PLANT ARCHITECTURE AND THE ALISMATIDAE

by

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De todas maneras, es muchos más importante darse cuenta del modo como un autor piensa en general, que catalogar al pormenor los hechos en que quizá abunden páginas de sus obras.

Léon Croizat

I would prefer not to think of this as a finished piece of work. Let it be instead the first question.

ABSTRACT

Plant architecture, particularly that of the shoot system, is discussed in terms of historical and current ideas. Landmark studies such as the works of Holttum, Hallé and Oldeman, etc. are reviewed in the development of a more deductive approach to plant architecture. The architecture of the subclass Alismatidae is reviewed, using the approach developed, as follows. Detailed morphogenetic studies of members of the Alismatales and Najadales, undertaken to elucidate characteristic architectural elements, are used in conjunction with extensive information in the literature. The architecture of the subclass shows distinct patterns within the diversity of forms observed. These patterns are identified and related through the consideration of component morphogenetic proceses. Major points of interest in the architecture of this group include apical bifurcation and the integration of vegetative and reproductive architecture.

RESUME

L'architecture des plantes, particulièrement celle de la tige feuillée, est discutée en termes historiques et contemporains.

Les travaux de marque, tels ceux de **HOLTTUM**, **HALLE** et **OLDEMAN**, ... etc., sont repris dans le but de développer une approche plus déductive de l'architecture des plantes. L'architecture de la sous-classe des Alismatidae a été révisée d'après ce mode d'approche. Des études morphogénétiques détaillées de certaines Alismatales et Najadales, choisies pour clarifier des éléments architécturaux typiques, sont utilisées et reliées aux informations tirées de la littérature. L'architecture de cette sous-classe présente certains patrons distincts parmi les divèrses formes observées. Ces patrons sont identifiés et integrés en considérant les composantes des processus morphogénétiques. Les principaux points d'intérêt concernant l'architecture de ce groupe incluent la bifurcation apicale et l'intégration architecturale des structures végétatives et reproductrices.

Traduit par Dr. M. Dubuc-Lebreux

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PREFACE

This thesis was partially produced in the form of original papers suitable for submission to journals in accordance with Section 4.2.7, Paragraph (h) of the Faculty of Graduate Studies and Research Announcement of rules and regulations for submitting a thesis. Three papers, published by the author in the Canadian Journal of Botany in 1979 (v. 57, pp. 1418-1438, 2325-2352 and 2353-2373) have been incorporated as individual sections in Chapter 2. References for these papers have been assembled into the bibliography at the end.

All figures and tables are numbered according to the chapter in which they appear. They are placed at the end of each chapter. Legends appear to the left of the figures, and are identified by the same page numbers.

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CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

Knowledge is the accumulation of facts and the understanding of these facts in a systematic context. In the opinion of the author, this thesis contributes to both these aspects of knowledge.

In terms of elucidation of facts, the current work provides comprehensive developmental studies of the vegetative morphology of *Alisma triviale*, *Sagittaria cuneata*, *S. latifolia*, *S. lancifolia* and *Butomus umbellatus*, and of the vegetative and reproductive morphology of *Triglochin striata*. Less detailed studies of vegetative morphology of *Alisma gramineum*, *Sagittaria subulata*, *S.* "*Sinensis*" and *S.* "*microphylla*" have also been made. Wherever possible, details of different stages of the life cycle, including seed and seedling, and variation within and between populations have been described. Besides general descriptions, some of the major points brought to light include the following:

-- While the size, shape and extent of development of the species studied may vary from population to population, the basic architecture (branching pattern) remains constant in each species.

-- Phyllotaxy is spiral in seed and seedling stages in all Alismatacean species studied, contrary to previous reports in the literature.

-- The relatively precocious initiation and development of a clearly lateral bud topographically associated with the inflorescence is found in *Alisma triviale*, *Sagittaria lancifolia*, *Butomus umbellatus*, and *Triglochin striata*.

-- In Alisma triviale, there is a gradient of increasing development of axillary buds with proximity to the next inflorescence.

-- In Sagittaria cuneata and S. latifolia, an axillary bud is found in the axil of every foliage leaf including the one subtending the continuation shoot. There is no difference in the extent of axillary bud development.

-- In Sagittaria cuneata and S. latifolia, the membranous "prophyll" of the continuation shoot initially subtends the inflorescence. Its edges grow out to surround the continuation shoot later in development.

-- Stolon system development in Sagittaria subulata, S. "Sinensis", and S. "microphylla" follows a very precise pattern: formation of prophyll, scale leaves, and foliage leaves, and the occurrence of internodal elongation, and resumption of upright growth, do not vary from one stolon segment to another.

-- The seed and seedling stages of S. lancifolia have an upright axis as in other species of Sagittaria. The rhizomatous adult form develops secondarily.

-- The rhizomatous organization of Butomus umbellatus is established at the time of seed germination. It is not comparable to that of Sagittaria lancifolia.

-- The development of the relatively precocious lateral bud topographically associated with the inflorescence, and the development of ordinary axillary buds into bulbils, and their respective roles in vegetative propagation in B. umbellatus, are distinct, and the two are distinguishable throughout the growing season.

-- Floral development in Triglochin striata is trimerous, typical of monocotyledonous flowers. There is no evidence to support the interpretation of the flower as a compressed inflorescence branch.

This study also represents the development of a comprehensive approach to plant architecture, and the application of this approach to the subclass Alismatidae. It provides new insights and perspectives to the subject, including the following:

-- It includes a critical evaluation of current concepts of branching, especially terminal branching, and the application of these concepts. The decision process whereby apical branching is determined to be terminal or lateral, and whereby the organization of the plant is determined to be monopodial or sympodial, is analyzed.

-- The interpretation of the controversial apical bifurcation in Butomus umbellatus is placed on a systematic basis as a result of the above analysis.

-- The approach to plant architecture developed, based on variable occurrence of component morphogenetic processes, allows a more dynamic approach to the understanding of plant organization and form. It need not be restricted to shoot systems.

-- The contribution of the current work is not so much in the conclusions drawn about architecture in the Alismatidae, since these are based on available data only, as in the provision of a method by which future, more detailed data may be analyzed.

— Despite a lack of detailed data within certain groups, patterns of organization are recognized in the diverse taxa of the subclass Alismatidae.

Foreword : Generalization and Description

The description of plant form and architecture is not as simple as one would like it to be. The fact that it is loaded with observational and theoretical biases is a problem which has been recognized by various authors (for example, Rudwick, 1968; Sattler, 1978). Or as Hesse (1970) has pointed out, there is no theory independent language for the description of any observation. The words of a language themselves embody some conceptual view of the world at large, and the terminology for the description of plants is no different. These concepts are not only the results of sensible experience, but also of theoretical and cultural tradition, and above all the generalization of these experiences. Thus any theory unifying the generalized concepts can be no more than generalization itself.

Yet while, in the extreme, theories often become petrified into dogma, and serve to reinforce original observational biases and reject variation and exceptions, the immense practicality and thus also validity of some form of generalization cannot be denied. For whatever reasons of physiology, ecology, mechanics or sheer happenstance, patterns do emerge among the observational data, patterns more or less adequate for the formulation of good generalizations. For there is, at least in the author's opinion, yet to be a better way to convey the ideas and concepts of, say, a "dog" in its multitude of breeds, or a "cat" or "bird", or for that matter, a "leaf". It is the entrapment of perception and thought by rigid applications of generalizations that provide a wealth of pitfalls, and ultimately, of pseudoquestions (Sattler, 1966). Or as Lorch so succinctly put it, "Above all, the carrying afield of ostensive definitions into regions where they do not apply, necessarily involved the crossing of the "high confidence" boundary through the surrounding region of decreasing confidence to that peripheral zone of meaninglessness." (Lorch, 1963).

Perhaps the above is more true in the descriptive complexities of the biological view of the world than anywhere else. Here words largely replace symbols, equations, boundary conditions, and other mathematical definitions of the more rigorously quantifiable world of physical phenomena. Description of the biological compounds the intricacies of that of the physical into an almost entirely new and far more complex level of interactions. Here exceptions abound, requiring no modification of the generalization for explanation unless the latter has since become, fixed in the mind of the observer, an immutable law of nature.

Botany and its basic subset of descriptive morphology is no different. General categories and names have been created since the earliest days of languages, so that it is only by using the terminology of "leaf", "stem",... etc. as the generalizations that they are rather than rigid categories that one may hope to rationally consider the organization of plant form. The last point cannot be emphasized too strongly, and the discussion of plant architecture here is made with this uppermost in mind.

INTRODUCTION

The generation of plant form in its diversity is a fascinating question. Plant form develops under the constraints of its environment, under the limits of the geometry of three dimensional space, and the physics, chemistry and biology of this space. To try and grasp the construction of plant form, plant architecture, in detail, for all plants, is obviously an impossible task. This is an attempt to establish a method to study one small group. Even given these restrictions, the task is a collection of history, theories, ideas, and data, and hampered by a lack of data. For cohesiveness and readability of this effort therefore, a brief introduction and outline is in order.

The subclass Alismatidae (Monocotyledones) consists of marsh, freshwater, estuarine and marine plants, and is chosen for its relatively small size, availability of information on its architecture in the literature, and above all for the frequent unusualness of this architecture.

First of all, the salient historical ideas and understanding of architecture of the higher plants is discussed. From this review, an approach to analyzing the architecture of the Alismatidae is developed. These two components form the first chapter, "Plant Architecture".

In the second chapter, entitled "Architecture in the Alismatidae", data on the development and organization of the Alismatidae is presented within a taxonomic framework, i.e., by orders and families. This includes both data from the literature and experimental studies by the author. The latter are in three sections and integrated into the appropriate families. As a result of this organization, each of these sections is presented as a self-contained unit similar to the format under which they were published (Lieu, 1979a, 1979b, 1979c).

The third chapter discusses the data presented in the second chapter using the ideas developed in the first one. After a brief introduction, major issues in the architecture of the Alismatidae are considered. This is followed by a section where the specific growth forms are discussed and interrelated. This chapter synthesizes the efforts of the preceding chapters, and is titled "Plant Architecture and the Alismatidae".

Finally, a section titled "Conclusions" is presented to summarize the entire study.

CHAPTER I

PLANT ARCHITECTURE

By the end of the nineteenth century, crystallographers had enumerated thirty two different patterns of symmetry that crystals can show. Then a Russian crystallographer visited the Alhambra, the thirteenth century Moorish palace in Spain, and realized that the mosaics on the walls and floors displayed all the known varieties of crystalline symmetry. Taking a theme and working out variations, the artist had exhausted the geometry of symmetry.

INTRODUCTION

The diversity of plant form has always fascinated botanists and laymen alike. Unlike animals, there is constant evidence of an increasing, changing complexity: a flush of new leaves, a branch, blossoms, and fruits, in various sequences. This seemingly open, indeterminate, "adding on" type of growth in plants has been described as "architecture", and "architectural" by some (e.g., Bidwell, 1974), particularly in contrast to the highly determinate form and development of animals, for example the quadriped plan of so many vertebrates.

Yet as morphological studies have shown, this architectural type of growth, to pursue the analogy further, often follows a blueprint far more closely than the apparent indeterminism may indicate. In addition to certain physical laws that must be obeyed, there are restraints imposed by the very characteristics of the growth processes themselves. The result is a limit to the options of organization that a plant can have. Furthermore, factors such as ecology and energetics may also superimpose additional boundaries on the viability of different growth forms through natural selection. Though environmental trauma such as climate or predators do often modify the form of a plant, this does not obliterate the validity of the inherent patterns of growth and organization as exemplified by such as the tree models described by Hallé, Oldeman and Tomlinson (1978).

Growth is the production of new biomass in the form of increasing cell size or number or both. The filamentous (one dimensional), monolayer sheet (two dimensional), and multilayer sheet (three dimensional) modes of growth in the algae illustrate some aspects of the basic geometry of growth. A mark of the increasing complexity in the organization of plants is the occurrence of localized rather than diffuse growth, in the form of meristems, localized, undifferentiated groups of cells. From a three dimensional point of view, growth is usually radial, dorsiventral or axial in nature. Radial growth, with equal growth in all three dimensions, results in cells arranged in concentric spheres of increasing diameter. Dorsiventrality is the result of greater growth in only two dimensions (length and width), while axial growth, where growth is pronounced in only one dimension usually, results in an elongated structure. This is diagrammed in Fig. 1.1. With increasing size, dorsiventral, and especially axial growth are often necessary to the maintenance of an adequate surface area to volume ratio. This is true of any organism, and examples outside the vascular plants include the kelps or giant brown algae and the massive elkhorn corals.

Among the higher plants, organization of the plant body is generally distinctly axial in nature. Beginning with the single embryonic axis in the seed, growth occurs primarily at the ends of the axis, at the shoot and root apices. Additional axes are produced by a proliferation of the total number of apical meristems. Though intercalary meristems and cambia are also integral to plant growth, these are usually secondarily derived from the products of the apices, so that the basic architecture of the plant is dependent on the apical meristems and their subsequent fates.

There are, naturally, exceptions to the axial mode of plant organization. Examples such as Welwitschia (Martens 1977), the extremely simplified duckweeds (Lemnaceae) (Arber, 1919; Brooks, 1940; Hillman, 1961), and the unique phyllomorph structure of some species of Streptocarpus (Gesneriaceae) (Jong 1970, 1973; Jong and Burtt, 1975) come readily to mind. However, it is possible to describe a very large proportion of the higher plants in terms of axial organization.

Because of the difficulties of access, relatively little is known about the growth patterns of root axes, although Jenik (1978) has contributed significantly to the overall understanding of this subject in woody plants. Instead, most of the literature on plant growth and architecture is restricted to the above-ground parts, i.e., usually the system derived from the shoot apices. Thus "plant architecture" has often become synonymous with "shoot architecture". The following discussion is also restricted to the shoot system only.

In a system of shoot architecture, there are two interacting levels of organization. Firstly, there is that of the organization of a single shoot: the activity of the apical meristem may be considered ultimately to produce all other structures such as leaf, inflorescence or other meristems. The second is the interaction of all shoot apices of a plant, and their activities to produce plant form. Obviously, a consideration of the latter is entirely dependent upon the understanding and conceptions of the former. In the following sections, some of the major ideas on these two topics are reviewed.

THE CLASSICAL SHOOT MODEL

Botanists have always sought to understand and therefore superimpose order upon the diversity of plant organization. The most basic of these efforts is probably that of taxonomy, the classification of plants, by a "natural" or phylogenetic scheme. Although ideally this scheme is based on all plant characteristics, historically there has been a far greater emphasis on reproductive structures. A more ecologically oriented approach is that of categorizing plants by their physiognomy, simply as trees, shrubs and herbs, or more elaborately, as in Raunkiaer's system of life forms based on the position of the perennating buds (Braun-Blanquet, 1932; Raunkier, 1934). From a structural point of view, the focus of plant architecture is on the shoot system, the "skeleton" of the plant. The emphasis is largely on the processes and dynamics of apical growth and proliferation, since all other structures are ultimately produced by the apical meristem.

The pivotal importance of the shoot system in plant organization was recognized very early in the history of modern botany. Indeed, much of the traditional generalizations of shoot organization and growth originated in the late eighteenth and early nineteenth century. The ideas of acknowledged founders such as Goethe and A.-P. de Candolle, imbued with the Zeitgeist of these botanists, i.e., Naturphilosophie (Eyde, 1975a, 1975b) and Essentialism (Sattler, 1974), form a conceptual framework which, while modified and refined, remain a cornerstone of modern botany, as the Classical Shoot Model.

According to this model, a shoot consists of the discrete subentities of caulome ("stem" or "axis" sensu lato) and phyllome ("leaf" sensu lato). Caulome and phyllome may then be further subdivided into smaller, exclusive categories. In addition, caulome and phyllome are produced by and inserted on caulomes, and only caulomes.

As botanists rejected the essentialistic philosophy even while the generalizations associated with it became entrenched and eventually accepted as "natural law", there became a need to explain the departures from this model. Exceptions were justified by additional concepts such as "precocious development" and "congenital fusion", or the catch all and indeed circular category of "adventitious growth". Unfortunately, regardless of whether or not these concepts have any real value to the understanding of growth and organization of plants, they are most frequently adhered to in the current literature, either explicitly or implicitly, with no consideration of their origins.

The historical development of the Classical Shoot Model and the invalidity of its rigid application in dealing with plant architecture has been discussed in detail by Sattler (1966, 1974). His objections, with which this author concurs, are briefly as follows:

1. The model cannot deal with structures intermediate between the defined categories.

2. The assumption that positional relationships of organs are absolute is unrealistic given the current knowledge of the diversity of plant architecture.

Both points, especially the latter, will come up again in the discussion of plant architecture from the principles of meristem and axis formation in a later section.

Sattler (1974) offered an explicit alternative in what he termed a "new conception" (c.f. model) of the shoot. This allows both for intermediates in the form of a semi-quantitative homology of organs, for example, part "leaf" and part "stem", and for heterotopy, changes in the position of inception of organs, e.g., on the leaf rather than on the stem (Sattler, 1975). Like numerical taxonomy, application of quantitative homology encounters difficulties in the actual assignment of numerical values to a feature or an aspect of a feature. On the other hand, conceptually, a semi-quantitative approach serves the function of emphasizing the frequently continuous nature of variations in morphological features.

Sattler's approach has met with favourable responses (e.g., Meyen, 1973; Fisher, 1976). On the other hand, authors such as Phillipson (1978) have maintained that adventitious buds and positional relationships in development as part of the Classical Shoot Model are sufficient to account for all seeming deviations. These objections to Sattler's model have been cogently answered by the following quote from Dickinson (1978):

> "...his point of view...seems to dismiss both the occurrence of heterotopy (i.e. ontogenetic and spatial relations are not absolutely constant) and the problems of interpreting products of ontogenetic displacement. While admittedly these are relatively infrequent phenomena, which can readily be interpreted merely as deviations from typical behaviour, this disregards hologenetic processes and their possible evolutionary significance, and ignores the disadvantages of the ensuing concepts of "adventitious" origin and congenital fusion. "

The problem of an excessively rigid application of the generalizations of the Classical Shoot Model, and attempts to justify deviations with ad hoc and catch-all processes, is a recurrent one throughout this discussion. The view of the classical model as an empirically derived model with no rigid or underlying "rules" (Tomlinson, personal communication) would be a more viable alternative. However, the more absolute application of the classical model, either implicitly or explicitly, is still by far the more prevalent in the literature.

Regardless of any controversy concerning models of the shoot, much progress has been made in the understanding of plant architecture and the morphogenetic processes involved in its generation. The literature on shoot architecture or growth forms (from the German term "Wuchsform"), in particular that of the herbaceous plants, is far too abundant to mention here except for the landmark studies that contribute to the conceptual framework of plant organization and architecture. These key studies are discussed briefly below.

RECENT IDEAS ON PLANT ARCHITECTURE, ESPECIALLY THOSE OF HALLÉ, OLDEMAN AND TOMLINSON

Holttum (1955) was the first to make the generalization that monocots are usually sympodial in organization. In recent years, there has been a resurgence of interest in the morphology of monocots (prevalent in the tropics and thus ignored by the tradtional temperate zone botanists). This includes McClure's work on the bamboos (McClure, 1967), and especially Tomlinson's papers on a number of families (Tomlinson, 1966-1973). The work of the latter author on the Scitaminae, Marantaceae, and Tillandsia (Bromeliaceae, Spanish moss) showed how apparently different growth forms are but variations of a basic pattern with intensification, reduction, and minor modifications of certain elements.

Concurrent with this revival of interest in the monocots, Hallé and Oldeman (1970) published a monograph on the branching patterns of tropical trees where they referred to the visible expression of these patterns as "architecture", a term prevalent in the French literature. By observing certain variable features of growth, these authors generated 21 actual and 3 theoretical "models" of growth. Furthermore, each model is named after a botanist whose work these authors considered to have contributed significantly to the field.

This comprehensive and novel approach, accompanied by Hallé's elegant illustrations and the increasing interest in tropical botany and whole plant morphology, was enthusiastically received by many botanists. It is a mark of its appeal among French-speaking and non-French-speaking botanists alike that an English translation was shortly published thereafter (Hallé and Oldeman, 1975). The subject was also a central theme to the Fourth Cabot Symposium at Harvard University (Tomlinson and Zimmermann, 1978).

The inspiration for the work of Hallé and Oldeman can be traced back to Corner's approach in the development of his Durian Theory of angiosperm phylogeny (Corner 1949, 1964). Hallé and his brother (N. Hallé) had translated this and introduced it to the French literature, and Hallé and Oldeman acknowledged it as "un véritable catalyseur". In brief, the Durian Theory postulates "phases" of tree evolution such that the massive, arillate fruits (megaspermy) of, for example, the durian, are the primitive and ancestral type. Out of mechanical necessity, these must be borne on massive (pachycaulous) stems and twigs. By the principle of "axial conformity" (which is part of the Durian Theory), these axes also bear large, compound leaves (megaphylls). From this, by means of a second principle of "dimunition upon ramification" acting in conjunction with the above one of axial conformity, the small seeded (microspermous), thin branched (leptocaulous) trees and herbaceous plants were derived. This scheme is shown in Fig. 1.2.

The Durian Theory per se is not particularly well accepted among the many proposed schemes of angiosperm evolution. Critics object to the seemingly arbitrary choice of the arillate fruit as the starting point, and even more to the simplistic, broad theorizations on tropical ecology and evolution (e.g., Croizat, 1970). Just as Croizat's criticisms were directed against the assumptions of the Durian Theory and not the scheme of evolution of the life forms themselves, the monograph by Hallé and Oldeman drew inspiration from the theory, but was based on extensive field observations. These authors recognized different architectural models based on growth characteristics of the shoot system such as the presence of branching, the equivalence of axes, etc.

The simpler of the models of Hallé and Oldeman correspond directly to phases in Corner's scheme. For example, Holttum's model (monocaulous, monocarpic), Corner's Model (monocalous, polycarpic and monopodial), and Chamberlain's Model (monocaulous, polycarpic and sympodial, or "pseudomonocaulous" in

Corner's terminology), are equivalent to the monocarpic and polycarpic ancestral type of Corner's "Cycad Phase". Tomlinson's model (monocaulous, with suckering), is identical to the "Monocotyledonous Phase". Beyond these, the two schemes diverge. The concept of inflorescence position (lateral versus terminal) is retained and used specifically in the work of Hallé and Oldeman. But instead of the variations from megaspermy to microspermy and pachycauly to leptocauly, these authors considered comparisons of rhythmic and continuous growth, plagiotropy and orthotropy, and the differentiation of trunk (main axis) and branches.

However, although Hallé and Oldeman emphasized above all the patterns of tree organization and growth, they also provided a scheme of the evolution of meristem functioning similar to Corner's on the evolution of tree forms. Corner's principles of axial conformity and dimunition upon ramification were explicitly revived in a later version of the architectural models. This appeared in a book entitled "Tropical Trees and Forests" produced in collaboration with Tomlinson (Hallé, Oldeman and Tomlinson, 1978), where a substantial section was devoted to tropical forest ecology. The development of ideas on architectural models in the two works may profitably be compared and contrasted.

As mentioned above, the scheme of Hallé and Oldeman is mainly based on six pairs of generally mutually exclusive characteristics:

1. presence and absence of branching
2. homogeneity and heterogeneity of axes
3. differentiation of orthotropic and plagiotropic axes
4. terminal and lateral position of inflorescence
5. rhythmic and continuous growth
6. monopodial and sympodial trunk organization.

This is summarized in Table 1.1.

The models of Hallé and Oldeman were incorporated almost unchanged in the collaboration between Hallé and Oldeman and Tomlinson. Modifications to the scheme included the addtition of a new model (McClure's Model), the realization of two previously "theoretical" models by the discovery of trees that actually conformed to these, and the suppression of a third theoretical model for which no example could be found. Also, dichotomy was accepted as an integral part of morphogenesis, although Hallé and Oldeman had been reluctant to state this definitively for Schoute's Model in their earlier work. Hallé, Oldeman and Tomlinson also included a key to all models. The organization of this key varied from the scheme of Hallé and Oldeman (1970, page 115) mainly where models with differentiated axes were concerned. The changes reflect a greater emphasis on the consideration of branching parameters and dynamics in the later work. These two schemes (Tables 1.1 and 1.2) are discussed in detail below.

One of the major differences between the original and the new work is the removal of considerations of orthotropy versus plagiotropy in the latter. Hallé and Oldeman recognized three types of axis orientation, orthotropy, plagiotropy, and plagiotropy "by apposition". The last category drew some of the strongest comments from Croizat-Chaley (1973), also the major critic of the Durian Theory (Croizat, 1970). Croizat-Chaley objected to the use of the term "plagiotropy", a well defined phenomenon of shoot dorsiventrality, distichous phyllotaxy, diageotropism and horizontal orientation (Roux, 1968), to cover a superficially similar situation of general horizontal orientation of the axis and the appearance of dorsiventrality as a result of internodal torsion (Hallé and Oldeman, 1970, p102). He considered all "torsions" to be petiolar and not axial, and simply a light response; therefore, "plagiotropy by apposition" as defined would be at best an environmentally induced phenomenon, and not the result of distinct morphogenetic attributes of a plant itself.

The problem of plagiotropy is addressed in detail by Hallé, Oldeman and Tomlinson. They considered shoot orientation to be a continuum of increasing organization of the apex, from orthotropic, radially symmetric axes, to apparently plagiotropic ones by secondary leaf orientation and sometimes anisophylly ("reversible plagiotropy") to the clearly plagiotropic as defined by Roux ("irreversible plagiotropy"). This is summarized in Table 1.3.

In relation to this, these authors also contrasted growth by apposition, i.e., displacement by a more vigorous lateral, to growth by substitution, i.e., replacement of a terminal inflorescence or an aborted terminal apex by a lateral. These two aspects of growth are discussed separately, and are implicitly applicable to both orthotropic and plagiotropic branches. Both growth by apposition and growth by substitution result in sympodial structures, though the former type may more easily be identified as such (Fig. 1.3a). Plagiotropy by apposition as used by the authors is the result of the association of appositional growth with reversible plagiotropy frequently found in branches: the original axis becomes orthotropic in orientation, and often forms a short shoot (Fig. 1.3b).

The other major reorganization of the second key is the result of the introduction of the concept of "modular construction". As defined by Prévost (1972, 1978), the module (or "article" in French) is a unit produced by an apical meristem, of limited activity, which also produces new meristem(s) repeating the same sequence of development. The emphasis is on the limited activity of the apical meristem. By definition then, sympodial growth by the substitution of equivalent units is modular, whereas growth by apposition of the same is modular only if the displaced axis terminates by abortion or flowering fairly shortly thereafter (Figs. 1.3a, 1.4a).

Disregarding the more rigid definition used in plant demography (Harper and White, 1974), the idea of modular construction is a most useful and attractive one. It defines repeating patterns of plant architecture at a level below that of the entire plant and above that of individual organs _per se_. By providing this intermediate between the two widely separated levels, it allows a more hierarchical representation of plant organization and morphogenesis that facilitates understanding and modelling (Lindenmayer, 1977, 1978; Lieu, in prep.). As used by these authors for homogeneous axes, modular growth defines a regularly repeating unit of branching organization in the pattern of tree growth. However, its application in conjunction with models with heterogeneous axes seems to be inconsistent, and is discussed further below.

In addition to the association of appositional growth of branches with reversible plagiotropy described above, an analysis of the partitioning of the models in the key given by Hallé, Oldeman and Tomlinson also indicates that, contrary to Prévost, sympodial branch growth by substitution is not considered modular (Fig. 1.4a). For example, Massart's Model includes the possibility of both monopodial branches, and sympodial branches of successive units of substitution growth. In Nozeran's Model, the trunk shows growth by substitution, and is considered modular by definition (Halle, Oldeman and Tomlinson, 1978, p.107). Like Massart's Model, its branches may be monopodial or sympodial by substitution (Halle, Oldeman and Tomlinson, 1978, p.91). However, in the key given, both models are excluded from the group of models with "modular construction, at least of plagiotropic branches" (Fig. 1.4b).

Thus, as it is used here, "modular construction" implies a narrow group of models with branches of "growth by apposition and inflorescence in a terminal position". However, this is likely the result of greater emphasis on the modular aspect of construction as defined, to differentiate, as in a taxonomic key, this group of models from the rest of the scheme. Though this may achieve the desired results, it seems somewhat contrary to the purpose of using the concept of modular construction as an organizational unit in the understanding of plant architecture.

The work of Hallé and Oldeman was based on extensive observations and analyses of tropical trees and verified by detailed later studies (e.g., Hallé, 1971, Hallé and Mabberley, 1976). From these, some of the growth processes most important to architecture were derived and used to generate the models by varying each in turn. By doing so, three theoretical models to which no species were known to conform were generated. In the key produced in conjunction with Tomlinson, trees conforming to two of these models were observed while the third (Theoretical Model II) was suppressed for lack of observable examples. This is indicative of overall shifts in emphasis in the later work that seem to represent the influence of the third collaborator, P.B. Tomlinson (e.g., Tomlinson, 1973, 1978). On one hand, much attention was paid to the detailed elements of tree architecture themselves, particularly the dynamic relationships of shoot organization and interaction; on the other, the emphasis was on the architectural models of known plants.

The original scheme devised by Hallé and Oldeman considered possible models by permutations of a number of characteristics. The key of Hallé, Oldeman and Tomlinson resembles a taxonomic one, concerned mainly with distinguishing between existent models by known features of growth. Obviously, given the increased detail of elements of growth considered, an explicit model for each and every permutation can only be cumbersome. Thus it may be justifiable to use one growth process to distinguish certain models and implicitly combine or ignore its alternatives in the description of others. (An example is the possibility of branches of either monopodial or sympodial by substitution growth in the models of Nozeran and Massart.) To be sure, the difference between the two works is one of approach. Yet one cannot help sensing some impatience with theoretical considerations on the part of the later work.

Also, despite the statements that the named architectural models act as named points of reference or "semantic pegs" in the biological continuum, Halle, Oldeman and Tomlinson also admitted that these models are categories delimited by definition. Though this may be non-typological from the point of view that a taxonomic point of reference is not given (e.g., the Cycad Model, or the Euphorbia Model), named models do tend to emphasize "models" or "types" of growth rather than the possibly continuous processes of growth that these authors detailed. Only the inferences of taxonomic and phylogenetic relationships are avoided. In fact, although the models were initially recognized by empirical processes, and although Halle (1978) also stressed the intraspecific variations in and interconvertibility of the models to which a plant species may belong as a result of sex, environment, genetic mutations both Mendelian and cytoplasmic, pathology and other traumatic effects, the importance of discrete, well defined models, each named after and dedicated to a particular botanist, remains.

The concept of using branching patterns or models to understand plant architecture can be extended to growth habits other than the tree. While Corner first suggested that herbaceous plants may be phylogenetically derived from microspermous (and leptocaulous or pachycaulous) trees (Corner, 1949), Halle and Oldeman discussed the phylogenetic and ontogenetic concept of "miniaturization" of architectural models as herbs, particularly to take advantage of the inherently short biological cycle in seasonal climates. Yet the original models were formulated based on observations of tropical trees. Rhizomatous growth ,though not suckering which is included in Tomlinson's Model, common to many herbaceous plants was not taken into serious consideration since a diageotropic main axis certainly does not lead to the conventional "tree" form. In this regard, Jeannoda-Robinson (1977) had suggested a system of "prostrated parallels" whereby the horizontal main axis of herbs is considered equivalent to the tree trunk in the models. In their later work, Halle, Oldeman and Tomlinson introduced McClure's Model (heterogeneous axes with basitonic branching producing "new (usually subterranean) trunks") to account for many of the rhizomatous herbs. In the same work, the concept of miniaturization is also discussed in greater detail. Mechanisms for this process, explicitly or implicitly phylogenetic, are suggested. These include reduction in size, neoteny, fragmentation (the equivalence of a herbaceous plant with only part of a particular model), and also the loss of orientation of the original upright axis.

In summary, the monograph of Hallé and Oldeman attempted to identify the important features of plant organization and their possible roles in architecture; their later work in conjunction with Tomlinson is built upon this, but it is, at the same time, more pragmatic in its concern with identification and description of plant models and ecology, and more phylogenetic in approach. On one hand, the formulation of McClure's Model characterizes a practical "adding on" approach taken to deal with new architectural plans as required. On the other, the assignment of rhizomatous Nypa to Schoute's Model with upright species such as Hyphaene thebaica may be correct by definition (i.e., dichotomous branching and phylogenetic loss of axis orientation), but not very satisfactory especially in the light of the more sophisticated considerations given to growth parameters in many of the other models.

Despite this, it cannot be denied that the approach of these authors has tremendous appeal for and thus influence upon much of the current studies of shoot organization, and upon all aspects of botany in general. Indeed, the current work draws significantly upon concepts formulated by these authors. The alternative is to use a more deductive approach, beyond the original scheme in the monograph by Hallé and Oldeman. This would stress the features of growth, systematically varying them to explore all possible options of organization independent of physiological and ecological significance (Meyen 1973, 1978), and is further explored below.

SOME OTHER IDEAS, ESPECIALLY THOSE OF MEYEN

While the work of Hallé and Oldeman and Hallé, Oldeman and Tomlinson emphasizes growth forms as a result of certain morphogenetic processes such as branching and branch orientation, there are, naturally, other approaches to the study of plant form.

Horn (1971) studied trees from the point of view that the evolution of tree geometry is a mathematical optimization process of the total photosynthetic area. Based on this, leaf shadows and the amount of shading and exposed photosynthetic area are calculated. From these calculations, Horn derived two strategies of canopy structure, the formation of monolayers, and that of multiple layers. The mathematical consequences of these two structures indicate that the monolayer canopy is more shade tolerant than the multilayer, and is also capable of casting more complete shadows, thus inhibiting undergrowth. Horn discusses these results, as well as some general geometric considerations of tree crown shape, in relation to ecological adaptations, particularly in forest succession. He also gives evidence of the confirmation of these ideas in the field, and generally provides the framework for much further analysis on plant geometry and ecological strategies. However, the field identification of monolayer and multilayer trees has not been specified.

Horn's approach is followed in great detail in conjunction with that of Hallé and Oldeman by Honda and Fisher (1978; see also Fisher and Honda, 1977, 1979) for the tree species Terminalia catappa. The authors analyzed tree geometry in terms of leaf orientation, leaf size, branch angle and branch unit length, and found substantial conformity between real trees and the mathematically derived model of optimum leaf exposure. Subsequently, these authors were able to extend their predictions of optimal tree geometry to 32 other tropical species (Fisher and Honda, 1979b).

Bell (1976, 1979; Bell and Tomlinson, 1980), on the other hand, has modelled the consequences of hexagonal rhizome growth generated by a few simple branching rules by means of a digital computer model. The importance of this approach is that these rules incorporate an element of probability (e.g. the probability that a bud will develop into a branch) whereas previous models have been deterministic. In this way, the apparently random spatial location of colonies of herbaceous perennials over a number of growing seasons can easily be simulated.

Stevens, in his popular book "Patterns in Nature" (Stevens, 1974), approached the problem of form from a different, more fundamental level. As he amply illustrated in the opening pages, there are aspects of form that are direct results of physical and mathematical constraints, for example, the shapes resulting from packing equilateral triangles around a central point, or the formation of five and only five regular polyhedra from joining a single type of plane figure (such as a triangle or a pentagon), or the minimization of total path length by a branching pattern consisting of three-way joints.

In a different vein of morphological analysis is the nomothetical approach proposed by Meyen (1973, 1978). Nomothetical is defined as an orientation leading to the establishment of certain inherent laws to which natural phenomena, in this case the presence and combinations of plant forms, are subject. Meyen described this approach to be one of an "as-if'ism" (Meyen, 1978), an analysis of form and its variation without recourse and reduction to considerations of developmental dynamics, causality and functionality; i.e., as if ecology, physiology and other related concerns do not exist. The superimposition of these factors are removed so that the intrinsic rules of form may be revealed.

As defined, this approach may, in the extreme, be justifiably accused of being pseudoscience and divorced from reality (Tomlinson, personal communication). However, in its more moderate conception, i.e., a generally deductive approach where the apparently unlikely, e.g., epiphylly, is not rejected outright or considered a freak because of its rarity, nomothetical morphology can offer new and different perspectives to plant architecture.

In his nomothetical approach to plant morphology, Meyen provides a formal systems approach to plant morphology. Morphological features, e.g., leaf shape, is defined as a "meron" (Fig. 1.5). A meron may show variations, either discrete or continuous, which are termed "modalities". The totality of these variations is the "polymorphic series", while conceptual and physical processes of modality transform link the modalities in a multidirectional manner. The same feature and its variations, i.e., a polymorphic series, may be found in a number of taxa, in which case the sum of all modalities in these taxa form a "repeating polymorphic series". This Meyen later termed a "refrain" (Meyen, 1978). The main example Meyen gave of a repeating polymorphic series and its constituents is that of leaf segmentation, a feature (or meron) which occurs to varying extents (modalities) in different taxa.

Meyen emphasized the statistical nature of merons and refrains among taxa, deriving three main principles from the diversity of frequency of merons and refrains. These are:

1. The taxonomic range of a given polymorphic series (PS) or repeating polymorphic series (RPS) is not a constant; i.e., one species of a genus may show merons of the entire RPS, but in other genera, only two or more species together can exhibit the full refrain.

2. The systematic value of the same modality varies from one taxon to another.

3. The number of modalities (or degree of polymorphism) of the same meron in different taxa can be different; e.g., one genus may show only one modality while another shows the entire refrain of several modalities.

Attention is also given to the fact that rarely occurring modalities which would commonly be considered a deviation or monstrosity in a particular taxon is often a normal or predominant form in another (the so-called Krenke's Rule).

From this point of view it can be suggested that the genome of a taxon contains the requisite coding for the entire refrain. The transition from one subtaxon to another represents a vectorized displacement of mechanisms responsible for the frequency of certain modalities rather than the much slower change of the general potentiality itself. This vectorized displacement in evolution may proceed in a web of directions, so that the corresponding modi of structural transformation from one modality to another cannot be correlated to and is independent of evolutionary trends or directions.

The combination of features from taxon to taxon may be represented as a multidimensional lattice (a two dimensional one of which is illustrated in Fig. 1.6). When more than one taxon is considered, the lattice becomes a probability distribution of taxa showing different modalities, or modalities each represented in certain taxa. Though this distribution may frequently be clustered around certain combinations of modalities, leaving large gaps around others (i.e., forming a degenerate lattice, or conforming to what D'Arcy Thompson (1942) considered as the Principle of Discontinuity), these unrealized combinations are not "prohibited", merely low in frequency.

The appeal of Meyen's ideas lies in the fact that they systematically consider form as an independent entity, and in terms of frequencies of variations (modalities) of a morphological feature (meron) without reduction to (and therefore by) other disciplines such as ecology and evolution, or the Classical Shoot model. Each meron may be defined a priori by the consideration of morphogenetic processes. Alternatively, merons can be assembled from observations of a particular feature among one or more taxon. In addition, structurality is not sacrificed to generalizations (i.e., high frequency events) that have evolved conceptually into dicta (i.e., absolute occurrences).

The consideration of plant forms or modalities in terms of frequency or probability distributions rather than the traditional and rigid categories may be likened to the differrence between classical Newtonian (discrete) physics and the probabilistic approach of modern physics and physical chemistry today. It is also consistent with the ideas of partial homology proposed by Sattler (1966, 1974).

CONSIDERATION OF GROWTH FORMS FROM COMPONENT PROCESSES

Between Hallé and Oldeman and Meyen, some fundamentals of a comprehensive approach to plant architecture have been laid down. In generating the architectural models of tropical trees, Hallé and Oldeman emphasized the validity of taking a theme (in this case tree growth) and describing all the major variations. Meyen, by his nomothetical morphology, provides the conceptual framework for analyzing theme and variation in plant form, both theoretically and in relation to real phenomena.

To benefit from this combined approach to plant architecture, it is valuable to reconsider in some detail the processes of the growth and development of the shoot system. Disregarding the extremitites of the Classical Shoot Model and other artificial constraints, it is possible to consider the shoot system of the higher plants from first principles. A biological system such as the shoot system must operate under physical (including spatial and geometric), chemical and biological constraints. Examples of the first two include considerations such as the geometry of packing (e.g., Thompson, 1942; Stevens, 1974), the casting of shadows (Horn, 1971), the mechanics of physical structures, and surface area to volume ratio limitations. Without quibbling over what exactly constitutes life (from the Greek word "bios" meaning mode of life), biological requirements generally include energy input to overcome entropy, informational storage (the genetic code as we know it), the facility for self duplication, and, especially in the more complex organisms, growth.

As mentioned in a previous section, growth is the increase of mass by increasing cell number and/or size. The geometry of cell division determine much of the geometry of multicellular form, i.e., whether filamentous, sheet-like, spherical or cylindrical. The same approach may be used with an analysis of axial growth characteristic of the higher plants.

Axial growth, producing a linear structure with two ends or apices, occurs as a result of localized growth at two points 180 degrees apart, or of diffuse growth where the plane of cell division is largely perpendicular to the length of the axis. In the higher plants, the cells of the axis away from the apices, i.e., cells of relatively greater age, develop further and are differentiated from the apical cells by their form and decreased ability to divide and produce new cells. (How this may affect or be a result of the control of whole plant development is an intriguing question concerning the physical "operation" of the plant that will not be speculated upon here.)

The shoot system of a plant is significantly determined by the developmental events of the apex: its growth rate, differentiation, and increase in number. While the shoot apex is defined as a group of embryonic cells which produce primary tissue precursors (Esau, 1976), it may also be subject to some level of differentiation or organization (Hallé, Oldeman and Tomlinson, 1978). This is manifested in the different characteristics of orthotropic and plagiotropic apices, with their associated symmetry and phyllotaxy. In addition, the apical meristem may differentiate, usually irreversibly, to become an inflorescence (reproductive apex), or other specialized structures such as tendrils and spines. The differentiated apices may in turn proliferate and form more of the same. However, they are generally determinate, and do not contribute to the formation of new shoot axes. Thus the discussion of plant architecture in general may reasonably be focussed on vegetative meristems.

Beginning with the single shoot apex of the embryo plant, a single axis is developed. In the simplest case, there is no increase in the number of apices, i.e., no meristem proliferation occurs. There is a single axis which eventually terminates by the transition from a vegetative to a reproductive apex. (This is contrasted with Holttum's Model (Hallé and Oldeman, 1970) in which meristem proliferation may have produced lateral buds, but these are suppressed in the normal course of development.) All other growth forms encountered would entail an increase in the number of vegetative meristems.

As has been amply illustrated by the work of Hallé and Oldeman (1970) and Hallé, Oldeman and Tomlinson (1978), a diversity of plant architecture may be described in terms of patterns of meristem proliferation and development, commonly referred to as branching. Therefore, a detailed discussion of branch formation is included to assess the possible architectural forms that result from branching.

CONSIDERATIONS OF BRANCH FORMATION

The processes involved in branch formation include the following features:

1. pattern and distribution of meristems
2. mode of meristem formation
3. subsequent development of meristems

The complex interactions of these attributes over time have resulted in various concepts such as prolepsis and syllepsis, neoformation and preformation, pleonanthy and hapaxanthy, etc., which are reviewed in detail for tree forms by Hallé, Oldeman and Tomlinson (1978, Chapter 2).

Though a large body of information, both observational and experimental, has been accumulated regarding axis initiation and differentiation, relatively little deals conclusively with the mechanisms involved. A large number of the morphogenetic processes, the link between the "influences" and form, remain black boxes. This is in part because of the indeterminate and yet highly integrated nature of plant growth. In fact, it is often difficult to establish whether experimentally obtained results are induced aberrations or of genuine significance (Steeves, 1976).

Morphologists frequently postulate mechanisms for the generation of plant form and architecture, yet most often these cannot be confirmed except by indirect inference with its inherent problems. One may speak broadly of meristem interactions inferred from experimental data (e.g., Lang, 1973; Hicks, 1980), but these are difficult to isolate or confirm in the natural system. Therefore, much of the study of plant architecture must largely rest on description, whether static or dynamic. A case in point is the study of phyllotaxy. Though this field has intrigued many since the time of Goethe, and various models have been able to simulate the actual patterns found in nature (Adler, 1974; Mitchison, 1977; Veen and Lindenmayer, 1977), as yet there is no proven theory on the generation of phyllotaxy itself. Nevertheless this in no way diminishes the studies in terms of their contribution to the understanding of plant form.

The approach to branching taken here is a descriptive, hierarchical one amenable to eventual modelling by digital computer programs (Lieu, in prep.). Accordingly, branch formation may be considered in terms of two conceptually separable components: the actual initiation or production of one or more meristems, and the subsequent development and expansion of the new meristem(s). The first is necessary and sufficient for meristem production; however, the second is necessary for the formation of branches (in the common, macroscopic sense of the word), and the development of all but the simplest monoaxial structures. Discussion of the possible casual mechanisms is beyond the scope of this effort and has not been included.

I. Distribution of new meristems

Without speculating on the physiological and morphogenetic mechanisms that may be involved, it can be said that new meristems may be initiated during some part or all of the life cycle of a plant when conditions are favourable to their production. The first consideration is therefore the temporal aspect of meristem proliferation, even though the result is a spatial distribution of additional meristems along the plant axis.

The internal conditions favourable to meristem production, as those favourable to other morphogenetic processes, may be continuous from the start of the life cycle, or may be reached later on, i.e., a certain "age" or stage of development must be reached. In addition, meristem production may be periodic, being related to internal or external influences or both. This may be subdivided into rhythmic and intermittent (diffuse) types. The difference between these two may be a semantic or observational one. Rhythmic processes are usually those where the periodicity is predictable, whereas intermittent ones are those with no regular (and therefore predictable) periodicity. The fact that their occurrence cannot be correlated with other obvious phenomena does not mean that it is not causally or otherwise related to some internal or external event. Many species of the Alismatidae show rhythmic meristem production (see Chapter 2), as do species of the Ampelidaceae (Bugnon, 1952; Moens, 1956; Millington, 1966). On the other hand, plants such as Flagellaria indica may be considered to branch intermittently (Tomlinson, 1970b).

Once the conditions required for meristem production are satisfied, one may proceed to consider the location and mode of formation of the new meristem. It should be pointed out, however, that in reality this need not be a linear sequence of events: location and mode of formation may have significant influences on the conditions required for meristem production.

The location and mode of meristem production pose some of the greater challenges to the rigidities of th Classical Shoot Model. To recapitulate, according to this model, branching in higher plants is associated with two positional attributes:

1. A shoot or axis is produced laterally on another shoot.
2. The insertion of one shoot on another is axillary in position.

While these are fairly good generalizations, they are too often thought to be necessary conditions to plant organization. An axis is usually produced on another through the participation of the apical meristem. This process is not so much due to the identity of the axis as to the functional attributes of the undifferentiated embryonic cells that characterize its apical meristem. It is a limitation of the biological system with its differentiation of cells to provide "division of labour" that a new meristem can only be developed from less differentiated cells; i.e., cells where the options of development have not been reduced through the selection of a particular developmental pathway. Therefore, given non-inhibited, meristematic or dedifferentiated cells, i.e., morphogenetic conditions favourable to meristem proliferation, there is no a priori reason that new apical meristems (or any structure for that matter) cannot be formed. The reason for the generalization that axes are usually found one on another holding true must be sought elsewhere. In fact, shoot axes do occur on leaves and inflorescences as well as on other shoots, though their relative infrequency may be due to structural and ecological reasons.

The case of epiphyllous initiation of not only shoots, but leaves and inflorescences, on leaves, has been comprehensively reviewed recently (Dickinson, 1978). It is clear from this review that almost all of these are cases of leaf or floral epiphylly, i.e., cases where the leaf-borne structures are relatively small and limited in growth. This may be simply for mechanical reasons, since the leaf is not usually a rigid, reinforced structure, and is in all likelihood incapable of supporting a shoot system of sustained growth. Another possibility is the more temporary nature of the leaf and its function as a photosynthetic unit. As such there is little adaptive value in its evolution into a bearer of large, indeterminate shoot systems. As a result, shoot epiphylly usually involves small systems as in Begonia sinuata (Dickinson, 1978) or vegetative propagules which are discussed below. Where the leaf and especially its main axis is massive or well strengthened, more extensive shoot systems do occur on it; for example, epiphyllous inflorescences in the Meliaceae (Corner, 1964; Mabberley, 1979), or the epipetiolar branching in the Arecaceae (Fisher, 1973a; Fisher and Dransfield, 1977, 1979). The lack of shoot systems per se on inflorescences is probably due to the same reasons as the rarity of shoot epiphylly, though some irreversibility of the differentiation to form reproductive structures may also be postulated.

On the other hand, vegetative propagules, small, condensed shoots or shoot systems with the potential of indeterminate vegetative growth, do occur on leaves. A well known example of this is the succulent genus Bryophyllum (Kalanchoë), and Dickinson (1978) lists others. Sterilization of the inflorescence to form buds or turions is well known among aquatic plants of all families (Sculthorpe,1967), and plants such as Allium and Agave and many members of the succulent family, Crassulaceae. Unlike permanent or long term shoot systems, propagules become autonomous by detachment or rooting, and do not require extensive mechanical or nutritive support from the "parent" structure. As such it is a viable alternative option of plant organization and architecture.

In the case where a shoot axis does originate on another, there is ample evidence for its non-axillary position. Meristems may be produced in an extra-axillary position, for example, Thalassia testudinum (Tomlinson and Bailey, 1972) and Musa (Barker and Steward, 1962; Fisher, 1978). Axes may also occur in leaf positions without an axillating leaf, for example, Pinguicula vulgaris (Raju, 1969) and the Nymphaceae (Cutter, 1957, 1961). The latter may be considered a special case of axes in extra-axillary positions. In this case, the morphogenetic factors are likely to be more complex, and interrelated with mechanisms of phyllotaxy, leaf initiation and organ determination.

II. Modes of Meristem Formation

Regardless of the axillary or extra-axillary location of the meristem, laterality (which implies a shoot of order n producing meristems of the order n+1 as opposed to terminality where the product apices may be considered equal in order) is also not an immutable given. Shah and Unnikrishnan (1971) differentiated three types of non-terminal production of meristems. These are, in increasing distance from the apex, proliferation by a sector of the apex, by a detached meristem, and by dedifferentiation of differentiated tissue. Yet the position and process of the origin of meristems in fact intergrade from the undisputably lateral to the apparently terminal with no clear distinction. Terminal branching as a morphogenetic process in the higher plants is often a controversial issue (e.g., Brunaud, 1971 and Bugnon, 1971, versus Nolan, 1969 and Tomlinson and Posluszny, 1977a, 1977b), and is discussed in greater detail below.

Terminal Branching

Terminal branching, that is to say meristem proliferation at the apex, challenges the Classical Shoot Model tenet of the lateral origin of branches. The historical development of the ideas of terminal versus lateral branching is an interesting one. For various theoretical reasons, opinions have been (and are) divided as to what precisely constitutes terminal branching. And as will be evident throughout this discussion, the quest for a phylogenetic relationship and a "natural" (evolutionary) view of the plant world has time and again been the prime mover in the development of certain concepts of branching.

The Classical Model of the shoot considers terminal meristem proliferation to be a primitive feature because of its prevalence as dichotomy (where two apices are produced) among the algae and lower vascular plants, and its infrequency among the higher plants. Unfortunately, terminal branching as a morphogenetic process in the higher plants is then rejected by the circular argument that it is a primitive feature.

Another reason for this putative primitiveness is the phylogenetic implications of the Telome Theory (Zimmermann, 1959; Stewart, 1964). According to this theory, sympodial and monopodial growth (with lateral branching) were derived evolutionarily from dichotomy of the apex by the process of overtopping and reduction (see Fig. 1.7). While this theory is seldom used explicitly in the study of angiosperms, it is not without influence upon botanic thinking to date.

Initially, the process of dichotomy in plants in general (and other cases of terminal branching by extension, such as trichotomy) was a simple idea of the division of the apical meristem into two more or less equal parts (Sachs, 1874; Campbell, 1917). Yet as the "dichotomy equals primitiveness" idea took hold, its proponents seized upon any evidence that the product apices (apex) may be comparable to a lateral axis and thus be interpretable as a "precocious lateral bud" rather than "true dichotomy" to uphold their point of view. Under this scheme, to qualify as truly dichotomous, many other criteria must be met. Thus the occurrence of meristem proliferation by the partition of the apex found in various groups, e.g. Ampelidaceae (Goebel, 1928; Bugnon, 1952, Millington, 1966), Asclepiadaceae (Bugnon, 1955; Brunaud, 1971) and Apocynaceae (Boke, 1947; Prevost, 1972, 1978), are often not regarded as "truly terminal" by the above authors. Partition or dichotomy of the inflorescence apex, on the other hand, is accepted since the inflorescence is considered to show more indications of "primitive traits" (Brunaud, 1971). However, there have also been authors who recognized the occasional occurrence of dichotomy in vegetative growth in the monocots (Schoute, 1909; Troll, 1937; Emberger, 1960). These authors believed in the existence of an "angular leaf" which acts as a "bisector" of the apical meristem whose growth is interrupted (Emberger, 1960).

The dissenting opinions on the existence of "true dichotomy" would eventually result in attempts to define it more critically. Yet as late as 1968, Gréguss, based largely on external morphology of adult plants, published a scheme for the polyphyletic origin of dichotomously branching monocots and non-dichotomously branching dicots (Gréguss, 1968; also Bock, 1962; for a refutation, see Tomlinson, Zimmermann and Simpson, 1970).

In his work on Asclepias syriaca, Nolan (1969) redefined true dichotomy to be the division of the apex into two new apices without subtending organs or abortion of the original apical meristem, i.e., what he described as an autonomous mode of origin, such that equality of size of the product apices and their subsequent development are not necessary preconditions. The presence of organs subtending a single partition product is generally taken to imply its axillary origin and increasing precocious development in evolution. This would therefore not constitute true dichotomy (which is terminal, not lateral) and Nolan called it pseudodichotomy. Abortion of the original apical meristem with the formation of two new ones (axillated or otherwise) is termed paradichotomy. The scheme is shown in Fig. 1.8. The cessation or interruption of growth at the apex has been defined as part of the process of dichotomy by some authors (Sachs, 1874; Emberger, 1960) but not by others (Campbell, 1918; Foster and Gifford, 1974). Nolan rejected the former approach since the interruption of growth could represent phylogenetic abortion of the main apex, and the two resultant apices, by implication, would be lateral in nature.

At about the same time, Bugnon formulated a scheme of dichotomy and lateral branch formation based on the distinct polarity of cell lineages which may be observed in the algae and applied by extension to the higher plants (Bugnon, 1967). He recognized three main groups of dichotomous branching: division of a clearly present apical cell to form two new ones; the physical separation of cell lineages; and the cessation of growth of one or more cell lineages where growth is by marginal initials. This scheme is shown in Fig. 1.9.

The same idea was elaborated upon in a scheme of fundamental branching types (Bugnon, 1971; Fig. 1.10). According to this, terminal branching (or in its most common form, dichotomy) is defined by a constancy in the polarity of growth and involves the entire apex while lateral branching consists of the creation of a second meristem by localized lateral growth before longitudinal polarity is resumed. A third category, "resolutive branching" deals with branching before growth polarity is established, usually in axillary complexes (Bugnon, 1956).

The schemes of Nolan and Bugnon constitute two different solutions to the problem. On one hand, Nolan has generally taken the traditional concepts of the Classical Shoot Model and added an unequivocal definition of the types of terminal branching. On the other, Bugnon has presented a rather novel approach based on cell lineages and the polarity of growth. This approach may be used to interpret other morphological structures (Bugnon and Turlier, 1977) including those of a controversial nature, for example, the peltate leaf and carpel (Sattler, personal communication).

In theory, the use of polarity of growth via cell lineages to define terminal and lateral growth is a very appealing one. The idea may be analogous to the tracing of various differentiated tissues to the three original dermal layers in early embryonic development in animals, an integral part of embryology and zoology. However, there are both theoretical and practical objections to the tracing of cell lineages in plant growth.

Firstly, the open architectural growth of plants is very different from the closed, determinate pattern of organization of animal embryogenesis. Thus the tracing of cell lineages _per se_ may not be as meaningful as the influences and regulators of morphology that act upon the plant due to position, internal age or external factors (i.e., topophysis, cyclophysis and periphysis, _sensu_ Hallé, Oldeman and Tomlinson) to name but a few.

Secondly, given an axis of a certain number of cells in width or diameter, dichotomy by separation of cell lineages and by cessation of growth of certain of these lineages in Bugnon's scheme would necessarily result in the diminishing size of successive branches unless there is an increase in the number of cell lineages. Yet any increase in the number of cell lineages necessarily involves a plane of cell division not entirely parallel to the length of the axis. Thus it would inevitably involve lateral growth sensu Bugnon. There can be no increase in width without some element of lateral polarity. The difference rests only between a diffuse lateral growth and a more localized one. Any but an extremely gradual increase in width of the axis would constitute lateral polarity and lateral branching as defined.

In the case of higher plants, the vegetative apical meristem may be quite constant in size except for the period of establishment growth (Tomlinson, 1973). Alternatively, there may be minor to marked fluctuations due to leaf initiation and development. Usually, the apical meristem broadens considerably only shortly before branching at or near the apex. Thus, in Bugnon's scheme, this would constitute lateral branching by definition. Also, from the practical point of view, cell lineages in higher plants are not clear cut as in the algae, and often are not easily observable by histological techniques (Fisher, 1976). Nor for the most part, given the isodiametry of meristematic cells, is the polarity of cell division and growth distincly parallel ("terminal") or perpendicular ("lateral") to the axis itself.

Nevertheless, it is not so much the observational difficulty (which is genuine enough) that precludes dichotomy from the morphogenetic processes of higher plants, but the definition of dichotomy itself in this scheme. Just as the definition of dichotomy by the division of the apical cell cannot be applied to the higher plants (Foster and Gifford, 1974), to reject dichotomy by the presence of a noticeable broadening of the apex (i.e., as "indications of lateral polarity") seems both a priori and unjustifiable. Thus while it may be a useful approach to the understanding of apical organization and morphogenesis where cell lineages can be unequivocally determined, the scheme proposed by Bugnon is limited in actual applications.

Nor is Nolan's scheme entirely satisfactory; according to this, true dichotomy is simply a category for any and every phenomenon not directly explicable by the "apex and axillary bud" organisation of the Classical Shoot Model.

Thus despite these attempts at definition, the existence of dichotomy in higher plants is still a matter of interpretation and opinions. Indeed, the terms "apical bifurcation" and "partition" have often been used in an interpretatively neutral sense for the description of the physical phenomenon itself (Nolan, 1969; Wilder, 1975), and is adhered to in the current discussion.

Partition of the apex into equal or subequal parts is known in many taxa (Table 1.4), and almost as many are the criteria in use for and against considering these partitions to be dichotomous. The criteria are listed in Table 1.5 with the pertinent references. It is clear that there are two components in the current understanding of dichotomy. The first is the description of the physical phenomenon of bifurcation or partition of the apical meristem. The criteria for this process, considered by some to be true dichotomy, has long been recognized (e.g., Sachs, 1874; Campbell, 1918; for a historical review, see Nolan, 1969). The second is an attempt to describe, as much as possible, any apparent bifurcation as a derived condition from the apex and axillary (lateral) bud organization. The criteria involved in each of these two components are discussed in detail below.

For the description of the physical phenomenon of dichotomy, an equality of the resultant apices in size and position, at least in early ontogeny, is almost the universally accepted criterion for the process of dichotomy. (The exception is Nolan's scheme, where size and fate of the apices need not be equal.) The question is therefore what constitutes equivalence of product apices.

Firstly, apices produced by bifurcation may be both vegetative or both reproductive, or one of each. The equivalence of differentiation after dichotomy may be explicitly stated (Sachs, 1874), but is more freqently implied. While Nolan based his definition of dichotomy on <u>Asclepias</u>, where a vegetative and a reproductive apex are distinguishable from the outset, the author agrees with Fisher's suggestion that the formation of both types of apices by bifurcation be considered an intermediate case (Fisher, 1976).

Secondly, equality of size and other developmental aspects of the product apices may vary in duration. Most authors admit the possibility of unequal development of size and dominance after an initially equal partition of the apex (e.g., Sachs, 1874, Troll, 1937; Foster and Gifford, 1974). In fact, Emberger has devised the special cases of isotony and anisotony for equivalence and non-equivalence of the subsequent development of product apices.

Another factor is simply that of biological variability. It is difficult to define where equality in size and position ends and lateral growth begins in the continuity presented by diverse examples. To further complicate the issue, one or the other of the resultant apices recognized in relation to the rest of the plant may be "larger" or "higher" with no consistency (e.g., in <u>Butomus</u>, Butomaceae, Charlton and Ahmed, 1973). The latter phenomenon has led some authors to claim greater validity for the use of positional criteria in the determination of dichotomy, and this is discussed below.

The explanation of any apical bifurcation in terms of a main and lateral axis organization to uphold the Classical Shoot Model now precedes any consideration of the inherent processes of branching at the apex; i.e., one must first be able to show that the bifurcation is not really lateral (<u>sensu</u> Classical Shoot Model) before dichotomy can be suggested. This is exemplified by Nolan's scheme, where "true dichotomy" only occurs when all other lateral bud interpretations (e.g., "paradichotomy" and "pseudodichotomy") fail. To this end, many accessory criteria "indicative" of lateral growth have been devised, though these are almost inevitably positional and phylogenetic ones.

First of all, as mentioned previously, Shah and Unnikrishnan (1971) have shown that a lateral axis may originate at a varying distance from the apex: from formation by dedifferentiation of differentiated tissue on the mature axis to development from a detached meristem several plastochrons old to being derived directly from a sector of the main apex. The proximity to the apex is associated with increasingly early development of the lateral, so that where it is found directly on the apex, the term "precocious"is usually used in the literature. The continuum to terminal branching, conceptually so natural, is cut off by the attribute of the Classsical Shoot Model which states that branching can only be axillary and lateral.

Secondly, there must be no evidence of interruption or cessation of activity of the apex prior to bifurcation (Nolan, 1969), since this would "indicate" abortion of the apex with the result that both bifurcation products may be interpreted as precocious lateral buds. As a result of the close relationship of the possible mechanisms of apical abortion, dormancy and rhythmic growth (e.g., Hallé, Oldeman and Tomlinson, 1978), a lack of the last-named feature has also been suggested in support of an interpretation of dichotomy (Tomlinson and Posluszny, 1977a, 1977b).

Thirdly, and most commonly, the presence of a leaf arranged such that it subtends one of the resultant apices is taken to indicate that the subtended apex is a precocious development of the axiliary bud of that leaf; the other apex is a continuation of the original apex (Nolan, 1969; Tomlinson, 1967, 1971, 1973; Ecole, 1974; Foster and Gifford, 1974). As a result of the precocious lateral bud interpretation, features associated with axillary buds of the plant in question are often used to support this. For example, the position of the resultant apex in relation to the centre of the axil of the subtending leaf is critical to the acceptance or rejection of dichotomy (Tomlinson, 1971; Fisher, 1976). The presence of a "shell zone" of relatively narrow cells characteristic of lateral buds (Shah and Patel, 1972) around a product apex is also considered indication of its laterality (Wilder, 1975). Another piece of evidence for precocious lateral bud development is the normal pattern of distribution and other characteristics of the regular axillary buds. Similarity of the "precocious" and "non-precocious" axillary buds would support this interpretation, and vice versa. For example, should leaves of the plant undergoing apical bifurcation not normally subtend axillary buds, the occurrence of "precocious lateral branching" would be less tenable (e.g., Flagellaria, Tomlinson and Posluzny, 1977b). Another example is the case where the leaf "subtending" the precocious bud already has other buds, either vegetative or reproductive, in its axil (Tomlinson, 1971; Fisher, 1974, 1976). While it may be that serial axillary buds, different in their development and precocity, may be postulated, this seems to be stretching the interpretation too far to be of any value (Lieu, 1979b).

It must be emphasized that the idea of precocious lateral branching (with or without abortion of the main apex) is either a typological or a phylogenetic one. The typological approach believes in a fundamental "type" for plant structures and organization such that all else is derived from this original and most basic type. The phylogenetic approach differs in that the fundamental "type" of the typologist is considered the ancestral or primitive condition from which others arose by processes of evolution. The bifurcation of the apex is likewise considered as a condition derived conceptually or through evolution from the fundamental or primitive plan of organization, i.e., an axillary bud which was once developed further away from the apical meristem.

Certainly, a series of increasingly precocious lateral buds, in taxa closely related to one in which apical bifurcation occurs, may make phylogenetic implications more difficult to reject. In this respect, Brunaud (1971) advocates the use of comparative morphology to determine the terminal-lateral organization of bifurcation products. This approach is also found in the "part-for-part" (and therefore positional) comparisons found in much of Wilder's work (Wilder, 1974-1975).

There are additional criteria which are used less frequently. One of these, also based on the equivalence of axes, is that of vasculature (Tomlinson and Bailey, 1972). Disregarding the doctrine of vascular conservatism (which suggests that better vascularized apex, if present, is the continuation of the main axis and the other as the lateral, for a review, see Schmid, 1972), differences in vascular supply may be seen as a reflection of the biochemical and physiological conditions of the resultant meristems themselves. As vascular differentiation usually occurs later than bifurcation per se, the problem of the duration of equivalence of axes arises again. Also, while early differentiation of the product apices cannot necessarily be taken as a refutation of dichotomy, their persistent similarity in development has been used to support the occurrence of the same (Tomlinson, 1971; Tomlinson and Bailey, 1972; Boke, 1976). On the other hand, the use of only adult morphology and vascular anatomy (Gréguss, 1961, 1968) has been shown to be quite inadequate (Tomlinson, Zimmermann and Simpson, 1970). Other evidence for dichotomy includes the presence of an angular leaf (Troll, 1937; van der Hammen, 1947-1948; Emberger, 1960) which is now disproven, and mirror imagery of the phyllotaxy of the resultant axes (Tomlinson, 1971; Halle and Oldeman, 1970) which has also since been rejected as inconstant (Fisher, 1974, 1976; Tomlinson and Posluszny, 1977).

In conjunction with the precocious lateral branching interpretation is the interpretation of the resultant apices as the continuation of the main axis (if any) and the lateral axis, i.e., whether the growth is sympodial or monopodial. Again there are many criteria used to indicate one or another (Table 1.6), and like those for dichotomy, these criteria may either be physical or phylogenetic in origin.

Of the physical criteria, the apex that is larger, taller or at a higher level of insertion is generally considered terminal though interpretations to the contrary have been made based on other characteristics (e.g., Tomlinson and Vargo, 1966). The difficulty of biological variation has already been mentioned above for the determination of dichotomy. Other anatomical or physiological criteria include polarity of growth (Bugnon, 1971), vascular (procambial) continuity (Tomlinson and Bailey, 1972), and the presence of a shell zone (Wilder, 1974 - 1975). Continuity of phyllotaxy after bifurcation is also considered evidence for monopodial growth (Tomlinson and Vargo, 1966; Charlton and Ahmed, 1973), while a rhythmicity in leaf production has been taken to indicate a sympodial one (Serguéeff, 1907). However, the latter is a doubtful criterion, since apical bifurcation is likely to affect other apical processes more than ordinary lateral branching would.

As may be expected, the phylogenetic arguments for determining monopodial and sympodial growth are inextricably linked to those determining precocious lateral branching. The presence of a subtending leaf is used to "indicate" a "lateral" axis, though both resultant apices may be leaf-subtended, with no indication of the previous abortion of the terminal apex (Wilder, 1975; Brunaud, 1976). Again comparative morphology and "part-for-part" comparisons are critical to the interpretation. However, neither Bugnon (1952, 1955) nor Brunaud (1971) considers an axillant leaf to be necessary. The latter author required only the presence of a leaf in a normally prophyllar position on one or more of the resultant apices (as revealed by a "diagramme de ramification") as necessary and sufficient evidence of a lateral axis (Brunaud, 1971). The criterion of a morphologically distinct prophyll as suggested by Tomlinson (1973), on the other hand, is more representative of some physiological differentiation of the lateral axis.

The question, ultimately, has always been one of classification. As in taxonomy or any other situation requiring some formulation of discrete categories, or points of reference in a continuum, definitive criteria must be chosen. In this case, although it is possible to select an arbitrary set of criteria to support whatever system of classification one might want to (and indeed sometimes the use of criteria to support one conclusion or another in the works cited above may border upon the ecletic), two major, non-exclusive but often contrary approaches to apical bifurcation are discernible. One is generally based on the processes of ontogeny while the other attempts to interpret the phenomenon in terms of phylogenetic derivation from some original plan following the dictates of the Classical Shoot Model. Each approach has its set of criteria to "determine" the absence or presence of "true dichotomy" and each values certain observable criteria above others; for example, vascularization over initial size of the resultant apices (Tomlinson and Bailey, 1972).

Though most authors use both ontogenetic and phylogenetic arguments in support of their conclusions, these approaches in themselves are basically antagonistic. The recent schemes of Bugnon (1967 - 1971) and Nolan (1969), though coming to different conclusions, are both phylogenetic by their structuring of the definition of dichotomy. Bugnon's definition precludes dichotomy of higher plants while Nolan's considers it only when the precocious lateral bud interpretation cannot be used. Terminal branching, including the special case of dichotomy as a strictly ontogenetic phenomenon is favoured by Fisher (1976), and Tomlinson and his co-authors (e.g., Tomlinson and Posluszny, 1977; Hallé, Oldeman and Tomlinson, 1978). In fact, Tomlinson and Posluszny have rejected the presence of a leaf in an axillant position _per se_ as evidence of precocious branching, since one product of bifurcation is inevitably axillated by a leaf in plants with distichous or near distichous phyllotaxy.

Given the continuum between clearly terminal and clearly lateral branching in various species, one might justifiably suggest a partial or semi-quantitative homology approach to branching at the apex. While conceptually satisfying, partial homology is difficult to implement beyond qualitative descriptions. The problems are similar to those associated with numerical taxonomy, i.e., which criteria to adopt and which to reject, or whether or not some criteria may be more important than others such that the scheme should be weighted. The latter example suggests that in the use of objective, numerical methods, there is still a large element of subjectivity in converting the qualitative into quantitative measures. However, while partial homology may be applied to morphogenetic processes of the ontogenetic approach, from a phylogenetic standpoint, there is no real alternative but the lateral bud interpretation in the classical conception of the shoot, i.e., there are not two (or more) points of reference from which a partial homology can be drawn. The essential nature of the Classical Shoot Model upon which the phylogenetic arguments are based (Sattler 1966) is not amenable to this approach.

It is not necessary to belabour the point of the inadequacies of the Classical Shoot Model. On the other hand, descriptive morphology based on an ontogenetic approach does provide a less biased view of plant organization compatible with the suggestions of Meyen's nomothetical morphology (Meyen, 1973, 1978). According to this, the "meron" of meristem proliferation consists of a continuous series of modalities where the new meristems are produced at decreasing distances from the apex (Fig. 1.11).

Fasciation

A different form of terminal meristem proliferation not discussed above is that of fasciation. This entails an increase in size or girth rather than in the actual number of apical meristems. It is usually associated with reproductive structures, for example, the inflorescence of Celosia (Amaranthaceae), or of some of the Compositae, or the increase in carpel number from two to many in tomato cultivars. Fasciation in vegetative morphology is considered as teratological or pathogenic, and of little importance to the principles of plant organization and morphogenesis. The best known example of vegetative fasciation is the prized flabellate or undulating "crested" forms of cacti such as Echinocereus reichenbachii (Boke and Ross, 1978).

Jonsson (1970) and Boke and Ross (1978) have shown the development of fasciated (flabellate) forms as the result of a single linear meristem showing varying levels of activity through its entire length (Fig. 1.12) rather than the result of activity restricted only to the ends of the meristem (Buxbaum 1950; Fig. 1.12). With the exception of a pathological response, proliferation of meristematic tissue by fasciation can be physically and conceptually compared to the broadening of the apex during terminal branching such as dichotomy. In addition, Jonsson (1972, 1973) has shown that fasciation may also be the result of multiple meristems arising from dichotomies, but where separate axes are not formed (Fig. 1.12). Meristems from these dichotomies may then undergo further dilation to form new linear meristems.

In a comprehensive approach to the results obtained so far, Boke and Ross considered it possible to regard dichotomy as fasciation followed by defasciation (the production of "normal" shoots of radial symmetry from flabellate ones). They interpret the entire range of fasciated forms reported in the literature in these terms. (In contrast, Jonsson (1973) regarded dichotomy and fasciation to be separate teratological events.) According to the approach of Boke and Ross, the flabellate axes with multiple meristems mentioned above occur where the defasciation process is incomplete. In this view, meristem proliferation at the apex producing vegetative, reproductive, or mixed apices could be regarded, at least phenomenologically, as the result of the processes of fasciation and defasciation alone.

It is also possible to consider this approach, in light of Meyen's work, as follows: the linear and radial apical meristems are two modalities in the meron of apical organization, while fasciation and defasciation are the processes of modality transformation linking them. This may be further integrated into the larger view of meristem organization and proliferation through the mechanism of dichotomy proposed by Boke and Ross. However, as yet the processes of fasciation and defasciation have not been well defined mechanistically except in the distinct cases mentioned above. While some component of the organization of apical meristems must be involved in all cases, it remains to be seen whether, morphogenetically, these processes have the general applicability suggested by Boke and Ross.

In summary, proliferation of the axis is the first step in the development of the architecture of the shoot system. Although much of the growth and development of the shoot system conform to the generalizations of the Classical Shoot Model, the full extent of the branching process in the higher plants is better described by considering all possibilities from component morphogenetic processes, and without resorting to phylogenetic interpretations.

III. Subsequent Development of New Meristems

After its production, a new meristem may then undergo a period of inhibition, growth, further proliferation, differentiation, or some combination of these processes. In terms of the macroscopic architecture of the plant, however, the meristem is of minor importance until it develops further into a distinct axis. This is especially true in the case of monopodial, lateral branching, or in the rare case of terminal branching where one or more meristems then is inhibited, resulting in an unequal, apparently "main-and-lateral" organization.

Meristem initiation and expansion may be fairly close in time, (syllepsis), or there may be a period of inhibition, e.g., a year, before expansion occurs (prolepsis). In the latter case, protective structures such as scales may be well developed. This period of inhibition can, in principle, occur at any stage before significant development of the axes, and be of variable duration. In the extreme case, the new meristem may be permanently suppressed or aborted at an early stage. On the other hand, terminal branching and equal development of the product meristems may functionally be the most rapid development following meristem proliferation. (For a review of the physiological control of bud development and inhibition, see Rubinstein and Nagao, 1976).

Another feature of plant architecture that is affected by the timing of axis development is the occurrence of basitony and acrotony. In basitony, the axes are developed at the base of another axis; in acrotony, branching occurs near the apex. While acrotonic branches may be proleptic or sylleptic, basitonic axes are suppressed or formed from dedifferentiated tissue, and thus proleptic. These two modes of branch formation are really two ends of a continuum, but the majority of cases do tend to fall close to either extremes, resulting in distinctive growth forms.

In addition to the general basitonic or acrotonic modes of axis development, a further pattern related to timing of development is superimposed on acrotonic development. Branches formed along a main axis may be developed continuously or discontinuously. In the latter case, the occurrence of branching may be diffuse and follow no predictable pattern, or it may follow a regular pattern in accordance with some internal or external rhythm.

Diversity in the form of axes, particularly where there is at least an apparent main axis and lateral branches organization, may also result from the number and arrangement of meristems produced in a localized region of the main axis. These new, lateral meristems most commonly occur singly, but may also be found in multiples. Of the latter group, the most common are the serial and collateral arrangements (parallel and perpendicular to the longitudinal leaf axis respectively), though other arrangements have also been described (Troll, 1937). In addition to these, Tomlinson (1973) distinguishes a group of meristems in which the original lateral meristem has produced new meristems resulting in a complex of two or more orders (or generations). Alternatively, two or more new meristems are derived by near equal division of the original such that "main" and "lateral" relationships are not easily distinguishable, i.e., the "resolutive branching" described by Bugnon (1971). McClure (1967) has given many examples of complex multiple meristems in the bamboos.

However, most important of all may be the structural differentiation of the axis itself, a component in axis organization applicable through the full range of terminal and lateral branching. Features of axis differentiation include, among others, the following major ones:

1. Level of organization.
   This includes the levels of orthotropic, reversibly plagiotropic and irreversibly plagiotropic as described by Hallé, Oldeman and Tomlinson mentioned in an earlier section. Concomitant with these levels are characteristic features such as geotropism and phyllotaxy.

2. Phyllotaxy.
   Though the geotropy and organizational level of an apex may determine its radial or bilateral symmetry, a number of phyllotactic patterns are possible, especially within the former group. Phyllotaxy has a significant effect on plant architecture since most lateral branches are

leaf associated.

3. Internodal elongation.
   Stebbins (1973, 1974) considered elongation by intercalated meristems one of the major factors leading to the rise of the angiosperms. Internodal elongation may dramatically affect the form of a plant if not the actual branching pattern and frequency.

4. Formation of more branches.
   The axis may in turn undergo meristem proliferation, resulting in an increased number of apices.

The differentiation of an axis may recapitulate the features of the axis upon which it was formed so that it is a replica of the previously formed axis (what Halle, Oldeman and Tomlinson termed "equivalent" axes). Alternatively, two axes may be different. Frequently, there is a change in the geotropism and phyllotaxy, for example orthotropic trunks and plagiotropic branches characteristic of many trees, or plagiotropic rhizomes with upright shoots. The formation of short shoots on trees is an example of a decrease in the extent of internodal elongation from one axis to another.

More extreme differentiations, often reflecting function and ecology, particularly for vegetative reproduction, are often found. These are exemplified by the formation of tubers or stolons and runners from orthotropic axes, orthotropic ("aerial") short shoots from rhizomes and stolons, or even geotropic rhizomes from orthotropic shoots (Cordyline, Fisher, 1973b).

Another major feature is determinism of growth. Frequently, an axis which is greatly differentiated from the axis upon which it is produced (as in some of the examples above) is also limited in growth. Determinism is particularly associated with reproductive and certain other specialized structures. The production of inflorescences results in a highly complex system of production and differention determinate meristems. Newly produced apical meristems may also develop into very distinctive morphological structures of limited growth, for example spines (e.g. *Bougainvillea*, *Crataegus*) and tendrils which may or may not show a morphological continuum with the inflorescence (Ampelidaceae). From an organizational point of view, the important distinction between determinate and indeterminate axes is the ability to produce new meristems which contribute significantly to the architecture of the whole plant.

Anatomical and morphological differentiation of the plant body, e.g., the variety of leaves and flowers *sensu lato*, fruits, epidermal structures, etc., in turn increases the apparent diversity of form by orders of magnitude. However, these do not alter the basic architecture or skeleton of the shoot system.

Table 1.1 Architectural Models with Differentiated Axes (after Hallé and Oldeman, 1970)

Branch Characteristics		Position of Inflorescence	Trunk Growth	Trunk Organization	Architectural Model
plagiotropic	sympodial by apposition	terminal	rhythmic	sympodial	Koriba, Prevost
				monopodial	Fagerlind
			continuous	monopodial	Petit
		lateral	rhythmic	sympodial	Theoretical II
				monopodial	Aubreville
			continuous	monopodial	Theoretical I
	monopodial, sympodial by substitution		rhythmic	sympodial	Nozeran
				monopodial	Massart
			continuous	monopodial	Roux, Cook
orthotropic		terminal	rhythmic		Scarrone
			continuous		Theoretical III
		lateral	rhythmic		Rauh
			continuous		Attims

Table 1.2 Key to the Architectural Models with Differentiated Axes. (After Hallé, Oldeman and Tomlinson, 1978).

Level of Branching	Branch Modularity	Trunk Organization	Trunk Growth	Plagiotropic Branch Growth	Architectural Model
basitonic					McClure
acrotonic	modular	sympodial			Koriba, Prevost
		monopodial	rhythmic		Fagerlind
			continuous		Petit
	non-modular	sympodial			Nozeran
		monopodial	rhythmic	by apposition	Aubreville
				**	Massart
			continuous	by apposition	Theoretical I
				**	Roux, Cook

** sympodial by substitution, or monopodial

Table 1.3 Types of Axes Defined By Hallé, Oldeman and Tomlinson (1978)

Axis type	Stability	Level of Differentiation	Phyllotaxis	Secondary Leaf Orientation
Orthotropy	stable	low	spiral, decussate	little
Reversible Plagiotropy	unstable	low	spiral, decussate, often with anisophylly	pronounced
Irreversible Plagiotropy	stable	high	distichous, decussate	pronounced

Table 1.4 Taxa of Plants Showing Apical Bifurcation

a. Both product apices vegetative:

Flagellaria (Flagellariaceae)
Hyphenae (Arecaceae)
Mammillaria (Cactaceae)
Nannorrhops (Arecaceae)
Nypa (Arecaceae)
Thalassia (Hydrocharitaceae)

b. One apex vegetative, the other usually reproductive:

Blumenbachia (Loasaceae)
Lycopersicum (Solanaceae)
Myosotis (Boraginaceae)
Nicotiana (Solanaceae)
Alismataceae
Ampelidaceae
Apocynaceae
Aponogetonaceae
Asclepiadaceae
Butomaceae
Cucurbitaceae
Hydrocharitaceae
Juncaginaceae
Limnocharitaceae
Najadaceae
Strelitziaceae
Zannichelliaceae

Table 1.5 Criteria Used to Determine the Occurrence of Dichotomy

Criterion	Studies in which the criterion is used	
	to support dichotomy	to reject dichotomy/not considered
a. Based on ontogeny		
1. Equality of bifurcation products.	Sachs, 1874 Campbell, 1917 Emberger, 1960 Tomlinson, 1970, 1971 Brunaud, 1971 Ecole, 1974 Boke, 1976 Fisher, 1976 Tomlinson and Posluszny, 1978	Nolan, 1969
2. Equality of development of products with no indication of dominance by either.	Tomlinson, 1971 Tomlinson and Bailey, 1972 Foster and Gifford, 1974 Boke, 1976	Emberger, 1960
3. Appearance at maturity.	Gréguss, 1968	Tomlinson, Zimmermann and Simpson, 1970
4. Growth polarity unchanged.	Bugnon, 1971 Brunaud, 1971	Fisher, 1976
b. Based on the interpretation of derivation from an apex and lateral bud organization.		
1. Absence of interruption of apical activity.	Bugnon, 1971 Tomlinson, 1971 Prévost, 1972 Ecole, 1974 Fisher, 1974 Tomlinson and Posluszny, 1977	
2. Absence of rhythmic growth.	Nolan, 1969 Tomlinson and Posluszny, 1977	

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Table 1.5 Continued.

Criterion	Studies in which the criterion is used to support dichotomy	 to reject dichotomy/not considered
3. Absence of subtending leaf to indicate laterality of bifurcation product.	Nolan, 1969 Tomlinson, 1971, 1973 Ecole, 1974 Foster and Gifford, 1974 Fisher, 1976 Tomlinson and Posluszny, 1977	Brunaud, 1971 Tomlinson and Posluszny, 1978
4. Absence of axilary buds on plant.	Tomlinson and Posluszny, 1977	
5. Presence of an inflorescence in the axil of leaf subtending bifurcation product(s).	Tomlinson, 1971 Fisher, 1974, 1976	
6. Absence of a positional or morphological prophyll on one or both bifurcation product(s).	Brunaud, 1971 Tomlinson, 1973	Tomlinson, 1971
7. Different extent of vascularization in product apices.	Gréguss, 1968 Tomlinson and Bailey, 1972	
8. Positional comparison of various organs.		Brunaud, 1971 Wilder, 1974-1975
c. Other criterion.		
1. Mirror imagery of phyllotaxy on shoots produced by bifurcation.	Tomlinson, 1970 Fisher, 1974 Tomlinson and Posluszny, 1977	Fisher, 1976
2. Angular leaf or bissector.	Troll, 1937 Emberger, 1960.	Generally disregarded

Table 1.6 Criteria Used to Determine Terminal and Lateral Apices Produced by Bifurcation

Criterion	Studies in which the criterion is	
	considered	not considered necessary
a. Based on anatomical and physiological features of the apex.		
1. Level of insertion of apices.	general	
2. Size of apices.	general	Tomlinson and Vargo, 1966
3. Height of apices.	general	
4. Polarity of cell lineages.	Bugnon, 1970 Brunaud, 1971	Fisher, 1976
5. Vascularization.	Tomlinson and Bailey, 1972	
6. Presence of a shell zone.	Wilder, 1974-1975	
7. Interruption of phyllotaxy.	Tomlinson and Vargo, 1966 Charlton and Ahmed, 1973	
8. Rhythmic growth.	Serguéeff, 1907	
b. Based on homology of parts.		
1. Presence of a subtending leaf	general	Bugnon, 1970 Brunaud, 1971
2. Morphological prophyll.	Tomlinson, 1973 Fisher, 1974	
3. Positional prophyll	Brunaud, 1971	
4. General part-for-part comparison.	Brunaud, 1971, 1974 Wilder, 1974-1975	

Figure 1.1 Geometry of Multicellular Growth. (See discussion in text.)

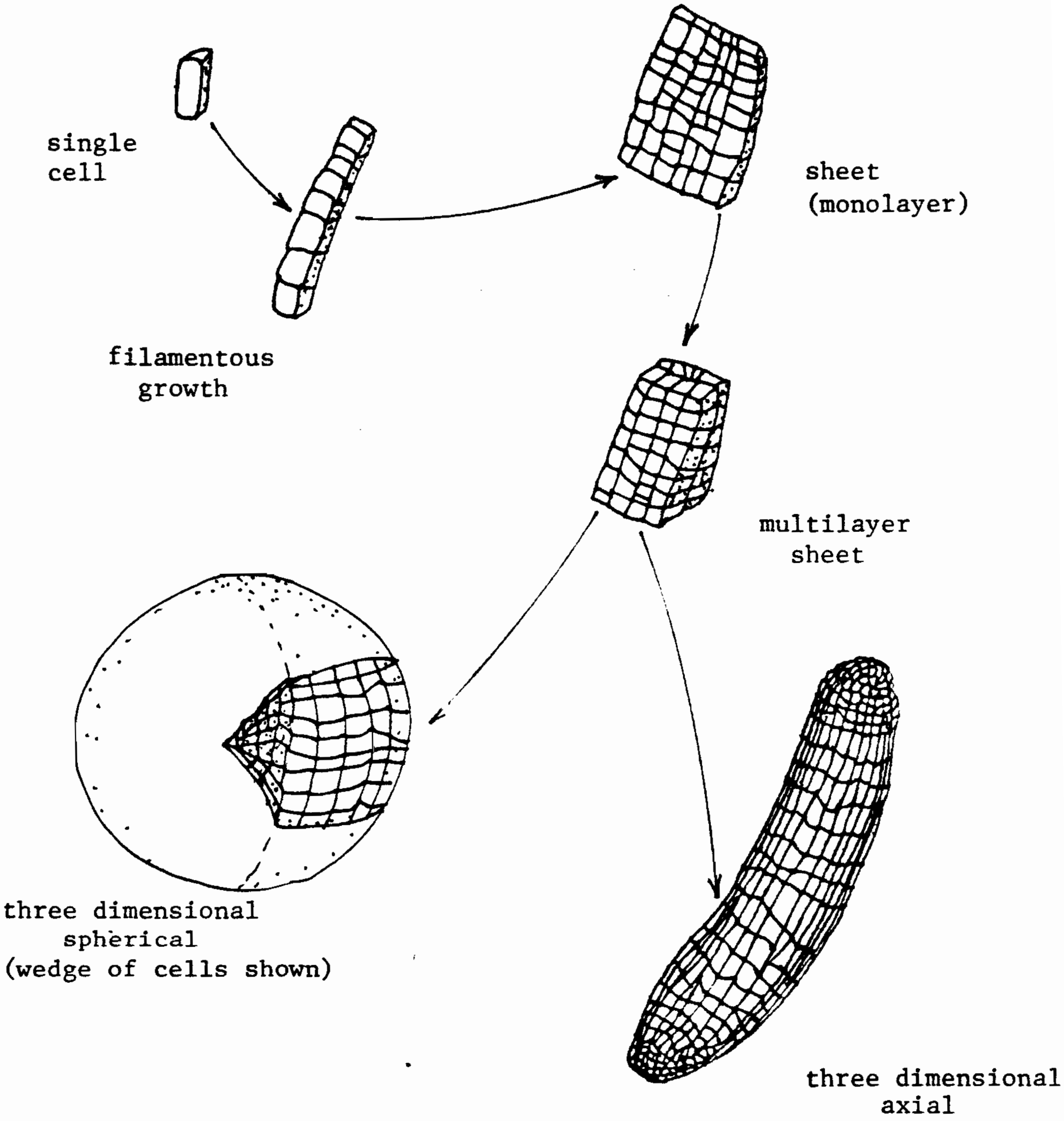

single
cell
filamentous
growth
sheet
(monolayer)
multilayer
sheet
three dimensional
spherical
(wedge of cells shown)
three dimensional
axial

Figure 1.2 Corner's Scheme for the Evolution of Tree Architecture.

a. Cycad Phase: megaphylly, megaspermy, monocaulous, inflorescence lateral or terminal.

b. Monocotyledonous Phase: Cycad Phase plus the occurrence of suckering.

c. *Carica* Phase: Stem less massive compared to the Cycad Phase, sparse branching, some internodal development, herbaceous derivatives.

d. *Dysoxylon* Phase: Megaphylly, mega- or microspermy, much branching, inflorescence lateral or terminal, spiral or decussate phyllotaxy.

e. *Magnolia* Phase: Megaphylly or microphylly, otherwise same as the Dysoxylon Phase.

f. *Myristica* Phase: Microphylly, alternate or decussate leaves in one plane, herbaceous derivatives.

Note: Each leaf is outlined by a dotted line.

--●-- inflorescence

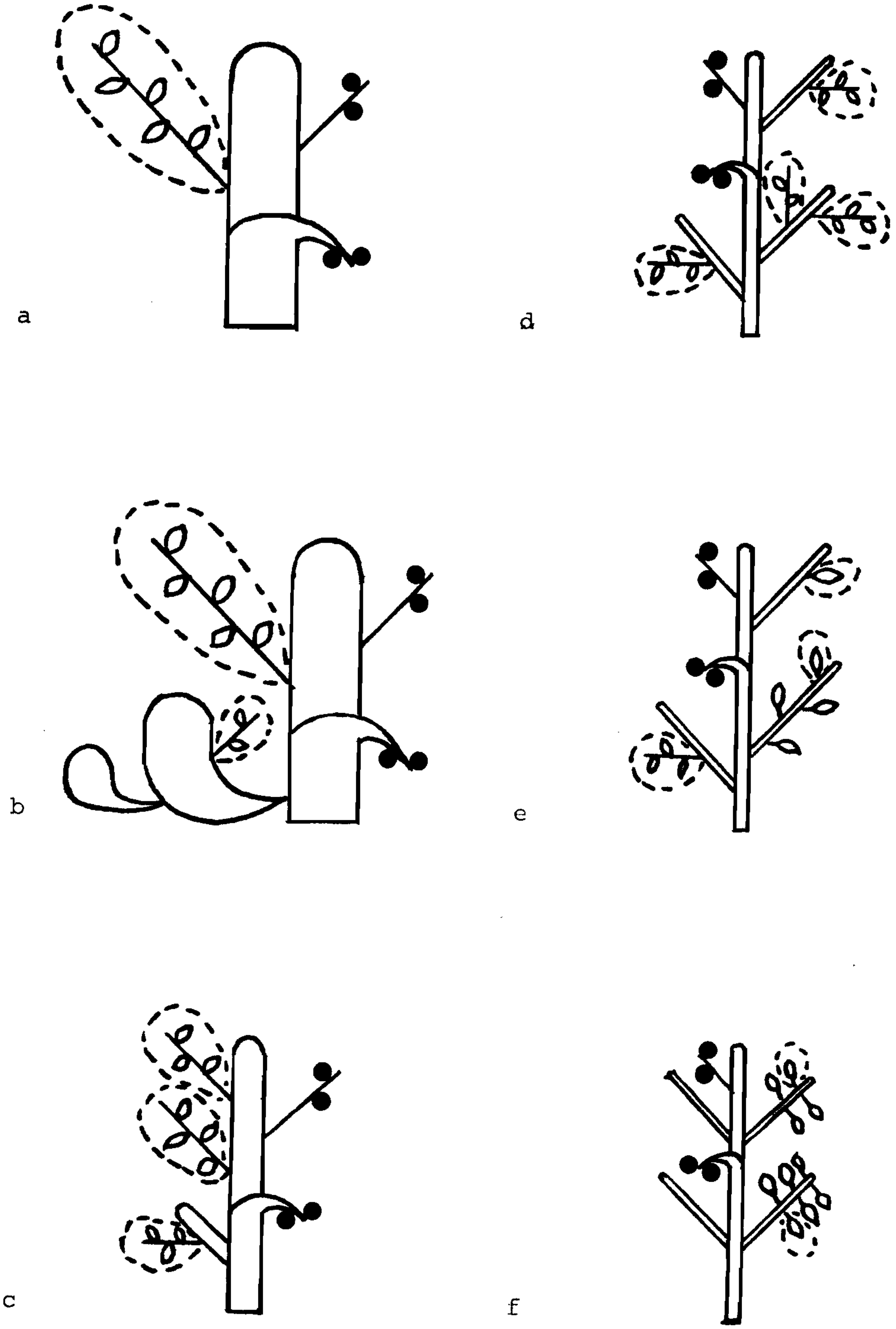

a
d
b
e
c
f

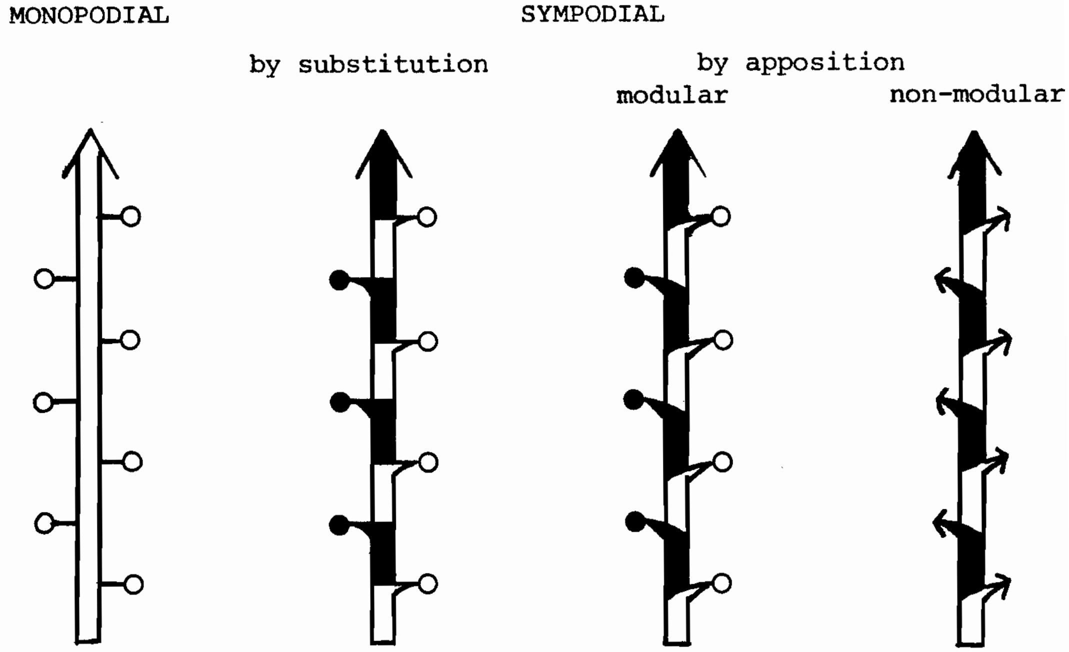
Figure 1.3 Different Types of Axis Organization as Defined by Hallé, Oldeman and Tomlinson (1978).

a. Variation in axial structure: monopodial growth; sympodial growth by substitution and by apposition. (See text for further discussion.)

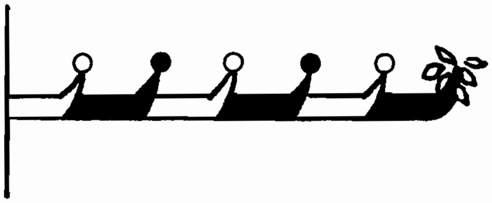
b. Branch structure: plagiotropic by apposition with reversal to orthotropy in each successive unit.

Note: ● o termination of apical growth

⟹ continuation of growth


MONOPODIAL
SYMPODIAL
by substitution
by apposition
modular
non-modular

a



b

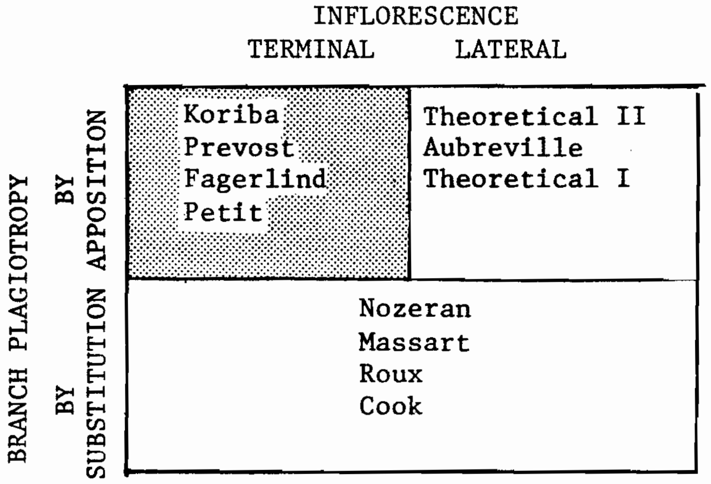
Figure 1.4 Architectural Models with Modular Construction _sensu_ Hallé, Oldeman and Tomlinson.

a. In relation to type of plagiotropic growth and position of inflorescence.

b. In relation to modularity of trunk and branch.

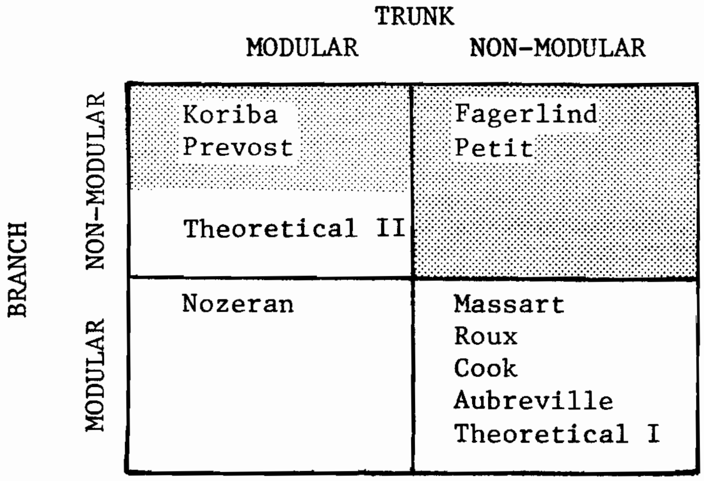
Note: Shaded area indicates modular construction _sensu_ Hallé, Oldeman and Tomlinson. (See text for discussion.)

a



		INFLORESCENCE TERMINAL	INFLORESCENCE LATERAL
BRANCH PLAGIOTROPY	BY APPOSITION	Koriba Prevost Fagerlind Petit	Theoretical II Aubreville Theoretical I
BRANCH PLAGIOTROPY	BY SUBSTITUTION	Nozeran Massart Roux Cook	

b



		TRUNK MODULAR	TRUNK NON-MODULAR
BRANCH	NON-MODULAR	Koriba Prevost Theoretical II	Fagerlind Petit
BRANCH	MODULAR	Nozeran	Massart Roux Cook Aubreville Theoretical I

Figure 1.5 Illustration of Nomothetical Morphology as Applied to Leaf Segmentation. (After Meyen, 1978.)

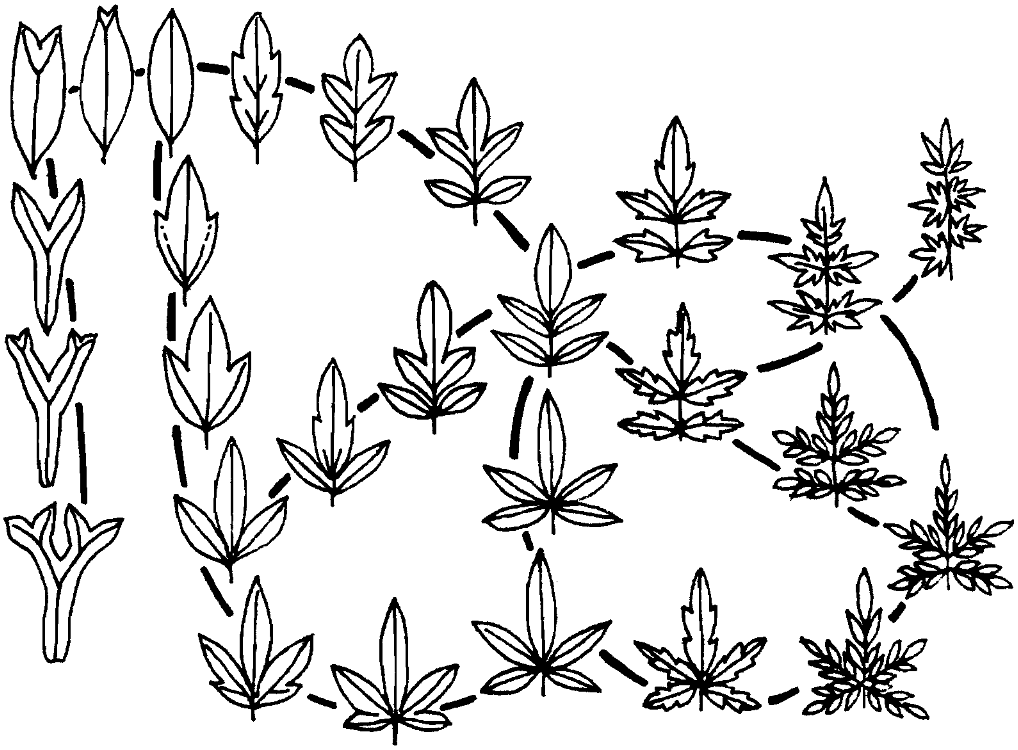


Figure 1.6 Lattice Representing the Probability Density Distribution from the Combination of Two Characteristics, A and B.

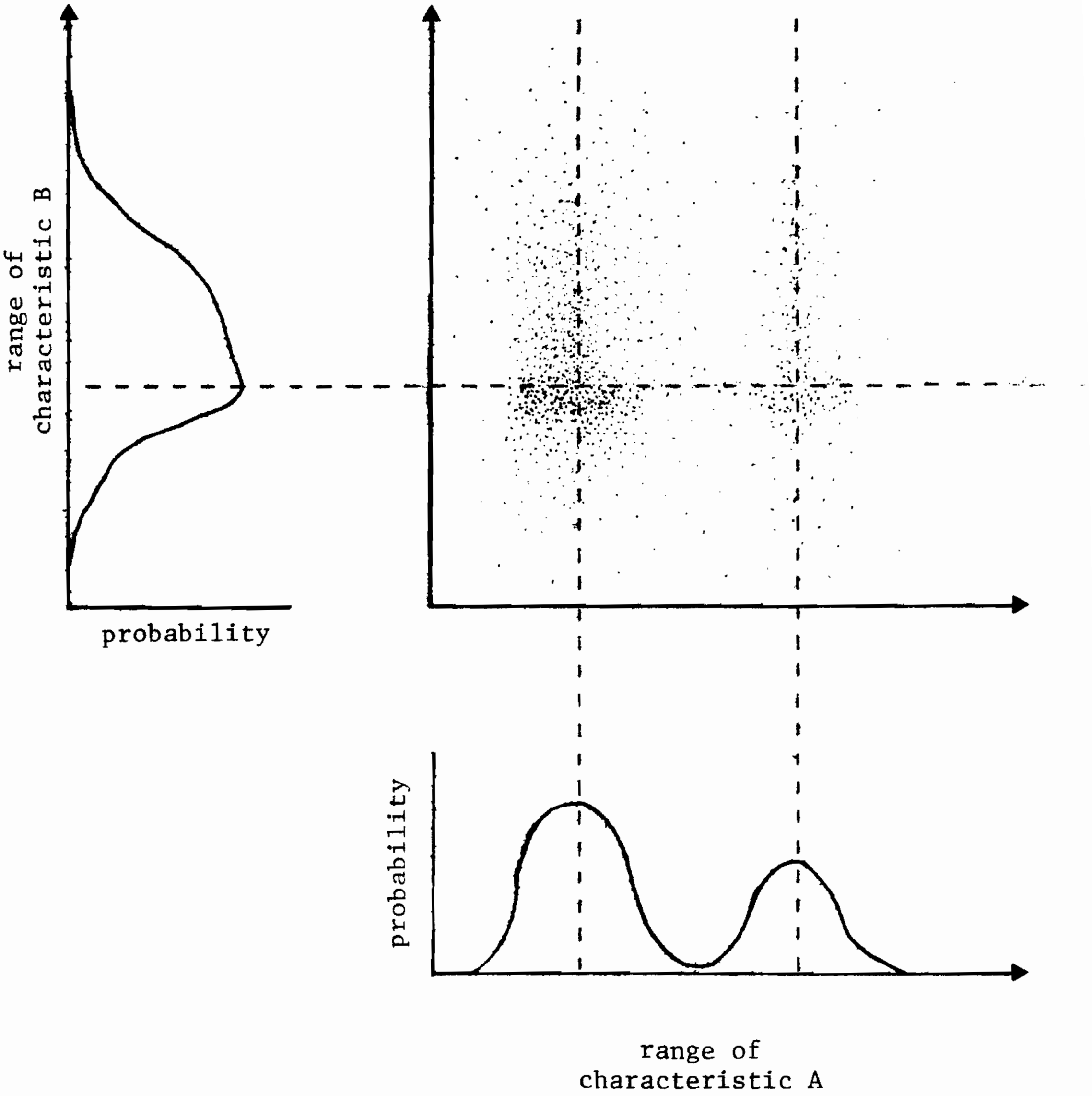

range of
characteristic B
probability
probability
range of
characteristic A

Figure 1.7 Simplified Diagram of some of the Processes According to the Telome Theory.

Note: Branch order included for the dichotomously branching case.

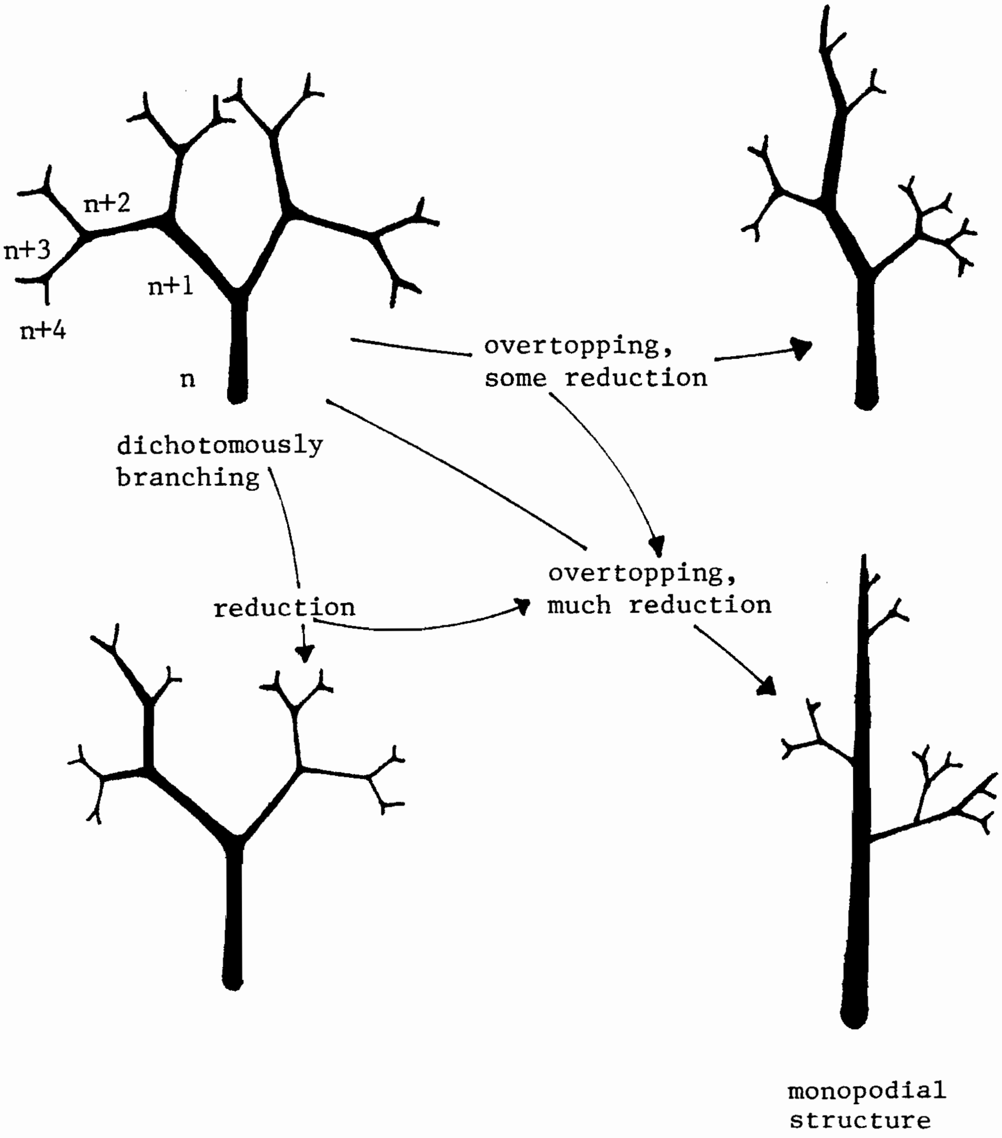

n+2
n+3
n+1
n+4
n
dichotomously branching
overtopping, some reduction
reduction
overtopping, much reduction
monopodial structure

Figure 1.8 Nolan's Classification of Apical Bifurcation.

a. True dichotomy.

b. Pseudodichotomy.

c. Paradichotomy.

d. Paradichotomy.

Note:
X — abortion of apical meristem
L — leaf
V — vegetative apex

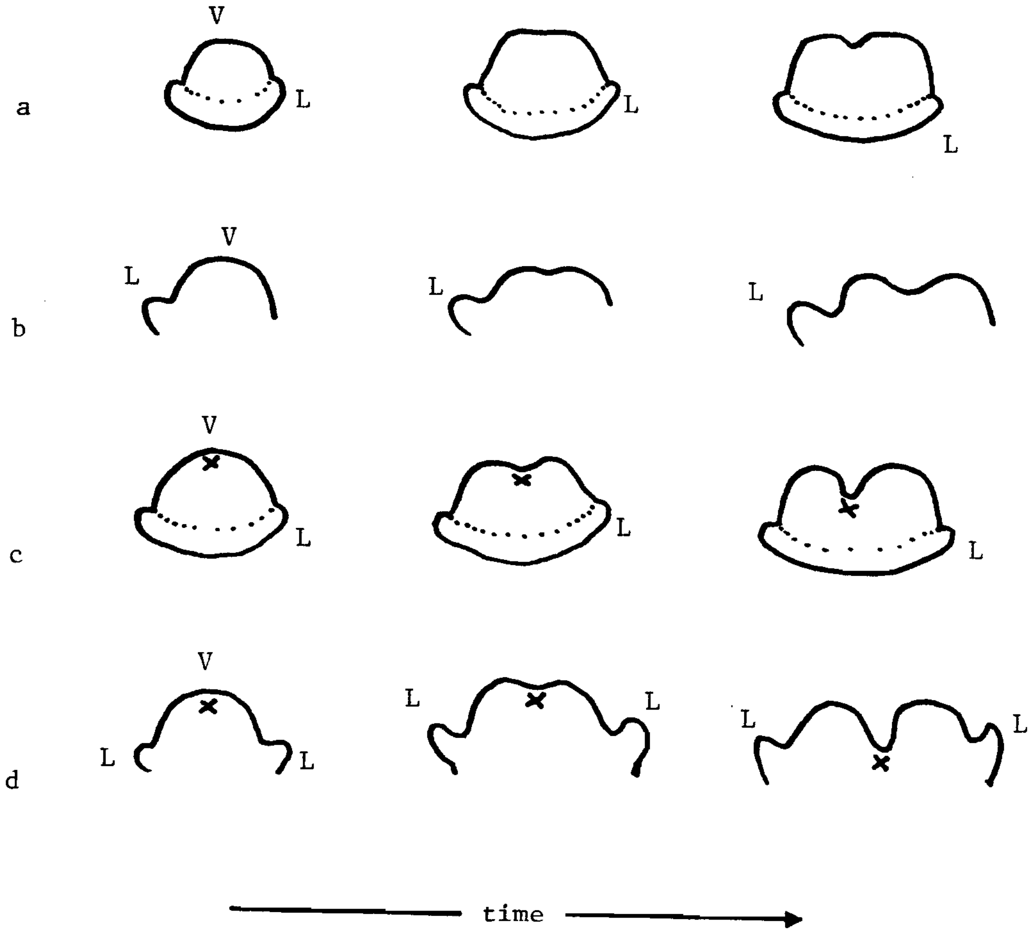

V
a
L
L
L
V
L
b
L
L
V
c
L
L
L
V
L
L
d
L
L
L
L
time

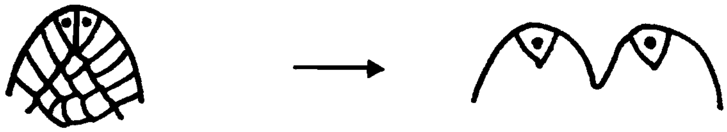
Figure 1.9 Bugnon's Definition of Dichotomy.

a. By division of the apical cell.

b. By separation of cell lineages.

c. By abortion of certain cell lineages.

Note: X — abortion of cell lineage


a


b

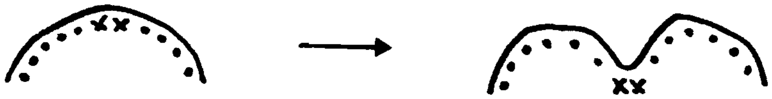

c

Figure 1.10 Bugnon's Classification of Branching Types Based on the Polarity of Cell Lineages.

a. Terminal branching.

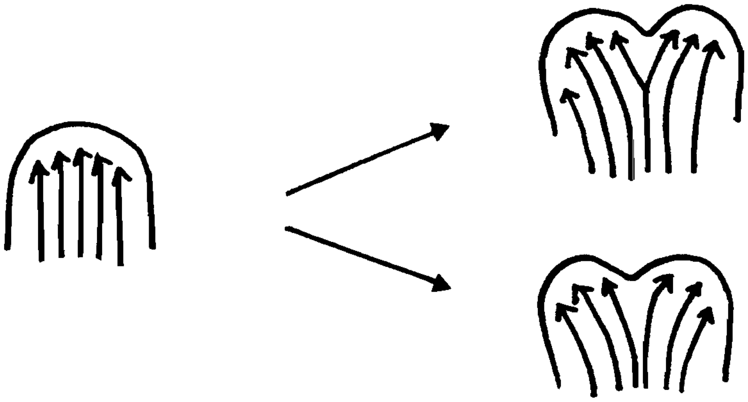
b. Lateral branching.

c. Resolutive branching.

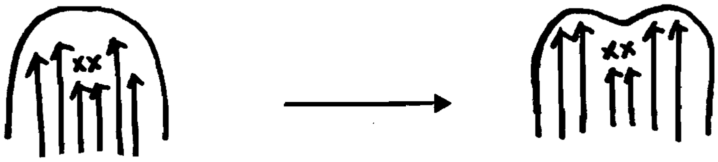
Note: XX — abortion of cell lineage

--> -- cell lineage

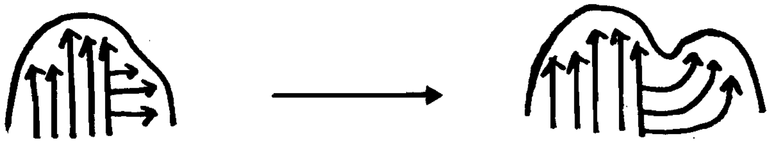
a



b



b



c

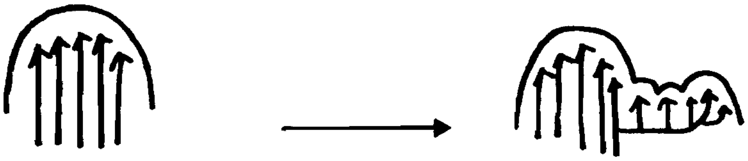


Figure 1.11 Different Modalities of the Meron of Meristem Proliferation.

Note: V — vegetative apex
L — leaf

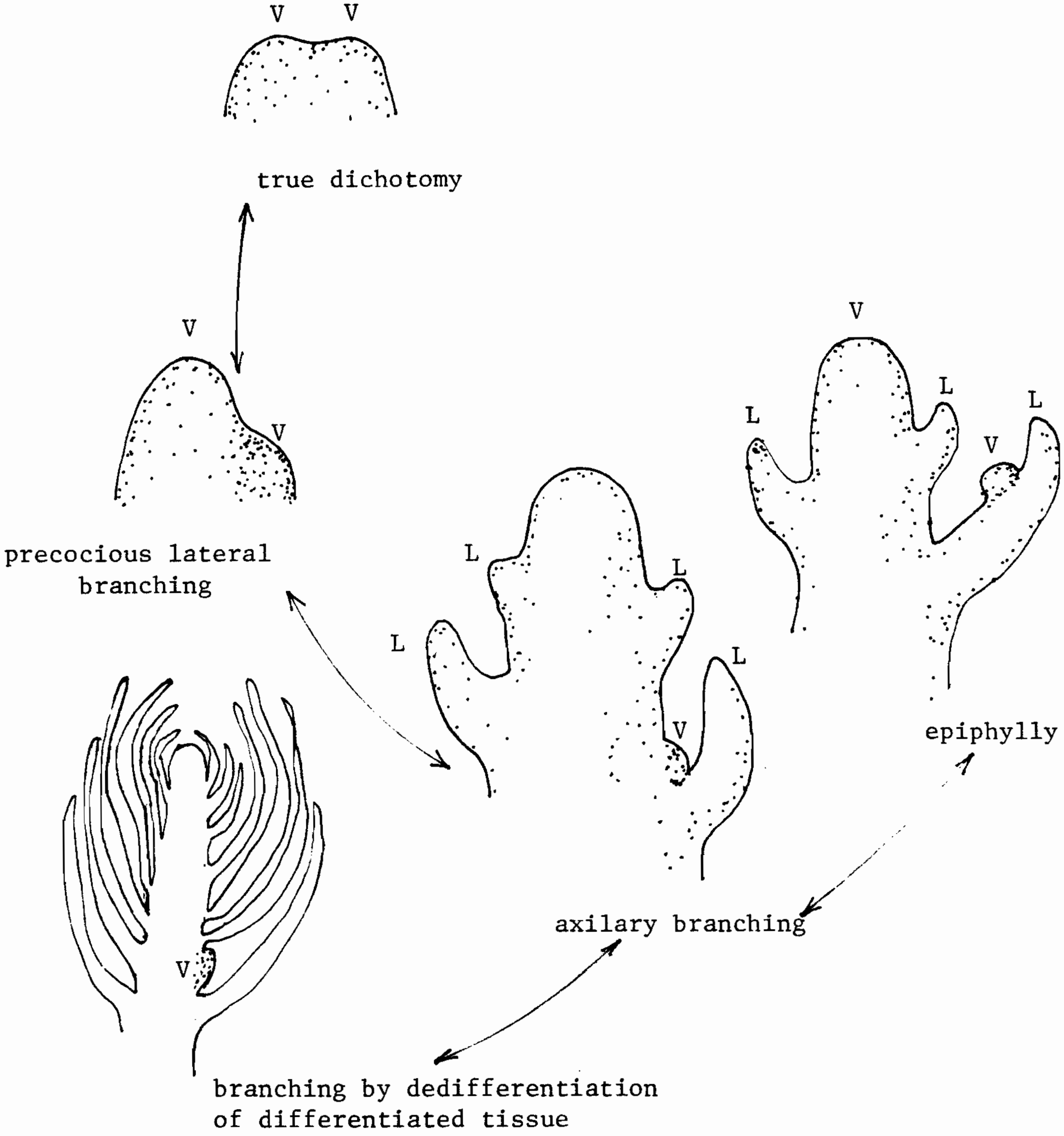
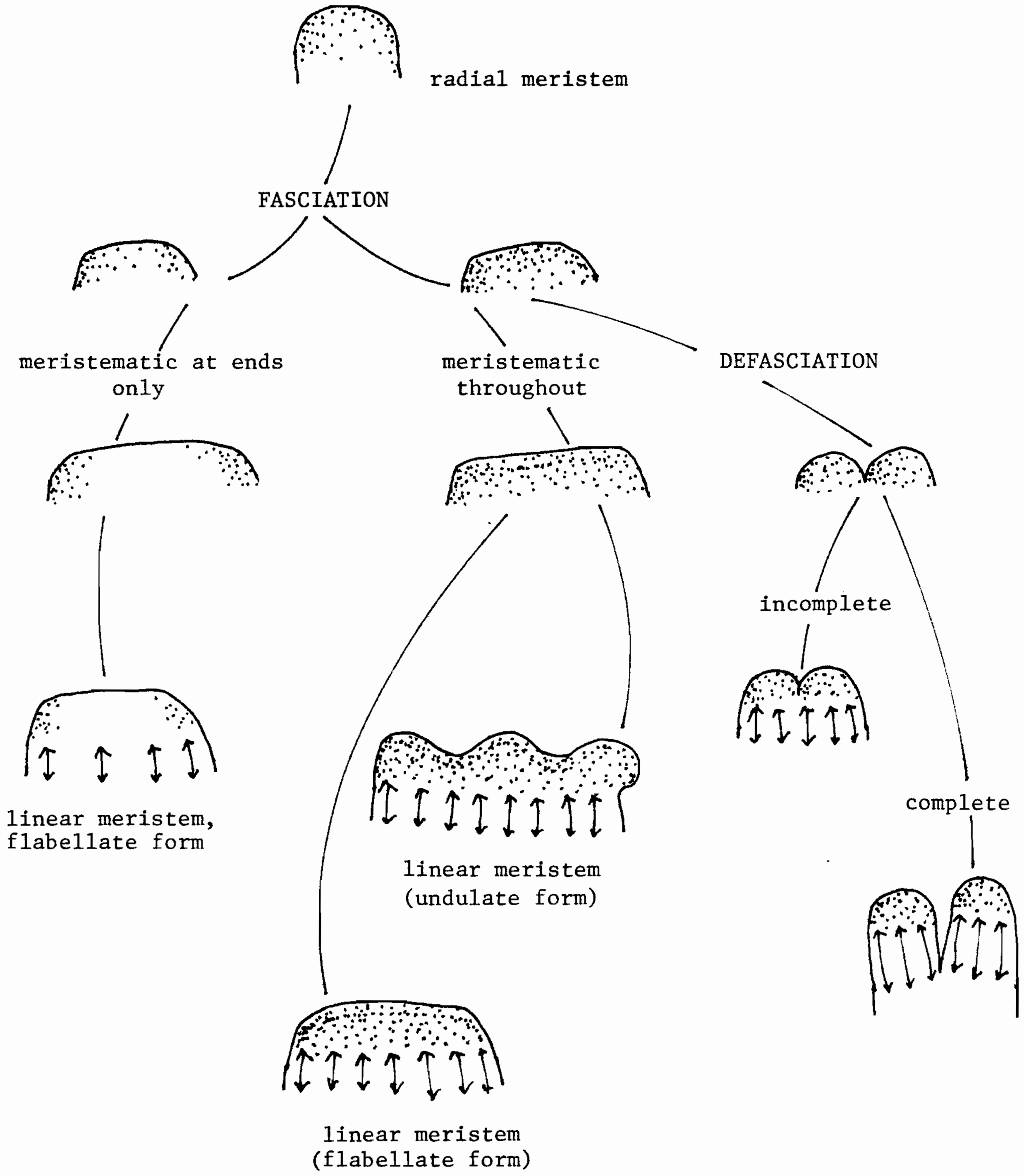

V V
true dichotomy
V
V
precocious lateral branching
V
L
L
L
L
L
V
L
L
L
V
epiphylly
axilary branching
V
branching by dedifferentiation of differentiated tissue

Figure 1.12 Radial and Linear Apical Meristems.

Note: <--> -- axial elongation


radial meristem
FASCIATION
meristematic at ends only
meristematic throughout
DEFASCIATION
incomplete
complete
linear meristem, flabellate form
linear meristem (undulate form)
linear meristem (flabellate form)

CHAPTER II

ARCHITECTURE
IN THE
ALISMATIDAE

INTRODUCTION

In the preceding chapter, the main features accounting for the diversity of plant architecture have been discussed in detail. These include the pattern of distribution of new meristems, the mode of meristem formation, and the subsequent development of the meristems formed.

If these features are indeed the only ones available to the organization of shoot systems, then, as in the patterns of symmetry in the Alhambra and in crystallography, there is a finite number of options of organization available to plant species. There is thus a finite number of variations on the theme of plant architecture underlying the seeming diversity. The analysis and interrelation of variations (modalities) upon a theme (meron) provides a powerful, comprehensive framework for the conceptualization of plant form. The question is then justifiably posed: how does this approach apply to real plants ?

Hallé and Oldeman and subsequent authors have applied their concepts of tree organization with great elegance to the generation of models of tree architecture. Though the models are based on varying characteristics of tree growth, the idea of systematically exploring all possible variations on a theme is not stressed; indeed, as discussed in Chapter I, less emphasis has been placed upon this since the appearance of the original Halle and Oldeman monograph. Although "true dichotomy" has since been accepted as part of the morphogenetic processes, the approach taken by most authors using the ideas of Hallé and Oldeman is largely a traditional one. (The mathematical optimizations of Honda and Fisher, drawing upon the ideas of Horn, are an example to the contrary.)

As defined, the models of Hallé, Oldeman and Tomlinson are not intended to cover the full spectrum of diversity in plant architecture. For example, the models are not always applicable where the architecture of herbaceous forms are concerned. Although attempts have been made to extend them by concepts such as miniaturization and "prostrated parallels" (Jeannoda-Robinson, 1977), these have not yet met with great success. Historically, herbaceous species have been described individually. Most of the past descriptions are in the German literature, notably the papers of Meusel and his coworkers (e.g., Meusel, Jaeger and Morchen, 1977; Meusel and Morchen, 1977). A systematic description of herbaceous architecture comparable to the Hallé and Oldeman tree models was never developed.

Furthermore, the approach of Hallé and Oldeman also becomes limited where plant organization beyond the accepted tenets of "traditional morphology" and the Classical Shoot Model are concerned. Hallé, Oldeman and Tomlinson have described their models as semantic pegs in the biological continuum, as manifestation of certain combinations of morphogenetic processes. Meyen's approach on the very same idea of variations on the theme of plant organization emphasizes instead the continuum. Whereas models sensu Hallé, Oldeman and Tomlinson imply variation in organization, nomothetical morphology centers explicitly upon it. The Hallé and Oldeman models, the "semantic pegs", may be considered a subset of the continuous and discrete modalities of merons of Meyen's nomothetical morphology. But can approaches such as Meyen's be applied to branching systems not accountable by the models ?

In this respect, aquatic vascular plants are particularly interesting to the study of plant architecture. As has been amply documented, there is often significant emphasis of vegetative reproduction over sexual reproduction in these plants (e.g., Sculthorpe, 1967). Although the mechanisms of hydrophilous pollination has evolved in a number of selected genera and species (Pettitt and Jermy, 1975; Ducker and and Knox, 1976; Yamashita, 1976), there is a gamut of successful methods of vegetative propagation by stolons, "pseudostolons" of all manners, turions, etc. This prevalence of the asexual mode of reproduction necessarily involves further elaboration of the branching process and branch organization, where the traditional concepts of branch and plant (as discussed in the previous chapter) are not always applicable; i.e., where modalities of the composite meron of branch and axis formation may be comparatively numerous.

From past and recent studies, it is evident that the aquatic subclass Alismatidae is one of the groups with distinct branching systems that are controversial and challenging to the ideas of traditional morphology. At a glance, it is also clear that the complexity of their organization cannot be adequately described by simple application or extension of the Hallé and Oldeman models. Though there are consistent patterns in their growth, these are not of the generic nature of "trunk orthotropic and monopodial, branches plagiotropic, modular, inflorescence terminal in position" descriptions of these models. Instead, the application of some of the less traditional concepts such as semi-quantitative and nomothetical morphology to these more complex structures would test the validity of these latter concepts of plant organization and architecture. A survey of the variations in form and organization within the subclass in the context of a more process oriented approach (as opposed to a phenomenon oriented one) would shed light on the organization of plants as a whole.

This approach is possible as a result of the level of interest in the Alismatidae. As a potential link between the monocots and dicots through the Nympheales, and because of their aquatic and marine habitat, there have been many studies on all aspects of the group since the beginning of modern botany. Studies on its vegetative morphology, in particular, are more detailed than those of many other taxa The recent resurgence of interest in the order (e.g., the Helobial Conference at Harvard University in 1976, and the publication of the Helobial Newsletter) has also contributed to detailed knowledge of whole plant morphology in the Alismatidae.

The subclass Alismatidae sensu Cronquist is separated into four orders, including the Alismatales, the Hydrocharitales, and the Najadales which, as suborders, make up Engler's order Helobiae. Although the fourth order, the Triuridales, has usually been included in the same grouping by recent authors (e.g., Takhtajan, 1966; Cronquist, 1968), the relationships of its subtaxa among themselves and to the other three orders are less well established. The Triuridales have not been included in the following discussion.

The survey of their architecture follows the organization of Taktajan and Cronquist, though the arrangement of genera within the families may follow those of other studies (e.g., Sculthorpe, 1967; Tomlinson and Posluszny, 1976). It should be emphasized that as the current study is made solely on a morphological and morphogenetic basis with no phylogenetic implications, the subscription to one arrangement or another is not as critical as it otherwise might be. The data are drawn from personal investigations and morphological studies described in the literature. Where no morphological studies per se are available, information is drawn from descriptions in taxonomic works, floras and keys and other studies as possible. The major sources, specifically cited and otherwise, are listed in Tables 2.1-2.3. The findings of the author are reproduced in detail here and discussed in context of the pertinent literature. Literature material is summarized in sections on each of the three orders. These are followed by a general discussion on the architecture of the subclass in Chapter 3.

In a survey of this scope, several provisions must be borne in mind. Although the subclass Alismatidae is relatively well studied, many of the subgroups, particularly the diverse tropical taxa, are little investigated. Detailed studies are frequently lacking; nor is it possible to verify the accuracy of all the information assembled. Furthermore, some of these taxa are known to show great plasticity in form (Tomlinson, personal communication). Thus any conclusion drawn about architecture in the

Alismatidae are quite far from being final. Rather, they may be subject to revision as more detailed data become available.

ALISMATALES

The Alismatales consists of about seventeen genera divided into two or three families. About twelve genera and 70 species make up the single family Alismataceae. The remainder, five genera and 12 species, are either included in the Butomaceae (Hutchinson, 1973), or divided between the monotypic Butomaceae and the family Limnocharitaceae (Takhtajan, 1966; Cronquist, 1968; Cook, 1974). In the following discussion, the order is divided into three families, and the genera within each are listed in Table 2.1. A survey of the growth forms in each genus and family is given in the following sections on the Alismataceae, Butomaceae and Limnocharitaceae respectively. Detailed investigations into the first two families were conducted as part of the current study and are included in the appropriate sections.

Alismataceae and Butomaceae

Members of the Alismataceae are usually perennials, with short, thick, corm-like stems bearing a rosette of leaves. Stoloniferous shoots, formed either by the development of lateral meristems, or by the sterilization of inflorescences, are frequent. Many of the genera in the family are, at least superficially, very similar in terms of their architecture. They are differentiated one from another through characteristics of floral structure and inflorescence organization.

The family Butomaceae is represented by the single species, Butomus umbellatus, the flowering rush. It has a thick, creeping rhizome bearing erect foliage leaves and showy inflorescences. It has been the subject of a number of morphological studies including floral development (Singh and Sattler, 1974), inflorescence development (most recently, Wilder, 1974) and sterilization (Lohammar, 1954), and rhizome morphology (Weber, 1956a). Studies on the architecture of Butomus, however, have given conflicting results (Charlton and Ahmed, 1973; Wilder, 1974).

The approach undertaken here is to study representatives of two genera of the Alismataceae, Alisma and Sagittaria, in detail in order to understand both the upright, corm-like vegetative axis, and the stoloniferous types of organization that do not result from sterilization of the inflorescence. (These highly vegetized inflorescences, referred to as pseudostolons, have been described in detail for Echinodorus tenellus by Charlton, 1968.) Representative species of the genus Alisma, which only has the congested upright vegetative axis, and the genus Sagittaria, where upright, corm-like axes and thin, creeping stolons both occur, were investigated in detail morphologically. Then a comparative study of a rhizomatous species of Sagittaria, S. lancifolia, and Butomus umbellatus was undertaken in order to evaluate the occurrence of rhizomatous growth in Alismatalean architecture. These studies are published as "Growth Forms in the Alismatales" parts I and

II (Lieu, 1979b, 1979c) and duplicated in the following sections. A brief discussion of the architecture of the species studied is included in each of these sections. These are followed by descriptions of the architecture of other genera in the Alismataceae. A more comprehensive discussion of organization in the order Alismatales, in relation to the rest of the subclass Alismatidae, is found in Chapter 3.

Growth Forms in the Alismatales. I. Alisma triviale and Species of Sagittaria with Upright Vegetative Axes.

Introduction

In recent years there have been many detailed organogenetic studies of growth form in the diverse groups of the Alismatidae, for example, the Alismataceae (Charlton, 1968; Charlton and Ahmed, 1973), Najadales (Posluszny, 1976), the Alismatidae (Wilder, 1974a, 1974b, 1974c), and various seagrasses (Tomlinson 1974; Tomlinson and Bailey, 1972).

The present study was undertaken for several reasons. First, the aim was to establish a basic plan of organization for the "rosette" members of the Alismatales and Hydrocharitales. This would then serve as a starting point in a comparative survey of growth forms of the subclass Alismatidae. Though only a few species have been studied at length (Alisma plantago-aquatica, Wydler, 1863; Echinodorus tenellus, Charlton, 1968; Ranalisma humile, Charlton and Ahmed, 1973, for example), the growth forms found in the Alismataceae clearly involve less complex structures than other families in the subclass. Within the Alismataceae, the genus Alisma is one of the simplest in organization. Wydler (1863) showed no developmental stages in his study of A. plantago-aquatica. With the availability of a simple technique for visualizing events at the apex (Sattler, 1968), Alisma triviale, a North American species closely related to A. plantago-aquatica is described in detail as the basic growth pattern.

In addition, previous investigations indicate that the inflorescence and continuation shoot in the Alismatidae are formed by apical bifurcation. This process is usually considered to be the result of precocious axillary (sympodial) branching. However, the interpretation of bifurcation products (as sympodial or monopodial) is not always clear cut, as in the case of

Butomus umbellatus (Charlton and Ahmed, 1973; Wilder, 1974a). Thus it is important to describe each case, stating the criteria used in making the interpretations.

The genus Sagittaria is of interest for two reasons.

1. It contains both upright (rosette) species and rhizomatous ones. An understanding of these two types of organization and their interrelationship may help clarify the debated growth form of Butomus. The upright growth form is considered in this study whereas the rhizomatous S. lancifolia is described in a comparative study with Butomus in the following section (Lieu, 1979c).

2. Many species of Sagittaria are also known to form dense meadows excluding other plants (e.g., Adams and Godfrey, 1961). A diversity of unique methods of "pseudostolon" and "stolon complex" formation has been demonstrated in the Alismataceae (Charlton, 1968, 1973) and in the Limnocharitaceae and Hydrocharitaceae (Wilder, 1974a, 1974b, 1974c). These methods of vegetative reproduction contribute to variation in plant organization and are of significant ecological importance. The questions are, therefore: What organogenetic mechanisms are involved in vegetative propagation in Sagittaria ? How do these compare with the ones already described in the literature ? How do they modify the basic plan of organization presented by Alisma triviale ?

Lastly, this study also takes into account the organogenesis of seeds and seedlings, and the consistency of organizational patterns within and between populations, factors that are not usually included in morphological work on the Alismatidae.

Material and Methods

Entire plants of Alisma triviale, Sagittaria cuneata and S. latifolia were collected over the growing season in 1976 from Morgan's Arboretum (Ste. Anne de Bellevue), Mont St. Hilaire, and Nun's Island, Quebec. Different populations of each were distinguished and investigated separately. A complete set of voucher specimens has been deposited in the McGill College Herbarium (MTMG).

Some material of Sagittaria subulata form subulata (Adams and Godfrey, 1961) was obtained in the flowering condition from Dr. J. French of the Fairchild Tropical Garden in Florida. This was collected from Fisheating Creek, Glades County, Florida in mid-October 1976. Owing to the small amount of material available, only a single voucher specimen was made and deposited in the Fairchild herbarium. In addition, two species of Sagittaria growing in the McGill University greenhouse and originally obtained from William Trickers Inc. (Saddle River, New Jersey) as Sagittaria "Sinensis" and S. "microphylla" were also studied. As neither of these has yet flowered, a positive identification to the species level is not possible.

Material for study was washed in water and fixed in 70% ethanol within 48 hours of collection, often after a preliminary dissection. This was then stained in alcoholic acid fuchsin, dissected, and photographed using the technique of Sattler (1968). All photographs have been reproduced at the same magnification (120x) to facilitate comparisons. The photographed specimens and others were then oriented in blocks of pith and dehydrated in a tert-butyl alcohol series and embedded in Tissue Prep (mp 61 degrees C, Fisher Scientific) using standard techniques. Serial sections were cut at 6 or 7 µm and stained in Johannsen's Safranin or fast green and safranin. From these, camera lucida drawings were made with a Zeiss microscope and drawing tube attachment.

Seeds of Alisma triviale were collected in 1976 whereas those of A. gramineum were obtained from Lake Champlain, New York, courtesy of Dr. W. Countryman. These were germinated under sterile conditions and ambient light in spring 1977; 6- to 8-week old seedlings were then transferred to soil under about 5 cm of water. A few seeds of Sagittaria cuneata were collected in 1976 and again in 1977. Attempts to germinate these, however, did not succeed.

The sample size of each observation, designated "n", is included in the results section. The specimens which appeared identical in organization to previous observations and thus not recorded in detail are not counted in the sample size, but simply indicated by a plus sign (+).

Phyllotaxy is given as Schimper and Braun fractions or as divergence angles. Time references in the descriptions are in terms of developmental events, as the actual time scale of these events was not studied.

Results

1. Alisma triviale Pursh. (1)

Alisma triviale is an emergent growing in shallow water in ditches and at edges of lakes and ponds. It consists of a short upright stem with a rosette of ovate-lanceolate leaves with long petioles (Fig. 2.1). Phyllotaxy is spiral, approximating 2/5. Flowering usually begins in early July, producing three large paniculate inflorescences per season. These are basically trimerous in organization. They are considered to be terminal in position (Wydler, 1863), with the continuation growth (also called the renewal growth) forming from a precocious lateral bud in the axil of the ultimate leaf; i.e., a sympodial structure. The plant is perennial. After the third inflorescence is formed, the renewal growth remains vegetative, overwintering and forming the axis the following year. Stem portions formed in the previous year disintegrate rapidly, but may occasionally be found attached to the current year's growth.

At the time that it is shed, each seed contains an incumbent embryo (Figs. 2.2c, 2.2d) with a large cotyledon. The cotyledon is terminal in appearance, having only a small aperture near its base where the edges of the sheath overlap (Fig. 2.3). Two plumular leaves would have been initiated. Phyllotaxy is spiral, with no evidence of distichy (Figs. 2.3c, 2.5b; n = 10+). A procambial trace links cotyledon to radicle, while a branch of this from below the level of the apex supplies the first foliage leaf (n = 6). At germination (Figs. 2.2d, 2.2e), the first foliage leaf emerges through the aperture in the encircling cotyledon. The hypocotyl and radicle elongate. Many fine root hairs are formed on the collet between them. Soon, adventitious roots develop at the base of the cotyledon. Three to five linear leaves are formed before the petiolate ones, regardless of water depth. Throughout vegetative development, the apex (Fig. 2.4a) has a single tunica layer and leaves are initiated by periclinal divisions beneath it

(Fig. 2.5c; n = 4). A median procambial strand develops in the leaf primordium by the second plastochron, and the encircling leaf base by the third. Spiral 2/5 phyllotaxy is indicated with the initiation of more leaves.

The first sign of inflorescence formation is the broadening of the apex, especially in the plane oblique to that of the last-formed leaf, to about twice its original size (Fig. 2.4b). This occurs by an increase in cell division though the tunica layer remains distinct and continuous. Bifurcation to form two equal or subequal apices occurs (Fig. 2.5e). Where subequal, the apex distal to the ultimate leaf is usually larger, and develops into the inflorescence; the other, off centre of the ultimate leaf axil, forms the continuation growth (Figs. 2.4c, 2.4d, 2.5e). At about the same time, localized periclinal and anticlinal divisions and cell enlargement beneath the tunica result in the appearance of a ridge of tissue between the two apices (Fig. 2.5f). This ridge eventually forms the membranous, two-keeled prophyll of the continuation growth. Positionally, it continues the phyllotaxy of the axis; i.e., it is located where the next leaf would have been had there been no inflorescence formation. The greater growth rate of the inflorescence results in a clear size difference soon after this (Fig. 2.4e), but the tunica remains continuous over both apices for a considerable period of development (Fig. 2.5f).

The foliage leaves formed after the prophyll also continue uninterrupted the phyllotaxy of the axis before inflorescence formation, the first leaf developing in the space between the ultimate leaf and the prophyll (Fig. 2.4f). At this time, the first bract of the inflorscence is formed on the side of the inflorescence distal to the continuation growth (Figs. 2.4f, 2.4g) as a result of anticlinal divisions and subsequent cell enlargement beneath it (Fig. 2.5f). In the same way, the second and third bracts, completing the lowest pseudowhorl, are formed on the proximal side of the inflorescence, opposite the first and second foliage leaves of the continuation growth, respectively. The first bract of the next whorl alternates between the first and second bracts of the first whorl. Inflorescence branch primordia are initiated in the same sequence as their subtending bracts (Fig. 2.4h). At the stage of formation of the first bract, the prophyll is distinct from both apices (Figs. 2.4f, 2.4g), extending laterally to enfold the continuation growth later in development (Fig. 2.4h). By the time a second foliage leaf is formed, the inflorescence is larger than the continuation growth, occupying most of the centre of the shoot system. The continuation growth is often hidden, compressed against the scape below the lowest branches (Fig. 2.4h). Eventually, it becomes larger than the inflorescence, displacing it to a more lateral position.

Usually, five foliage leaves are formed before another inflorescence is initiated; i.e., a cycle of six leaves including the membranous prophyll (Fig. 2.5d). Occasionally (2 plants out of 30), only four foliage leaves are formed before transition to flowering again. In these plants, the inflorescences lie along an orthostichy, that is, along a radius of the plant in cross section, as a result of the 2/5 phyllotaxy. In one plant, the second inflorescence was formed after four foliage leaves on the continuation shoot, but the third inflorescence was formed after five such leaves.

After the third inflorescence has been formed, the apex produces only foliage leaves. Up to 11 of these are found on plants collected in late August, but some do not expand until the following season. Inflorescence and floral development have been studied in detail by Charlton (1973) and Singh and Sattler (1972), and are not mentioned here.

Plants collected late in the season have axillary buds associated with all but the ultimate leaf below the first inflorescence. The continuation growth is generally considered an extremely precocious development of the axillary bud of the ultimate leaf. However, for simplicity, the term "precocious" is used here only for those buds not formed by bifurcation of the apex.

Each axillary bud first forms an adaxial prophyll (Fig. 2.3e). The first leaf is abaxial and to one side (Fig. 2.3f), depending on the direction of the genetic spiral; i.e., these buds may be homodromous or antidromous in relation to the main axis, with no regular pattern of distribution. Phyllotaxy and anatomy are similar to the main axis. Most buds are arrested at the three to five foliage leaf stage (Fig. 2.3f). On the other hand, the leaf in the axil of the penultimate leaf is precocious in development and seems less inhibited, often having up to 10 unexpanded foliage leaves (compare Figs. 2.3g and 2.3h). Above the first inflorescence, only the penultimate leaves subtend axillary buds. There is no synchronization of the development of main and axillary apices.

In one population (n = 20), the development of axillary buds, especially the precocious penultimate one, is more extensive. The first penultimate bud expands, forming a second order branch with adventitious roots. It may also initiate inflorescences after eight or more foliage leaves though branches with expanded inflorescences have not been collected. The secondary axis reiterates the pattern of the main axis. Only penultimate axillary buds are found. One or two axillary buds older than the first penultimate bud of the main axis may also initiate inflorescences, but these buds remain unexpanded and seem to play no role in the following season. No other variation in the basic plan of organization was found among the three populations investigated.

2. Alisma gramineum Gmel. (A. Geyeri)

Seeds of Alisma gramineum, an entirely submersed species similar to A. triviale, were also germinated under sterile conditions (Fig. 2.3a). The seed and embryo are slightly larger than those of A. triviale (compare Figs. 2.2a, 2.2b with 2.2c, 2.2d, and Figs. 2.3d, 2.5a with 2.3c, 2.5c), with spiral phyllotaxy evident from the cotyledon and two plumular leaves. The apex has a single-layered tunica with leaf initiation in subjacent layers (n = 6). No flowering stages have yet been obtained, but there is no difference in the pattern of organization between the vegetative phases of the two Alisma species.

3. Sagittaria latifolia Willd. (2)

Both Sagittaria latifolia var. latifolia and S. cuneata usually grow in shallow water, with a short upright stem bearing arrowhead-shaped leaves on long petioles. They are perennial and overwinter by means of corms (Bogin, 1955). These are developed from stolons which are also responsible for vegetative reproduction during the growing season (Fig. 2.6). Sagittaria cuneata flowered in July, 1976; S. latifolia also initiated inflorescences by this time, but these did not expand and flowering was not evident until mid-August. All three populations of the latter species are dioecious (n = 49+), as is usually the case (Wooten, 1971). These are staminate plants, so that seeds and seedling stages are not available. The two species are extremely similar in organization, and only the development of S. latifolia is described in detail though equivalent stages are shown for both species.

In spring, the corms break dormancy (Fig. 2.6c). Each develops an elongated, orthotropic internode before formation of the short, thickened stem. As a result, the plant and its parent corm are some distance away from each other. The apex has a one-layered tunica, with leaf initiation by periclinal divisions in the second and third layers (Fig. 2.9a). Phyllotaxy is 2/5. Leaf bases ensheathing the entire shoot apex are developed by the third plastochron (Figs. 2.7a, 2.7b), with the anodic edge exterior to the cathodic one (Fig. 2.10d). The asymmetry of the leaf base is further manifested in a shorter, thicker anodic side. The inflorescence is a raceme, with flowers arranged in pseudowhorls of three. It is generally considered to be terminal, with renewal growth by precocious lateral branching.

With the onset of flowering, the apex begins to broaden (Figs. 2.7c 2.7d, 2.9b) as a result of general cell division and enlargement. Two centres of growth are soon apparent. The one distal to the ultimate leaf formed before the transition becomes the inflorescence, while the proximal, off centre in the axil of this leaf, forms the continuation growth (Fig. 2.7e). Differences in developmental rates emphasize the appearance of a tall inflorescence with the continuation shoot apex on its lower flank. At about the same time, a ridge of tissue between the two is formed by cell expansion following periclinal and occasionally anticlinal divisions beneath the tunica. This ridge of tissue is oblique relative to the vertical (Fig. 2.7f) and lateral growth initially results in its edges enfolding part of the base of the inflorescence (Figs. 2.7g, 2.7h, 2.9d). Eventually it will form the membranous, two-keeled "prophyll" surrounding the continuation growth. A distinct tunica remains continuous over both inflorescence and continuation shoot primordia for a long period of time (Fig. 2.9b).

The first floral bract is initiated at about the same time as the prophyll, on the distal side of the inflorescence relative to the continuation growth (Figs. 2.7g, 2.9c). The second and third bracts are formed on the proximal side of the inflorescence opposite the first and second foliage leaves of the continuation growth, respectively. The first bract of the second pseudowhorl alternates between the first and second in a pattern similar to that described for Alisma triviale. The formation of floral primordia in the bract axils follows the same sequence. The mature inflorescence, usually a monaxial structure, is small in cross sectional area in relation to the whole plant (compare Figs. 2.20 and 2.21). Floral development of the staminate plant has been described by Singh and Sattler (1973).

The prophylls and foliage leaves of successive phases of vegetative growth are arranged such that the phyllotaxy of the axis appears uninterrupted by inflorescence formation. The genetic spirals of both inflorescence and continuation growth are homodromous with that of the original shoot (Fig. 2.10d). The prophyll begins to extend laterally to surround the continuation shoot after the latter has formed its first foliage leaf (Fig. 2.8a), this association becoming more pronounced with time (Figs. 2.8b, 2.8c).

Three foliage leaves (rarely a fourth, in 2 out of 53 cases) are formed before transition to inflorescence formation occurs again. Three inflorescences are initiated in a summer, though the first is often suppressed. After the third, the continuation growth remains vegetative, but it does not seem to overwinter and contribute to the population of the following year.

Axillary buds are associated with every leaf except the membranous "prophyll", the earliest bud visible being a mound of meristematic tissue in the axil of the fifth or sixth youngest leaf (Fig. 2.8d). A thick prophyll on the adaxial side (Figs. 2.8e, 2.8f, 2.10a) is followed in development by scale leaves formed from cells subjacent to the single layered tunica (Fig. 2.10b). A second tunica layer is sometimes observed (Fig. 2.10a). The first scale leaf is abaxial, its exact position being determined by the directionality of the genetic spiral of the bud (Figs. 2.8g, 2.8h). The latter is in turn independent of the symmetry of the main axis, following no set pattern along this. The same relationship of cathodic and anodic leaf edges holds for both scale and foliage leaves. There is no indication of relative precocity of any axillary bud, so that the one in the axil of the ultimate leaf (which "subtends" the continuation growth) is not out of place developmentally in the series of buds along the shoot axis.

Though initially the axillary buds are upright, differential growth soon results in the horizontal orientation characteristic of stolons. The apex retains its shape and stratification (Figs. 2.8i, 2.10c). Elongation of internodes begins with the seventh to tenth youngest bud. Up to six internodes may be produced before the stolon resumes upright growth (Fig. 2.6b), forming a new plant 40-60 cm from the parent plant. The daughter plant soon develops a root system. The rapid disintegration of the stolon made it impossible to determine whether these plants also initiate inflorescences in the same year. In the fall, perennating corms are formed by starch accumulation in the subapical internodes of stolons that have not yet developed into upright plants.

Sagittaria latifolia is extremely variable in leaf form (Arber, 1920; Stant, 1964). The population at Morgan's Arboretum (n = 25+) had very narrow blades whereas that of the overflow pond of Lac Hertel, Mont St. Hilaire (n = 10+) had more wedge-shaped ones. The latter plants also grew in chlorinated water. No variations in the basic plan of shoot organization were found. In addition, at the North Creek of Lac Hertel, plants of S. latifolia remained entirely submerged as a result of unusually high water levels in 1976. These plants (n = 14+) had very poorly developed, linear laminae, and were generally small in size. Inflorescences were initiated but remained unexpanded. Though not studied in detail, these plants showed the same pattern of organization as the other populations. The only difference seemed to be a general paucity of stolon development.

4. Sagittaria cuneata Sheldon (Fig. 2.11a)

Mature seeds of S. cuneata (Fig. 2.11c) were collected in 1977. The embryo, as in other members of the Alismataceae, is incumbent, with a large cotyledon which is terminal in appearance (Figs. 2.11d, 2.12a). Usually, two plumular leaves would have been formed in spiral arrangement, the first being positioned against the aperture of the cotyledonary sheath (Figs. 2.12b, 2.14a). Though attempts at germination were unsuccessful, it seems likely that the process is similar to the one described for Alisma triviale and A. gramineum. In the field, the first leaves, immersed, are usually linear. Floating and emergent leaves of the characteristic wedge shape are formed later. Whether flowering occurrs in the first year of growth is not known to the author.

Sagittaria cuneata overwinters by means of corms as does S. latifolia. Germination involves the elongation of an internode so that the new rosette plant is separated from the corm which decays rapidly (Fig. 2.11b). A sequence of immersed, linear leaves, and cuneate floating and aerial ones is formed.

The apex has a single-layered tunica (Fig. 2.15a; n = 4). Flowering occurs in July, the pattern of organogenesis being similar to that of S. latifolia (compare Figs. 2.12-2.15 with Figs. 2.7-2.10). However, the plants are usually smaller, especially in stem diameter, owing to less leaf-base growth and radial expansion. Three inflorescences are initiated per season, separated from each other in developmental sequence by a membranous bract ("prophyll") and three foliage leaves. After the third inflorescence is formed, uninterrupted vegetative growth occurs.

Floral initiation in relation to the development of the continuation growth is more rapid in S. cuneata than in S. latifolia (compare Figs. 2.13e, 2.13f with Figs. 2.8a-2.8c). The sequence of bract and floral primordia initiation is the same. *Sagittaria cuneata* is monoecious, and the first two (occasionally up to six) flowers formed are pistillate. (Floral and inflorescence development is described in detail by Singh and Sattler, 1977.) The first-formed bract sometimes subtends a branch rather than a flower. In such cases, all flowers formed on the branch are staminate.

In one case (n = 47+), the normally two-keeled membranous "prophyll" was replaced by two single-keeled ones. As the succeeding two prophylls were normal, this was attributed to the non-functioning of the meristem between the two keels during development.

The population of *S. cuneata* collected from the mouth of a sewage outlet on Nun's Island (n = 15+) grew in much deeper water than the one in Morgan's Arboretum (n = 22+). But except for larger size (over 60 cm tall), no variation in organization was found. Whether this size difference was due to water depth and (or) nutrient supply is not known, for in 1977, the outlet was dry, and very small plants less than 10 cm tall were found there (n = 10+). These flowered in late June, with no difference in the pattern of organization from the one described above.

5. *Sagittaria subulata* (L.) Buch., *S.* "*Sinensis*" and *S.* "*microphylla*"

Three other taxa of *Sagittaria* were studied. These differ from *S. latifolia* and *S. cuneata* mainly in that many plants are found connected on a single stolon instead of only one daughter plant per stolon (Fig. 2.16).

The upright axis of *S. subulata* form subulata (Adams and Godfrey, 1961; n = 13) follows the general pattern of *S. latifolia* and *S. cuneata*, with a non-leaf-subtended, racemose inflorescence typical of the genus. The inflorescence and continued vegetative growth are most likely formed by apical bifurcation. The continuation axis begins with a two-keeled, membranous prophyll (Fig. 2.17b). It is not clear whether this originates around the inflorescence base as in the other two species described above. The prophyll and successive leaves continue the spiral 2/5 phyllotaxy without interruption. No definite cycle of vegetative growth and inflorescence formation is found: the plants examined all continued vegetative growth after the production of a single inflorescence.

Each foliage leaf on the upright axis has an axillary bud, including the ultimate one that subtends the continuation growth. Each bud has an adaxial prophyll and three scale leaves before foliage leaves are formed. The prophyll and the first two scale leaves are distichous or near distichous in position (Figs. 2.18a, 2.18b). The divergence angle then decreases and the third scale leaf is placed in a more lateral position (Fig. 2.18b). Subsequent phyllotaxy of the foliage leaves approaches 2/5 (sometimes 3/8). Elongation of the axis occurs only at the internode between the prophyll and the first scale leaf (Fig. 2.18c) and begins as the scale leaf primordia are still developing. This internode eventually becomes the stolon segment, so that the prophyll alone remains attached to the parent plant. The upright axis bearing foliage leaves is formed by differential growth of the upper and lower sides of the stem between the scale leaves (Fig. 2.17d).

The axils of the prophyll and first two scale leaves are empty, whereas that of the third contains a very well developed axillary bud (Figs. 2.17a, 2.17b, 2.18e, 2.18f). This bud is apparent at an early stage, but developmental studies indicate that it is clearly lateral and not formed by a bifurcation of the apex (Fig. 2.18d). The formation of this bud is similar to axillary bud development in foliage leaves of S. latifolia and S. cuneata as well as S. subulata itself. The bud reiterates the entire sequence to form the next stolon segment; i.e., the "string" of upright plants is sympodial in structure.

The stolons are frequently as thick as the upright stems (Figs. 2.17d, 2.17e). With the disintegration of the prophyll (Fig. 2.16), their axillary origin is frequently obscured. The monaxial appearance of the stolon system is emphasized by the relatively late appearance of stolons from other axillary buds. Successive upright plants are similar in size and complexity as a result of the rapid formation of stolon segments. These plants form adventitious roots quickly (Fig. 2.17a), though the connecting segments persist for a long time.

The same pattern of stolon development is found in the two cultivated species of Sagittaria: S. "Sinensis" and S. "microphylla" (both n = 15+). As these have not yet flowered, it is impossible to identify the species, or describe the process of inflorescence formation.

A comparison of the two types of stolon development in Sagittaria is shown in Fig. 2.19.

Discussion

In Alisma triviale, A. gramineum, and Sagittaria cuneata, phyllotaxy including the cotyledon is found to be spiral from the outset. There is no evidence of a distichous arrangement gradually changing to a spirodistichous one as is commonly accepted (Hirmer, 1922). This observation differs also from Arber's illustrations which show Alisma plantago-aquatica seedlings with distichous phyllotaxy (Arber, 1925). No embryological studies were undertaken. However, investigations in other species of the Alismatidae indicate that the formation of the apparently terminal cotyledon and of the epicotyl each involves about half the active zone of the embryonic apex (Swamy, 1963; Swamy and Lakshmanan, 1962a, 1962b; Swamy and Parameswaran, 1963). The process of seed germination and growth is consistent with the observations of Arber (1920) and Kaul (1978). The relatively small seedlings have not been observed to flower in the first season. Vegetative growth remains fairly constant until flowering begins.

The upright vegetative axis may continue from season to season, as in Alisma triviale, or die in the fall, perennating instead by stem tubers or corms as in Sagittaria latifolia and S. cuneata. Stem tubers have also been described in detail in Sagittaria sagittifolia (Sculthorpe, 1967). Adams and Godfrey reported "small white swellings similar to a corm or tuber" in Sagittaria subulata, but from the illustrations shown (Figs. 1, 4, Adams and Godfrey, 1961), these correspond to the short, thickened upright stem (Fig. 2.17a) rather than the large overwintering structures of the other species.

The asymmetry of leaf bases, with the overlap by the anodic edge, has been reported in Limnobium spongia and Vallisneria americana (Wilder, 1974b, 1974c, respectively). On the other hand, overlap by the cathodic leaf edge was recorded in Musa (Barker and Steward, 1962). This asymmetry seems to be of common occurrence in the sheathing leaf bases of the monocotyledons.

In the species studied in detail, the formation of the inflorescence and continuation growth is by bifurcation of the apex into two equal or subequal portions. Positionally, the continuation growth is associated with the ultimate leaf before bifurcation, and the inflorescence with the penultimate leaf.

Flowering occurs from late June to early August in Alisma triviale, S. latifolia and S. cuneata. These species also show a distinct cycle of development in the successive vegetative phases and inflorescence formations. In Alisma, the vegetative phase consists of a membranous prophyll and five foliage leaves, whereas in the Sagittaria species only three foliage leaves are formed after the prophyll. Wydler (1863) found that increasingly fewer leaves were produced between inflorescences over the growing season in Alisma plantago-aquatica. Thus a definite vegetative phase may be another distinguishing characteristic between the European *A. plantago-aquatica* and North American *A. triviale*, sometimes considered the same species (Hendricks, 1957). *Sagittaria subulata* does not show a similar, well defined cycle of vegetative and reproductive growth. Periodicity between successive inflorescences or inflorescence complexes has been reported for many species of the Alismatidae, including *Aponogeton distachys* (Sergueeff, 1907), *Butomus umbellatus* (Charlton and Ahmed, 1973; Wilder, 1974a), and *Limnobium spongia* (Wilder, 1974b), etc., but none seem to be apparent in either *Echinodorus tenellus* (Charlton 1968) or *Ranalisma humile* (Charlton and Ahmed, 1973).

The membranous prophyll and foliage leaves are placed so that they continue uninterrupted the phyllotaxy before inflorescence formation. Thus successive segments of vegetative growth are homodromous with one another. This is the result of each new leaf being formed in an area, at least visually, of greatest space. The arrangement of floral or inflorescence bracts, in pseudowhorls of three, is also homodromous with foliage leaf phyllotaxy. Prophyll initiation in the species studied is, unlike *Echinodorus tenellus*,located beneath the tunica and therefore similar to foliage leaf initiation. In the cases of *S. latifolia* and *S. cuneata*, the edges of the prophyll first enfold the inflorescence base, surrounding the continuation shoot only by later growth. This may be contrasted with the case of *Ruppia maritima*, where the spathal bract originates as the prophyll of the renewal growth shoot (Posluszny and Sattler, 1974a).

Unlike *E. tenellus* and other species of Alismataceae with heterogeneous inflorescences (Charlton, 1973), pseudostolons were not found in the species studied. (Adams and Godfrey (1961) have reported the presence of young plantlets "at the lowest nodes of the inflorescence" in *S. subulata*, but this was not observed here.) Instead, these species are more variable in the distribution of axillary buds and their subsequent development.

In the simplest case, Alisma triviale, there is a gradient of increasing development of the axillary buds from the first leaves of the vegetative phase to the penultimate one before inflorescence formation. The continuation growth, off centre in the axil of the ultimate leaf, may be considered to be an extremely precocious lateral bud, a view supported by the fact that this leaf subtends no other buds. The penultimate buds are the only ones that develop on the main axis after the first inflorescence (Fig. 2.20) and on the second order axes. Any bud found below these buds is noticeably less developed. The same gradation has also been observed in Alisma plantago-aquatica (Wydler, 1863), Echinodorus tenellus (Charlton, 1968), and Ranalisma humile (Charlton and Ahmed, 1973). The increasing size of axillary buds with proximity to the next inflorescence is due to the greater number of leaf primordia, not larger primordia as is the case in Acorus (Kaplan, 1973).

In the species of Sagittaria studied, each foliage leaf, including the ultimate one before the inflorescence formation, subtends an axillary bud. This is in contrast to the observations of Charlton (1973). Though initially identical in organization and symmetry to those of Alisma, the axillary buds of Sagittaria soon grow out horizontally as stolons to form new plants. There is no precocity or period of inhibition along the upright vegetative axis as in Alisma, so that an uninterrupted gradient of buds and stolons of increasing size and complexity with age is present.

Two patterns of stolon development are found. Sagittaria cuneata and S. latifolia produce stolons with several elongated internodes. These stolons turn upright to form a single daughter plant some distance away. Alternatively, in the submerged taxa S. subulata, S. "Sinensis" and S. "microphylla", a sympodial stolon system is formed (compare Figs. 2.19a and 2.19b). Elongation of only the internode between the prophyll and the first scale leaf and the reiteration of the pattern of development by the axillary bud of the third scale leaf to form the next segment result in a "string" of plants similar in development and apparently one internode apart. This method of vegetative propagation seems to be of great importance and dense mats of plants are often found (Arber, 1920; Adams and Godfrey,1961). Though different in origin (axillary as opposed to apical, and sympodial rather than monopodial), there is much similarity in organization between the stolon system and the pseudostolons of Echinodorus, where upright vegetative axes usually develop from the axil of the first scale leaf of each pseudowhorl (Fig. 2.19).

The basic pattern of organization, as exemplified by Alisma triviale, is as follows: an upright vegetative axis, bearing a rosette of leaves in spiral arrangement, with successive phases of vegetative growth beginning by the formation of a membranous prophyll and terminating by apical bifurcation to form an inflorescence and a continuation growth (Fig. 2.20). This pattern of growth can be considered sympodial by the relative size and position of the inflorescence and continuation growth, and by the lack of a lateral bud in the axil of the ultimate leaf. This interpretation is well accepted in the literature.

For the Sagittaria species studied, the pattern of organization is complicated by the development of stolons (Fig. 2.21). At the same time, the case for precocious lateral branching is not as strong. In both S. latifolia and S. cuneata the continuation growth is clearly lower in position than the inflorescence early in development, and a shell zone indicative of axillary branching (Wilder, 1975) is occasionally found around the continuation growth. However, the ultimate leaf subtends its own axillary bud, which develops as other axillary buds do. If the continuation shoot is to be considered a precocious lateral bud, then serial axillary buds, separated by a long time interval between their initiation and very different in form, must be invoked. The presence of a bud in the axil of the leaf enclosing the bifurcated apex has been used as a criterion for nonaxillary interpretations of bifurcation in Chamaedorea and Strelitzia (Fisher, 1974 and 1976, respectively). The significance of a morphologically distinct prophyll as an indicator of sympodial growth is reduced in the light of the developmental history of the prophyll. The continuous phyllotaxy of successive vegetative phases may be considered support for a monopodial interpretation (Charlton and Ahmed, 1973). On the other hand, it may be argued that the situation in these two species of Sagittaria is "derived", whereas a study of S. lancifolia, a rhizomatous and putatively primitive species (Bogin, 1955), shows no stolon development and a lack of buds in the axil of the last foliage leaf before flowering (Lieu, 1979c). It is evident that a clear cut case of precocious axillary branching cannot be made, though the interpretation of sympodial organization without recourse to precocious axillary branching may be appropriate. In fact, given the understanding of axillary bud formation (e.g., Shah and Unnikrishnan, 1971), one may equally argue that where bifurcation to produce inflorescence and continuation growth involves a sufficiently large portion of the apex (as in Alisma triviale or Sagittaria lancifolia), meristematic tissue that might otherwise form the axillary meristem has been incorporated instead into the continuation growth. Where a lesser portion of the apex is involved (as in S. latifolia and S. cuneata), the ultimate axillary bud is formed normally. The problems of branching at or near the apex and its interpretation have been discussed in Chapter 1.

Though variations in size, leaf shape, and the extent of development are found within and between populations, the basic pattern and symmetry relationships are precise and rarely modified. The same well defined organization and growth have been reported for other genera and families, though not necessarily from different populations (e.g., Charlton, 1968; Wilder, 1974a, 1974b, 1974c, etc.). This reflects the high level of organization in the shoot systems of the Alismatidae.

A summary of the variation in the pattern of organization of the above and other Alismatacean species is listed in Table 2.4. It can be seen that growth forms in these species can be described by a relatively small number of morphological features.

Footnotes

(1) The populations under study were identified as *Alisma triviale* Pursh. in accordance with Fernald (1946) and Pogan (1963) rather than as *A. plantago-aquatica* var. *americanum* (Hendricks, 1957). This is also consistent with a previously published paper based on the same populations (Singh and Sattler, 1972).

(2) All species of *Sagittaria* were identified by Bogin's monograph (1955) on the genus.

Growth Forms in the Alismatales. II. Two Rhizomatous Species: *Sagittaria lancifolia* and *Butomus umbellatus*.

Introduction

In the recent literature on patterns of organogenesis in various groups of the Alismatidae, there has been some controversy over the development and branching relationships in *Butomus umbellatus*, monotypic member of the Butomaceae. Based on various characteristics, it has been interpreted to be either monopodial (Charlton and Ahmed, 1973), or sympodial (Wilder, 1974a) in growth. Part of the problem lies in the fact that this species, unlike most of the others studied, is rhizomatous but with a subterminal apex. The latter bifurcates to form the inflorescence and continuation growth, so that "terminal" and "lateral" relationships are difficult to assign.

The same growth habit is found in the genus *Sagittaria*, which also includes upright species. Of the former type, the species *Sagittaria lancifolia* bears a striking resemblance to *Butomus*, especially in the presence of a subterminal apex. The aim of the study is therefore to elucidate and compare the patterns of organization of the entire plant of both *S. lancifolia* and *Butomus* over their life cycles, including seedling and perennating strucutres as well as the adult plant. A previous study of the upright sagittarias (Lieu, 1979b) also serves as a possible basis for the understanding of the rhizomatous habit in *S. lancifolia*, and by comparison, *Butomus umbellatus*.

Material and Methods

Seeds and terminal portions of the rhizome of Butomus umbellatus were collected from Nun's Island, Quebec, in June and July of 1976. Similar collections were made for Sagittaria lancifolia in October 1976 near Miami International Airport, Miami, Florida. Voucher specimens for both species have been deposited at the McGill College Herbarium (MTMG).

The rhizomatous pieces were washed in water and fixed in 70% ethanol (Butomus) or formalin-acetic acid-alcohol (Sagittaria) within 48 h of collection, often after a preliminary dissection. These were then stained in alcoholic acid fuchsin, dissected, and photographed using the technique of Sattler (1968). All photographs but one have been reproduced at the same magnification (120x) to facilitate comparisons. (These magnifications are consistent with those used for the study of Alisma and upright species of Sagittaria (Lieu, 1979b).) The photographed specimens and others were then oriented in blocks of pith and dehydrated in a tert-butyl alcohol series and embedded in Tissue Prep (mp 61 degrees C, Fisher Scientific) using standard techniques. Serial sections were cut at 6 or 7 µm and stained in Johannsen's Safranin or fast green and safranin. From these, camera lucida drawings were made with a Zeiss microscope and drawing tube attachment.

Seeds of both species were germinated under sterile conditions and ambient light in spring 1977. Six- to eight-week old seedlings were then transferred to soil under about 5 cm of water.

The sample size of each observation, designated "n", is included in the results section. The specimens which appeared identical in organization to previous observations and thus not recorded in detail are not counted in the sample size, but simply indicated by a plus sign (+).

Results

1. Sagittaria lancifolia L.

Adult plants of Sagittaria lancifolia are rhizomatous, with two ranks of lanceolate leaves converging at the growing tip of the rhizome in a "V" shape (Fig. 2.22). The rhizome is partially or entirely buried in the substrate, and may reach 4-5 cm in thickness. The apex is usually subterminal, though occasionally (3 plants out of 45) it is terminal. Unlike the usual terminal apex of a rhizome, which occurs at the tip of the axis and is oriented horizontally, the subterminal apical meristem is situated on the upper side of the distal end of the rhizome so that its topographical tip is pointed upwards relative to the substrate. The growth of rhizomes with subterminal apices has been described in detail by Wilder (1974a).

Inflorescences seem to be leaf subtended and occur after every three to five leaves on any plant (41, 33 and 29 out of 108 cases, respectively). Vegetative phases of less than three or more than five leaves are less common (5 out of 108 cases in total). These inflorescences are monoecious and monaxial in the plants from the population studied. Inflorescences with first order branches in the lowermost whorl(s) are frequently found in other populations. In all plants observed (n = 30+), branching of the rhizome is from the very large axillary bud in apparently the same axil where the inflorescence is located (Figs. 2.26f, 2.26g). Smaller axillary buds are subtended by other leaves; however, they seem to be quickly hidden by the extensive growth of the leaf base and rhizome, and thus are difficult to locate in the fully expanded region of the rhizome. Whether the plant flowers throughout the year, or only seasonally, is not known to the author.

The seeds of S. lancifolia are similar to those of other members of the Alismataceae studied (Lieu, 1979b). The embryo is incumbent, with a large ligulate cotyledon folded back along the epicotyl (Figs. 2.23a, 2.23b, 2.23c). One or two foliage leaves are present at maturity of the seed. The divergence angle is significantly less than 180 degrees, so that distichous phyllotaxy is not established from the start (Figs. 2.24b, 2.27a). The apex is extremely small (n = 10+; compare Figs. 2.27b and 2.27c), with a single tunica layer (n = 4). A procambial strand links the cotyledon to the radicle, branching to the first foliage leaf (Fig. 2.27b).

At germination (n = 10+), the plumular leaves emerge through the aperture between the edges of the cotyledonary sheath (Fig. 2.23d), a region of relatively smaller cells (Fig. 2.24a). The first leaves are linear, and phyllotaxy is spiral. Many fine root hairs are developed on the collet between hypocotyl and radicle, and the first adventitious root soon appears at the base of the cotyledon (Fig. 2.23d). No difference is observed between these and other alismatacean seedlings described elsewhere (Lieu, 1979b). Establishment of the adult form may be a lengthy process. Six-month old seedlings (n = 4) still maintain upright growth and spiral phyllotaxy. A 7 1/2 month old seedling has just begun a gradual changeover to a distichous leaf arrangement (Fig. 2.23e). An increase in the divergence angle and extension of the axis in a horizontal rather than vertical direction are involved, but the conditions required for this transition are not known.

At the rhizomatous stage, the apex is still dome shaped (Fig. 2.24f), with little or no indication of dorsiventrality. Leaves are initiated at about 180 degrees from each other (Figs. 2.24d, 2.24e) by periclinal divisions beneath the single tunica layer (Fig. 2.27c; n = 3). The ensheathing leaf base and median procambial strand are both developed in the second plastochron (Figs. 2.24g, 2.27c). The sequence of leaf development is shown in Figs. 2.24c to 2.24g. The leaf base is asymmetric, as in S. cuneata and S. latifolia (Lieu, 1979b), but there is no regularity to the overlap of the anterior or posterior leaf edge around one another.

Flowering begins with the broadening of the apex in the plane of leaf insertion (Fig. 2.25a) by general cell division throughout the apex (Fig. 2.27d). Two distinct meristematic centres are soon evident (Figs. 2.25b, 2.25c). The leaf-axillated portion continues the vegetative growth while the leaf-opposed one develops into the inflorescence. The latter is often clearly larger and taller from the start (Figs. 2.25d, 2.25e), and occasionally a "shell zone" of narrower cells may be found between the two apices (Fig. 2.27e). There is no membranous bract produced between the two (Figs. 2.25f 2.27f), though the next appendage, a foliage leaf, is formed in this position later in ontogeny (Fig. 2.25g). The divergence angle between this leaf and the ultimate one before inflorescence formation is 180 degrees, so that the phyllotaxy of the rhizome continues uninterrupted.

The first bract and floral (or branch) primordia are formed on the distal side of the inflorescence relative to the continuation growth. This set of primordia is followed by an anterior and then a posterior one (relative to the direction of rhizome growth) at the same level (Fig. 2.25g). The fourth bract, the first of the next pseudowhorl, occurs between the first and the second at a slightly higher level. The relationship between these is not documented for the later pseudowhorls where bract and floral primordia are initiated in rapid succession. Thus the initial direction of the genetic spiral of the inflorescence depends on the side of the rhizome on which it is found (clockwise when it is on the left while facing the direction of growth of the rhizome and counterclockwise when it is on the right).

Usually, the first two to eight flowers are pistillate. As mentioned earlier, the flowers of the lowermost whorl(s) may be replaced by branches built on the same trimerous plan. These consist of staminate flowers only. Floral development is similar to that of S. cuneata (Singh and Sattler, 1977) and S. latifolia (Singh and Sattler, 1973), and will not be described.

At anthesis, neither the inflorescence nor the continuation growth is in a terminal position. Often the plane of distichy of the latter is also displaced from that of the older part of the rhizome. In addition, the first foliage leaf, next to the inflorescence, is compressed to form an externally two-keeled structure (Fig. 2.22). Further expansion of the rhizome of the continuation growth, however, soon displaces the leaf-opposed inflorescence into a lateral position, giving it the appearance of being subtended by what, in reality, is the penultimate leaf. The appearance of a monopodial construction is enhanced by the dissociation of the inflorescence from the base of the ultimate leaf that encircled it initially (Fig. 2.22). Thus the continuation growth is again in a terminal position. There is no external evidence of a change in the direction of growth of successive segments of vegetative growth that may indicate a sympodial organization. Since each continuation growth may have an odd or even number of leaves, successive inflorescences may be found on the same or alternate sides of the rhizome.

Axillary buds are distributed in an organized way along the rhizome during organogenesis. They are present in all leaf axils except those of leaves subtending the continuation growth, and the first leaf of the latter (Fig. 2.22). Each bud originates as a mound of meristematic tissue (Fig. 2.26a) which soon develops an adaxial prophyll (Fig. 2.26c; n = 30+). The first leaf is usually posterior in position (22 out of 30 cases), and phyllotaxy is distichous thereafter (Fig. 2.24h). The axillary bud is similar to the main apex in organization and anatomy. Occasionally, the divergence angle between successive leaves may be less than 180 degrees, giving the bud a spiral phyllotaxy (Fig. 2.26e; 5 out of 30 cases). Another anomaly is the occurrence of an adaxial first leaf (Fig. 2.26d; 3 out of 30 cases).

Though initiated 180 degrees from each other in a plane, the leaves are displaced from this plane of distichy by elongation of the rhizome to form an orthostichy along the length of either side (Fig. 2.22). The two lines of axillary buds, approximating the midpoints of the leaves, form a "V" subtending an angle of about 130 degrees between the apex and the fully expanded portion of the rhizome. This angle is the simple geometric consequence of the relative growth in thickness and length of the rhizome; i.e., the lesser the growth in thickness, the smaller is this angle, and vice versa.

The axillary bud of the penultimate leaf (i.e., on the same side as the inflorescence) is extremely early in development (Fig. 2.25g), being initiated shortly after inflorescence formation. Its apex is larger than those of other axillary buds (compare Figs. 2.27b and 2.27c), and at maturity it remains more developed and prominent (Fig. 2.26f). These buds are the only observed source of branching of the rhizome, and may expand soon after anthesis (Fig. 2.26g) and initiate their own inflorescences after only four to eight foliage leaves. At other times, they remain inhibited with 12 to 15 unexpanded leaves. The other axillary buds are often obscured by the development of the mass of rhizome and leaf base tissue.

Except for the development of inflorescence branches, there are no variations in pattern of organization between the different populations examined.

2. <u>Butomus umbellatus</u> L.

<u>Butomus umbellatus</u> is a rhizomatous emergent aquatic, with two ranks of leaves, triangular in cross section, converging at the apex to form a "V" (Fig. 2.28a, 2.29f). The apex is subterminal, on the dorsal side of the rhizome, located in the bulge formed by the leaf bases (Fig. 2.29f). It may occasionally (2 out of 45 plants) be terminal. The rhizome is brittle, 1-1.5 cm in diameter, and is constricted at the junction of the branch and main axis. Showy inflorescences appear in early June and are leaf-subtended, occurring after every seven (rarely nine) leaves on alternate sides of the rhizome. Every leaf subtends an axillary bud in a lateral-dorsal position except those subtending inflorescences (which are more median in location). The axillary bud on the same side as and immediately posterior to the inflorescence is better developed than the rest.

Unlike the species of Alismataceae studied, the seed of <u>Butomus</u> consists of a straight embryo, with a cylindrical cotyledon and a short hypocotyl and radicle portion (Figs. 2.29a, 2.29b). At the time the seed is shed, the apex within the cotyledonary sheath appears as a mass of cells with no discernible foliage leaves. A single procambial trace connects the cotyledon to the radicle. The cotyledon contains many starch granules.

Seeds of <u>Butomus</u> germinate readily under sterile conditions, the plumular leaves emerging from between the small-celled edges of the cotyledon (Fig. 2.29a). Leaf arrangement is distichous from the start (Figs. 2.29b, 2.31a). The leaves are rounded in cross section. Orthostichies of round-tipped root hairs are formed on the collet between the hypocotyl and the radicle, which is elongated (Fig. 2.29c). The first adventitious root is formed at the base of the cotyledon. The second forms at the base of the first foliage leaf on the opposite side (Fig. 2.29d). The anterior-posterior orientation of the axis is frequently apparent when two to three leaves have expanded, the anterior being marked by a bulging of leaf bases around the apex, as in the adult rhizome, and the posterior by a higher incidence of adventitious roots (Fig. 2.29e). Thus the basis of rhizomatous growth is established early in the developmental history of the plant. Viewed from the posterior (i.e., facing the direction in which the rhizome is growing), there seems to be an equal number of seedlings with the cotyledon on the left as on the right.

The apex is elongated in an anterior-posterior direction (Fig. 2.30c), with a single tunica layer (Fig. 2.32c; n = 4). Leaf initiation is by periclinal divisions beneath this (Fig. 2.32c), slightly posterior to the apex (Fig. 2.30d). Ensheathing leaf bases are developed by the second plastochron, with the rear edge surrounding the shorter and thicker anterior one (Fig. 2.32b). The median procambial strand is usually distinguishable at the end of the second or early in the third plastochron. The two ranks of leaves between the apex and the fully expanded rhizome form an angle of about 110 degrees. This is a result of the greater elongation of the rhizome relative to its growth in thickness when compared with S. lancifolia.

Inflorescence initiation involves some enlargement of the apex before bifurcation occurs (compare Figs. 2.30c and 2.30d with 2.31a and 2.31b). The plane of division is oblique to the rhizome axis, from the anterior on the side of the ultimate leaf to the posterior on the side of the penultimate leaf (Figs. 2.31a, 2.31d). Either one of the two product apices may be larger or higher (Fig. 2.31b versus Fig. 2.31c), though the one in the axil of the ultimate leaf, the more posterior, will form the inflorescence and is soon taller (Fig. 2.31d). The single tunica layer of the prebifurcation apex remains continuous over both apices for some time (Fig. 2.32d).

Inflorescence development begins with the formation of a bract on the anterior side proximal to the continuation growth (Fig. 2.31e), and has been described in detail (Wilder, 1974). No results to the contrary were obtained. Floral development has been investigated by Singh and Sattler (1974).

The continuation growth forms the first foliage leaf on the same side as the penultimate leaf so that the phyllotaxis of the rhizome continues uninterrupted (Figs. 2.31e, 2.31f. 2.32c). This occurs at about the same time as the formation of the first inflorescence bract. The inflorescence, though larger at one point, develops slowly when compared with the continuation growth which soons becomes the larger of the two (Figs. 2.31h, 2.31i). In addition, by the time the next inflorescence is initiated, the first one resembles a slightly elevated and enlarged axillary bud owing to its short peduncle and the three tapering bracts that surround the floral primordia. The bud-like appearance of the inflorescence is maintained long after the peduncle has carried it above the ensheathing leaf bases.

There is no cessation of inflorescence formation towards the end of the growing season. The rhizome produces leaves and inflorescences until the expanded leaves of the current year's growth are killed by frost. The unexpanded appendages overwinter and develop the following spring.

Phyllotaxy of the lateral buds is distichous, with the plane of distichy perpendicular to that of the main axis (Fig. 2.28b). Each bud first initiates an adaxial prophyll (Figs. 2.30e, 2.33a), followed by four to five scale leaves. The first of these is almost always (28 out of 30 cases) on the anterior side relative to the rhizome. Thus buds on either side of the rhizome are mirror images of each other. Anatomical organization is also similar to that of the main apex (Fig. 2.33b).

The youngest visible bud is found in the axil of the seventh to tenth youngest leaf. Development is inhibited after six to seven foliage leaves have been formed. (A series of axillary buds along a rhizome is shown in Figs. 2.30e to 2.30j).

The axillary bud of the leaf that is two plastochrons older than the ultimate leaf (and therefore on the same side of the rhizome and immediately posterior to it) is always precocious in development (Figs. 2.30f, 2.31g). Because of this relative precocity, there is often a sharp difference in the extent of development of buds in axils younger than this, or an abrupt absence of them. As the rhizome matures, this precocious bud is larger than the others, extruding from between the leaf bases (Fig. 2.29f). In addition to the prophyll and scale leaves, 6-10 foliage leaves are found. If horizontal elongation of the bud axis has occurred, then a small replica rhizome at right angles to the main one is formed (Fig. 2.33c). Often the apices of these buds are in various stages of bifurcation and inflorescence formation. The first four or five leaves on these branches may, but do not always, develop their own axillary buds (third order axes), repeating the same pattern and symmetry of organization. The most developed of these third order axes may have four to five scale leaves.

Later, by mid-July, the other axillary buds begin to develop into the so-called "bulbils" (Countryman, 1970). More leaves are formed. There is extensive vertical growth of the axis beneath the prophyll, and elongation of the internode between the prophyll and the first scale leaf (Figs. 2.34b to 2.34d). A parenchymatous stalk traversed by vascular bundles results (Fig. 2.33d). These bulbils are similar to those found in partially sterilized inflorescences of Butomus (Lohammar, 1954). The extent of development of the mature bulbil is comparable to that of the precocious axillary bud described above, with 11-13 leaves before inflorescence formation and often several leaves on the continuation growth (Fig. 2.33c). Bulbils have their own axillary buds with the same symmetry relationships. In addition, the better developed of these are also borne on short stems (Figs. 2.34e to 2.34g). The small, corm-like bulbils are easily detached from the parent axis. They germinate in the following spring, forming small individual plants.

The bulbils and precocious buds remain distinguishable despite their similarity in size. Firstly, the latter tends to be prominently ribbed along its length due to fibrous bundles in the prophyll (Fig. 2.34a). The bulbil, different in shape, is surrounded by a prophyll covered by clusters of tannin cells (Figs. 2.33d, 2.34d). The precocious axillary bud does not develop the short, thickened stem characteristic of bulbils, so that the apex is much closer to the point of attachment. Possibly as a result of this, the precocious bud is also more difficult to remove from the parent rhizome and contributes to local branching rather than dispersal as in the case of the bulbils.

Discussion

Despite considerable similarities in the adult form, Sagittaria lancifolia and Butomus umbellatus are quite different in organization. A comparison of the two species is listed in Table 2.5 (see also Figs. 2.22 and 2.28), and only the main features will be discussed here.

To begin with, the rhizomatous growth form in Sagittaria lancifolia is acquired during the development from seedling to adult form. Embryo and early seedling stages are very similar to other species of Sagittaria and Alisma studied (Lieu, 1979b). Distichous phyllotaxy characteristic of the mature plant of Butomus is established from the start, with a rapid determination of the anterior-posterior orientation. Apex shape and overlap of leaf sheath edge, which may be indicative of the spatial organization and directionality of growth processes, also support the ontogenetic and organizational differences of the rhizomatous habit in the two species.

The inflorescence of S. lancifolia is leaf-opposed, with the last leaf before its formation subtending the continuation growth. Its primordium is usually the larger product of bifurcation though neither is more anterior or posterior relative to the direction of rhizome growth. The first leaf of the continuation growth is a foliage leaf that does not subtend an axillary bud.

On the other hand, the inflorescence in Butomus is leaf-subtended, and may be the larger or smaller product of bifurcation. All leaves subtend either an axillary bud or an inflorescence. As a result of these basic differences, an interpretation of the rhizome of Butomus cannot be based on that of S. lancifolia, as has been suggested (Wilder, 1974a). Instead, each will be considered independently.

Though its continuation growth does not possess a morphologically distinct prophyll, the main axis of S. lancifolia is similar in organization to species of Alismataceae with upright vegetative axes (Lieu, 1979b). The only difference lies in the direction of extension of the axis, and thus also of phyllotaxy, features secondarily acquired early in the life cycle of the plant.

In terms of axillary bud distribution and development, S. lancifolia is more similar to Alisma and Echinodorus tenellus than to other species of Sagittaria, which have buds in all axils but those of the prophylls of continuation growths (Lieu, 1979b; Table 2.6). A sympodial construction may be postulated based on the relatively large size of the inflorescence primordium and the similarity to Alisma and Echinodorus, which are considered sympodia.

The rhizomatous habit, described as "horizontal rhizomes" in contrast with vertical ones by Bogin in his monograph on the genus Sagittaria, is also found in S. sprucei and S. rhombifolia of the subgenus Lophotocarpus, and S. graminea var. chapmanii and var. platyphylla of the subgenus Sagittaria (as is S. lancifolia) (Bogin, 1955). In addition, illustrations of S. graminea var. graminea and var. teres in a more recent revision of the genus (Rataj, 1972b) seem to show the same growth form. Sagittaria graminea is closely related to S. lancifolia with which it hybridizes readily (Bogin, 1955). Also, though spanning both subgenera, all taxa mentioned above are New World species closely related to the "plastic and primitive" S. montevidensis (subgenus Lophotocarpus) which has "changed but little from the ancestral prototype" (Bogin, 1955). The monographs mentioned above and illustrations available (e.g., Hoehne, 1955), as well as small amounts of living material observed, however, all indicate that S. montevidensis does not possess a rhizomatous habit. The same is true of S. guyanensis, an Old World species (Rataj, 1972a) considered a link between S. montevidensis and Echinodorus.

The rhizomatous habit in Sagittaria may thus be considered a secondary variation on the basic structure occurring in a group of related species. That this may involve relatively minor changes in plant organization is indicated by the interchangeability of orthotropic and plagiotropic growth documented by various authors (e.g., Tomlinson, 1961; Roux, 1968; Hallé and Oldeman, 1970).

The organization of Butomus umbellatus is consistent with the observations of Weber (1956), Charlton and Ahmed (1973), and Wilder (1974a). The presence of buds in all leaf axils except those subtending an inflorescence, the occurrence of relatively precocious axillary buds, and also the differentiation between these (which result in local branching) and other axillary buds which form bulbils later in the season, on the other hand, have not been reported by these authors.

The difficulty in the interpretation of the organization of Butomus is like that of interpreting other apical bifurcations discussed above. The presence of a subterminal apex, however, complicates the situation. The larger (higher) product of bifurcation is usually considered the main apex while the lower, more proximal one is considered a precocious lateral bud. Where growth is horizontal and terminal, the anterior (and distal) product may be more accurately interpreted as the "main apex", a consideration also proposed by Wilder (1974a). In the case of Butomus, where the histological apex points upwards and is situated on the dorsal side of the rhizome behind the latter's topographical apex, both criteria may be applied. The continuation growth is more anterior in position (implying a monopodial axis), but it is not always the larger in size at the time of bifurcation. Another piece of evidence in favour of "monopodial" growth may be the distribution of axillary buds; except for those which subtend inflorescences, all leaves subtend an axillary bud, including the one that positionally subtends the continuation growth. The latter would possibly be empty were the continuation growth to be considered its axillary bud.

Other arguments, both pro and con, have been advanced by Charlton and Ahmed (1973) and Wilder (1974a). One of the major points proposed by the latter is that of "part-for-part" comparisons. According to this, the inflorescence of Butomus is considered to be the main axis since those of related members of the Limnocharitaceae and Alismataceae are regarded as such. This form of comparison seems unjustifiable in view of the differentiation of Butomaceae from these families (a fact which Wilder (1974a) also recognized). The present study of rhizomatous organization in Sagittaria lancifolia (Alismataceae) and its comparison with Butomus also support the morphological distinctness of Butomaceae within the Alismatales.

Thus it would seem that a relatively stronger case may be made for a monopodial construction in Butomus umbellatus if a strict monopodial-sympodial system of stem organization is to be followed.

A phenomenon of note is the topographical association of an inflorescence and precocity of its nearest axillary bud (the continuation growth not being considered as such). While present in S. lancifolia and Butomus, it also occurs in Echinodorus tenellus (Charlton, 1968), Ranalisma humile (Charlton and Ahmed, 1973), Alisma plantago-aquatica (Wydler, 1863), A. triviale (Lieu, 1979b), Triglochin striata (Juncaginaceae, Lieu, 1979a) and probably other members of the Alismatidae. This most frequently contributes to the formation of branches that repeat the growth pattern of the main axis while the nonprecocious buds, where present, remain suppressed. The position and developmental fate of these buds may be attributable to some yet unidentified process in the organization and regulation of branching. It is interesting to note that in species of *Sagittaria* with upright vegetative axes studied, there are no such precocious buds. Instead, all but the prophylls of continuation shoots subtend axillary buds that rapidly grow out to form stolons and new plants.

Other Genera in the Alismataceae

With the exception of the occurrence of apical bifurcation, studies cited in the previous sections have shown that the genus *Alisma* is very simple in its architecture. It basically consists of a congested, upright stem that produces inflorescences at regular intervals to form the inflorescence and the continuation shoot.

The architecture of the genus *Sagittaria* is largely comparable to that of *Alisma*. In addition, axillary buds often develop into stolons (often described as slender rhizomes) or stolon systems that overwinter or contribute to vegetative reproduction. A secondary rhizomatous form is found in several species. These usually do not develop stolons and tubers. An analysis of the organization of selected species of *Sagittaria* is listed in Table 2.6.

Charlton has described the architecture of *Echinodorus tenellus* in detail (Charlton, 1968). This species is very similar to *Alisma* in organization, but also shows the development of partially vegetized inflorescences, which Charlton termed "pseudostolons", if the plant is submersed. The same ecological response is not found in submersed species of *Alisma*, such as *A. gramineum* (Lieu, 1979b).

Pseudostolons are of frequent occurrence in the genus *Echinodorus*. In addition, *E. parvulus* has been described to spread by slender rhizomes (Correll and Correll, 1975; Godfrey and Wooten, 1979). Whether this is similar to the stolons of *Sagittaria*, as it seems to be, or is merely a highly vegetized inflorescence (pseudostolon), is not clear. Stolons have not been reported for other species in the genus.

Most of the other genera of the Alismataceae can be compared to *Alisma* or *Echinodorus* in terms of their architecture. A comparison of the genera is shown in Fig. 2.35. The following discussion is drawn largely from Charlton's study on inflorescences in the Alismataceae (Charlton, 1973), and from various floras.

The genera *Burnatia*, *Damasonium* and *Limnophyton* do not possess pseudostolons or stolons. Although apical bifurcation has not been demonstrated for these taxa, it is likely that their organization is the same as that of *Alisma*. They differ in leaf morphology, and in inflorescence and floral structures.

The genera *Baldellia*, *Caldesia*, *Luronium*, and *Wisneria*, like *Echinodorus*, exhibit sterilization of the inflorescence and development of pseudostolons. In submerged forms of *Caldesia parnassifolia*, vegetative buds may replace flowers and inflorescence branches and function as turions (Glück, 1905). Prolonged growth of the pseudostolon has been reported in *Luronium natans* (Charlton, 1973), so that the plant greatly resembles the stolon system of species of *Sagittaria* such as *S. subulata*.

The symmetry and organization of the inflorescence of *Ranalisma humile* has been described in detail by Charlton and Ahmed (1973). Although the genus is considered very close to *Echinodorus* (e.g., Cook, 1974), "pseudostolons", when they do occur, are sympodial structures more similar in organization to members of the Limnocharitaceae such as *Hydrocleis*.

Limnocharitaceae

The Limnocharitaceae, sensu Takhtajan, consists of four genera, Hydrocleis, Limnocharis, Ostenia and Tenagocharis (Butomopsis). Cook (1974) equates Ostenia Buch. with Hydrocleis. No independent information on the architecture of Ostenia is available, although that of Hydrocleis has been studied in detail by Charlton and Ahmed (1973).

General descriptions of Tenagocharis indicate that it is very similar in organization to the genus Alisma (Alismataceae). Its architecture is simple, consisting of an upright vegetative axis with congested internodes producing inflorescences at intervals. There is normally no development of the axillary buds.

The morphology of Limnocharis has been described by Wilder (1974a). It has a congested, upright stem characteristic of the family. Inflorescence production is by apical bifurcation, forming a continuation shoot in the axil of the ultimate leaf. The inflorescence is a sympodial structure, a cincinnus (Micheli, 1881; Ronte, 1891; Wagner, 1918), where the ultimate bud develops into a new vegetative shoot. About 5 to 8 flowers are formed per inflorescence. Like the supernumerary vegetative buds that are also found in the inflorescence of Limnocharis, this is not an ecological response to submergence. The inflorescence is held erect above the water initially, but eventually falls over so that the new vegetative shoot roots in the substrate. No development of axillary structures has been reported.

The organization of Hydrocleis is very similar to that of Limnocharis and Ranalisma (Alismataceae). The inflorescence is produced by bifurcation of the apex. It is a sympodial structure like that of Limnocharis; however, elongation of the axis of every third flower bud after the first occurs. A vegetative bud develops at the proximal end of the elongated axis, as in Ranalisma, resulting in a sympodial structure of clusters of three flower and one vegetative buds very similar to the monopodial pseudostolons, of for example, Echinodorus. A summary of the architecture of the family is shown in Fig. 2.35.

HYDROCHARITALES

The order Hydrocharitales is represented by the single family, Hydrocharitaceae, consisting of fifteen aquatic and marine genera and about 115 species. The genera of the Hydrocharitaceae are listed in Table 2.2.

Hydrocharitaceae

As the largest family within the Alismatidae in terms of the number of species within it, Hydrocharitaceae is also the most variable in terms of its growth habit and architecture. Plants may be floating, partly emergent or submerged, and in the last category, include both aquatic and marine genera. In terms of its architecture, the family may be divided into three broad categories. These are as follows:

1. Stem erect, with internodal elongation.
2. Stem erect and congested, stolons usually also developed.
3. Rhizomatous, with or without erect short shoots.

These three architectural plans are discussed in sequence below, along with the genera which conform to them. This information is summarized in Fig. 2.36.

Group 1

This group exhibits the simplest plan of organization found in the Hydrocharitaceae. It includes the genera Egeria, Elodea, Hydrilla, Lagarosiphon, Maidenia, and Nechamandra.

The stem is erect, with whorls or pseudowhorls of 2 to 5 leaves. There is some internodal elongation. The plant is usually rooted to the substrate and submerged. Flowering is by apical bifurcation to form the inflorescence and continuation shoot (Brunaud, 1976, 1977).

The shoot is simple with no further branches in Maidenia (Cook,1974). Branching is axillary and irregular in Egeria, Elodea and Lagarosiphon (Brunaud, 1977; Ancibor, 1979). It appears to be axillary and more frequent in Nechamandra (Cook, 1974). A vegetative bud is usually found in the axil of one of the first leaves of the lateral branch in these species.

In Hydrilla, the pattern is somewhat more complex. An axillary bud develops a short stem with 5 to 7 closely arrranged pairs of scale leaves. New buds develop from the axils of these scale leaves into branch axes (Ancibor, 1979). This is comparable to the development of turions in many species of the Alismatidae where turions are formed.

Group 2

The second group of growth forms in the Hydrocharitaceae consists of plants with congested upright stems with or without the development of stolons by which rosette plants are attached to one another, In appearance, this group is most similar to the Alismataceae and Limnocharitaceae.

Of the six genera that have congested upright shoots, two do not develop stolons of any sort. These are the genera Blyxa and Ottelia. Although not studied in detail in either genus, given the prevalence of the process in inflorescence formation in the rest of the subclass, it is likely that the inflorescence is formed by apical bifurcation. The organization of the Hydrocharitaceous inflorescence (Kaul, 1970) is quite different from that of the Alismataceae (Charlton, 1973). However, it seems that the vegetative architecture of Blyxa and Ottelia is quite comparable to that of the simplest Alismataceae, the genus Alisma.

The remaining four genera are Hydrocharis, Limnobium, Stratiotes and the highly variable Vallisneria. They all exhibit the same plan of organization, with variations in details. Although intensively studied in the recent past (e.g., Bugnon and Joffrin, 1963; Cutter, 1963-1965; Wilder, 1974b, 1974c; Brunaud, 1976, 1977), the interpretation of this architectural plan remains fairly controversial, and is described below.

The apex of the upright vegetative axis bifurcates at regular intervals, e.g., one plastochron for Stratiotes, two for Limnobium, and three for Hydrocharis and Vallisneria. The apex in the axil of the ultimate leaf continues the growth of the upright axis. The other develops into a complex of axes which form one or more stolons and inflorescences (usually a total of three). The stolon apex further bifurcates after a regular period of scale leaf formation (two plastochrons in Limnobium and three in Hydrocharis and Vallisneria). The apex in the axil of the ultimate scale leaf continues the growth of the stolon while that in the axil of the penultimate scale leaf forms a new upright vegetative axis.

The controversy about this architectural plan lies in the interpretation of the products of bifurcation as sympodia or monopodia. Authors such as Bugnon and Joffrin (1963), Loiseau and Nougarède (1963) and Brunaud (1976, 1977) interpret the upright vegetative axis as a monopodium, i.e., the stolons are produced laterally. The stolon is interpreted to be a sympodial structure, turning up to form the next upright vegetative axis, and producing the next stolon or horizontal segment laterally, as in the rhizomatous growth form of many monocots (Holttum, 1955). Wilder, on the other hand, takes the reverse interpretation; the upright axis is considered to be a sympodium while the stolon is a monopodial structure. These conflicting views are diagrammed in Fig. 2.37. (It should also be mentioned that Cutter (1963-1965) has suggested that "it is probably best not to attempt to equate the buds" which are produced by bifurcation with "specific morphological categories" (Cutter, 1964).)

Group 3

The Hydrocharitaceae is also the only family in the Alismatidae with both aquatic and marine genera. The architecture of the three marine genera is comparable to the architecture of other marine genera in the Najadales. All three genera are characterized by rhizomatous growth; however, they exhibit a wide range in their levels of differentiation.

The simplest of the three is the monotypic genus Enhalus, which is one of the simplest of all the seagrasses. The vegetative axis is a monopodial rhizome bearing erect foliage leaves. Lateral meristems are produced in every other leaf axil, and develop into determinate inflorescences (Troll, 1931). Irregular vegetative branching via axillary buds repeat the pattern of the parent axis (Tomlinson, 1974).

The turtle grass, Thalassia, is also rhizomatous. However, its axes are dimorphic, with the production of erect short shoots bearing foliage leaves. Thalassia branches by apical bifurcation regularly (every 9, 11 or 13 leaves) to form an upright short shoot and a continuation of the rhizome axis. This is usually interpreted to be a monopodial system (Tomlinson and Bailey, 1972; Tomlinson, 1974; see however, Tomlinson and Vargo, 1966). Irregular vegetative branching of the erect short shoot by apical bifurcation produces new rhizome axes. Inflorescences are lateral on the short shoots. The organization of Thalassia is very regular and precise. There is a well defined periodicity of branching. Also, the exclusive production of short shoots on rhizomes and rhizomes on short shoot is indication of the high level of morphological organization.

The third Hydrocharitaceous seagrass is the pantropical genus Halophila. Like Thalassia, it has dimorphic axes, scale bearing rhizomes and short shoots with inflorescences in the lowest axils. The organization of the determinate short shoot varies with the sections found within the genus

(Balfour, 1879; den Hartog, 1957; Isaac, 1968; Tomlinson, 1974). and is not well understood. In general, in the sections Spinulosae and Microphila, the short shoot bears a pair of scale leaves and then 2 to 4 pairs of foliage leaves. New rhizome segments may be produced from an axillary meristem of one of basal scales. In the section Americanae, this axillary meristem may either produce a new rhizome segment or a new short shoot. In the section Halophila, the lateral shoot bears two basal foliage leaves before reversion to scale leaves. It continues growth as a scale bearing rhizome.

NAJADALES

Of the three orders under consideration, the order Najadales is the one in which partition into hierarchical levels is relatively controversial; for example the classifications of Takhtajan (1966), Sculthorpe (1967), Cronquist (1968) and den Hartog (1974) In fact, Hutchinson divides the same families and genera over five orders, Aponogetonales, Juncaginales, Najadales, Potamogetonales, and Triuridales. The current discussion largely follows Cronquist's scheme, except that the family Zosteraceae is divided into three families, Zosteraceae, Cymodoceaceae and Posidoniaceae . Thus, as defined here, the order Najadales consists of 10 families (instead of Cronquist's 8), and about 24 genera. This is detailed in Table 2.3. A summary of the architecture of the order is found in Fig. 2.38.

Aponogetonaceae

The family Aponogetonaceae is represented by the single genus Aponogeton. Grouped as one of the 10 families of the relatively large diverse order of Najadales, the Aponogetonaceae is generally regarded to be most closely related to the Scheuchzeriaceae and Juncaginaceae within the order (e.g., Kimura, 1956; Singh and Sattler, 1977b). Unlike other Najadalean families such as Zannichelliaceae and Najadaceae, these three families have relatively unspecialized floral structures; their flowers are regarded to be very similar to flowers in the Araceae and Liliaceae (Singh and Sattler, 1977b).

The genus Aponogeton consists of about 45 species (Cook, 1974). Although there has been substantial interest in the floral structure of Aponogeton because of its potentially intermediate position between the Alismatidae and other subclasses in the monocots, few studies have been made of the vegetative organization. Most of the current description is drawn from the work of Sergueéff (1907) on A. distachyus .

The adult plant of Aponogeton has a swollen stem, with congested internodes, and show seasonal constrictions. The divergence angle is slightly larger than 90 degrees, and foliage leaves seem to be initiated in pairs. The first leaf axil of the pair is empty. The second subtends the continuation apex which is produced by bifurcation to form inflorescence and vegetative apices. The continuation shoot repeats the same pattern of development. No vegetative branching, i.e., no meristem proliferation sensu Tomlinson has been observed.

Cymodoceaceae

There are five genera within the Cymodoceaceae. Rhizomatous in form, these show a full range of architecture with varying degrees of axis differentiation and either monopodial or sympodial organization. Inflorescences are generally described as "reduced" to one or two "flowers" terminating erect lateral shoots (e.g., den Hartog, 1970). Of the five genera, Halodule may be considered the simplest in architecture. Although there is some indication of the differentiation of erect annual and horizontal main axes, this distinction is not clear-cut. In a slightly more complex arrangement, long and short shoot differentiation is well established in the genus Cymodocea. Cymodocea seems very similar to Zostera and Phyllospadix in its vegetative architecture, with monomorphic but non-equivalent axes and monopodial growth. Internodal elongation in Cymodocea varies with seasonality (Bornet, 1864).

Further differentiation of axes results in shoot dimorphism in Syringodium. The main, horizontal rhizome bears only scale leaves while the erect short shoots bear only foliage leaves.

The two other genera, Amphibolis and Thalassodendron, differ from the rest in their sympodial shoot organization. There is often a proliferation of both rhizomes and erect shoots by branching of the first one or more nodes of the erect shoot. Furthermore, both these genera also show dimorphism of their axes.

Juncaginaceae

The family Juncaginaceae as defined here consists of five genera, Cycnogeton, Maundia, Tetroncium and Triglochin, and Lilaea which is sometimes placed in its own family, Lilaeaceae (Hutchinson, 1973; Cook, 1974). Although the family is described in Engler's Pflanzenreich in some detail, like the Scheuchzeriaceae, there is little information on its vegetative architecture.

Sparse information available for Maundia indicates that it is very similar to species of Triglochin with slender rhizomes. The two genera are differentiated definitively by ovule structure. Cycnogeton and Tetroncium are often not recognized as distinct genera from Triglochin (e.g., Cook, 1974), although Tetroncium, especially, is very different (Tomlinson, personal communciation).

The architecture of Triglochin striata is described in detail in the following section. The information is reproduced from a published paper by the author, Organogenesis in Triglochin striata (Lieu, 1979a). In summary, the architecture of T. striata consists of a sympodial system of slender rhizomes bearing scale leaves and erect, leafy shoots bearing inflorescences. The inflorescence and the continuation of the shoot axis are produced by bifurcation of the apex. Between the production of successive inflorescences, an average of three leaves are formed. New rhizome segments are usually produced by the development of an axillary bud topographically associated with the abaxial side of the inflorescence.

T. palustris is similar in organization, but Hill's study on T. maritima (Hill, 1900) does not provide enough information to determine its architecture. On the other hand, T. procera (Cycnogeton procera) of Australia presents a rather unique organization. A thick, horizontal rhizome resembling that of Butomus or Sagittaria lancifolia is produced. In addition, many of the roots end in tuberous structures. Whether or not these germinate, and their process of formation, are not known. Further studies of this species may provide interesting insights into the organization of the genus and family.

Lilaea seems comparable in architecture to Triglochin striata. The difference is that only one leaf is formed between successive inflorescences, which are also different from those of Triglochin and quite unique (Buchenau, 1903). Studies seem to indicate that this genus can be considered intermediate between the Najadales and the Alismatales (Posluszny, in prep., personal communication).

Organogenesis in Triglochin striata

Introduction

There have been many studies on the growth and development of the subclass Alismatidae in the recent literature, for example, Wilder (1973), Tomlinson (1974), Posluszny (1976) and Posluszny and Tomlinson (1977). In this group, the families Scheuchzeriaceae and Juncaginaceae are still relatively poorly known and a detailed investigation is required to understand the range of growth forms in the Alismatidae.

Inflorescence formation by apical bifurcation ,i.e., division of the apex into two equal or subequal parts, characteristic of many species of the subclass, has been observed in Triglochin maritimum (Juncaginaceae, Charlton, 1968). In this case, the process was interpreted to be precocious lateral branching rather than a true dichotomy as in, for example, Flagellaria (Tomlinson and Posluszny, 1977). The same mode of branching is likely to be an integral part of the organization of Triglochin striata. Vegetative propagation in the latter species is of particular interest since large stands are often formed by stoloniferous rhizomes (Long and Lakela, 1971). In a largely anatomical study, Hill (1900) mentioned briefly that the rhizome of T. maritimum "frequently forks into two branches", i.e., apical bifurcation may again be involved.

Floral development in Triglochin has been described briefly by Celakovsky (1901) and in greater detail in T. maritimum by Hill (1900). In addition, it has been suggested that the bractless flower is actually a reduced inflorescence branch of staminate and pistillate flowers as in other genera of the Najadales (Uhl, 1949; Eames, 1961). This interpretation is in turn basic to a new hypothesis on the origin of the monocot flower (Burger, 1977). In view of the difficulties of flower-inflorescence interpretations found in other members of the Najadales (Posluszny, 1976), a detailed study of floral development is included.

Materials and Methods

Plants of Triglochin striata were collected in October 1976 near the Fairchild Tropical Garden research laboratory on the Jennings Estate in Miami, Florida. Voucher specimens have been deposited in the herbarium at Fairchild and at the McGill College Herbarium (MTMG).

Whole plants were washed and preserved in formalin-acetic acid-alcohol within 48 h of collection, often after a preliminary dissection. These were then transferred to 70% ethanol and stained in alcoholic acid fuchsin, dissected, and photographed using the technique of Sattler (1968). All photographs have been reproduced at the same magnification (140x) to facilitate comparisons. The photographed specimens and others were then oriented in blocks of pith and dehydrated in a tert-butyl alcohol series and embedded in Tissue Prep (mp 61 degrees C, Fisher Scientific) using standard techniques. Serial sections were cut at 6 or 7 µm and stained in Johannsen's Safranin. Photographs of these sections were taken with a Zeiss Photomicroscope 2 and line drawings were made with a Zeiss microscope and camera lucida attachment.

Time references in the descriptions are in terms of developmental events, as the actual time scale of these events was not studied.

Results

The Shoot

Triglochin striata grows in stands in shallow, brackish water. Each plant consists of a relatively short stem (3-5 mm in diameter) with distichously arranged leaves half-cylindrical in cross section. It is usually connected to two to three other plants by thin, brittle stolons or stoloniferous rhizomes (Long and Lakela, 1971) up to 10 cm long. The inflorescence is a racemose spike of many short-pedicelled flowers with no subtending bracts (Fig. 2.39). Successive inflorescences along the axis are usually separated by two to three (sometimes more) foliage leaves.

Each flower produces three mature seeds and three aborted carpels (Figs. 2.40a, 2.40c). The embryo, dissected from the seed, is mainly a large cylindrical cotyledon. The radical and epicotyl are very small by comparison (Figs. 2.40b, 2.42a). There is one foliage leaf and the apex is extremely reduced, having a single tunica layer (Figs. 2.42b, 2.45a). Phyllotaxy of the embryo is distichous. Reserves are stored in the abundant starch granules in the cotyledon (Fig. 2.44a).

The adult plant also possesses a relatively small apex (Fig. 2.42c), though this usually has two tunica layers (Fig. 2.45c). Leaf initiations occur high on the apex (Fig. 2.45b) with long plastochrons. The median procambial trace and the leaf sheath are usually well developed before the initiation of a new leaf (Fig. 2.44b). There is frequently an enlarged portion at the tip of the ligulate leaf (Fig. 2.42d). This corresponds to the portion of the leaf above the ensheathing base of the preceding one and is probably related to the reduction of mechanical constraints to growth at this point.

Small, triangular intravaginal scales occur between the leaves (Figs. 2.42e, 2.43c). Lateral buds are found irregularly in leaf axils, but are most frequent in that of the penultimate leaf before bifurcation and thus topographically associated with the inflorescence (Figs. 2.40e, 2.41a, 2.42e). They are often first detected as a densely staining area at the base of the inflorescence apex (Fig. 2.45e). An adaxial prophyll is first formed on each lateral bud (Fig. 2.42e). The median plane of the first scale leaf formed after the prophyll is oriented 90 degrees from the vertical (or median of the prophyll). Phyllotaxy is subsequently distichous (Fig. 2.41b). Differential growth early in the development of the bud axis results in its horizontal orientation. The scale leaves may be distinguished from the square-topped foliage leaves by their triangular shape (Figs. 2.42c, 2.42f). The stolon is formed by elongation of the bud axis and expansion of scale leaves. After expansion of about six to eight scale leaves, it turns upright to form a new plant bearing foliage leaves; i.e., a clearly sympodial organization is found.

Apical expansion by generalized cell division (Fig. 2.45d) and bifurcation results in the formation of the inflorescence and a continuation shoot (Fig. 2.45e). The plane of bifurcation is usually at right angles to that of leaf insertion. Thus the inflorescence is leaf-opposed and the continuation shoot is found in the axil of the last leaf formed before the transition (Figs. 2.41a, 2.43a). Though the former is usually taller (Fig. 2.45e), the latter has a larger cross sectional area (Figs. 2.43a, 2.43b). The two tunica layers are often maintained after the two primordia have become distinct.

No morphologically distinct prophyll is formed on the continuation shoot. The first foliage leaf is opposite the last leaf before bifurcation and thus continues uninterrupted the phyllotaxy of the stem axis (Figs. 2.43c, 2.43d, 2.44c).

The inflorescence primordium enlarges but remains dome shaped while the first two leaves of the continuation shoot are initiated. The flattened ridge of the first leaf gives this shoot its characteristic shape (Figs.

2.43e, 2.44d). A ring of procambial strands soon develops in the inflorescence primordium (Figs. 2.44d, 2.44e). As the inflorescence begins to elongate, floral primordia are initiated acropetally by periclinal and anticlinal divisions in densely staining regions in subsurface layers (Figs. 2.43f, 2.44e, 2.51a). No bract primordia are formed (Figs. 2.46a, 2.51b). The length of the young inflorescence and thus the number of flowers each bears are highly variable. Flowers are arranged in approximate alternation in rows of four to eight. Each inflorescence may have 6 to 20 or more of these rows. A terminal flower is frequently found (Fig. 2.46b). Occasionally, a large floral primordium is found low on the inflorescence on the side distal to the continuation growth (Fig. 2.46a). However, this does not develop differently from the others and is indistinguishable in later stages. Elongation of the axis below the lowest flowers occurs rapidly (Fig. 2.40a). Further growth of the flower-bearing portion eventually scatters the flowers irregularly along the inflorescence axis.

The Flower

The flower of Triglochin striata is basically trimerous, with two whorls of three tepals each, two whorls of three stamens each, a whorl of three aborted carpels, and a whorl of developed carpels with sessile stigmas in alternation with each other (Figs. 2.40d, 2.47). The extent of stamen development is variable. Often, only the lowest median stamen is fully developed (Figs. 2.40d, 2.55a). The others remain as small staminodia. Other times, more of the stamens are developed, or none at all. Each stamen appears attached to the opposing tepal, and the two tend to be shed as a unit during seed development. When developed, the large size of the lowest stamen, coupled with the large pouch-like tepal opposite it, results in a zygomorphic appearance. In addition, the outer whorl of stamens often appears external to the inner whorl of tepals though their levels of insertion are about the same (Fig. 2.48i).

Floral development begins with the initiation of a tepal, usually but not always located on the lower median part of the floral primordium (Fig. 2.46b). Thus the median plane of the flower through the first tepal is usually parallel to the inflorescence axis. This primordium develops by divisions in the subepidermal layers and forms a ridge-like structure (Figs. 2.48a, 2.51c). Two other tepals are initiated one after another (Fig. 2.48b) so that, strictly speaking, they form a pseudowhorl as do other triplets of appendages. For simplicity, they are referred to as whorls in this description.

The first tepal of the inner whorl is initiated between the first and second outer ones, and the second between the first and the third (Figs. 2.48b, 2.49a, 2.51d). The first outer stamen primordium is initiated very shortly thereafter as a ridge of tissue opposite the first tepal (Figs. 2.48c, 2.51d) followed by the second and third in the same sequence as the outer tepals (Fig. 2.48d). At initiation these are clearly situated at a higher level than the inner tepals (Figs. 2.49b, 2.49c). The inner whorl of stamen primordia, more rounded in shape, is opposite the inner whorl of tepals. They are formed like the outer stamens by anticlinal and periclinal cell division and expansion beneath the epidermal layer (Fig. 2.51e).

The two rings of gynoecial primordia are formed as the thecae of the outer stamens are developed (Figs. 2.48e to 2.48g, 2.52b, 2.52c). A large portion of the floral meristem often remains at this stage (Figs. 2.48g, 2.52c). At the same time, the outer tepals expand and surround the floral bud. The inner ones do not increase appreciably in size and so appear to be at the same level as the rapidly expanding outer stamens (Figs. 2.48g, 2.49d). The inner carpels form bowl-shaped structures by upgrowth of the periphery of each primordium (Figs. 2.48h, 2.48i, 2.52d, 2.53a). A single ovule is formed at the base of the ventral wall (Figs. 2.48i, 2.50a). The outer whorl of carpels may form slight depressions (Fig. 2.50a) but usually they expand as a solid mass of tissue. The inner tepals begin to enlarge. Owing to the large size of the outer stamens now adjacent to them, the tepal edges often extend so that they are internal to the stamens (Figs. 2.48i, 2.49e, 2.49f).

The ovule develops as a basilar structure, initiating two integuments in quick succession (Figs. 2.50b to 2.50d). The outer integument is usually three cells thick whereas the inner one consists of two cell layers (Fig. 2.53b). A stalk is developed and an anatropous orientation attained later in development (Figs. 2.50e, 2.50f). The carpel walls grow upward at the same time and close over to form the stigmatic region (Fig. 2.50g) which later develops densely staining, uniseriate hairs (Figs. 2.50h, 2.53c). The aborted carpels remain small solid structures and do not form any stigmas (Figs. 2.50h, 2.55a).

Each appendage is supplied by a single vascular bundle originating from the massive one in the pedicel (Figs. 2.42d, 2.55a). This, in turn, is a branch from the ring of bundles in the inflorescence axis. The vascular bundle of the developed carpel is found in the dorsal wall. A branch from this innervates the ventral side of the ovule (Fig. 2.55b). Each aborted carpel also has a vascular bundle which is more central in location.

The extent of development of a stamen depends on its order of initiation. If a primordium remains rudimentary, then all others initiated after it are undeveloped. The inner whorl is almost always made up of staminodia and occasionally none of these develops beyond a superficially bilobed shape. The mature stamen has four thecae arranged in two extrorse lobes. The cells of the thecal walls are characterized by spiral thickenings (Figs. 2.54c). Staminodia may be a solid mass of tissue (Figs. 2.53c, 2.54b), may have the beginnings of thecal cavities (Figs. 2.54a, 2.54b), or may have thecae with no pollen grains (Fig. 2.54a).

Later in development, intercalary growth beneath each stamen and its opposite tepal results in the formation of a small common base (Figs. 2.54d, 2.55b). This accounts for the observation that they tend to break off as a unit. The vasculature, however, remains distinct (Fig. 2.55b).

Discussion

The organization of Triglochin striata is relatively simple and has much in common with species in the Alismatales (Lieu, 1979b, 1979c). The embryo consists mainly of a massive cotyledon and a small apex. Distichous phyllotaxy is established from the outset, as in Butomus umbellatus. Apical bifurcation results in the formation of a leaf-opposed inflorescence as in members of the Alismataceae, in particular rhizomatous Sagittaria lancifolia which also has distichous phyllotaxy (Lieu, 1979c). In organization, T. striata differs from upright species of Alismataceae mainly in the elongation of the axis and the absence of a morphologically distinct prophyll on the continuation shoot (see Table 2.7).

Axillary buds form clearly sympodial systems of stolons and new upright plants for vegetative propagation. These buds are irregular in occurrence and most often are topographically associated with the inflorescence, as they are in the axil of the penultimate leaf. They appear precocious in development, often developing before the appearance of the sheathing base of the next (the ultimate) leaf, so that they are formed directly on the base of the inflorescence apex. This association is found in many other members of the Alismatales (Lieu, 1979c).

A similar branching pattern is found in the related Lilaea subulata, where only one leaf is formed between successive inflorescences (Buchenau, 1903; Agrawal, 1952; Charlton, personal communication). The number of leaves between inflorescences varies from one to five (frequently three) in Triglochin striata.

Floral development in T. striata is similar to that described by Hill (1900) for T. maritimum. The flower of T. striata is based on a trimerous plan of alternating whorls of tepals, stamens, and carpels. There is no indication of an association of the petal and stamen primordia (the "CA complex") as in other members of the Alismatidae (Singh and Sattler, 1972, 1973). This is comparable to the pattern of organization also found in Aponogeton and quite characteristic of monocotyledons (Singh and Sattler, 1977), and would support the view that the family Juncaginaceae is closer to the Aponogetonaceae than to other members of the Alismatales (Singh and Sattler, 1977). The common occurrence of zygomorphy by the production of a single large stamen and the greater development of its opposite, lowermost median tepal probably follows the trend from actinomorphic hermaphroditic flowers to zygomorphic dioecious ones well known in aquatic groups (Eames, 1961; Sculthorpe, 1967).

Uhl (1947) and Eames (1961) consider the flower of Triglochin to be the reduced lateral branch of an inflorescence. Uhl (1947) based this interpretation on several criteria. Firstly, the three inner tepals and the points of origin of their vascular traces from the trace in the pedicel are located above the three outer stamens and the origins of their traces. This criterion, in turn, depends upon the independence of vasculature of the stamen and its adnate tepal: individual bundles "indicate" that the tepal is not an outgrowth of the stamen, but the perianth of a staminate flower. Should the tepals be considered staminal outgrowths, their location relative to other stamens would be immaterial. A second criterion is the extension of the floral axis, to which the carpels are attached, above the level of their insertion.

The current study shows that stamen inception is clearly after and above that of the inner whorl of tepals. Their relative positions later in development are a consequence of the short time interval separating initiations, and the different rates and timing of growth of their respective primordia. The outer stamen primordia develop rapidly to form thecae which extend beyond the plane of the small, less developed inner tepals, so that later growth at the edges of the latter is topographically internal to the stamens. The positional differences of these two whorls of appendages as shown by Uhl (1947) are much greater than those found in young or mature flowers of Triglochin striata and T. maritimum (Hill, 1900) and other species (Buchenau, 1903); nor is there a significant difference in the level of origin of the vasculature bundles from the central bundle in the pedicel.

Though a large portion of the floral meristem remains after gynoecial initiation in T. striata, there is no indication of the formation of an extended and independent central axis from which the carpels separate at maturity as reported in T. maritimum (Uhl, 1947). It seems likely that in T. striata the continuity of the carpel walls in early stages is a result of fusion along their ventral margins. In this species, the narrow, aborted carpels remain on flowers after the mature seeds have been shed. The floral axis to which these are attached does not extend significantly beyond their level of insertion. Illustrations of other species of Triglochin seem to support this conclusion (Buchenau, 1903).

Eames considered that in Triglochin, "a whorl of staminate flowers, separated by a whorl of bracts from a whorl of pistillate flowers" occurs, and that "The presence of bracts (not staminodes) between the stamen and the carpels in itself is sufficient evidence that this is not a true flower" (Eames, 1961; Uhl, personal communication). Though this statement is not illustrated, from the results of this study, the "bracts" emphatically referred to as not being staminodes are, in fact, the inner whorl of stamens that are almost always poorly developed.

Thus the flowers of Triglochin striata and T. maritimum (Hill, 1900) develop very regularly on a clearly trimerous plan. Positional relationships in the mature flower can be readily understood in terms of differential growth. The common base between stamen and opposing tepal, which results in their being shed as a unit and thus used to support the interpretation of staminate flowers, is a simple consequence of intercalary growth beneath both. In this respect it resembles the case of the stamen and its adnate tepal in Potamogeton (Posluszny, 1976). It seems unnecessary to assume that each stamen and its opposing tepal represent a staminate flower, or that the flower is actually a reduced inflorescence.

Uhl (1947) noted that in the closely related genus Scheuchzeria, as in Triglochin, the inner perianth parts stand above the outer whorl of three stamens, though the difference in position is "not as easily apparent". In view of the preceding results, it seems quite possible that this flower may also be organized on a plan of alternating trimerous whorls typical of monocotyledonous flowers rather than as a condensed inflorescence branch, though a detailed study would be required to confirm this.

In terms of developmental events, there is no apparent ambiguity in the delineation of flower and inflorescence in Triglochin striata as there is, for example, in Potamogeton (Posluszny, 1976). In this respect, this study does not support Burger's hypothesis (Burger, 1977) that the flower of monocotyledons originated by condensation of inflorescence branches in genera such as Triglochin. However, Burger relied more on vascular anatomy than ontogenetic evidence in his work, in which case the anatomy of T. striata may still be considered indicative of its having originated as a lateral branch. As in vegetative morphology, the problem is one of interpretation and choice of criteria. Emphasis on vasculature would support Burger's hypothesis whereas developmental studies indicate that the flower of Triglochin is comparable to the ordinary trimerous monocotyledonous flower.

Najadaceae

The Najadaceae is a cosmopolitan family represented by the single genus Najas, consisting of about 50 species (Cook, 1974). Obligate submergents, plants of Najas have slender, usually profusely branched stems, with flowers in the leaf axils.

Sattler and Gifford (1967) and Posluszny and Sattler (1976b) have shown that branching is monopodial. The apical meristem bifurcates to form a vegetative meristem and a meristem in the axil of the youngest visible leaf, the lower one of the subopposite pair characteristic of the genus. The vegetative meristem continues the growth of the main axis. The axillary meristem is considered to be lateral; it bifurcates again to form a floral meristem and a collateral, vegetative meristem which develops into the macroscopic branch. Because of the proximity in time of development of the two vegetative axes, they are very similar in appearance, and has been described as "dichotomously branching" in some floras (e.g., Correll and Correll, 1975). Although the above description is for N. flexilis, the species of Najas seem to be more differentiated by fine points of leaf and seed morphology (e.g., Clausen, 1936) and not architecture.

Illustrations sometimes show slender, rhizome like structures in the genus Najas (e.g., N. guadalupensis and N. marina, Godfrey and Wooten, 1979). This is enhanced by the frequency of rooting at internodes along the stem. Horizontal orientation of the main axis has been reported for Najas tenuifolia (Aston, 1973). The absence or presence of a relatively undifferentiated rhizome is discussed in greater detail in a later section.

Posidoniaceae

Consisting of only one genus, Posidonia, Posidoniaceae exhibits the simplest architecture among the trio of exclusively marine families, Zosteraceae, Cymodoceae and Posidoniaceae. The axes of Posidonia are monomorphic and equivalent, being horizontal rhizomes bearing foliage leaves. Proliferation of rhizomes, as in Amphibolis and Thalassodendron (both Cymodoceae), is by a "precocious" branch which "often simulates a dichotomy" (Tomlinson, 1974). The inflorescence of Posidonia, a racemose arrangement of spathes, is axillary in origin.

Potamogetonaceae

The Potamogetonaceae as defined here includes the two genera, Potamogeton and Groenlandia although den Hartog (1970) included the three exclusively marine families, Cymodoceae, Posidoniaceae and Zosteraceae, as subfamilies in the Potamogetonaceae.

The genus Potamogeton consists of about 100 cosmopolitan species (Cook, 1974), and is one of the most species rich genera in the entire Alismatidae. Although some of these species are difficult to distinguish and identify because of their similarities in both vegetative and reproductive features, the architecture of the genus is fairly straightforward.

The predominant form consists of a creeping rhizome producing erect stems bearing terminal inflorescences. Dimorphism between the two axis types is usual. Scale leaves are found on rhizomes, which may often also be thicker and white, red or buff in colour. Sympodial branching of the rhizome (Sauvageau, 1894, Arber, 1920) produces the erect shoots, which bear foliage leaves. The extent of branching of both rhizome and upright shoots vary from species to species. These descriptions indicate that rhizome branching follows a very regular pattern in this family. Continuation of the axes after inflorescence formation is by vegetative buds, in the axil of leaves immediately below the inflorescence, which are precocious in development (e.g., Posluszny and Sattler, 1973, 1974).

In other species, the rhizomatous axis is absent. Other aspects of architecture are consistent with the description above. Examples of this growth form include *P. pusillus* and *P. Berchtoldii*. Most frequently, these species are described to overwinter by means of turions, specialized axillary buds with compressed internodes and sometimes different leaf structure.

Turions are also developed by rhizomatous species such as *P. crispus*. However, this seems to be less frequent. Furthermore, terminal, tuberous bulblets have been observed at the tip of rhizome axes, for example, *P. pectinatus* and *P. filiformis* (Mason, 1957; Correll and Correll, 1975; Godfrey and Wooten, 1979). Although seasonal in nature and very similar in appearance to tubers produced by species of *Sagittaria* (Alismataceae), it is not clear whether or not these are overwintering structures.

The genus *Groenlandia* consists of only one species, *G. densa*, regarded by some authors as *Potamogeton densus*. The separation of this species into its own genus reflects differences in floral and inflorescence structure (Posluszny and Sattler, 1973). In terms of vegetative architecture, it is comparable to other *Potamogeton* species with both rhizomatous and erect axes.

Ruppiaceae

The family Ruppiaceae consists of one genus, Ruppia L., which includes 7 species. Found usually in brackish waters, Ruppia is considered to be of considerable ecological importance as a food supply to various wildlife species.

The species of Ruppia are sometimes considered to be a single, very polymorphic species (Cook, 1974). Nevertheless, the architecture of the species is relatively constant. The general organization of the plant is similar to that of Potamogeton with both rhizomatous and upright axes. The plant consists of slender rhizomes bearing slender, erect stems. These stems are usually profusely branched, and terminated by reproductive structures. Continuation of the erect axis results from the precocious development of vegetative buds in the axils of leaves immediately below the inflorescence (Posluszny and Sattler, 1974b).

The rhizome is initially a monopodial structure, but it becomes sympodial later in development (Tomlinson, personal communication). There is no evidence of shoot dimorphism in terms of leaf type on either axis. In fact, Godfrey and Wooten (1979) have reported rhizomes where upright stems are lacking and leaves arise directly on the rhizome. The definition of rhizomes solely by its horizontal orientation, particularly in the more slender and delicate species of the Najadales, is discussed in greater detail at a later section.

Scheuchzeriaceae

The Scheuchzeriaceae is a monogeneric family, represented by the genus Scheuchzeria. The genus is not well studied, and has variously been placed within different groups of the Alismatidae, for example in the Najadaceae (Butcher, 1961), or in the Alismatales (Hutchinson, 1973), or not recognized at all (Cook, 1974). The description of the architecture of Scheuchzeria is based upon various descriptions in floras. Morphological studies currently under way (Posluszny, personal communication) may provide new insights in the near future.

The plant of Scheuchzeria consists of a creeping rhizome giving rise directly to erect, elongated shoots. In this regard, it is at least superficially similar to species of Triglochin (Juncaginaceae) with slender, sympodial rhizome systems. Initial results of recent investigations of the genus, however, seem to indicate a more complicated plan of organization (Posluszny, personal communication).

The mode of inflorescence formation is unknown. Flowers of the inflorescence are subtended by large bracts. Although some authors consider the "flower" to be an inflorescence branch (e.g., Uhl, 1947; Eames, 1961; Burger, 1977), it it likely that the structure may be interpreted to be a flower (Lieu, 1979a) rather than comparable to some of the complexes described for other families of the Najadales such as the Zannichelliaceae or Najadaceae (Posluszny, 1976).

Zannichelliaceae

Historically, the Zannichelliaceae has been considered to comprise of three freshwater genera, Zannichellia, Althenia and Lepilaena (e.g., Cook, 1974). The exclusively marine family, Cymodoceaceae, is also considered by some authors to be part of the Zannichelliaceae (e.g., Aston, 1973; Cook, 1974). Recent detail studies have resulted in the division of the genus Zannichellia into two genera, Zannichellia and Pseudalthenia (Vleisia, Tomlinson and Posluszny, 1976; Posluszny and Tomlinson, 1977). The latter scheme is followed here; indeed, much of the information presented below is drawn from the studies of Posluszny and Tomlinson (1977).

All four genera have slender rhizomes bearing scale leaves producing erect branches bearing foliage leaves sympodially (Reinecke, 1964; Posluszny and Tomlinson, 1977). The extent of dimorphism differs from one genus to another; for example, rooting occurs only at the nodes of the rhizome in Althenia (Prillieux, 1864) whereas rooting may occur at all internodes in other genera. The architecture of the four genera mainly differs in the organization of their erect shoots.

Both Althenia and Lepilaena are sympodial in the development of fertile shoots. The erect stem is terminated by a reproductive meristem formed by bifurcation of the apex. The other product of the bifurcation is a vegetative apex in the axil of the last leaf formed before bifurcation. It is considered to be lateral, and continues the growth of the axis briefly, before transition to the next bifurcation. Renewal growth terminated by the production of a flower or inflorescence occurs in the axillary buds of several leaves below the flower, and this pattern is reiterated as the renewal growths themselves are terminated by flowering.

In Pseudalthenia, this pattern of organization is modified slightly. The main shoot is usually monopodial, and vegetative initially. Distally, it produces axillary sympodia of fertile shoots similar to the shoots of Lepilaena and Althenia. In addition, proximal, short shoots terminated by a female flower are found. These produce lateral monopodia of the same organization as the main shoot described above.

Zannichellia shows the most complex organization of the four genera. The erect shoot is terminated by a female flower produced by bifurcation of the apex. The other product of bifurcation is the renewal shoot. It is in the axil of the ultimate leaf formed before bifurcation. The penultimate leaf subtends a shoot that terminates in a male flower after the production of a single leaf and a prophyll. The leaf proximal to the penultimate one is a membranous sheath which surrounds this compressed "nodal complex" (Posluszny and Sattler, 1976a). Proliferation of axes is the result of the development of a vegetative meristem formed during the bifurcation to form the male flower. Both this and the renewal shoot formed during the formation of the female flower reiterate the pattern of development.

Zosteraceae

The family Zosteraceae is subdivided into three genera, Zostera, Heterozostera, and Phyllospadix. In terms of their vegetative morphology, these three show only minor differences from one to another. The vegetative axes are usually described as monomorphic but not all equivalent (Tomlinson, 1974); i.e., although only foliage leaves are produced, there is a clear distinction between the horizontal main axis and the erect, annual axes on which flowers, if present, are usually borne. These flowering shoots, bearing obvious sympodia of spathes and spadices characteristic of the family, are often referred to as generative shoots.

The genus Phyllospadix is distinguished from the others by a lack of internodal elongation of the rhizome, resulting in the congestion of successive leaves. It also shows a monopodial organization of long and short shoots. Heterozostera and Zostera both show internodal elongation. However, the former routinely produces erect shoots sympodially whereas Zostera, like Phyllospadix, follows a monopodial arrangement. Tomlinson has suggested that the turning up of the rhizome apex to form a generative shoot in Zostera may occur, resulting in sympodial organization. An annual form of Zostera marina L. seems to consist solely of the development of an erect generative shoot (Keddy and Patriquin, 1978).

Table 2.1 Genera of Alismatales with Selected References

Alismataceae	
Alisma	Wydler, 1863 Lieu, 1979b
Baldellia	
Burnatia	
Caldesia	
Damasonium	
Echinodorus	Charlton, 1968
Limnophyton	
Luronium	
Machaerocarpus	
Ranalisma	Charlton and Ahmed, 1973
Sagittaria	Charlton, 1973 Lieu, 1979b Lieu, 1979c
Wisneria	
Butomaceae	
Butomus	Weber, 1956a Charlton and Ahmed, 1973 Wilder, 1974 Lieu, 1979c

Table 2.1 Genera of Alismatales with Selected References (cont'd)

Limnocharitaceae

Hydrocleis	Charlton and Ahmed, 1973
Limnocharis	Wilder, 1974a
Ostenia	
Tenagocharis	

Table 2.2 Genera of Hydrocharitales with Selected References

Hydrocharitaceae

Blyxa	
Egeria	
Elodea	Wylie, 1904 St. John, 1965 Brunaud, 1976
Enhalus	Svedelius, 1904 Cunnington, 1912 Troll, 1931 Tomlinson, 1974
Halophila	Balfour, 1879 den Hartog, 1957 Isaac, 1968 Tomlinson, 1974
Hydrilla	Ancibor, 1979
Hydrocharis	Cutter, 1963 Cutter, 1964 Cutter, 1965 Bugnon and Joffrin, 1963 Loiseau and Nougarède, 1963
Lagarosiphon	
Limnobium	Wilder, 1974b
Maidenia	
Nechamandra	
Ottelia	
Stratiotes	Brunaud, 1976

Table 2.2 Genera of Hydrocharitales with Selected References (cont'd)

Thalassia	Pacasio and Santos, 1930 Tomlinson and Vargo, 1966 Tomlinson and Bailey, 1972
Vallisneria	Bugnon and Joffrin, 1962 Wilder, 1974c

Table 2.3 Genera of Najadales with Selected References

Aponogetonaceae	
Aponogeton	Engler, 1886 Serguéeff, 1907 Riede, 1920 van Bruggen, 1970 Singh and Sattler, 1977
Cymodoceaceae	
Amphibolis	Sauvageau, 1891 Ostenfeld, 1916 den Hartog, 1970 Tomlinson, 1974
Cymodocea	Bornet, 1861 Sauvageau, 1891 den Hartog, 1970 Kay, 1971 Tomlinson, 1974
Halodule	den Hartog, 1970 Tomlinson, 1974
Syringodium	Sauvageau, 1891 Ostenfeld, 1916 den Hartog, 1970 Tomlinson, 1974 Posluszny and Tomlinson, 1978
Thalassodendron	Sauvageau, 1891 den Hartog, 1970 Tomlinson, 1974

Table 2.3 Genera of Najadales with Selected References (cont'd)

Juncaginaceae	
Cycnogeton	
Lilaea	Buchenau, 1903 Agrawal, 1952 Posluszny, in prep. Charlton, unpub.
Maundia	Buchenau, 1903
Tetroncium	Buchenau, 1903
Triglochin	Hill, 1900 Buchenau, 1903 Uhl, 1947 Lieu, 1979a
Najadaceae	
Najas	Magnus, 1870 Campbell, 1897 Miki, 1937 Sattler and Gifford, 1967 Posluszny and Sattler, 1976b Posluszny, 1976
Posidoniaceae	
Posidonia	Grenier, 1869 Ostenfeld, 1916 Weber, 1956b den Hartog, 1970 Tomlinson, 1974 Kuo and Cambridge, 1978

Table 2.3 Genera of Najadales with Selected References (cont'd)

Potamogetonaceae	
Groenlandia	Posluszny and Sattler 1973 Posluszny, 1976
Potamogeton	Sauvageau, 1894 Posluszny and Sattler 1974a Posluszny, 1976
Ruppiaceae	
Ruppia	Graves, 1908 Gamerro, 1968 Poslusny and Sattler, 1974b Posluszny, 1976
Scheuchzeriaceae	
Scheuchzeria	
Zannichelliaceae	
Althenia	Prillieux, 1864 Posluszny and Tomlinson, 1978
Lepilaena	Posluszny and Tomlinson, 1978
Pseudalthenia	Posluszny and Tomlinson, 1978
Zannichellia	Campbell, 1897 Reinecke, 1964 Posluszny and Sattler 1976a Posluszny, 1976 Posluszny and Tomlinson, 1978

Table 2.3 Genera of Najadales with Selected References (cont'd)

Zosteraceae		
	<u>Heterozostera</u>	
		Setchell, 1933
		den Hartog, 1970
		Tomlinson, 1974
	<u>Phyllospadix</u>	
		Dudley, 1893
		den Hartog, 1970
		Tomlinson, 1974
	<u>Zostera</u>	
		Setchell, 1929
		Setchell, 1933
		Taylor, 1957
		Bugnon, 1963
		den Hartog, 1970
		Tomlinson, 1974

Table 2.4 Comparison of Features in the Pattern of Organization of the Alismataceae

	Alisma triviale	*Sagittaria latifolia* *Sagittaria cuneata*	*Sagittaria subulata*	*Echinodorus tenellus**	*Ranalisma humile†*
Upright vegetative axes	×	×	×	×	×
Phyllotaxy	Spiral $\frac{2}{5}$	Spiral $\frac{2}{5}$	Spiral $\frac{2}{5}$	Spiral	Spiral
Apical bifurcation	×	×	×	×	×
Leaf subtending continuation shoot	Ultimate	Ultimate	Ultimate	Ultimate	Ultimate
Morphologically distinct prophyll	×	×	×	×	—
Periodicity between inflorescences	5 foliage leaves	3 foliage leaves	—	—	—
Pseudostolon	—	—	—	Monopodial	Sympodial
Axillary bud: gradient of precocity	×	—	—	×	×
Stolon	—	Single new plant	Series of new plants	—	—
Environmentally induced flowering	×	×	—	—	Not studied

x - Feature present
---- - Feature absent

* Based on Charlton (1968).
\+ Based on Charlton and Ahmed (1973).

Table 2.5 Comparison of *Sagittaria lancifolia* and *Butomus umbellatus*

Sagittaria lancifolia	*Butomus umbellatus*
Seedling phyllotaxy spiral, gradually changing to distichous	Seedling phyllotaxy distichous from start, early establishment of anterior–posterior orientation
Rhizome 4–5 cm thick	Rhizome 1–1.5 cm thick
Distichous phyllotaxy	Distichous phyllotaxy
Leaf with lanceolate blade	Leaf triangular in cross section
Apex radially symmetrical	Apex elongated in direction of rhizome axis
No pattern to the overlap of anterior or posterior leaf edge around the other	Posterior edge of leaf sheath surrounds anterior one
Inflorescence leaf opposed, continuation growth leaf subtended	Inflorescence leaf subtended, continuation growth leaf opposed
Inflorescence primordium formed by apical bifurcation usually taller and larger	Inflorescence primordium formed by apical bifurcation may or may not be larger than continuation growth
Plane of bifurcation parallel to rhizome axis, neither product more anterior	Plane of bifurcation at an angle to rhizome axis, continuation growth in a more anterior position
Shell zone found occasionally	Shell zone not found
Phyllotaxy of continuation growth continues uninterrupted by that of the rhizome before bifurcation, as does that of inflorescence	Phyllotaxy of continuation growth continues uninterrupted by that of the rhizome before bifurcation, that of inflorescence does not
Continuation growth has no morphologically distinct prophyll, first foliage leaf externally two-keeled by compression against inflorescence	Continuation growth has no morphologically distinct prophyll, first foliage leaf similar to others due to slow growth of inflorescence
First foliage leaf does not subtend axillary bud	First foliage leaf subtends an axillary bud
Precocity of axillary bud of penultimate leaf	Precocity of axillary bud of leaf before the penultimate one
Precocious bud dominant in lateral branching	Precocious bud dominant in lateral branching
Other axillary buds poorly developed on mature rhizome	Other axillary buds form bulbils for dispersal later in season

Table 2.6 Comparison of Features in the Pattern of Organization in Some Species of the Alismatales

	Alisma triviale	*Sagittaria latifolia* *Sagittaria cuneata*	*Sagittaria subulata*	*Echinodorus tenellus**	*Ranalisma humile†*	*Sagittaria lancifolia*	***Butomus umbellatus***
Vegetative axis	Upright	**Upright**	Upright	**Upright**	Upright	**Rhizomatous**	**Rhizomatous**
Phyllotaxy	**Spiral $\frac{2}{5}$**	**Spiral $\frac{2}{5}$**	**Spiral $\frac{2}{5}$**	Spiral	**Spiral**	**Distichous**	**Distichous**
Apical bifurcation	×	×	×	×	×	×	×
Ultimate leaf subtends	Continuation growth	Continuation growth	Continuation growth	Continuation growth	Continuation growth	Continuation growth	**Inflorescence**
Morphologically distinct prophyll	×	×	×	×	—	—	—
Periodicity between inflorescences	**5 foliage leaves**	**3 foliage leaves**	Variable	Variable	Variable	Variable	**7 (9) leaves**
Pseudostolon	—	—	—	Monopodial	**Sympodial**	—	—
Precocious axillary bud	**Penultimate**	—	—	**Penultimate**	**Penultimate**	**Penultimate**	***p* − 1**
Other axillary buds	**Usually suppressed**	**Stolon forming a new plant**	**Stolon forming a new plant**	**Usually suppressed**	**Usually suppressed**	**Usually suppressed**	**Form bulbils**

x - Feature present
—— - Feature absent

* Based on Charlton (1968).
+ Based on Charlton and Ahmed (1973).

Table 2.7 Comparison of Features in the Pattern of Organization in Species of Alismataceae with Upright Axes, *Sagittaria lancifolia* and *Triglochin striata*

	Alismataceae	*Sagittaria lancifolia*	*Triglochin striata*
Vegetative axis	Upright	Horizontal	Upright
Axis elongation	—	X	X
Phyllotaxy	Spiral	Distichous	Distichous
Apical bifurcation	X	X	X
Leaf subtending continuation growth	Ultimate	Ultimate	Ultimate
Morphologically distinct prophyll	Usually present	—	—
Periodicity between inflorescences	Variable with species	2–8	1–5 Usually 3
Distribution of axillary buds	Regular	Regular	Irregular
Rapidly developed axillary bud	When present in penultimate leaf axil	In penultimate leaf axil	In penultimate leaf axil
	Contributes to local branching	Contributes to local branching	Forms sympodial stolon system

x - Feature present
--- - Feature absent

List of Abbreviations for Figs. 2.1 to 2.21

Br - bract or its primordium
Co - cotyledon
F - flower or its primordium
I - inflorescence or reproductive apex
IS - intravaginal scales (multiseriate hairs)
L - foliage leaf or its primordium
Pr - prophyll or its primordium
R - root or its primordium
S - scale leaf or its primordium
St - stolon
V - vegetative apex

a - axillary, e.g., aV, apex of axillary shoot
p - penultimate, e.g., Lp, penultimate leaf before transition to inflorescence formation
pr - procambial strand
r - removed, e.g., rL, leaf removed
u - ultimate, e.g., Lu, ultimate leaf before transition to inflorescence formation

List of Symbols for Figs. 2.1 to 2.21

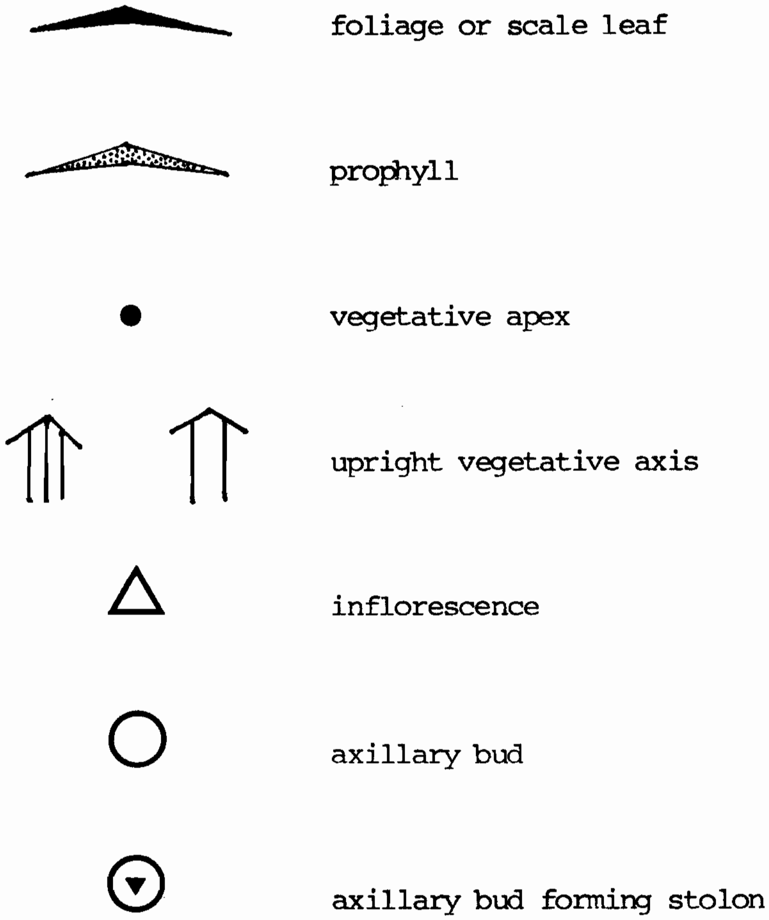


Figure 2.1 Vegetative Plant of <u>Alisma</u> <u>triviale</u>.

Figure 2.2 Seed Germination and Seedling of Alisma.

a. Seed of Alisma gramineum. x10.

b. Embryo dissected from the seed of A. gramineum. Arrowhead indicates the aperture in the cotyledonary sheath. x10.

c. Seed of Alisma triviale. x10.

d. Seed germination in A. triviale. The primary root (R) does not develop much further. Note collet of fine root hairs. x10.

e. One week old seedling of A. triviale. The first plumular leaf (L) and adventitious root (arrowhead) are evident. x5.

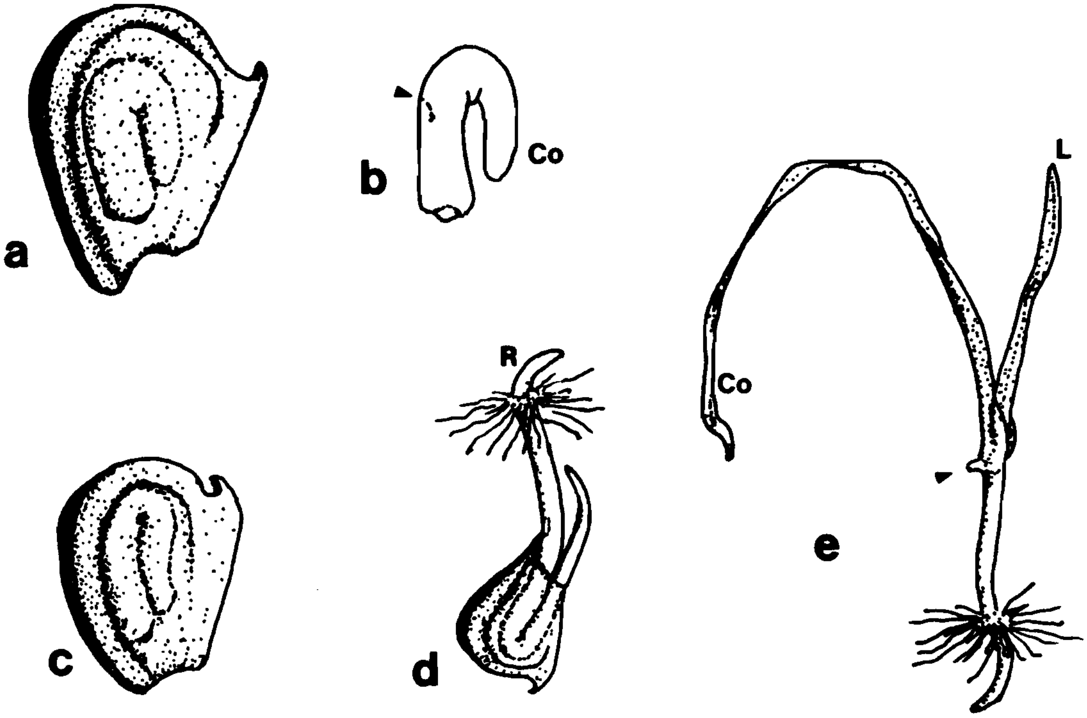

a
b
Co
L
R
Co
e
c
d

Figure 2.3 *Alisma triviale* and *Alisma gramineum*.

a. Stages of seed germination in *A. gramineum*. x3.

b. Embryo of *A. triviale*, showing aperture at the base of the cotyledon (Co). One edge of the sheath overlaps the other (arrowheads). Note the file of narrow cells. x120.

c. Embryo of *A. triviale*, with cotyledon removed. Two plumular leaves (L1 and L2) have been formed. The aperture in the cotyledonary sheath is directly behind L1. x120.

d. A stage of *A. gramineum* similar to fig. c. A portion of the sheath remains (arrowhead). Phyllotaxy is spiral. Note size difference from *A. triviale*. x120.

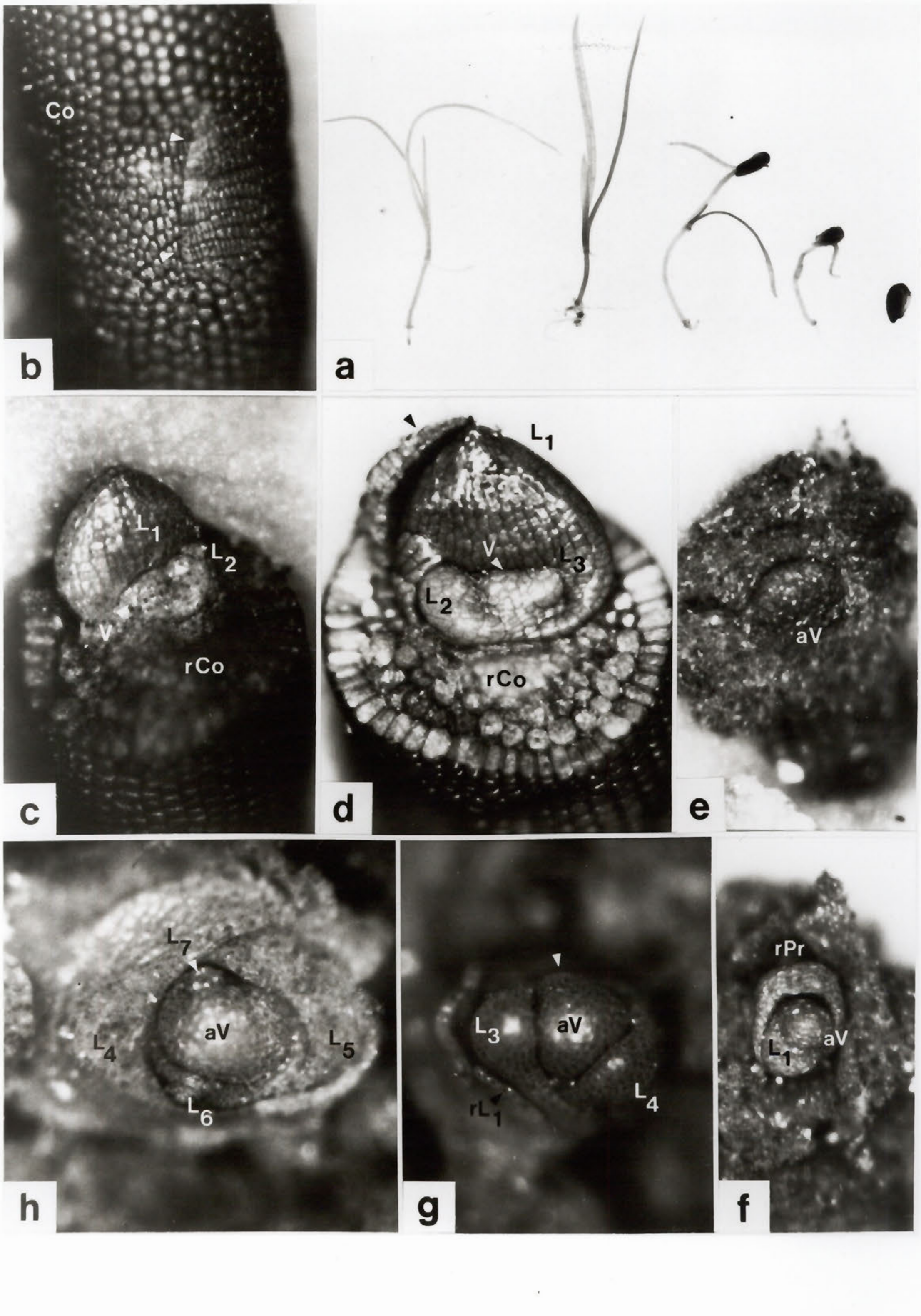
e. - h. Axillary bud development in *A. triviale*, top view. x120.

e. First visible sign of an axillary bud as a mound of meristematic tissue (aV).

f. Slightly older stage, with a prophyll (rPr) and the first leaf (L1). (L1). The genetic spiral is counterclockwise.

g. Mature axillary bud (aV) shown in the same orientation (position of prophyll at top of figure). The prophyll and first two leaves have been removed; the fifth leaf has just been initiated (arrowhead) in line with the prophyll, i.e., 2/5 phyllotaxy.

h. Precocious axillary bud of the penultimate leaf, same plant as in fig. g. A seventh leaf (L7) is visible. Note the clockwise genetic spiral.



Co
b
a
L_1
L_2
V
rCo
c
L_1
V
L_3
L_2
rCo
d
aV
e
L_7
L_4
aV
L_5
L_6
h
L_3
aV
rL_1
L_4
g
rPr
L_1
aV
f

Figure 2.4 Inflorescence Formation in *Alisma triviale*.

a. Vegetative apex showing leaf initiation (arrowhead). x120.

b. Top view of the broadening apex at the start of inflorescence formation. x120.

c. Bifurcation of the apex to form the inflorescence (I) and the continuation shoot (V) which is proximal to the ultimate leaf formed before the transition (Lu). x120.

d. Top view of a slightly later stage than fig. c. The prophyll (Pr) is distinct as a ridge between the two apices. x120.

e. View from the side of the ultimate leaf (Lu) shows the development of the size difference between inflorescence (I) and the continuation growth (V). x120.

f. Top view of a still later stage. The first leaf of the continuation growth (L1) has been initiated. Bracts (Br) subtending lateral inflorescence branches are being initiated. The first bract is always farthest from the continuation growth while the second and third (not yet visible here) are proximal, opposite the first and second foliage leaves on the continuation shoot. x120.

g. Side view of the same stage as fig. f. The prophyll (Pr) does not surround either apex. x120.

h. An older stage. Inflorescence branches (I') are forming rapidly. Arrowheads indicate the edges of the prophyll (Pr) which now begin to surround the continuation growth (V). x120.

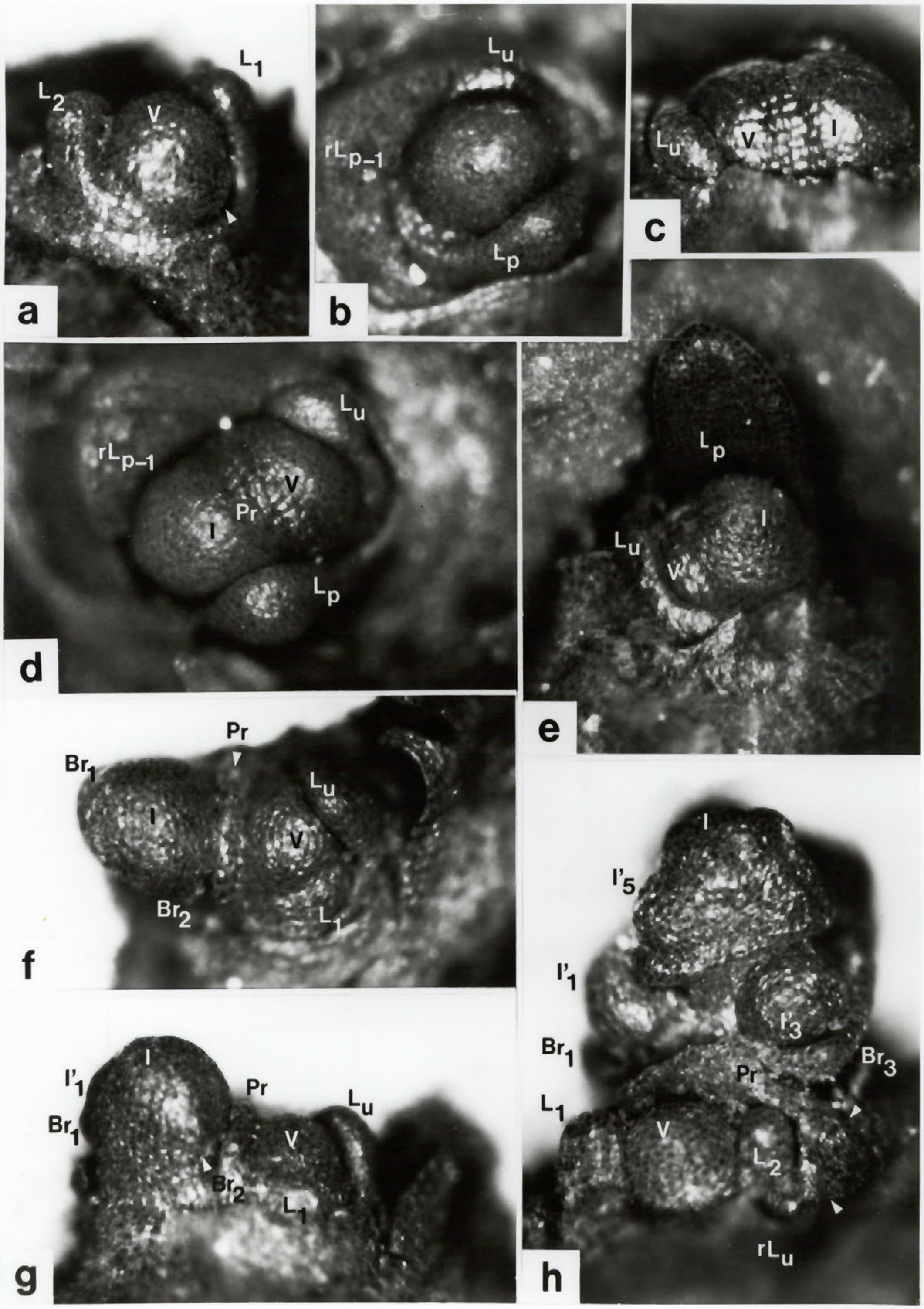

L1
L2
V
a
Lu
rLp-1
Lp
b
Lu
V
I
c
Lu
rLp-1
V
Pr
I
Lp
d
Lp
I
Lu
V
e
Pr
Br1
I
Lu
V
Br2
L1
f
I
I'1
Pr
Lu
Br1
V
Br2
L1
g
I
I'5
I'1
I'3
Br1
Pr
Br3
L1
V
L2
rLu
h

Figure 2.5 Camera Lucida Drawings of Sections through *Alisma triviale* and *A. gramineum*.

a. Cross section through an embryo of *A. gramineum* similar to the stage shown in Fig. 2.3d. Note structure of the cotyledonary sheath (arrowhead) and spiral phyllotaxy. x112.

b. Outline of the same stage in *A. triviale*. x112.

c. Longitudinal section through a vegetative apex of *A. triviale*. Arrowhead indicates leaf initiation. This is comparable to the stage in Fig. 2.4a. x112.

d. Outline of a cross section through the shoot apex of *A. triviale*. The penultimate leaf (Lp) subtends both continuation shoot (V) and inflorescence (I). x66.

e. Longitudinal section through the apex of *A. triviale* after inflorescence formation has begun (as in Fig. 2.4c). x112.

f. Longitudinal section of a slightly older stage, through both the inflorescence (I) and the continuation growth (V). x112.

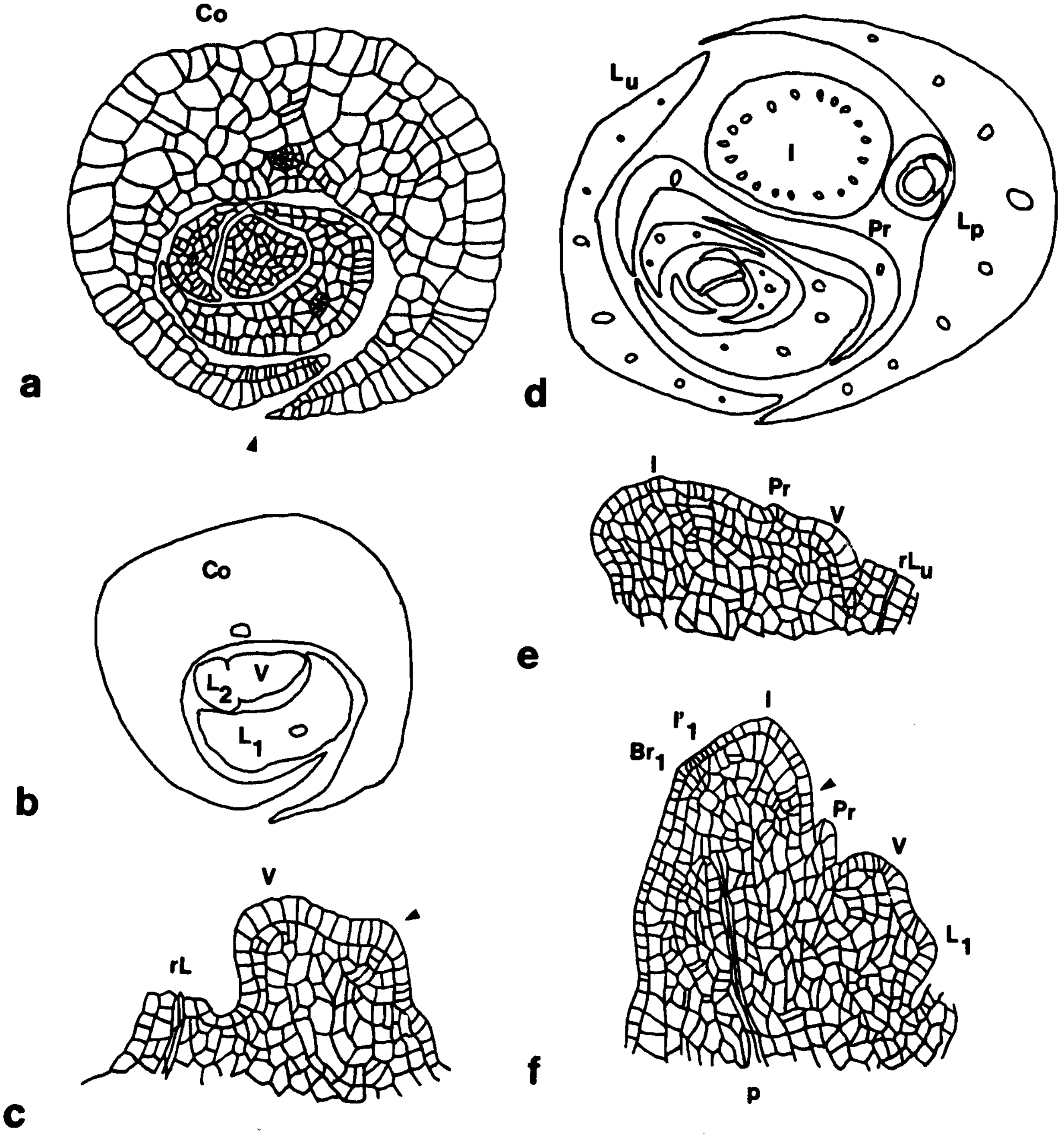

Co
a
Lu
I
Pr
Lp
d
Co
L2
V
L1
b
I
Pr
V
rLu
e
V
rL
c
I
I'1
Br1
Pr
V
L1
f
p

Figure 2.6 Sagittaria latifolia.

a. Vegetative plant. x0.4.

b. Stolon beginning to develop into a new upright axis. x0.4.

c. Germination of overwintering corm. Arrowhead indicates the base of the new plant. x0.4.


c
a
b

Figure 2.7 Stages in the Development of Sagittaria latifolia.

a. Side view of a vegetative apex with three foliage leaves. Lateral meristems (arrowheads) resulting in the characteristic leaf shape have developed on the oldest leaf (L1). x120.

b. Same stage as the above, with the eldest leaf shown removed to show the initiation of a new leaf (L4). The leaf bases develop rapidly and overlap (arrowhead). x120.

c. Side view of an apex at the start of inflorescence formation. x120.

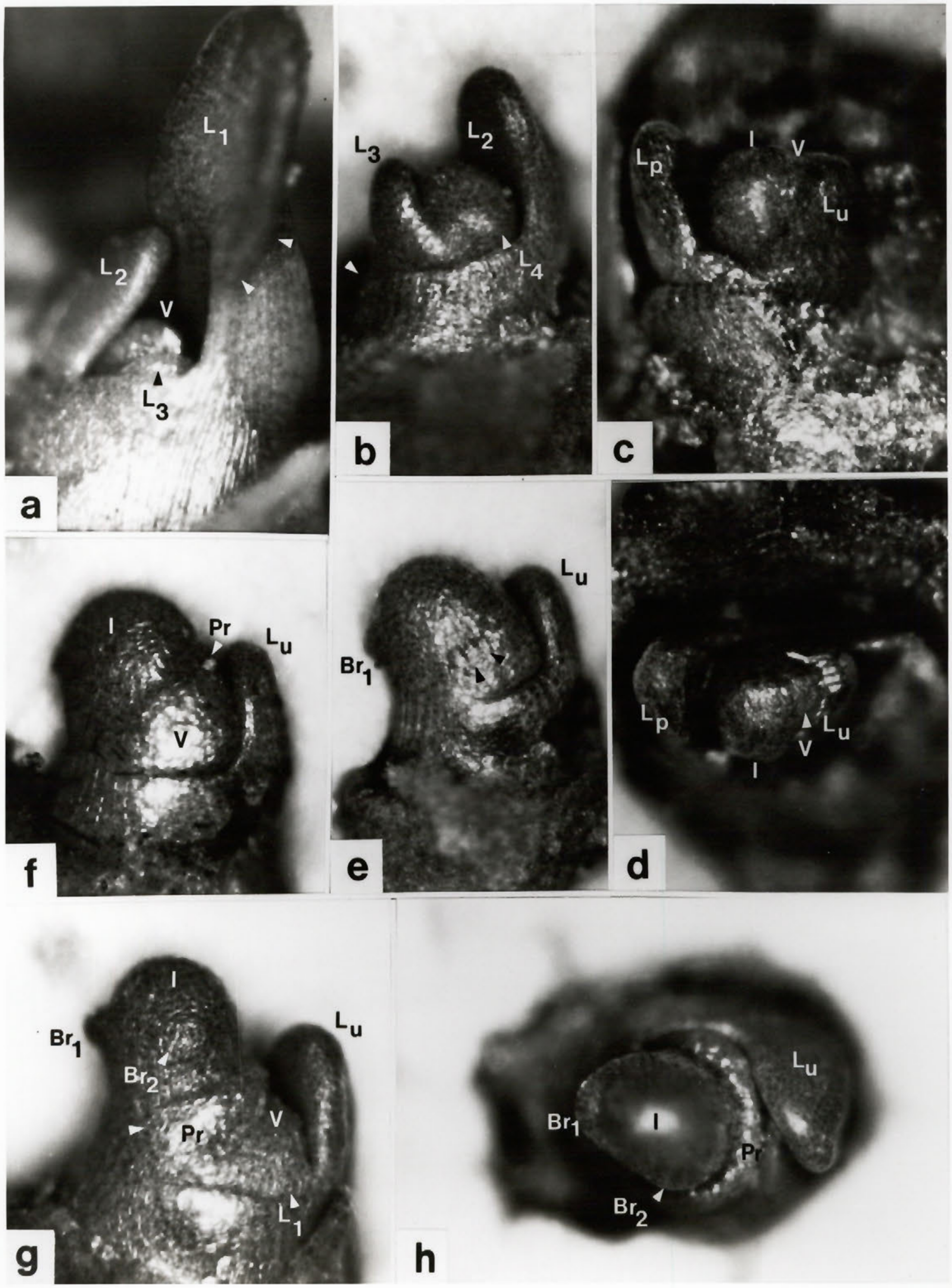
d. Top view of the same stage. The inflorescence (I) portion is much larger than that of the continuation growth (V). x120.

e. Side view of the beginning of prophyll formation (arrowheads). The first floral bract (Br1) has been formed on the far side. x120.

f. Slightly older stage than fig. e. The prophyll (Pr), more prominent, is oblique in relation to the vertical. x120.

g. Side view of yet older stage. The prophyll (Pr) begins to enfold the base of the inflorescence (arrowhead). x120.

h. Top view of a similar stage showing the sequence of floral bract initiation. The prophyll clearly surrounds the base of the inflorescence. x120.



a
L_1
L_2
V
L_3
b
L_3
L_2
L_4
c
L_p
I
V
L_u
f
I
Pr
L_u
V
e
L_u
Br_1
d
L_p
L_u
V
I
g
I
Br_1
L_u
Br_2
Pr
V
L_1
h
L_u
Br_1
I
Pr
Br_2

Figure 2.8 Stages in the Development of Sagittaria latifolia (cont'd).

a. Side view of a young inflorescence (I) and continuation growth (V). The edges of the prophyll (arrowheads) are beginning to grow around the latter. x120.

b. Side view of an older stage where three leaves have initiated on the continuation shoot. The prophyll (Pr) now clearly envelops the latter. The taller inflorescence tends to "lean" over the shoot. x120.

c. View of the same stage from the side of the continuation shoot. Arrowhead indicates the formation of the first bract of the second pseudowhorl. x120.

d. Youngest visible axillary bud seen in top view. x120.

e. Side view of a young axillary bud where the formation of an adaxial prophyll (Pr) has just begun. x120.

f. Slightly older stage than fig. e. The apex becomes more rounded in shape (see also fig. d) as it becomes distinct from the prophyll. x120.

g. Side view showing the initiation of the first scale leaf on the abaxial side of the axillary bud. x120.

h. Top view of an axillary bud, with the prophyll (Pr) and three scale leaves (S1, S2 and S3) arranged spirally. x120.

i. Side view of the apex of a stolon. Compared with the main apex, the leaves are smaller and the internodes better developed. x120.

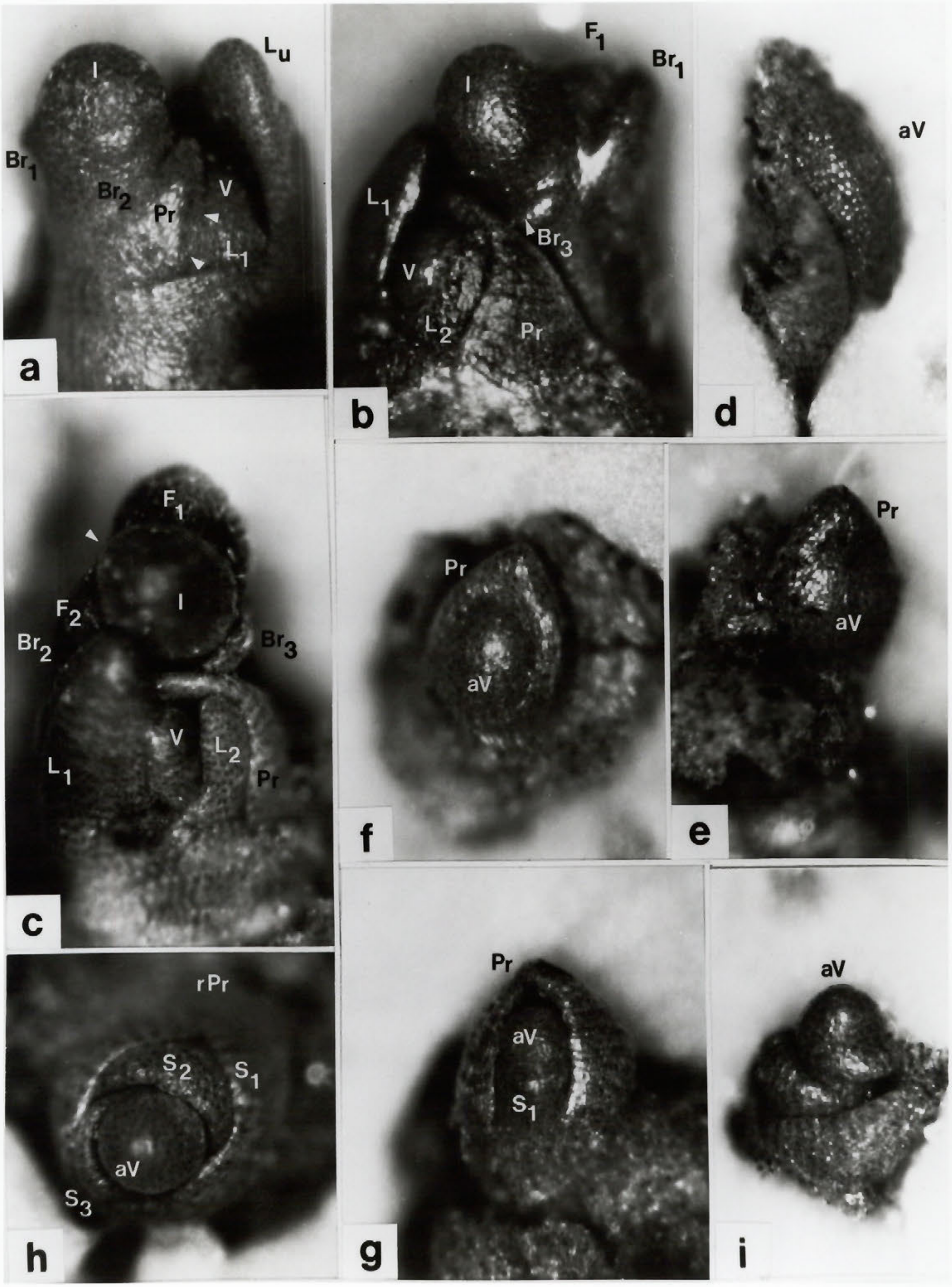

I
L_u
Br_1
Br_2
Pr
V
L_1
a
F_1
Br_1
I
L_1
Br_3
V
L_2
Pr
b
aV
d
F_1
F_2
I
Br_2
Br_3
V
L_2
L_1
Pr
c
Pr
aV
f
Pr
aV
e
rPr
S_2
S_1
aV
S_3
h
Pr
aV
S_1
g
aV
i

Figure 2.9 Camera Lucida Drawings of Sections through Sagittaria latifolia.

a. Longitudinal section through a vegetative apex. There is a single tunica layer. Leaf initiation indicated by the arrowhead. x180.

b. Longitudinal section through the stage shown in Fig. 2.7e. Prophyll initiation is indicated by the arrowhead. No distinct shell zone is found, and the tunica remains continuous over both centres of growth. x180.

c. Longitudinal section through an older stage where a floral primordium (Fl) is developing. Arrowhead indicates the prophyll. This is slightly younger than the stage in Figs. 2.8b and 2.8c. x180.

d. Cross section through a stage comparable to Fig. 2.8c. The two-keeled prophyll enfolds the bases of both inflorescence and continuation shoot. x180.

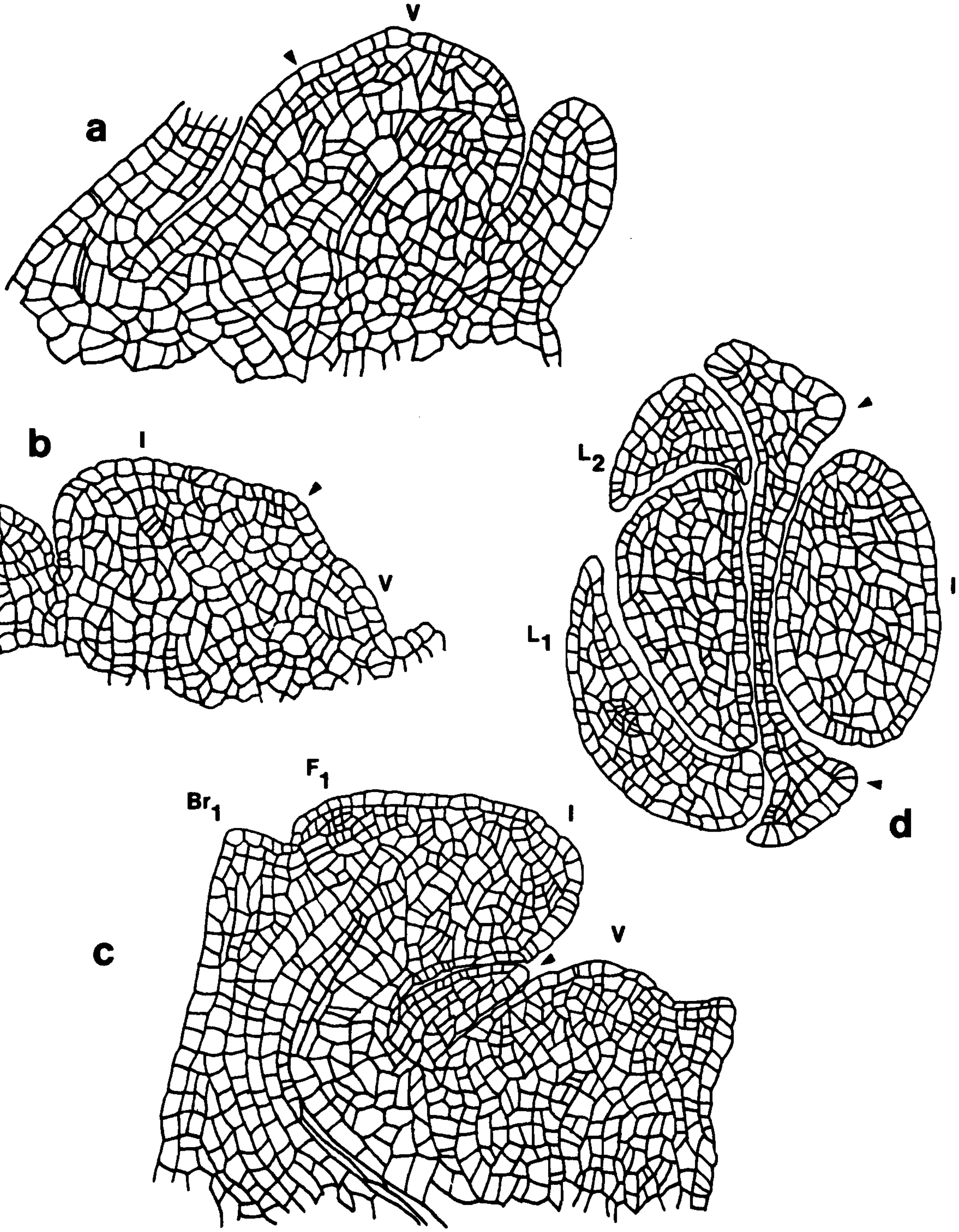

v
a
b
I
v
L2
L1
I
d
F1
Br1
I
c
v

Figure 2.10 Camera Lucida Drawings of Sections through _Sagittaria latifolia_ (cont'd).

a. Longitudinal section through the axillary bud (aV) and its prophyll (Pr) shown in Fig. 2.8e. x180.

b. Longitudinal section through an older axillary bud. Note leaf initiation by periclinal divisions beneath the single tunica layer (arrowhead). Intravaginal scales (IS) are also shown. x180.

c. Longitudinal section through a young stolon that has just penetrated the base of its subtending leaf. Procambial development (pr) and elongation of internodes by intercalary growth (arrowheads) are evident. x180.

d. Outline of the cross section through a shoot tip showing its organization. x66.

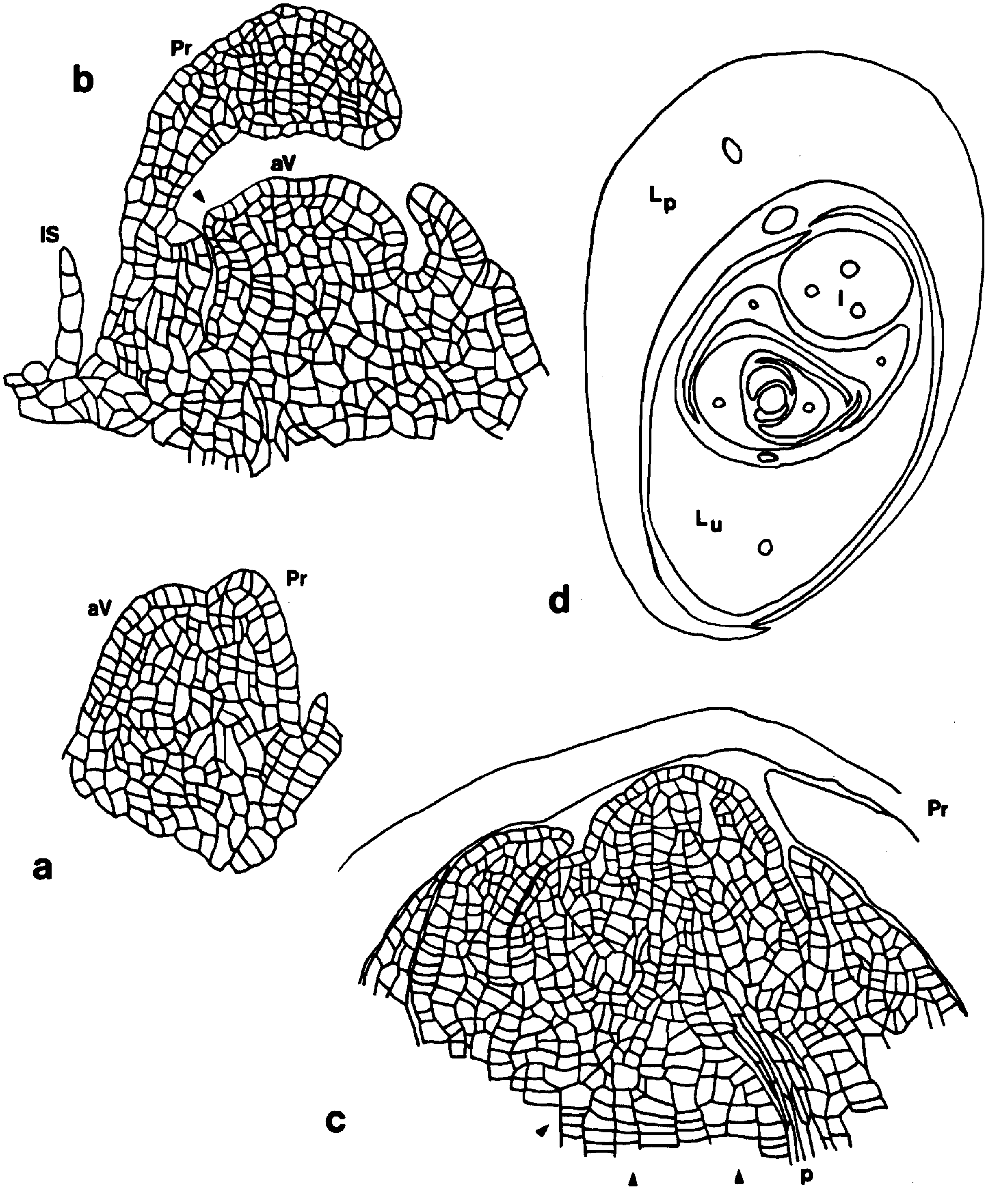

b
Pr
aV
IS
aV
Pr
a
Lp
l
Lu
d
Pr
c
p

Figure 2.11 _Sagittaria_ _cuneata_.

a. Vegetative plant showing linear, immersed leaves and sagittate floating and aerial ones. An overwintering corm is developing from a stolon (arrowhead). x1.

b. Corm germination. Arrowhead indicates the base of the plant formed some distance above it. x2.

c. Mature seed. x15.

d. Embryo dissected from the seed, showing the characteristic incumbent cotyledon (Co) and aperture in the cotyledonary sheath. x15.

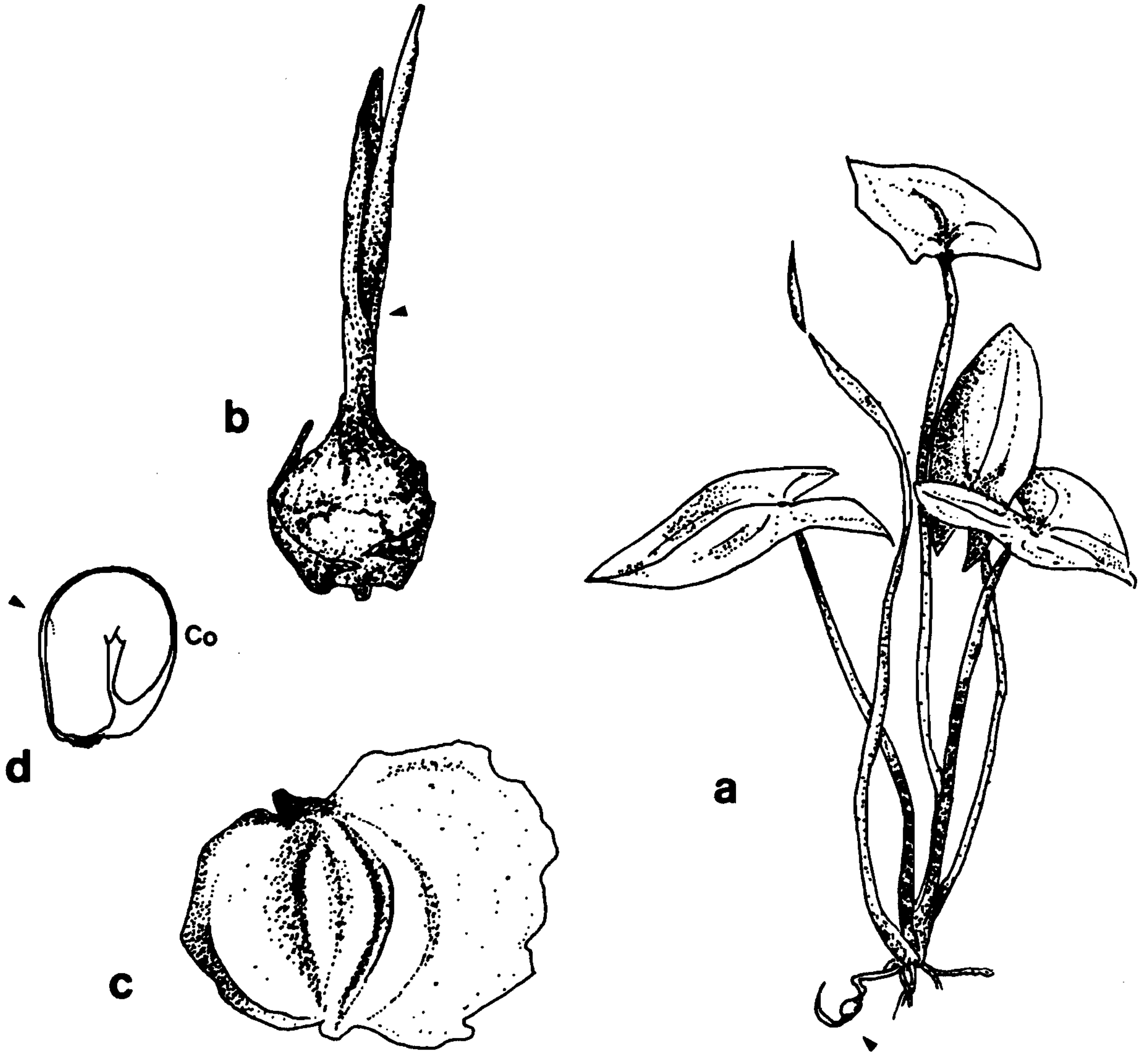

b
d
Co
a
c

Figure 2.12 Development in Sagittaria cuneata.

a. Embryo dissected from mature seed, showing the aperture in the cotyledon (arrowheads) associated with narrow files of cells. x120.

b. Apex (V) of the stage in the stage in fig. a. with the first two leaves (L1 and L2). Note spiral phyllotaxy. x120.

c. Top view of the vegetative apex of a mature plant. Phyllotaxy is spiral. x120.

d. Top view of the youngest stage of axillary bud found. An adaxial prophyll (Pr) is distinguishable. x120.

e. Side view of an older stage than fig. d. x120.

f. Side view of an axillary bud with the formation of the first scale leaf (S1) on the abaxial side. x120.

g. Side view of a stolon apex. x120.

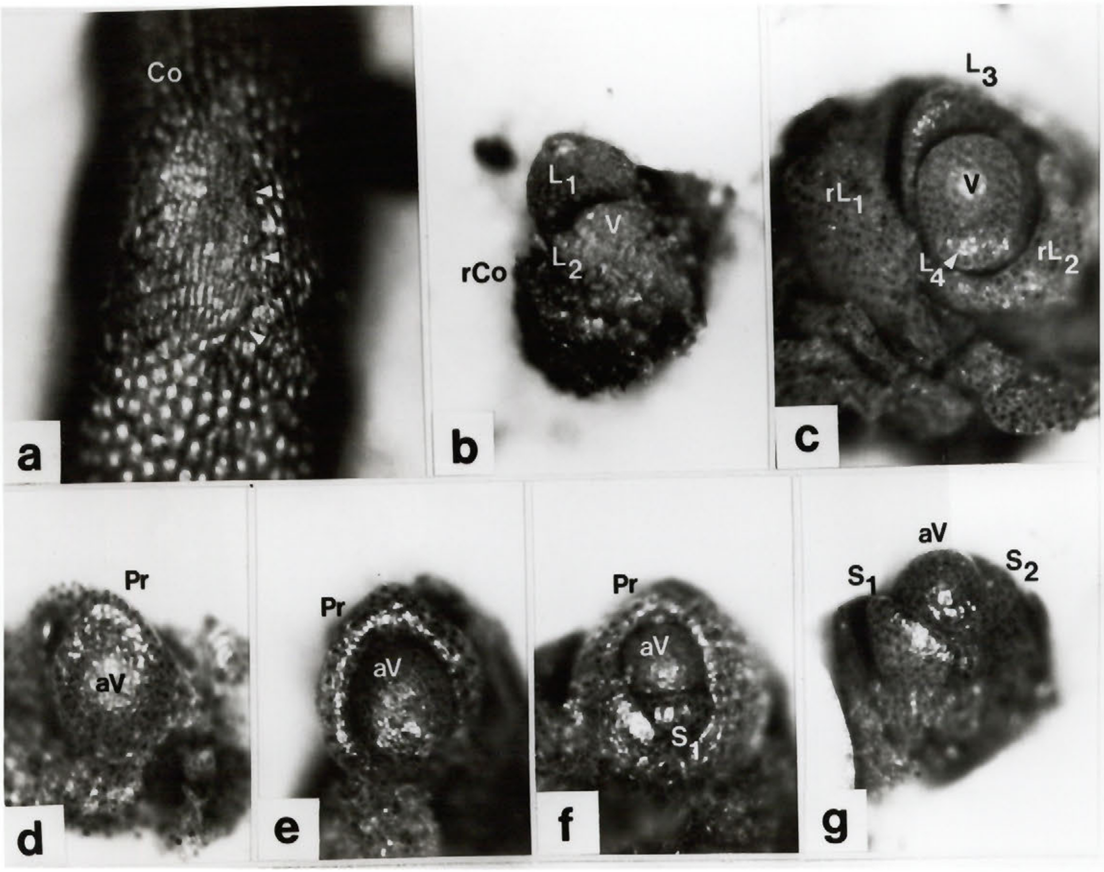

Co
a
L_1
V
rCo
L_2
b
L_3
rL_1
V
L_4
rL_2
c
Pr
aV
d
Pr
aV
e
Pr
aV
S_1
f
aV
S_1
S_2
g

Figure 2.13 Inflorescence Formation in Sagittaria cuneata.

a. Side view of a vegetative apex just after leaf initiation (arrowhead). x120.

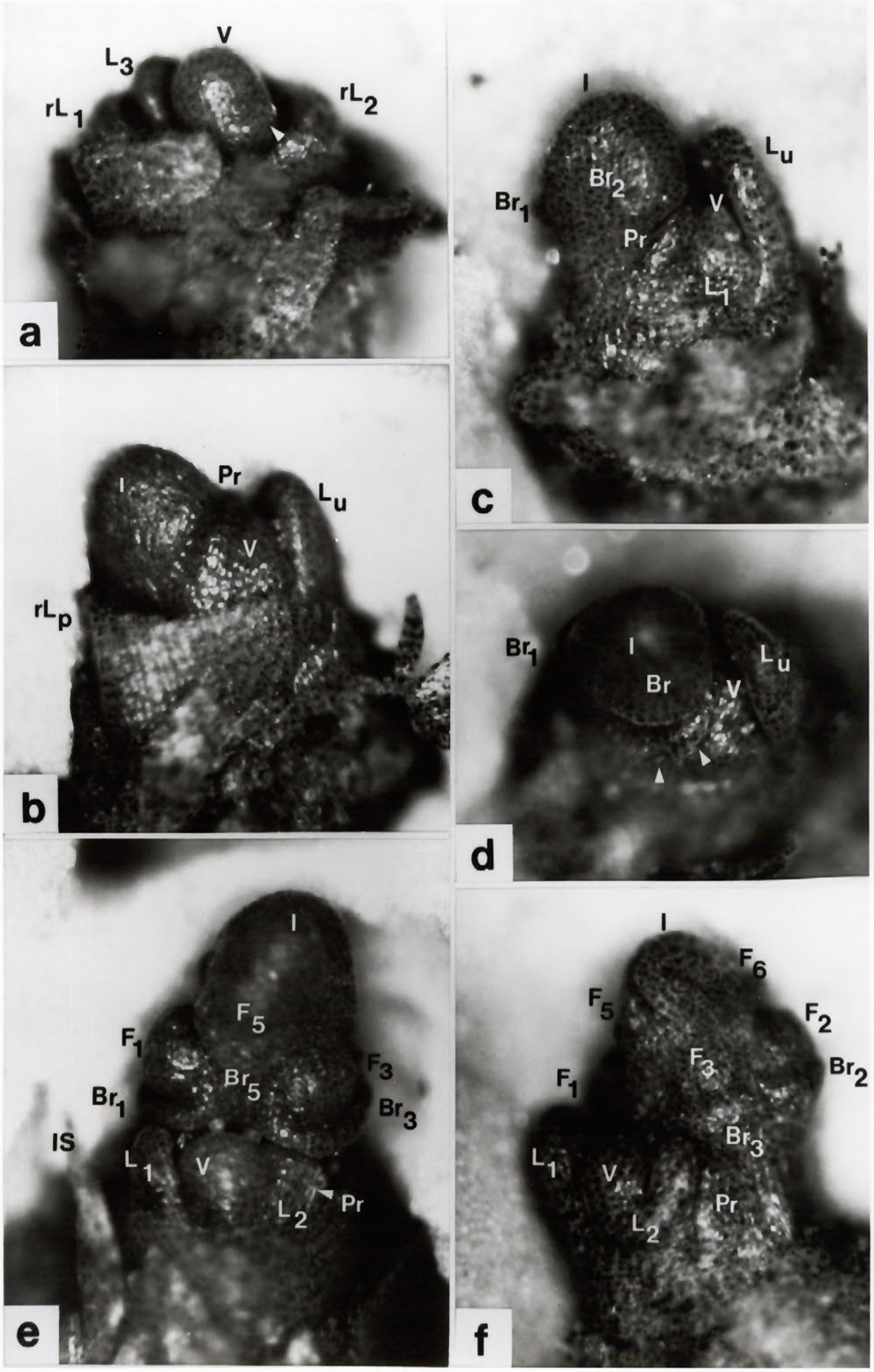
b. Side view of a young inflorescence (I) and continuation growth (V). The inflorescence is distal to the ultimate leaf formed before transition (Lu). x120.

c. Side view of a later stage where the first foliage leaf of the continuation growth (L1) has been formed. x120.

d. Top view of the same stage as fig. c, showing the sequence of bract and flower initiation. The prophyll (arrowheads) surrounds the base of the inflorescence rather than that of the continuation growth. x120.

e. Side view of a later stage where the second foliage leaf of the continuation shoot is formed. Note the presence of intravaginal scales (IS). x120.

f. Stage similar to the one in fig. e, side view. The inflorescence is slightly more differentiated and the edges of the prophyll are beginning to enfold the continuation shoot. x120.



a
V
L3
rL1
rL2
b
I
Pr
Lu
V
rLp
c
I
Lu
Br2
Br1
V
Pr
L1
d
Br1
I
Lu
Br
V
e
I
F5
F1
Br5
F3
Br1
Br3
IS
L1
V
L2
Pr
f
I
F6
F5
F2
F3
Br2
F1
Br3
L1
V
L2
Pr

Figure 2.14 Camera Lucida Drawings of Sections through Sagittaria cuneata.

a. Cross section through the embryo showing its spiral phyllotaxy. x180.

b. Longitudinal section of the vegetative apex in Fig. 2.13a. There is one tunica layer. Leaf initiation is indicated by the arrowhead. x180.

c. Longitudinal section of a young axillary bud with an adaxial prophyll (Pr). x180.

d. Longitudinal section through an older axillary bud. Scale leaf initiation is occurring on the flank of the apex above the first scale leaf (S1). x180.

e. Longitudinal section of the stolon apex shown in Fig. 2.13g. x180.

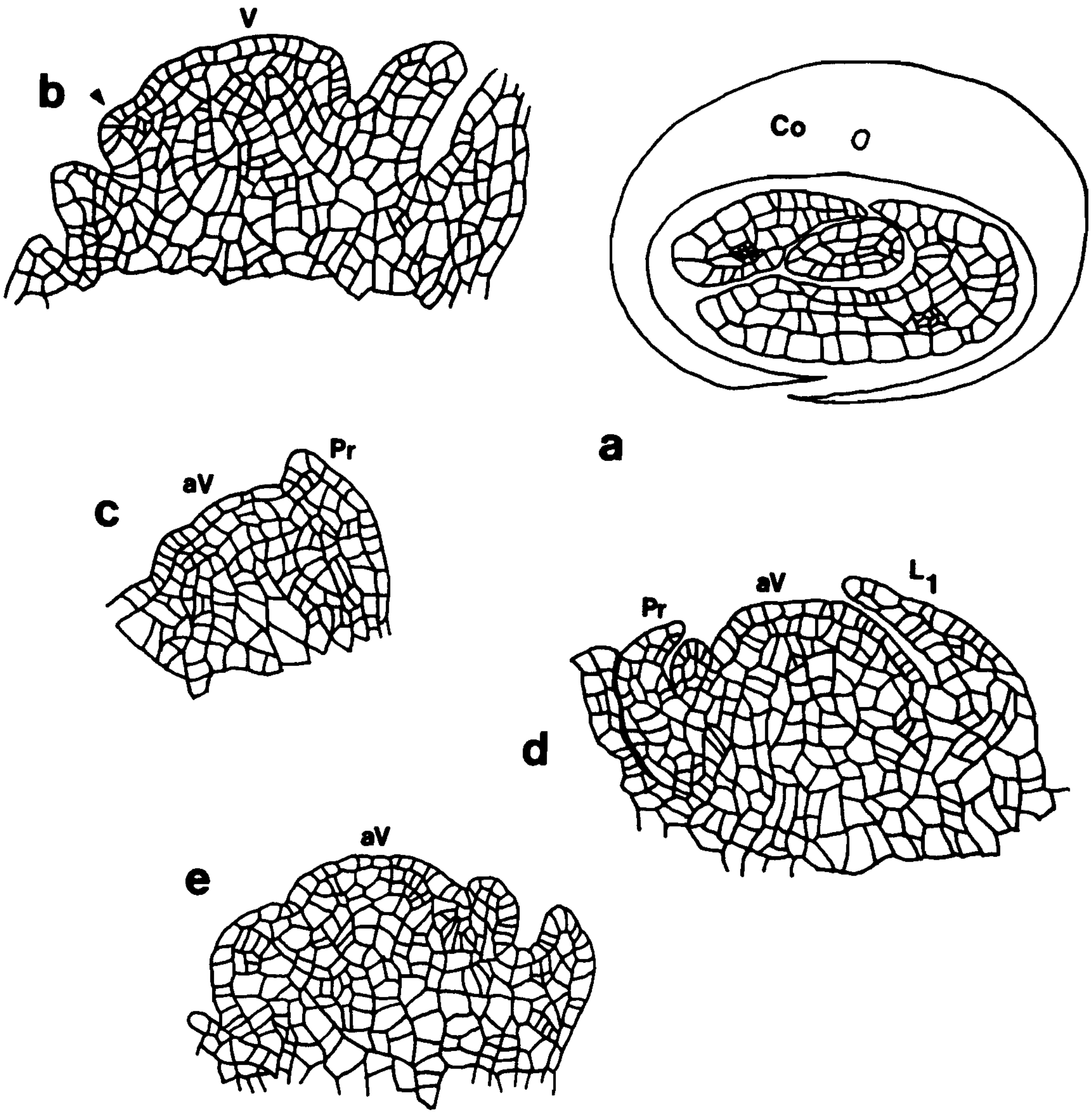

V
b
Co
a
Pr
aV
c
Pr
aV
L1
d
aV
e

Figure 2.15 Camera Lucida Drawings of Sections through *Sagittaria cuneata* (cont'd).

a. Longitudinal section through an apex that has just undergone bifurcation. Initiation of the prophyll is occurring (arrowhead). A shell zone may be discerned between the young inflorescence (I) and the continuation growth (V). x180.

b. Longitudinal section of the stage shown in Fig 2.13e. The prophyll is indicated by the arrowhead. Procambial differentiation has begun. x180.

c. Cross section through a stage similar to the one in Fig. 2.13d showing the edges of the two-keeled prophyll around the inflorescence base and the continuation shoot. x180.

d. Outline of the cross section through the shoot apex of a plant showing its organization. All leaves except the prophyll subtend an axillary bud, and three foliage leaves are found between successive inflorescences. x66.

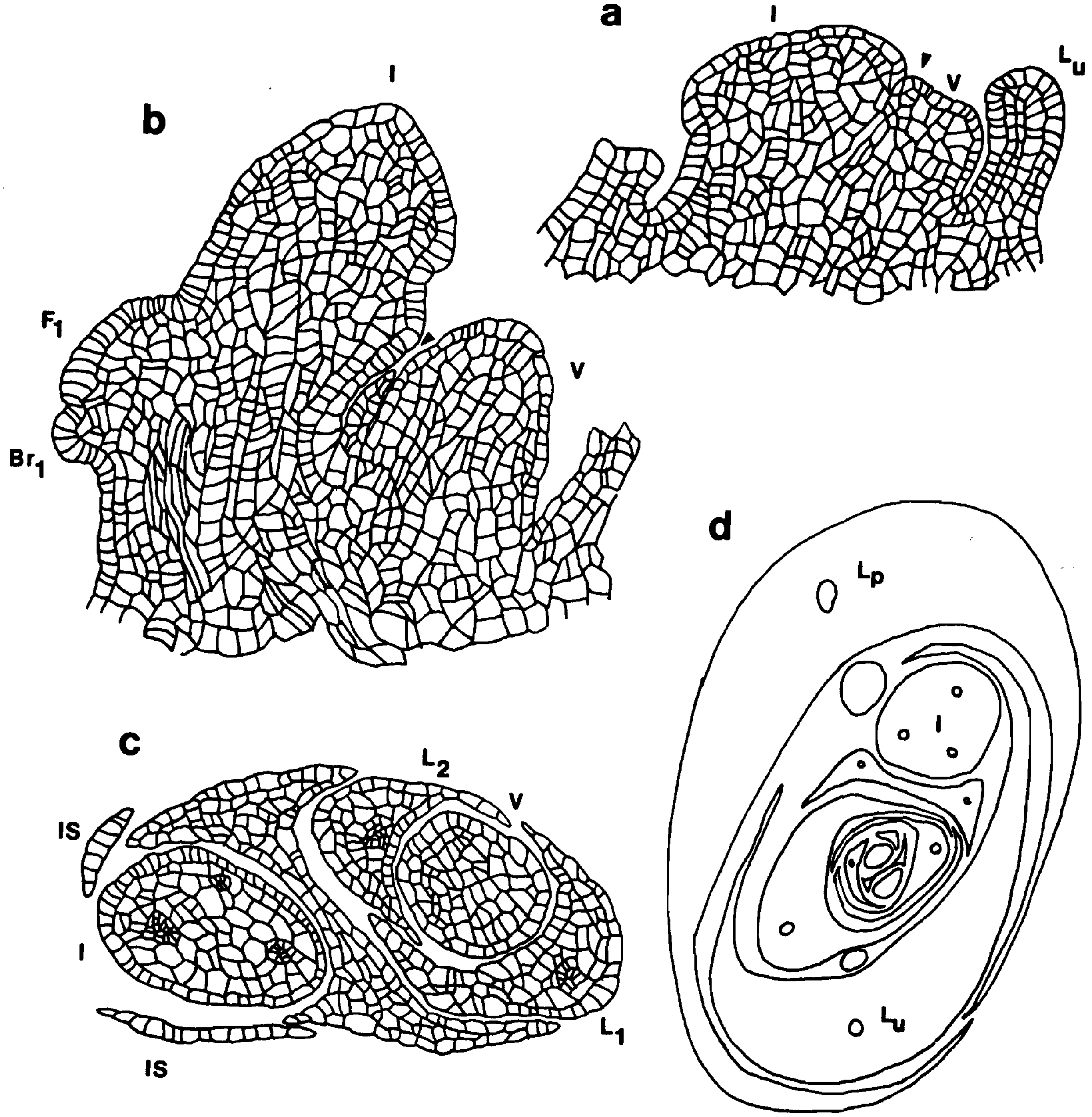

a
I
V
L_u
b
I
F_1
Br_1
V
c
L_2
V
IS
I
L_1
IS
d
L_p
I
L_u

Figure 2.16 Vegetative plants of Sagittaria "Sinensis".

Three upright axes are linked by stolons. The prophyll of the third stolon segment (arrowhead) has not yet disintegrated. A fourth plant is developing to the right of the youngest plant (arrowhead). x1.

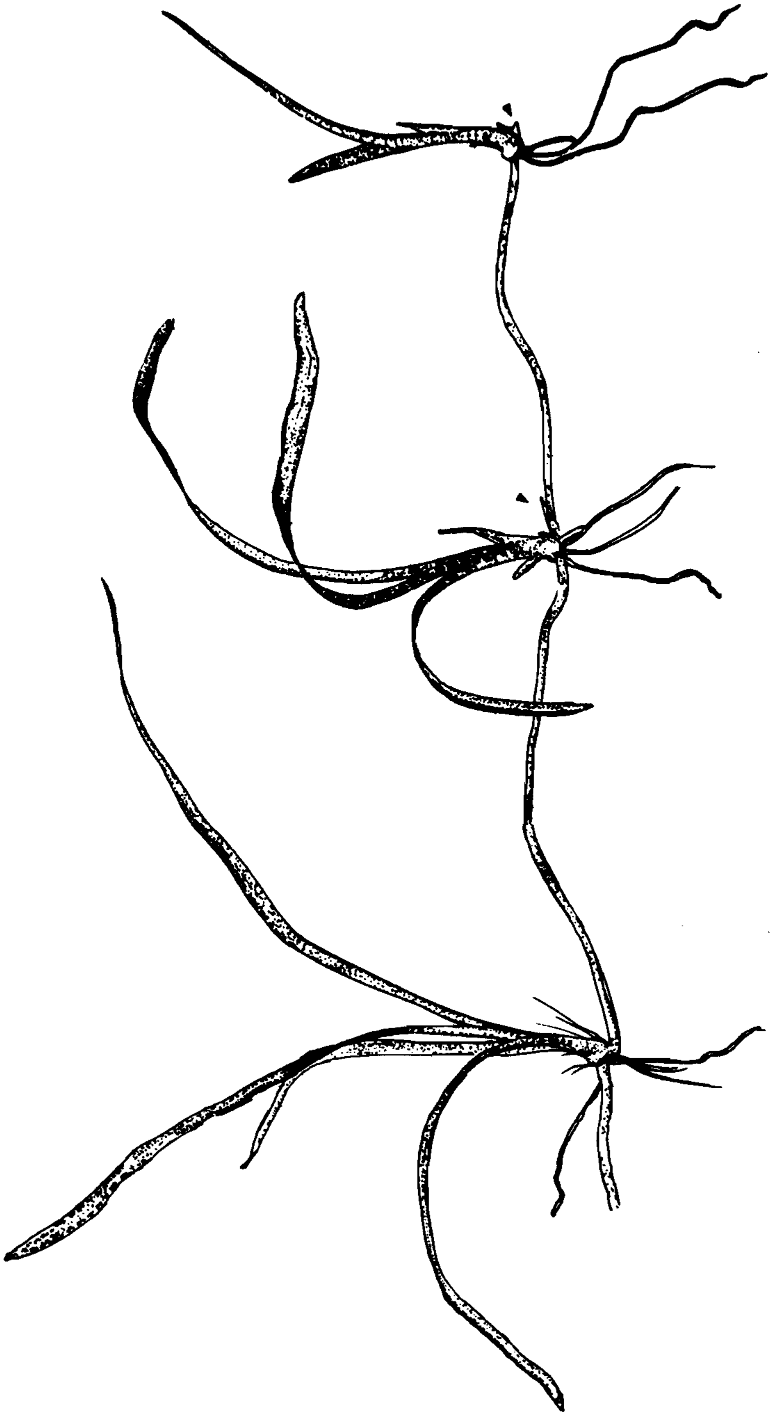


Figure 2.17 Sagittaria subulata.

a. Terminal plant of a stolon system. The three scale leaves have been removed, showing adventitious roots (R) initiating and the presence of a precocious axillary bud (arrowhead) in the axil of the third scale leaf. x5.

b. Shoot apex showing the typical organization of inflorescence (I) and continuation growth (V) surrounded by a membranous prophyll (arrowheads). x2.

c. Side view of a slightly later stage than fig.a. A new stolon segment (St) has just penetrated the scale leaves. x5.

d. View of the same stage from the other side. The scale leaves have been removed to show the differential growth of internodes resulting in the upright orientation of the daughter plant. x5.

e. Oblique top view of the same stage, with most of the foliage leaves removed. Note relative size and orientation of the upright axis and the new stolon segment (St). x5.

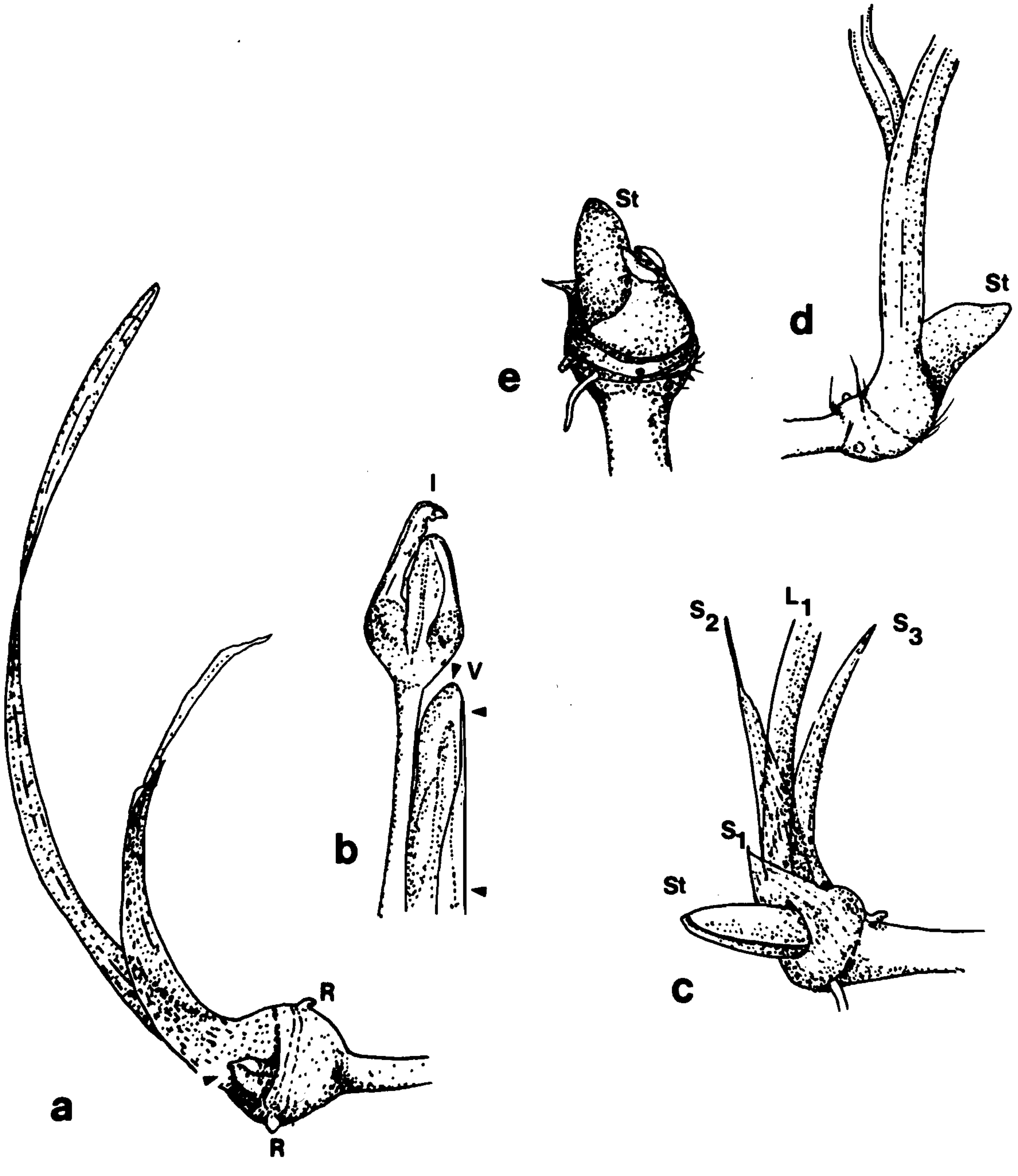

St
e
d
St
I
V
b
S2
L1
S3
S1
St
c
R
a
R

Figure 2.18 Development of Stolon Segments.

a. - e. Sagittaria subulata.

a. Side view of the precocious lateral bud in the axil of the third scale leaf. The first scale leaf (S1) is opposite the adaxial prophyll (Pr). x120.

b. Top view of an older stage where all three scale leaves have been formed. The prophyll is removed to show the arrangement of scale leaves. x120.

c. Side view of a stage slightly older than the one in fig. b. Note internodal elongation, between the prophyll (removed) and the first scale leaf (S1), indicated by arrowheads. A foliage leaf (L1) has been formed. x120.

d. Side view of a stage where two foliage leaves have been formed. No axillary bud is yet distinguishable in the axil (arrowhead) of the third scale leaf (rS3). x120.

e. Side view of a later stage with three visible leaf primordia. The axillary bud that will form the new stolon is now apparent (arrowheads). x120.

f. A later stage in Sagittaria "Sinensis". An adaxial prophyll (Pr) has been formed on the precocious axillary bud. Note the large size of the bud relative to its parent axis. x120.

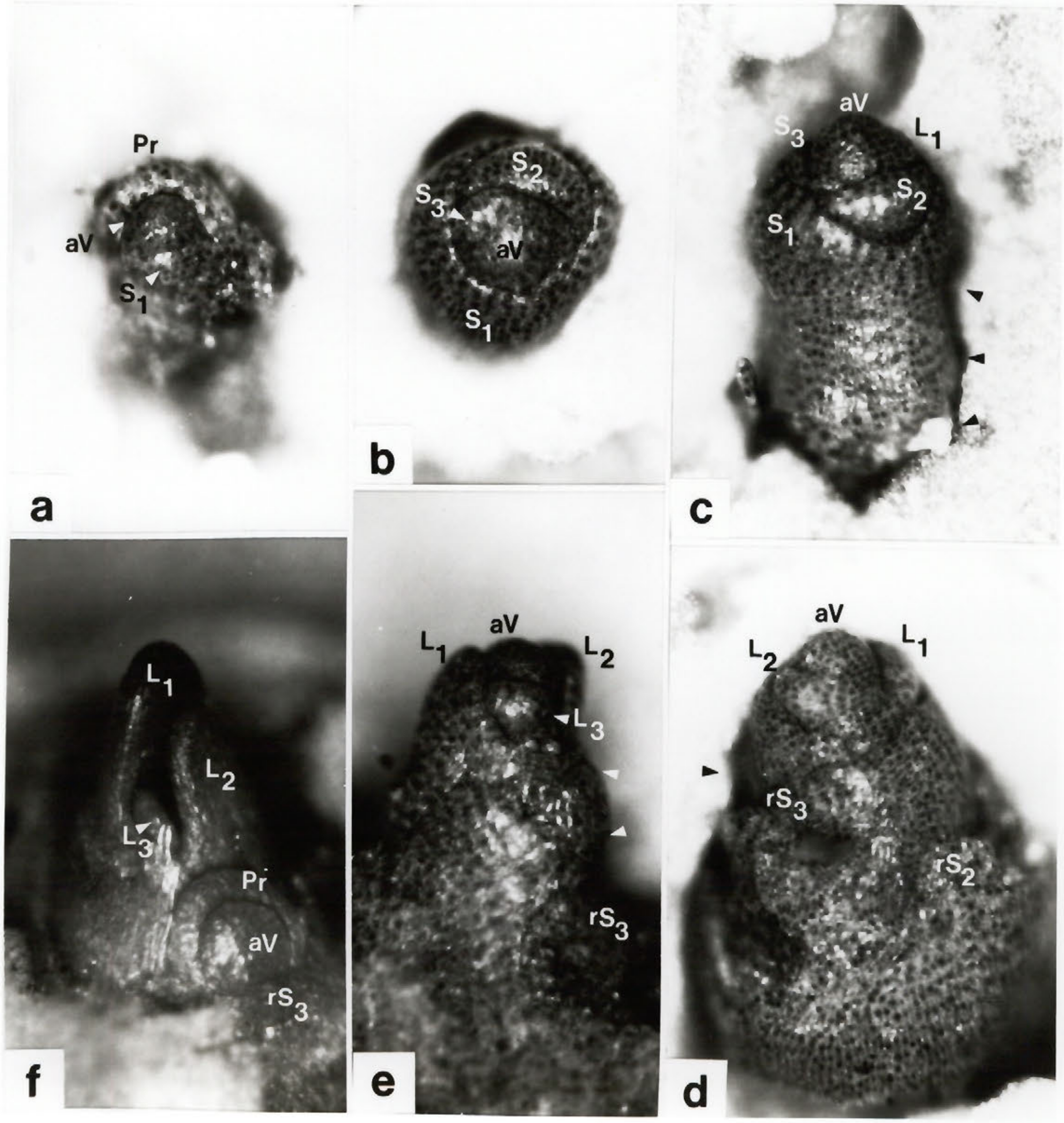

Pr
aV
S1
a
S2
S3
aV
S1
b
aV
S3
L1
S2
S1
c
L1
L2
L3
Pr
aV
rS3
f
L1
aV
L2
L3
rS3
e
aV
L2
L1
rS3
rS2
d

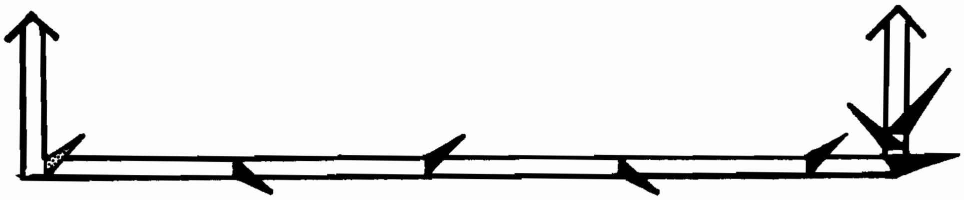
Figure 2.19 Schematic Diagram Showing Stolon and Pseudostolon Systems and Their Relationships.

a. Stolon of Sagittaria latifolia and S. cuneata. A single long segment is found. It has four to six scale leaves, with internodes of about equal length, before vertical growth occurs. The upright axis produces several scale leaves before foliage leaf formation.

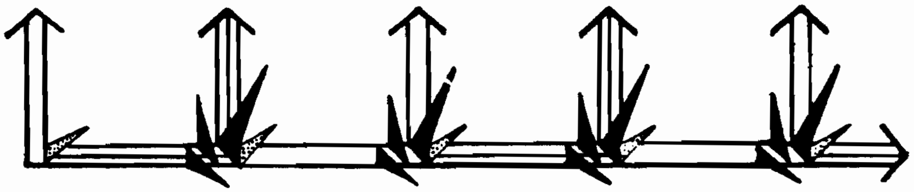
b. Stolon system found in Sagittaria subulata, S. "Sinensis" and S. "microphylla". Each segment is formed by the elongation of the internode between prophyll and first scale leaf only. Two more scale leaves are formed before foliage leaf production. A precocious lateral bud in the axil of the last scale leaf repeats the pattern to form the next segment, i.e., a sympodial organization.

c. Pseudostolon found in Echinodorus tenellus (Charlton, 1968). The inflorescence produced by apical bifurcation grows out horizontally, forming pseudowhorls of three scale leaves. Upright vegetative axes are developed from buds in the axils of these leaves, i.e., a monopodial organization.

a



b



c

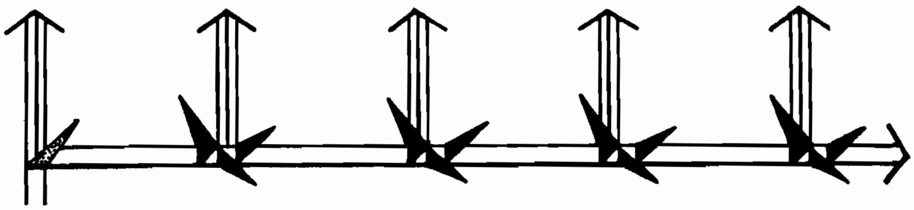


Figure 2.20 Diagrammatic Representation of the Organization of *Alisma triviale*, plan view. The genetic spiral is counter-clockwise. Only two inflorescences are shown.

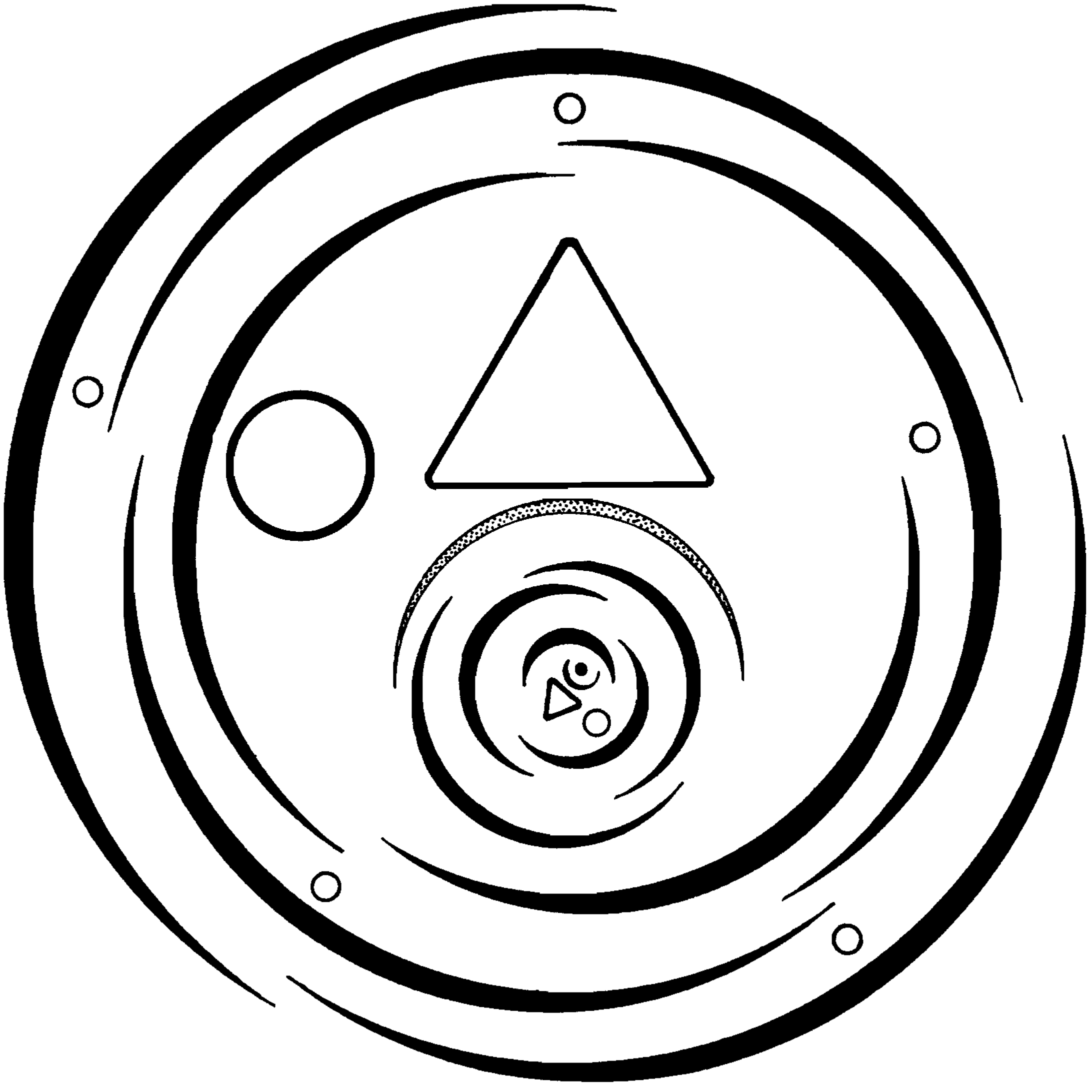
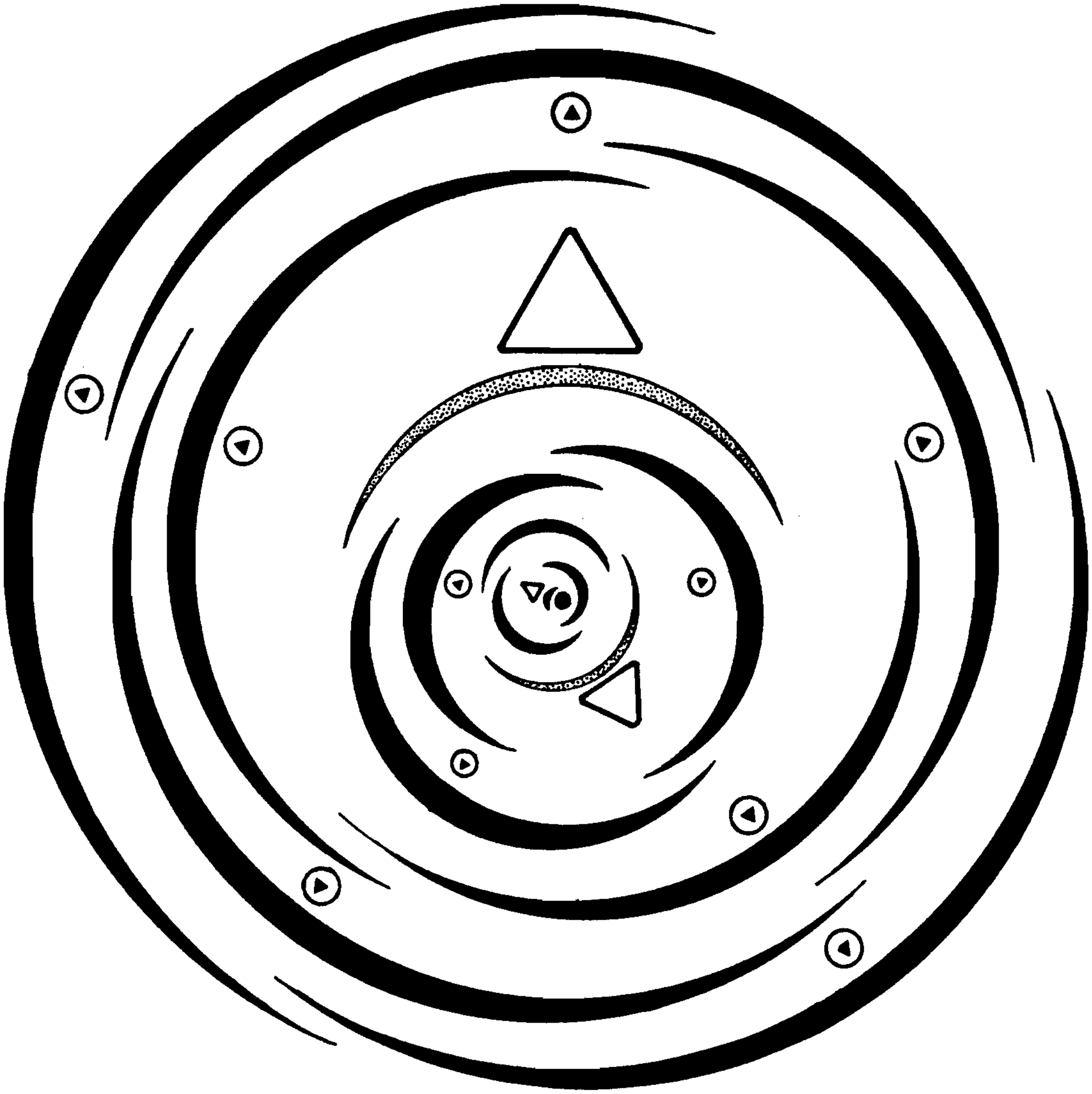


Figure 2.21 Diagrammatic Representation of the Organization of Sagittaria latifolia and S. cuneata, plan view. The genetic spiral is counterclockwise. Three inflorescences are shown.



List of Abbreviations for Figs. 2.22 to 2.34

A - anterior
Br - bract or its primordium
Co - cotyledon
F - flower or its primordium
I - inflorescence or reproductive apex
IS - intravaginal scales (multiseriate hairs)
L - foliage leaf or its primordium
P - posterior
Pr - prophyll or its primordium
R - adventitious root or its primordium
V - vegetative apex

a - axillary, e.g., aV, apex of axillary shoot
p - penultimate, e.g., Lp, penultimate leaf before transition to inflorescence formation
r - removed, e.g., rL, leaf removed
u - ultimate, e.g., Lu, ultimate leaf before transition to inflorescence formation

List of Symbols for Figs. 2.22 to 2.34

⌃	foliage or scale leaf
⊓	prophyll of axillary bud
●	vegetative apex
△	inflorescence
◇	axillary bud

Figure 2.22 Diagrammatic Representation of the Shoot System of *Sagittaria lancifolia*.

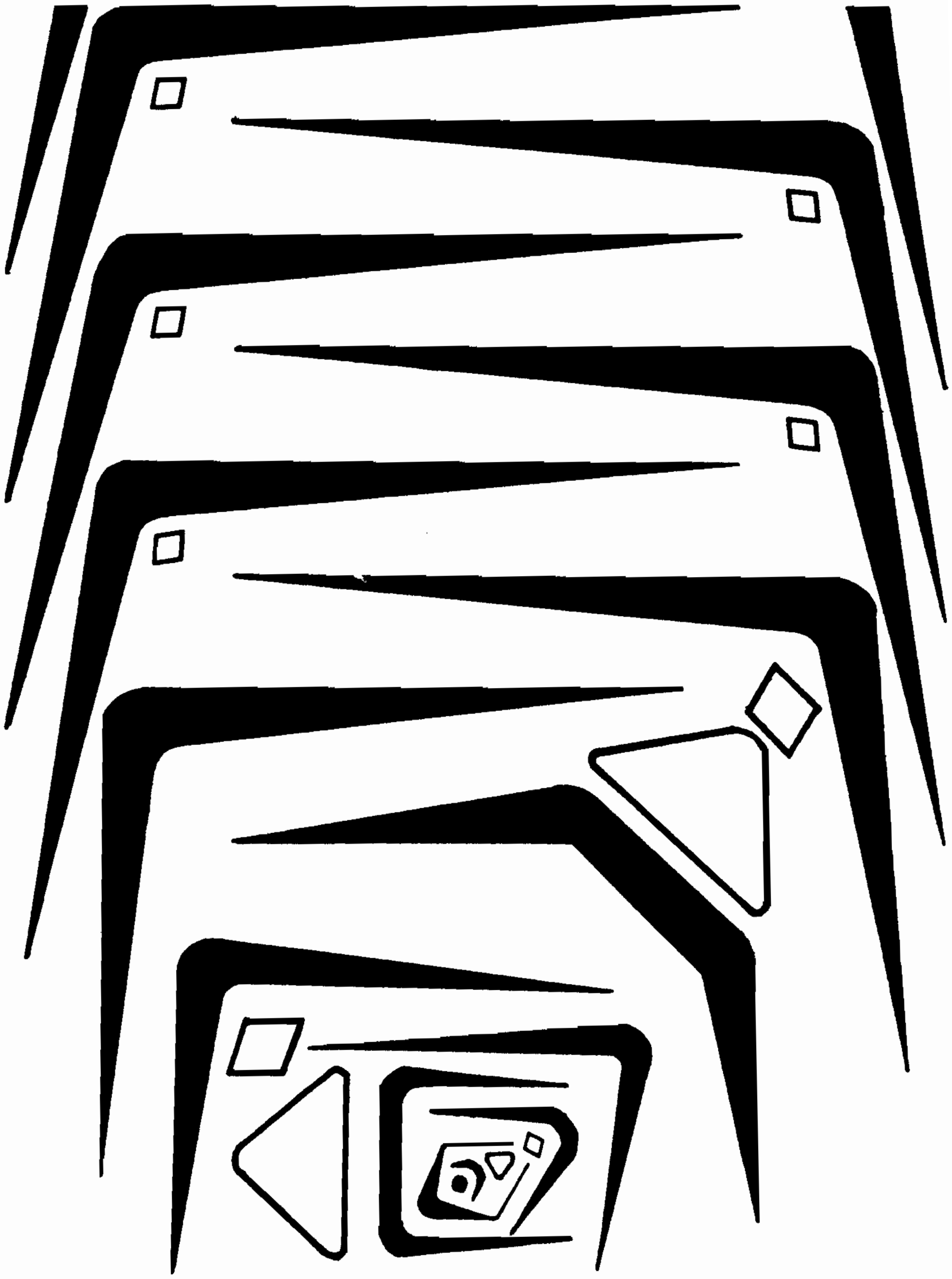


Figure 2.23 Seed Germination and Seedling of Sagittaria lancifolia.

a. Seed. x20.

b. Embryo plant dissected from seed. x20.

c. Embryo plant dissected from seed, showing more clearly the typical slit between the cotyledonary sheath (arrowhead), and the folded cotyledon. x20.

d. Newly germinated seedling. The radicle elongates and the collet is covered by fine root hairs (arrowheads). The first adventitious root (R) usually forms at the base of the cotyledon (Co). From the orientation of the first plumular leaf (L1), the spiral phyllotaxy is obvious. x10.

e. Seven and a half month old plant. A short upright stem has been formed. Rhizomatous growth is just beginning with the gradual changeover to distichous phyllotaxy by increasing divergence angle (L4, L5, L6). x10.

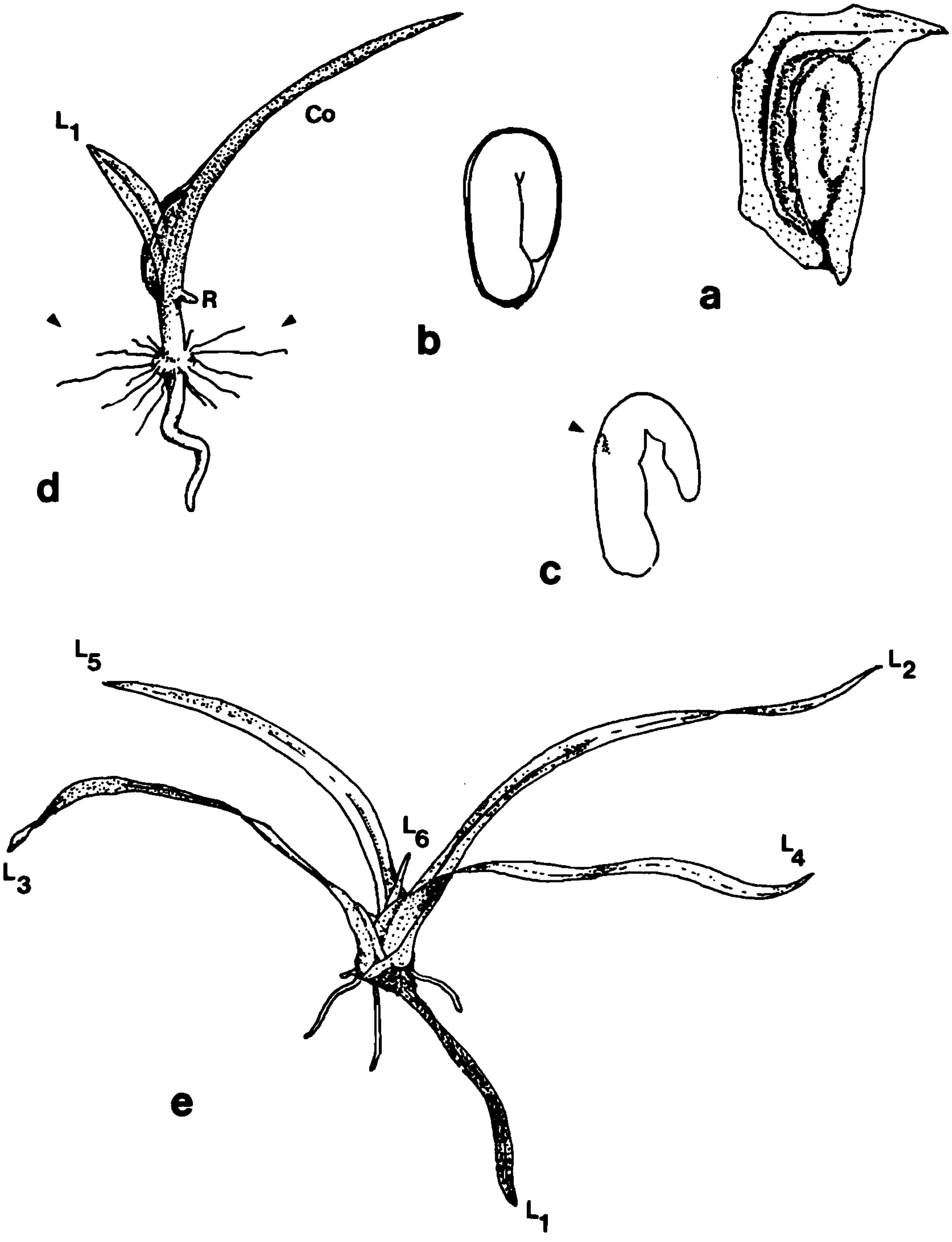

L1
Co
R
a
b
c
d
L5
L2
L6
L3
L4
e
L1

Figure 2.24. Vegetative Development in Sagittaria lancifolia.

a. Embryo plant dissected from the seed. Note the characteristic files of narrow cells forming the overlapping edges of the cotyledonary sheath (arrowheads). x120.

b. Side view of the apex of the embryo plant (V) after the cotyledon has been removed (rCo). Two leaves have already been formed (L1, L2). x120.

c. High angle view of the vegetative apex (V) with a single leaf primordium (L1). x120.

d. Top view of a slightly later stage than fig. c. A new leaf (L2) has just been initiated. x120.

e. Side view of the same stage as fig. d. The new primordium is located high on the apex (V), reducing the size of the latter significantly. x120.

f. High angle view of a slightly later stage than figs. d and e. The leaf two plastochrons old (L1) is beginning to develop its ensheathing leaf base. x120.

g. Vegetative apex showing size relationships of successive leaves. The distichous phyllotaxy is obscured by the position of the oldest leaf (L1), which has been partially broken off and dislodged. x120.

h. High angle view of a newly expanded axillary bud. Phyllotaxy is also distichous, and it is very similar to the main apex. Intravaginal scales (IS) may be observed. x120.

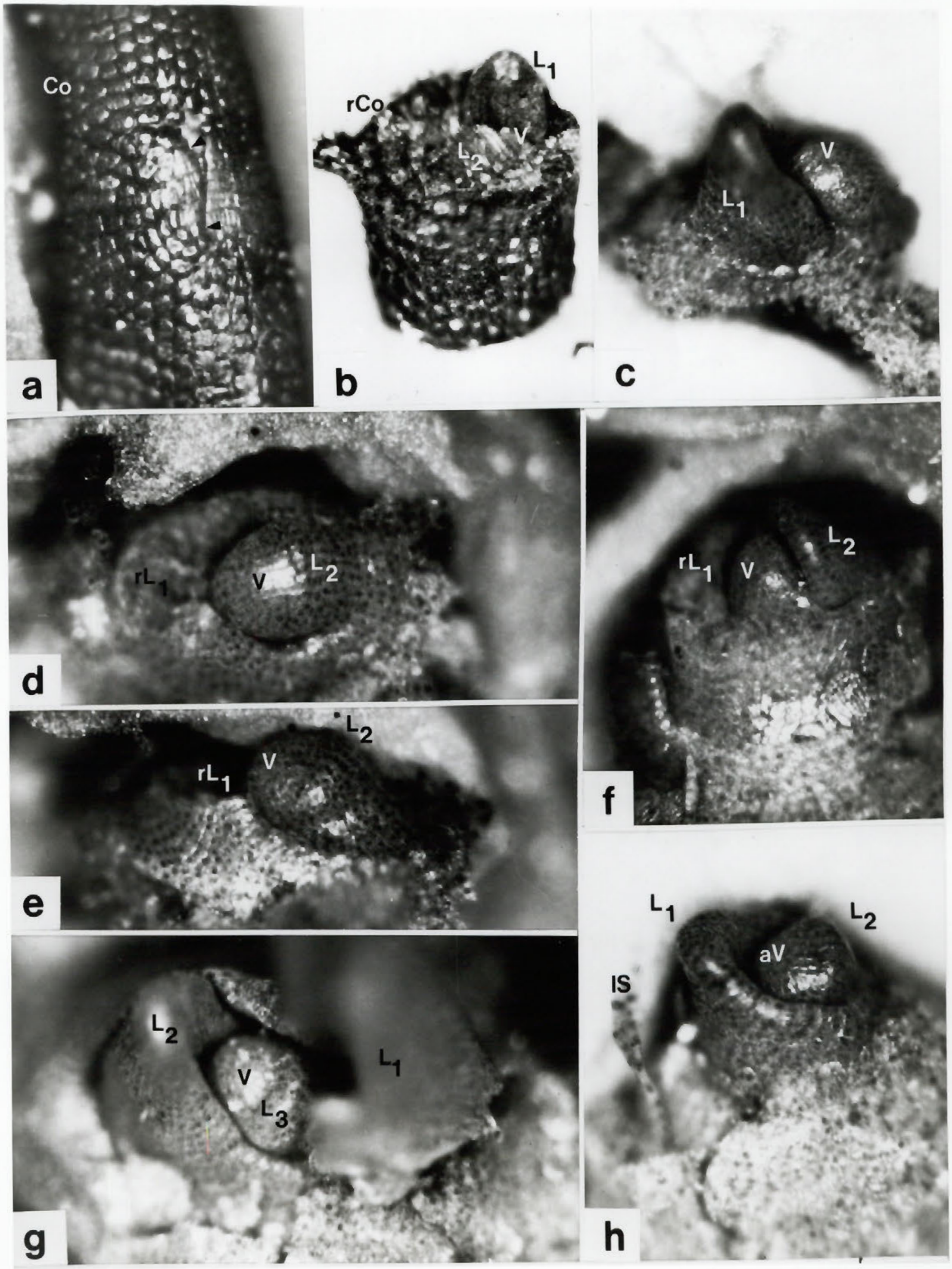

Co
a
rCo
L_1
L_2
V
b
V
L_1
c
rL_1
V
L_2
d
L_2
rL_1
V
e
rL_1
V
L_2
f
L_2
V
L_3
L_1
g
L_1
L_2
aV
IS
h

Figure 2.25 Inflorescence Development in Sagittaria lancifolia.

a. Side view of an apex that is just beginning to broaden. Arrowhead marks eventual location of the inflorescence. x120.

b. Top view of a slightly later stage than fig. a. Two new apices (I and V) are distinct. x120.

c. Side view of the same stage as fig. b. The ultimate leaf (rLu) subtends the continuation growth (V). The latter is very similar in size and height to the inflorescence primordium (I) at this stage. x120.

d. Top view of an older stage. The inflorescence primordium (I) grows rapidly in comparison with the continuation growth (V). x120.

e. Side view of a stage similar to that of fig. d. The continuation growth (V) now appears to be situated on the flank of the inflorescence primordium (I). x120.

f. Side view of a stage where the two apices are distinct. No prophyll has yet been formed between the two (arrowhead). x120.

g. Anterior side view of an older inflorescence (I) with a continuation growth that has developed three foliage leaves. Bract and flower primordia (Br1F1, Br2F2, etc.) have been formed. A very precocious axillary bud (aV) is associated with the axil of the penultimate leaf and is thus situated at the base of the inflorescence. x90.

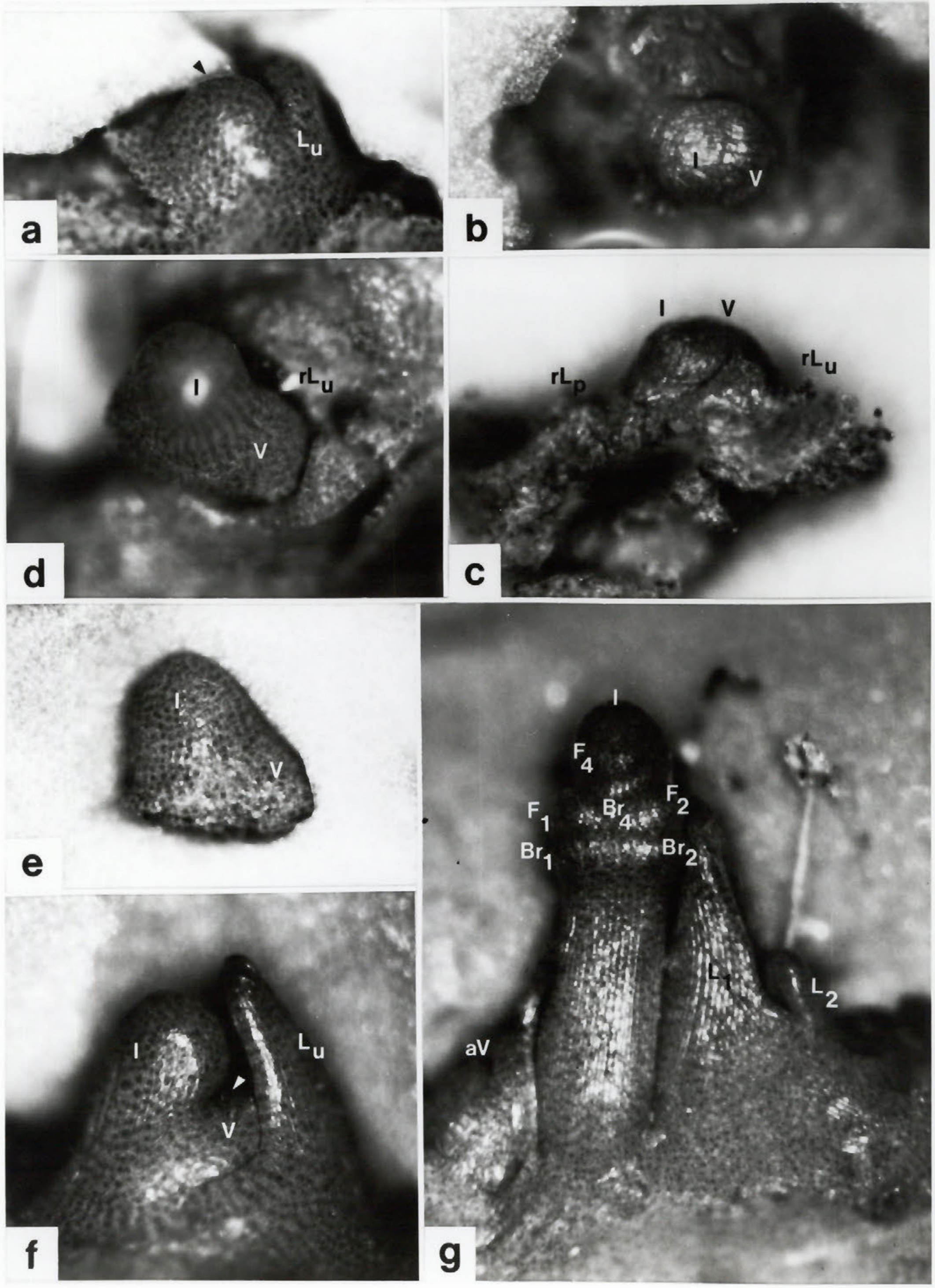

a
Lu
b
I
V
d
I
rLu
V
c
I
V
rLp
rLu
e
I
V
f
I
Lu
V
g
I
F4
F1
Br4
F2
Br1
Br2
L1
L2
aV

Figure 2.26 Axillary Bud Development in <u>Sagittaria</u> <u>lancifolia</u>.

a. Side view of the youngest visible axillary bud (aV). No appendages have yet been formed. x120.

b. Side view of the axillary bud of the penultimate leaf before inflorescence formation. Note its large size (compare with fig. c) and the associated intravaginal scales (IS). x120.

c. Side view of an ordinary axillary bud after the development of an adaxial prophyll (Pr). x120.

d. Side view of an axillary bud with the normal adaxial prophyll and an anomalous adaxial first leaf (L1). x120.

e. Top view of an axillary bud showing spiral phyllotaxy. The arrowheads indicate the midpoint of each leaf. x120.

f. Side view of the terminal portion of a mature rhizome. The large axillary bud (arrowhead) is associated with the penultimate leaf and is topographically situated at the base of the inflorescence (I). x0.3.

g. Side view of the terminal portion of a mature rhizome. Two consecutive precocious axillary buds have developed into secondary axes (arrowheads). x0.5.

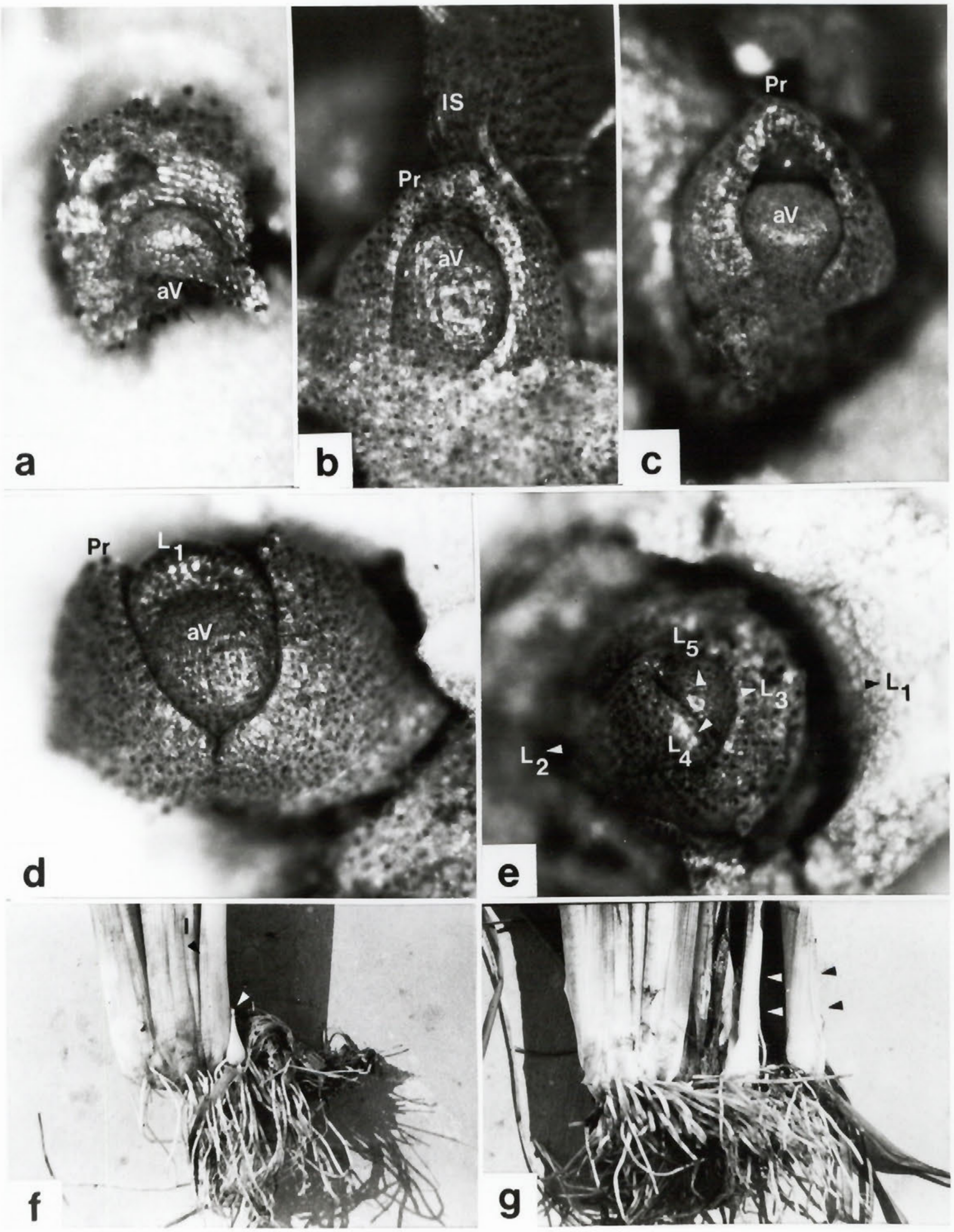

aV
a
IS
Pr
aV
b
Pr
aV
c
Pr
L_1
aV
d
L_5
L_3
L_1
L_2
L_4
e
f
g

Figure 2.27 Camera Lucida Drawings of Sections through _Sagittaria lancifolia_.

a. Cross section through the embryo plant of an ungerminated seed showing spiral phyllotaxy. The apex is relatively small. Note presence of intravaginal scales. x180.

b. Median longitudinal section through a stage similar to fig. a, showing the apex with a single tunica layer and one leaf (L1) with procambial strand (arrowhead). x180.

c. Median longitudinal section of a vegetative apex at about the same stage as the one in Fig. 2.25c. Leaf initiation is occurring (arrowhead), and a procambial trace is present in the preceding leaf primordium. x180.

d. Median longitudinal section of the stage shown in Fig. 2.25a showing the broadening of the apex (arrowheads) by general cell division. x180.

e. Median longitudinal section of a stage younger than the one in Fig. 2.25e. This is perpendicular to the plane of bifurcation. The single tunica layer remains, and a shell zone (arrowhead) is found between the inflorescence (I) and the continuation growth (V). x180.

f. Median longitudinal section through the stage in Fig. 2.25f. No prophyll is formed between the two products of bifurcation, and no shell zone can be distinguished in this case. x180.

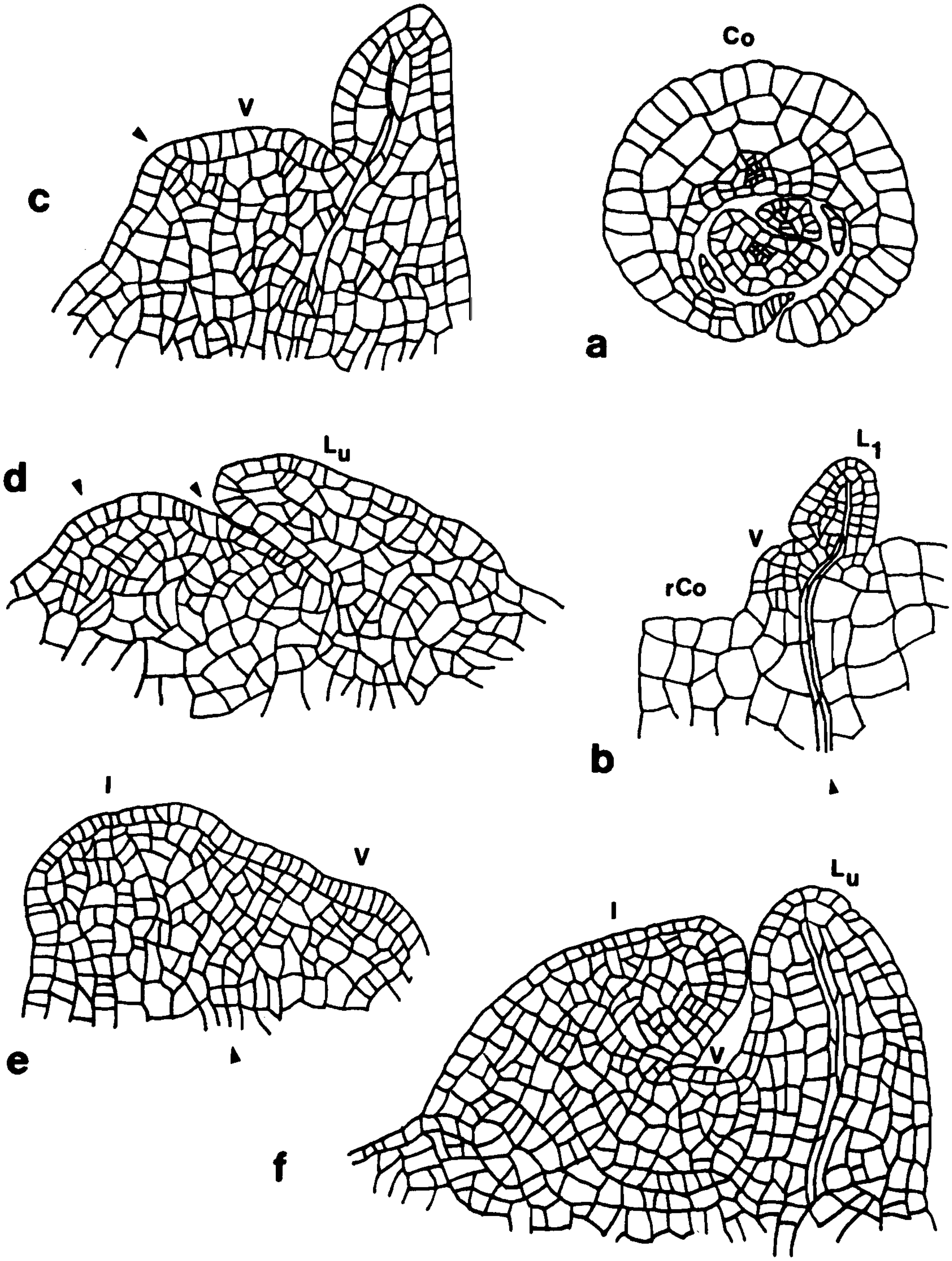
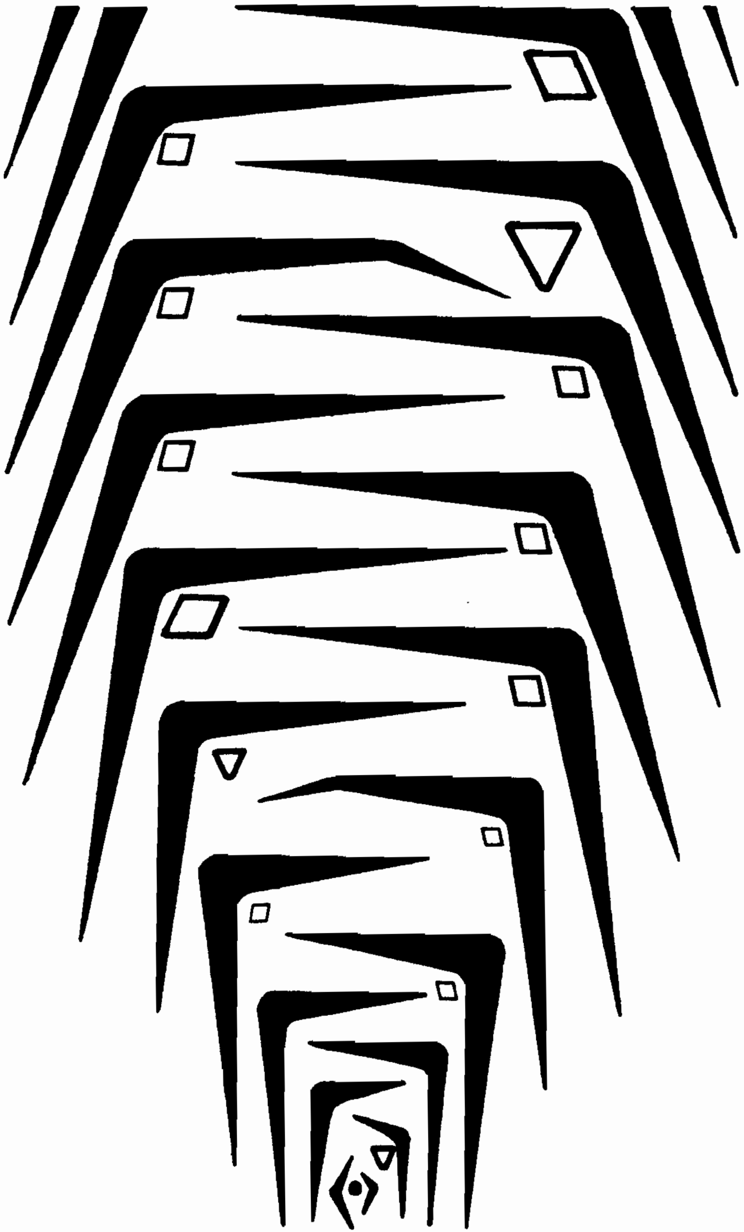
Co
V
c
a
Lu
d
L1
V
rCo
b
I
V
e
Lu
I
V
f

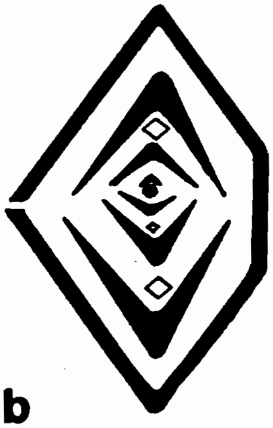
Figure 2.28 Diagrammatic Representation of Butomus umbellatus.

a. Shoot system of a mature plant. The anterior end is towards the lower edge of page.

b. The organization of an axillary bud. The orientation of fig. a is maintained, i.e., the anterior end of the main axis is towards the lower edge.



a



b

Figure 2.29 Seed Germination and Adult Form in Butomus umbellatus.

a. Seed with sculptured seed coat. x22.

b. Embryo plant dissected from the seed. Though it also has the typical slit between the cotyledonary sheath (arrowhead), the cotyledon (Co) itself is straight and not folded. x22.

c. Seed germination. Many fine root hairs develop on the collet (arrowhead). x22.

d. Young seedling. Phyllotaxy is distichous from the start. The first adventitious root (R) forms at the base of the cotyledon (Co), while the second appears on the opposite side (arrowhead). x11.

e. Six week old seedling. Already the anterior-posterior (A, P) orientation is well established. The apex is located within the small bulge of leaf bases on the anterior side (arrowhead). x11.

f. Terminal portion of a mature rhizome. The leaves, in two ranks, converge at the apex (arrowhead). Inflorescences (I) are leaf-subtended and are associated with a well developed bud in the axil of the leaf just posterior to it (arrow). x0.75.

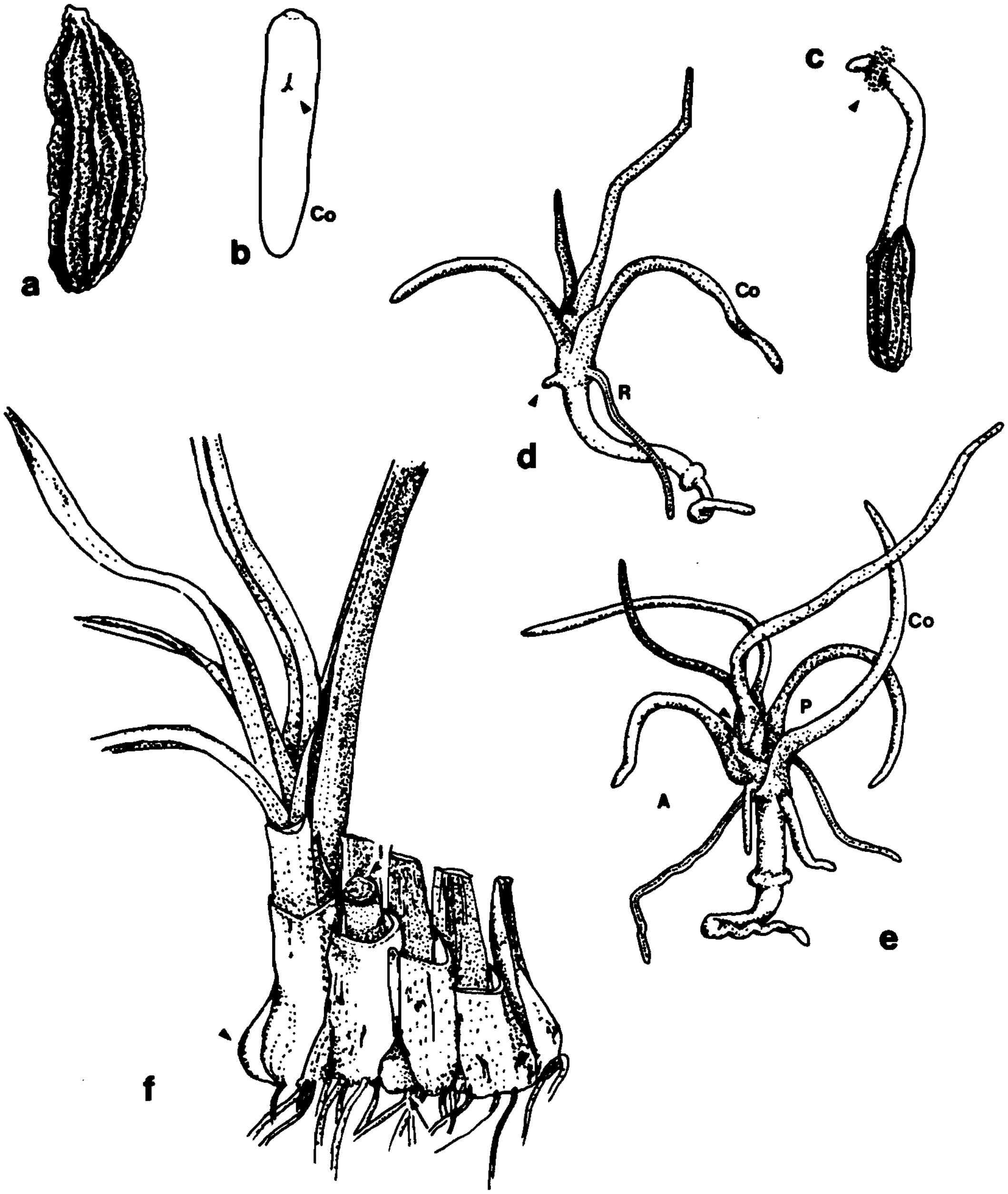

a
b
Co
c
d
Co
R
e
Co
P
A
f

Figure 2.30 Vegetative Development in Butomus umbellatus.

a. Embryo plant dissected from the seed. Arrowhead indicates the opening between the edges of the cotyledon. x120.

b. Apex of newly germinated seedling, where two foliage leaves have been formed. Phyllotaxy is distichous (arrowheads indicate the midpoint of removed leaves). Note small size of the apex. x120.

c. High angle view of the vegetative apex (V) of a mature rhizome. Leaf initiation (L3) takes place on the lower flanks of the apex. x120.

d. Top view of the vegetative apex of a mature rhizome. An earlier stage of leaf initiation is shown. Phyllotaxy is distichous, with an elongated apex. The anterior side is towards the top of the figure. x120.

e. - j. Side views of a series of axillary buds along a rhizome, from the anterior to posterior. The anterior end of the rhizome is on the right for figs. g and i, and on the left for figs. f, h and j. x120.

e. Youngest visible axillary bud. An adaxial prophyll (Pr) is already present.

f. Precocious axillary bud associated with the leaf two plastochrons older than the one subtending the inflorescence. Though in the axil of a relatively young leaf in this series, it has already formed a prophyll (rPr), and four, possibly five leaf primordia.

g. Next youngest bud. The first leaf is on the anterior side and a third leaf primordium (L3) has just been initiated.

h. Axillary bud with three distinct leaf primordia. Note intravaginal scales (IS) on the edge of the adaxial prophyll.

i. The prophyll (Pr) surrounding the axillary bud has been partially removed. A fourth leaf primordium (L4) has just been initiated.

j. This bud is four plastochrons older than the one shown in fig. f, but its extent of development is similar. The prophyll (rPr) and first leaf (rL1) have been removed. The latter is on the posterior side of the bud, an unusual position.

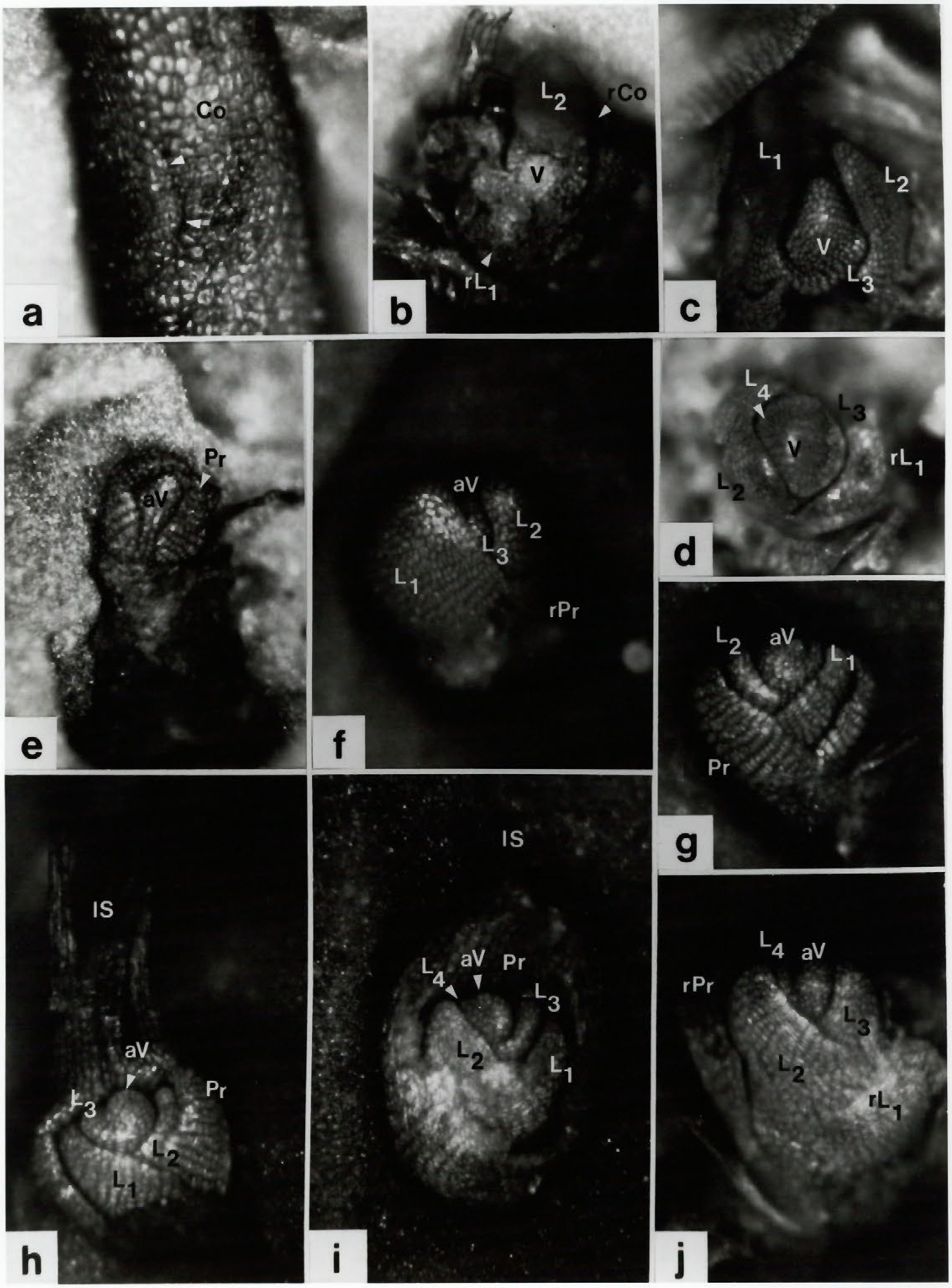

Co
a
L_2
rCo
V
rL_1
b
L_1
L_2
V
L_3
c
Pr
aV
e
aV
L_2
L_3
L_1
rPr
f
L_4
L_3
V
rL_1
L_2
d
L_2
aV
L_1
Pr
g
IS
aV
L_3
Pr
L_2
L_1
h
IS
L_4
aV
Pr
L_3
L_2
L_1
i
L_4
aV
rPr
L_3
L_2
rL_1
j

Figure 2.31 Development of the Inflorescence of Butomus umbellatus.

a. Top view of the beginning of inflorescence formation. The apex broadens and two new apices are formed: an anterior continuation growth (V) and a posterior inflorescence (I) subtended by the ultimate leaf (Lu). x120.

b. Side view of the stage shown in fig. a. In this case, the vegetative apex (V) is slightly higher than the inflorescence (I). x120.

c. Side view of a later stage than figs. b and c. The anterior end is on the right. The inflorescence primordium (I) is slightly taller than the continuation growth (V). x120.

d. View from the anterior side of an older stage. The inflorescence (I) is much higher than the continuation growth (V), and the leaf subtending it (Lu) is mostly hidden by the one, two plastochrons older, immediately posterior to it (Lp-1). x120.

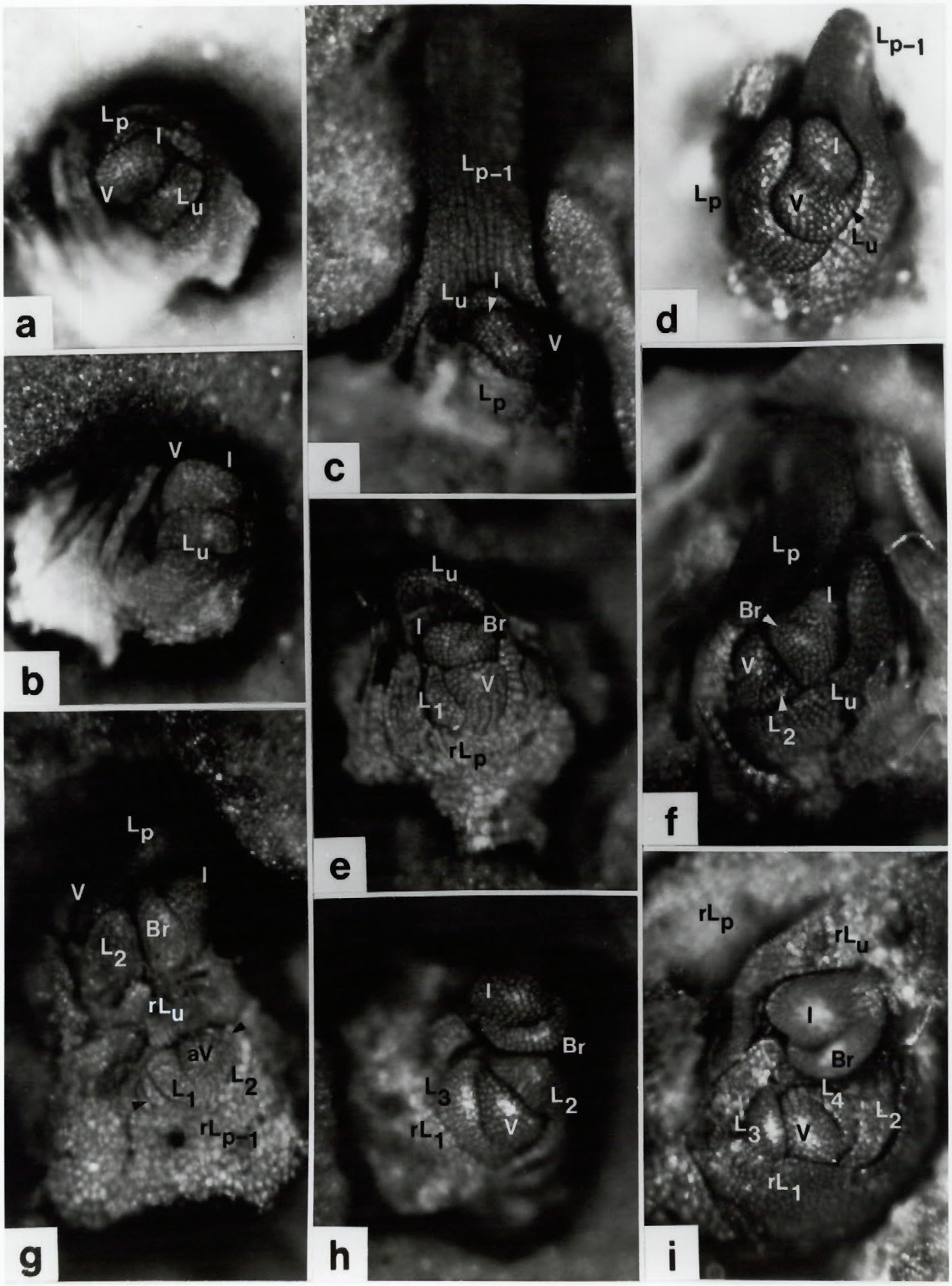
e. A bract (Br) has been initiated on the inflorescence (I). The first foliage leaf (L1) formed on the continuation growth (V) continues the phyllotaxy prior to apical bifurcation. x120.

f. Anterior view of a slightly older stage than fig. e. A second foliage leaf (L2) is found. Note size difference of the two apices. x120.

g. Posterior view from a later stage, showing a precocious axillary bud (aV) in the axil of the leaf posterior to the one subtending the inflorescence (rLp-1). It has already formed an adaxial prophyll (arrowheads) and two leaves (L1, L2). x120.

h. Top view showing a continuation growth with three leaf primordia and the associated inflorescence with a single bract. x120.

i. Top view of a stage with four leaf primordia on the continuation growth. There is little concurrent development of the inflorescence, which still has only one bract as in fig. d. The continuation growth is now substantially larger than the inflorescence (compare with fig. f). x120.



a
L_p
I
V
L_u
b
V
I
L_u
c
L_{p-1}
L_u
I
V
L_p
d
L_{p-1}
I
L_p
V
L_u
e
L_u
I
Br
V
L_1
rL_p
f
L_p
Br
I
V
L_u
L_2
g
L_p
V
I
Br
L_2
rL_u
aV
L_1
L_2
rL_{p-1}
h
I
Br
L_3
L_2
rL_1
V
i
rL_p
rL_u
I
Br
L_4
L_3
V
L_2
rL_1

Figure 2.32 Camera Lucida Drawings of Sections through the Main Axis of *Butomus umbellatus*.

a. Median longitudinal section through the apex of a newly germinated seedling. The tunica is one cell layer thick and phyllotaxy is distichous. The cotyledon (rCo) and first leaf (rL1) have been removed. Note the first adventitious root (R) at the base of the former. Xylem elements are already present. x180.

b. Median longitudinal section through a vegetative apex (V) showing a single tunica layer. A fourth leaf is initiating by periclinal divisions beneath it on the lower flank of the apex (on the right). There is little size change in the apex with leaf initiation. x180.

c. Median longitudinal section showing the broadening of the apex during inflorescence formation. The inflorescence (I), proximal to the ultimate leaf (Lu), is higher than the continuation growth (V). No shell zone is detectable. This stage is similar to the one shown in Fig. 2.31c. x180.

d. Median longitudinal section of a later stage than fig. c. A third foliage leaf is initiating on the continuation growth (arrowhead). The inflorescence has only a single bract. x180.

e. Outline of the cross section of a rhizome apex shortly after apical bifurcation. The precocious lateral bud (aV) is on the same side of the rhizome as the inflorescence (I). The posterior edge of the leaf sheath surrounds the anterior one. x66.

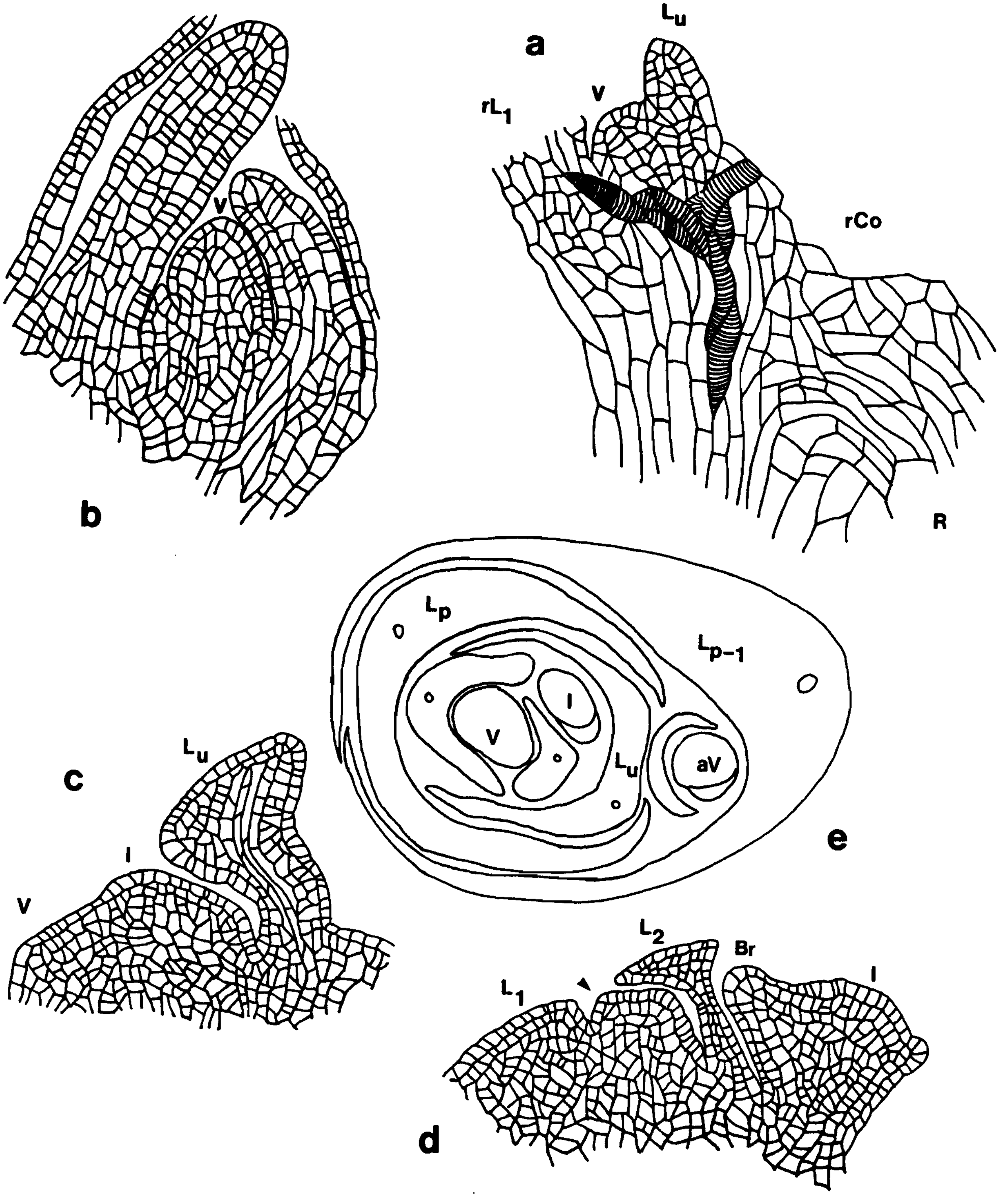

a
L_u
V
rL_1
rCo
R
b
V
c
L_u
l
V
L_p
L_{p-1}
l
V
L_u
aV
e
L_2
Br
L_1
l
d

Figure 2.33 Camera Lucida Drawings of Sections through Axillary Structures of Butomus umbellatus.

a. Longitudinal section through an axillary bud initiating a first leaf on its anterior side (on the right) beneath the single tunica layer. The adaxial prophyll (Pr) is beginning to surround the entire bud. x180.

b. Median longitudinal section of a developed axillary bud. The fifth leaf is just initiating on the right. Part of the sheathing base of the second leaf (L2) is also present between the first (L1) and the third (L3). x180.

c. Outline of the cross section of a well developed bulbil. The organization is very similar to that of the rhizome. The leaves form two ranks converging at the apex, as indicated by axillary buds which are represented by circles. An inflorescence (I) has already been initiated. (Compare with Fig. 2.32e). x66.

d. Cross section showing part of the parenchymatous "stalk" of a bulbil. Tannin cells (shown in black) and a small procambial trace (at the top of the figure) are shown. x180.

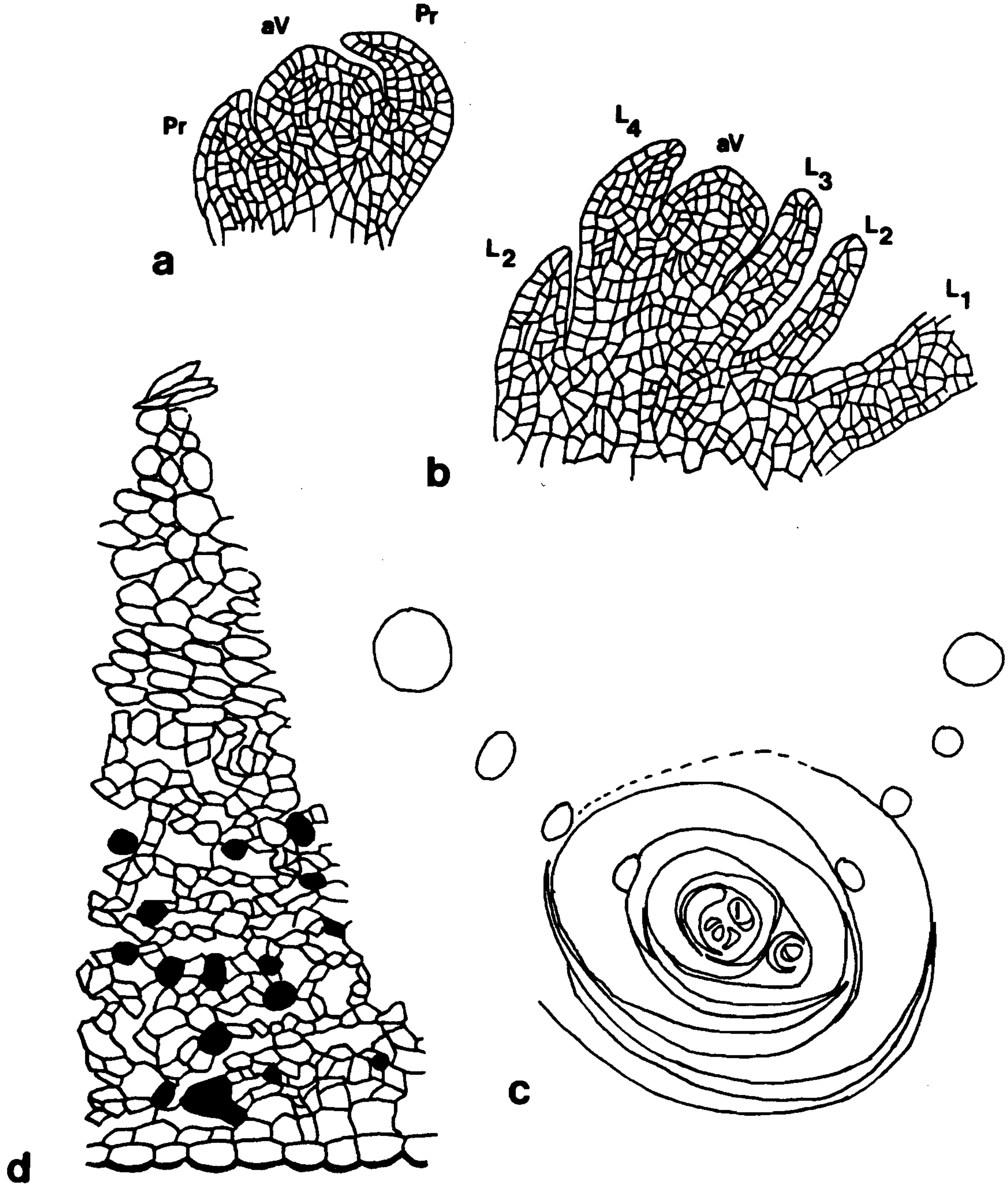

aV
Pr
Pr
a
L4
aV
L3
L2
L2
L1
b
c
d

Figure 2.34 Axillary Buds of Butomus umbellatus.

a. Axillary bud associated topographically with the inflorescence (precociously formed in the axil of Lp-1, see Fig. 2.31g). Its prophyll is often strongly ribbed. x5.

b. Non-precocious axillary bud during the first part of the growing season. x5.

c. Axillary bud in mid-season, beginning to expand and develop into a bulbil. x5.

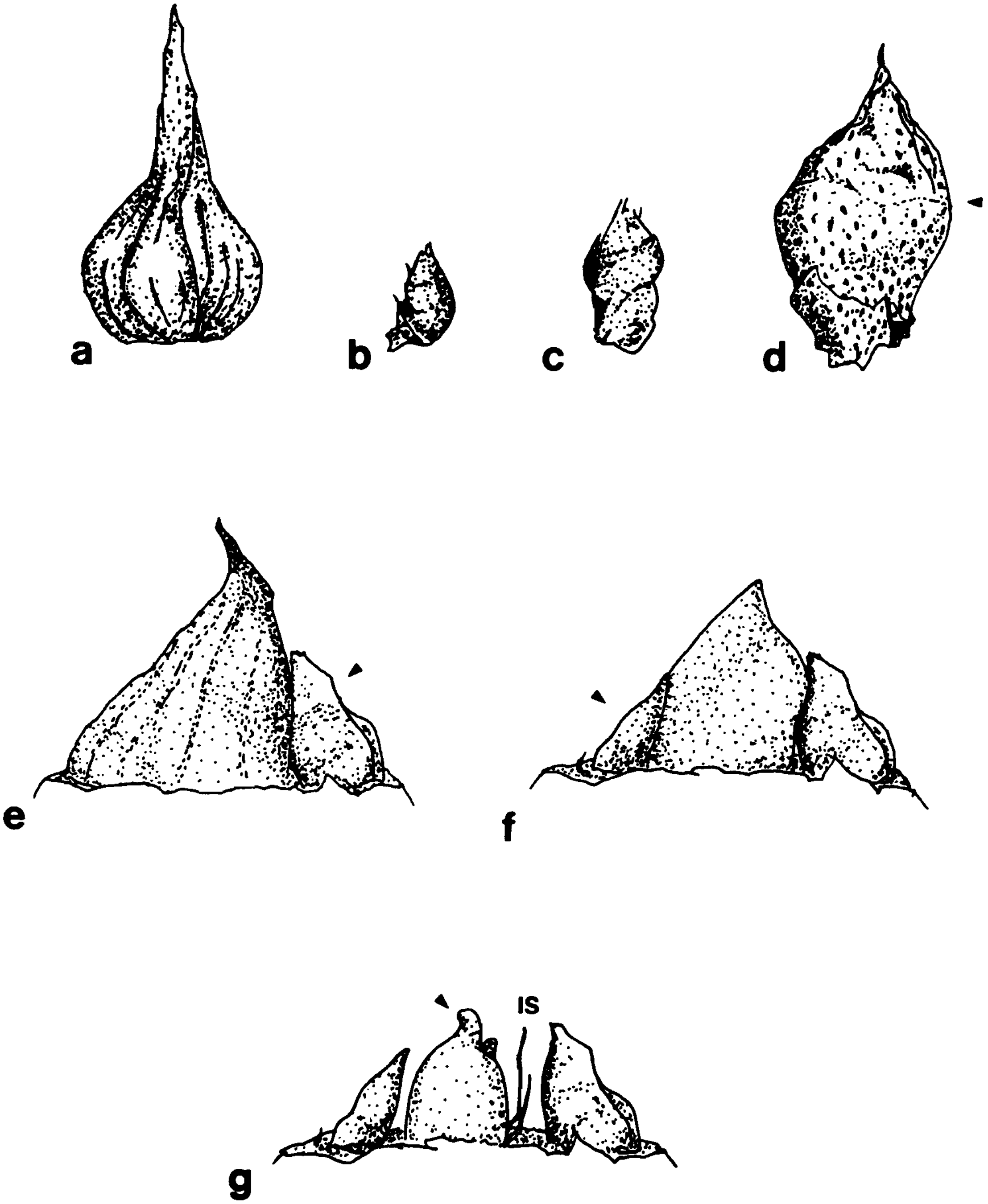
d. Fully developed bulbil found in the latter half of the growing season. A short stalk is formed, the level of prophyll insertion being marked by an arrowhead. The surface is covered with scattered tannin cells. x5.

e. - g. Bulbil with successive leaves dissected away.

e. The first leaf, usually anterior in position relative to the main axis, is removed. A very large and well developed bud, similar in organization to the bulbil itself, is found in its axil (arrowhead). x10.

f. The second leaf, on the posterior side (left of figure) also subtends a well developoed axillary bud. x10.

g. No bud is found in the axil of the third leaf. The fourth leaf is indicated by an arrowhead. Note the presence of intravaginal scales (IS). x10.


a
b
c
d
e
f
IS
g

List of Symbols Used for Figs. 2.34 to 2.38

↑	-- vegetative axis
⫯	-- flower
●	-- inflorescence
▶—	-- ultimate leaf formed before bifurcation
▷—	-- penultimate leaf formed before bifurcation
×	-- scale leaf
≡	-- axis with congested internodes
╪	-- axis with internodal elongation

Figure 2.35 Summary of Architectural Forms in the Alismatales.

a. Simple upright vegetative axis with congested internodes.

b. Upright vegetative axis with congested internodes. Formation of stolons or stolon systems from lateral buds.

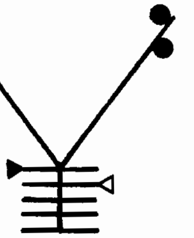
c. Rhizomatous, with congested internodes. Branching from lateral buds.

d. Upright vegetative axis with congested internodes. Formation of pseudostolons with lateral vegetative buds which develop into new upright axes.

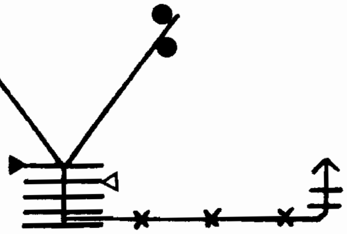
e. Upright vegetative axis with congested internodes. Repeated bifurcation of inflorescence apex to form floral buds and vegetative buds which develop into new upright axes.

Note: Genera which correspond to these forms are listed below each figure by family.

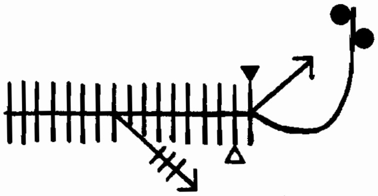
A:Alismataceae
B:Butomaceae
L:Limnocharitaceae



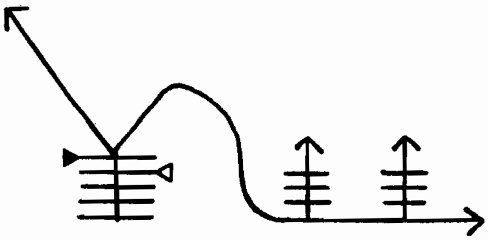
a Alisma (A)
Burnatia (A)
Damasonium (A)
Limnophyton (A)
Tenagocharis (L)



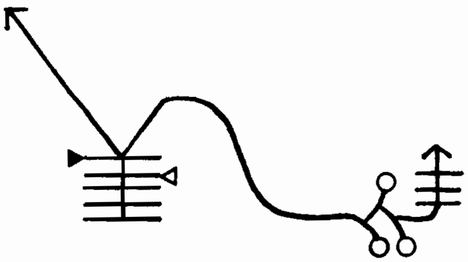
b Sagittaria (A)



c Sagittaria (A)
Butomus (B)



d Baldellia (A)
Caldesia (A)
Echinodorus (A)
Luronium (A)
Wisneria (A)



e Ranalisma (A)
Hydrocleis (L)
Limnocharis (L)
Ostenia (L)

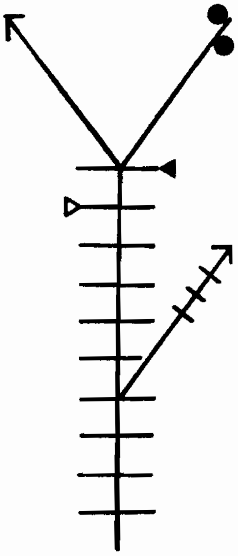
Figure 2.36 Summary of Architectural Forms in the Hydrocharitales.

a. Upright vegetative axis with internodal elongation. Lateral branching frequent except in Maidenia.

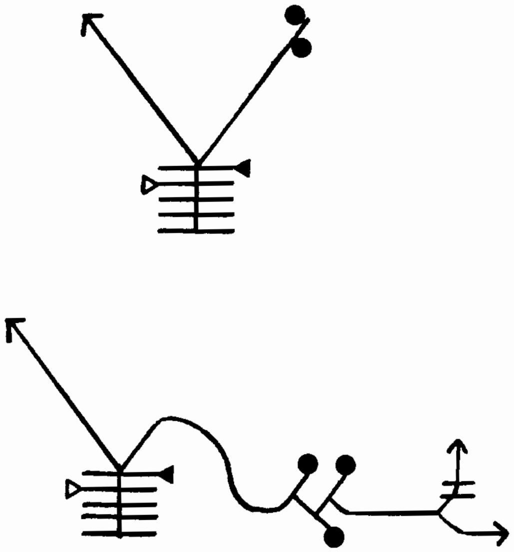
b. Upright vegetative axis with congested internodes. Reproductive apex may form an inflorescence (as in Blyxa and Ottelia), or bifurcate repeatedly to form vegetative axes and inflorescences on pseudostolons (sensu lato).

c. Rhizomatous. Axes dimorphic if upright shoots are formed.

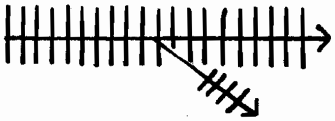
Note: Genera which correspond to these forms are listed below each figure.



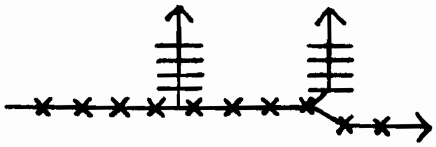
a Egeria
Elodea
Hydrilla
Lagarosiphon
Maidenia
Nechamandra



b Blyxa
Hydrocharis
Limnobium
Ottelia
Stratiotes
Vallisneria



c Enhalus



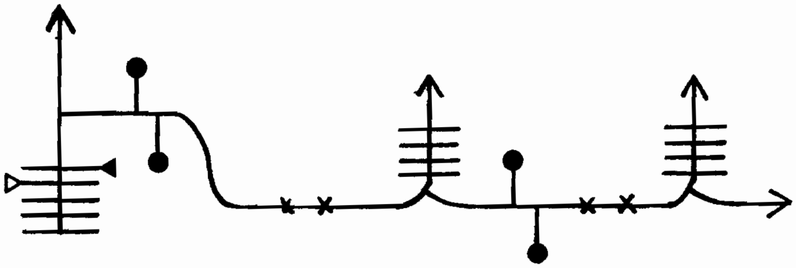
Halophila
Thalassia

Figure 2.37 Interpretations of the Rosette Architecture in the Hydrocharitales.

a. Upright vegetative axis monopodial. Reproductive axis lateral, forming inflorescences and segment of stolon, but eventually turning upright to form a new vegetative axis, i.e., a sympodial stolon organization.

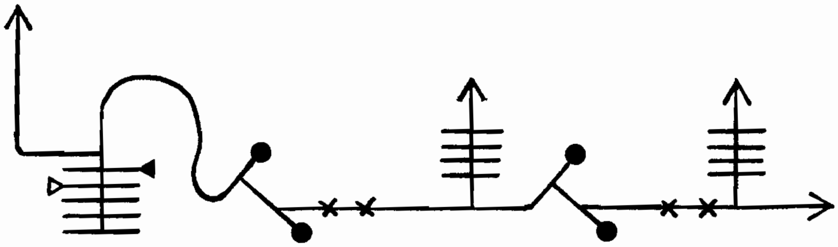
b. Upright vegetative axis sympodial. The terminal reproductive axis bifurcates to form inflorescence and vegetative bud systems and a stolon segment. The stolon produces an new upright axis laterally before the pattern of development is repeated.

Note: Authors adhering to each interpretation are listed below the figure.



a

Bugnon and Joffrin, 1962
Loiseau and Nougarede, 1963
Brunaud, 1977



b

Wilder, 1974

Figure 2.38 Summary of Architectural Forms in the Najadales.

a. Upright vegetative axis with congested internodes. Stolons may or may not be formed.

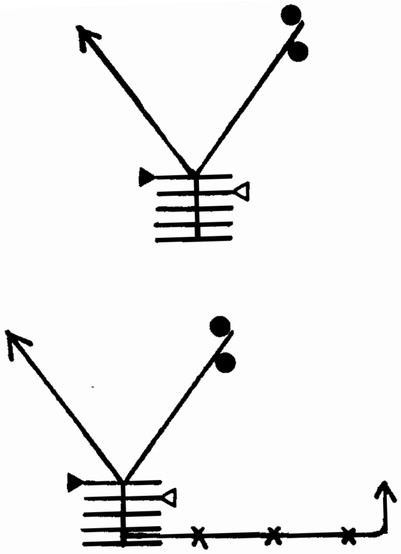
b. Vegetative axis with internodal elongation and frequent branching. Differentiation of upright and horizontal axes mainly by orientation, occasionally also by duration of growth. Case of sympodial branching shown.

c. Vegetative axis with internodal elongation and frequent branching. Upright and horizontal axes clearly dimorphic. Case of sympodial branching shown.

d. Rhizomatous axis with congested internodes.

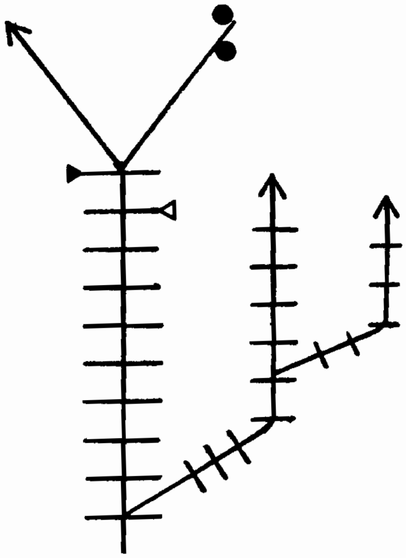
Note: Genera which correspond to these forms are listed below by family below each figure.

A:Aponogetonaceae
C:Cymodoceaceae
J:Juncaginaceae
N:Najadaceae
P:Posidoniaceae
Po:Potamogetonaceae
R:Ruppiaceae
S:Scheuchzeriaceae
Z:Zannichelliaceae
Zo:Zosteraceae



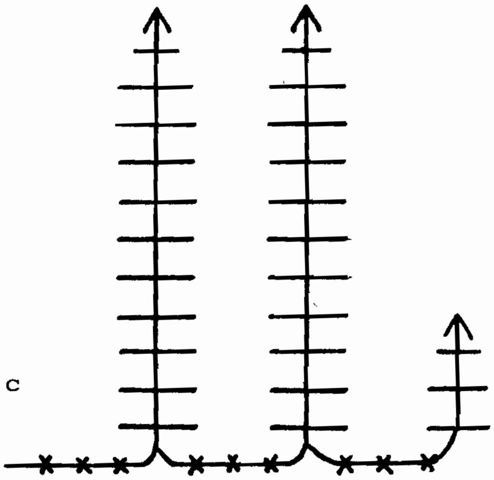
a

Aponogeton (A)
Cycnogeton (J)
Lilaea (J)
Maundia (J)
Scheuchzeria (S)
Tetroncium (J)
Triglochin (J)



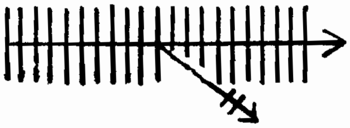
b

Cymodocea (C)
Heterozostera (Zo)
Najas (N)
Phyllospadix (Zo)
Ruppia (R)
Zostera (Zo)



c

Althenia (Z)
Amphibolis (C)
Groenlandia (Po)
Lepilaena (Z)
Potamogeton (Po)
Pseudalthenia (Z)
Syringodium (C)
Thalassodendron (C)
Zannichellia (Z)



d

Halodule (C)
Posidonia (P)
Triglochin (? Cycnogeton, J)

List of Abbreviations for Figs. 2.39 to 2.55

A - stamen or its primordium
Co - cotyledon
F - flower or its primordium
G - carpel or its primordium
G' - aborted carpel or its primordium
I - inflorescence or reproductive apex
In - integument or its primordium
IS - intravaginal scales (multiseriate hairs)
L - foliage leaf or its primordium
O - ovule or its primodrdium
Pr - prophyll or its primordium
R - adventitious root or its primordium
T - tepal or its primordium
V - vegetative apex

a - axillary, e.g., aV, apex of axillary shoot
i - inner, e.g., Ini, inner integument
o - outer, e.g., Ino, outer integument
p - penultimate, e.g., Lp, penultimate leaf before transition to inflorescence formation
pr - procambial strand
r - removed, e.g., rL, leaf removed
u - ultimate, e.g., Lu, ultimate leaf before transition to inflorescence formation

List of Symbols for Figs. 2.39 to 2.55

●	vegetative apex
○	inflorescence axis
▼⃝	axillary bud developing to form stolon
◓	foliage leaf
◠	scale leaf
⌒	tepal
⏢	stamen (size indicates extent of development)
△	carpel
◎	ovule with two integuments

Figure 2.39 Mature Plant of Triglochin striata. x0.5.

Figure 2.40 Reproductive Structures of Triglochin striata.

a. Mature seed. x20.

b. Embryo plant and integuments dissected from the seed. x20.

c. Undeveloped carpel. x20.

d. Flower at anthesis. Note zygomorphy. x20.

e. Young inflorescence and continuation growth. Note intravaginal scales and the presence of a well developed axillary bud (arrowhead). x10.

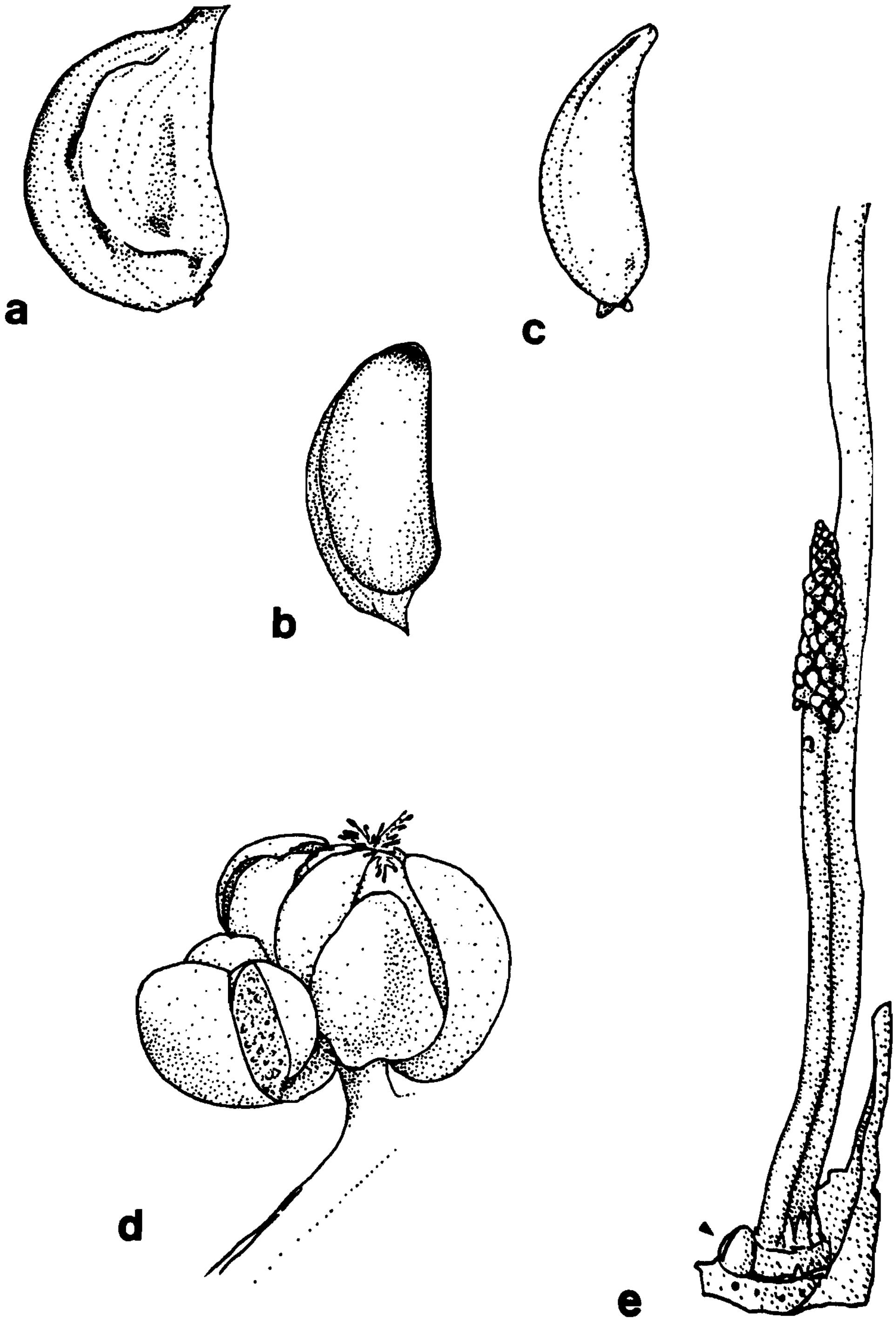
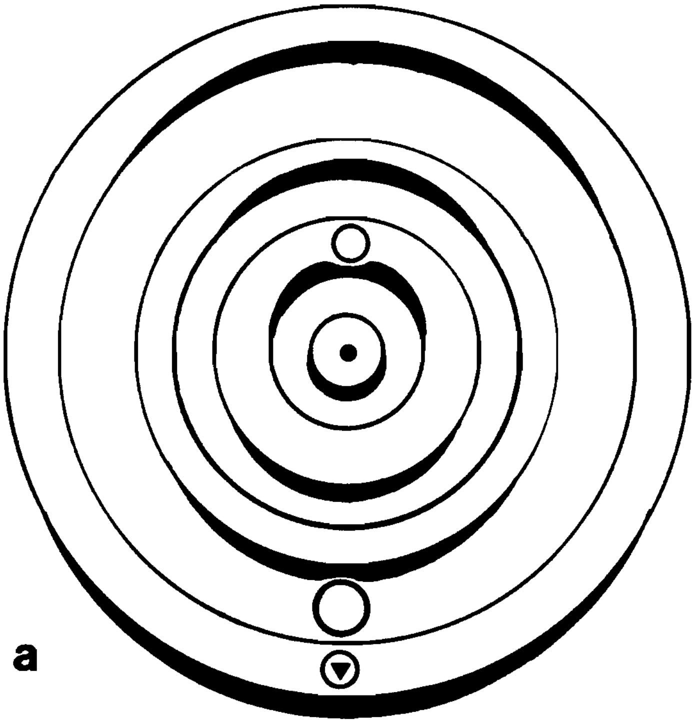

a
c
b
d
e

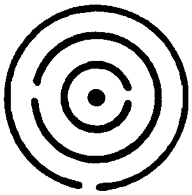
Figure 2.41 Diagrams Showing the Organization of *Triglochin striata*.

a. Mature plant.

b. Axillary bud.



a



b

Figure 2.42 Vegetative Growth. x140.

a. Lower part of embryo plant dissected from seed. The collet (small arrowheads) and the aperture between the cotyledon edges (large arrowheads) are evident.

b. Apex of an embryo plant. The cotyledon (rCo) has been dissected away to show a single leaf (L1) and a very small apex (arrowhead).

c. Vegetative apex of a mature plant (V). One foliage leaf (L1) is attached.

d. Apex of a mature plant at about the same stage as fig. c. The two leaves (L1, L2) exhibit distichous phyllotaxy. The bulge of the tip of the older leaf (arrowheads) is the portion that extrudes above the sheathing base of the preceding leaf.

e. Development of an axillary bud in the axil of the penultimate leaf before inflorescence formation (rLp). The base of the inflorescence (I), damaged, is surrounded by the sheath of the ultimate leaf (Lu). Triangular intravaginal scales (IS) are present.

f. Apex of an axillary bud more developed than the one in fig. e. Note the triangular shape of the scale leaf (arrowhead) in comparison with a foliage leaf (e.g., fig. c).

g. An axillary bud prior to axial elongation to form a stolon.

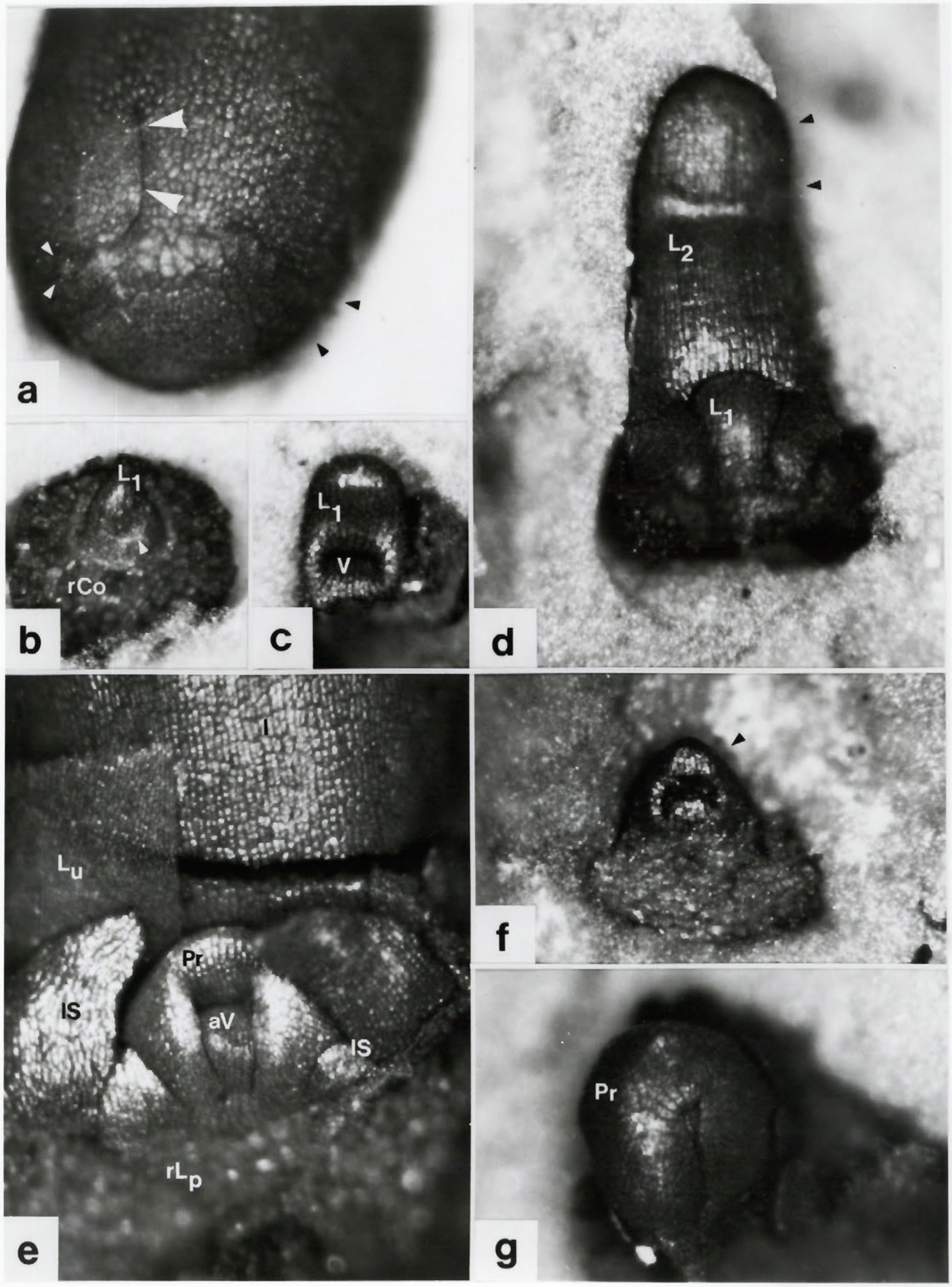

a
L_1
rCo
b
L_1
V
c
L_2
L_1
d
I
L_u
Pr
IS
aV
IS
rL_p
e
f
Pr
g

Figure 2.43 Inflorescence Development. x140.

a. Top view of the bifurcation of the apex to form an inflorescence (I) and a continuation growth (V). The latter is found in the axil of the last leaf formed prior to bifurcation (Lu).

b. Side view of the stage shown in fig. a. Though higher than the continuation growth (V), the inflorescence primordium (I) is narrower in diameter.

c. Slightly later stage than the one in figs. a and b, showing the size and positional relationships of the inflorescence (I), the first leaf of the continuaton growth (Ll), and the last leaf before bifurcation (Lu). Note also the formation of an axillary bud (large arrowhead) and intravaginal scales (small arrowheads).

d. Side view of about the same stage as fig. c. The first leaf (Ll) is formed on the continuation growth opposite the ultimate leaf and thus continues uninterrupted the phyllotaxy of the main axis. The location of the apex is indicated by an arrowhead. The inflorescence (I) is dome-shaped at this stage.

e. A later stage than fig. d, where a second foliage leaf is usually being initiated. The first leaf (Ll) begins to elongate. The inflorescence remains dome-shaped.

f. Side view of an elongating inflorescence (I) on which floral primordia (arrowheads) are being initiated. An axillary bud (black arrowhead) is beginning to form at the base of the inflorescence in the axil of the penultimate leaf (rLp).

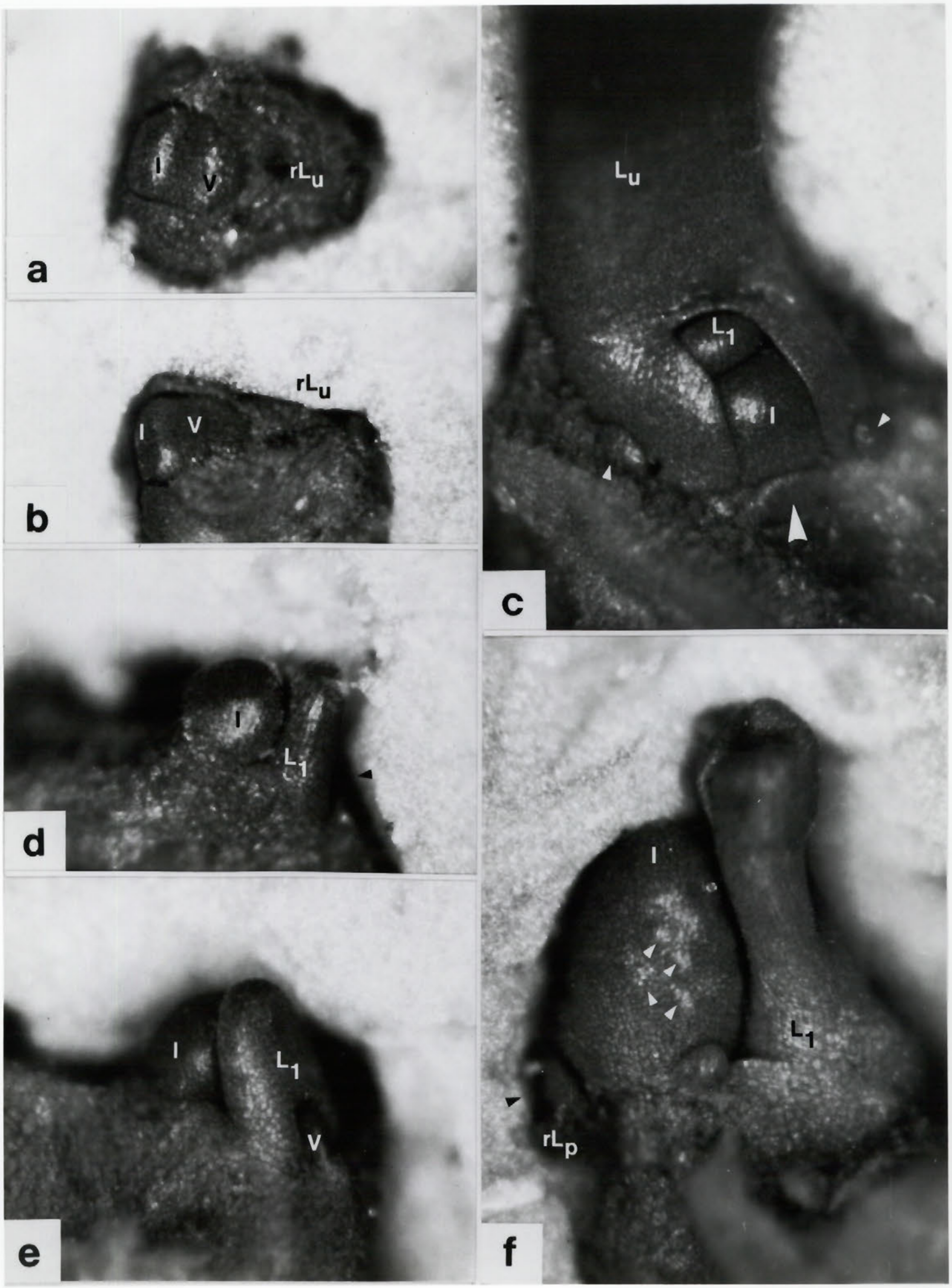

a
I
V
rL_u
b
rL_u
I
V
c
L_u
L_1
I
d
I
L_1
e
I
L_1
V
f
I
L_1
rL_p

Figure 2.44 Sections through Stages Showing Vegetative Growth and Apical Bifurcation. x224.

a. Median longitudinal section of an embryo with one foliage leaf (L1) and a small apex (arrowhead). A procambial trace connects this to the radicle (R) where the collet is indicated (black arrowheads). Reserve storage is in the form of starch granules (white arrowheads.

b. Median longitudinal section of a vegetative apex similar to the one shown in Fig. 2.42d. Note bulge at the tip of the older leaf.

c. Median longitudinal section of an apex shortly after bifurcation. Much of the dome-shaped inflorescence (I) retains the two tunica layers. A partially damaged foliage leaf (L1) has been formed by the continuation growth (V) which also has two tunica layers.

d. Median longitudinal section of an older stage than fig. c. A ring of procambial strands (arrowheads) has begun to develop in the inflorescence. The median procambial strand of the first leaf is evident. A second leaf is being initiated on the continuation growth apex (black arrowhead).

e. Cross section of an inflorescence (I) and the first leaf of the continuation growth. Floral primordia are beginning to form by divisions in the subepidermal layers (arrowheads).

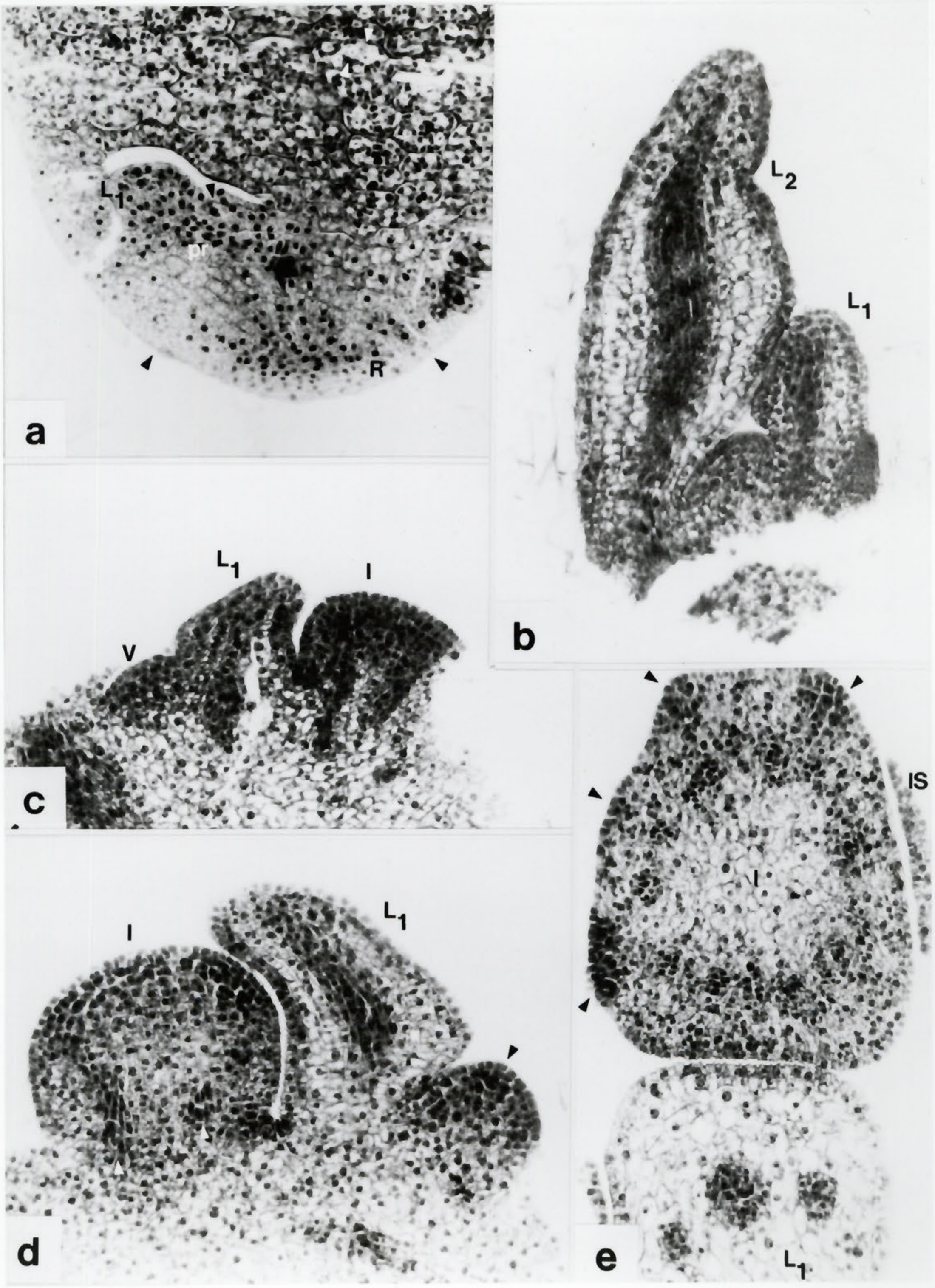

L_1
pr
R
a
L_2
L_1
b
L_1
I
V
c
I
L_1
d
IS
I
L_1
e

Figure 2.45 Median Longitudinal Sections through Stages of Vegetative Growth and Apical Bifurcation. x560.

a. The apex of the embryo is extremely reduced, with only one tunica layer.

b. Vegetative apex of a mature plant. Leaf initiation occurs by periclinal divisions in the second tunica layer high on the apex (arrowhead).

c. Vegetative apex (V) showing two tunica layers. A procambial trace (pr) is beginning to develop in the youngest leaf (L2).

d. An apex in the process of bifurcation to form an inflorescence (I) and a continuation shoot (V). The two tunica layers are present over much of the two product apices. This stage is slightly younger than the one in Figs. 2.43a and 2.43b.

e. A later stage in inflorescence development. Procambial traces (pr) are beginning to develop. Stippling indicates the densely staining cells (aV) which later form a lateral bud in the axil of the penultimate leaf (not shown) near the base of the inflorescence.

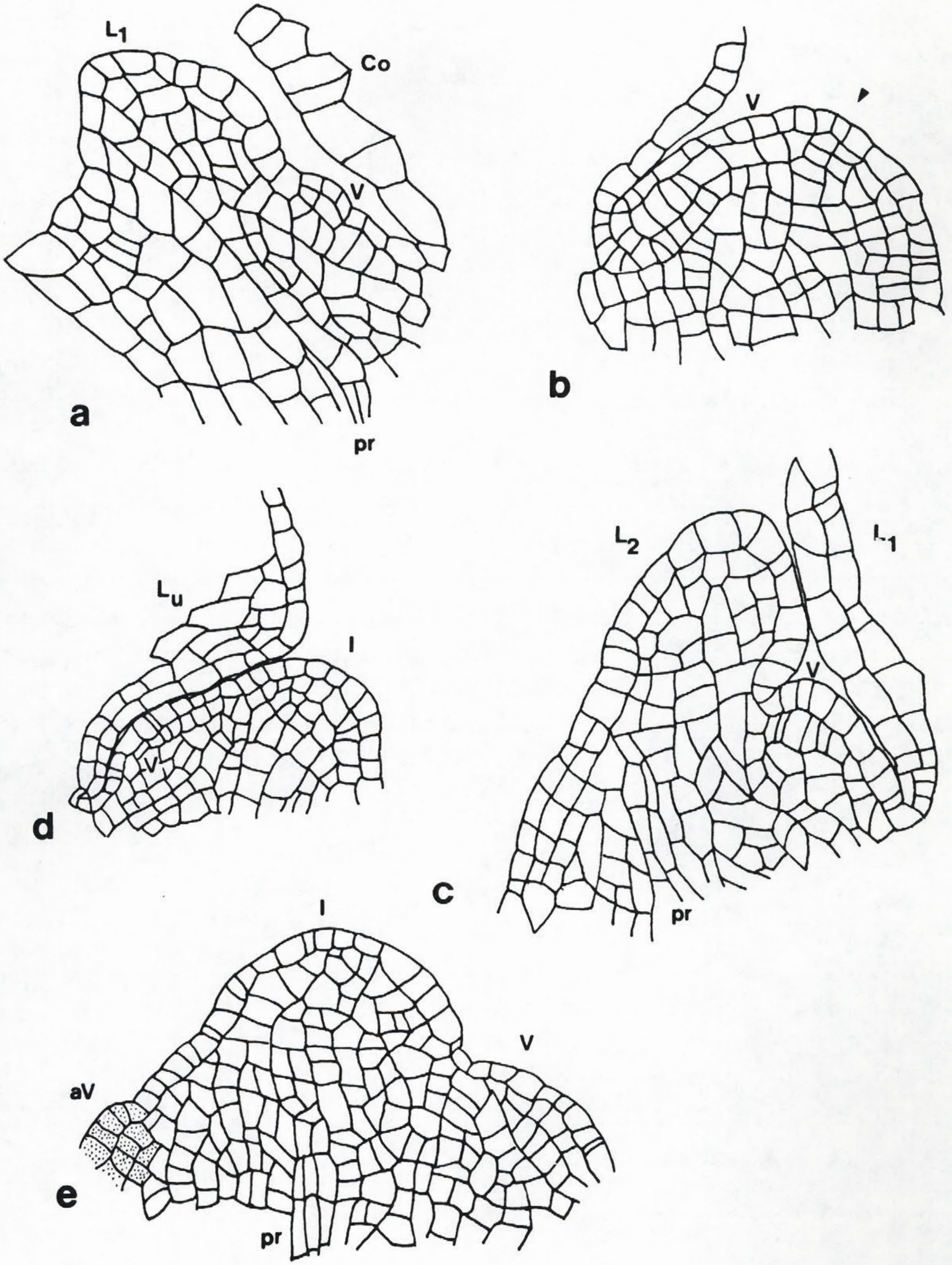
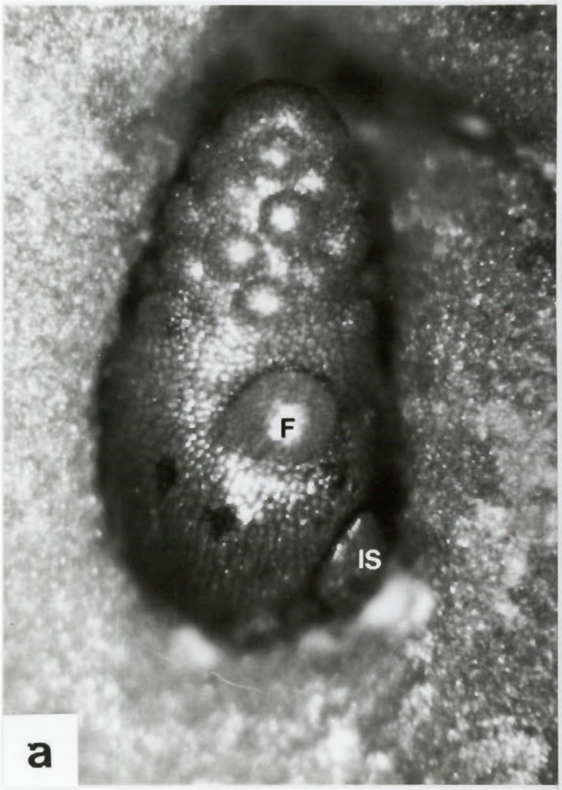

L_1
Co
V
a
pr
V
b
L_u
l
V
d
L_2
L_1
V
c
pr
l
V
aV
e
pr

Figure 2.46 Inflorescence Development. x140.

a. View of young inflorescence from the abaxial side relative to the continuation shoot. Some elongation and floral initiation have occurred. A particularly large floral primordium (F) is found.

b. Side view of a relatively small inflorescence with a terminal flower (large arrowhead). The first formed tepal of each flower is often very large and pouch-like, and oriented so that its median is parallel to the inflorescence axis (black arrowheads). In other flowers, the first tepal is less developed and the flower may be oriented at an oblique angle (white arrowheads).


F
IS
a


b

Figure 2.47 Floral Diagram of Triglochin striata.

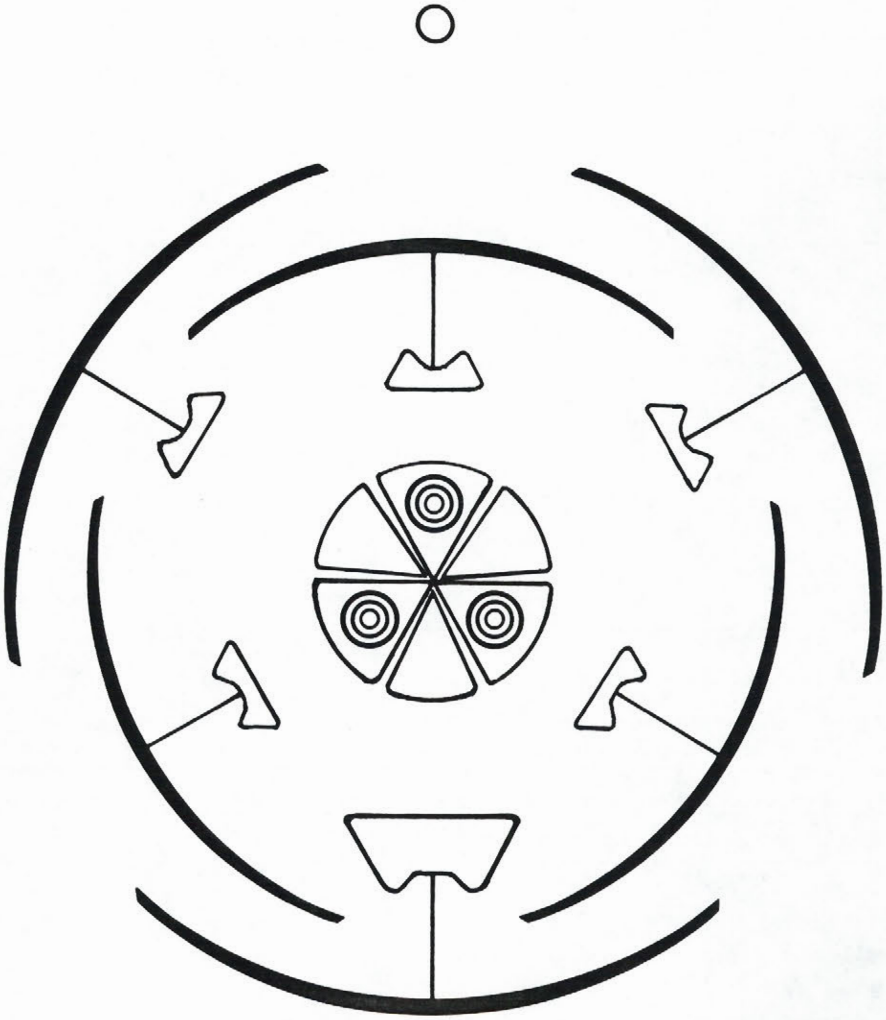


Figure 2.48 Floral Development. x140.

a. - i. Top view. All buds oriented so that the first formed tepal is lowermost in each figure.

a. The first tepal of the outer whorl (Tol) is formed on the lower side of the floral primordium (relative to the inflorescence axis). The other members of the whorl are beginning to form (arrowheads).

b. The outer whorl of tepals have developed. The first tepal of the inner whorl is being initiated between the first and second tepals of the outer whorl (arrowhead).

c. Both whorls of tepals are apparent. The first of the outer whorl of stamens (arrowhead) is forming opposite the first outer tepal (Tol).

d. A slightly later stage than fig. c where a second stamen primordium is visible (arrowhead). The direction of appendage formation is reversed.

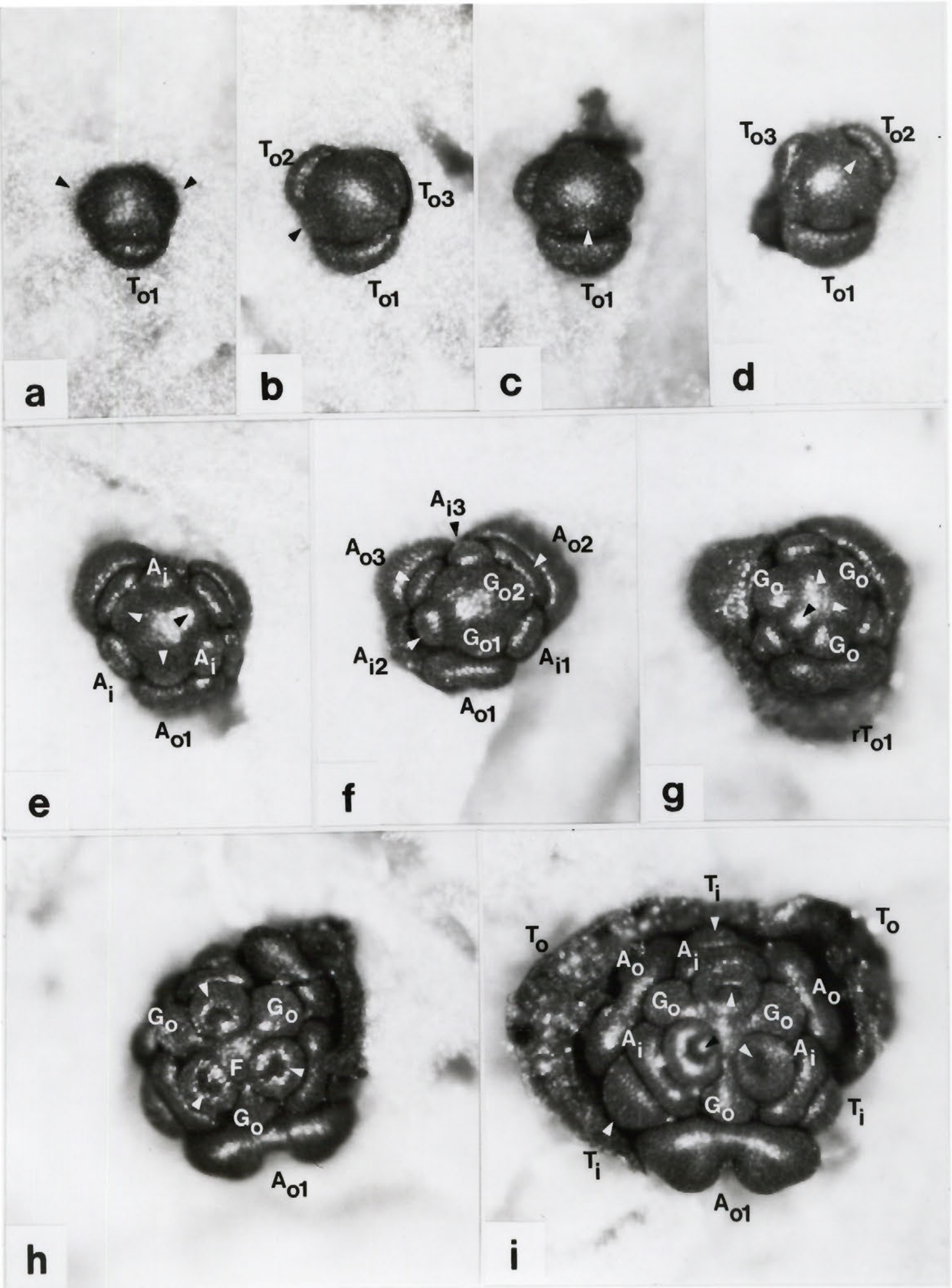
e. The pouch-like first tepal has been removed. A second staminal whorl (Ai) is formed in sequence opposite the inner whorl of tepals. The initiation of carpels is visible (arrowheads).

f. A stage slightly later than fig. e. The sequential initiation of members of each whorl is very clear in this case.

g. Three gynoecial primordia forming the inner whorl opposite the inner tepals and stamens are visible (arrowheads).

h. The inner whorl of carpels form bowl-shaped structures (arrowheads) while the outer whorl remains undeveloped. A large portion of the floral apex (F) remains.

i. A single ovule develops at the base of the adaxial wall of the inner carpels. The inner tepals appear internal to the outer stamens.



To1
a
To2
To3
To1
b
To1
c
To3
To2
To1
d
Ai
Ai
Ai
Ao1
e
Ai3
Ao3
Ao2
Go2
Go1
Ai2
Ai1
Ao1
f
Go
Go
Go
rTo1
g
Go
Go
F
Go
Ao1
h
Ti
To
To
Ao
Ai
Ao
Go
Go
Ai
Ai
Go
Ti
Ti
Ao1
i

Figure 2.49 Side View Showing the Relationship of the Inner Tepals and Outer Stamens. x140.

a. Initiation of an inner tepal (arrowhead).

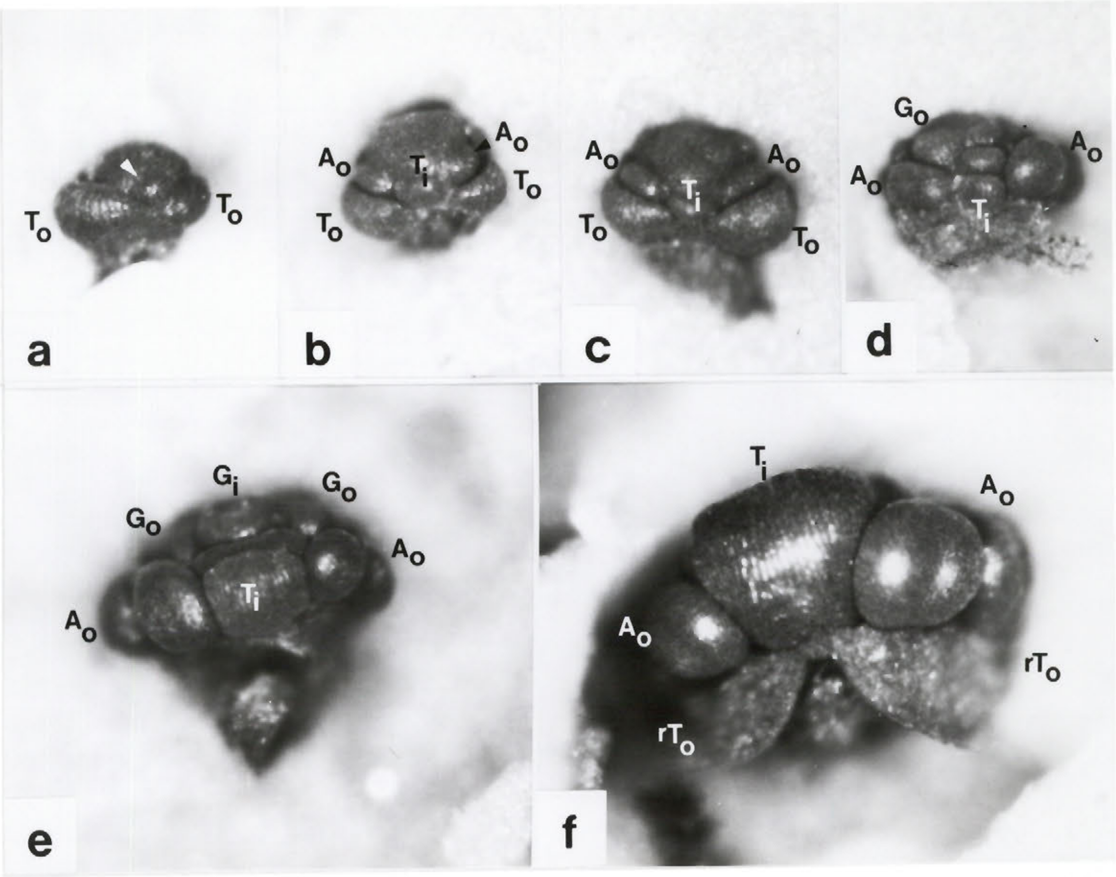
b. The outer stamens (Ao) have been initiated above and in alternation with inner tepals (Ti).

c. A later stage comparable to Fig. 2.48e. The stamens are still clearly above the inner tepals (Ti).

d. The outer stamens expand rapidly laterally and are soon much larger than the inner tepals. They still appear to be inserted at a higher level. (The outer tepals have been removed.)

e. A stage similar to the one shown in Fig. 2.48i. The inner tepals and outer stamens are now inserted at about the same level due to the differential growth of their bases. As the inner tepals begin to expand, their edges grow in such a way that they become internal to the outer whorl of stamens.

g. Slightly older stage than that of Fig. 2.50a. The inner tepals have expanded to cover the inner ring of stamens and the outer stamens appear to be inserted below these tepals.



a
T_o
T_o
b
A_o
T_i
A_o
T_o
T_o
c
A_o
A_o
T_i
T_o
T_o
d
G_o
A_o
A_o
T_i
e
G_i
G_o
G_o
A_o
T_i
A_o
f
T_i
A_o
A_o
rT_o
rT_o

Figure 2.50 Development of the Gynoecium. x140.

a. Top view of a late stage where the outer tepals have been removed. The inner tepals have expanded and their margins may be internal or external to the outer stamens. There may be some rudimentary development of the outer whorl of carpels (arrowhead).

b. Later stage in ovule development. The aborted carpels are usually a solid mass of tissue (arrowhead).

c. A single integument (arrowhead) has developed around the ovule.

d. The development of a second, outer integument (Ino).

e. A slightly later stage than fig. d. A basilar stalk may be distinguished (arrowhead).

f. Anatropous, bitegmic ovule of a flower at anthesis.

g. The development of a stigmatic surface (arrowheads) at the top of the carpel wall. The aborted carpels (G') remain undifferentiated.

h. Sessile stigma of large unicellular and multicellular hairs.

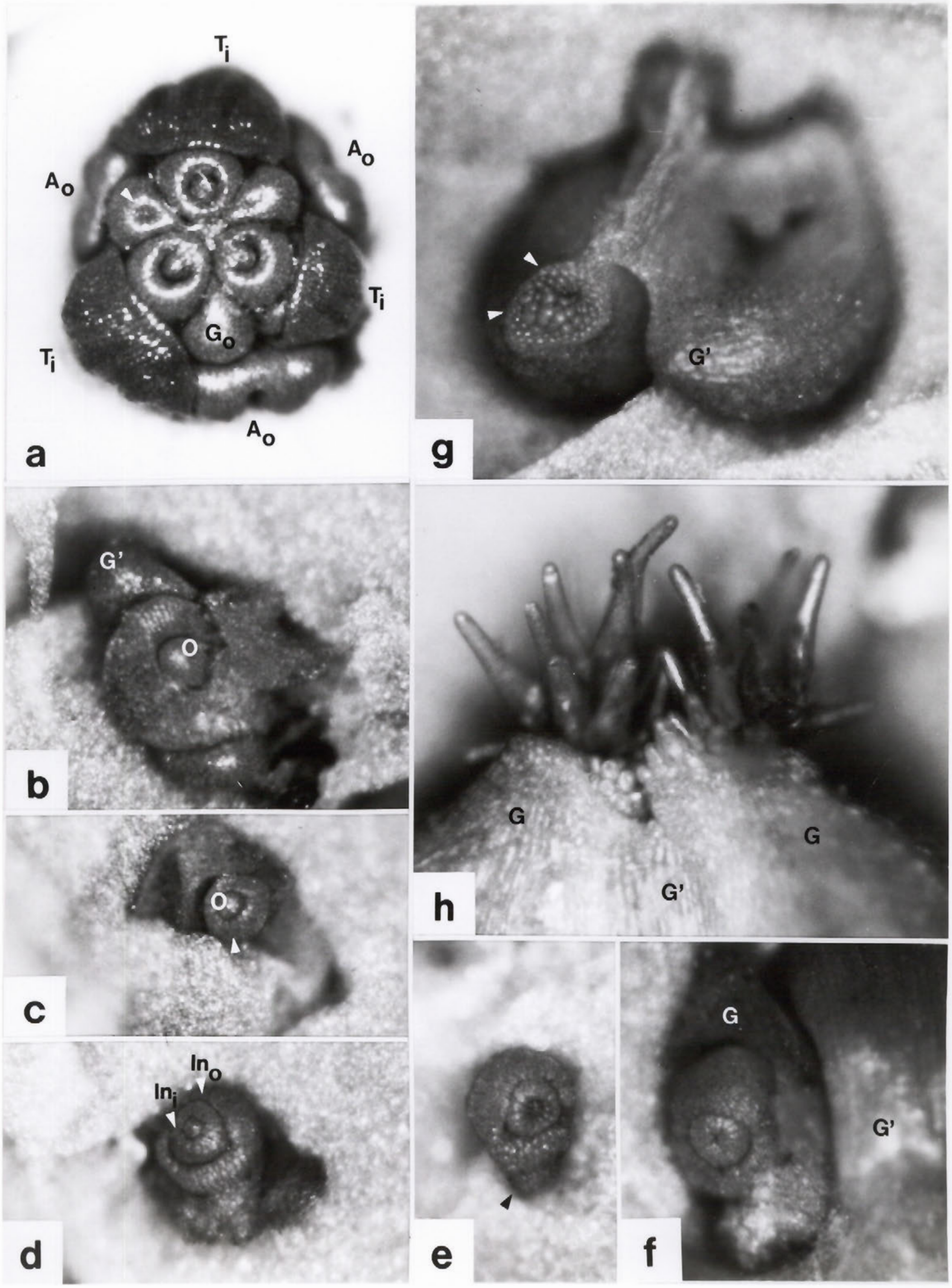

Ti
Ao
Ao
Ti
Go
Ti
Ao
a
G'
g
G'
O
b
G
G
G'
h
O
c
In o
In i
d
e
G
G'
f

Figure 2.51 Sections Showing Stages of Floral Development.

a. Cross section of part of an inflorescence (I) where floral primordia (F) are being initiated by periclinal and anticlinal divisions. The dense staining of the cells involved is indicated by stippling. The cells near the centre of the inflorescence are relatively enlarged and vacuolated. x560.

b. Longitudinal section of a later stage of floral initiation similar to the one shown in Fig. 2.46a. The floral primordia (F) are congested on the inflorescence (I). Procambial traces are indicated by hatched lines. x224.

c. Median longitudinal section of a very young floral primordium (F) comparable to the one shown in Fig. 2.48a. The first tepal primordium is being initiated (arrowhead). x560.

d. Median longitudinal section of a stage comparable to the one in Fig. 2.48d showing the formation of an inner tepal. The first stamen primordium is just being initiated (arrowhead). x560.

e. Median longitudinal section of a floral bud slightly younger than the one shown in Fig. 2.48e. The inner stamens (Ai) have formed and an outer gynoecial primordium is just visible (arrowhead). x560.

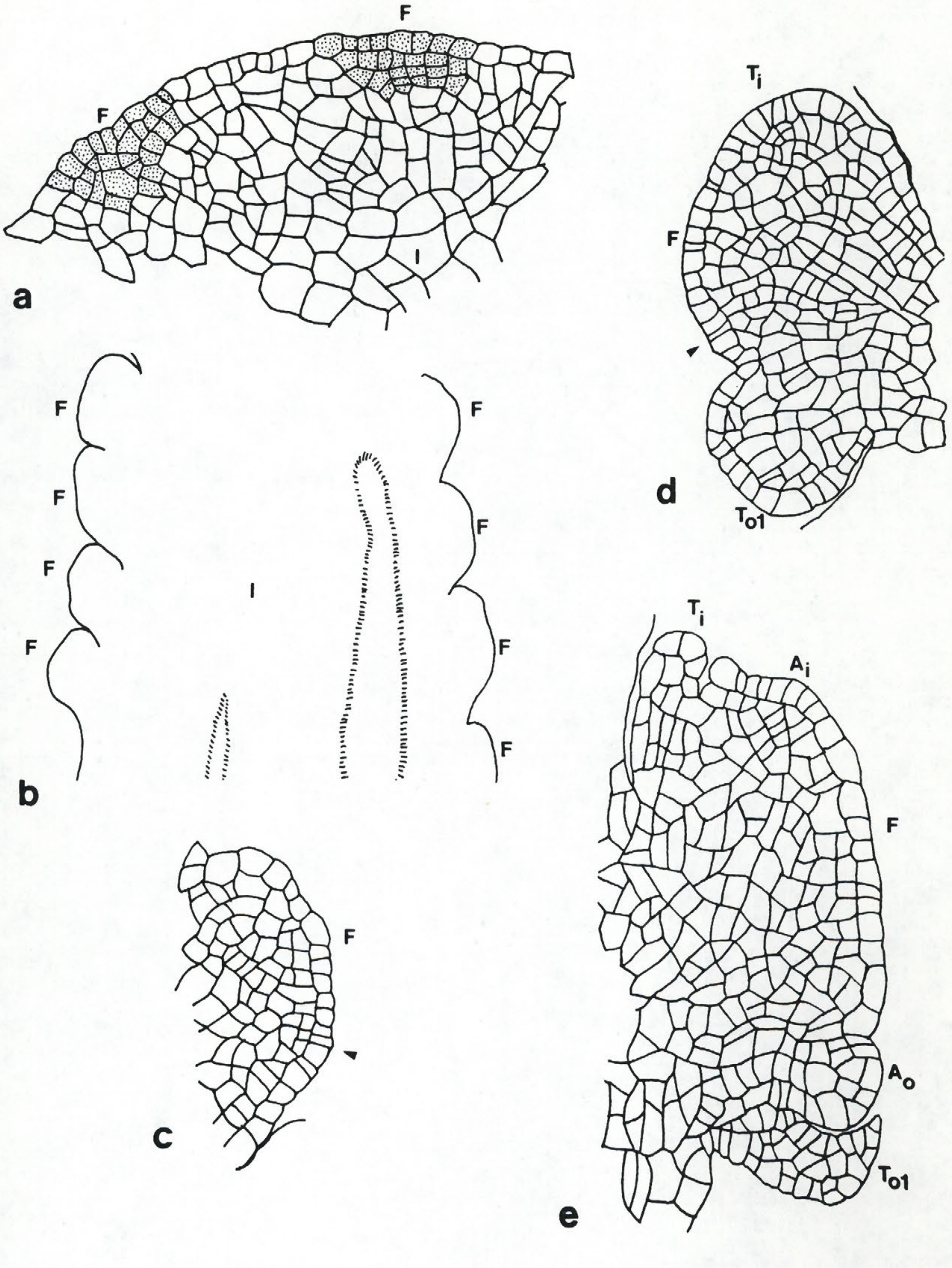

F
F
I
a
F
F
F
F
I
F
F
F
F
b
F
c
T_i
F
T_{o1}
d
T_i
A_i
F
A_o
T_{o1}
e

Figure 2.52 Sections Showing Stages of Floral Development (cont'd).

a. Median longitudinal section of the bud shown in Fig. 2.48e, where an outer ring of gynoecial primordia (Go) has been formed. The outer stamens (Ao) are already larger than the inner tepals (Ti) at this stage. x560.

b. Longitudinal section of a stage showing the formation of the inner gynoecial primordia (arrowhead). A relatively large residual floral apex with larger, vacuolated cells is found. x560.

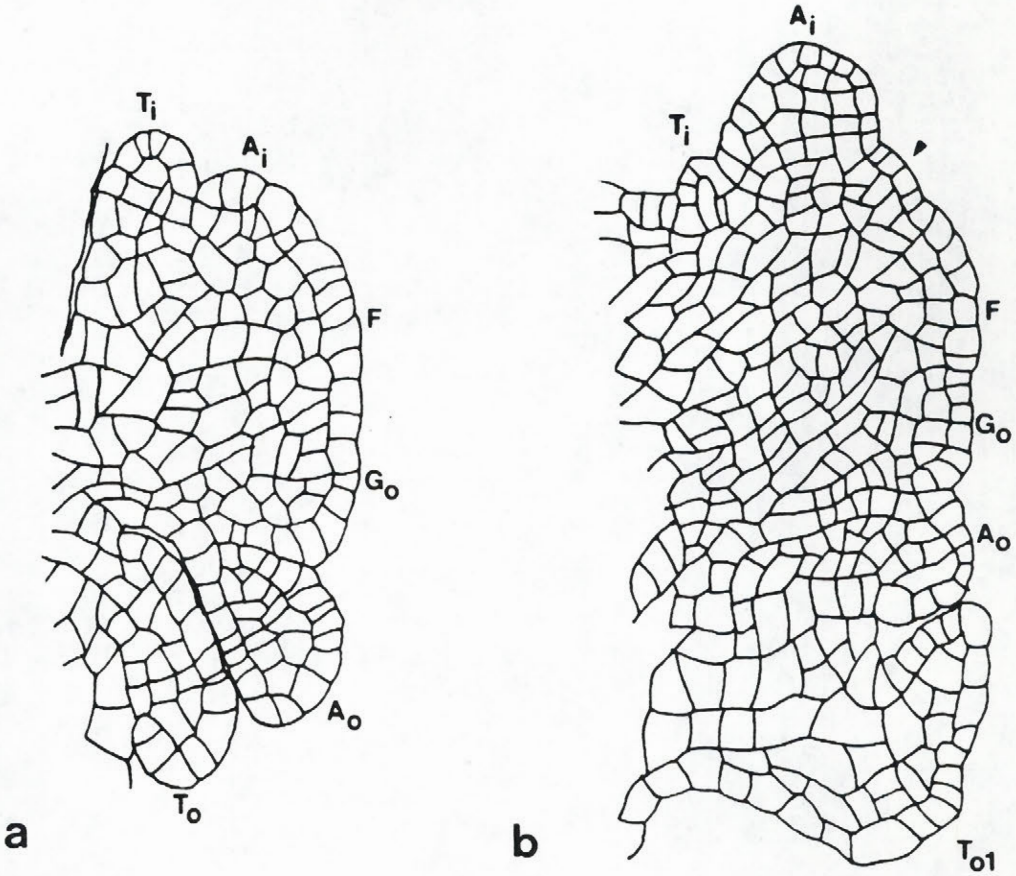

T_i
A_i
F
G_o
A_o
T_o
a
A_i
T_i
F
G_o
A_o
T_{o1}
b

Figure 2.53 Longitudinal Sections through the Flower and Gynoecium. x224.

a. Section through a flower at an angle to the median plane. The bowl shape of an inner carpel (Gi) is indicated by arrowhead.

b. Developed carpel with ovule (O). The outer integument (Ino) is three cell layers thick while the inner one (Ini) consists of only two cell layers. The basal stalk is indicated by the arrowhead. A single procambial strand (pr), running through the abaxial side of the carpel, is shown.

c. Near median section showing a carpel (Gi) with its single ovule and the development of the stigmatic surface in the form of large, elongated cells (arrowheads). The stamen at its base (Ai) remains a rudimentary mass of tissue.

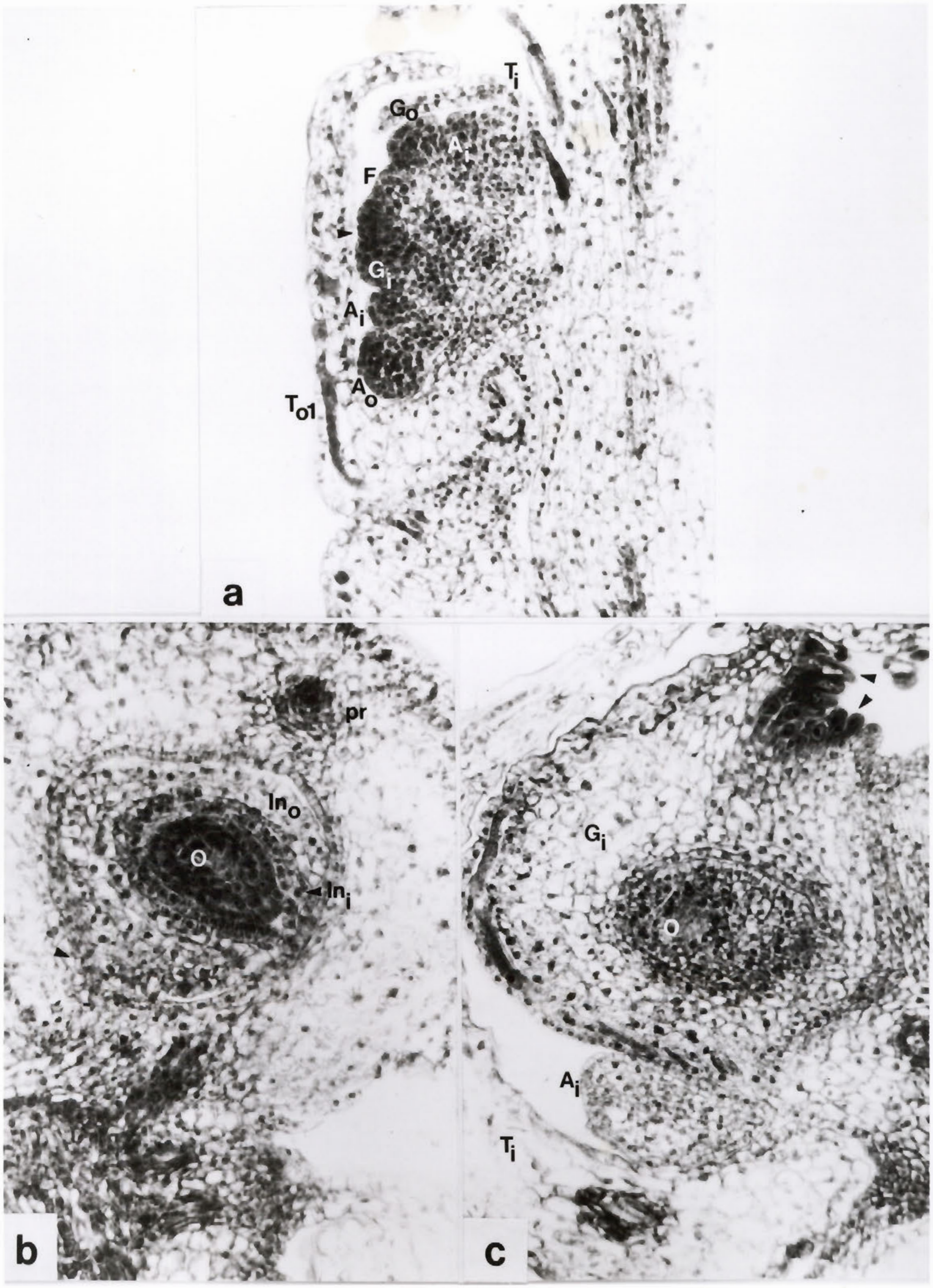

T_i
G_o
A_i
F
G_i
A_i
A_o
T_{o1}
a
pr
In_o
O
In_i
b
G_i
O
A_i
T_i
c

Figure 2.54 Sections Showing Stamen Development. x224.

a. Cross section of a mature flower with two relatively undeveloped stamens. Despite the smallness of the outer stamens (Ao), its size relationship to the inner tepal (Ti) in earlier development is such that the latter still appears internal in position. Note the aborted locules of the outer stamen.

b. Cross section of a mature flower. Part of the inner stamen shown (Ai) is almost solid tissue (arrowhead), as are the carpels of the outer whorl (G').

c. Cross section of the thecae of the lowest stamen (Aol) of the flower shown in fig. b. The pollen grains are well developed. Note the spiral thickenings on the cells of the thecae wall (arrowheads).

d. Near median longitudinal section through the lowermost tepal (Tol) and the stamen opposite it (Aol). The two are attached to each other due to intercalary upgrowth to form a common base (arrowheads). Each is supplied by a separate vascular bundle.

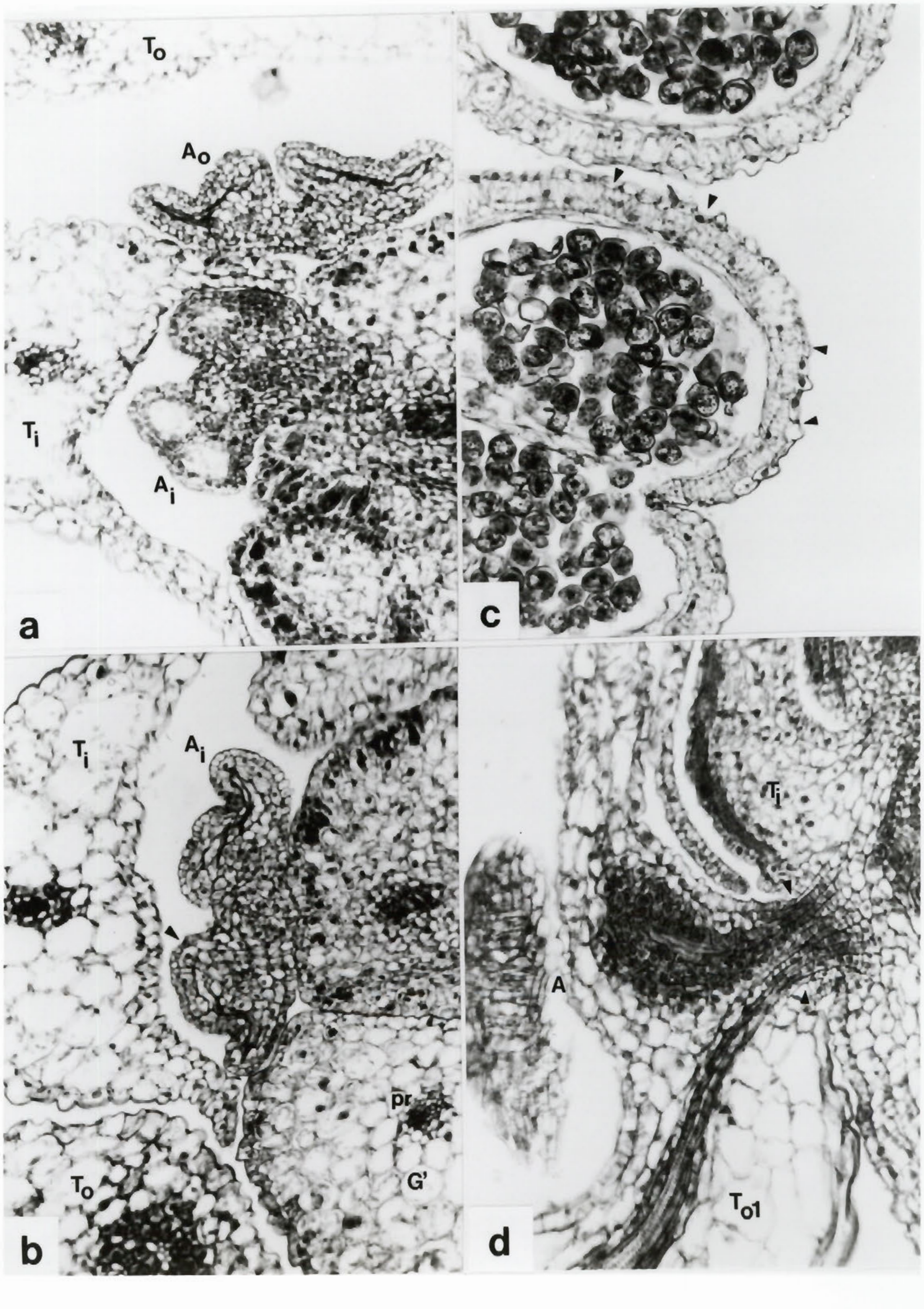
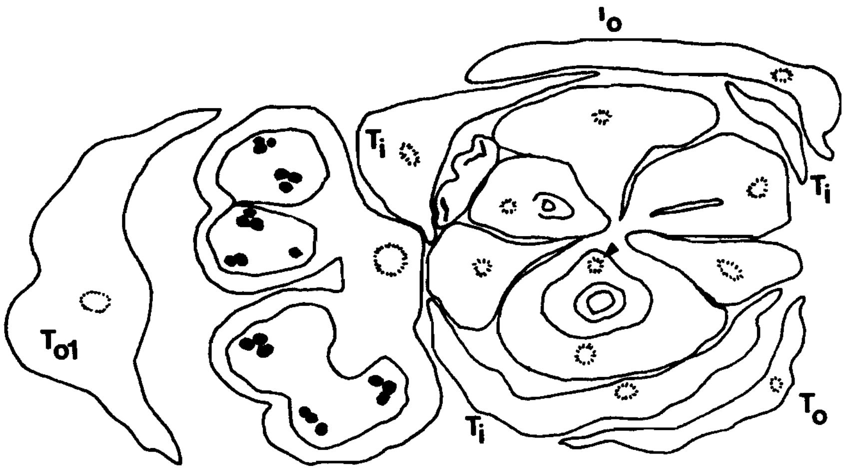

To
Ao
Ti
Ai
a
c
Ti
Ai
pr
G'
To
b
Ti
A
To1
d

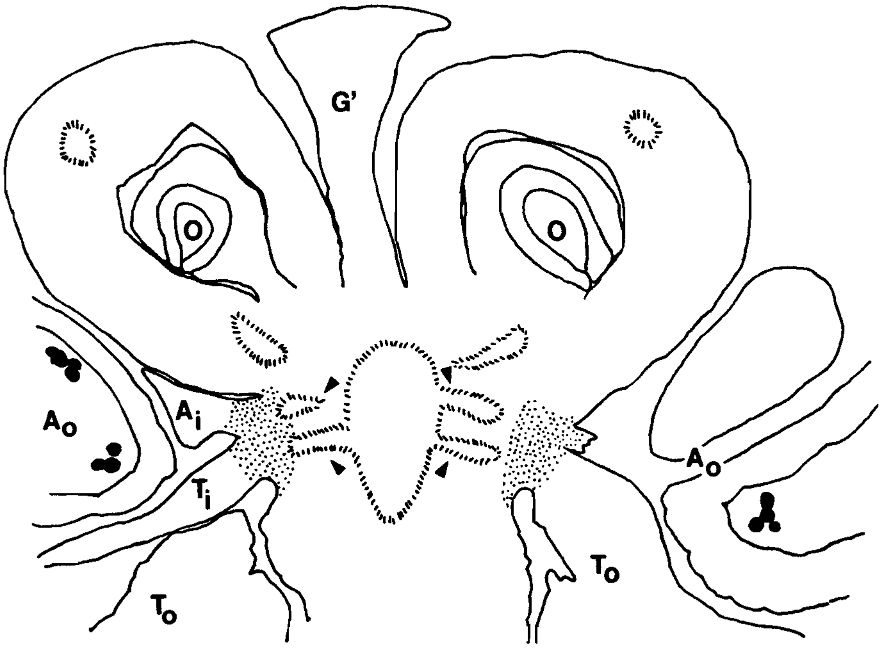
Figure 2.55 Sections through the Flower.

a. Outline drawing of an oblique cross section of a mature flower. The lowest stamen (Aol) is extremely well developed and external to the inner tepals (Ti). Only a few pollen grains are shown. Each appendage has a single vascular bundle (indicated by hatched lines), as does the bitegmic ovule (arrowhead). x45.

b. Longitudinal section through a mature flower. Vascular bundles are indicated by hatched lines. Each stamen and its opposing tepal share a common base due to intercalary upgrowth (stippled area). Their separate vascular bundles are indicated by arrowheads. Note hemitropous appearance of ovules at this stage. x60.



a



b

CHAPTER III

PLANT ARCHITECTURE
AND THE
ALISMATIDAE

INTRODUCTION

In Chapter 1, it was suggested that plant architecture may be understood through an analysis of the existing variations and characteristics of the shoot systems and their morphogenetic processes, and the efforts of Hallé, Oldeman and Tomlinson and other authors in this regard were discussed. It was further suggested that aquatic plants, in particular the subclass Alismatidae, show more complex architecture that is not accountable by the Hallé and Oldeman type models. A more general analysis of the organization of the shoot systems in this subclass, based in part on the nomothetical morphology of Meyen, was proposed.

In this approach, elements or merons of the organization of the shoot system are considered on an a priori basis: given an axial system, what are the architectural processes or elements that result in different growth forms or architectural plans? Some of these elements are discussed in detail in the first chapter. These elements include the characteristics of the shoot itself, e.g., shoot organization and differentiation, orientation, internodal elongation, and the production of new axes. The variations (modalities) that may be found for each specific architectural element or feature (meron) of the shoot system (in the subclass Alismatidae in this case) are evaluated through a survey of the subclass. The architectural plans found in the taxon can then be generated through combinations of the modalities and merons.

From the previous chapter describing the plans of organization in the Alismatidae, it is clear that there are consistent repetitions of certain architectural elements from one taxon to another. Some of these, discussed in detail in Chapter 1, include internodal elongation, especially at selected internodes, resulting in pseudowhorls of leaves separated by long internodes, selective development of axillary buds, and the variation in their time of development. Distinct periodicity in many of these processes adds further regularity to the patterns formed. However, although many aspects of plant organization in the Alismatidae can be described in terms of the elements suggested in Chapter 1, other architectural features of the subclass are beyond the norm in the morphogenesis of higher plants. The interpretation of these features are often controversial when attempts are made to deal with them in terms of the more "conventional" plans of plant organization, i.e., in terms of the classical conception of the shoot and shoot organization. In order to discuss the architecture of the subclass meaningfully, it is necessary to consider some of these elements in greater detail.

As is amply clear from the previous chapters, the understanding and interpretation of the growth forms of the Alismatidae, as in other taxa, depend entirely upon conceptions about the shoot system. Yet the generalizations of shoot organization that apply to the majority of the higher plants are not representative of the subclass. The one example that springs to mind immediately is the interpretation of the bifurcation of the apex in terms of main and lateral axes and therefore in terms of a sympodial or monopodial organization. Another is the frequently mixed nature of the vegetative and reproductive architecture: the vegetization of the inflorescence in the Alismatales and Hydrocharitales on one hand, and on the other, the morphological series in the Najadales, where floral or inflorescence development becomes increasingly integrated into the vegetative organization of the plants. These features are discussed in greater detail below.

APICAL BIFURCATION

Apical bifurcation to form either an inflorescence and a vegetative axis or two vegetative axes is found in many species of the Alismatidae that have been studied in detail. Yet apical bifurcation is inconsistent with the traditional view of the organization and development of shoot systems of higher plants. To recapitulate briefly, this view of the shoot in higher plants is that the shoot consists of shoot and leaf, such that all leaves and shoots are borne on, i.e., lateral to, other shoots. Terminal meristem proliferation is thought to be primitive, and basically next to impossible in the angiosperms.

Given this conception of shoot organization, and the need to maintain its total validity and applicability, it comes as no surprise that apical bifurcation in the Alismatidae has almost inevitably been interpreted as a precocious lateral branching process. Terminal or apical processes are cast into a classical framework by the assumption of the derivation of the apical process from a lateral one, either conceptually for the typologists, or phylogenetically by the others. This approach is quite consistently adhered to in the literature, so that the current controversy, for the most part, lies in whether the plant is sympodial or monopodial, i.e., which of the products of bifurcation is to be considered terminal, and which lateral.

The criteria and arguments used in support of terminal or lateral branching and of a sympodial or a monopodial interpretation in higher plants have been discussed in detail in Chapter 1. The problem remains that depending on the criteria selected, a case may be made for either interpretation (e.g., Charlton and Ahmed, 1973 vs. Wilder, 1974a, see also Lieu, 1979c; Wilder 1974b, 1974c, vs. Brunaud 1976, 1977). There are generally two kinds of criteria used to evaluate the products of bifurcation: those which are based directly on the anatomical and physiological features of the apex, and those which are based directly on interpretations in terms of phylogenetic and typological derivation (Table 1.6).

Criteria based on physiological and anatomical evidence include features such as the size, height and level of insertion of the apices, polarity of cell lineages, vascularization, presence of a shell zone, interruption of the phyllotaxy of the axis from the original to the continuation shoot, and the rhythmicity of growth. There is no uniformity in the organization of members of the Alismatidae in relation to some of these criteria. For example, either one of the bifurcation products may be larger or taller in Butomus umbellatus (Charlton and Ahmed, 1973; Lieu, 1979c). On the other hand, the complexity of some of the shoot systems, e.g., Najas flexilis (Posluszny and Sattler, 1976b, Figures 2-14), makes the determination of the height or level of insertion of the apices difficult at best. Often, the results from the use of different criteria are conflicting: for example, in Triglochin striata, the apparently "lower" apex which ultimately forms the continuation shoot is also larger in girth. In yet other species, a sympodial growth form seems quite tenable (e.g., Alisma triviale, Lieu, 1979b). For other criteria such as the polarity of cell lineages, or the appearance of rhythmic growth, the validity or at least applicability of the criterion itself is in doubt.

The alternative approach used is to interpret the products of apical bifurcation in terms of derivation from a clearly lateral branching process by drawing homologies. The "lateral" axis is "indicated" if it is subtended by a leaf in an axillant position, or if it bears a morphological prophyll or a leaf in a prophyllar position. The difficulties and contradictions in the use of these criteria are discussed in detail in Chapter 1. The developmental history of the morphologically distinct prophyll in Sagittaria latifolia and S. cuneata (Lieu, 1979b, Chapter 2) and in Ruppia maritima (Posluszny and Sattler, 1974b) present examples of the problems encountered in selection of criteria for evaluating plant architecture.

A modification of the above is the "part-for-part" comparisons proposed by Wilder (1974-1975) for the Alismatidae itself. Instead of homologies based on the position of the bifurcation products in relation to the rest of the plant body, the main and lateral axes are determined by their ultimate development: inflorescences in the subclass are considered to always be terminal, and the continuation of the axis lateral. In so doing, positional homologies may be overridden. Correlations can be made between the eventual "fate" of the product apices and their position in relation to the plant, particularly to the ultimate and penultimate leaves formed before bifurcation. For example, the inflorescence is associated with the ultimate leaf and the continuation shoot with the penultimate leaf in the Alismataceae and Limnocharitaceae, and some taxa within the Najadales; the topographic associations are reversed in the Butomaceae and Hydrocharitaceae. According to the part-for-part comparison sensu Wilder, the inflorescence is terminal, and its position in relation to the rest of the plant is a variation with taxonomic groups within the subclass (Wilder, 1975).

One interesting question this approach does raise is whether or not the bifurcation in the subclass is the "same" process; i.e., whether general considerations may apply to the whole subclass, or if analyses must be made on a case-by-case basis. Part-for-part comparisons, evidently, regard all bifurcations as comparable in the production of a terminal inflorescence and a lateral continuation shoot regardless of their positions. On the other hand, to emphasize positional homologies would mean that two "different" processes occur: terminal inflorescence with a continuation shoot in the axil of the ultimate leaf (sympodial growth) and lateral inflorescence in the axil of the penultimate leaf (monopodial growth). It should be emphasized that the application of general considerations to the subclass in drawing homologies assumes that the subclass is a natural one.

Given the current state of our knowledge, the genetic and physiological control processes that govern the determination of the developmental pathway for each of the products of bifurcation, and of bifurcation itself, remain very much black boxes. There is no evidence to support the assumption that position (in relation to the ultimate and penultimate leaves) or identity (vegetative or reproductive apices) is related to the "terminal" and "lateral" attributes in the Alismatidae. Thus, the assignment of these attributes to one or the other morphological feature is basically arbitrary.

Therefore, with regard to the apical bifurcation in the Alismatidae, the situation is at an impasse. The identification of terminal and lateral members of the bifurcation is far from a forgone conclusion. Rather, each apex shows characteristics of both terminal and lateral apices, and partial homologies (Sattler, 1974) may be drawn. Given the level of effort that has been devoted to the issue, it seems unlikely that it can be objectively and unequivocally resolved. The more important question is whether the resolution of the controversy contributes to the understanding of plant architecture, and particularly that of the Alismatidae.

Traditionally and conceptually, sympodial growth can be thought of as an elaboration of monopodial growth. In sympodial growth, the growth of the original axis has been terminated or displaced, and the continuation of the main axis is by the development of a lateral bud. Most frequently, the same basic unit of organization is repeated, i.e., the replacement unit is itself replaced by another identical one, so that the main axis is a succession of higher order segments. The classic example is, of course, the sympodial rhizomes and suckering of the monocots (Holttum, 1955; the "monocotyledonous phase" of Corner, 1949; "Tomlinson's Model", Hallé and Oldeman, 1970).

The example of the sympodial monocotyledonous rhizome is also one of the simpler cases of modular growth, where a series of architectural elements are associated to form a unit of the overall growth form, such that this unit is then repeated at more, or less, frequent intervals (Prévost, 1972, 1978; Hallé, Oldeman and Tomlinson, 1978). As discussed in Chapter 1, modular growth in its broadest sense is a powerful concept in the understanding of plant architecture. Architectural elements, grouped into modules, reveal patterns in the generation of plant form above the level of organs and organ systems such as leaf or flower. The identification of modules in plant growth emphasizes the high level of integration and organization that is not suggested by the common descriptions of "open" or "indeterminate growth". Although Hallé, Oldeman and Tomlinson (1978) have used a restricted definition of modular growth in the architecture of tropical trees, where main and lateral relationships of the axes are clearly defined (see Chapter 1), there is no _a priori_ reason against using this concept in a wider sense in the Alismatidae.

Faced with the unresolved controversy over the interpretation of apical bifurcation characteristic of the subclass Alismatidae, both as to whether it indeed represents derivation through precocious development of a lateral bud, and as to whether it is a monopodial organization or a sympodial one if lateral branching is truly involved, it is proposed that an alternative approach be taken to architecture in the Alismatidae.

Architecture of the taxa of Alismatidae usually consists of distinct modules of growth which are generally, but not necessarily, initiated and terminated by apical bifurcations. If this latter process can be treated as a valid variation in the continuous meron of meristem proliferation rather than a typological or phylogenetic derivation from some other condition, then the problems, or pseudoproblems posed by the assumption of derivation is avoided. The incorporation of apical bifurcation into the continuum of branch production suggested by Shah and Unnikrishnan (1970) is a natural one consistent with the nomothetical approach proposed by Meyen (1973, 1978). It rejects the absolute application of the view that axes can only arise laterally on other axes.

At the same time, the replacement of sympodial units by modules of growth increases the generality of the approach. Sympodial growth by itself refers only to the replacement of successive segments of an axis by higher order branches. The concept of modular growth allows for the assessment of repeating series of architectural elements independent of their modes of origin. The two concepts of growth overlap significantly, so that there may seem to be very little difference in the choice between them. However, the generality of the latter would obviate much of the controversy over the terminal and lateral nature of bifurcation and bifurcation products.

This approach does not reject the use of the descriptors "sympodial" and "monopodial" entirely, since these two terms do convey vital information in many instances. It merely avoids the pseudoquestions resulting from the rigid adherence to the classical conception and terminology of the shoot, so that the repetition of architectural elements and patterns may be revealed.

DIFFERENTIATION OF AXES

The differentiation of vegetative axes plays an important role in the generation of different growth forms. Some of the main features of differentiation include the orientation and duration of growth, phyllotaxy and apex organization, and leaf shape (see Chapter 1). In the Alismatidae, the most common differentiation of axes is the development of both rhizomes and upright shoots. As is illustrated by the variety of seagrasses, differentiation may range from the very distinct, where there are significant morphological differences between the two axis types produced in precise succession, to situations where the difference is mainly in the orientation of the axis and its duration of growth. Examples of the former include Thalassia (Hydrocharitaceae) and Thalassodendron (Cymodoceaceae), where thick rhizomes with scale leaves bear upright short shoots with strap shaped foliage leaves. Examples of the latter include species of Zostera, Heterozostera and Posidonia (Posidoniaceae).

When the aquatic genera are considered, a similar range of forms may be found, particularly in the Najadales. Species of Zannichelliaceae and Potamogetonaceae have generally slender rhizomes with distinct scale leaves. However, in the Ruppiaceae and and possibly the Najadaceae, there is no differentiation of leaf type between rhizomes and upright shoots. Descriptions of rhizomes usually refer to their horizontal orientation and the presence of roots. The lack of a marked dimorphism poses a problem of interpretation. Unlike land plants, aquatic plants grow in a denser medium which supports the plant form and counteracts gravity. A lack of lignification of the shoot system results in generally limp forms where the orientation is determined by water depth and movement. Furthermore, rooting at the nodes is frequent. As a result, the differentiation between rhizome (horizontal stem) and upright axis may be somewhat arbitrary in these families.

In this regard, another point of interest in the description of shoot systems in the aquatic environment is the distinction between rhizome and stolon. General use of the term stolon implies a horizontal axis, usually of a lateral origin, and links the main plant to a new one as a mode of vegetative propagation (e.g., Sagittaria or Vallisneria). Yet sympodial rhizomes are organizationally no different from sympodial stolon systems, especially where both rhizome and stolon are slender and bearing scale leaves, e.g., Potamogeton and Sagittaria species respectively, or where the stolon ends in a tuberous thickening, e.g., in species of Sagittaria. The sole difference rests in the "nature" of the upright axis. If this is considered a new "offspring" plant, then the horizontal axis is a stolon. If the upright axis is thought to be a branch, then the horizontal axis is a rhizome. From the descriptive literature, it is clear that this decision has often been arbitrarily made, and any data drawn from such sources must be analyzed with this in mind. This ambiguity of terminology also serves to emphasize the basic similarity of the architecture of rhizomatous and stoloniferous growth forms in many cases.

INTEGRATION OF VEGETATIVE AND REPRODUCTIVE ARCHITECTURE

Another form of differentiation between axes is the production of inflorescences. Although in the simplest case this may be a solitary flower, many inflorescences are complex shoot systems involving a large number of floral meristems. The inflorescence or reproductive axis is usually differentiated from vegetative axes in many features such as internodal elongation, branching, or the presence of scale leaves instead of foliage leaves. Another part of the classical conception of the shoot is the idea of the irreversibility of the transition from a vegetative apex to a reproductive one (e.g., Gifford and Corson, 1971; Steeves and Sussex, 1974). An inflorescence may be terminal on the main axis, or lateral in position, however, it is not usually intercalated between two successive phases of vegetative growth.

In this respect, the Alismatidae again deviates from the norm. Variations in the reproductive structure of the subclass Alismatidae may be viewed in two general and intergraded perspectives: the vegetization of inflorescences, and the close intermixing of elements of vegetative and reproductive architecture.

Some of the structures found in the Alismatidae may be easily "derived" in terms of sterilization of inflorescences, or replacement of floral buds by vegetative ones. This is found in many genera of land plants as well as in aquatic plants. Examples of these include species of Agave and Allium. The presence of vegetative buds has been reported for many genera of the Alismataceae (Charlton, 1973). Furthermore, the scape of the inflorescence is often horizontal, or falls over. The development of vegetative buds on these axes result in a stolon-like appearance, and account for the term "pseudostolon". Pseudostolon development is frequently, but not necessarily, an ecological response to submergence of the plant.

In Ranalisma (Alismataceae), Limnocharis (Limnocharitaceae) and some of the rosette Hydrocharitaceae with stolons, vegetative and reproductive components are further integrated. The inflorescence frequently involves a series of buds produced by successive apical bifurcations, the last of which, instead of developing into a flower or flowers, forms a new vegetative axis.

In the Najadales, the vegetative structures may often be inextricably linked to the reproductive ones, e.g., in the Najadaceae (Sattler and Gifford, 1967; Posluszny and Sattler, 1976b) or Zannichelliaceae (Posluszny and Sattler, 1976a) where highly reduced male and female "flowers" and "precocious" vegetative branches are closely associated in "nodal complexes" formed by a series of apical bifurcations. References to these mixed growth forms as "inflorescences" do not appear to be appropriate. In the following discussion they are usually referred to as "reproductive axes", a term that is comparable to the description "generative shoots" used for seagrasses (e.g., den Hartog, 1974).

To consider architectural forms entails the consideration of both vegetative and reproductive axes. On the other hand, other species in the Najadales have flowers which some believe to be extremely condensed inflorescence branches or reproductive axes (Uhl, 1947; Eames, 1960; Burger, 1977). However, detailed investigations usually indicate that while possibly showing some characteristics of inflorescences (Groenlandia, Posluszny and Sattler, 1973), these may satisfactorily be described as flowers (Hill, 1900; Cronquist, 1968; Lieu, 1979a). In these taxa, the reproductive and vegetative organization of the plant body remain relatively distinct, and architectural considerations need not include the former.

In summary, although Hallé, Oldeman and Tomlinson have suggested that the organization of the reproductive axes of a plant do not contribute significantly to its architecture (Hallé, Oldeman and Tomlinson, 1978), this clearly cannot be applied to these members of the Alismatidae. Instead, the combination of vegetative and reproductive elements of architecture are integral parts of the modules of growth in the majority of species surveyed in Chapter 2.

ARCHITECTURAL FORMS AND THEIR GENERATION

Despite some of the difficulties of interpretation described above, a survey of the subclass Alismatidae seem to show three major forms:

1. "Rosette" plants with congested upright vegetative axes
2. Plants with elongated upright vegetative axes
3. Rhizomatous forms with or without upright axes.

However, there are many more similarities between the three types than the apparent grouping may indicate. Since all three forms are found in both Hydrocharitales and Najadales, while only the first and the third are found in the Alismatales, this discussion will use this order as a starting point.

As was discussed in the first chapter, the generation of plant architecture is dependent on the proliferation and differentiation of axes, and particularly by repetition of certain modules or sequences of growth processes. Likewise, it is possible to analyze the architecture of the Alismatidae in terms of growth processes and modules.

Conceptually, one may consider the basic unit of architecture in the Alismatales to be an upright vegetative axis, with congested internodes and spiral phyllotaxy. The unit is terminated by the occurrence of an apical bifurcation to produce a reproductive axis in the axil of the penultimate leaf and a vegetative axis (the continuation shoot) in the axil of the ultimate leaf. This unit is initiated either by the previous bifurcation, by germination of a seed, or by development of axillary buds (Fig. 3.1). This is typical of species of _Alisma_, _Burnatia_, _Damasonium_, and _Limnophyton_ (all Alismataceae) and probably _Tenagocharis_ (Limnocharitaceae).

A variation on this theme is the secondarily horizontal orientation of rhizomatous _Sagittaria lancifolia_ and similar species in the same genus

(Fig. 3.1b). Rhizomatous Butomus umbellatus exhibits the opposite positional symmetry of the products of bifurcation; i.e., the reproductive axis is in the axil of the penultimate leaf, and the vegetative axis is in the axil of the ultimate leaf. Rhizomatous growth is also apparent at the initiation of each module. However, the architecture of Butomus can be represented by modular units of congested axes terminated by apical bifurcation, maintaining the basic Alismatalean module of growth while altering positional symmetry and orientation (Fig. 3.1c).

On the other hand, other species of Sagittaria provide further variation in the development of propagation by stolons which are clearly lateral structures. When a series of stolons, i.e., a stolon system, is developed, a very specific pattern of growth is followed (Lieu, 1979b). Each stolon (or stolon segment) and its associated upright axis can be compared to an axillary bud where elongation of one or more of the first internodes have occurred (Fig. 3.2). The development of tubers by accumulation of reserves in the subapical internodes of stolons that have not yet developed the upright axis, in turn, represents merely a temporal halt to this mode of growth: in spring, the tubers germinate by the development of one internode, followed by the development of the usual congested axis and foliage leaves.

Other genera of the Alismataceae are characterized by the integration of vegetative elements of architecture into the reproductive structures. This has been described in detail for Echinodorus and more generally in the rest of the family (Charlton, 1968, 1973 respectively). In Echinodorus, as well as Baldellia, Caldesia, Luronium and Wisneria, the reproductive structure produced by apical bifurcation may be strictly reproductive (as in genera such as Alisma) or may have flower buds replaced by vegetative ones that grow into new upright axes, i.e., pseudostolons. The similarity of pseudostolons with their pattern of pseudowhorls of scale leaves and upright axes separated by long internodes to stolon systems in Sagittaria has been pointed out (Fig. 2.19, see also Lieu, 1979b).

In the pseudostolons of Echinodorus, meristem proliferation to form the new upright vegetative axis is evidently lateral. Other variations on the combination of vegetative elements into reproductive forms exist. Most of these, like Echinodorus, appear stoloniferous. Therefore the term "pseudostolon" may, broadly speaking, include any reproductive axis which has the attributes of a stolon.

In Limnocharis (Limnocharitaceae), the production of floral buds of the reproductive axis is by a series of bifurcations, usually interpreted as a cincinnus (e.g., Wilder, 1974a). One of the two last apices produced develops into a new upright axis. Elongation occurs only below the lowest floral bud.

In Ranalisma (Alismataceae) and Hydrocleis (Limnocharitaceae), the growth of the reproductive axis is initially similar to Limnocharis (compare Figs. 3.3a, b, and c). After a number of floral buds are produced, an apical bifurcation produces one meristem which develops into the new upright vegetative axis while the other is displaced by elongation to repeat the sequence of development of the reproductive axis again and again indefinitely. The number of flowers produced between these long internodes is set, and depend on the genera. The macroscopic appearance of the plant is similar to a stolon system bearing a cluster of flowers (if they do develop) at the base of each upright axis.

The integration of vegetative and reproductive elements of architecture described in the preceding paragraphs can be generalized for the order Alismatales. It has already been pointed out that the stolon system of Sagittaria and the pseudostolon of Echinodorus have much in common morphologically although the former is clearly "sympodial" and the latter is "clearly monopodial". In addition, the vegetization of the reproductive structures of Limnocharis, and Hydrocleis and Ranalisma, is very much comparable to the development of stolons and stolon systems respectively in

Sagittaria species also (Fig. 3.4). In the stolons of species such as Sagittaria cuneata or S. latifolia, the single axillary meristem develops into the upright axis. In Limnocharis, the single meristem produced by apical bifurcation bifurcates further to produce floral buds and a single vegetative axis. Where an axillary bud at the base of the upright axis produces the next stolon segment in species such as Sagittaria "microphylla" and S. "Sinensis", the apex produced in the same bifurcation that produced the vegetative apex in Hydrocleis and Ranalisma undergoes elongation on its proximal side to produce the next segment of pseudostolon, sensu lato.

Therefore, the basic unit of congested, upright vegetative axis may be initiated by, in addition to seed development, axillary bud development, apical bifurcation of the vegetative axis itself, lateral branching, or apical bifurcation of a reproductive axis. If one considers all these processes to be modalities in the meron of meristem proliferation, then the commonality of certain architectural elements of both reproductive and vegetative structures becomes evident. The importance of the results engendered by this approach will be further demonstrated as the remainder of the subclass is discussed.

Architectural forms parallel to those described for the Alismatales may be found in the Hydrocharitales and Najadales. The basic unit of congested upright vegetative axis terminating in apical bifurcation to form vegetative and reproductive axes is found in all the rosette genera of the Hydrocharitales mentioned in Chapter 2. Of these, Blyxa and Ottelia do not develop stolons or pseudostolons, so that at least superficially they are very similar to Alisma. However, more detailed developmental studies are required to confirm this. The same applies to the genus Aponogeton of the Najadales.

However, more interesting patterns of architectural plans are revealed when the rosette species of Hydrocharitaceae with stolons (or pseudostolons) are considered. As described previously, the genera Hydrocharis, Limnobium, Stratiotes and Vallisneria share the same plan of organization. The apex of the upright vegetative axis bifurcates at regular intervals to form a vegetative apex and a reproductive apex. The latter then bifurcates a number of times to produce a maximum of three inflorescence and stolon axes. The stolon axis bifurcates again to produce a new upright axis and a continuation of the stolon system. Elongation of the stolon occurs below every other bifurcation, beginning with the segment proximal to the second bifurcation producing the upright vegetative axis. The entire sequence of developmental processes may be repeated, or as in the case of Vallisneria, only the production of upright axes is repeated (Fig. 3.5).

Traditionally, the architecture of these species has been considered a series of sympodial horizontal and monopodial upright units (e.g., Bugnon and Joffrin, 1963). This would mean that the architecture of the group is very simple, and consistent with many other rhizomatous monocots. More recently, Wilder (1974b, 1974c) has suggested an exactly reversed interpretation based on part-for-part comparisons with related species. It should be pointed out that in the Alismatidae, where all species oberved show apical bifurcation to produce inflorescence and continuing vegetative shoot, part-for-part comparison may be somewhat arbitrary; the assumption that inflorescences are always terminal in position, therefore all structures are sympodial because of their terminal inflorescences, is circular at best.

From the point of view of architectural elements, there is a great deal of similarity between these four genera of Hydrocharitaceae and Ranalisma and Hydrocleis of the Alismatales. Fig. 3.6 shows diagrammatically the two architectural plans. There is a reversal of the position of the products of bifurcation, the inflorescence or pseudostolon being in the axil of the penultimate leaf in the Alismatalean species and in the axil of the ultimate leaf in the Hydrocharitalean species. Entire inflorescences are produced on the pseudostolons in the latter group rather than simply floral buds produced in the former. Furthermore, the upright vegetative axis is associated with the antecedent floral structures in the Alismatalean species and with the subsequently formed ones in the Hydrocharitalean species. This last feature results from the occurrence of internodal elongation at different points along the pseudostolon axis: between the upright axis and the floral buds subsequent to it in the former, and between the axis and its antecedent inflorescence buds in the latter.

Once the emphasis on monopodial versus sympodial organization and the idea of derivation is removed, the artificial barrier of pseudoquestions is dismissed. What remains instead is the organizational features of the different modalities of branch formation and internodal elongation.

Internodal elongation of the upright axis in the Najadales and Hydrocharitales result in further variations in the growth forms. Species of the emergent families of Scheuzeriaceae and Juncaginaceae show some degree of internodal elongation, although their axes remain stiff and brittle rather than limp as in the submerged forms in these two orders. Sympodial stolons are well documented for the genera Triglochin (Juncaginaceae, Fig. 3.7f). (The organization of the apparently rhizomatous T. procera of Australia is not well studied.)

The remainder of the species showing internodal elongation are submerged in habit. Their organization may again be related to the simple upright unit of vegetative growth first identified for the Alismatales. Maidenia (Hydrocharitaceae) may be considered an analogue of this simplest case, with the additional feature of internodal elongation: each upright axis flowers by apical bifurcation to form the inflorescence and continuation shoot. No lateral branches are usually formed (Figs. 3.7a, c).

In other species of the Hydrocharitaceae, namely Egeria, Elodea, Lagarosiphon and Nechamandra, development of axillary branches occurs (Figs. 3.7b, d). This is seldom found in the rosette species of the Alismatidae, except for the development of stolons and stolon systems. Yet the difference between these branches and stolons is mainly a period of axis dimorphism in the case of the latter, where a horizontal axis segment bearing only scale leaves is produced (compare Figs. 3.7d, e). The situation of Hydrilla (also Hydrocharitaceae) is only a little more complex in that a turion-like axis is produced, and branching occurs by development of vegetative buds on this axis.

The transformation from this pattern to that of the Potamogetonaceae, Zannichelliaceae, Ruppiaceae and Najadaceae involves two features of growth. Firstly, the production of branches is much more freqent in the above four families, particularly from axils closest to the bifurcating apex. Secondly, the development of the upright axis from morphologically distinct, sympodial rhizome systems, is also common (Fig. 3.7f). In the Zannichelliaceae, bifurcation may occur only on lateral shoots (Pseudalthenia), or on both main and lateral ones. The product of bifurcation that normally develops into the continuation shoot, often bifurcates again after the production of one or two leaves. In Althenia filiiformis, only a single reduced leaf or bract is formed, and the shoot system is comparable in organization to a cincinnus (Posluszny and Tomlinson, 1977).

The occurrence of successive bifurcations is prevalent among the pseudostolons of the Limnocharitaceae and Hydrocharitaceae. In fact, the organization of that of Limnocharis has also been described as a cincinnus (e.g., Micheli, 1881, Wilder, 1974a). However, organizationally, the so-called sympodial genera of Zannichelliaceae is more similar to an elongated, branched, Alisma. The reproductive axis produced by the initial bifurcation results only in an inflorescence. The other, the continuation shoot, bifurcates again to produce further inflorescences and vegetative axes.

A similar plan occurs in the genus Najas. Apical bifurcation of the main axis produces a continuation shoot and another apex which bifurcates again immediately to form a floral bud and another vegetative axis. The latter develops rapidly to repeat the same pattern of organization. The two vegetative axes are extremely close in development, so that the adult plant has often been erroneously described as "dichotomously branching" (e.g., Correll and Correll, 1975). Organizationally, Najas may be compared to genera such as Limnocharis. Although radically different in appearance, the difference between the two architectural plans lies mainly in the number of floral buds produced by bifurcation of the reproductive axis, and the rate of development of the vegetative axes (Fig. 3.8).

Up to this point, the architecture of the seagrass families, Cymodoceaceae, Posidoniaceae and Zosteraceae, and the marine Hydrocharitaceous genera, have not yet been considered. Studies on the architecture of the seagrasses have been reviewed by Tomlinson (1974). Although morphological studies have been carried out for selected species of seagrasses (e.g., Bornet, 1864; Ostenfeld, 1916; Setchell, 1929; Tomlinson and Bailey, 1972), one is immediately struck by the relative scantiness of detailed studies of whole plant development and morphology when compared with the literature on the freshwater taxa (although even many of these are not studied in detail).

Developmental studies of aquatic Alismatidae have shown the extensive integration of vegetative and reproductive architecture discussed in an earlier section. This feature is likely to play a significant role in the architecture of the seagrasses also. This idea is supported by the recent study by Tomlinson and Posluszny (1978), which showed the development of "precocious renewal growth shoots" in the inflorescence of Syringodium filiforme. This characteristic is comparable to the production of continuation shoots by apical bifurcation in aquatic families of Najadales such as Ruppiaceae of Zannichelliaceae described in Chapter 2 (also Posluszny 1976; Posluszny and Tomlinson, 1977).

Although the details of vegetative and reproductive organization and development of the seagrasses are not as well studied as the freshwater Alismatidae, their vegetative architecture may be related to that of the freshwater taxa. In the seagrasses, the overall emphasis shifts slightly more towards the horizontal axis. All these plants are characterized by rhizomatous growth, although most also develop some form of upright axes.

Again, one may start with the relatively simpler growth forms. These include the genera Enhalus (Hydrocharitaceae) and Posidonia (Posidoniaceae), which have monomorphic rhizomes bearing erect leaves. Branching is diffuse and irregular in both, but axillary buds are found in Enhalus and apical bifurcation occurs in some species of Posidonia. Inflorescences are described as lateral and rare in occurrence (Tomlinson, 1974). Enhalus has congested internodes while periods of long and short internodes alternate in Posidonia. With minor variations, the plan of orgnization of these genera are comparable to those of Butomus and the rhizomatous Sagittaria species in the Alismatales.

The remainder of the genera all have upright short shoots which may or may not be morphologically distinct from the rhizome. Only the latter kind are referred to as dimorphic (Tomlinson, 1974). In addition to shoot differentiation, these genera are usually distinguished by their modes of upright axis production: monopodial branching, sympodial branching, or apical bifurcation. The last name group is usually considered sympodial, although Tomlinson and Bailey (1972) have interpreted the bifurcation in Thalassia (Hydrocharitaceae) as monopodial branching. Figs. 3.9 and 3.10 show the partitioning of the genera in relation to the two features, shoot differentiation and upright axis production.

The organization of Heterozostera (Zosteraceae) is the simple, sympodial one characteristic of many monocots. Amphibolis and Thalassodendron (Cymodoceaceae) differ from Heterozostera in the occurrence of a distinct shoot dimorphism. In addition, while erect shoots can produce other erect shoots directly, the production of new rhizomes is often associated with basal nodes of upright shoots in both Amphibolis and Thalassodendron. The vegetative architecture of Heterozostera and these two genera can be compared with that of the Ruppiaceae and Potamogetonaceae respectively. Although interpreted as a monopodial structure (Tomlinson and Bailey, 1972), the architecture of Thalassia is very similar to that of Amphibolis and Thalassodendron. However, its organization is more precise, particularly in that new rhizomes can be formed on short shoots, and short shoots only on rhizomes.

Likewise there is a certain pattern to the organization of the seagrasses with monopodial rhizomes with or without shoot dimorphism. Phyllospadix, Cymodocea, Zostera and Halodule are all monomorphic, usually monopodial genera where the horizontal rhizome is only produced by branching of the rhizome (or long shoot) itself. Short shoots end in terminal flowers during the reproductive period in Cymodocea and Halodule. Sympodially branched generative shoots are produced in Zostera and Phyllospadix. Long shoots in Zostera and Halodule may also be terminated by flowering, resulting in a sympodial organization.

Syringodium differs from this group in three features. It has dimorphic axes, reproductive structures may be terminal or lateral (not just terminal) in position, and rhizomes or long shoots may be produced on either long or short shoot (not just on the long shoot itself).

The organization of the short shoot of Halophila varies with the taxonomic subgroups. A pair of basal scale leaves are formed, and new rhizome segments, or rhizome segments or short shoots are developed from the axils of the scale leaves in Sections *Spinulosae* and *Microphila*, and *Americanae* respectively. Two to four foliage leaves are formed before reversion to rhizomatous growth in Section *Halophila*. Inflorescences are positioned in the axils of the basal scale or foliage leaves.

Thus, even though relatively little detail on exact branching relationships and on integration of vegetative and reproductive architecture in the seagrasses, patterns of organization can still be recognized. Furthermore, architectural plans in the simpler growth forms can be related to other freshwater Alismatidae (compare Figs. 3.7 and 3.10).

The prevalence of the horizontal axis in the seagrasses has been pointed out. In the simpler forms such as *Enhalus* and *Posidonia*, these can be compared to *Butomus umbellatus* and species of *Sagittaria*. The growth of these species, in particular *Sagittaria lancifolia*, can be described as a horizontal variation on the congested upright vegetative axis unit basic to other Alismatales. This is analogous to the "prostrated parallels" idea suggested by Jeannoda-Robinson (1977) discussed in Chapter 1, where the rhizome is considered in terms of a prostrated or horizontal analogue to the upright axis. Superficially, this seems to be an attractive idea. However, as has been pointed out in the same chapter, this overlooks the processes and characteristics inherent to orthotropic, "upright" growth and plagiotropic, "prostrated" growth.

Furthermore, the gradation of architectural forms from upright axes with horizontal stolons or pseudostolons to sympodial or monopodial rhizomes with upright shoots in the architecturally more complex taxa of the Alismatidae cannot be described in terms of prostrated parallels. In these genera, analogies cannot be drawn between the upright axes and the rhizome system. Architectural forms in the Alismatidae with rhizomes do not develop in parallel with upright axes. Instead, the horizontal axis is integrated into the repertoire of variations or modalities of shoot axes in the subclass.

SUMMARY

Despite the lack of information on the reproductive architecture of the seagrasses, it can be seen that the complexity of architecture in the Alismatidae can be described by combinations of morphogenetic elements. The diversity of form encountered in the subclass can be accounted for by variations in these combinations and their transformations one to another. Figure 3.11 shows some of the variety of growth forms in the Alismatidae by genus, and the major relationships between these forms in terms of their architectural elements.

From this analysis, several basic and non-exclusive elements are identified. These include the following:

1. Meristem proliferation by a continuum of processes ranging from monopodial branching through apical bifurcation to sympodial branching. Products of the proliferation may be reproductive, vegetative, or a combination of both.

2. The time of development and position of the additional meristem(s).

3. The differentiation of axes. This includes differences in geotropic response and its associated morphology, the occurrence and location of internodal elongation, and the number and differentiation of organs on the axis.

4. Combinations of the above three processes; e.g., the development of stolons may be thought of as proximal meristem proliferation and differentiation of elongated, diageotropic axes with scale leaves.

These are the features suggested through deduction in Chapter 1.

From the basic unit of organization (such as Alisma) described in Chapter 2, the growth forms of the Alismatidae may be transformed one to another by variations in the occurrence and specific details of these four elements. For example, in terms of branching pattern and shoot architecture, the occurrence of internodal elongation and vegetative branching is the major difference between the basic unit of growth of Alisma and many of the submerged genera of Najadales. Successive bifurcation of the reproductive axis and formation of new upright axes characterize diverse rosette genera of Alismatales and Hydrocharitales such as Ranalisma, Hydrocleis and Stratiotes. These are differentiated one from another largely by the location of internodal elongation and other details of differentiation such as number of flowers or leaves.

Less frequent transformations between growth forms include the relationship of Limnocharis flava to Najas flexilis, where the difference between the branching patterns of the two lies in the timing and extent of additional axis development. The common organization of the stolon system of Sagittaria subulata and the pseudostolon of Echinodorus differ only in their mode of origin: from an axillary bud in the former and a bifurcation product in the latter.

There is a precise grouping of processes into modules in each taxa. These modules are then reiterated in the course of development and growth of the plant. This view allows for a convenient analogy between the realization of instructions in the genetic program of the development of plant form, and the execution of instructions in digital computer programs. Modularity and reiteration of basic units at all levels may be compared to the use of subroutines and subprograms in computer programming, resulting in the requirement of a simpler instruction set to achieve the same goal, be it generation of plant form or problem solving.

Variation in form results from the different combinations of the modules or subroutines. Although three major forms are identified in the current effort, one cannot overstate the importance of the interrelation these forms by varying the occurrence of component morphogenetic processes in each. This emphasis results in a more dynamic, non-typological approach to plant architecture, which can also account for the plasticity and variation that is found in nature.

Another advantage of the approach taken here is that it permits a more comprehensive and unified view of growth forms in the Alismatidae than has been previously attempted. A framework within which diverse architectural plans may be evaluated is created. This is independent of interpretation and its associated problems characteristic of previous approaches to growth forms in the subclass (e.g., Wilder, 1975). Although much of the existent information on the architecture of the Alismatidae has been reviewed and satisfactorily placed in the context of the current approach, a great deal still remains to be learned, particularly where the seagrasses are concerned. This framework for the study of Alismatidae architecture also allows for the incorportation of new observational data as they become available.

List of Symbols Used

↑ -- vegetative axis

○ -- flower

● -- inflorescence

▶— -- ultimate leaf formed before bifurcation

▷— -- penultimate leaf formed before bifurcation

× -- scale leaf

╪ -- axis with congested internodes

┼ -- axis with internodal elongation

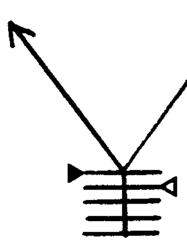
Figure 3.1 Simplified Diagrams of Basic Architectural Units

a. Basic upright vegetative axis, as in the genus Alisma. Note that the continuation shoot is in the axil of the ultimate leaf formed before bifurcation.

b. Horizontal vegetative axis found in Sagittaria lancifolia. Axillary branching to form new rhizome occurs proximal to the bifurcation.

c. Horizontal vegetative axis found in Butomus umbellatus. Successive units of growth and axillary branching are shown. Note that the continuation shoot is in the axil of the penultimate leaf.

a



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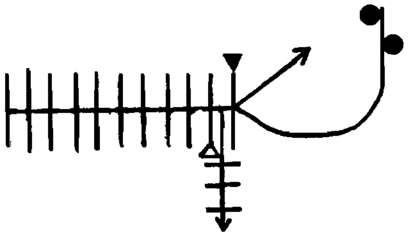

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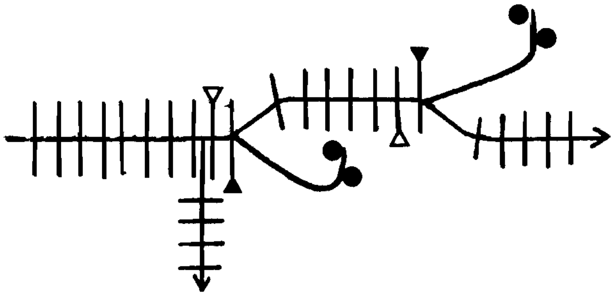
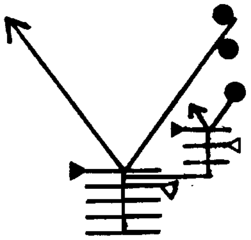


Figure 3.2 Simplified Diagrams of Upright Axes Showing Axillary Branching

a. Axillary branch reiterates development of the main axis. Found in certain populations of *Alisma triviale*.

b. Axillary stolon bearing scale leaves and forming a single new axis; e.g., *Sagittaria cuneata*, *S. latifolia*.

c. Formation of sympodial stolon system with multiple new axes: each segment of the stolon consists of one internode between the prophyll and the first scale leaf; e.g., *S. subulata*.



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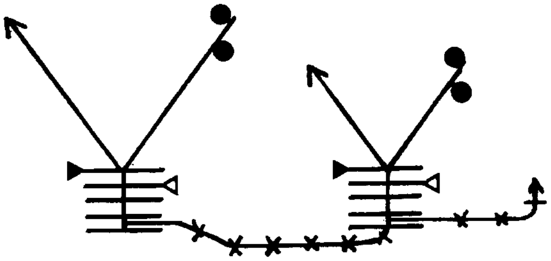

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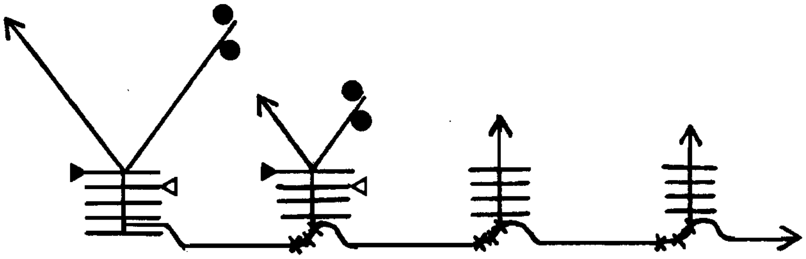


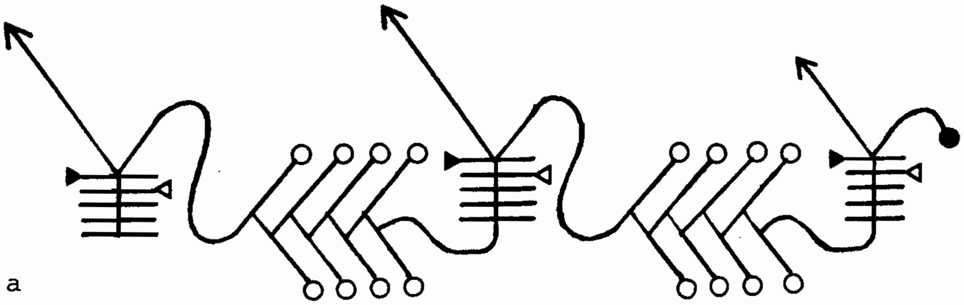
c

Figure 3.3 Diagrams Showing Interrelationship Between Various Species of Alismataceae and Limnocharitaceae

a. *Limnocharis flava* (Limnocharitaceae).

b. *Hydrocleis nymphoides* (Limnocharitaceae).

c. *Ranalisma humile* (Alismataceae).



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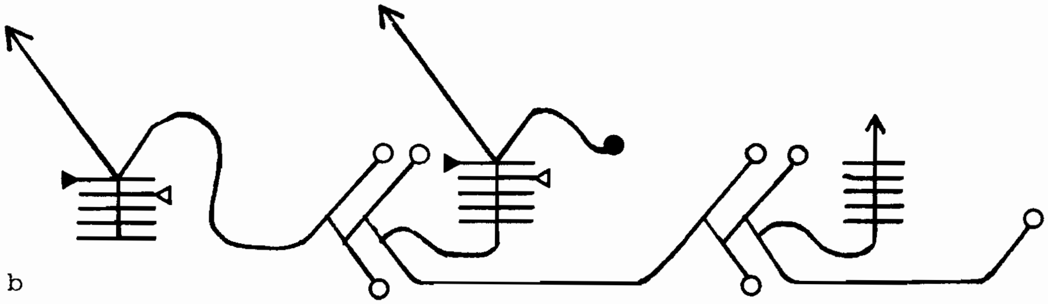

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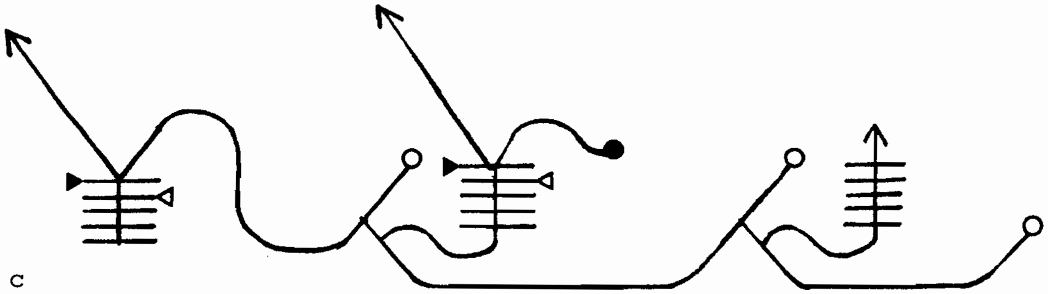

c

Figure 3.4 Development of New Upright Vegetative Axes by Bifurcation of the Reproductive Axis and by Axillary Branching

a. Limnocharis flava. A single upright vegetative axis is formed per reproductive axis.

b. Sagittaria cuneata. Stolon with a single vegetative axis.

c. Ranalisma humile. Multiple upright vegetative axes are formed per reproductive axis.

d. Sagittaria subulata. Stolon system with multiple vegetative axes.

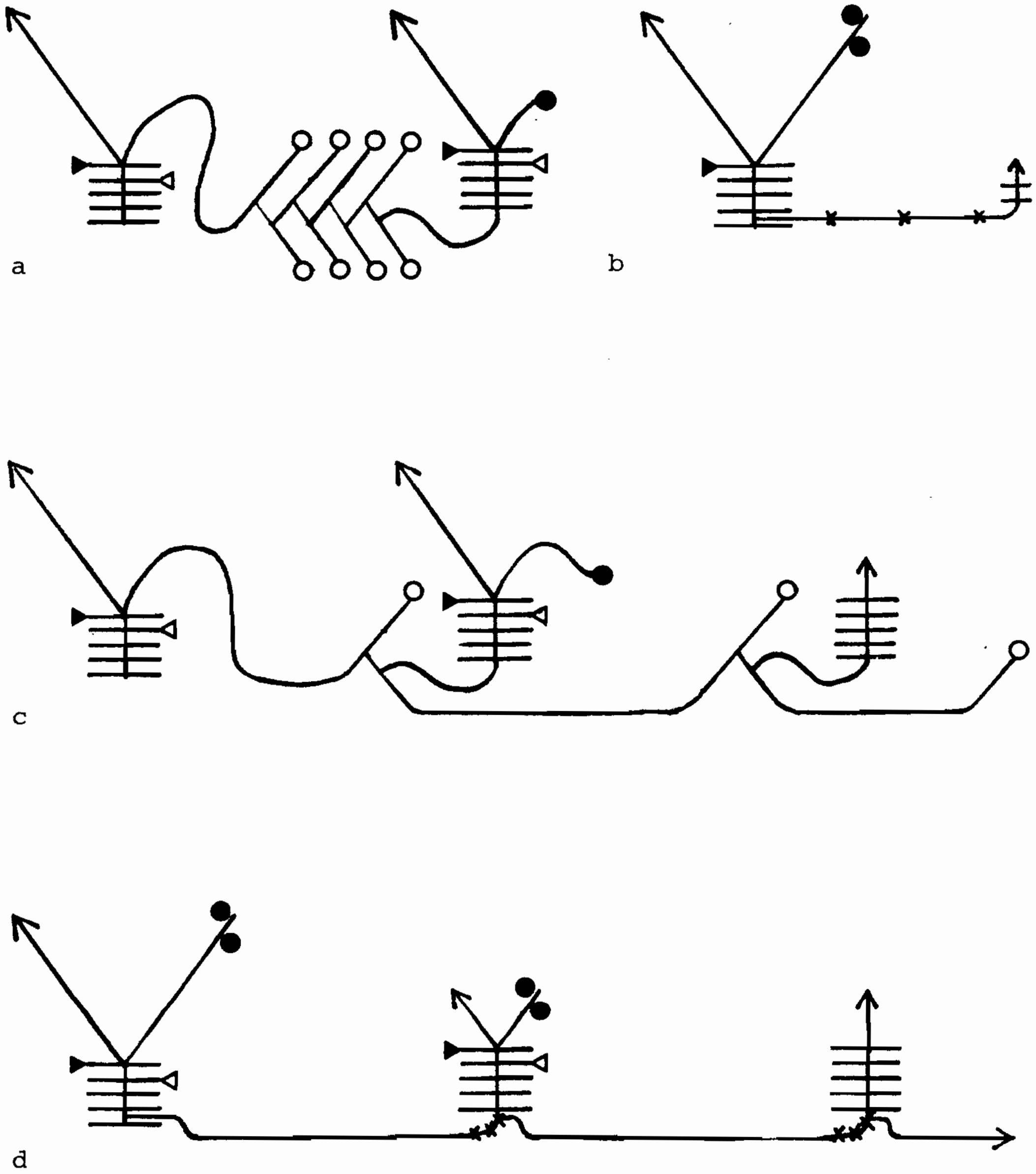
a
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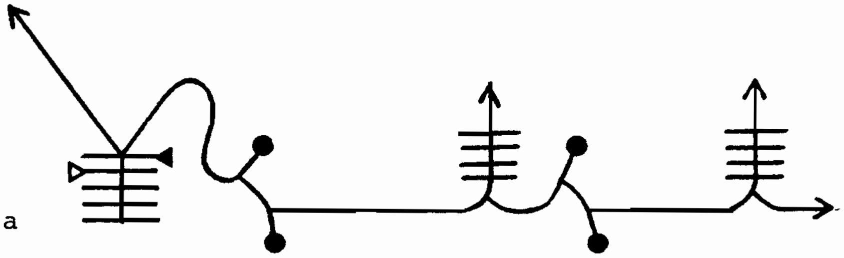
Figure 3.5 Simplified Diagrams Showing Organization of the Reproductive Axis in the Hydrocharitales

a. Usual development of reproductive axis. A first series of bifurcations produce sterile and fertile components and a stolon axis. The last-named bifurcates again to produce an upright vegetative axis and a continuation of the stolon axis. Internodal elongation occurs proximal to the upright axis. This sequence is then repeated.

b. Pistillate *Vallisneria americana*. After the first upright vegetative axis is formed, successive units of stolon axis only bifurcates to form more upright axes without forming inflorescences.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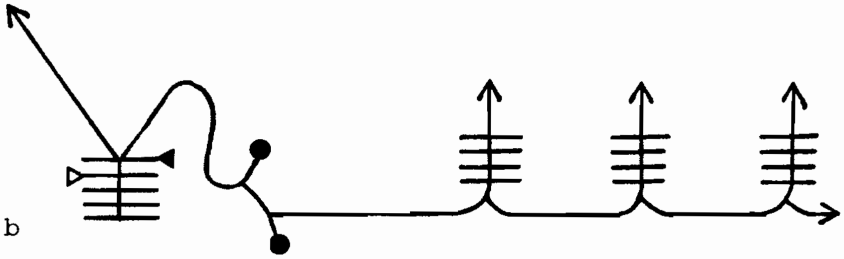
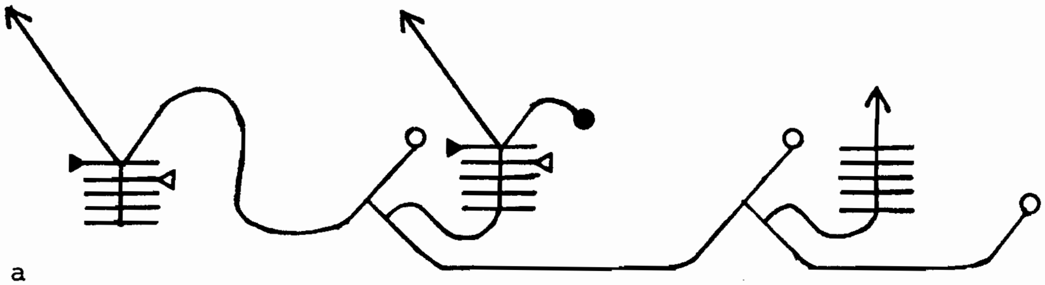

b

Figure 3.6 Comparison of the Organization of the Reproductive Axes in the Limnocharitaceae and the Hydrocharitaceae

a. *Ranalisma humile* (Limnocharitaceae). The reproductive axis is in the axil of the penultimate leaf. Internodal elongation occurs distal to the upright vegetative axis so that this axis is topographically associated with antecedent floral bud(s).

b. *Limnobium spongia* (Hydrocharitaceae). The reproductive axis is in the axil of the ultimate leaf. Internodal elongation occurs proximal to the upright vegetative axis so that this axis is topographically associated with subsequently formed inflorescences.



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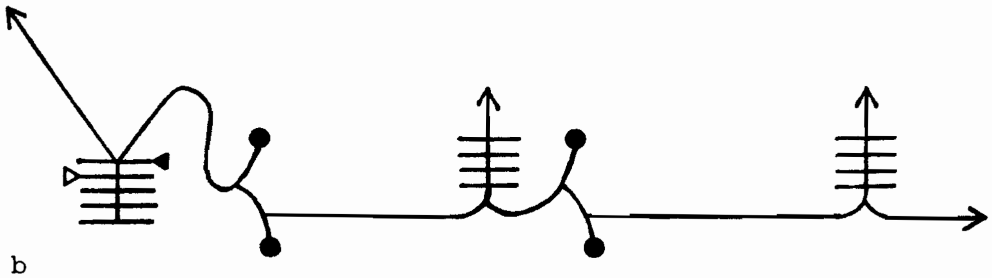


b

Figure 3.7 Comparison of Axillary Branching in Rosette and Elongated Species of the Alismatidae

a. Basic upright vegetative axis found in Alisma. Duplicated from Fig. 3.1a for easy comparison.

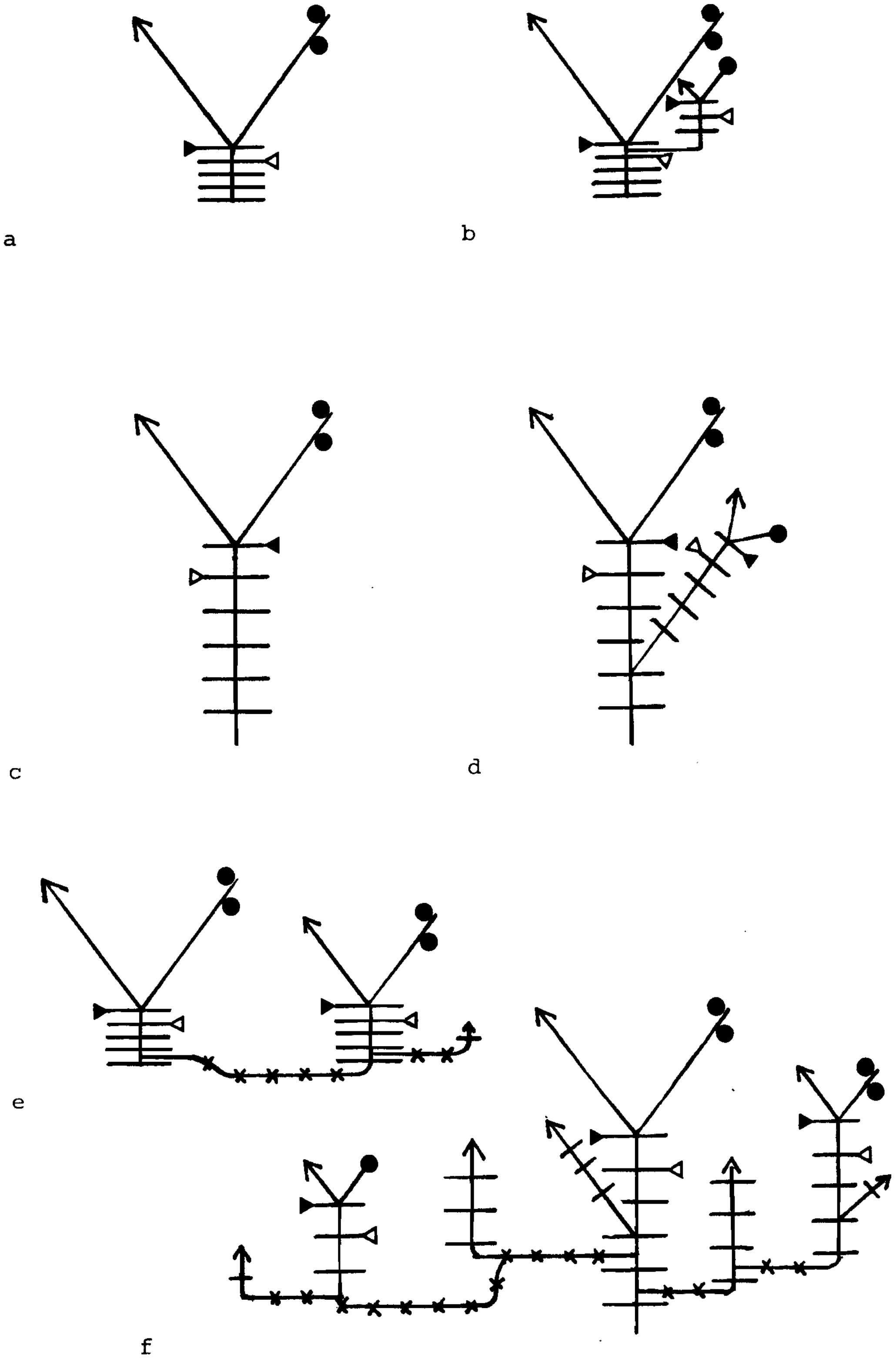
b. Axillary branching. Duplicated from Fig. 3.2a for easy comparison.

c. Simple upright vegetative axis with internodal elongation, no branching. Flowering by apical bifurcation. Found in Maidenia (Hydrocharitaceae, Cook, 1974).

d. Elongated axis with axillary branching, flowering by apical bifurcation. Typical of genera such as Elodea, Egeria and Lagarosiphon (Hydrocharitaceae).

e. Stolon formation. Duplicated from Fig. 3.2b for easy comparison.

f. Formation of horizontal axes which are usually distinct morphologically. These may be referred to as rhizomes or as stolons. Axillary branching also prevalent. This is characteristic of most species of the Potamogetonaceae.


a
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f

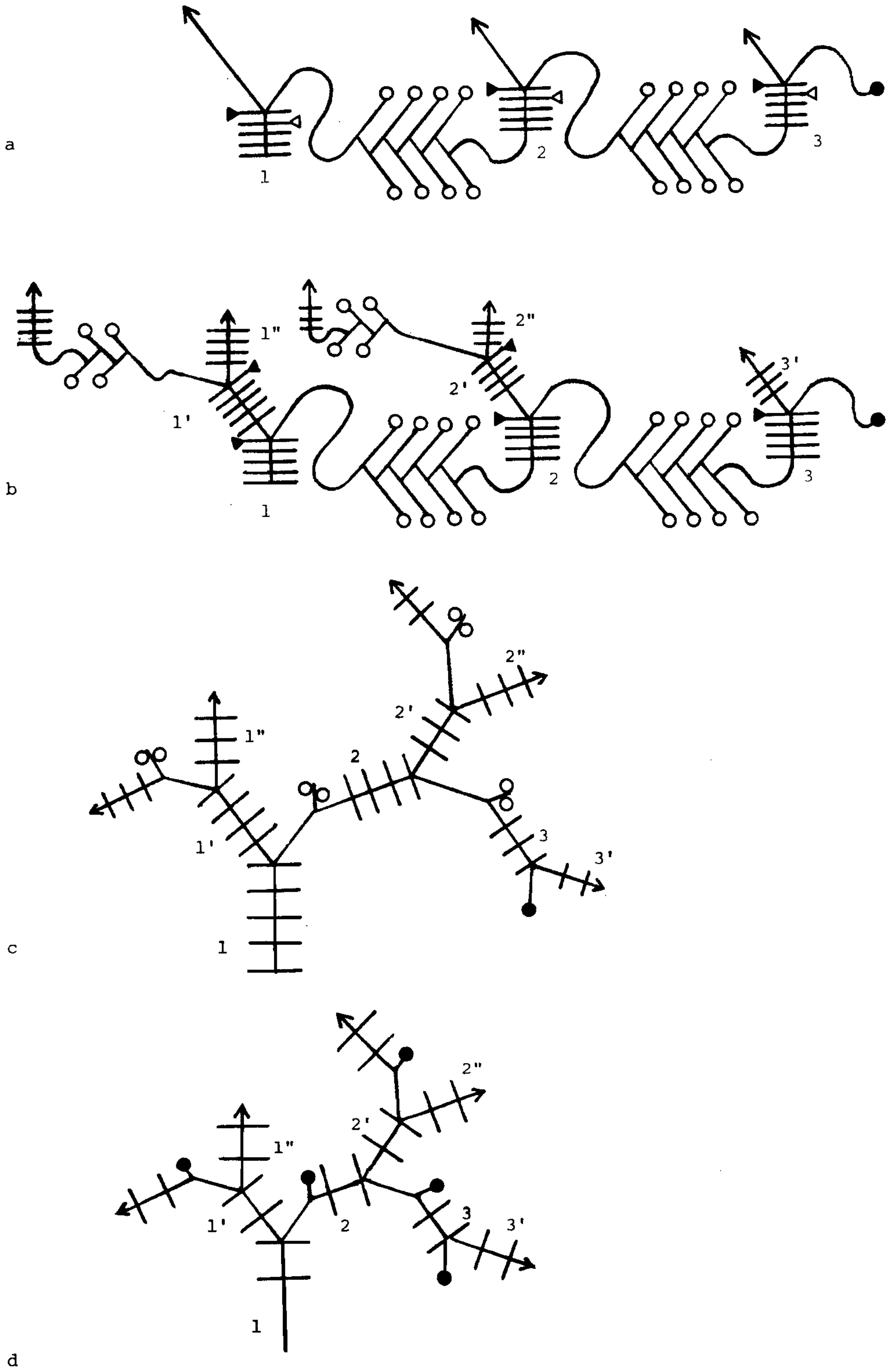
Figure 3.8 Relationship of the Growth Forms of Limnocharis flava (Limnocharitaceae) and Najas flexilis (Najadaceae)

a. Diagram of Limnocharis flava, showing a series of upright vegetative axes produced by bifurcation of the reproductive axes.

b. Diagram of Limnocharis flava, similar to Fig. 3.8a but showing also successive bifurcations of the upright vegetative axes.

c. Rearrangement of Fig. 3.8b to represent the upright vegetative axes as segments in a single plant.

d. Diagram of Najas flexilis.


a
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2"
3
3'
d
1"
1'
1
2
2'
2"
3
3'

Figure 3.9 Diagram Showing the Partitioning of the Marine Genera of Alismatidae in Relation to Two Architectural Elements, Meristem Proliferation and Axis Differentiation.

Axes Dimorphic	Halophila Syringodium	Thalassia	Amphibolis Thalassodendron
Axes Differ in Orientation	Cymodocea Phyllospadix Zostera	---	Heterozostera
Axes Differ in Duration of Growth	Halodule	---	---
Axes Monomorphic	Enhalus	Posidonia	---
	Monomorphic Branching	Apical Bifurcation	Sympodial Branching

Figure 3.10 Diagrams Showing the Architecture of the Marine Genera of Alismatidae

a. *Halophila* and *Syringodium*.

b. *Thalassia*.

c. *Amphibolis* and *Thalassodendron*.

d. *Cymodocea*, *Phyllospadix* and *Zostera*.

e. *Heterozostera*.

f. *Halodule*.

g. *Enhalus*.

h. *Posidonia*.

Note: This follows the arrangement shown in Fig. 3.9.
Internodal elongation is not shown in detail.

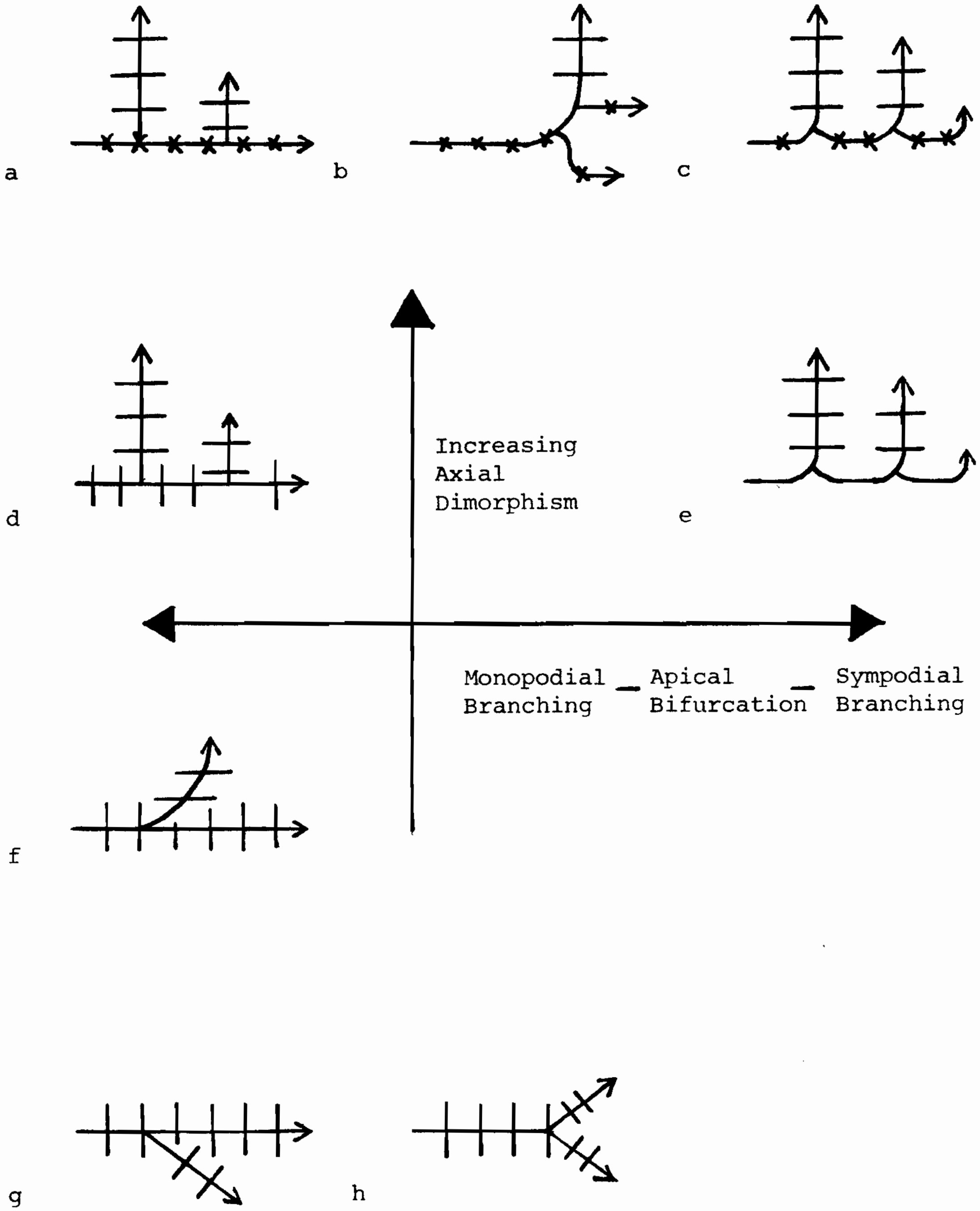
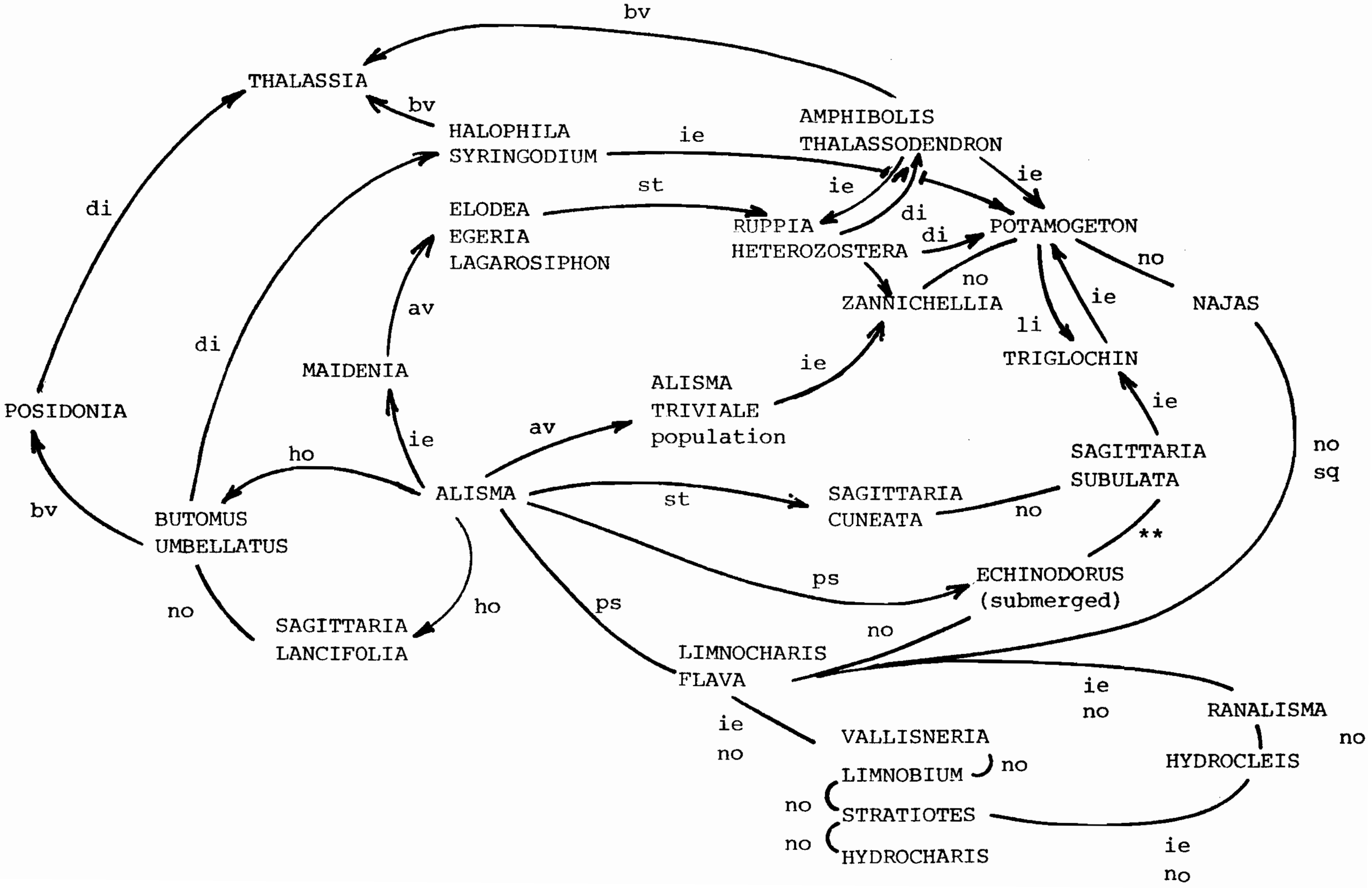

a
b
c
d
Increasing
Axial
Dimorphism
e
Monopodial Branching – Apical Bifurcation – Sympodial Branching
f
g
h

Figure 3.11 Diagram of Some Major Relationships Between Basic Growth Forms in the Alismatidae

Abbreviations used:

av -- occurrence of axillary branching
bv -- branching by apical bifurcation
di -- increasing dimorphism of axes
ho -- horizontal orientation of main axis
ie -- variation in or increasing internodal elongation
li -- increasing lignification of axis
no -- differences in the number or differentiation of parts
ps -- development of pseudostolon
sq -- changes in relative rate and timing of development
st -- development of horizontal stolons or rhizomes
** -- differences in the origin of structure, axillary vs. by apical bifurcation

Arrowheads indicate directionality of change denoted by abbreviations. No evolutionary or derivational direction is implied. Arrowheads may be reversed by suitably changing the processes represented by the abbreviations.


bv
THALASSIA
bv
HALOPHILA
SYRINGODIUM
ie
AMPHIBOLIS
THALASSODENDRON
ie
ie
st
ELODEA
EGERIA
LAGAROSIPHON
di
di
RUPPIA
HETEROZOSTERA
di
POTAMOGETON
no
no
ZANNICHELLIA
NAJAS
ie
li
av
di
MAIDENIA
ie
TRIGLOCHIN
ALISMA
TRIVIALE
population
ie
POSIDONIA
av
ie
SAGITTARIA
SUBULATA
no
sq
ho
ALISMA
st
SAGITTARIA
CUNEATA
no
bv
BUTOMUS
UMBELLATUS
**
ECHINODORUS
(submerged)
ps
no
ho
ps
SAGITTARIA
LANCIFOLIA
no
LIMNOCHARIS
FLAVA
ie
no
RANALISMA
no
ie
no
VALLISNERIA
LIMNOBIUM
no
HYDROCLEIS
no
STRATIOTES
no
HYDROCHARIS
ie
no

CONCLUSIONS

Based on the current study, several major conclusions may be drawn with regard to the study of plant architecture in general, and to the study of the architecture of the Alismatidae specifically.

1. The architecture of plant shoot systems may be considered in terms of the formation and differentiation of new axes. These may be subdivided into various component morphogenetic processes or elements. Formation of new axes may range from axillary branching to terminal processes such as dichotomy. Major elements of axis differentiation include processes such as the level of apical organization, axis orientation and phyllotaxy, the occurrence of internodal elongation, and physiological and anatomical differentiation.

2. These morphogenetic processes are frequently grouped into precise sequences, or modules, which are repeated over the course of plant development and growth. The reiteration of modules, i.e., modular growth *sensu lato*, requires a comparatively simpler (genetic) instruction set for the development of form.

3. Variation in the occurrence and specific details of a relatively small number of architectural processes can result in a diversity of forms. The interrelationships of these forms are web-like because of the combinatorial nature of the variations.

4. Apical bifurcations such as those found in the Alismatidae are contrary to the absolute application of the Classical Shoot Model. Adherents of this view usually interpret these to be derivations from axillary branching through precocious bud development. However, these interpretations depend largely upon the selection of criteria which are considered to "determine" terminal or lateral branching.

5. Monopodial and sympodial interpretations of apical bifurcation usually cannot be made unequivocally; like terminal and lateral branching, these depend on the selection of criteria used.

6. Problems associated with the understanding of architectural forms in which apical bifurcation occurs are largely pseudoproblems resulting from extreme extensions of the Classical Shoot Model. The acceptance of apical bifurcation as a process in the continuum of meristem proliferation along an axis, on the other hand, allows progress in the study of plant architecture.

7. The integration of vegetative and reproductive architecture is an important element in the growth form of many members of the Alismatidae.

8. Given the above, a unified approach to the architecture of the Alismatidae can be developed. This is based upon modular growth sensu lato, and the transformation of modules into one another through variations in their component processes. It is independent of interpretations of apical bifurcation, and allows for easy incorporation of new data.

9. Based on the approach developed in the present study, the diversity of the rosette species of Alismatidae, and the submerged, elongated species of the Hydrocharitales and Najadales, are accounted for and interrelated by variations of a few key architectural processes.

10. Although more detailed information is required for the seagrass taxa, particularly in regard to their reproductive architecture, growth forms in this group may be related to those of the freshwater species in the same way as is outlined in the previous conclusion.

11. The approach developed allows for a more dynamic analysis of plant organization and form and need not be restricted to shoot architecture alone.

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