Amer. J. Bot. 75(1): 56–84. 1988.

SURVEY OF SHOOT ORGANIZATION IN THE ARACEAE[1]

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ABSTRACT

Shoot organization is examined in 87 species from 29 genera representing all six subfamilies of the Araceae and of *Acorus*, which has been placed in a separate family. Within each taxonomic group examined, the details of shoot organization are presented, including the types of segments and articles which make up the shoot, the degree of expansion of leaf blades, and the placement of buds along the shoots. Literature on shoot organization of the 29 genera is reviewed. The degree of correlation between shoot organization characteristics and systematic groupings is examined, and the utility of these characteristics for systematics is evaluated. It is found that within the taxa observed, the pattern of shoot organization provides a distinctive "fingerprint" at the generic or sectional level, sufficient for determination of the group. Some patterns which appear are pointed out: taxa with bisexual flowers usually produce a single inflorescence at the terminus of a vegetative article. A few taxa with bisexual flowers produce pairs of inflorescences at the ends of articles. Multiple inflorescences (more than two) at an article terminus occur only among taxa with unisexual flowers. Multiple inflorescences are associated with anisophyllous or homeophyllous sympodial growth, while single or paired inflorescences are associated with homeophyllous or intermittent homeophyllous sympodial growth. These patterns might be understood as the result of selection for flexibility of reproductive effort and of seasonal reproduction.

A GENERAL SCHEME of shoot organization in the Araceae was presented in Ray (1987c), and a discussion of the diversity of leaf types in the Araceae was presented in Ray (1987b). The terminology developed in these two papers is used here. This paper will look more closely at the details of shoot organization, to show variations which occur within each of the eleven patterns described in the overall scheme. One type of variation which occurs is the degree of development of the blades of leaves at various positions in the organization of the shoot. For example, in most species the prophyll is a cataphyll, but in some it is a foliage leaf. In most species the sympodial leaf is a foliage leaf, but in some it is a reduced leaf or a cataphyll. The degree of blade development of the sylleptic mesophyll varies widely. Another variable characteristic is the number of times that a given unit of construction is repeated. For example, in intermittent homeophyllous growth, the homeophyllous article is repeated a variable number of times. Similarly, in intermittent homeophyllous growth, the number of monopodial segments in the anisophyllous article separating homeophyllous episodes is also variable. The placement of vegetative buds is variable. In most taxa, buds are lacking on sympodial segments, but they are present in some taxa. Buds are usually present on monopodial segments, but in some taxa they are only rarely present. The presence of buds on mesophyll segments is highly variable, although it tends to be consistent within a species.

Another characteristic that will be detailed is the presence or absence, and the kind of bud found on the base of the peduncle of the inflorescence terminating a vegetative article. If no bud is present, or if a vegetative bud is present, the species will be able to produce at most a single inflorescence with each vegetative article. If there is a bud on the peduncle base which can develop into a single inflorescence, then the species will produce at most two inflorescences with each vegetative article. If there is a bud on the peduncle base which can develop into an inflorescence sympodium (either axillary, gorgonoid, or mixed), then the species will be able to produce an essentially unlimited number of inflorescences with each vegetative article. In other words, when an inflorescence sympodium is produced, the individual plant will be able to adjust the number of inflorescences that it allows to mature in accordance with the resources that it has available for reproduction, with no upper limit imposed by the shoot organization. Which of these

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[1] Received for publication 31 December 1986; revision accepted 23 April 1987.

This study was supported in part by a grant from the University of Delaware Research Foundation. I wish to thank Angela Blaschke, Mike Grayum, Susanne Renner, Sue Thompson, and Michael Zacks for their assistance, and James French, Mike Grayum, and Dan Nicolson for their critical reviews of the manuscript.

patterns are found in a species will have a profound impact on the phenological characteristics of the species and on its life history characteristics.

In addition to bringing out more details of shoot organization, this paper has three other aims. The first is to bring together everything known about the shoot organization of the taxa that I have observed, and to present it in such a way that persons working on a specific taxon can easily locate the relevant information for their taxon. In this respect not only my own observations will be presented, but all literature references to shoot organization of the genera that I have observed. The second aim is to assess the degree to which the characteristics of shoot organization are useful to systematists in classifying groups within the Araceae. In this respect the various characteristics of shoot organization will be examined to see how stable each characteristic is at each level of classification: subfamily, genus, section, series, and species. The third aim is to look for any interesting patterns in shoot organization within the family. These observations will go beyond the correlations between shoot organizations and systematics to look at unexpected correlations between various morphological and developmental characteristics.

MATERIALS AND METHODS—The study reported here was conducted primarily in the Sarapiquí region of northeast Costa Rica, principally at 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 in the living collections of the New York Botanical Garden and the Missouri Botanical Garden.

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 prepared by the author and by P. B. Tomlinson. Shoot organization has been examined in 87 species from 29 genera in 22 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, as described in Ray (1987c), by using more and different kinds of symbols. Engler used only N, L, and S for cataphyll, foliage leaf, and spathe and spadix respectively. The symbols used here and described in Ray (1987c) are: P = *p*rophyll, B = *b*racteole, E = m*e*sophyll, C = mesobra*c*teole, M = *m*onopodial leaf, S = *s*ympodial leaf, I = *i*nflorescence (spathe and spadix), and X = inflorescence (spadi*x* without spathe). In some cases where greater specificity is desired, subscripts will be added to the right of the symbols just listed, as follows: s = *s*ylleptic, p = *p*roleptic, c = *c*ataphyll, r = *r*educed leaf, e = *e*xpanded leaf (foliage leaf). These terms are used in the sense described in Ray (1987b). In addition to these refinements that were used in Ray (1987c), this paper will consider additional details requiring the use of additional symbols.

The subscript 'b' will be used to indicate the presence of a vegetative *b*ud on a segment. The subscript indicating the bud will be placed on the left side of the principal symbol to stress that it refers to the bud on the internode subtending the leaf, not to the bud in the axil of the leaf. Sympodial segments bear both a sympodial leaf and a prophyll; thus, two symbols connected by a vertical line appear in each schematic diagram for each sympodial segment. If a bud occurs on a sympodial segment, the 'b' subscript will be placed to the left of the prophyll symbol 'P', rather than the sympodial leaf symbol 'S'. I have chosen this convention because it seems logical that buds on sympodial segments are likely to be associated with the internode subtending the prophyll, rather than the internode subtending the sympodial leaf. The new axis, of which the prophyll is the first leaf, develops from the sylleptic bud positioned directly below the point of overlap of the edges of the sheath of the sympodial leaf, on the internode subtending the sympodial leaf; thus, the bud of this internode is "used up" in the formation of the new axis. Proleptic vegetative buds on sympodial segments are always placed directly below the point of overlap of the edges of the sheath of the prophyll, and so would reasonably be associated with the internode subtending the prophyll.

The subscript 'o' indicates that an organ is ab*o*rted by becoming necrotic at a very early stage of development, while still in the primordial state. It will usually be applied to the inflorescence, either the inflorescence terminating a vegetative article or in an expanded diagram of an inflorescence sympodium to show which inflorescences have necrosed. The subscript 'w' (*w*aiting) will be used to indicate that a leaf is a resting cataphyll. The subscripts 'o' and 'w' will be placed on the right side of the principal symbol.

The structures surrounding the inflorescence terminating a vegetative article will be considered in more detail than in Ray (1987c). The terminal inflorescence will be symbolized with the letters I or X as indicated above, and subscripts will be used to indicate what kind of bud, if any, develops on the peduncle base. In keeping with other bud notation, the subscript will be on the left side of the inflorescence symbol. The subscripts to be used are as follows: l = (*l*one) no bud on the peduncle base, b = a vegetative *b*ud on the peduncle base, t = (*t*wo) the bud on the peduncle base develops into a second inflorescence, a = the bud on the peduncle base develops into an *a*xillary inflorescence sympodium, g = the bud on the peduncle base develops into a *g*orgonoid inflorescence sympodium, x = the bud on the peduncle base develops into a mi*x*ed axillary gorgonoid inflorescence sympodium, u = the bud on the peduncle base develops into an inflorescence sympodium but it is *u*ncertain if it is an axillary or a gorgonoid sympodium.

Superscripts will be used to indicate in some cases the nature of the observation on which the data is based, as follows: s = leaf type implied by *s*car on stem, and b = observation based on leaf primordia contained in apical *b*ud. The superscripts will appear on the right side of the primary symbol, and they are added as a note of caution, that the accuracy of the data may be affected by the nature of the observation. When the leaf has abscised, or is still in the primordial condition, it is possible to distinguish easily between monopodial and sympodial leaves, but it can be very difficult to know if the blade was or will be expanded or reduced. Generally, no superscript will be used, meaning that a fully developed and intact leaf was observed. The symbols used in the construction of Englerian shoot organization diagrams are summarized in Table 1.

The method of construction of the schematic diagrams is described in the methods section of Ray (1987c). When more than one subscript is listed, it means that all of the observed conditions have been observed within a species. When more than one subscript is listed, followed by a ? mark, it means that it is known that at least one of these conditions occurs, but there is uncertainty as to which. When a bud is sometimes present and sometimes absent from a given position on a shoot, the subscripts 'lb' will be used together without a question mark, to indicate this variability.

Species authors and vouchers were listed for most species dealt with in this paper in Ray (1987b, c); therefore, they will not be repeated here. The relevant information will be given for any species not previously treated.

RESULTS—The data will be presented in accordance with the phylogenetic arrangement of species, following the scheme presented in Grayum (1984). The 29 genera are arranged into 22 tribes and six subfamilies (plus the Acoraceae) as follows:

Acoraceae: *Acorus*
Gymnostachyoideae: *Gymnostachys*
Pothoideae
  Spathiphylleae: *Spathiphyllum*
  Anthurieae: *Anthurium*
  Anadendreae: *Anadendrum*
  Monstereae: *Heteropsis, Rhaphidophora, Monstera, Stenospermation, Rhodospatha*
Philodendroideae
  Callaea: *Calla*
  Callopsideae: *Callopsis*
  Anubiadeae: *Anubias*
  Aglaonemateae: *Aglaonema*
  Homalomeneae: *Homalomena*
  Peltandreae: *Peltandra*
  Asterostigmateae: *Spathicarpa*
  Philodendreae: *Philodendron*
  Dieffenbachieae: *Dieffenbachia*
Colocasioideae
  Colocasieae: *Alocasia*
  Caladieae: *Caladium, Xanthosoma, Syngonium*
Lasioideae
  Symplocarpeae: *Symplocarpus, Orontium*
  Lasieae: *Urospatha*
Aroideae
  Pinellieae: *Pinellia*
  Pistieae: *Pistia*
  Arisaemateae: *Arisaema*

Acoraceae—Acorus: As described in Ray (1987b), I advocate an interpretation of the shoot organization of *Acorus calamus,* based on the idea that the sheath of the sympodial leaf is fused with the peduncle. Thus, what has been interpreted as the spathe (Engler, 1877; Hotta, 1971) is actually the blade of the sympodial leaf. I come to this conclusion simply because that is what it looks like, and because of the anatomical observations of Van Tieghem (1867) that the so-called peduncle has two independent vascular systems, an outer ring and an inner V. As I have no special symbol

TABLE 1. *Summary of symbols used in Englerian diagrams*

Principal symbols:

B = *b*racteole
C = mesobra*c*teole
E = m*e*sophyll
I = *i*nflorescence (spathe and spadix)
M = *m*onopodial leaf
P = *p*rophyll
S = *s*ympodial leaf
X = inflorescence (spadi*x* without spathe)

Right subscripts:

c = *c*ataphyll
e = *e*xpanded leaf (foliage leaf)
o = ab*o*rted
p = *p*roleptic
r = *r*educed leaf
s = *s*ylleptic
w = *w*aiting (resting cataphyll)

Left subscripts: all but "b" are used only in the inflorescence sympodium

a = *a*xillary inflorescence sympodium
b = vegetative *b*ud
g = *g*orgonoid inflorescence sympodium
l = *l*one inflorescence, no bud on peduncle base
t = *t*wo, the bud on the peduncle base develops into a second inflorescence
u = *u*ncertain, inflorescence sympodium axillary or gorgonoid
x = mi*x*ed axillary gorgonoid inflorescence sympodium

Superscripts:

b = observation based on leaf primordia contained in apical *b*ud
s = leaf type implied by *s*car on stem

for adnate structures, I will indicate the fusion of the sympodial leaf and inflorescence by leaving out the line connecting the two. Based on my interpretation, the shoot organization of *Acorus calamus* corresponds to the following schematic diagram:

$$\begin{array}{c} \vdots \\ \{{}_{b}P_{es}\text{–}{}_{b}E_{e}\text{–}({}_{b}M_{e})\text{–}S_{e}X\} \\ \vdots \end{array}$$

Gymnostachyoideae—Gymnostachys anceps: This Australian species has the most unusual shoot organization seen. Two individuals were examined in the greenhouse at the Harvard Forest, and some serial sections prepared by P. B. Tomlinson were studied. The vegetative part of the shoot had a near homeophyllous shoot organization, with each article containing three or four leaves (see diagram, bottom of page).

The diagramed individual was not destructively sampled; thus, it was not possible to look in the leaf axils for the presence of buds. However, the serial sections were examined for the presence of vegetative buds, and it was found that they were absent from most segments. In fact, only a single vegetative bud was found after considerable search. Thus, the bud-free shoot indicated would appear to be typical.

In the schematic, the inflorescence sympodium is represented with the symbol I_z because the inflorescence sympodium of *Gymnostachys* is unique. In the position indicated by I_z in the above diagram is an entire shoot system which is very complex in structure. It consists of a monopodial shoot bearing only monopodial cataphylls, in the axils of which occur diphyllous sympodial inflorescence sympodia. The flowering shoot system conforms to the following diagram:

$$\begin{tikzcd}
& I_d \arrow[d, dash] & & I_d \arrow[d, dash] & & I_d \arrow[d, dash] \\
\cdots M_c \arrow[r, dash] \arrow[d, dash] & M_c \arrow[r, dash] & M_c \arrow[r, dash] \arrow[d, dash] & M_c \arrow[r, dash] & M_c \arrow[r, dash] \arrow[d, dash] & M_c \cdots = I_z \\
I_d & & I_d & & I_d &
\end{tikzcd}$$

Spathes are lacking from the diphyllous sym-

$$\begin{tikzcd}
\begin{array}{l} P_{es}\text{–}E_e\text{–}M_e\text{–}M_e\text{–}I_z \\ \vdots \end{array} \arrow[dr, dash] & & P_{es}\text{–}E_e\text{–}M_e\text{–}M_e\text{–}I_z \arrow[dr, dash] & & \begin{array}{r} P_{es}\text{–}E_e\text{–}M_e\text{–}I_z \\ \vdots \end{array} \\
& P_{es}\text{–}E_e\text{–}M_e\text{–}I_z \arrow[ur, dash] & & P_{es}\text{–}E_e\text{–}M_e\text{–}I_z \arrow[ur, dash] &
\end{tikzcd}$$

$$\text{or} \quad \begin{array}{c} \vdots \\ \{P_{es}\text{–}E_e\text{–}(M_e)_{1\text{–}2}\text{–}I_z\} \\ \vdots \end{array}$$

podial inflorescence sympodium, represented by I_d in the above diagram which have the following structure:

$$\{\overset{\vdots}{B}_c\text{–}C_c\text{–}\underset{\vdots}{X}\} = I_d$$

Pothoideae—Spathiphyllum: Observations of four species suggest that the genus is uniformly anisophyllous sympodial. Variation between species occurs with respect to the presence of buds on the peduncle base and on the mesophyll segment. Buds are always absent from the sympodial segment. All leaves have expanded blades except the prophyll and the mesophyll which are cataphylls. The mesophyll is directly superposed to the prophyll. The species *S. laeve* fits the schematic diagram below. In a shoot which had flowered twice, the intervening article had five leaves. Three articles were examined:

$$\{\overset{\vdots}{P}_{cs}\text{–}{}_bE_c\text{–}({}_bM_e)\text{–}\underset{\vdots}{S}_e\text{–}{}_lI\}$$

The species *S. friedrichstalii* fits the schematic diagram below. Note that vegetative buds are sometimes but not always present on the peduncle base, but were always absent from the mesophyll segment. Five articles were examined: three had vegetative buds on the peduncle base; two did not. No shoots with two successive flowering events were examined; however, the shoots examined had at least five to ten monopodial segments in succession.

$$\{\overset{\vdots}{P}_{cs}\text{–}E_c\text{–}({}_bM_e)\text{–}\underset{\vdots}{S}_e\text{–}{}_{lb}I\}$$

The species *S. fulvovirens* and *S. phryniifolium* both fit the schematic diagram below. Buds were present on both the mesophyll segment and the peduncle base. Articles contain from four to seven leaves. Eight articles of *S. fulvovirens* were examined, and two articles of *S. phryniifolium* were examined:

$$\{\overset{\vdots}{P}_{cs}\text{–}{}_bE_c\text{–}({}_bM_e)_{1-4}\text{–}\underset{\vdots}{S}_e\text{–}{}_bI\}$$

Anthurium: Observations of 14 species including 9 of the 15 sections of *Anthurium* listed by Croat (1983, 1986) suggest that two patterns of shoot organization occur in the genus. The two species (*A. clidemioides* and *A. flexile*) in the section *Polyphyllium* have anisophyllous sympodial growth, while all of the remaining species have triphyllous sympodial growth. The species *A. clidemioides* conforms to the schematic diagram below, based on observation of several articles. Two complete articles observed had six leaves each.

$$\{{}_b\overset{\vdots}{P}_{cs}\text{–}{}_bE_e\text{–}({}_bM_e)_{\sim 3}\text{–}\underset{\vdots}{S}_e\text{–}{}_bI\}$$

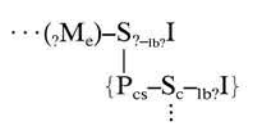
Observations of several articles of *A. flexile* subsp. *flexile* show the species to conform to the schematic diagram below. Note that cataphylls are scattered haphazardly along the stem, such that any leaf, be it monopodial, sympodial, or mesophyll, may be a cataphyll or a foliage leaf. (Prophylls are always cataphylls.) On one individual examined, it appeared that nine of 22 leaves were cataphylls (not counting prophylls). Successive inflorescences on a single shoot were not observed, but as many as 13 monopodial segments were observed preceding a sympodial segment, and as many as five were observed following.

$$\{{}_b\overset{\vdots}{P}_{cs}\text{–}{}_bE_{ec}\text{–}({}_bM_{ec})\text{–}\underset{\vdots}{S}_{ec}\text{–}{}_bI\}$$

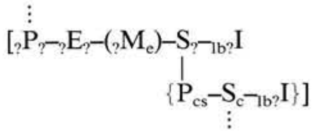
Numerous articles of each of the remaining species have been examined, and they all conform to precisely the same pattern of triphyllous sympodial growth, with no variation either within or between species with respect to the placement of buds or the development of leaf blades. Each article of the shoot includes a sylleptic prophyll and mesophyll, both of which are cataphylls, a sympodial leaf which is a foliage leaf, and a solitary terminal inflorescence. Vegetative buds are formed only on the sympodial segment and on the peduncle base. The species observed to fit this pattern are *A. 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*, and *A. upalaense*. These species conform to the following diagram:

$$\{{}_b\overset{\vdots}{P}_{cs}\text{–}E_c\text{–}\underset{\vdots}{S}_e\text{–}{}_bI\}$$

Anadendrum: A specimen of *A. microstachyum* (de Vr. et Miq.) Backer et Alderw. was examined in the herbarium of the New York Botanical Garden (R. S. Williams 2364, from the Philippines). It was possible to recognize the growth as intermittent diphyllous sympodial, according to the diagram below. Although this specimen was not observed to return to the production of anisophyllous articles,



$$\begin{array}{l}\cdots({}_{?}M_{e})\text{–}S_{?\text{–}lb?}I\\ \qquad\qquad |\\ \qquad\quad \{P_{cs}\text{–}S_{c}\neg_{lb?}I\}\\ \qquad\qquad\qquad \vdots\end{array}$$



$$\begin{array}{l}\vdots\\ [{}_{?}P_{?}\text{–}{}_{?}E_{?}\text{–}({}_{?}M_{e})\text{–}S_{?}\neg_{lb?}I\\ \qquad\qquad\qquad\quad |\\ \qquad\qquad\qquad \{P_{cs}\text{–}S_{c}\neg_{lb?}I\}]\\ \qquad\qquad\qquad\qquad\quad \vdots\end{array}$$

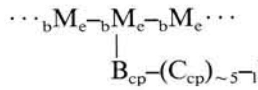
it must do so, as the homeophyllous articles do not bear foliage leaves.

Heteropsis: Live flowering material of *Heteropsis* has not been observed; however, flowering material has been examined in the herbarium. Growth of some species is monopodial, while others appear to be proleptic anisophyllous sympodial.

Among sympodial species, examination of numerous specimens (many mislabeled *H. oblongifolia*) consistently showed that flowering occurs terminally on short shoots bearing about eight leaves. The first of these leaves had always abscised; thus, it was not possible to examine their morphology. The first scars were closely spaced indicating proleptic development. The last three or four leaves were usually present and had well developed blades. Given that the first few leaves were consistently missing, they were probably short-lived cataphylls; experience has shown that foliage leaves do not regularly abscise rapidly. While inflorescences on the herbarium sheets were always in a terminal position on these short shoots, scar patterns on stems suggested that after a period of rest, the shoot would be renewed from the axil of the penultimate leaf. This pattern was most clearly seen in *H. melinonii* (Engl.) Jonk. & Jonk. This pattern can be summed up by the following diagram:

$$\begin{array}{l}\ \vdots\\ \{P_{cp}\text{–}(E_{cp})_{2}\text{–}({}_{b}M_{e})_{3\text{–}6}\text{–}S_{e}\neg I\}\\ \qquad\qquad\qquad\qquad\qquad\quad \vdots\end{array}$$

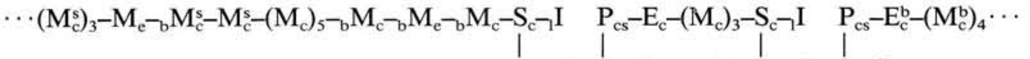
Among monopodial species, flowering occurred on short shoots bearing several bracts. These shoots were greatly reduced, with a total length of about 1 cm. There were no buds on these shoots, which makes shoot renewal after flowering impossible. This pattern was found in the type specimens of *H. oblongifolia* and *H. salicifolia.* The organization of these shoots is summarized in the following diagram:



$$\begin{array}{l}\cdots{}_{b}M_{e}\neg{}_{b}M_{e}\neg{}_{b}M_{e}\cdots\\ \qquad\qquad\ |\\ \qquad\qquad B_{cp}\text{–}(C_{cp})_{\sim 5}\neg I\end{array}$$

Rhaphidophora: One shoot of *R. decursiva* was examined in the conservatory of the New York Botanical Garden. This species has an unusual shoot organization in that most of the leaves on the shoot are short-lived monopodial cataphylls. There are very few foliage leaves on the shoot; only two of the 29 segments examined had foliage leaves, and these were both monopodial leaves. Buds were also sparsely distributed and seemed to occur in loose association with the foliage leaves. Buds occurred only on the segment bearing the foliage leaf, or on the segment immediately preceding or following the foliage leaf. Four of the 29 segments had buds. Although many of the monopodial cataphylls were represented only by scars, the cataphyll scars were clearly distinctive from the scars of monopodial foliage leaves, in that they were much thinner. Sympodial leaves, mesophylls, and prophylls were all cataphylls, inflorescences were solitary without buds on the peduncle bases, and the overall shoot organization is anisophyllous sympodial. The shoot had the organization indicated below:

Monstera: Of the five species of *Monstera* examined closely, three clearly showed intermittent diphyllous sympodial growth, one may exhibit this pattern, and the fifth seemed to be proleptic anisophyllous sympodial. There is considerable developmental diversity in the genus *Monstera.* More species must be ex-



$$\begin{array}{l}\cdots(M_{c}^{s})_{3}\text{–}M_{e}\neg{}_{b}M_{c}^{s}\text{–}M_{c}^{s}\text{–}(M_{c})_{5}\neg{}_{b}M_{c}\neg{}_{b}M_{e}\neg{}_{b}M_{c}\text{–}S_{c}\neg I\quad P_{cs}\text{–}E_{c}\text{–}(M_{c})_{3}\text{–}S_{c}\neg I\quad P_{cs}\text{–}E_{c}^{b}\text{–}(M_{c}^{b})_{4}\cdots\\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\quad |\qquad\quad |\qquad\qquad\qquad\qquad |\qquad\quad |\\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\quad P_{cs}\text{–}E_{c}\text{–}S_{c}\neg I\qquad\qquad P_{cs}\text{–}E_{c}\text{–}S_{c}\neg I\end{array}$$

$$\begin{array}{l}\ \vdots\\ \{P_{cs}\text{–}E_{c}\text{–}({}_{lb}M_{ce})\text{–}S_{c}\neg I\}\\ \qquad\qquad\qquad\qquad\quad \vdots\end{array}$$

amined in order for this genus to be understood. Numerous individuals of *M. adansonii* var. *laniata* were examined and were found to fit the intermittent diphyllous pattern below. The number of leaves on anisophyllous articles has not been counted, but they are numerous, e.g., more than 10.

$$\begin{array}{rl}
\vdots\qquad\qquad\qquad\qquad\qquad & \\
[P_{cs}-({}_{b}E_{c})_{1-2}-({}_{b}M_{e})- & S_{e}\neg I\\
 & |\\
 & \{P_{cs}-S_{c}\neg I\}_{0-9}]\\
 & \qquad\quad\vdots
\end{array}$$

Examination of a shoot of *Monstera spruceana* growing in the conservatory of the New York Botanical Garden showed the intermittent diphyllous pattern (bottom of page, upper figures).

Examination of several individuals of *M. tenuis* shows the shoot to conform to an intermittent diphyllous pattern as shown in the diagram below. The mesophyll segment may or may not have a bud; the bud was present on four out of six mesophyll segments. It is not known if the mesophyll has an expanded or reduced blade, and it is not known if there is a bud on the peduncle base.

$$\begin{array}{rl}
\vdots\qquad\qquad\qquad\qquad\qquad\qquad & \\
[P_{cs}\neg_{1b}E_{?}-({}_{b}M_{e})_{11-15}- & S_{e}\neg_{1b?}I\\
 & |\\
 & \{P_{cs}-S_{c}\neg_{1b?}I\}_{1-4}]\\
 & \qquad\quad\vdots
\end{array}$$

Two individuals of *M. diversifolia* were examined, in each of which the inflorescence had recently released its fruit and abscised. One of the individuals had a diphyllous article, suggesting that the species may sometimes exhibit intermittent diphyllous sympodial growth. In one individual, the renewal shoot had not emerged from the bud enclosed by the prophyll, even though the inflorescence had abscised. This suggests that there is a period of rest before the renewal shoot develops, indicating at least partial prolepsis. In this respect, it is interesting to note that in the individual with the developed renewal shoot, there were two mesophylls that were cataphylls, followed by a monopodial leaf with a reduced blade, a pattern typical of proleptic morphology. It is not known if there is a bud on the peduncle base. The two individuals showed the following two patterns (bottom of page, lower figure).

Most individuals of *M. glaucescens* examined have shown no signs of intermittent homeophyllous sympodial growth. However, a single specimen included a single diphyllous article. (See diagram at the top of p. 63.) Growth seems to be anisophyllous sympodial, with signs of prolepsis, as indicated by renewal shoots resting in the prophyll while the inflorescence matures. Possibly very vigorous specimens may show intermittent diphyllous growth. Another interesting characteristic of this species is that some individuals show monopodial cataphylls scattered along the stem, in a manner similar to *Anthurium flexile.* In one entirely monopodial shoot examined, it seemed that half of the monopodial leaves were cataphylls, and the cataphylls always occurred in adjacent pairs separated by one or two adjacent monopodial foliage leaves. Three flowering shoots examined showed the following patterns:

$$\begin{array}{rllll}
\cdots E_{r}-({}_{b}M_{e})_{6}- & S_{r}-_{1}I & & & P_{cs}{}^{b}\cdots\\
 & | & & & |\\
 & \{P_{cs}- & S_{c}-_{1}I\}_{2} & P_{cs}{}^{b}- & S_{c}{}^{b}-_{1}I^{b}\\
 & & | & | & \\
 & & P_{cs}-E_{c}-E_{r}-({}_{b}M_{e})_{5}- & S_{r}-_{1}I^{b} &
\end{array}$$

$$\begin{array}{rl}
\vdots\qquad\qquad\qquad\qquad\qquad\quad & \\
[P_{cs}-E_{c}-E_{r}-({}_{b}M_{e})- & S_{r}\neg I\\
 & |\\
 & \{P_{cs}-S_{c}\neg I\}]\\
 & \qquad\quad\vdots
\end{array}$$

$$\begin{array}{rll}
\cdots({}_{b}M_{e})- & S_{r}-_{1b?}I & \\
 & | & \\
 & P^{s}- & S^{s}\neg_{1b?}I^{s}\\
 & & |\\
 & & P^{s}-({}_{b}E_{c})_{2}\neg_{b}E_{r}\cdots
\end{array}$$

$$\begin{array}{rl}
\cdots({}_{b}M_{e})- & S_{e}\neg_{1b?}I\\
 & |\\
 & P_{c}-({}_{b}E_{c}{}^{b})_{2}\neg_{b}M_{e}{}^{b}\cdots
\end{array}$$

$$\begin{tikzcd}
\cdots({}_bM_e)_5- & S_?^s{-}_?I^s \arrow[d, dash] & & \\
 & P_c^s\neg{}_bE_c- & S_c\neg I \arrow[d, dash] & P_c\neg{}_bE_c^b-({}_bM_e^b)_2\cdots \\
 & & P_c-({}_bE_c)_2-({}_bM_e)_2- & S_c\neg I \arrow[u, dash]
\end{tikzcd}$$

$$\begin{tikzcd}
\cdots({}_bM_e)_4- & S_?^s{-}_?I \arrow[d, dash] & & P_c\neg{}_bE_c- \arrow[d, dash] & S_c{-}_?I_o^b \arrow[d, dash] \\
 & P_c^s\neg{}_bE^s-({}_bM_e)_4- & & S_c\neg I & P_c\neg{}_bE_?^b-({}_bM_e^b)_2\cdots
\end{tikzcd}$$

$$\begin{tikzcd}
\cdots{}_bM_e- & S_e\neg I \arrow[d, dash] & \\
 & P_{cs}- & S_c\neg I \arrow[d, dash] \\
 & & P_c^b-E_?^b-E_?^b\cdots
\end{tikzcd}$$

$$\begin{tikzcd}
\cdots({}_bM_e)_5- & S_c\neg I \arrow[d, dash] \\
 & P_c\neg{}_bE_c^b-({}_bM_e^b)_2\cdots
\end{tikzcd}$$

The proleptic, or partially proleptic *Monstera* appear to conform to the following generalized scheme:

$$\{\overset{\vdots}{P}_c-({}_bE_c)_{\sim 2}-({}_bM_e)-\underset{\vdots}{S}_{cre}\neg I\}$$

Stenospermation: Examination of two species shows growth to be anisophyllous sympodial; however, most of the articles are pentaphyllous, indicating an approximation of pentaphyllous homeophyllous sympodial growth. The prophyll is a cataphyll, the mesophyll is a cataphyll or a reduced leaf depending on the species, and the sympodial leaf is a foliage leaf. Vegetative buds are lacking from the mesophyll segments and the sympodial segments; are always present on the monopodial segments; and are apparently absent from the peduncle bases. The growth of *S. angustifolium* conforms to the following diagram:

$$\{\overset{\vdots}{P}_{cs}-E_c-({}_bM_e)_{2-4}-\underset{\vdots}{S}_e\neg I\}$$

A shoot of *S. spruceanum* was examined in the conservatory of the New York Botanical Garden and found to conform to the following diagram:

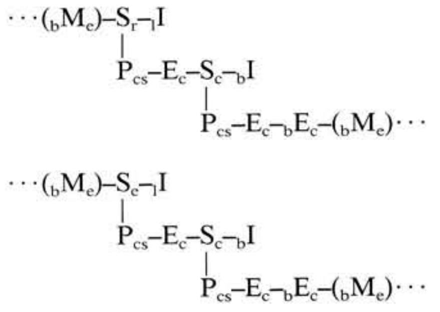
$$\{\overset{\vdots}{P}_{cs}-E_r-({}_bM_e)_{2-4}-\underset{\vdots}{S}_e\neg_{b?}I\}$$

Rhodospatha: In the two species examined, the smaller species was found to be anisophyllous sympodial, and the larger species was found to be intermittent triphyllous sympodial. In the smaller species, *R. forgetii,* the sympodial leaf may be a cataphyll or a reduced leaf, the first mesophyll segment has a cataphyll and no bud, there may be a second mesophyll segment with a reduced leaf and a bud, and there may or may not be a bud on the base of the peduncle. The following patterns were seen in *R. forgetii* (bottom of page).

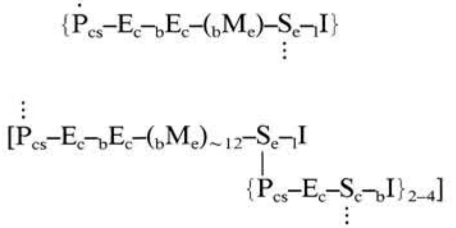
Smaller individuals of *R. wendlandii* showed anisophyllous sympodial growth; however, large and vigorous individuals showed unmistakable intermittent triphyllous sympodial growth. The sympodial leaf of an anisophyllous article is usually a fully developed foliage leaf, though on one occasion it was a reduced leaf less than half the normal length. Buds are not found on the bases of peduncles of inflorescences terminating anisophyllous articles. All three of the leaves of the homeophyllous articles—the prophyll, the mesophyll, and the sympodial leaf—are cataphylls. The only buds found on the homeophyllous articles are vegetative buds on the peduncle bases. The bud on the peduncle base of the last homeophyllous article before returning to anisophyllous growth is significantly larger than the bud on the preceding homeophyllous articles. Upon return to anisophyllous growth, there are two mesophyll segments with cataphylls: the second has a bud but the first does not. The following patterns were found (see top of p. 64):

$$\begin{tikzcd}
\cdots({}_bM_e)- & S_r\neg l \arrow[d, dash] & P_c-E_c- \arrow[d, dash] & S_c\neg I \arrow[d, dash] \\
 & P_{cs}-E_c\neg{}_bE_c\neg{}_bM_e- & S_c\neg I & P_{cs}-E_c\cdots
\end{tikzcd}$$

$$\{\overset{\vdots}{P}_c-E_c\neg{}_bE_r-({}_bM_e)-\underset{\vdots}{S}_c\neg I\} \qquad \{\overset{\vdots}{P}_c-E_c-({}_bM_e)-\underset{\vdots}{S}_r\neg I\} \qquad \{\overset{\vdots}{P}_c-E_c-({}_bM_e)-\underset{\vdots}{S}_r\neg_b I\}$$



$$\begin{array}{l}
\cdots({}_bM_e)-S_r\neg I\\
\qquad|\\
\qquad P_{cs}-E_c-S_c\neg_b I\\
\qquad\qquad\quad|\\
\qquad\qquad\quad P_{cs}-E_c\neg_b E_c-({}_bM_e)\cdots\\
\\
\cdots({}_bM_e)-S_e\neg I\\
\qquad|\\
\qquad P_{cs}-E_c-S_c\neg_b I\\
\qquad\qquad\quad|\\
\qquad\qquad\quad P_{cs}-E_c\neg_b E_c-({}_bM_e)\cdots
\end{array}$$



$$\begin{array}{l}
\qquad\vdots\\
\qquad\{P_{cs}-E_c\neg_b E_c-({}_bM_e)-S_e\neg I\}\\
\qquad\qquad\qquad\qquad\qquad\qquad\vdots\\
\vdots\\
[P_{cs}-E_c\neg_b E_c-({}_bM_e)_{\sim 12}-S_e\neg I\\
\qquad\qquad\qquad\qquad\qquad\qquad|\\
\qquad\qquad\qquad\qquad\qquad\qquad\{P_{cs}-E_c-S_c\neg_b I\}_{2\text{–}4}]\\
\qquad\qquad\qquad\qquad\qquad\qquad\qquad\vdots
\end{array}$$

Philodendroideae—Calla: Observations of several individuals of *C. palustris* consistently yielded the following pattern: the sympodial leaf and the mesophyll are normal foliage leaves; the prophyll is a cataphyll. Buds are absent from the peduncle base, the sympodial segment, the mesophyll segment, and the first segment following the mesophyll segment, but present on all other segments. Although the species is temperate, no evidence of resting cataphylls was found.

$$\begin{array}{l}
\vdots\\
\{P_{cs}-E_c-M_e-({}_bM_e)_{0\text{–}12}-S_e\neg I\}\\
\qquad\qquad\qquad\qquad\qquad\vdots
\end{array}$$

Callopsis: A single shoot of *C. volkensii* was examined in the propagation range of the New York Botanical Garden. Buds were not observed, but may have been present. Growth was triphyllous sympodial with the bud on the peduncle base developing into a single inflorescence, resulting in a pair of inflorescences at the end of each vegetative article. The prophyll was a cataphyll; the mesophyll and the sympodial leaf were foliage leaves:

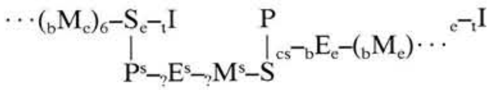
$$\begin{array}{l}
\vdots\\
\{P_{cs}-_{?}E_c-_{?}S_e-_{\iota}I\}\\
\qquad\qquad\quad\vdots
\end{array}$$

Anubias: As an experiment, an unmounted herbarium specimen of an unidentified species of *Anubias* at the Carnegie Museum of Natural History was rehydrated in soapy water and dissected. The process worked well, and the specimen was determined to be anisophyllous sympodial, corresponding to the following diagram (bottom of page, upper diagrams).

Aglaonema: Several individuals of *A. commutatum* growing in a single pot in the author's office were examined. The sympodial leaf and the mesophyll sometimes have reduced blades, and sometimes are cataphylls. A bud is sometimes present on the sympodial segment, never present on the mesophyll segment, and always present on all other segments. The bud on the peduncle base develops into a gorgonoid inflorescence sympodium. In all six articles observed, there were three visible inflorescences terminating each vegetative article:

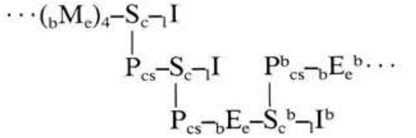
$$\begin{array}{l}
\quad\vdots\\
\{{}_{\mathrm{Ib}}P_{cs}-E_{cr}-({}_bM_e)-S_{cr}-_{g}I\}\\
\qquad\qquad\qquad\qquad\vdots
\end{array}$$

Homalomena: Two species were examined at the New York Botanical Garden, and both appeared to be anisophyllous sympodial. A single shoot of *H. picturata* was examined in the propagation range and found to conform to the diagram below (bottom of page, lower diagrams). The mesophylls and monopodial leaves had fully expanded blades, while the prophylls and sympodial leaves were cataphylls. Buds were absent from sympodial segments, but present on all other segments. Buds were not visible on the peduncle bases.



$$\begin{array}{l}
\cdots({}_bM_e)_6-S_e-_{\iota}I \qquad\qquad P \qquad\qquad\qquad\qquad\qquad {}_e-_{\iota}I\\
\qquad\quad| \qquad\qquad\qquad\quad |_{cs}\neg_b E_e-({}_bM_e)\cdots\\
\qquad\quad P^s-_{?}E^s-_{?}M^s-S
\end{array}$$

$$\begin{array}{l}
\quad\vdots\\
\{P_{cs}\neg_b E_e-({}_bM_e)-S_e-_{\iota}I\}\\
\qquad\qquad\qquad\qquad\qquad\vdots
\end{array}$$



$$\begin{array}{l}
\cdots({}_bM_e)_4-S_c\neg I\\
\qquad\quad|\\
\qquad\quad P_{cs}-S_c\neg I \qquad P^b{}_{cs}\neg_b E_e{}^b\cdots\\
\qquad\qquad\quad| \qquad\qquad\quad |\\
\qquad\qquad\quad P_{cs}\neg_b E_e-S_c{}^b\neg I^b
\end{array}$$

$$\begin{array}{l}
\quad\vdots\\
\{P_{cs}\neg_b E_e-({}_bM_e)-S_c\neg I\}\\
\qquad\qquad\qquad\qquad\qquad\vdots
\end{array}$$

A single shoot of *H. rubescens* was observed in the conservatory and found to correspond to the diagram at the bottom of p. 65. All leaves had expanded blades, except the prophyll and bracteoles which were cataphylls. Buds were present on all segments, including sympodial and mesophyll segments. The bud on the peduncle base produces a mixed axillary gorgonoid inflorescence sympodium.

Peltandra: Numerous individuals of *P. virginica* were observed, and growth was found to be anisophyllous sympodial in conformance with the diagram below. Observations were made during the growing season; thus, it was difficult to determine if resting cataphylls were present. Dissection of the apical bud of individuals collected in September suggests that the first leaf of the apical bud (the first immature leaf, enclosed by the petiole sheath of the last developed leaf of the season) has a significantly reduced blade, and thus may be a resting cataphyll. It appears that more than one article may be produced in a season, therefore, resting cataphylls may not be present on all the articles. All other leaves seem to be foliage leaves with the exception of the prophyll and bracteole, which are cataphylls. Buds are rare, occurring only on the monopodial segments immediately preceding sympodial segments. Peduncle bases bear buds which develop into single inflorescences; thus, all vegetative articles are terminated by a pair of inflorescences.

$$\begin{array}{c@{}c@{}c@{}c@{}c}
 & \vdots & & & \\
\{ & P_{cs} & -E_e-(M_e)_{0-7}-(M_w)_{0-1}-(M_e)_{0-7}-{}_bM_e- & S_e & -{}_tI\} \\
 & & & \vdots &
\end{array}$$

Spathicarpa: Several shoots of *S. sagittifolia* were examined at the Carnegie Museum of Natural History and at the New York Botanical Garden. Growth was found to be triphyllous sympodial. The prophyll and bracteole are cataphylls, the mesophyll and sympodial leaf are foliage leaves. Buds occur only on the mesophyll segment. The bud on the peduncle base develops into a single inflorescence; thus, each vegetative article is terminated by a pair of inflorescences, as shown in the diagram below:

$$\begin{array}{c@{}c@{}c@{}c@{}c}
 & \vdots & & & \\
\{ & P_{cs} & -{}_bE_e- & S_e & -{}_tI\} \\
 & & & \vdots &
\end{array}$$

Philodendron: Shoot organization in *Philodendron* falls into three distinct groups: all species not in the section *Pteromischum* are diphyllous sympodial, all species in the section *Pteromischum* are anisophyllous sympodial, but some of these are proleptic and some are sylleptic. The 18 non-*Pteromischum* species observed were *P. 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,* and *P. wilburii.* All of these species are diphyllous sympodial, the prophyll is a cataphyll, the sympodial leaf is a foliage leaf, and there is a bud on the sympodial segment. It is likely that the bud on the peduncle base in all species develops into an axillary inflorescence sympodium; however, there have not been sufficient observations made to confirm this for all species. (See Table 2.) With these uncertainities about the inflorescence sympodia of some species, it appears that all of these species conform to the following diagram:

$$\begin{array}{c@{}c@{}c@{}c@{}c}
 & \vdots & & & \\
\{ & {}_bP_{cs} & - & S_e & -{}_aI\} \\
 & & & \vdots &
\end{array}$$

An interesting minor variation in the inflorescence sympodium was observed in two species, *P. fragrantissimum* and *P. davidsonii.* In these two species, the inflorescence immediately following the sympodial leaf always aborts, as in the diagram below where the inflorescence sympodium is described more explicitly. Mayo (1986) also reports this pattern for *P. ecordatum,* known to be closely related to *P. fragrantissimum.*

$$\begin{array}{r@{}c@{}l}
\cdots S_e- & I_o & \\
 & | & \\
\{ & B_c & -I\} \\
 & & \vdots
\end{array}$$

More variation was found among the anisophyllous sympodial members of *Philodendron* section *Pteromischum.* This section divides very neatly into two series, based on whether renewal of the shoot after flowering is proleptic or sylleptic. The species with proleptic shoot renewal are *P. aurantiifolium, P. chavarrianum, P. fontianum* Groat and Grayum ined.

$$\begin{array}{r@{}l}
\cdots({}_bM_e)_5- & S_e-{}_xI \\
 & | \\
 & {}_bP_{cs}-{}_bE_e-{}_bM_e{}^b\cdots
\end{array}$$

$$\begin{array}{c@{}c@{}c@{}c@{}c}
 & \vdots & & & \\
\{ & {}_bP_{cs} & -{}_bE_e-({}_bM_e)- & S_e & -{}_xI\} \\
 & & & \vdots &
\end{array}$$

TABLE 2. *Elements of shoot organization in the Araceae*

Species	1	2	3	4	5	6	7	8	9	10	11	12
Acoraceae 1/1												
Acorus calamus	a	—	s	e	e	e*	o	p	p	l	?	b
Gymnostachyoideae 1/1												
Gymnostachys anceps	a	—	s	e	e	—	—	—	a	*	n	b
Pothoideae 8/17												
Spathiphyllum friedrichsthalii	a	—	s	c	c	e	a	a	a	lb	n	b
S. fulvovirens	a	—	s	c	c	e	a	a	p	b	n	b
S. laeve	a	—	s	c	c	e	a	a	p	l	n	b
S. phryniifolium	a	—	s	c	c	e	a	a	p	b	n	b
Anthurium atropurpureum var. *arenicolum*	h	3	s	c	c	e	a	p	a	b	n	b
A. bakeri	h	3	s	c	c	e	a	p	a	b	n	b
A. clavigerum	h	3	s	c	c	e	e	p	a	b	n	b
A. consobrinum	h	3	s	c	c	e	a	p	a	b	n	b
A. formosum	h	3	s	c	c	e	a	p	a	b	n	b
A. interruptum	h	3	s	c	c	e	a	p	a	b	n	b
A. lancifolium	h	3	s	c	c	e	e	p	a	b	n	b
A. ochranthum	h	3	s	c	c	e	a	p	a	b	n	b
A. pentaphyllum var. *bombacifolium*	h	3	s	c	c	e	e	p	a	b	n	b
A. subsignatum	h	3	s	c	c	e	e	p	a	b	n	b
A. trinerve	h	3	s	c	c	e	e	p	a	b	n	b
A. upalaense	h	3	s	c	c	e	a	p	a	b	n	b
section *Polyphyllium*												
A. clidemioides	a	—	s	c	e	e	e	p	p	b	n	b
A. flexile ssp. *flexile*	a	—	s	c	ec	ec	e	p	p	b	n	b
Anadendrum microstachyum	i	2	s	c	?/—	?/c	?	?	?/—	lb?	?	b
Heteropsis oblongifolia	m	—	p	—	—	—	—	—	—	l	n	b
Rhaphidophora decursiva	a	—	s	c	c	c	a	a	a	l	n	b
Monstera adansonii var. *laniata*	i	2	s	c	cm/—	e/c	a	a	p/—	l	n	b
M. diversifolia	i?	2?	?	c	cm/—	er/?	a	a	p/—	lb?	n	b
M. glaucescens	a	—	p?	c	cm	c	a	a	p	l	n	b
M. spruceana	i	2	s	c	cm/—	r/c	?	a	a/—	l	n	b
M. tenuis	i	2	s	c	?/—	e/c	a	a	pa/—	lb?	n	b
Stenospermation angustifolium	a	—	s	c	c	e	e	a	a	l	n	b
S. spruceanum	a	—	s	c	r	e	a	a	a	lb?	n	b
Rhodospatha forgetii	a	—	s	c	cm	cr	a	a	a	lb	n	b
R. wendlandii	i	3	s	c	cm/c	e/c	a	a	a	l/b	n	b
Philodendroideae 9/45												
Calla palustris	a	—	s	c	e	e	e	a	a	l	n	b
Callopsis volkensii	h	3	s	c	e	e	a	?	?	t	n	us
Anubias sp.	a	—	s	c	e	e	?	a	p	t	?	us
Aglaonema commutatum	a	—	s	c	cr	cr	a	pa	a	g	n	us
Homalomena picturata	a	—	s	c	e	c	?	a	p	l	n	us
H. rubescens	a	—	s	c	e	e	?	p	p	x	n	us
Peltandra virginica	a	—	s	c	e	e	a	a	a	t	y	us
Spathicarpa sagittifolia	h	3	s	c	e	e	a	a	p	t	n	um
Philodendron aromaticum	h	2	s	c	—	e	o	p	—	?	n	us
P. brunneocaule	h	2	s	c	—	e	o	p	—	?	n	us
P. cretosum	h	2	s	c	—	e	o	p	—	a	n	us
P. davidsonii	h	2	s	c	—	e	o	p	—	a	n	us
P. fragrantissimum	h	2	s	c	—	e	o	p	—	a	n	us
P. grandipes	h	2	s	c	—	e	o	p	—	a	n	us
P. ligulatum	h	2	s	c	—	e	o	p	—	?	n	us
P. mediacostatum	h	2	s	c	—	e	o	p	—	a	n	us
P. platypetiolatum	h	2	s	c	—	e	o	p	—	?	n	us
P. pterotum	h	2	s	c	—	e	o	p	—	a	n	us
P. radiatum	h	2	s	c	—	e	o	p	—	a	n	us
P. rothschuhianum	h	2	s	c	—	e	o	p	—	u	n	us
P. sagittifolium	h	2	s	c	—	e	o	p	—	u	n	us
P. scandens	h	2	s	c	—	e	o	p	—	?	n	us
P. tenue	h	2	s	c	—	e	o	p	—	?	n	us

TABLE 2. *Continued*

Species	1	2	3	4	5	6	7	8	9	10	11	12
P. tertivenarum	h	2	s	c	—	e	o	p	—	u	n	us
P. tripartitum	h	2	s	c	—	e	o	p	—	?	n	us
P. wendlandii	h	2	s	c	—	e	?	?	—	?	n	us
P. wilburii	h	2	s	c	—	e	o	p	—	?	n	us
proleptic *Pteromischum*												
P. aurantiifolium	a	—	p	—	—	e	e	a	—	l	n	us
P. chavarrianum	a	—	p	—	—	e	e	a	—	l	n	us
P. fontianum	a	—	p	—	—	?	p	a	—	?	n	us
P. inaequilaterum	a	—	p	—	—	?	e	a	—	a	n	us
P. pluricostatum	a	—	p	—	—	e	p	a	—	b	n	us
P. rigidifolium	a	—	p	—	—	e	e	a	—	?	n	us
sylleptic *Pteromischum*												
P. lewisii	a	—	s	c	r	r	e	a	p	a	n	us
P. mediavaginatum	a	—	s	c	r	r	e	a	p	?	n	us
P. radicans	a	—	s	c	r?	r	e	a	p	?	n	us
P. viaticum	a	—	s	c	r	r	a	a	p	a	n	us
Dieffenbachia beachiana	a	—	s	c	e	c	e	a	p	?	n	us
D. cf. *longispatha*	a	—	s	c	e	c	e	a	p	a	n	us
D. cf. *oerstedii*	a	—	s	c	e	r	e	a	p	a	n	us
D. cf. *seguine*	a	—	s	c	e	c	e	a	p	a	n	us
Colocasioideae 4/15												
Alocasia plumbea	i	3	s	c	e	e/c	a	a	a	t	n	us
Caladium bicolor	a	—	s	c	e	e	a	p	p	t	y?	us
Xanthosoma violaceum	a	—	s	c	e	e	a	p*	a*	g	n	us
Syngonium birdseyanum	a	—	s	c	e	e	e	a	a	?	n	us
S. macrophyllum	a	—	s	c	e	e	o	a	a	g	n	us
S. podophyllum var. *peliocladum*	a	—	s	c	e	e	o	a	a	g	n	us
S. rayi	a	—	s	c	e	e	?	?	?	g	n	us
S. schottianum	a	—	s	c	e	e	?	a	a	g	n	us
S. triphyllum	a	—	s	c	e	e	o	a	a	g	n	us
Lasioideae 3/13												
Symplocarpus foetidus	h	2	s	ec	e	—	—	—	p	l	y	b
Orontium aquaticum	h	4	s	e	e	c	a	a	a	t	n	b
Urospatha friedrichsthalii	h	3	s	c	e	e	a	p	a	b	n	b
Aroideae 3/18												
Pinellia ternata	h	3	s	c	e	e	a	a	a	l	n	us
Pistia stratiotes	h	3	s	c	e	c	a	p	a	l	n	us
Arisaema triphyllum	a	—	s	c	c	er	a	a	a	l	y	us

The following are the column definitions:

1) Growth of the mature stem is *m*onopodial (m), *a*nisophyllous sympodial (a), *h*omeophyllous sympodial (h), or *i*ntermittent homeophyllous sympodial (i).
2) When homeophyllous articles are present, are they diphyllous (2), triphyllous (3), or tetraphyllous (4). (Inflorescence sympodia are treated separately, column 10.)
3) Do articles originate by *p*rolepsis (p) or *s*yllepsis (s).
4) For sylleptic articles, does the prophyll have an *e*xpanded blade (e) or is it a *c*ataphyll (c).
5) For sylleptic articles, does the mesophyll have a normal *e*xpanded blade (e) or is it a *c*ataphyll (c), or does it have a partially *r*educed blade (r); (m) indicates that there is *m*ore than one sylleptic mesophyll on anisophyllous articles. When a prophyll is followed directly by a sympodial leaf, it is considered that there is no mesophyll.
6) Does the sympodial leaf have a normal *e*xpanded blade (e), or is it a *c*ataphyll (c), or is the blade partially *r*educed (r).
7) On the sympodial segment, is the sympodial leaf attachment hyp*o*phyllous (o), hyp*e*rphyllous (e), *p*eraphyllous (p), or *a*mbiphyllous (a).
8) Is a bud *p*resent (p) or *a*bsent (a) on the sympodial segment, below the point of overlap of the sheath edges of the prophyll, and generally axillary to the blastophyll.
9) For sylleptic articles, is a bud *p*resent (p) or *a*bsent (a) on the mesophyll segment.
10) Is there a *l*one inflorescence with no bud on its peducle base (l), a solitary inflorescence with a vegetative *b*ud on its peduncle base (b), *t*wo inflorescences (t), an *a*xillary inflorescence sympodium (a), a *g*orgonoid inflorescence sympodium (g), or a mi*x*ed axillary gorgonoid inflorescence sympodium (x), (u) indicates that an inflorescence sympodium is formed containing more than two inflorescences, but it is *u*ncertain if it is an axillary or a gorgonoid sympodium.
11) Does the shoot rest seasonally, within resting cataphylls (y), or not (n).

$$\{\overset{\vdots}{P}_{cp}\text{–}(E_c)_{1\text{–}3}\text{–}({}_bE_r)_{1\text{–}2}\text{–}({}_bM_e)\text{–}\underset{\vdots}{S}_e\text{–}_{\neg}I\}$$

$$\{\overset{\vdots}{P}_{cp}\text{–}(E_c)_{1\text{–}3}\text{–}({}_bE_r)_{1\text{–}2}\text{–}({}_bM_e)\text{–}\underset{\vdots}{S}_e\text{–}_{b}I\}$$

$$\{\overset{\vdots}{P}_{cp}\text{–}(E_c)_{1\text{–}3}\text{–}({}_bE_r)_{1\text{–}2}\text{–}({}_bM_e)\text{–}\underset{\vdots}{S}_e\text{–}_{a}I\}$$

MG 6153 (MO, CR), P. *inaequilaterum* Liebm. MG 2797 (MO), *P. pluricostatum,* and *P. rigidifolium.* In *P. fontianum* and *P. inaequilaterum,* flowering has not been observed, and the classification of the shoot as proleptic is based on examination of the scar pattern of the shoot (the presence of shortened internodes at the beginning of each article). Although flowering in *P. inaequilaterum* has not been observed, examination of the scars of the peduncle bases suggests the presence of an axillary monophyllous inflorescence sympodium, which would make this species unique for the series. All remaining species in the series have either no bud on the peduncle base or a vegetative bud on the peduncle base. The number of monopodial leaves in each article range from few to many. This series of the section *Pteromischum* is proleptic anisophyllous sympodial and conforms to the diagrams at the top of the page which differ only in the nature of the bud on the peduncle base.

The species that have been observed to fall into the sylleptic series of the section *Pteromischum* are *P. lewisii, P. mediavaginatum, P. radicans,* and *P. viaticum.* The growth of these species is sylleptic anisophyllous sympodial and conforms to the diagram on the left below. The prophyll was a cataphyll; the mesophyll and sympodial leaves were reduced leaves. Buds were absent from the sympodial segment but present on all other segments. The bud on the peduncle base developed into an axillary inflorescence sympodium in all species in which the relevant observations were made. It was observed that the inflorescence sympodium of *P. radicans* contains more than two inflorescences, but it was not observed if the configuration was axillary or gorgonoid. Also, in this same species, the mesophyll observed was not fully mature; thus, it was not possible to determine with certainty if it was to be a reduced leaf or a fully expanded leaf. In *P. mediavaginatum,* the inflorescence was not observed; therefore, it was not possible to determine what kind, if any, of bud was present on the peduncle base. In *P. lewisii* a most remarkable event was observed on one shoot. The sylleptic prophyll of a renewal shoot directly subtended an inflorescence, which configuration indicates a monophyllous article. My notes show the shoot to conform to the diagram on the right below; however, I am in doubt as to the position of origin of the final article. I was not fully aware of the uniqueness of the configuration until the shoot had been fully dissected, and then it was too late to recheck and reconsider. The number of monopodial leaves in an article ranges from few to many.

$$\{\overset{\vdots}{P}_{cs}\text{–}_{b}E_r\text{–}({}_bM_e)\text{–}\underset{\vdots}{S}_r\text{–}_{a}I\}$$

$$\begin{array}{rl} \cdots({}_bM_e)\text{–} & S_r\text{–}_aI \\ & | \\ & S^b{}_{cs}\text{–}_aI^b \\ & | \\ & P^b{}_{es}\text{–}_{?}E^b\text{–}_{?}M^b\cdots \end{array}$$

←

12) Flowers are *b*isexual (b) or *u*nisexual (u). If flowers are unisexual, it is also indicated if the sexes are *m*ixed together on the spadix (m), or segregated into *s*eparate portions of the spadix (s).

When both anisophyllous and homeophyllous articles are present, and some characteristic differs between the two types of articles, a slash (/) will be used with the anisophyllous condition on the left and the homeophyllous condition on the right. If more than one condition is listed in a column, it means that all of those have been observed in the species, unless they are followed by a (?) symbol, which means one of those conditions occurs, but it is not certain which one. The symbol (–) means that the character is not applicable.

* See explanation in text. The numbers following the subfamilial names indicate the proportion of the genera sampled in each subfamily.

$$\{\overset{\vdots}{\mathrm{P}}_{cs}\text{–}{}_{b}\mathrm{E}_{e}\text{–}({}_{b}\mathrm{M}_{e})\text{–}\underset{\vdots}{\mathrm{S}_{r}}\text{–}{}_{a}\mathrm{I}\} \qquad \{\overset{\vdots}{\mathrm{P}}_{cs}\text{–}{}_{b}\mathrm{E}_{e}\text{–}({}_{b}\mathrm{M}_{e})\text{–}\underset{\vdots}{\mathrm{S}_{c}}\text{–}{}_{a}\mathrm{I}\}$$

Dieffenbachia: Four species have been examined and found to be anisophyllous sympodial. In all species the prophyll was a cataphyll, the sympodial leaf was a cataphyll or a reduced leaf, and the mesophyll was a normal foliage leaf. Buds were always absent from the sympodial segment but otherwise present on all segments. The bud on the base of the peduncle develops into an axillary inflorescence sympodium. The species examined were *D. beachiana* Croat and Grayum ined. BEH 8122 (DUKE), *D. cf. longispatha, D. cf. oerstedii,* and *D. cf. seguine.* The prophyll and sympodial leaf were cataphylls in *D. beachiana, D. cf. longispatha* and *D. cf. seguine,* and a reduced leaf in *D. cf. oerstedii.* The single specimen of *D. beachiana* examined was in poor condition; thus, the determination of the degree of blade development was based on the examination of senescent leaves. The number of leaves per article varied from species to species, but there are generally many. For example, in *D. cf. oerstedii,* there are consistently about 12 or 13 leaves per article. The four species fit the diagrams at the top of the page.

Alocasia: Several individuals of *A. plumbea* were examined, and all were found to be intermittent triphyllous sympodial in growth. All prophylls and bracteoles were cataphylls. In anisophyllous articles all other leaves were fully developed foliage leaves. In homeophyllous articles, the sympodial leaves as well as the prophylls were cataphylls, while the mesophylls were foliage leaves. Buds were not present on homeophyllous articles, while on anisophyllous articles they were present on all segments except for mesophyll segments and sympodial segments. The bud on the peduncle base develops into a single inflorescence, so that each vegetative article is terminated by a pair of inflorescences. All individuals conformed to the pattern illustrated at the bottom of the page.

Caladium: Several individuals of *C. bicolor* (Aiton) Vent. were examined. New growth develops from the upper center of an underground corm, which appears to be the swollen older portion of the stem. Only a few leaves were visible on any individual. The first of these in most cases were cataphylls, about six in a series, each longer than the preceding one. It is not clear if these are resting cataphylls or proleptic mesophylls. Without observing the plants in other seasons, it is not possible to know if they rest seasonally with the apex protected by seasonal cataphylls. Alternatively, the shoots might develop from one of the many buds covering the surface of the corm, in which case the cataphylls could be proleptic mesophylls. The former possibility seems more likely, given that the leaves always come out of the center of the circular corms and are surrounded by concentric rings representing leaf scars. One observation which casts doubt on this interpretation is that the leaves developing in the apical bud all seemed to have well-developed blades; thus, there was no sign of next season's resting cataphylls.

Sylleptic mesophylls, sympodial leaves, and monopodial leaves had fully developed blades, while bracteoles, prophylls, and what were apparently resting cataphylls, were cataphylls. Buds were present on all segments, including the sympodial and mesophyll segments. The bud on the peduncle base develops into a single inflorescence, such that each vegetative article is terminated by a pair of inflorescences.

An interesting characteristic of these shoots is that three of the four individuals examined had flowered twice, and in all three cases these inflorescences were separated by a tetraphyllous article. This raises an interesting question. Would it be appropriate to classify this species as intermittent homeophyllous sympodial if, on flowering, only a single homeophyllous article is produced? I feel that this would be appropriate, if the short article produced in each flowering season always has the same number of segments. In this case it would be desirable to examine more specimens before making a determination. This species must be either anisophyllous sympodial or intermittent tetra-

$$\begin{array}{l}
[\overset{\vdots}{\mathrm{P}}_{cs}\text{–}\mathrm{E}_{e}\text{–}({}_{b}\mathrm{M}_{e})_{12-14}\text{–}\mathrm{S}_{e}\text{–}{}_{t}\mathrm{I}\\
\hphantom{[\mathrm{P}_{cs}\text{–}\mathrm{E}_{e}\text{–}({}_{b}\mathrm{M}_{e})_{12-14}\text{–}}|\\
\hphantom{[\mathrm{P}_{cs}\text{–}\mathrm{E}_{e}\text{–}({}_{b}\mathrm{M}_{e})_{12-14}}\{\mathrm{P}_{cs}\text{–}\mathrm{E}_{e}\text{–}\underset{\vdots}{\mathrm{S}_{c}}\text{–}{}_{t}\mathrm{I}\}_{1-5}]
\end{array}$$

phyllous sympodial. Pending the examination of more material, I have classified *C. bicolor* as anisophyllous sympodial in Table 2. Based on the interpretation of the cataphylls as resting cataphylls, the individuals observed fit the diagrams at the bottom of the page.

Xanthosoma: A single shoot of *X. violaceum* was examined and found to be anisophyllous sympodial. All leaves were foliage leaves except for the prophyll and bracteoles. On most segments, there was a large vegetative bud in the standard position, below the point of overlap of the edges of the petiole sheath. However, in addition, a series of smaller accessory buds flanked the primary bud, arranged along the node and completely encircling the stem. Both the primary bud and the series of accessory buds were present on every segment, including the sympodial segment; however, on the mesophyll segment the accessory buds were present but the primary bud was absent. In the diagram below, the presence of a series of accessory buds on a segment will be indicated by a subscript 'a' to the left of the principal symbol. The bud on the base of the peduncle developed into a gorgonoid inflorescence sympodium. Each article contained numerous leaves. The shoot conformed to the following diagram:

$$\begin{array}{l}\quad\ \ \vdots\\ \{{}_{ba}\mathrm{P}_{cs}-{}_{a}\mathrm{E}_{e}-({}_{ba}\mathrm{M}_{e})-\mathrm{S}_{e}-{}_{g}\mathrm{I}\}\\ \qquad\qquad\qquad\qquad\quad\ \vdots\end{array}$$

Syngonium: Six species were examined and all were found to be anisophyllous sympodial. In every case, the prophyll and bracteoles were cataphylls, and all other leaves were fully developed foliage leaves. In all species examined, buds were present on all segments except the sympodial segment and the mesophyll segment. (Bud placement was not observed in *S. birdseyanum* and *S. rayi.*) Multiple inflorescences were not observed in *S. birdseyanum,* but in all other species, the bud on the peduncle base developed into a gorgonoid inflorescence sympodium. Flowering is very rare in *S. birdseyanum.* In all examples observed by the author, the single inflorescence produced at flowering aborted in the primordial state, while still less than 5 mm in length. The shoot of *S. birdseyanum* is represented in the diagram on the right below; the diagram to the left corresponds to five other species observed—*S. macrophyllum, S. podophyllum* var. *peliocladum, S. rayi, S. schottianum,* and *S. triphyllum*:

$$\begin{array}{l}\ \vdots\\ \{\mathrm{P}_{cs}-\mathrm{E}_{e}-({}_{b}\mathrm{M}_{e})-\mathrm{S}_{e}-{}_{g}\mathrm{I}\}\\ \qquad\qquad\qquad\quad\ \vdots\end{array}\qquad\begin{array}{l}\ \vdots\\ \{\mathrm{P}_{cs}-\mathrm{E}_{e}-({}_{b}\mathrm{M}_{e})-\mathrm{S}_{e}-\mathrm{I}_{o}\}\\ \qquad\qquad\qquad\qquad\ \vdots\end{array}$$

Symplocarpus: Several individuals of *S. foetidus* were examined, and all were found to conform to a strict diphyllous sympodial pattern. Renewal shoots develop from the bud of the peduncle base; thus, there is no sympodial leaf, as the spathe is in that position. Both the prophyll and the mesophyll are fully developed foliage leaves. Buds occur only on the mesophyll segments. Since the renewal shoots develop from the peduncle bases, inflorescences are solitary, and I will characterize them as lacking buds on the peduncle bases. (In actuality the buds on the peduncle bases develop into renewal shoots.)

This temperate species rests seasonally, and resting cataphylls are formed. Both prophylls and mesophylls are modified into cataphylls by the resting phase. It appears that usually four resting cataphylls are formed in each season. Most inflorescences are aborted; generally only those associated with the articles bearing resting cataphylls actually develop to maturity. Shoots conform to the following pattern:

$$\begin{array}{l}\quad\vdots\\ [\{\mathrm{P}_{w}-{}_{b}\mathrm{E}_{w}-{}_{l}\mathrm{I}\}_{\sim 2}\\ \qquad\qquad\quad\ \ |\\ \qquad\qquad\quad\{\mathrm{P}_{es}-{}_{b}\mathrm{E}_{e}-{}_{l}\mathrm{I}_{o}\}_{3-4}]\\ \qquad\qquad\qquad\qquad\qquad\vdots\end{array}$$

Orontium: Several individuals of *O. aquaticum* were observed. Growth conforms to a strict tetraphyllous sympodial pattern. The prophyll, mesophyll, and monopodial leaf are normal foliage leaves, while the sympodial leaf and the bracteole are cataphylls. No vegetative buds were observed; thus, they must be fairly sparsely distributed. Although the species is temperate, no sign of resting cataphylls was observed. The bud on the peduncle base develops into a single inflorescence, so each vegetative article is terminated by a pair of inflorescences. One or both inflorescences of a pair are often aborted at an early stage of development. One highly unusual feature of this species is the configuration and morphology of the sympodial leaf. In every other species that

$$\begin{array}{l}\cdots({}_{b}\mathrm{M}_{w})-\mathrm{S}_{e}-{}_{t}\mathrm{I}\qquad\quad {}_{b}\mathrm{P}_{cs}-{}_{b}\mathrm{E}_{e}-({}_{b}\mathrm{M}_{e})\cdots\\ \qquad\quad\ \ |\qquad\qquad\qquad\quad\ |\\ \qquad\ \ {}_{b}\mathrm{P}_{cs}-{}_{b}\mathrm{E}_{e}-{}_{b}\mathrm{M}_{e}-\mathrm{S}_{e}-{}_{t}\mathrm{I}\end{array}\qquad\qquad\begin{array}{l}\quad\vdots\\ \{{}_{b}\mathrm{P}_{cs}-{}_{b}\mathrm{E}_{e}-({}_{b}\mathrm{M}_{ew})-\mathrm{S}_{e}-{}_{t}\mathrm{I}\}\\ \qquad\qquad\qquad\qquad\quad\ \vdots\end{array}$$

I have examined the back side of the leaf faces 180 degrees away from the renewal shoot. In *O. aquaticum,* the back of the sympodial leaf is turned only slightly to the side. This unusual configuration, in combination with being a fairly small cataphyll developing next to a much larger shoot, results in the sympodial leaf having a two-keeled morphology, virtually identical to that of a bracteole. Another unusual feature of *O. aquaticum* is that it lacks a spathe, a character which is supposed to define the family Araceae. The shoot conforms to the following diagram:

$$\{\overset{\vdots}{\mathrm{P}}_{e}-\mathrm{E}_{e}-\mathrm{M}_{e}-\underset{\vdots}{\mathrm{S}}_{c}-_{t}\mathrm{X}\}$$

Urospatha: Several individuals of *U. friedrichsthalii* were examined and found to strictly conform to triphyllous sympodial growth. The prophyll was a cataphyll, the mesophyll and sympodial leaf were both normal foliage leaves. Buds were present only on the sympodial segment and the peduncle base. The peduncle base bears a vegetative bud; thus, inflorescences are solitary. The buds on the peduncle bases are large and persist after the inflorescences have senesced. The shoot conforms to the following pattern:

$$\{{}_{b}\overset{\vdots}{\mathrm{P}}_{cs}-\mathrm{E}_{e}-\underset{\vdots}{\mathrm{S}}_{e}-_{b}\mathrm{I}\}$$

Pinellia: Several individuals of *P. ternata* were examined and found to conform to a triphyllous sympodial pattern of growth. The prophyll was a cataphyll; the mesophyll and sympodial leaves were normal foliage leaves. No buds were observed on the stems; however, buds did form on the petiole and at the base of the lamina. The inflorescence was solitary and no bud was visible on the peduncle base. Growth conforms to the following diagram:

$$\{\overset{\vdots}{\mathrm{P}}_{cs}-\mathrm{E}_{e}-\underset{\vdots}{\mathrm{S}}_{e}\neg\mathrm{I}\}$$

Pistia: Several individuals of *P. stratiotes* were examined. The organization of the shoot was extremely difficult to determine, because the foliage leaves lack a sheath, and their base does not wrap around either the shoot or a terminal inflorescence. For this reason, it is difficult to determine with confidence the correct order of the leaves along the shoot. According to my best interpretation, the shoot is triphyllous sympodial. The prophyll is a cataphyll which is an extremely thin, transparent, seamless bag enveloping the renewal shoot. The mesophyll is the foliage leaf, which although apparently a monopodial leaf, does not have a sheath encircling the stem. The sympodial leaf is a cataphyll, which like the prophyll is an extremely thin and transparent structure. However, the sympodial leaf, unlike the prophyll, is an open structure, encircling the terminal inflorescence. Because of the uncertainty associated with the ordering of the leaves caused by the mesophylls lacking a sheath encircling the stem, it is difficult to determine which segment the buds are associated with. The lack of nodes makes it difficult to define segments, but the buds appear to be only on the sympodial segments. The inflorescences are solitary and there is no sign of a bud on the peduncle base. With considerable uncertainty, *Pistia* shoots seem to conform to the diagram below. An alternative interpretation of *Pistia* shoot organization is provided in the discussion.

$$\{{}_{b}\overset{\vdots}{\mathrm{P}}_{cs}-\mathrm{E}_{e}-\underset{\vdots}{\mathrm{S}}_{c}\neg\mathrm{I}\}$$

Arisaema: Several individuals of *A. triphyllum* were examined and growth was found to be anisophyllous sympodial. In addition, seasonal resting occurs, with resting cataphylls. Each article consists of a prophyll, which is a cataphyll and the following in this order: about five resting cataphylls; a monopodial leaf which is a normal foliage leaf and has a bud on the segment; a sympodial leaf, which is usually a foliage leaf; and a solitary inflorescence with no bud on the peduncle base. There appears to be only a single bud on each article—on the monopodial segment preceding the sympodial segment. Growth is as follows:

$$\{\overset{\vdots}{\mathrm{P}}_{cs}-(\mathrm{M}_{w})_{5\text{–}6}\neg_{b}\mathrm{M}_{e}-\underset{\vdots}{\mathrm{S}}_{re}\neg\mathrm{I}\}$$

DISCUSSION—*Literature review*—I will begin the discussion by comparing my notes on shoot organization with those of Engler, Krause, and other authors. Irmisch (1874) established the principles of shoot organization in the Araceae, upon which Engler (1877) built. Engler introduced the use of "Englerian" schematic diagrams, which I have elaborated here. The bulk of Engler's observations on aroid shoot organization were presented in Engler (1877), with some additional observations presented in Engler (1879). Comments on shoot organization presented by Engler and Krause in the 1905–1920 Das Pflanzenreich series were in large part simply repeats of data already presented in Engler (1877).

Although Engler (1877) sketched details of shoot organization, he devoted as much or more attention to details of phyllotaxy, and something related to phyllotaxy which might be called "dromicity." Engler classified the growth of shoots as "homodromous," "antidromous," or "poikilodromous." These terms refer to the sense in which successive leaves of the shoot are rolled before they unfurl. If successive leaves are rolled in the same sense (all right-handed or all left-handed), the growth is homodromous. If successive leaves alternate in the direction of rolling (left, right, left, right . . .), then growth is antidromous. If the sense of rolling is inconsistent, then growth is poikilodromous. The direction that a leaf was rolled is often reflected in asymmetries of the mature blade. Once it has been confirmed that an asymmetry in the mature blade is a result of the sense of rolling of the immature blade, the rolling pattern of the shoot can be determined without examination of the shoot apex.

The illustrations of aroids presented in various works, particularly the drawings of Schott (1984) and the Das Pflanzenreich series of Engler and Krause, are detailed and lifelike, and are useful for the identification of species. They would appear to be useful for the determination of characteristics of shoot organization. It turns out, however, that they are not accurate in these details. The most serious and frequent error is that sympodial leaves, except in the homeophyllous *Philodendron* and *Anthurium,* are drawn like monopodial leaves, with their sheathing bases wrapped around the shoot. Because of this error, if one interpreted shoot organization from the drawings, one would conclude that most species are monopodial with axillary inflorescences.

I will now present a review of previous literature on shoot organization of the 29 genera that I have treated in this paper.

Acorus calamus: Engler (1877) gives a somewhat ambiguous interpretation of the *Acorus* shoot. He refers to a "foliage leaf-like spathe whose lower section is fused with the peduncle." His illustration shows the spathe as an adnate structure which is a fused spathe and foliage leaf. (This detail is only visible in the original color coded plate.) However, his schematic diagram (Engler, 1905) interprets the foliar piece as a spathe. In essence, it seems that he has observed the same organization that I have, but he insists in calling the terminal foliar piece a spathe. He is unwilling to consider it as a sympodial leaf or to consider the spathe as absent. Instead, he attributes to this foliar piece characteristics of both a foliage leaf and a spathe, so as not to commit himself strongly to either. Engler considers the renewal shoot to arise from the axil of the ultimate rather than the penultimate leaf. This interpretation would indicate that the last foliar piece is not a leaf, but a spathe. Irmisch (1874) also describes the sympodial leaf base as a peduncle. Kaplan (1970) describes anisophyllous sympodial growth and says that renewal shoots arise from the axil of the penultimate leaf, which corresponds with my interpretation; however, he did not address the issue of the spathe.

Gymnostachys anceps: Engler (1877) describes the same structure that I have observed. His interpretation differs from mine in that he refers to the foliar piece that I have called a mesobrateole as a spathe. In his interpretation, each new article of a monophyllous inflorescence sympodium arises from a position axillary to the spathe. I consider the spathes to be absent, and articles of the diphyllous inflorescence sympodium to arise from a position axillary to the mesobracteole. The difference is essentially a semantic one, and in no way do our observations of actual shoot organization differ. French and Tomlinson (1981a) describe growth of the main shoot as anisophyllous sympodial growth with three or four leaves per article in agreement with my observations. They also describe the unusual flowering shoot as follows: "its axis bears a series of lateral, cincinnus-like aggregates of spadices, each spadix associated with a narrow, scale-like (never spathe-like) bract."

Orontium aquaticum: Engler's (1877) description of this species is somewhat confused because the figure he provides of a section of a shoot apex does not correspond to the description in his figure legend, nor does it correspond even remotely to my observations. In the description in the text he refers to what must be the sympodial leaf as a spathe and notes that it is not in the position typical of a spathe. It is found at the bottom of the peduncle rather than in the normal position directly subtending the spadix at the top of the peduncle. He does not mention that inflorescences are always produced in pairs, nor that articles are homeophyllous. Given his interpretation of the sympodial leaf as a spathe, he considers the renewal shoot to originate from a position axillary to the last leaf of the article, rather than the penultimate leaf as is typical of most Araceae.

The problem with Engler's interpretations of *Acorus, Gymnostachys,* and *Orontium* is that in each case he feels compelled to classify the last foliar piece before the spadix as a spathe, regardless of its morphological characteristics. This seems reasonable in as much as the spathe is considered to be one of the defining characteristics of the family Araceae (Standley, 1944; Standley and Steyermark, 1958; Hutchinson, 1959; Nicolson, 1979). Hotta (1970) describes the familial characteristic as "forming spadix and usually enclosed by spathe." For the subfamily Acoroideae including *Acorus* and *Gymnostachys* he describes the character as "the leaf like spathe not enclosing the spadix." However, these three genera are atypical in many respects, and the absence of a spathe (in my interpretation) is only one of many characteristics that set these genera apart. Engler (1920c) allows for the absence of a spathe only in "the last axillary blooming branch of *Pothoidium.*"

In the case of *Orontium,* if one interprets the last foliar piece before the spadix as the spathe, then the inflorescence which develops on the peduncle base must be interpreted as a spathe and spadix not subtended by a bracteole. It would be unusual in the extreme for a shoot to originate without a prophyll or bracteole. What is more, the foliar piece subtending the second spadix is in the position of and has the two-keeled morphology of a bracteole, and has none of the morphological characteristics typical of a spathe. Engler did not note the presence of the second inflorescence, which was invariably present in the specimens I examined.

Engler (1920c) states that shoots are renewed from the axil of the ultimate, rather than the penultimate leaf, only in *Acorus, Gymnostachys, Orontium, Lysichiton, Symplocarpus,* and exceptionally in *Calla.* (French and Tomlinson [1981c] repeat this statement, but it is not clear if they base the statement on their own observations or on reference to Engler and Krause.) I can confirm this statement only for *Symplocarpus.* (I have not observed *Lysichiton.*) In *Gymnostachys* there are actually three leaves (a monopodial cataphyll, a bracteole, and a mesobracteole) between the renewal shoot and the nearest inflorescence. Apparently, Engler is treating the entire flowering shoot system of *Gymnostachys* as the inflorescence. It would, however, be correct to say that in *Gymnostachys, Symplocarpus,* and possibly in *Lysichiton,* there is no sympodial leaf, and by Engler's interpretation, sympodial leaves are also lacking in *Acorus.* Engler's interpretation of *Orontium* as lacking a sympodial leaf is simply erroneous; it is the spathe which is lacking.

Spathiphyllum: Engler (1877) describes this genus as anisophyllous sympodial, and his diagram of a cross section of a shoot apex confirms that the mesophyll is a cataphyll which is directly superposed to the prophyll. The drawing appears to incorporate an error, in that one of the inflorescences is not subtended by a sympodial leaf. Similar errors were made for *Monstera* and *Homalomena* (see below). French and Tomlinson (1981b) describe anisophyllous sympodial growth.

Anthurium: Engler (1877) describes shoot organization of the species outside of section *Polyphyllium* as triphyllous sympodial, and his description corresponds with mine in most details. The only point on which my observation differs from his is in that he claims that the internode separating the prophyll and mesophyll is as a rule very short, while that separating the mesophyll from the sympodial leaf is somewhat longer. My observations indicate that precisely the reverse is true. Note in Table 2 that the sympodial leaf placement is ambiphyllous in most species, which indicates that usually there is no separation between the mesophyll and the sympodial leaf. I have observed no homeophyllous species in which the sympodial segment is longer than the mesophyll segment; generally, the mesophyll segment is significantly longer than the sympodial segment. Meusel (1951) illustrates triphyllous sympodial growth by means of a schematic drawing. Blanc (1977, 1978), Croat (1983, 1986), and Madison (1987b) describe triphyllous sympodial growth in agreement with my observations.

Engler (1879) provides a schematic diagram and Latin description of anisophyllous sympodial growth in section *Polyphyllium.* In reference to this section, Croat (1983, 1986) does not discuss the shoot organization, but lists as a definitive character for the section "1-ribbed cataphylls lacking." This is a reference to the sylleptic mesophyll, which in the other sections of the genus is a 1-ribbed cataphyll and occurs every third leaf on the shoot. In section *Polyphyllium* the sylleptic mesophyll is usually a foliage leaf. However, it is not correct to say that 1-ribbed cataphylls are lacking in the section, because of the peculiar tendency for leaves in *A. flexile* to be reduced to cataphylls. In this species, 1-ribbed cataphylls are scattered irregularly along the stem, and they may be mesophylls, monopodial cataphylls, or sympodial cataphylls. (The prophylls are 2-keeled cataphylls.) Croat and Baker (1978), by reference to Engler (1877, 1879), do describe anisophyllous growth for section *Polyphyllium.* However, they also emphasize the absence of 1-keeled cataphylls as a sectional characteristic, which is not correct. A more appropriate sectional characteristic would be that growth is anisophyllous sympodial. This is the characteristic which most significantly sets *Polyphllium* apart from the other sections, which are all triphyllous sympodial.

Anadendrum: Engler (1877) describes "*Anadendron*" by saying that it behaves like *Monstera obliqua,* which he describes as intermittent diphyllous sympodial (see below). This agrees with my observations.

Heteropsis: Engler (1877) describes monopodial organization of the shoot system of this genus, with flowers formed terminally on axillary short shoots. He indicates that the short shoots bear only cataphylls, which suggests that he only observed monopodial species. Blanc (1978) confirms monopodial growth with flowering on lateral short shoots. French and Tomlinson (1981a) describe monopodial growth with axillary inflorescences.

Rhaphidophora: Engler (1877) also notes the unusual preponderance of monopodial cataphylls on the stems of some species, often observing five to six cataphylls for each foliage leaf. The shoot is described as anisophyllous sympodial, and his illustrations of cross sections of shoots and his schematic diagram are in agreement with my observations. Blanc (1978) also illustrates anisophyllous sympodial growth with numerous monopodial cataphylls. Holttum (1955) reports homeophyllous sympodial growth for this genus but does not provide details, making reference to Meusel (1951). Examination of Meusel's schematic drawing of *R. pertusa* shows that Meusel actually illustrates anisophyllous growth with numerous monopodial cataphylls. French and Tomlinson (1981b) describe anisophyllous sympodial growth.

Monstera: Engler (1877) provides illustrations of a cross section of a stem, and schematic diagrams, which show an anisophyllous article followed by a series of six diphyllous articles. Although he does not illustrate the return to anisophyllous growth, his text description states that it will occur. Engler and Krause (1908) provide a schematic diagram of two diphyllous articles sandwiched between two anisophyllous articles. They describe this as the development of a rhipidium. In short their description matches my observation of intermittent diphyllous growth. The drawing of a shoot cross section in Engler (1877) shows the sympodial cataphylls on the homeophyllous articles arranged as if they were monopodial cataphylls, that is, wrapped around the entire shoot rather than only the inflorescence. This is probably erroneous. Blanc (1978) illustrates anisophyllous growth in *Monstera* but does not comment on intermittent diphyllous growth. Madison (1977) explicitly describes intermittent diphyllous sympodial growth and provides both an original schematic diagram in the Englerian style and a lifelike drawing of such a shoot with the leaves and inflorescences removed. Meusel (1951) illustrates intermittent diphyllous sympodial growth by means of a schematic diagram. French and Tomlinson (1981b) describe anisophyllous sympodial growth.

Stenospermation: Gómez (1983) describes growth as anisophyllous sympodial with an inflorescence sympodium and provides an Englerian style schematic diagram. However, the idiosyncratic schematic diagram was lifted unaltered from Croat (1981). The diagram is correct as used by Croat for *Syngonium* but is not appropriate for *Stenospermation,* as my observations indicate that the latter does not have an inflorescence sympodium. In her species descriptions, she states, "Inflorescence usually one or more per axil" in reference to *S. angustifolium* which I observed to have inflorescences which were solitary with no bud on the peduncle base. Of *S. sessile* she states, "Inflorescence usually solitary, sometimes 2–3 per axil." If this is true, it would be most extraordinary, for only in *Orontium* have I observed more than one inflorescence to terminate a vegetative article in a species with bisexual flowers. Perhaps Gómez observed intermittent homeophyllous growth and misinterpreted it; however, I doubt that even intermittent homeophyllous growth occurs. French and Tomlinson (1981b) describe anisophyllous sympodial growth.

Rhodospatha: Engler (1877) is fairly vague on this genus, as he examined only sterile material, but he provides a schematic diagram indicating growth as anisophyllous sympodial. Apparently, he did not observe intermittent homeophyllous growth as I did. Blanc (1978) illustrates anisophyllous growth and apparently did not observe intermittent homeophyllous growth. French and Tomlinson (1981b) describe anisophyllous sympodial growth.

Calla: Engler (1877) describes the shoot as anisophyllous sympodial, in agreement with my observations. However, he describes the presence of resting cataphylls, which I did not observe, because my observations were made in midsummer. He also describes the occasional presence of a second inflorescence at the end of a vegetative article. His description indicates that this second inflorescence arises from the bud on the peduncle base, and that there is a bracteole followed by two or three spirally arranged spathes subtending the spadix. This is a highly unusual observation which I cannot confirm. Dudley (1937) provides a schematic drawing of a mature shoot and describes growth as anisophyllous sympodial with a single inflorescence terminating each article, and indicates that there are 9 to 15 leaves on each article. She describes seasonal resting, but makes no suggestion that there are resting cataphylls, and she confirms that there are sometimes multiple spathes subtending a spadix. Meusel (1951) illustrates anisophyllous sympodial growth with a schematic drawing.

Callopsis volkensii: French and Tomlinson (1983) report anisophyllous sympodial growth, based on a general statement about the subfamily in which they place it. Apparently, they did not notice that growth is homeophyllous.

Anubias: Engler's (1877) comments on this genus are brief and vague with respect to shoot organization. He says that the sympodial leaf is a cataphyll which may subtend an inflorescence sympodium. If this is what he is saying, it does not correspond to my observations, but he may be dealing with other species. French and Tomlinson (1981b) report anisophyllous sympodial growth.

Aglaonema: Engler (1879, 1915) provides schematic diagrams indicating anisophyllous sympodial growth, which agrees with my observations. He also indicates the presence of an inflorescence sympodium, however he does not specify whether it is axillary or gorgonoid. Nicolson (1969) describes growth as anisophyllous sympodial with an inflorescence sympodium. He provides a drawing of a shoot of *A. commutatum,* showing the arrangement of the inflorescence sympodium (which appears to be gorgonoid in the drawing) and the continuation shoot. He also comments on the presence of a bud on the sympodial segment. His observations agree in detail with my own. French and Tomlinson (1981d) report anisophyllous sympodial growth.

Homalomena: Engler (1877) describes and illustrates the mixed axillary gorgonoid inflorescence sympodium of *H. rubescens.* Engler and Krause (1912) provide a schematic drawing and a drawing of a cross section of a shoot of *H. pygmaea.* These clearly indicate anisophyllous sympodial growth with axillary monophyllous inflorescence sympodia. However, there appears to be an error in the cross section drawing. The first inflorescence sympodium is not subtended by a sympodial leaf, while the next two inflorescence sympodia are. It is likely that all inflorescence sympodia are subtended by sympodial leaves. Schematic diagrams in Engler and Krause (1912) also show anisophyllous sympodial growth with either axillary or unspecified inflorescence sympodia. These observations agree in general with my own. French and Tomlinson (1981d) report anisophyllous sympodial growth.

Peltandra: Engler (1877) briefly describes this genus as anisophyllous sympodial with a pair of inflorescences at the end of each article, in agreement with my observations. Goldberg (1941) provides an excellent and detailed description of shoot organization in *P. virginica.* He confirms anisophyllous sympodial growth with a pair of inflorescences terminating each vegetative article, and indicates that vegetative buds generally only occur on the internode subtending the blastophyll of the renewal shoot. He also notes that articles on mature plants generally contained from four to six leaves. He is unclear as to whether resting cataphylls occur. He provides a sketch of a shoot cross section and an Englerian schematic diagram. French and Tomlinson (1981d) report anisophyllous sympodial growth.

Spathicarpa: Engler (1877) indicates by means of schematic diagrams that growth is anisophyllous sympodial, and he states that multiple inflorescences frequently occur, in agreement with my observations. His schematic diagrams indicate numerous monopodial cataphylls along the stem, which presumably may be resting cataphylls. I did not observe this, but we examined different species, and the specimens I observed were growing indoors, relatively free of seasonal influences. French and Tomlinson (1983) report anisophyllous sympodial growth, based on a general statement about the subfamily in which they place it.

Philodendron: Engler (1877) describes and provides a schematic diagram of the non-*Pteromischum* shoot organization. He indicates diphyllous sympodial growth with axillary monophyllous inflorescence sympodia, in agreement with my observations. The illustration in Irmisch (1874), reprinted in Engler and Krause (1912), of a *Philodendron* shoot is peculiar because he shows two successive sympodial leaves, the first of which is hypophyllous, while the second is hyperphyllous. In such non-*Pteromischum* species, all sympodial leaves are hypophyllous. Irmisch also provides a drawing of a cross section of a shoot which confirms that the inflorescence sympodium has an axillary arrangement. Blanc (1977, 1978) and Ritterbusch (1971) also confirm diphyllous sympodial growth in *Philodendron.* Blanc (1978) illustrates the axillary monophyllous inflorescence sympodium of *Philodendron.* Meusel (1951) illustrates diphyllous sympodial growth by means of a schematic drawing. French and Tomlinson (1980) describe diphyllous sympodial growth.

Engler (1879) provides a schematic diagram and Latin description of anisophyllous sympodial growth in section *Pteromischum.* Because he simply indicates two cataphylls at the beginning of each article, it is not clear if his observations were based on proleptic or sylleptic species. Blanc (1978, 1980) describes shoot organization in section *Pteromischum* as monopodial, claiming that inflorescences are formed at the end of monocarpic branches. Madison (1978a) provides a similar description of section *Pteromischum,* apparently based on his own observations. Ray (1987c) discussed this confusion, which probably arose because of prolepsis. In proleptic *Pteromischum* the renewal shoot does not appear until well after the inflorescences have dispersed their fruit and senesced. Thus, anyone observing inflorescences would always find them to be at the terminus of the shoot with no sign of shoot renewal. French and Tomlinson (1981d) describe monopodial growth in the section *Pteromischum,* with "inflorescences that are terminal on lateral branches." However, they refer to and may have been influenced by Blanc (1978, 1980). They also make the correct but unusual statement that a few species of *Philodendron* are anisophyllous sympodial, but they give no explanation as to the basis of this statement.

Dieffenbachia: Engler (1877) describes anisophyllous sympodial growth for this species and indicates that inflorescence sympodia are formed with as many as five to seven inflorescences. However, he does not indicate if the inflorescences are axillary or gorgonoid in their branching. Meusel (1951) illustrates anisophyllous sympodial growth with an axillary inflorescence sympodium by means of a schematic drawing. French and Tomlinson (1981d) report anisophyllous sympodial growth.

Alocasia: Engler (1877) provides a schematic diagram in which growth is anisophyllous sympodial with a pair of inflorescences terminating each article. Blanc (1978) illustrates anisophyllous sympodial growth, with numerous monopodial cataphylls. They apparently did not observe intermittent homeophyllous growth.

Caladium: Engler (1877) provides a schematic diagram showing anisophyllous growth, occasionally with monopodial cataphylls, in agreement with my observations. However, he indicates a solitary inflorescence with each article, in contrast to my observation of two inflorescences with each article, but we examined different species. Engler also refers to the presence of monopodial cataphylls being related to seasonal growth, which is a strong indication that these are resting cataphylls. Madison (1981) provides "Inflorescences solitary or a few in a monochasium" as a generic characteristic. In reference to *C. bicolor* he states, "Inflorescences solitary or borne two or three together." This is a most interesting observation, considering that I observed the bud on the peduncle base to develop into a single inflorescence. If his statement that there are sometimes as many as three inflorescences is correct, then it casts doubt either on the thoroughness of my examination of the inflorescence sympodium of *C. bicolor,* or on the conception that there is a fundamental distinction between the formation of a single inflorescence on the peduncle base, as opposed to the formation of an inflorescence sympodium on the peduncle base. Alternatively, we may have observed different varieties, which differed in shoot organization.

Madison (1981) also states that *Caladium* occurs mostly in regions with a pronounced seasonal climate, and that they have intermittent above-ground vegetative growth. These comments would support the notion that there are resting cataphylls on *C. bicolor.* Although the species was observed in the relatively aseasonal Sarapiquí region, it is not native to the region, where it is grown as an ornamental.

Xanthosoma: Engler (1877) provides a schematic indicating anisophyllous sympodial growth with an inflorescence sympodium, and he mentions the presence of accessory buds, all of which correspond to my observations. However, he does not indicate if the inflorescence sympodium is axillary or gorgonoid. Madison (1981) provides "Inflorescence usually several in a monochasium" as a characteristic of the genus, in apparent reference to the presence of a monophyllous inflorescence sympodium.

Syngonium: Engler (1877) provides a schematic diagram indicating anisophyllous sympodial growth in agreement with my observations. However, his diagrams also explicitly indicate that the inflorescences are organized as an axillary inflorescence sympodium, which they are not, and we have observed the same species. His schematic of the inflorescence sympodium of *Syngonium* is identical to the schematic for *Philodendron,* although the former is gorgonoid and the latter is axillary. Croat (1981) describes growth as anisophyllous sympodial with an unspecified kind of inflorescence sympodium, but his description is based on reference to Engler (1877). Blanc (1978) and French and Tomlinson (1980) describe anisophyllous growth.

Symplocarpus: Engler's (1877) description is based on examination of a dried specimen, and therefore not surprisingly, deviates significantly from my own observations. He does show shoot renewal from the axil of the ultimate rather than the penultimate leaf, but he describes the shoot as anisophyllous. He clearly did not recognize the diphyllous growth, a mistake that could be easily made with dried material, as prophylls are like normal foliage leaves, and many inflorescences abort at a very early stage of development. Engler (1920c) states that only in *Acorus, Gymnostachys* and *Orontium* is the prophyll a foliage leaf. Engler (1877) notes that the prophyll is sometimes a foliage leaf, but he apparently failed to notice the regular shoot renewal in *Symplocarpus.*

Rosendahl (1911) correctly described the diphyllous sympodial growth, the presence of resting cataphylls, and the tendency of inflorescences to abort unless they are on the articles bearing resting cataphylls. Rosendahl severely berates Krause (1908) for claiming that foliage leaves and inflorescences are produced in alternate years, and refers to "an imaginative original drawing showing the plant in its flowerless year." While I do not believe that there is an alternation of leaf and flower production between years, I don't find Krause's drawing to be "imaginative," because in *Symplocarpus* the inflorescence emerges in the spring before the first foliage leaves appear. Krause (1908) gives two illustrations: one showing the flower in the early spring before the leaves have emerged, the other showing the plant later in the season when the leaves have emerged and flowering has passed.

Urospatha: Engler (1877) provides a schematic diagram and describes a regular succession of articles with a constant leaf number and speculates that this may not be a constant for the genus. These observations are in agreement with my determination of triphyllous sympodial growth. In correspondence with my observations, he shows the prophyll to be a cataphyll, the mesophyll and sympodial leaf to be foliage leaves, and a solitary inflorescence with each article. French and Tomlinson (1981c) describe growth as anisophyllous sympodial.

Pinellia: In conflict with my observations, the schematic diagram provided by Engler (1877) indicates anisophyllous sympodial growth with frequent monopodial cataphylls or resting cataphylls. The text describes the placement of buds on the petioles rather than on the stems. The text also indicates that triphyllous articles of the type I observed are predominant. Irmisch (1874) provides an illustration of a cross section of an apex which clearly shows triphyllous sympodial growth. French and Tomlinson (1983) report anisophyllous sympodial growth, based on a general statement about the subfamily in which they place it.

Pistia: Engler (1877) provides an extended description of *Pistia,* along with a schematic diagram and several drawings of cross sections. He describes the leaf that I have called the sympodial leaf as a "membranaceous sheath part" and apparently considers it to be a stipule, though he does not like to use the term stipule. He then disregards this leaf in the construction of his schematic diagram, which results in a diphyllous sympodial rather than a triphyllous sympodial pattern. Engler considers renewal shoots to arise from the axil of the prophyll, which means that what I have described as the mesophyll would be the sympodial leaf. According to Engler, *Pistia* grows according to the diagram below, which is diphyllous sympodial. Blanc (1978) also describes growth as diphyllous sympodial, though he places the bud on the sympodial segment. Arber (1920) also accepts the interpretation of what I have called the sympodial leaf as a ligule of the subtending leaf. She provides sketches of a series of sections through a shoot of *P. stratiotes,* but unfortunately the shoot is vegetative; thus, the nature and arrangement of the articles of the mature shoot cannot be ascertained from her information. Meusel (1951) illustrates diphyllous sympodial growth by means of a schematic drawing. I am uncertain about my triphyllous sympodial interpretation of *Pistia,* but offer it as an alternative to consider.

$$\begin{matrix} \vdots & & \\ \{P_{cs} & -S_{e} & \neg_{b} I\} \\ & \vdots & \end{matrix}$$

Arisaema: Engler (1877) describes growth as anisophyllous sympodial with numerous resting cataphylls and only one or two foliage leaves at the end of each article. This corresponds to my observations. Murata (1984) provides an excellent presentation of the diversity of shoot organization in this genus. He makes the observation that in some species, the renewal shoot does not originate from the segment of the leaf subtending the inflorescence, but may arise further back on the shoot. I have never observed shoot renewal from lower down on the shoot in any taxa; thus, this is a very significant observation and a most unusual characteristic. He provides schematic drawings to illustrate shoot organization. I will interpret his drawings into the following Englerian diagrams:

$$\{\overset{\vdots}{P_c}-({}_bM_w)\neg{}_bM_e-\underset{\vdots}{S_e}\neg{}_bM_c\neg{}_bM_c\neg{}_bI\} \qquad \{\overset{\vdots}{P_c}-({}_bM_w)-\underset{\vdots}{S_c}\neg{}_bM_e\neg{}_bM_e\neg{}_bI\}$$

$$\{\overset{\vdots}{P_c}-({}_bM_w)\neg{}_bM_e-\underset{\vdots}{S_c}\neg{}_bI\} \qquad \{\overset{\vdots}{P_c}-(M_w)-({}_bM_w)\neg{}_bM_e-\underset{\vdots}{S_e}\neg I\}$$

Comments: A few general observations come out of this literature review. Because a general scheme for the understanding of shoot organization has not previously been available, earlier authors have generally been imprecise in their descriptions. The use of "Englerian" schematic diagrams, or other diagrammatic representations, has generally added precision in the absence of a vocabulary for shoot organization. However, it is surprising how many of these representations are erroneous. The most widespread error has been to represent taxa, through either verbal descriptions or schematic diagrams, as anisophyllous when they are actually either homeophyllous or intermittent homeophyllous. It would appear that many of these errors have arisen out of relatively superficial observations. In general, the older literature is not a reliable source of information on shoot organization.

Systematic relationships—Now I would like to examine systematic relationships shown by the developmental/morphological characters that I have examined. It is important to remember that all of the characteristics described here apply to fully mature shoots. Many of these characteristics are different in juvenile shoots.

At the species-level there is a very high degree of consistency in character-states. The few exceptions in which a character varies within a species are shown in Table 2 as double entries in certain of the columns. The data presented here probably underrepresent the degree of variation within species, because in many species only a few articles were sampled. Of the 80 species with sylleptic shoot renewal examined, in 76 the sylleptic prophyll was a cataphyll and in 4 it was a foliage leaf; no species showed variation in this trait except *Symplocarpus,* in which the prophyll is sometimes reduced to a cataphyll by seasonal resting. The mesophyll was a cataphyll in 24 species, in 5 a reduced leaf, in 28 a foliage leaf, and in 2 the trait was variable as follows: in one species it varies between being a foliage leaf and a cataphyll and in one species it varies between being a reduced leaf and a cataphyll. The monopodial leaves were foliage leaves in 45 species (mature diphyllous and triphyllous homeophyllous species lack monopodial leaves, because prophylls and mesophylls are not considered to be monopodial leaves), and in 6 species they were sometimes cataphylls and sometimes foliage leaves. (In three of these species the cataphylls are resting cataphylls.) The sympodial leaf was a cataphyll in 9 species, in 5 a reduced leaf, in 58 a foliage leaf, and in 10 the trait was variable as follows: in two species it was usually a foliage leaf but sometimes a cataphyll; in two species it was sometimes a reduced leaf and sometimes a cataphyll; in one it was sometimes a foliage leaf and sometimes a reduced leaf. In four intermittent homeophyllous species the sympodial leaf was a foliage leaf on anisophyllous articles and a cataphyll on homeophyllous articles; in one intermittent species it was a reduced leaf on anisophyllous articles and a cataphyll on homeophyllous articles. The placement of the sympodial leaf was ambiphyllous in 31 species, hyperphyllous in 21 species, hypophyllous in 22 species, and peraphyllous in 2 species. There was a bud on the mesophyll segment in 23 species, in 34 species there was no bud on the mesophyll segment, and in one species the trait was variable. There was a bud on virtually all monopodial segments in 46 species, and in 5 species there usually was not; all but one of the latter (*Rhaphidophora*) are temperate species. There was a bud on the sympodial segment in 37 species, in 42 there was not, and in one the trait varied. There was no bud on the peduncle base in 15 species, in 18 species there was a vegetative bud on the peduncle base, in two species the trait varied between these two states, and in five species there was uncertainty as to which of these two traits occurred.

While most of the above traits showed at least some variation within species, the overall scheme of the organization of the shoot and the inflorescence sympodium is a very conservative character which does not vary at all within species. However, the shoot organization generally is not expressed until an individual is mature. Juveniles of most species are monopodial. Sympodial growth generally does not appear until the stem thickness approaches the dimension typical of the mature stem. Intermittent homeophyllous species may first become anisophyllous as the stem thickens, and only express intermittent homeophyllous growth when the maximum stem thickness has been reached. In 7 species, the bud on the peduncle base developed into a single inflorescence, in 13 species into an axillary inflorescence sympodium, in 7 species into a gorgonoid inflorescence sympodium, and in one species into a mixed axillary gorgonoid inflorescence sympodium. In three species it is known that an inflorescence sympodium is produced, but it is not known if it is axillary or gorgonoid, though the three are undoubtedly axillary like their congenerics. In one species the shoot was monopodial; in all the rest it was sympodial. In 43 species growth was anisophyllous sympodial, 37 were homeophyllous sympodial, and 7 were intermittent homeophyllous sympodial. Among the anisophyllous sympodial species, 35 were sylleptic, and 8 were proleptic. All homeophyllous species are sylleptic. One or two of the intermittent homeophyllous species may be proleptic in the initiation of anisophyllous articles; the rest appear sylleptic. Among the homeophyllous species, 20 were diphyllous; 16, triphyllous; and one, tetraphyllous Among the intermittent homeophyllous species, 5 were diphyllous; 2, triphyllous.

At the generic level, many of the traits examined are still consistent, while others become quite variable. However, it is difficult to assess in general the degree of variability among species within genera, because in most of the genera examined only a single species was sampled. The following lists of character distributions serve more to indicate the distribution of characters among sampled genera than the variability of characters within genera.

Of the 28 sympodial genera examined, in 24 the sylleptic prophyll was a cataphyll and in 4 it was a foliage leaf (the latter are all temperate or subtropical genera); no genera showed variation in this trait (except in *Symplocarpus,* see above). The sylleptic mesophyll was always a cataphyll in 5 genera, and in 18 always a foliage leaf. In *Philodendron,* sylleptic mesophylls occur only in the sylleptic series of the section *Pteromischum* where they are reduced leaves. In 3 genera the trait was variable as follows: in *Anthurium* the mesophyll is a cataphyll, except in section *Polyphyllium,* where it is usually a foliage leaf. (In *A. flexile* it is occasionally a cataphyll.) In *Stenospermation,* the mesophyll is a cataphyll in one species and a reduced leaf in the other. In the one species of *Aglaonema* examined the mesophyll varies between a cataphyll and a reduced leaf. The monopodial leaves were foliage leaves in 18 genera, and in 5 genera they were sometimes cataphylls and sometimes foliage leaves.

The sympodial leaf was a cataphyll in 4 genera, in 13 a foliage leaf, and in 9 the trait was variable as follows: in *Anthurium* the sympodial leaf is always a foliage leaf except in *A. flexile,* where any leaf can occasionally be a cataphyll. In the one species of *Aglaonema* examined, the anisophyllous species of *Rhodospatha* and in the genus *Dieffenbachia* the sympodial leaf is sometimes a reduced leaf and sometimes a cataphyll. In the one species of *Arisaema* examined, the sympodial leaf is usually a foliage leaf but sometimes a cataphyll. In *Homalomena* the sympodial leaf is a cataphyll in one species and a foliage leaf in the other. In *Philodendron* the sympodial leaf is a foliage leaf in all species except the sylleptic series of section *Pteromischum,* where it is a reduced leaf. In the intermittent homeophyllous genera *Monstera, Rhodospatha,* and *Alocasia,* the sympodial leaf is always a cataphyll in homeophyllous articles, while in anisophyllous articles it is a foliage leaf in *Alocasia* and *Rhodospatha,* but in *Monstera* it is sometimes a foliage leaf and sometimes a reduced leaf. The placement of the sympodial leaf was ambiphyllous in 16 genera, ambiphyllous or hyperphyllous in 4 genera, hypophyllous in one genus, and in two genera it varied as follows: in *Syngonium* most species are hypophyllous, though one species is slightly hyperphyllous. In *Philodendron* every variation is found: non-*Pteromischum* are hypophyllous, sylleptic *Pteromischum* are hyperphyllous or ambiphyllous, and proleptic *Pteromischum* are hyperphyllous or peraphyllous.

There was a bud on the mesophyll segment in 7 genera, in 15 genera there was no bud on the mesophyll segment, and in 4 genera the trait was variable as follows: in *Philodendron* sylleptic mesophyll segments occur only in the sylleptic series of the section *Pteromischum,* where a bud is always present. In *Anthurium* there is no bud on the mesophyll segment except in section *Polyphyllium.* In the genera *Spathiphyllum* and *Monstera,* the presence of a bud on the mesophyll segment varies between species: three of four *Spathiphyllum* have buds, three *Monstera* have buds, one *Monstera* lacks buds, and one *Monstera* is variable. There was virtually always a bud on monopodial segments in 15 genera, in 5 genera there usually was not, and in 6 homeophyllous genera monopodial segments were not present—if the mesophyll segment is not considered to be a monopodial segment. There was a bud on the sympodial segment in 6 genera, in 15 there was not, and in 3 the trait varied as follows: in the one species of *Aglaonema* the bud is sometimes present and sometimes absent; in the genus

Homalomena, one species has the bud and the other doesn't; in the genus *Philodendron* the bud is absent from the sympodial segment in all species of the section *Pteromischum,* but present in all other species. There was no bud on the peduncle base in 9 genera, in 2 genera there was a vegetative bud on the peduncle base, in 2 genera the trait varied between these two states, and in 2 genera it was not clear which of these two states was present. In addition, among the proleptic *Pteromischum,* one species had a vegetative bud on the peduncle base, two lacked buds, and one apparently had an axillary inflorescence sympodium.

At the generic level, as at the species level, most of the above mentioned traits showed at least some variability, at least among some genera in which more than a single species was sampled. The overall scheme of organization of the shoot and of the inflorescence sympodium was consistent among most genera, but varied in a few, usually in the larger genera. The bud on the peduncle base developed into a single inflorescence in 7 genera, in one genus into an axillary inflorescence sympodium, and in 3 genera into a gorgonoid inflorescence sympodium. In two genera the trait varied as follows: in *Homalomena* the bud was sometimes absent and sometimes developed into a mixed axillary gorgonoid inflorescence sympodium. In the genus *Philodendron,* all species had axillary inflorescence sympodia, except for the proleptic *Pteromischum* in which all but one species lack inflorescence sympodia. Exclusively anisophyllous sympodial growth was found in 16 genera, all of which were sylleptic. Exclusively homeophyllous sympodial growth was found in 7 genera, one of these was diphyllous, 5 were triphyllous, and one was tetraphyllous. Growth was exclusively intermittent homeophyllous in 2 genera, in one of these the homeophyllous phase was diphyllous, and in one it was triphyllous. In addition, four genera varied between anisophyllous and homeophyllous or intermittent homeophyllous growth as follows: *Anthurium* is triphyllous sympodial except for the section *Polyphyllium* which is sylleptic anisophyllous, and *Philodendron* is diphyllous sympodial except for the section *Pteromischum,* one series of which is sylleptic anisophyllous while the other series is proleptic anisophyllous. Most *Monstera* are intermittent diphyllous sympodial, but it appears that some are proleptic anisophyllous. One *Rhodospatha* was intermittent triphyllous sympodial while the other was anisophyllous sympodial.

The above distributions of characteristics represent the observations of 29 genera of the 110 genera recognized in the Araceae and Acoraceae. Because only 26% of the genera have been sampled, it is probably not reasonable to assume that the relative proportions of the various kinds of shoot organization in the sample (e.g., anisophyllous, homeophyllous, intermittent) are representative of the family as a whole. The sample is strongly biased toward new world lowland wet forest and temperate taxa.

At the subfamilial level, most of the traits become variable. The Acoraceae and the Gymnostachyoideae each contain only a single species, and their characteristics can be seen in Table 2. In the subfamily Pothoideae, 8 of the 17 genera have been sampled. Among these, growth was monopodial, anisophyllous sympodial, triphyllous sympodial, intermittent diphyllous, and intermittent triphyllous. All prophylls were cataphylls. All mesophylls were cataphylls except for foliage leaves in *Anthurium* section *Polyphyllium* and reduced leaves in a species of *Stenospermation.* The development of sympodial leaves was mixed. The placement of sympodial leaves on the sympodial segments was either ambiphyllous or hyperphyllous. The placement of buds on segments was variable. On the peduncle base, there was either no bud or a vegetative bud. The bud on the inflorescence sympodium never developed into a single inflorescence or into an inflorescence sympodium in the Pothoideae sampled.

In the subfamily Philodendroideae, only 9 of the 45 genera have been sampled. Among these, growth was found to be proleptic anisophyllous sympodial, sylleptic anisophyllous sympodial, diphyllous sympodial, and triphyllous sympodial. Intermittent homeophyllous sympodial growth was not seen in this subfamily. All prophylls were cataphylls. Mesophylls and sympodial leaves were predominantly foliage leaves. The placement of sympodial leaves on sympodial segments was quite variable, including all conditions: ambiphyllous, hyperphyllous, hypophyllous, and peraphyllous. The placement of buds on segments was mixed. The bud on the peduncle base was also highly variable, with every possible condition represented: no bud, a vegetative bud, a single inflorescence, an axillary inflorescence sympodium, a gorgonoid inflorescence sympodium, and a mixed axillary gorgonoid inflorescence sympodium.

In the subfamily Colocasioideae, 4 of 15 genera were sampled. Among these, growth was anisophyllous sympodial and intermittent triphyllous sympodial. Prophylls were cataphylls, and mesophylls and sympodial leaves were foliage leaves (except on homeophyllous articles). The placement of the sympodial leaf on the sympodial segment was ambiphyllous, hypophyllous, or hyperphyllous. The placement of buds on segments was variable. The bud on the peduncle base developed either into a single inflorescence or into a gorgonoid inflorescence sympodium.

In the subfamily Lasioideae only 3 of 13 genera were sampled. All three were homeophyllous, though they represent all three of the homeophyllous conditions: diphyllous, triphyllous, and tetraphyllous. Two of the three genera were temperate, and in these the prophyll was a foliage leaf. Mesophylls were foliage leaves, and sympodial leaves were mixed. (*Symplocarpus* lacks a sympodial leaf.) When present, sympodial leaves were ambiphyllous. The placement of buds on segments was variable. On the peduncle base, there was either no bud, a vegetative bud, or the bud developed into a single inflorescence.

In the subfamily Aroideae, only 3 of 18 genera were sampled. These were either triphyllous sympodial or anisophyllous sympodial. Prophylls were in all cases cataphylls, while mesophylls and sympodial leaves were mixed. The placement of sympodial leaves was in all cases ambiphyllous. Buds were absent from mesophyll segments and mixed on sympodial segments. Buds were never present on the peduncle base.

Summary: The details of shoot organization are highly consistent at the level of species, series, sections, and genera. At the subfamilial level, most characteristics are variable. Shoot organization characteristics appear to have their greatest utility to systematists at the generic and sectional levels. Some patterns appeared at the subfamilial level, but more genera must be sampled in order to determine if these patterns will hold up. More genera must be sampled before it will be possible to look for patterns at the tribal level. In this paper, the pattern of shoot organization has been fully resolved in 33 genera or sections. Among these groups, the pattern of shoot organization is a distinctive "fingerprint," which is sufficient to identify the genus or section. When the pattern of shoot organization becomes known for more genera, it is likely that overlaps will occur. Nonetheless, these patterns will remain useful in characterizing genera and sections.

Patterns in shoot organization—The placement of the sympodial leaf on the sympodial segment, where internodes are elongated, generally does not vary within a genus. (In this comparison, ambiphyllous placement is ignored, because in these species the sympodial segment is so short that leaf placement does not show a preference for either the upper or the lower node.) The most striking exception to this is the genus *Philodendron.* We have within this one genus every variation of leaf placement: ambiphyllous, hypophyllous, hyperphyllous, and peraphyllous. The only other exception occurs in the genus *Syngonium,* in which most species the leaf is hypophyllous, except in one hyperphyllous species. In this latter species, however, the sympodial segment is rather short, so the difference is not so striking.

With respect to the characteristics examined in this study, the section *Pteromischum* of the genus *Philodendron* was unusually diverse in characters which are otherwise generally conservative. We find within this one section both proleptic and sylleptic anisophyllous growth. In the proleptic series of the section alone, placement of the sympodial leaf varies between hyperphyllous and peraphyllous, and the peduncle base may have no bud, a vegetative bud, or an axillary inflorescence sympodium. What holds the section together is that all species of *Pteromischum* are anisophyllous in a genus which is otherwise homeophyllous. However, the section divides neatly into two series on the basis of whether growth is proleptic or sylleptic. This distinction correlates with a number of other characteristics, arguing strongly for dividing this section.

I have commented elsewhere (Ray, 1987c) that intermittent homeophyllous sympodial growth can be the most difficut form of shoot organization to recognize in a species. This is because it may only be exhibited in the largest and most vigorous individuals. I believe that this observation may be extended to the variation among species within a genus. It looks as though certain genera may be characteristically intermittent homeophyllous sympodial, but that this pattern may only manifest itself among the species with the largest stem diameters. Species in these genera, in which the maximum stem diameter achieved by an individual is relatively small, will be anisophyllous sympodial.

Another interesting pattern is that with only a few exceptions, flagellar shoots (sensu Blanc, 1980; Ray, 1987b) do not occur in species with homeophyllous growth. Flagellar shoots are almost universal among climbing species with anisophyllous or intermittent homeophyllous growth, but almost totally lacking among climbing species with homeophyllous growth. This illustrates that developmental patterns may correlate in complex and presently inexplicable ways. More details are given in Ray

(1987a, b). This pattern will be the subject of a future paper.

Perhaps one of the most strikingly conservative characters observed was the bud on the peduncle base. It is possible to make the generalization that species with bisexual flowers have either no bud on the peduncle base, or a vegetative bud on the peduncle base. In a few cases the bud develops into a second inflorescence, but these species never develop multiple inflorescences. Therefore, this characterisic follows subfamilial lines: multiple (more than two) inflorescences are found only in the Philoedendroideae and the Colocasioideae. *Gymnostachys* might be considered another exception, but I consider it to be simply unique. The "inflorescence sympodium" of *Gymnostachys* differs from all other taxa in being diphyllous sympodial rather than monophyllous sympodial. Rather than thinking of it as an inflorescence sympodium, I consider it to be a complex and condensed lateral shoot system.

A related observation is that intermittent homeophyllous growth is found only in taxa with a fixed inflorescence number (e.g., no bud on the peduncle base, a vegetative bud on the peduncle base, or a single inflorescence developing on the peduncle base). It appears that intermittent homeophyllous growth may be an alternative strategy for allowing species which produce a fixed number of inflorescences with each vegetative article to flexibly adjust their reproductive effort while flowering seasonally. This flexibility is greatest among species which produce inflorescence sympodia.

I suspect that the patterns just discussed can be understood as the result of evolution within the family directed by two interacting selective pressures. One pressure is for the ability to flexibly adjust the reproductive effort to the condition of the individual at a given time. The other pressure is to be able to compress the reproductive activity into whatever season of the year is the best time for reproduction.

It appears that the primitive morphological condition in the family is a peduncle with either no bud or a vegetative bud on the peduncle base. This condition follows subfamilial lines; usually it is the only condition found in taxa exhibiting the primitive condition of bisexual flowers (with a few exceptions where a second inflorescence develops from the peduncle base). The condition of no bud or a vegetative bud on the peduncle base results in a fairly inflexible reproductive pattern, in that an individual may produce either one inflorescence at the end of each vegetative article, or by selective abortion of the floral primordia, no inflorescence. Faced with these limitations, selection would favor short, possibly homeophyllous articles, so that potential inflorescences are produced as frequently as possible. However, this would tend to prevent seasonal flowering. Since the inflorescence primordia would be produced as the leaves are produced throughout the year, a vigorous individual would need to mature all of these inflorescences, regardless of the season in which they were produced. *Anthurium* is an example of the fullest development of this strategy. Although it is triphyllous sympodial, it produces one inflorescence (and two cataphylls) with each foliage leaf, and it appears that in the wild, vigorous individuals flower year round—inflorescences are only rarely aborted.

The next most advanced state is to have a second inflorescence develop on the base of the peduncle, resulting potentially in a pair of inflorescences. This morphology allows for a considerable increase in the flexibility of reproductive output, in that each article can produce two, one, or no inflorescences. However, the strategy is still limited to at most two inflorescences per article and should be subject to the same forces as described above.

The most advanced state of the floral morphology is the development of an inflorescence sympodium, either axillary, gorgonoid, or mixed. This allows the plant to mature as many inflorescences with each vegetative article as it has resources to support. There does not seem to be a morphological limit to the number of inflorescences that can develop in an inflorescence sympodium. There are always undeveloped inflorescence primordia in reserve, even in cases where 10 inflorescences actually develop to maturity. With this kind of flexibility, it is feasible for flowering to become highly seasonal, with all flowering of an individual or a population occurring within a brief period of time each year. It appears that taxa with inflorescence sympodia, such as *Dieffenbachia* or *Philodendron,* are a good deal more seasonal than those without.

Intermittent homeophyllous sympodial growth appears to be a less effective means of achieving the reproductive flexibility of the inflorescence sympodium morphology. In the most highly developed forms of this kind of growth, such as that found in *Monstera* and *Rhodospatha,* the shoot temporarily ceases the production of foliage leaves, while each short article produces a single inflorescence and two or three cataphylls. This allows for the relatively rapid serial production of inflorescences. I would predict that intermittent homeophyllous sympodial species would exhibit a degree of seasonality intermediate between that shown by species with inflorescence sympodia, and nonintermittent species lacking inflorescence sympodia.

At present, I do not have adequate phenological data to support the above speculations on the relationships between developmental patterns and seasonality. However, I hope to obtain such data in the near future and will report the results when they become available.

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