

# DIVERSITY OF SHOOT ORGANIZATION IN THE ARACEAE<sup>1</sup>

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## ABSTRACT

Morphological units in the Araceae are discussed and defined. The fundamental unit is the *segment* (an internode and its leaf or leaves), of which there are two basic types, the monopodial segment and the branching segment. Segments are assembled into chains to form *articles* (also called *axes*), which terminate in inflorescences, and are the product of the activity of a single apical meristem. Successive articles are assembled into chains which are physiognomically unbranched *shoots*. Shoot organization in the Araceae is discriminated into types on the basis of five characteristics: whether the shoot is renewed after flowering, whether renewal axes are proleptic or sylleptic, whether renewal axes develop from an axillary position, whether renewal axes have a variable or a constant number of leaves, and the number of leaves on renewal axes with a constant leaf number. The types of growth are described, illustrated, and organized into a hierarchical scheme, and a terminology is provided. A list of species representing each of the types is given.

SHOOT ORGANIZATION patterns were characterized for most genera of Araceae by Irmisch (1874), Engler (1877, 1879, 1905, 1911, 1915, 1920a, b, c), Engler and Krause (1908, 1912, 1920), and Krause (1908). They described the shoot organization of the Araceae with the aid of sketches of transverse sections through shoots, and schematic diagrams in which they listed the order of leaves on stems and showed the position of origin of new axes. The schematic diagrams of Engler and Krause were constructed principally from three symbols: N = Niederblatt (cataphyll), L = Laubblatt (foliage leaf), S = Hüllblatt mit Kolben (spathe with spadix). Occasionally they also used the symbols: C = cotyledon, and Sp. = spadix without spathe. Since most of the diagrams were built with only two symbols for leaf types (foliage leaves and cataphylls), there remains some ambiguity as to some details of shoot organization and what kinds of leaves are involved.

Since the time of Irmisch, Engler, and Krause, additional material has become available, showing patterns they did not describe. In addition, some observations presented here conflict with some of their statements and diagrams. Although they described the growth patterns for many genera, they never presented an overview of how these patterns vary throughout the family, nor did they provide

any scheme for classifying, or terminology for describing, the different types of shoot organization. Engler (1877) presented a classification in which he placed the genera into seven groups based largely on overall growth habit (creeping, climbing, shrub, etc.) and phyllotaxy, rather than the actual details of shoot organization.

Madison (1978) provided a limited overview of shoot organization in the Araceae. Being very brief, it describes only four growth patterns, not recognizing some additional patterns. An additional problem with Madison's classification, is that it erroneously describes *Philodendron* section *Pteromischum* as monopodial. Madison does not indicate the source of his information; however, the same error was repeated by Blanc (1980), who was clearly reporting his own observations. This error has now become commonplace (French and Tomlinson, 1981; Croat, 1984; Grayum, 1984), by reference to the work of Madison and Blanc. Oddly, Engler (1879) correctly described the shoot organization of *Pteromischum* as sympodial, but none of these authors mentioned the conflicting nature of their statements.

The most complete modern discussion of shoot organization in the Araceae is that provided by Blanc (1978). I have little criticism of the work of Blanc, and view my own work as complementary, adding my own observations, emphasis, and point of view to his. While my own work is restricted to the discussion of physiognomically unbranched shoots, Blanc (1978, 1980) also discusses branching patterns. In addition, Blanc (1977a, b, 1978) examines the anatomy of the shoot apex in monopodial and sympodial shoots, which I do not do.

<sup>1</sup> Received for publication 21 October 1986; revision accepted 29 December 1986.

This study was supported in part by a grant from the University of Delaware Research Foundation. I thank Angela Blaschke, Michael Grayum, and Susanne Renner for their assistance, and Thomas Croat, Dylan Hannon, and Dan Nicolson for their critical reviews of the manuscript.

This classification of shoot organization in the Araceae has been written in order to draw attention to some classes of shoot organization which have not been described, to draw attention to some details that have received little or no mention by previous authors, to clarify the situation in *Philodendron* section *Pteromischum*, and most importantly to attempt to provide a coherent overview of the diversity of shoot organization patterns in the Araceae. I do not presume that my scheme is comprehensive. In fact I am drawing on much more limited material than did Engler, as I will base my classification entirely on my own observations of a subset of the species found in the Sarapiquí region of Costa Rica and in the wild or in cultivation in the United States, and adding observations of some herbarium specimens from elsewhere.

In addition to describing the diversity of shoot organization in Araceae, the diversity is classified, and a terminology is provided that makes it possible to refer specifically to certain types of shoot organization. It has been observed that various aspects of development, phenology, and life history characteristics correlate with shoot organization. In order to begin a discussion of these relationships, a terminology is needed which makes it possible to refer with precision to the class of shoot organization involved. In addition, if it is to be possible to use details of shoot organization as characters in systematic studies, then it must be possible to refer discriminately to various types of organization to describe how they correlate with phylogeny. For these reasons a precise and detailed terminology for shoot organization in the Araceae is presented in this paper.

In essence, what is presented here is an "architectural analysis" in the sense of Hallé, Oldeman, and Tomlinson (1978). However, this analysis is restricted to patterns of development of physiognomically unbranched shoots. The analysis of Hallé et al. (1978), directed specifically at trees, dealt in large part with branched systems. The concept of architectural analysis deals primarily with the way branches are arranged on a plant. By examining branching patterns, Blanc (1978) described aroids which fit several architectural models. This paper will only detail the growth of single physiognomically unbranched shoots. Hallé et al. (1978) described only three models for unbranched shoot systems, out of 23 models discussed. The third model, Chamberlain's model, describes the physiognomically unbranched shoots of most of the Araceae, regardless of which model the branched plant as a whole

represents. All of the patterns described in the present paper (except the first, monopodial) fit this model. However, the organization will be described in greater detail in order to show many variations that may occur within Chamberlain's model.

**MATERIALS AND METHODS**—The study reported here was conducted primarily in the Sarapiquí region of northeastern Costa Rica, principally at the Finca El Bejuco biological station. The vegetation of the area, described in detail by Holdridge et al. (1971), is characterized as the transition between Tropical Wet and Premontane Wet Forest life zones in the Holdridge System (Tosi, 1969). Additional observations of live material were made in the wild in the northeastern United States, and on the living collections of the New York Botanical Garden, the Missouri Botanical Garden, and the Carnegie Museum of Natural History.

The observations described here are based largely on notes, drawings, photographs, and measurements made on live material from February 1983 to December 1986. However, some observations were made on dried specimens from the herbarium of Finca El Bejuco, the United States National Herbarium, the Carnegie Museum of Natural History, and the New York Botanical Garden, and on serial sections of preserved material. Shoot organization has been examined in 87 species from 27 genera in 20 tribes representing all six subfamilies and the separate family (Acoraceae) into which *Acorus* has been placed (based on the classification scheme of Grayum, 1984).

The schematic diagrams presented in this paper are based on the method of Engler (1877). His technique is refined somewhat by using more different kinds of symbols. Engler used only N, L, and S for cataphyll, foliage leaf, and spathe and spadix respectively. The symbols used here are: P = prophyll, B = bracteole, E = mesophyll, C = mesobracteole, M = monopodial leaf, S = sympodial leaf, I = inflorescence (spathe and spadix), and X = inflorescence (spadix without spathe). In some cases where greater specificity is desired, subscripts will be added to these symbols, as follows: s = sylleptic, p = proleptic, c = cataphyll, r = reduced leaf, e = expanded leaf (foliage leaf). These terms are used in the sense described in Ray (1987). In addition, I will use the symbols  $_a$ I to refer to axillary monophyllous inflorescence sympodia,  $_g$ I to refer to gorgonoid monophyllous inflorescence sympodia, and  $_x$ I to refer to mixed axillary gorgonoid monophyllous inflorescence sympodia. (See explanation in results, below.)





morphological units of which aroids are constructed are considered: *segment*, *article*, and *shoot*.

*Articles*—The term *article* is used in a manner essentially the same as used by Blanc (1978), and roughly synonymous with the term *module* as used by Hallé et al. (1978). The definition of article used is: "An article is produced by the activity of a single meristem, i.e., from the initiation of the meristem to its termination by abortion, or the onset of sexuality." If the apex of the article is destroyed by an external factor such as mechanical damage or desiccation, and then replaced by the release of a bud, the replacement axis will be considered to be a part of the same article. However, replacement of the apex is not a part of the development of an article in the absence of traumatic damage. Sometimes the term *axis* will be used as a synonym for article, thus one may speak of *monoaxial* or *polyaxial* shoot organization.

Articles may be *anisophyllous* meaning that they have a variable number of leaves, or *homeophyllous* meaning that they have a fixed number of leaves. When sylleptically produced, anisophyllous articles usually consist of a prophyll, followed by a mesophyll, followed by a variable number of monopodial leaves or cataphylls, followed by a sympodial leaf, followed by a terminal inflorescence which rarely aborts. When proleptically developed, anisophyllous articles differ from those sylleptically developed in that they have several proleptic mesophylls following the prophyll.

Among homeophyllous articles, several kinds were observed: *monophyllous*, which consist of a bracteole followed by a terminal inflorescence; *diphyllous*, which consist of a prophyll, followed by a sympodial leaf or a mesophyll, followed by a terminal inflorescence which often aborts; *triphyllous*, which consist of a prophyll followed by a mesophyll, a sympodial leaf, and a terminal inflorescence; and *tetraphyllous*, which consists of a prophyll, followed by a mesophyll, a monopodial leaf, a sympodial leaf, and terminating in an inflorescence. In all classes of articles, the first internode of the article, which subtends the prophyll or bracteole, is adnate to one of the last internodes of the previous article, which subtends the bracteole, sympodial leaf, or inflorescence. These two fused internodes and their associated leaves form a single *sympodial segment* (see below).

*Shoots*—The term *shoot* will be used in a manner synonymous with the term *tige* (= stem) of Blanc (1978), and somewhat similar to the

term *caul* as used by Hallé et al. (1978). The definition of shoot used is: "The shoot is physiognomically unbranched. It may be the product either of one apical meristem or several apical meristems which function in sequence. It is a morphological entity constituted by a single article, or a linear succession of articles." While the shoot is a clearly circumscribed morphological unit, it is also a physiognomic concept, referring to the linearity of the entity. While the shoot may technically be branched, the branches will be arranged end to end so that the shoot retains a linear configuration and superficially appears unbranched. The term *caul* will be used synonymously with the term *shoot*; therefore, it may be said that shoots are by definition *monocaulous*, but may be either monoaxial or polyaxial. A plant which is *polycaulous* has many shoots and thus is visibly branched, however, this paper will deal only with monocaulous systems. The term *stem* will refer to the shoot, excluding the leaves.

*Segments*—I have described the segment previously (Ray, 1986) as an internode and its associated leaf(s) and bud. There are two basic types of segments in the Araceae: the *monopodial segment* and the *branching segment*. The monopodial segment consists of an internode with or without a bud toward the proximal end and a monopodial leaf or cataphyll at the distal end. In the monopodial segment, the base of the leaf forms a sheath which wraps around the stem, attaching at the upper node. The bud is positioned directly below the point where the two edges of the petiolar sheath meet after wrapping around the stem (usually axillary to the leaf of the preceding segment).

It is worth noting that I do not follow the convention of associating the bud with the leaf in whose axil it occurs. The primary reason for this is that buds are often moved up on the internode to such an extent that they have no obvious physical connection with the subtending leaf. It is generally accepted that leaves are associated with the subtending internode. It seems logical that the bud which is thoroughly embedded in this internode should be associated with the segment, rather than associating with the bud above the leaf axil, which has no obvious physical connection with either the leaf or the internode of the segment.

Within the Araceae I have observed that while buds are not consistently positioned in the leaf axil, they are consistently positioned below the point of overlap of the petiole sheath. The distinction becomes most obvious when two successive leaves are directly superposed. This situation is found in *Spathiphyllum* in

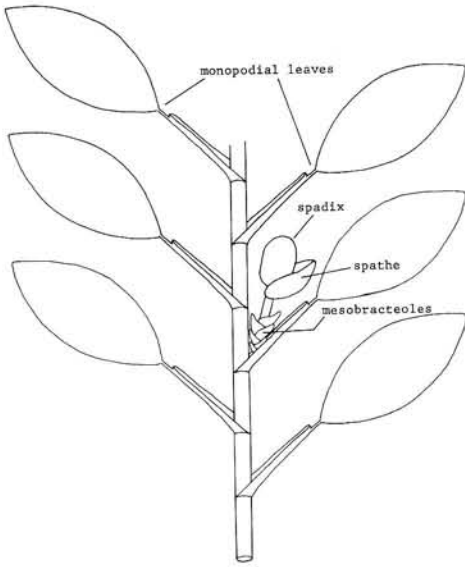


Fig. 1. True monopodial growth, based on Engler's (1905) drawings of *Pothos*. Flowering is terminal on lateral short shoots bearing only a few leaves, the bracteole and mesobraceoles, in this case all cataphylls. All leaves on the main shoot are monopodial leaves.

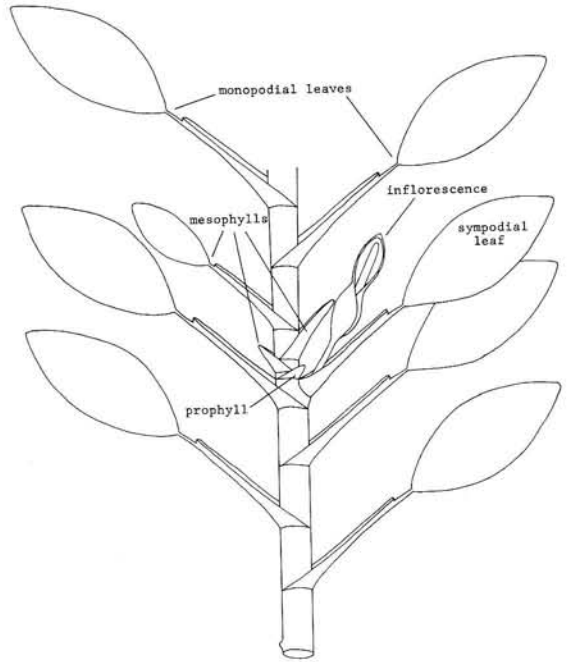


Fig. 2. Proleptic sympodial growth, based on some species of *Philodendron* section *Pteromischum*. After flowering, the bud that will produce the renewal shoot, rests for a unknown period of time, generally until after the fruit has been dispersed. The new shoot then emerges showing proleptic morphology, with a series of proleptic mesophylls.

which the mesophyll is directly superposed to the prophyll. In those species with a bud on the internode between the two leaves (*S. fulvovirens*, *S. laeve*, *S. phrynifolium*), the bud does not occur in the position axillary to the prophyll, but opposite it, below the point of overlap of the sheath edges of the mesophyll. Similarly, in gorgonoid monophyllous inflorescence sympodia (Fig. 5, see description below) branching occurs from a nonaxillary position, below the point of overlap of the sheath.

Branching segments are more complex than monopodial segments because they represent the junction between two articles, or even two shoots. A single branching segment contains elements of each of two different articles. It consists of two internodes which are fused, forming an internode which bifurcates, initiating a new article by the development of a bud. At the basal node of the branching segment is a leaf scar encircling the stem. At this node there will be a leaf (the blastophyll) pertaining to the preceding segment, which may be a monopodial leaf or cataphyll, a sylleptic mesophyll, or a sylleptic prophyll or bracteole. Because the segment bifurcates, there are two "distal" ends, each with a leaf scar encircling the axis. However, either one of the axes may elongate more than the other within the segment, such that one or the other (or neither) of the two "distal" leaf scars may actually be at the proximal end of the segment. The more

proximal of the two will be diverted to the side (Fig. 2, 3, 7-11).

The distal end pertaining to the higher order axis formed by development of a bud is encircled by a leaf scar at which there will be a prophyll or bracteole, either sylleptic or proleptic, depending on the timing of development of the bud. The other distal end pertaining to the continuation of the original axis is also encircled by a scar. The kind of leaf found at this node depends on which of two kinds of branching segments we are concerned with.

A branching segment may occur where a shoot produces a higher order shoot resulting in polycaulous construction. A branching segment may also occur when a shoot terminates in an inflorescence, and a higher order shoot is produced to renew the original shoot, resulting in sympodial monocaulous construction. In the latter case, the branching segment will be called a *sympodial segment*, a class of branching segment. To refer to branching segments of the former type, the term *monopodial branching segment* is used.

At the distal node of the original axis of a monopodial branching segment, we will find simply the next monopodial leaf on the shoot.

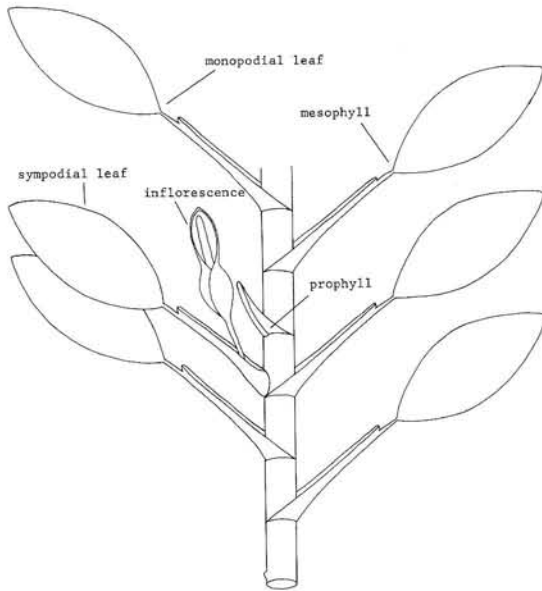


Fig. 3. Sylleptic sympodial growth, based on a number of genera, such as *Dieffenbachia*. At the same time as the terminal inflorescence develops, or perhaps even before, the bud in the axil of the penultimate leaf develops without rest, often producing a sylleptic mesophyll with a fully developed blade.

At the distal node of the original axis of a sympodial segment, we will find a foliar organ which may be a sympodial leaf or cataphyll, or the spathe.

Branching segments (both monopodial and sympodial) in which the higher order axis develops proleptically do not have a bud, because the one and only bud of the segment is used in the formation of the new axis. In Araceae, to my knowledge, all monopodial branching segments develop proleptically; therefore, none of them will have buds remaining. Among sympodial segments which develop sylleptically, there may or may not be a bud in a position below the point of overlap of the sheath edges of the prophyll (opposite the sympodial leaf and axillary to the blastophyll), depending on the species: they are always present in *Philodendron* (except section *Pteromischum*) and *Anthurium*, and usually absent in other genera.

Four classes of sympodial segments are recognized, which differ in configuration depending on which internode elongates. There are *hypophyllous* segments (Fig. 3, 7), in which the scar of the sympodial leaf borders the lower end of the sympodial segment, contiguous with the scar of the blastophyll. (This is typical of *Philodendron* excluding *Pteromischum*.) There are *hyperphyllous* segments (Fig. 2, 8) in which the scar of the sympodial leaf borders the scar

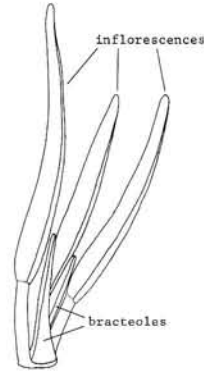


Fig. 4. Axillary monophyllous sympodial growth. A bud on the base of the peduncle of the inflorescence (left) terminating a vegetative axis develops into a shoot bearing only a single leaf (a bracteole) and an inflorescence (right). Another shoot consisting of a bracteole and an inflorescence (center) develops from a bud on the peduncle base of the second inflorescence, axillary to the bracteole. This branching may continue indefinitely, as each new inflorescence has a bud developing on its peduncle base axillary to the subtending bracteole.

of the prophyll at the upper end of the sympodial segment. (This is typical of *Anthurium*.) In many taxa, the sympodial segment is so short that the scar of the sympodial leaf borders on both ends of the segment, contiguous with the scars of both leaves, at both the lower and upper ends of the segment. These will be called *ambiphyllous* (Fig. 9–11). An additional variation has been observed in two proleptic members of *Philodendron* section *Pteromischum*, *P. fontianum* Croat & Grayum ined. (Grayum 6153 MO, CR), and *P. pluricostatum*, in which the internode subtending the sympodial leaf is elongated and supersedes the point of attachment of the prophyll. This will be called *peraphyllous* (not illustrated). In *P. pluricostatum* the prophyll scar is moved down on the sympodial segment, and the renewal axis is diverted to the side.

There exists another kind of sympodial segment worth mentioning. When gorgonoid inflorescence sympodia are formed (see description below), the segment consists of an indefinite number of adnate internodes, each newer axis branching from the same side of the lower order axis in a neatly linear arrangement. All of the internodes are greatly reduced. The lower end of the segment is subtended by the sympodial leaf. The upper end of the segment incorporates the peduncle of the internode terminating the original axis, but also includes an indefinite number of bracteoles in a row, representing multiple axes. Because this single segment has multiple axes and associated brac-



Fig. 5. Gorgonoid monophyllous sympodial growth. As in Fig. 4, a bud on the base of an inflorescence (left) terminating a vegetative axis, develops into a shoot bearing a bracteole and an inflorescence (center). Now, however, the next shoot (right) develops not from a position on the peduncle base axillary to the bracteole, but on the reduced internode subtending the bracteole, below where the sheath edges of the bracteole overlap. Successive shoots develop in similar positions, producing a series of successively younger shoots, arranged neatly in a row. The segment subtending the bracteoles is a gorgonoid segment.

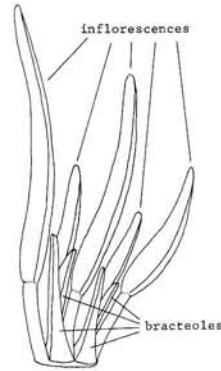


Fig. 6. Mixed axillary gorgonoid monophyllous sympodial growth, based on *Homalomena rubescens*. As in Fig. 5, successive buds develop on the reduced internode subtending the bracteole. However, in addition, buds develop on the peduncle bases in positions axillary to the bracteoles. The two smallest inflorescences in the illustration are the ones developing from the axillary position. A gorgonoid segment is produced.

teoles at the upper end, I will call it a *gorgonoid segment* (Fig. 5).

*Shoot organization:* The scheme by which the various kinds of shoot development are organized in the Araceae is outlined as follows:

1. Monopodial (Fig. 1)
2. Sympodial
  - 2.1 Anisophyllous
    - 2.1.1 Proleptic (Fig. 2)
    - 2.1.2 Sylleptic (Fig. 3)
  - 2.2 Homeophyllous
    - 2.2.1 Monophyllous
      - 2.2.1.1 Axillary (Fig. 4)
      - 2.2.1.2 Gorgonoid (Fig. 5)
      - 2.2.1.3 Mixed axillary gorgonoid (Fig. 6)
    - 2.2.2 Diphyllous (Fig. 7)
    - 2.2.3 Triphyllous (Fig. 8)
    - 2.2.4 Tetraphyllous (Fig. 9)
    - 2.2.5 Pentaphyllous?
  - 2.3 Intermittent homeophyllous
    - 2.3.1 Intermittent diphyllous (Fig. 10)
    - 2.3.2 Intermittent triphyllous (Fig. 11)
    - 2.3.3 Intermittent tetraphyllous?

In order to clarify the details of the classes of shoot organization, a schematic illustration, interpretative diagrams, and a list of species exhibiting the different types are presented for each category. There exists considerable variation even within each of these categories. Variations within a pattern relate to whether a bud is present on a given internode, whether the blade of a leaf in a given position is ex-

panded or reduced, how many times a repeated unit is repeated, and what kind of inflorescence sympodium if any is present. These variations will be elaborated upon in Ray (in press).

In all aroids, flowering is terminal, resulting in the termination of the activity of the apical meristem as it is consumed in the production of the inflorescence. Sympodial and monopodial Araceae are distinguished by whether the shoot is renewed after flowering or not. The former grow sympodially, forming polyaxial shoots. The latter grow monopodially, forming only monoaxial shoots, but have a greater tendency to be polycaulous.

1. Monopodial—Shoots, in the absence of traumatic damage, are normally produced by the continued activity of a single apical meristem. I have observed the organization of monopodial shoots only in herbarium specimens, the drawings and schematic diagrams in Engler (1905), and the drawings of Bogner (1975). These observations suggest that flowering occurs on proleptic lateral branches which are short shoots bearing only a few leaves (presumably a proleptic prophyll or bracteole and mesophylls or mesobracteoles), and terminating in an inflorescence without the development of a continuation shoot (Fig. 1).

There is only a single species of monopodial Araceae in the Sarapiquí region, *Heteropsis oblongifolia*. I have not observed this species in flower and I cannot state with confidence the details of the organization of this category. I include a diagram of the shoot organization as I interpret it from examination of herbarium specimens. The flowering lateral short shoots appear to develop proleptically, and in addi-



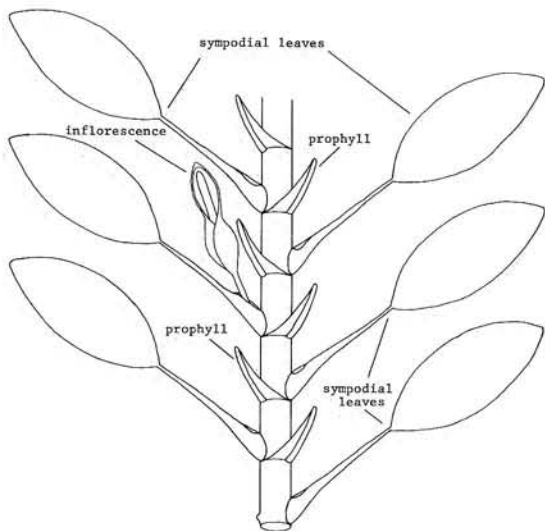


Fig. 7. Diphyllous sympodial growth, based on *Philodendron*. Each article bears a prophyll and a sympodial leaf followed by a terminal inflorescence. In many instances the terminal inflorescence aborts, and so is not visible.

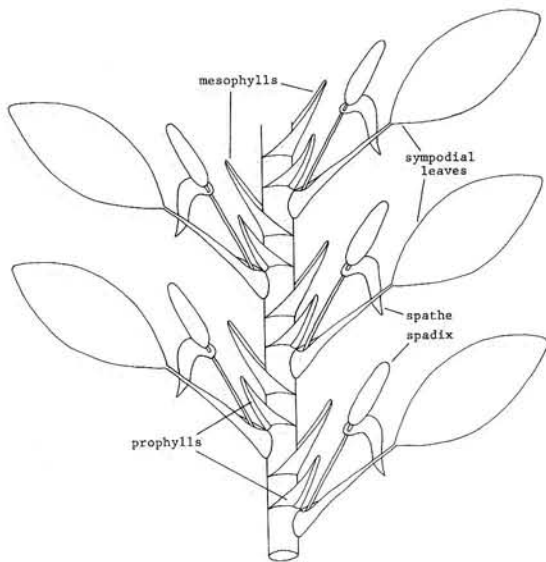
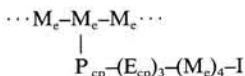


Fig. 8. Triphyllous sympodial growth, based on *Anthurium*. Each article bears a prophyll, a mesophyll, a sympodial leaf, and a terminal inflorescence. In *Anthurium*, the inflorescence usually develops to maturity.

tion to the proleptic prophyll and mesophylls, *Heteropsis* generally has a few monopodial leaves subtending the terminal inflorescence, as follows:



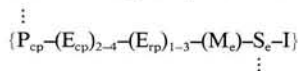
2. In sympodial—Aroids development of the shoot is interrupted by flowering, as the apical meristem is consumed in the formation of the inflorescence. However, unlike monopodial aroids, growth of the shoot is continued by the development of a new article from the axil of a leaf just below the inflorescence. In most taxa the new article develops in the axil of the penultimate leaf, in some taxa the ultimate leaf.

Sympodial taxa can be divided into three groups: anisophyllous, in which the plant is constructed entirely from anisophyllous articles; homeophyllous, in which after possibly producing a single initial anisophyllous article, all subsequent growth is by a succession of homeophyllous articles; and intermittent homeophyllous, in which anisophyllous and homeophyllous articles alternate, with groups of few to many (e.g., 1 to 10) successive homeophyllous articles being separated by one or a few anisophyllous articles.

2.1. Anisophyllous sympodial—Taxa may be grouped into those species in which the renewal article develops sylleptically, and those in which the renewal article develops proleptically.

2.1.1. Proleptic anisophyllous sympodial—Figure 2 illustrates the proleptic renewal of a shoot after flowering, with the proleptic prophyll and mesophylls visible. The renewal of the stem after flowering occurs by the same process by which the stem is renewed after damage to the apex, and also by the same process found in proliferative branching (resulting in a polycaulous shoot system). The morphology of the beginning of the new article is the same in each case, a proleptic prophyll followed by a series of proleptic mesophylls on segments with reduced internodes.

The only species in which proleptic renewal is believed to occur is a subset of *Philodendron* section *Pteromischum*. The remaining *Pteromischum* are sylleptic anisophyllous sympodial. However, I also suspect several species of *Monstera* of having proleptic shoot renewal. Six of the ten species of section *Pteromischum* of Finca El Bejuco fall in to this category: *Philodendron aurantiifolium*, *P. chavarrianum*, *P. fontianum*, *P. inaequilaterum* Liebm. (Grayum 2797 MO), *P. pluricostatum*, and *P. rigidifolium*; as well as *P. guttiferum* Kunth (Schunke 9691, USNH) from South America. The growth of these species is illustrated in Fig. 2 and in the interpretative diagram, below.



2.1.2. Sylleptic anisophyllous sympodial—In this pattern of growth, a variable number



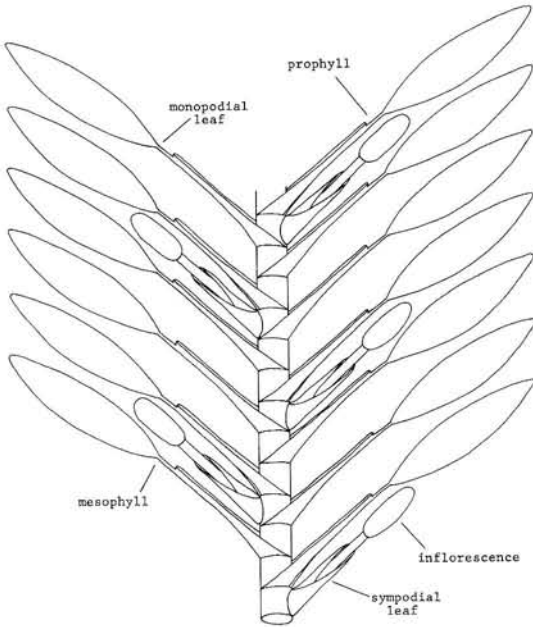


Fig. 9. Tetraphyllous sympodial growth, observed only in *Orontium aquaticum*. Each article bears a prophyll which is a foliage leaf, a mesophyll, a monopodial leaf, a sympodial leaf which is a cataphyll, and a terminal inflorescence. In *Orontium*, the sympodial leaf has an unusual configuration: the back of the leaf is turned only about 90 degrees from the renewal shoot, as compared with 180 degrees in all other species I have observed. In addition, the sympodial leaf is morphologically like a bracteole, being a two keeled cataphyll. Another unusual feature of *Orontium* is that it lacks a spathe.

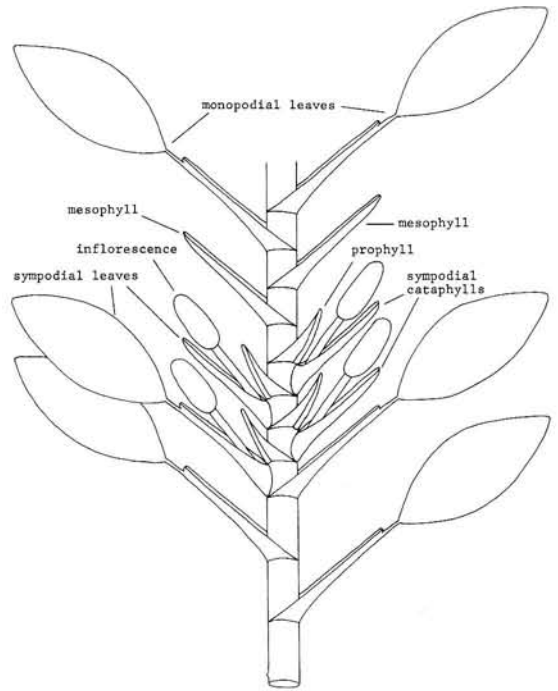
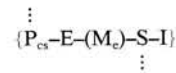


Fig. 10. Intermittent diphyllous sympodial growth, based on *Monstera*. After the flowering of an anisophyllous article, a series of diphyllous articles are produced, each containing a prophyll, a sympodial cataphyll, and a terminal inflorescence. After the last diphyllous article, the new anisophyllous article which continues the growth of the shoot starts with a prophyll and two mesophylls. The inflorescences are drawn without spathes, as if they have already abscised.

of monopodial segments are formed by each article, before it terminates in an inflorescence. The shoot is then renewed sylleptically, the new axis beginning with a sylleptic prophyll and usually a single mesophyll which may be a cataphyll, a reduced leaf, or a foliage leaf. Sylleptic anisophyllous sympodial growth has been observed in the following species: *Acorus calamus*, *Aglaonema commutatum*, *Anthurium clidemioides*, *A. flexile* ssp. *flexile*, *Arisaema triphyllum*, *Caladium bicolor*, *Calla palustris*, *Dieffenbachia beachiana* Croat & Grayum ined. BEH 8122 (DUKE), *D. cf. longispatha*, *D. cf. oerstedii*, *D. cf. seguine*, *Gymnostachys anceps*, *Homalomena picturata*, *H. rubescens*, *Monstera glaucescens*, *Peltandra virginica*, *Rhaphidophora decursiva*, *Rhodospatha forgetii*, *Spathiphyllum friedrichsthalii*, *S. fulvovirens*, *S. laeve*, *S. phrynifolium*, *Stenospermatium angustifolium*, *S. spruceanum*, *Syngonium birdseyanum*, *S. macrophyllum*, *S. podophyllum* var. *peliocladum*, *S. rayi*, *S. schottianum*, *S. triphyllum*, *Xanthosoma violaceum* and the following members of section *Pteromischum*: *Philodendron lewisii*, *P. mediavaginatam*, *P.*

*radicans*, and *P. viaticum*. The growth of these species is illustrated in Fig. 3 and represented in the schematic diagram below. Only *Acorus* and *Gymnostachys* differ significantly from the diagram. Details of their growth will be given in Ray (in press).



2.2. Homeophyllous sympodial—Taxa may be divided into groups based on the number of leaves in the homeophyllous articles. The patterns will be called *monophyllous sympodial*, *diphyllous sympodial*, *triphyllous sympodial*, or *tetraphyllous sympodial*, depending on the number of leaves in the article.

2.2.1. Monophyllous sympodial—Construction occurs when multiple inflorescences are formed by the development of a usually condensed “inflorescence sympodium” in the axil of a single sympodial leaf on a shoot (Fig. 4–6). Because these flowering shoots are usually condensed, they do not affect the monocaulous appearance of the shoots from which they

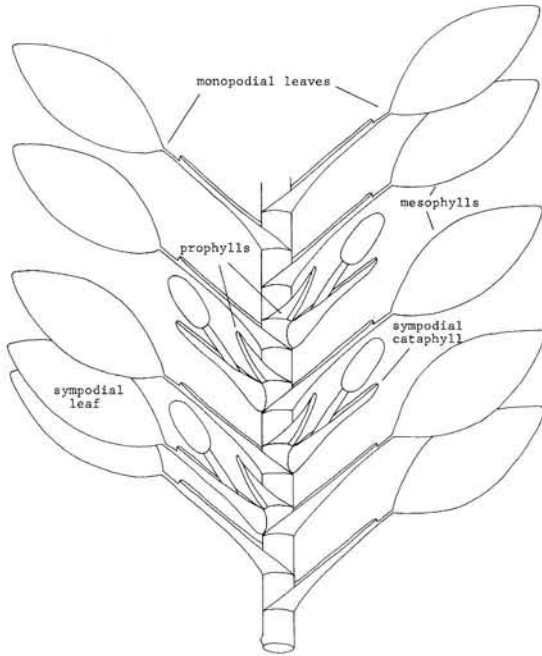


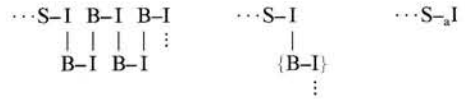
Fig. 11. Intermittent triphyllous sympodial growth. After the flowering of an anisophyllous article, a series of triphyllous articles are produced, each containing a prophyll, a mesophyll, a symphyllal cataphyll, and a terminal inflorescence. After the last triphyllous article, the growth of the shoot is continued by a new anisophyllous article. The inflorescences are drawn without spathes.

emerge. However, a photograph of *Culcasia angolensis* in Knecht (1980) shows that sometimes the inflorescence sympodium can be extended, making the plant polycaulous. Each inflorescence of the sympodium terminates an article bearing a single leaf (a sylleptic bracteole).

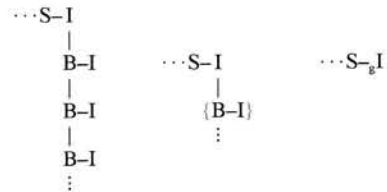
Monophyllous sympodial growth occurs in three ways among the species I have observed. In one kind, each higher order article on the inflorescence sympodium develops from a bud on the base of the peduncle, in the axil of the bracteole of the next lower order article. This will be called *axillary monophyllous sympodial* (Fig. 4). In another kind, each higher order article on the flowering shoot develops from the bud on the internode subtending the bracteole (of the next lower order article); the developing bud is positioned below where the edges of the bracteole sheath overlap. This is a very unusual kind of branching because the branches are not arising from an axillary position. This kind of branching produces a gorgonoid segment. This will be called *gorgonoid monophyllous sympodial* (Fig. 5). In a third type of monophyllous sympodial growth, new shoots arise from positions both axillary and nonaxillary to the bracteoles. This will be called

*mixed axillary gorgonoid monophyllous sympodial* (Fig. 6).

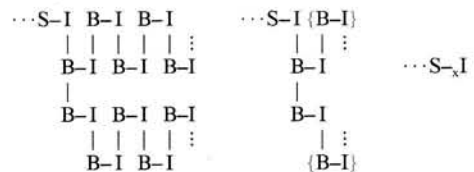
2.2.1.1. Axillary monophyllous sympodial—This kind of growth is highly uniform, and corresponds to Fig. 4 and to the schematic diagram below. Axillary monophyllous inflorescence sympodia have been observed in the following species: *Dieffenbachia cf. longispatha*, *D. cf. oerstedii*, *D. cf. seguine*, *Philodendron cretosum*, *P. davidsonii*, *P. fragrantissimum*, *P. grandipes*, *P. lewisii*, *P. mediacostatum*, *P. pterotum*, *P. radiatum*, and *P. viaticum*. As inflorescence sympodia develop in the axils of single symphyllal leaves, it can be quite complex to represent both the organization of the vegetative shoot and the flowering shoot in the same schematic diagram. Therefore, when diagramming vegetative shoots, the inflorescence sympodium will be abbreviated with a single symbol. The axillary monophyllous inflorescence sympodium will be represented with the symbol  $\text{aI}$  as indicated by the three equivalent schematic diagrams below.



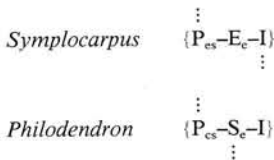
2.2.1.2. Gorgonoid monophyllous sympodial—This kind of growth is also highly uniform, and corresponds to Fig. 5 and the three schematic diagrams below. Gorgonoid monophyllous inflorescence sympodia have been observed in the following species: *Aglaonema commutatum*, *Syngonium macrophyllum*, *S. podophyllum* var. *peliocladum*, *S. rayi*, *S. schottianum*, *S. triphyllum*, and *Xanthosoma violaceum*. This kind of inflorescence sympodium will be abbreviated with the symbol  $\text{gI}$ .



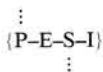
2.2.1.3. Mixed axillary gorgonoid monophyllous sympodial—This pattern of growth has been observed only in *Homalomena rubescens*. It is represented in Fig. 6 and in the three equivalent schematic diagrams shown below. I will abbreviate this kind of inflorescence sympodium with the symbol  $\text{xI}$ .



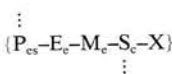
2.2.2. Diphyllous sympodial—This pattern occurs in two basic forms, conforming to the schematic diagrams below. In one pattern, observed only in *Symplocarpus*, the renewal axis develops from the axil of the last leaf of each article, while in the other pattern the renewal axis develops from the axil of the first leaf of each article (Fig. 7). Diphyllous sympodial growth has been observed in the following species: *Philodendron aromaticum*, *P. brunneocaule*, *P. cretosum*, *P. davidsonii*, *P. fragrantissimum*, *P. grandipes*, *P. ligulatum*, *P. mediacostatum*, *P. platypetiolatum*, *P. pterotum*, *P. radiatum*, *P. rothschuhianum*, *P. sagittifolium*, *P. scandens*, *P. tenue*, *P. tertivenarum*, *P. tripartitum*, *P. wendlandii*, *P. wilburii*, and *Symplocarpus foetidus*.



2.2.3. Triphyllous sympodial—This pattern is represented in Fig. 8 and conforms to the schematic diagram below. Triphyllous sympodial growth has been observed in the following species: *Anthurium atropurpureum* var. *arenicolum*, *A. bakeri*, *A. clavigerum*, *A. consobrinum*, *A. formosum*, *A. interruptum*, *A. lancifolium*, *A. ochranthum*, *A. pentaphyllum* var. *bombacifolium*, *A. subsignatum*, *A. trinerve*, *A. upalaense*, *Calloopsis volkensii*, *Pinellia ternata*, *Pistia stratiotes* (determination of shoot organization is uncertain for *Pistia*, see Ray, in press for details), *Spathicarpa sagittifolia*, and *Urospatha friedrichsthalii*. There is considerable variation between the genera with respect to which of the three leaves of each article has a developed or reduced blade.



2.2.4. Tetraphyllous sympodial—This kind of growth has been observed in only one species, *Orontium aquaticum*. The shoot organization is illustrated in Fig. 9 and conforms to the diagram below.



2.2.5. Pentaphyllous sympodial?—By far, most of the articles observed in *Stenospermatum spruceanum* are constructed with five leaves. However, scattered among them are articles with more or fewer leaves. It looks as though this species is programmed for pentaphyllous sympodial growth, but that control

mechanisms are not adequate to consistently produce articles consisting of five leaves. This may be an indication of a practical limit on the number of leaves in homeophyllous growth. I have classed *S. spruceanum* as anisophyllous.

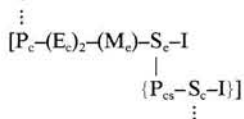
2.3. Intermittent homeophyllous sympodial—This is a combination of anisophyllous sympodial and homeophyllous sympodial growth. After one or more initial anisophyllous articles, the shoot may produce a series of homeophyllous articles. As many as nine diphyllous articles have been observed, each of which bears a sylleptic prophyll and a sympodial cataphyll, following the first inflorescence in *Monstera adansonii* var. *laniata*. After the last homeophyllous article of a series, the shoot produces one or more anisophyllous articles. At the next episode of flowering the stem may again produce an indeterminate number of homeophyllous articles in succession.

This may be the most difficult pattern to recognize in practice with confidence. The reason for this is that species which show intermittent homeophyllous sympodial growth can easily be mistaken for anisophyllous sympodial, if the individuals observed are not of sufficient size. Intermittent homeophyllous individuals may flower sporadically when they are not fully mature, or not growing under optimal conditions. Similarly, anisophyllous species may exhibit several flowering episodes in close succession when they reach their maximum size and are growing under the most optimal conditions.

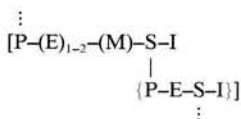
However, intermittent homeophyllous growth, when clearly expressed, is an unmistakable pattern distinct from either anisophyllous or homeophyllous growth. The homeophyllous episode of intermittent homeophyllous species will be as rigidly constant as in strictly homeophyllous species, unlike the very loose pattern of rapid succession seen in extremely vigorous anisophyllous species. Furthermore, in some intermittent homeophyllous taxa (*Monstera*, *Rhodospatha*), the homeophyllous episode occurs with the production of cataphylls only, with no foliage leaves produced for the duration of homeophyllous growth. This seems to represent a high degree of specialization of the homeophyllous episode, which sets it apart from the rapid succession flowering of anisophyllous species, and from the foliage leaf-bearing articles of strictly homeophyllous species.

2.3.1. Intermittent diphyllous sympodial—The diphyllous articles of *Monstera* differ from those in *Philodendron* in that the blade of the sympodial leaf is expanded in *Philodendron* and reduced in *Monstera*, and a bud is present in a position axillary to the prophyll in *Philo-*

*dendron*, but this bud is absent in *Monstera*. Intermittent diphyllous sympodial growth has been observed in the following species: *Monstera adansonii* var. *laniata*, *M. diversifolia*, *M. spruceana*, and *M. tenuis*. This kind of growth is illustrated in Fig. 10 and corresponds to the schematic diagram below.



2.3.2. Intermittent triphyllous sympodial—This kind of growth has been observed in the following species: *Alocasia plumbea* and *Rhodospatha wendlandii*. Growth of this kind is illustrated in Fig. 11 and conforms to the schematic diagram below.



2.3.3. Intermittent tetraphyllous sympodial?—Some indications of this kind of growth have been found in *Caladium bicolor*. In all three individuals which were observed to flower twice in a season, the two flowering events were separated by a tetraphyllous article, suggesting the possibility of intermittent tetraphyllous sympodial growth. However, more observations would be needed to confirm this. This species has been classified as anisophyllous sympodial. For further discussion, see Ray (in press).

DISCUSSION—*Terminology*—I would like to discuss the use of terminologies for morphological units and classes of shoot organization by previous authors.

*Segment*: The concept of the segment, also known as a *phyton*, *phytomer*, or *shoot unit*, has not been universally accepted. Arber (1930) dismissed it as follows: "The phyton theory seems to me to belong to that group of overingenious, academic conceptions which are difficult to discuss because they bear so little relation to reality." White (1979) reviewed the literature and concluded that support for the concept is mixed, and that it seems to be more applicable to monocots than to dicots. Ray (1986) presented data that suggest the segment may have some developmental integrity in Araceae. I use the concept because nodes are well defined in the Araceae, making the segment a useful concept for organizing lists of parts occurring along shoots. That is, each leaf and bud may be associated with a specific internode for the purpose of description and construction of schematic diagrams.

*Articles and shoots*: In developing these terms, I carefully examined the analogous definitions in Blanc (1978) and Hallé et al. (1978). I found the usage of terms by Blanc to be highly consistent and suited to my purposes, and have therefore adopted essentially the same definitions as his. In usage, my term *article* is the same as his term *article*, and my term *shoot* is the same as his term *tige*. It is no surprise that Blanc and I should have settled on equivalent definitions of these terms, as we are attempting to describe the same organisms. It is worth noting that in his Latin descriptions, Engler (1879) used the terms *axes* and *caudicis* in a manner equivalent to my *article* and *shoot*, respectively.

My terminology differs more from that of Hallé et al. (1978). These differences may arise out of the fact that they are describing a much greater diversity of plants, which are, for the most part, polycaulous. In Hallé et al. (1978), my term *article* is close to their terms *module* and *axis*, and my term *shoot* is similar to their terms *caul* and *sympodium*. However, their definitions differ from mine in some details, and are less consistent than I would like. The definition of *module* provided by Hallé et al. (1978) does not appear to differ significantly from my term *article*.

The term *caul* of Hallé et al. (1978) is defined as follows: "*Monocaulous* (monocaulous), with reference to trees with a single trunk or visible stem of the plant (from the Greek *καυλος* = stem or stalk). This may be the product either of one apical meristem or of several apical meristems which function in sequence. A complementary term is *acaulous* (acaulous), without a trunk, as in plants with underground stems. Polycaulous (polycaulous) we have not used, since it means a 'tree with several trunks,' which is a contradiction to the usual definition of a tree. It should be used to describe shrubs . . ." Thus the term *caul* would seem to be like my shoot, except that, at least in reference to trees, they prefer that it be applied only to the first order shoot, which emerges from the ground.

The term *axis* as used by Hallé et al. (1978) would also appear to be identical to my *article*, according to their description: "an axis is the product of a single apical meristem . . . Polycaxial trees are usually visibly branched, but this is not always so, as is exemplified by Chamberlain's model where we have a monocaulous (apparently unbranched) tree which is polyaxial." However, in the glossary definition of *sympodium* they use the term *axis* in the sense of my *shoot*: "a single axis formed by a series of lateral meristems in sequence." In this case the term *axis* is not being used synonymously



with module and article, but is being used to substitute for *caul*, in the general case where a *caul* may or may not be a trunk. Thus it seems that Hallé et al. (1978) use *axis* sometimes in the sense of article and sometimes in the sense of shoot. An example of this kind of conflicting use is found in the description of Fagerlind's Model: "Plagiotropism of the branch tiers is established early by apposition growth which also results in the multiplication of branches by forking below the evicted parent axis" (p. 168), where *axis* is used in the sense of article, and "there is some tendency for continued development of an axis by substitution growth even after it has flowered" (p. 172), where *axis* is used in the sense of shoot.

It would seem that the only term in Hallé et al. (1978) that is equivalent to my *shoot* is *sympodium*, as the above definition indicates. However, in their description of Lecuwentberg's model, they clearly use it in a different sense: "Two or more branches per module; sympodium three-dimensional, nonlinear, clearly branched." This usage to describe a branched system seems to conflict with their glossary definition which stresses the linear quality. There seems to be no term in Hallé et al. (1978) which is equivalent to my *shoot*. In spite of the inconsistent terminology, they provide a precise analysis of shoot systems by means of a careful dissection and presentation of the data, using well-constructed diagrams.

Types of articles—I have provided a terminology for types of articles: *anisophyllous*, *homeophyllous*, *tetraphyllous*, *triphyllous*, *diphyllous*, and *monophyllous*. Blanc (1978) has also provided a terminology for types of articles. His terminology differs from mine in that it places a great emphasis on whether leaf blades are expanded or not, whereas my terminology does not consider leaf expansion at all. When he uses the terms *pléiophylle* (more leaves), *monophylle* (one leaf), and *aphylle* (no leaves), to describe classes of articles, he is counting only the foliage leaves on the article. Any number of reduced leaves may occur in each of these three kinds of articles.

His term *pléiophylle* is applied to the same articles that I have termed *anisophyllous*, except that it excludes articles composed principally of reduced leaves. His term *monophylle* describes articles which I would describe as *triphyllous* or *diphyllous*, because there are one or two cataphylls, even though there is only one foliage leaf. He uses the term *pseudomonophylle* to describe *anisophyllous* articles in which most of the leaves are reduced, and in which all but one of the foliage leaves senesce quickly. He uses the term *aphylle* to describe articles without foliage leaves, which includes

the articles that I have termed *monophyllous*. He would describe the *diphyllous* articles of *Monstera* and the *triphyllous* articles of *Rhodospatha* as *aphyllous* because none of their leaves are foliage leaves. He also includes, under the term *aphyllous*, *anisophyllous* articles without foliage leaves and bearing only reduced leaves (e.g., stolon shoots produced in *Monstera* seedlings and climbing flagellar shoots of *Philodendron linnaei* Kunth).

Classes of shoot organization—I will review some of the terms that have been used by other authors to refer to the various classes of shoot organization that I have described. *Monopodial* shoots have been described as *monopodial* by most authors (Blanc, 1977a, 1978; Grayum, 1984; Madison, 1978).

Engler and Krause (1912) referred to the mixed axillary gorgonoid *monophyllous* inflorescence *sympodium* of *Homalomena rubescens* as a "double helicoid flowering system" (doppelschraubeligen Blütenstands-systems).

Proleptic *sympodial* growth has not been unambiguously described by previous authors. Blanc (1980) and Madison (1978) described these species as *monopodial*, but their descriptions indicate that they were not aware that the shoot is renewed after flowering. Blanc based his description on observations of *Philodendron guttiferum* in Guyana. Blanc (1980) refers to *P. guttiferum* as having "monocarpic lateral branches." I have examined specimens of *P. guttiferum* from South America in the U.S. National Herbarium, and have confirmed that the shoot organization is *proleptic anisophyllous sympodial*. Engler (1879) more accurately described the shoots of *Philodendron* section *Pteromischum* as *pleiophyllis*, but it is not clear whether he was basing his observations on *sylliptic* or *proleptic Pteromischum*. His schematic diagram shows two *cataphylls* at the beginning of the article. My observations show that the *sylliptic* species have only a single *cataphyll* (the *prophyll*) at the beginning of each article, while the *proleptic* species have several *cataphylls* (the *prophyll* and some *mesophylls*) at the beginning of each article. Therefore it is difficult in this case to know if Engler is referring to *sylliptic* or *proleptic sympodial* growth, though *proleptic* is more likely.

The term "monophyllous sympodial" (Madison, 1978; French and Tomlinson, 1980, 1981; Grayum, 1984) has been applied to *Philodendron* (excluding section *Pteromischum*) and *Anthurium* (excluding section *Polyphyllium*), but is something of a misnomer, as the articles in these shoots actually produce two leaves in *Philodendron* (one *sylliptic prophyll* and one *sympodial leaf*), and three leaves in *Anthurium* (one *sylliptic prophyll*, one *syl-*

leptic mesophyll, and one sympodial leaf). Ritterbusch (1971) refers to the "monophyllous sympodial" stems of *Philodendron* as a "monochasial sympodium." Evidently these terms are based on a count of foliage leaves. I call this kind of growth *homeophyllous sympodial*.

The term "polyphyllous sympodial" (Madison, 1978; French and Tomlinson, 1980, 1981; Grayum, 1984) is more accurate in that these shoots usually have many leaves in each article. However, they occasionally produce articles with as few as one or two leaves. The more important criterion is that they produce a variable number of leaves, as compared to the homeophyllous sympodial species which produce a precisely determined and constant number of leaves per article. Therefore, I will refer to "polyphyllous sympodial" growth as *anisophyllous sympodial*.

Blanc (1977a) takes the somewhat unconventional position of using the term *monopodial* to refer to the growth of polyphyllous articles, and using the term *sympodial* to refer only to the homeophyllous sympodial growth of *Philodendron* and *Anthurium*, which he would describe as being composed of monophyllous articles.

The results presented in this paper have been organized around a hierarchical scheme for the classification of shoot organization, and only the broad outlines of these patterns have been discussed. In Ray (in press), I will present more detailed analyses of shoot organization, and the data will be organized systematically. It will then be possible to more easily consider how these characters correlate with phylogeny. Future papers will also discuss how shoot organization characteristics correlate with the facility for vegetative dispersal, and with life history characteristics.

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