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LEAF TYPES IN THE ARACEAE[1]

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ABSTRACT

Leaf types in the Araceae are described and classified on the basis of their morphology and functional role. Four classes are recognized on the basis of their association with the initiation of new shoot axes, the continuation of axes, the resting of axes, or the termination and renewal of axes. The basic types are described with the terms leaf, prophyll, mesophyll, bracteole, mesobracteole, cataphyll, and blastophyll. These terms are modified with the terms monopodial, sympodial, proleptic, sylleptic, resting, flagellar, stolon, reduced, and foliage. This represents an unconventional terminology because some of the modifiers refer to the structure of the stem to which the leaves are attached, rather than to the form of the leaf itself. The intent is to draw attention to the impact of shoot organization on leaf form, and to develop a leaf terminology that will aid in describing shoot organization.

LEAF TYPES in the Araceae have been described by previous authors in terms of lamina venation, and shapes such as pinnate, hastate, perforate, digitate, pedate, entire, sagittate, etc. In addition, some attention has been given to the development of sheaths, genicula, and pulvini on the petioles. Also, the presence of reduced leaves, cataphylls, has been noted (Engler, 1920; Hotta, 1971; Croat and Bunting, 1979; Grayum, 1984). In this study the more common types of leaves are described and classified primarily on the basis of their relationship to the organization of the shoot. No attention is given to the shape of the lamina, but a distinction is made between those leaves in which the lamina is fully expanded, and those in which the lamina is reduced or absent. No consideration is given to the pulvinus or geniculum, but the development of the petiolar sheath as it relates to shoot organization is considered. Different kinds of reduced leaves are recognized, and a terminology to distinguish between the various types is provided.

This classification of leaf types has been prepared because a recognition of certain classes of leaves, and the development of a terminology for them, ease the discussion of shoot organization. Other authors who have recently described shoot organization in the Araceae have also found it necessary to develop a more specific terminology for various leaf types. Ritterbusch (1971) developed terms for the distinct leaf types associated with monopodial growth and sympodial growth. Blanc (1977b) recognized the distinctions made by Ritterbusch, and carefully defined his terms in order to avoid confusion between foliage leaves and reduced leaves. In addition, Blanc noted the different forms of two kinds of reduced leaves.

Engler (1877) provided a comprehensive description of shoot organization throughout the entire family. However, he had no terminology to distinguish between the different foliage leaves of monopodial and sympodial growth. He used several terms to refer to reduced leaves, but these were not applied consistently. Many of the terms were used interchangeably and provided no discriminatory power. Engler's descriptions of shoot organization are at times difficult to follow because one does not know what kind of leaf, or even which leaf, he is referring to.

For this paper, shoot organization has been examined in 83 species from 27 genera in 20 tribes representing all six subfamilies and the separate family (Acoraceae) into which *Acorus* has been placed (on the basis of the classification scheme of Grayum, 1984), and it has been found useful to develop a more specific leaf terminology than that provided by previous authors. The leaf terminology presented here is not intended to be a comprehensive classification of leaf types in the Araceae as it is based entirely on species encountered in the Sarapiquí' region of Costa Rica, and those accessible in the northeastern United States, in the wild or in cultivation.

MATERIALS AND METHODS—The study reported here was conducted primarily in the Sarapiquí' region of northeastern Costa Rica, principally at Finca El Bejuco biological sta-

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TABLE 1. *Leaf types found in various species of Araceae*

Species	P_s	B_s	E_s	M	D	R	S
Acorus calamus L.	e	—	e	e	—	?	e*
Aglaonema commutatum Schott	c	c	cr	e	—	—	cr
Alocasia plumbea Van Houtte MG 1796 (DUKE)	c	c	e	e	—	—	ce
Anthurium atropurpureum Schultes and Maguire var. *arenicolum* Croat TBC 50358f	c	—	c	?	—	—	e
A. bakeri Hook.f. MG 2216	c	—	c	?	—	—	e
A. clavigerum Poepp. and Endl. BEH 12169 (MO)	c	—	c	e	—	—	e
A. clidemioides Standl. GSH 939 (MO)	c	—	e	e	fm	—	e
A. consobrinum Schott MG 6527 (MO)	c	—	c	?	—	—	e
A. flexile Schott ssp. *flexile* JF 8717 (MO)	c	—	ec	ec	fm	—	ce
A. formosum Schott MG 2880 (DUKE)	c	—	c	—	—	—	e
A. interruptum Sodiro MG 2415 (DUKE)	c	—	c	?	—	—	e
A. lancifolium Schott MG 3060 (DUKE)	c	—	c	?	—	—	e
A. ochranthum C. Koch MG 2109 (DUKE)	c	—	c	e	—	—	e
A. pentaphyllum (Aubl.) G. Don var. *bombacifolium* (Schott) Madison TBC 35684 (MO)	c	—	c	e	—	—	e
A. subsignatum Schott KFG 34 (MO)	c	—	c	e	—	—	e
A. trinerve Miq. MG 2833 (DUKE)	c	—	c	?	—	—	e
A. upalaense Croat and Baker MG 2383 (DUKE)	c	—	c	?	—	—	e
Arisaema triphyllum (L.) Schott	c	—	c	e	o	+	re
Caladium bicolor (Aiton) Vent.	c	c	e	e	—	+?	e
Calla palustris L.	c	—	e	e	—	—	e
Callopsis volkensii Engl. NYC 263/82	c	c	e	?	—	—	e
Dieffenbachia cf. longispatha Engl. and Krause MG 2225 (DUKE)	c	c	e	e	—	—	c
D. cf. oerstedii Schott BEH 8606 (DUKE)	c	c	e	e	—	—	r
D. cf. seguine (L.) Schott MG 2288 (DUKE)	c	c	e	e	—	—	c
Gymnostachys anceps R. Br. MH 4325	e	c	e	e	—	—	—
Heteropsis oblongifolia Kunth MG 2698 (DUKE)	—	—	—	e	f	—	—
Homalomena picturata (Linden and André) Regel. NYC	c	—	e	e	o	—	c
H. rubescens (Roxb.) Kunth NYC 241/79	c	c	e	e	?	—	e
Monstera adansonii Schott var. *laniata* (Schott) Madison MG 5322 (MO)	c	—	c	e	f	—	ec
M. diversifolia Croat and Grayum ined. [MG 5281] (MO)	c	—	c	e	f	—	re
M. glaucescens Croat and Grayum ined. MG 2858 (DUKE)	c	—	c	ec	?	—	c
M. spruceana (Schott) Engler NYC	c	—	c	e	?	—	rc
M. tenuis C. Koch TBC 35712 (MO)	c	—	?	e	fo	—	ce
Orontium aquaticum L.	e	c	e	e	—	—	c
Peltandra virginica (L.) Kunth	c	c	e	e	—	+	e
Philodendron aromaticum Croat and Grayum ined. BEH 10733 (DUKE)	c	?	—	e	—	—	e
P. aurantiifolium Schott MG 2906 (DUKE)	—	—	—	e	f	—	e
P. brunneocaule Croat and Grayum ined. MG 2790 (DUKE)	c	?	—	—	fym	—	e
P. chavarrianum Croat and Grayum ined. BEH 11147 (MO)	—	—	—	e	f	—	e
P. cretosum Croat and Grayum ined. MG 1894 (MO)	c	c	—	e	—	—	e
P. davidsonii Croat MG 2829 (MO)	c	c	—	e	—	—	e
P. fragrantissimum (Hook.) Kunth MG 5541 (MO) BEH 13308 (DUKE)	c	c	—	e	fym	—	e
P. grandipes Krause MG 1758 (DUKE)	c	c	—	e	—	—	e
P. lewisii Croat and Grayum ined. TBC 44316 (MO)	c	c	r	e	f	—	r
P. ligulatum Schott MG 2800 (DUKE)	c	?	—	e	—	—	e
P. mediacostatum Croat and Grayum ined. MG 1915 (DUKE)	c	c	—	e	—	—	e
P. mediavaginatum Croat and Grayum ined. MG 2756 (MO)	c	?	r	e	—	—	r
P. platypetiolatum Madison MG 2247 (DUKE)	c	?	—	e	—	—	e
P. pluricostatum Croat and Grayum ined. MG 2842 (MO)	—	—	—	e	f	—	e
P. pterotum C. Koch and Aug. BEH 8150 (MO)	c	c	—	e	—	—	e
P. radiatum Schott TBC 35680 (MO)	c	c	—	e	—	—	e
P. radicans Croat and Grayum ined. MG 5335 (MO)	c	?	r?	e	—	—	r
P. rigidifolium Krause MG 2808 (DUKE)	—	—	—	e	f	—	e
P. rothschuhianum (Engl. and Krause) Croat and Grayum comb. ined. MG 2120 (DUKE)	c	c	—	e	—	—	e
P. sagittifolium Liebm. MG 2306 (MO)	c	c	—	e	—	—	e
P. scandens C. Koch and Sello MG 2565 (MO)	c	?	—	—	—	—	e
P. tenue C. Koch and Aug. TBC 35691 (MO)	c	?	—	—	—	—	e
P. tertivenarum Croat and Grayum ined. MG 5564 (MO)	c	c	—	—	—	—	e

TABLE 1. *Continued*

Species	P_s	B_s	E_s	M	D	R	S
P. tripartitum (Jacq.) Schott TBC 44227 (MO)	c	?	—	e	—	—	e
P. viaticum Croat and Grayum ined. MG 2816 (MO)	c	c	r	e	f	—	r
P. wendlandii Schott BEH 9086 (DUKE)	c	?	—	e	—	—	e
P. wilburii Croat and Grayum ined. [MG 4759] (MO)	c	?	—	—	—	—	e
Pinellia ternata (Thunb.) Breit.	c	—	e	e	—	?	e
Pistia stratiotes L.	c	—	e	e	—	—	c
Rhodospatha forgetii N. E. Br. MG 2896 (DUKE)	c	—	c	e	?	—	cr
R. wendlandii Schott MG 5551 (MO)	c	—	c	e	f	—	ce
Rhaphidophora decursiva (Roxb.) Schott NYC 4086	c	—	c	ce	?	—	c
Spathicarpa sagittifolia Schott NYC ex. KBG	c	c	e	e	—	—	e
Spathiphyllum friedrichsthalii Schott MG 2089 (DUKE)	c	—	c	e	o	—	e
S. fulvorvirens Schott BEH 9750, 9995 (DUKE)	c	—	c	e	—	—	e
S. laeve Engl. MG 5314 (MO)	c	—	c	e	—	—	e
S. phryniifolium Schott MG 2910 (DUKE)	c	—	c	e	—	—	e
Stenospermation angustifolium Hemsl. BEH 9481 (DUKE)	c	—	c	e	—	—	e
S. spruceanum Schott NYC	c	—	r	e	—	—	e
Symplocarpus foetidus (L.) Nutt.	e	—	e	e	—	+	—
Syngonium birdseyanum Croat and Grayum ined. MG 2786 (DUKE)	c	?	e	e	f	—	e
S. macrophyllum Engl. BEH 9835 (MO)	c	c	e	e	f	—	e
S. podophyllum Schott var. *peliocladum* (Schott) Croat BEH 12787 (MO)	c	c	e	e	f	—	e
S. rayi Croat and Grayum ined. MG 2959 (DUKE)	c	c	e	e	f	—	e
S. schottianum Wendl. ex Schott TBC 35686 (MO)	c	c	e	e	f	—	e
S. triphyllum Birdsey ex Croat TBC 35675 (MO)	c	c	e	e	f	—	e
Urospatha friedrichsthalii Schott BEH 8221, 8337 (DUKE)	c	—	e	e	—	—	e
Xanthosoma violaceum Schott	c	c	e	e	?	—	e

The letters heading the seven columns correspond to the following code: P_s = sylleptic prophyll, B_s = sylleptic bracteole, E_s = sylleptic mesophyll, M = monopodial leaf, D = dispersal leaf, R = resting cataphyll, S = sympodial leaf. Entries in the rows correspond to the following code: '+' indicates that the leaf type is present, '—' that the leaf type has not been observed and is presumed to be absent, and '?' that not enough information is available or that there is some doubt. Where applicable, entries in the columns are letters corresponding to the following code: e = expanded leaf (foliage leaf), r = reduced leaf (compared to adjacent monopodial leaves), c = cataphyll (blade absent or rudimentary), s = sylleptic, p = proleptic, m = monopodial, y = sympodial, f = flagellar leaf, o = stolon leaf. Multiple entries in a column indicate that all of the conditions indicated have been observed (the trait may be variable). Brackets indicate that the collection was not made from the Sarapiquí region. GSH = Hartshorn, JF = Folsom, MG = Grayum, BEH = Hammel, TBC = Croat, KFG = Grove, MH = Margaret Howard, MO = Missouri Botanical Garden, CR = National Herbarium of Costa Rica, NYC = living material from New York Botanical Garden. *See explanation in text of my interpretation of the sympodial leaf in *Acorus*.

tion. 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 have been made on species living wild in the northeastern United States, and in living collections at the New York 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 herbarium specimens and on serial sections of shoot apices.

Table 1 indicates which leaf types are found in each of the species observed. Some leaf types were not systematically observed and so are not listed in the table. For example, any species which produces axillary buds that rest will have proleptic prophylls and mesophylls. Therefore, it is expected that most species have proleptic prophylls and mesophylls, and no effort is made to systematically determine their presence or absence in any species. Where there is not enough information as to the occurrence of a certain leaf type, a '?' is placed in the table.

All drawings and photographs were made by the author.

RESULTS—Leaves observed can be divided into four major types: those associated with the initiation of new shoot axes, with the continuation of axes, with the resting of axes, and with the termination and replacement of axes.

Axis initiation—In most species of Araceae, the specialized leaves associated with the initiation of new shoot axes are reduced leaves

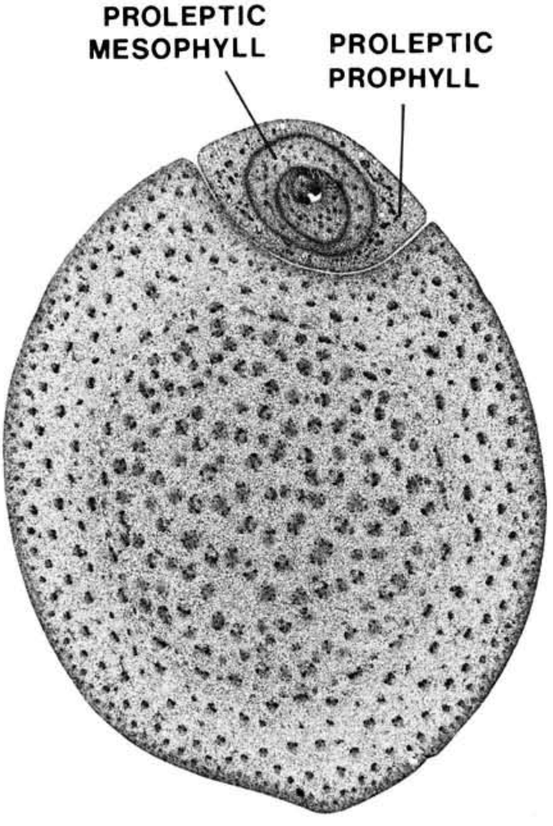

Fig. 1. Section of *Syngonium macrophyllum* showing the leaf arrangement in an axillary bud. The 2-keeled form of the proleptic prophyll is visible. Three presumed proleptic mesophylls are seen within the prophyll.

or cataphylls. Leaves whose blades are absent or rudimentary are generally described as "cataphylls." The term "reduced leaf" will be applied when the leaf blade is about 10–70% of the normal leaf length. Leaves whose blades are reduced below 10% of normal length will be called "cataphylls." Leaves whose blades are not reduced will be called "foliage leaves." However, there are many types of cataphylls and reduced leaves, and it is useful to develop a more specific terminology to refer to them. With respect to the initiation of new axes, leaves are considered to fall into four groups: prophyll, which is the first leaf on a new vegetative axis; mesophylls, which are leaves immediately following the prophyll; bracteole, which is the first leaf on a short shoot terminating in an inflorescence; and mesobracteoles, which are leaves following the bracteole.

Prophylls and mesophylls: There is some disagreement over the use of the term prophyll. Some authors define prophyll as the first leaf on a stem (Swartz, 1971), while others equate prophyll to bracteole and define it more narrowly as the first leaf on a stem which subtends a flower or inflorescence (Usher, 1966; Jackson, 1971). The present paper follows Arber (1925) and Tomlinson (1970), who use the broader definition of prophyll (the first leaf on a new axis), and define those subtending inflorescences as a subtype, bracteole.

Monocotyledons have only a single prophyll or bracteole lying between the main axis and the lateral branch, with its back to the main axis. Prophylls and bracteoles are generally unlike other kinds of leaves because they are usually 2-keeled. Generally, other leaves have a single rib. Apparently, the 2-keeled form is due to the compression resulting from the crowded development between the main axis and the lateral branch (Arber, 1925; Tomlinson, 1970; Kaplan, 1973).

Actually, when branching occurs, the two shoots must share the space in the developing apex, and both are affected by the crowding. Both shoots tend to take on the D-shape that causes the keels. It can be seen in Fig. 1 that both the prophyll, and the stem adjacent to it, are 2-keeled. The smaller of the two shoots will have the most strongly developed keels. Generally, it is the new shoot that is initially smaller, and thus it tends to be the prophyll that is markedly keeled. However, in some cases the relative sizes of the two shoots are such that the newer shoot is larger. In the case of *Orontium aquaticum,* the renewal shoot is much larger than the terminus of the original shoot. The leaf subtending the terminal inflorescence is a cataphyll, and the prophyll subtending the renewal shoot is a fully developed foliage leaf. In this case it is the terminal cataphyll that is strongly keeled, not the prophyll. This terminal cataphyll very strongly resembles a typical 2-keeled bracteole.

Sometimes additional reduced leaves follow the prophyll. Tomlinson (1970) suggests the use of the word "mesophyll" to describe these additional reduced leaves. This terminology is adopted here and the analogous term "mesobracteole" is added to refer to analogous leaves following the bracteole on an inflorescence short shoot.

Syllepsis and prolepsis: Prophylls, bracteoles, mesophylls, and mesobracteoles are considered to fall into two main groups on the basis of whether they are associated with proleptic or sylleptic shoot renewal. Proleptic shoots develop from a bud that has rested. In proleptic development, the first few segments (sensu Ray, 1986) of the shoot have greatly shortened internodes (e.g., 1–3 mm in length), usually lack axillary buds, and have cataphylls or reduced leaves. In the first of these leaves

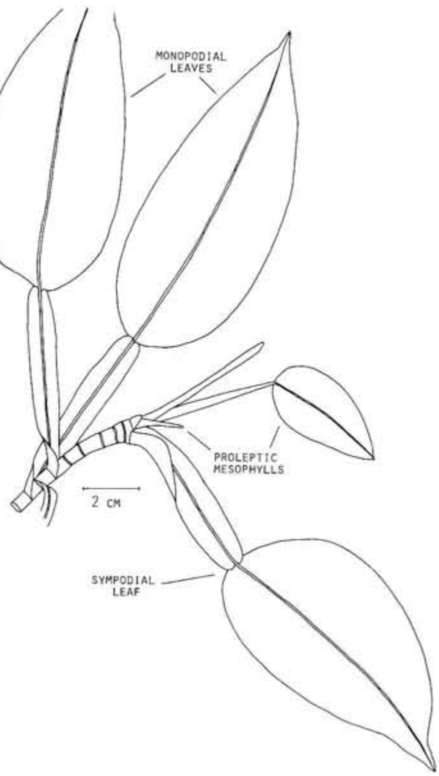

Fig. 2. Proleptic shoot development in *Philodendron aurantiifolium*. The two large leaves at the top are monopodial leaves. The large leaf at the bottom is a sympodial leaf. The inflorescence has abscised. Note that the sheath of this sympodial leaf is as fully developed as those of the monopodial leaves. The proleptic shoot develops axillary to the monopodial leaf preceding the sympodial leaf (not shown). Four proleptic mesophylls are shown on the continuation shoot of this sympodial branch. The first leaf visible on the axillary shoot is a 1-ribbed leaf whose back faces away from the main axis. Thus this first leaf is probably the first mesophyll rather than the prophyll. It is likely that the prophyll disintegrated when the new shoot began to expand.

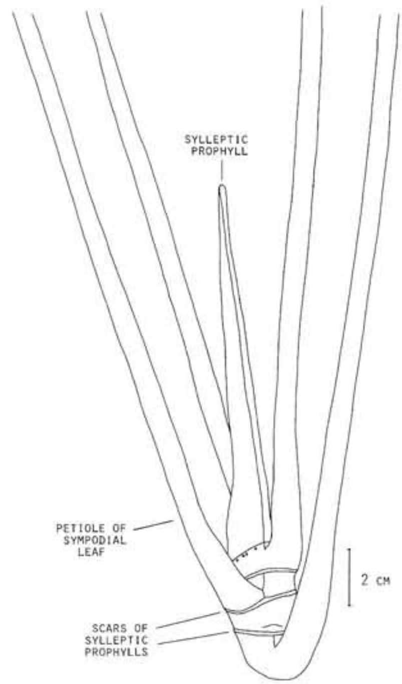

Fig. 3. Illustration of a large sylleptic prophyll in *Philodendron grandipes*. The prophyll is at the apex of the shoot and is surrounded by the petioles of four sympodial leaves.

the blade is missing, and all that remains is a shortened sheath. The sheath is longer in each successive leaf. Then the blade appears, and the blade is longer in each successive leaf until the normal leaf size is reached. Thus there is a gradual transition from the smallest leaf to the normal leaf, with intermediate forms showing a full gradation between the two extremes (Fig. 2). The number of leaves involved in the transition depends on the species.

The first leaf on a proleptic shoot is the budscale leaf, which is here called the "proleptic prophyll" (Fig. 1). The cataphylls and reduced leaves which follow will be called "proleptic mesophylls" (Fig. 1, 2). The proleptic prophyll of aroids apparently always has the 2-ribbed construction typical of the prophylls of monocots. However, the form is often not obvious to the naked eye, as the leaf is usually quite small, simply covering the axillary bud. The two-keeled form can be most easily seen in serial sections (Fig. 1). Some exceptions to this are found, for example in *Acorus calamus* and *Urospatha friedrichsthalii,* where the proleptic prophyll attains a greater size and the two-keeled structure is clearly visible.

Sylleptic shoots develop from a bud which has not rested, but which develops simultaneously with the main axis. The first leaf of the new shoot is a usually 2-keeled prophyll, which is called a "sylleptic prophyll" (Fig. 3; see also Fig. 4, 6, 7, 11). Unlike the proleptic prophyll, the sylleptic prophyll is generally large enough (2–50 cm in length) for the 2-keeled structure to be obvious to the naked eye. The segment following the prophyll has an internode of roughly normal length, may have a bud axillary to the prophyll, and is terminated by a leaf which will be called the "sylleptic mesophyll" (Fig. 4; see also Fig. 11). Generally, no more than the first two leaves of a sylleptic branch are reduced; thus, there will generally be no more than a single sylleptic mesophyll with a reduced or absent blade. In many cases, the leaf following the sylleptic prophyll is not morphologically distinct from the normal

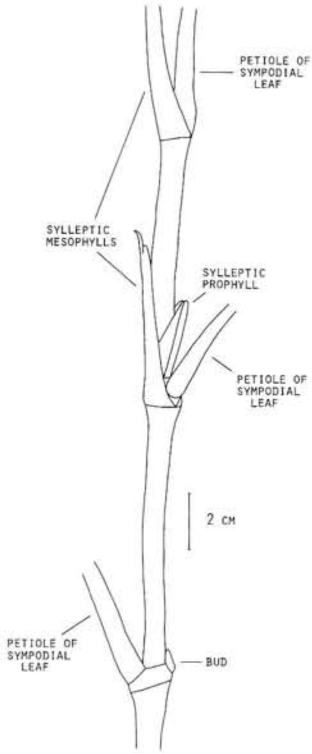

Fig. 4. Stem of *Anthurium clavigerum*. Each sympodial leaf is followed by a short internode and a sylleptic prophyll, then a long internode and a sylleptic mesophyll, then a short internode and another sympodial leaf. The divergence angle between foliage leaves on this stem is about ¼. The stem has been rotated so that all leaves appear in profile.

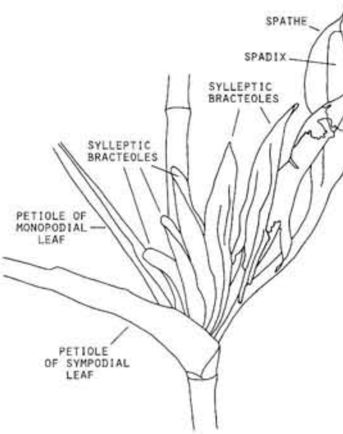

Fig. 5. A drawing of *Syngonium podophyllum* var. *peliocladum,* showing the sylleptic bracteoles, each subtending a single inflorescence. Note that the first inflorescence (on right) is not subtended by a bracteole, as it is the terminus of the shoot, rather than the beginning of a new shoot. Each inflorescence which follows is a new shoot, and so is subtended by a bracteole. The three youngest bracteoles (on left) show the 2-keeled structure. The shape of the next older bracteole is distorted by the inflorescence developing within. The next two oldest bracteoles (on right) have been ruptured by the developing inflorescences, and have senesced and turned brown, but the remnants are visible.

monopodial leaves which follow it, but the first leaf following the prophyll will always be called a mesophyll, regardless of the degree of development of its blade. When more than one reduced leaf or cataphyll follow the sylleptic prophyll, they will all be called mesophylls.

In most cases, the mesophyll has a normal 1-ribbed structure, rather than the 2-keeled structure typical of the prophyll. However, in *Spathiphyllum fulvovirens,* the sylleptic mesophyll is directly superposed to the prophyll. On the condensed stem of *Spathiphyllum,* this mesophyll is apparently growing under the same compressed conditions as the prophyll. Therefore, it is also 2-ribbed, although the keels are not as sharp as those of the prophyll. The sylleptic mesophyll of *Stenospermation angustifolium* is also directly superposed to the prophyll, but is 1-ribbed. In this species, the internodes are fairly elongate. This perhaps reduces the congestion, allowing the mesophyll to develop the more "normal" 1-ribbed structure. The distinction between prolepsis and syllepsis and its relation to morphology have been discussed and illustrated by Donoghue (1981, 1982) and Hallé, Oldeman, and Tomlinson (1978).

Bracteoles and mesobracteoles: In some species, when the axis terminates in an inflorescence, the inflorescence axis itself branches sylleptically, with each new branch containing only a sylleptic prophyll and an inflorescence. These are the cataphylls which would be called prophylls under the more restricted usage of the term (Usher, 1966; Jackson, 1971). In the present paper, these leaves will be called "sylleptic bracteoles" (Fig. 5). They have the 2-keeled form and are morphologically identical to the "sylleptic prophyll" described earlier. They differ only in that they directly subtend an inflorescence, rather than a vegetative shoot (Fig. 6).

I have observed flowering in monopodial aroids only in herbarium specimens. These observations, along with illustrations of Engler (1905) and Bogner (1975), seem to suggest that these taxa produce flowers on proleptic short shoots. Therefore, we would expect to find "proleptic bracteoles" and "proleptic mesobracteoles." The former term is just a bracteole on a proleptic flowering shoot. The term mesobracteole is just the analog of a mesophyll on a flowering shoot. Mesobracteoles have not

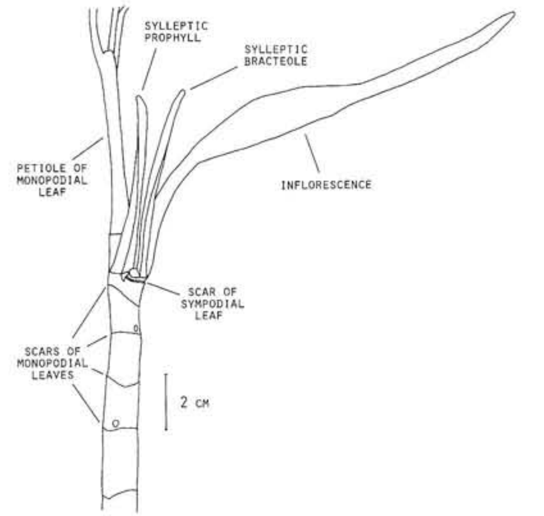

Fig. 6. Comparison of sylleptic prophyll and sylleptic bracteole in *Dieffenbachia oerstedii*. The prophyll, on the left, subtends the renewal shoot. The bracteole, on the right, subtends the second inflorescence. The first inflorescence, whose scar is visible, has abscised. Note that the prophyll and bracteole are about the same size and shape. They differ only in that the former subtends a vegetative axis, and the latter a reproductive axis.

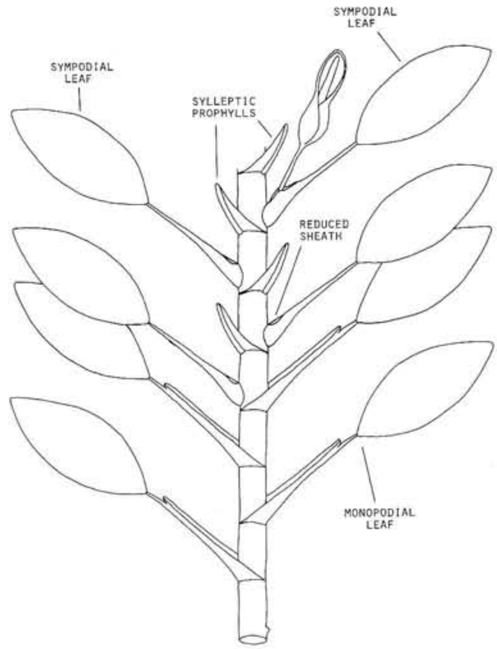

Fig. 7. Schematic drawing showing monopodial and sympodial leaves, and the sylleptic prophylls. The lower four foliage leaves are monopodial leaves, showing the well-developed sheaths. The next three foliage leaves are sympodial leaves showing the greatly reduced sheaths characteristic of *Philodendron* and *Anthurium*. The topmost foliage leaf is a sympodial leaf subtending a developed inflorescence, showing the sheath with an intermediate degree of development. Following each sympodial leaf is a sylleptic prophyll.

been observed in sylleptic flowering shoots. However, Engler's (1905) illustrations of *Pothos* clearly show what appear to be proleptic mesobracteoles. The bracteoles are not visible, but proleptic bracteoles are likely to be as reduced as proleptic prophylls. In *Heteropsis*, the flowering shoot bears about eight leaves, the last several of which are normal foliage leaves. In this case it seems sufficient to describe the shoot as bearing a proleptic prophyll and several proleptic mesophylls followed by some monopodial leaves before the terminal inflorescence. It would seem to be appropriate to use the term mesobracteoles only where leaves are substantially reduced due to their position of subtending the inflorescence, as appears to be the case in the *Pothos* illustrated by Engler (1905) and Bogner (1975).

To my knowledge, all proleptic prophylls and proleptic mesophylls are cataphylls or reduced leaves. Most sylleptic prophylls in the Araceae have reduced blades; exceptions, with expanded blades, are found in the temperate genera *Acorus, Orontium,* and *Symplocarpus* and in the subtropical *Gymnostachys*. Sylleptic mesophylls are more variable. Often they have expanded blades and are not morphologically distinct from monopodial leaves (see definition below). However, sylleptic mesophylls which are cataphylls or reduced leaves are found in many genera, most notably in the genus *Anthurium,* where a sylleptic prophyll and a sylleptic mesophyll with the blade rudimentary or absent alternate with each sympodial foliage leaf (see definition below) on mature stems (Fig. 4). The variation in blade development of sylleptic mesophylls is indicated in Table 1.

Axis continuation—Monopodial leaves: When an aroid shoot is growing monopodially, without interruption of the activity of the apical meristem by terminal flowering or seasonal resting, successive segments are produced by the continued activity of a single meristem. The sheaths of the petioles on monopodial shoots are usually well developed and the base of the sheath wraps around the stem at the node (Fig. 7; see also Fig. 2, 5, 8, 9). These leaves will be called "monopodial leaves." Virtually all monopodial leaves are foliage leaves with expanded blades. The only exceptions observed are in *Monstera glaucescens, Rhaphidophora decursiva,* and *Anthurium flexile* ssp. *flexile,* one of two species in the section *Polyphyllium.* In these species reduced monopodial leaves are scattered irregularly along climbing

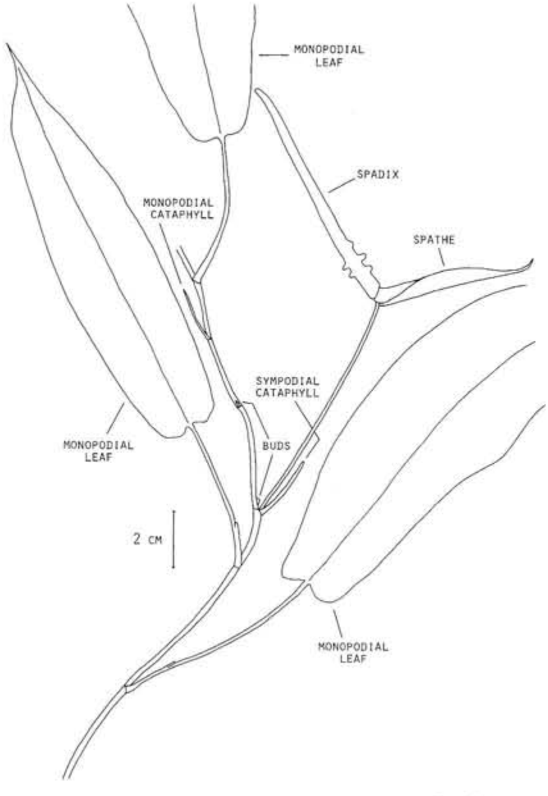

Fig. 8. Drawing of *Anthurium flexile* ssp. *flexile* showing a monopodial cataphyll (top), and a sympodial cataphyll (subtending inflorescence). The foliage leaves are monopodial leaves.

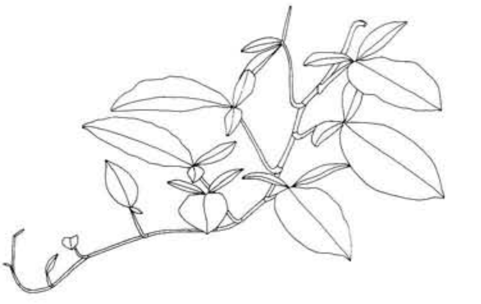

Fig. 9. Drawing of descending shoot of *Syngonium standleyanum* Bunting MG 1841 (DUKE) showing transition from monopodial leaves (on right) to flagellar leaves (on left).

stems. In *R. decursiva* the cataphylls greatly outnumber the foliage leaves. These short-lived leaves essentially consist of a sheath which is 1-ribbed and has no blade. These will be called "monopodial cataphylls" (Fig. 8).

Dispersal leaves: Many climbing aroids produce elongate shoots with reduced leaves, which serve the function of vegetative dispersal. Blanc (1980) described these shoots in some detail and called them "flagelles" or "stolons." I have also described flagelles (Ray, 1981, 1983a, b) using different terminology, but I will follow the terminology of Blanc here. In most species, flagellar shoots develop when a climbing shoot overgrows its support and begins to hang down. Successive segments are of a decreased diameter, and the internodes become elongated, with a correlated reduction in leaf size (Ray, 1986). Therefore, we see a gradual reduction in the size of the lamina on successive segments once the stem begins to descend (Fig. 9).

When the form of the segments that make up the flagelle has stabilized after the transition from the climbing form, the lamina is reduced to a degree that depends on the species. In *Syngonium triphyllum* the lamina is reduced to a mere vestige, with 1% or less of the area of the preceding laminas. In *Philodendron aurantiifolium* the lamina is reduced to a length of about 3 cm, compared to a length of about 15 cm for the fully developed lamina on the ascending shoot. The term cataphyll is generally reserved for leaves whose blades are absent or completely rudimentary; thus, one might be reluctant to call such a 3 cm leaf a cataphyll, yet it is precisely homologous to the fully reduced leaf on the flagellar shoots of *S. triphyllum.* This has caused indecision by some authors who have attempted to describe these leaves. Madison (1977) described them as "cataphylls," "scale leaves," and "highly reduced sickle-shaped foliage leaves." Engler and Krause (1908) called them "cataphylls with entirely or much reduced blades or foliage leaves with small blades." Because these leaves originate through a gradual process of reduction of successive leaves, and because the final form sometimes has a substantial blade, they will not be called cataphylls, but rather "flagellar leaves" (Fig. 9). When a flagellar shoot makes contact with a tree, it begins to climb, and the internodes of successive segments rapidly shorten, causing the leaf blades to become large. The climbing shoot will then very gradually begin to thicken again.

Flagelles are produced almost exclusively by stems growing monopodially. However, monophyllous sympodial (definition below) flagelles have been observed in two species: *Philodendron fragrantissimum* and *P. bruneocaule.* The reduced leaves borne on these stems may be distinguished by the term "sympodial flagellar leaves" (Fig. 10). It is not necessary to modify the term "flagellar leaf" with the adjective "monopodial" because, with the exceptions just mentioned, it appears that all flagellar leaves are monopodial. Where there might be ambiguity, the term "monopodial flagellar leaves" could be used.

The other kind of elongate shoot produced

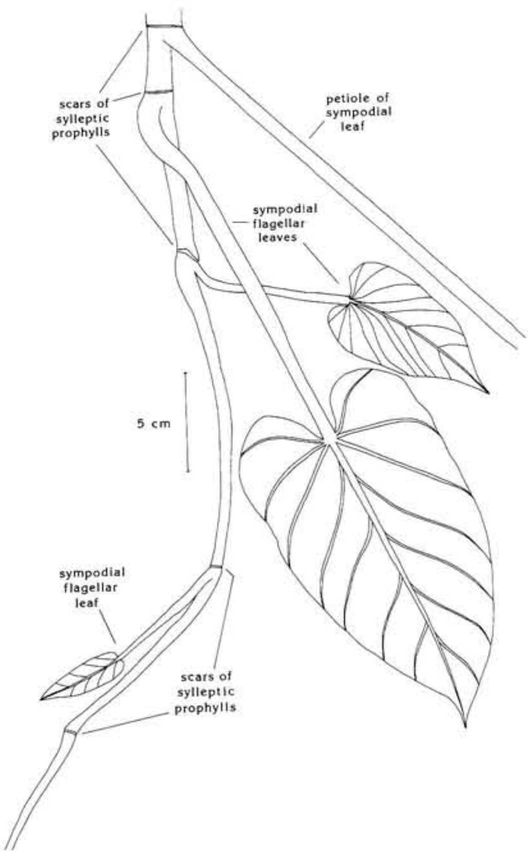

Fig. 10. Drawing of descending shoot of *Philodendron fragrantissimum* showing transition from sympodial leaves to sympodial flagellar leaves. The segment of the last leaf shown (bottom) is followed by a monopodial segment with a monopodial flagellar leaf (not shown). Adapted from a drawing by Mark Murphy.

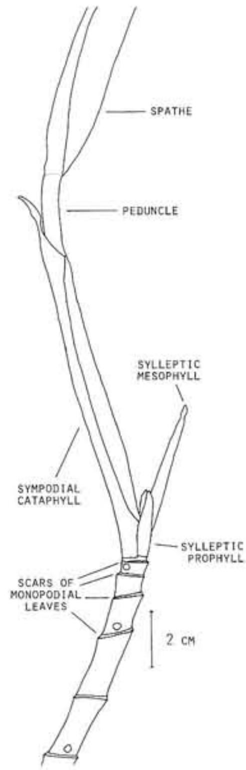

Fig. 11. Drawing of *Rhodospatha forgetti* showing a sympodial cataphyll enveloping the peduncle. To the right of the cataphyll are a sylleptic prophyll and a sylleptic mesophyll.

in the Araceae for the purpose of vegetative dispersal and reproduction is the stolon. Blanc (1980) has emphasized the differences between the stolon and the flagelle. Flagelles originate by transformation of the primary shoot axis, while stolons are initiated as lateral branches, and leaves do not go through successive reduction. Therefore, it seems reasonable to give the reduced leaves on these stems a separate name, "stolon cataphylls." Stolon cataphylls have been observed in *Arisaema triphyllum, Homalomena picturata,* and *Spathiphyllum friedrichsthalii.* In addition, stolons may be produced by germinating seeds, as in *Monstera tenuis.* Stolons probably occur in other of the genera I have observed, but I have not consistently searched for them.

Axis resting—In strongly seasonal environments such as temperate climates, aroids are forced into a period of dormancy. In some species this results in the annual production of reduced leaves which will be called "resting cataphylls." Resting cataphylls protect the shoot apex while the plant is devoid of foliage leaves during a period of dormancy (usually related to seasonal factors), distinguishing them from monopodial cataphylls. A good example of this is found in *Arisaema triphyllum,* which produces several cataphylls at the end of each year's growth.

The state of rest and morphological reduction of the blade may be imposed on various types of leaves, i.e., monopodial leaves, sympodial leaves, or prophylls. For example, in *Symplocarpus,* prophylls are foliage leaves, and on mature stems prophylls alternate with monopodial leaves in a manner similar to monophyllous sympodial growth of *Philodendron* stems. Therefore, when the stem rests, the leaves which are reduced are both prophylls and monopodial leaves.

The concept of seasonal resting can be easily confused with the concept of prolepsis. For example, in *Symplocarpus,* the bud enclosed within a resting prophyll might be considered proleptic because it rests. However, the morphology of overwintering prophylls and the shoots which develop from them is like that of sylleptic rather than of proleptic shoots. For example, these shoots do not have proleptic mesophylls; in fact, the one leaf, which by definition is a sylleptic mesophyll, generally has an expanded blade. An analogous situation has been described for *Viburnum* by Donoghue (1981, 1982).

This seeming paradox that overwintering shoots have sylleptic rather than proleptic morphology, in spite of having rested, can be resolved by thinking of prolepsis as the resting of a bud relative to the development of the primary axis. If the primary axis and the bud rest together, as in a period of dormancy, then their development remains simultaneous and therefore sylleptic. In this view, prolepsis occurs only when the bud rests while the parent shoot continues development.

Axis termination and replacement—Sympodial leaves: When aroids flower, the shoot apex is consumed in the production of the inflorescence, or of an inflorescence primordium which aborts (Engler, 1920; Ritterbusch, 1971; Blanc, 1977b; Madison, 1978a). The shoot is then continued by the development of a bud axillary to the penultimate leaf (except in the temperate genera *Acorus, Orontium, Lysichiton, Symplocarpus,* and *Calla,* and the subtropical *Gymnostachys* in which the new stem develops in the axil of the monopodial leaf immediately preceding the inflorescence [Engler, 1920]. My own observations conflict with Engler's, in that I observe *Acorus, Orontium,* and *Calla* to produce renewal shoots from the axil of the penultimate leaf. Dudley [1937] confirms my observations on *Calla.* See Ray [in press] for more details). The continuation shoot grows in the same direction as the preceding shoot, pushing aside the inflorescence and (with the above exceptions) the terminal leaf which envelops the developing inflorescence in its petiole base (Fig. 3, 4, 7). In sympodial growth the petiole base of the terminal leaf does not encircle the stem, but rather the often aborted terminal inflorescence, and therefore the sheath, is not always well developed.

These leaves encircling the terminal inflorescences will be called "sympodial leaves." This terminology does not imply that sympodial leaves develop in a sympodial fashion, but rather that they are associated with sympodial growth of the stem. They occur at the junction between two axes and are the foliage leaves of sympodial segments (sensu Ray, 1986). The sympodial leaf can be most easily distinguished from the monopodial leaf by observing if the petiole base surrounds the stem, as illustrated in Fig. 7.

Sympodial leaves vary considerably in the development of the sheath. In *Anthurium* (except section *Polyphyllium*) and *Philodendron* (except section *Pteromischum*), the sheath of the sympodial leaf is rudimentary during sympodial development, being generally less than 1 cm in length. If the inflorescence develops, the sheath may be more developed, as it wraps around the peduncle which emerges from the sheath (Fig. 7). However, the sheaths of such sympodial leaves are generally much less developed than those of monopodial leaves. This was also noted by Ritterbusch (1971).

A striking reduction of the sheath in sympodial leaves has been observed only in *Anthurium* and *Philodendron,* in which development of the mature stem is monophyllous sympodial. In those taxa with polyphyllous sympodial development, the sympodial leaves have sheaths as fully developed as the sheaths of monopodial leaves (Fig. 2, 5). The term "monophyllous sympodial" indicates that only one foliage leaf is produced by each continuation shoot before terminating in an inflorescence, while "polyphyllous sympodial" indicates that a variable number of foliage leaves, usually more than one, is produced by each continuation shoot before terminating in an inflorescence. These terms will be discussed in more detail and revised in Ray (1987). If one desired to distinguish between the sympodial leaves which differ so greatly in sheath development, one could use the terms "reduced sheath sympodial leaf" and "developed sheath sympodial leaf." Another interesting variation is found in *Stenospermation,* where, in sympodial leaves, the lower half of the petiole consists of a tubular sheath enclosing the peduncle. Tubular sheaths are found in both monopodial and sympodial leaves of *Arisaema triphyllum.*

While sympodial leaves generally have expanded blades, there are some exceptions. In some species of the genus *Monstera,* when an individual matures, it will switch for a time to a form of growth analogous to monophyllous sympodial growth, in which the sympodial leaves (at least after the first sympodial leaf) have no blades. Similarly, the sympodial leaves of *Rhodospatha forgetii* are reduced. I will call these leaves "sympodial cataphylls" (Fig. 11). One may also note that in Fig. 8, the leaf subtending the inflorescence in *Anthurium flexile* is a cataphyll; so in this instance it also is a "sympodial cataphyll." The illustrations in Croat and Baker (1978) show that this leaf is sometimes a foliage leaf, and thus a "sympodial leaf." My observations confirm this. In many cases the sympodial leaf has a blade too large for it to be classed as a cataphyll, but the blade is substantially reduced in comparison with adjacent monopodial leaves. The variation in blade development of sympodial leaves is indicated in Table 1.

In the above listed temperate genera in which the renewal shoot originates from the axil of the ultimate rather than the penultimate leaf, there is no sympodial leaf. The last leaf on each axis is a normal monopodial leaf with its petiole base encircling the stem. I would, however, like to offer a different interpretation of the organization of the *Acorus* shoot. My examination suggests that in *Acorus* the tubular sheath of the sympodial leaf is fused to the peduncle to form a single adnate structure composed of the sympodial leaf and the inflorescence. The peduncle is completely enclosed and hidden by the tubular sheath, and only the spadix emerges from the open end of the sheath. The structure which has been described as the "spathe" is the blade of the sympodial leaf; no spathe is present. Van Tieghem's (1867) description of the vasculature of the "peduncle" of *Acorus* supports my interpretation. Van Tieghem points out that there are two completely separate vascular sytems in the *Acorus* "peduncle," while other aroids have only a single vascular system in the peduncle. He describes an outer cylinder and an inner V of vascular bundles. I interpret the outer cylinder as corresponding to the leaf sheath and the inner V as corresponding to the peduncle. This interpretation supports the movement to separate *Acorus* from the family Araceae (Tomlinson, 1980; Grayum, 1984; Walker, 1986) by suggesting that *Acorus* lacks a spathe, and by the uniqueness of the adnate leaf and peduncle.

Tragblatt: The German term "Tragblatt" refers to a leaf that subtends a branch—that is to say, that a branch develops from the bud axillary to the Tragblatt. The branch may be sylleptic or proleptic, and the Tragblatt may be a foliage leaf, a reduced leaf, or a cataphyll. The morphology of the Tragblatt is not affected by the development of a shoot in its axil. In this sense the Tragblatt differs from all the other classes of leaves defined here. In all other cases, some aspects of the morphology of the leaves is affected by their position in the organization of the shoot. However, it is sometimes convenient to refer to the leaf subtending a new axis. D. H. Nicolson (personal communication) has suggested "hypoblastophyll" (foliar element below shoot) as a Greek derived term for Tragblatt, or the shorter term "blastophyll," which I will use. Since blastophylls are apparently present in all aroids, they are not included in Table 1.

Table 1 contains a list of species observed, which are principally from the Sarapiquí and Delaware regions or from a cultivated source, indicating which of the leaf types are found in each of the species. The table also indicates in many cases if the leaf blades are expanded or reduced. Proleptic prophylls and mesophylls are not listed as they were not systematically observed, and are presumed to occur in most or all species.

DISCUSSION—Having described the various leaf types, I would like to review some of the literature to show how leaf terminology has been used in the past. There has been little recognition of the distinction between the principal types of foliage leaves, sympodial and monopodial. Workers have generally referred to them indiscriminately as "leaf" (Goldberg, 1941; Nicolson, 1969; Hotta, 1971; Blanc, 1977a, b, 1978, 1980; Croat and Baker, 1978; Madison, 1978a, b; Croat and Bunting, 1979; Ray, 1981, 1983a, b; Croat, 1983a); "foliage leaf" (Engler and Krause, 1912, "Laubblatt"; Goldberg, 1941; Galil, 1978; Madison, 1978a, b; French and Tomlinson, 1980, 1981); or "assimilatory leaf" (Blanc, 1980, "feuilles assimilatrices").

Some workers have recognized the difference between monopodial leaves and sympodial leaves and have described them. Blanc (1977b) described monopodial leaves as "leaves with blade, petiole and sheath developed," and sympodial leaves as "sheath reduced, petiole and blade developed." In their key to the Araceae of La Selva, Croat and Grayum (unpublished) describe monopodial leaves as "leaf with petiole sheath encircling stem at base," and sympodial leaves as "leaf with petiole arising from the side of stem (the base not encircling the stem)." Grayum (1984) describes the "fully sheathed leaves of juvenile monopodial phase" and the "totally sheathless leaves [of] sympodial branching." Goldberg (1941) referred to the sympodial leaf as the "ultimate leaf."

Although these workers recognized the differences between monopodial and sympodial leaves, none of them developed a terminology to distinguish them. Ritterbusch (1971) was the only one to do so, recognizing the differing degree of development of the sheaths of monopodial and sympodial leaves in the species of his study. He described these two types of leaf as open-sheath leaves (offenscheidige Laubblätter) and closed-sheath leaves (geschlossenscheidige Laubblätter), respectively. In addition, Ritterbusch recognized the intermediate sheath development of sympodial leaves in which the inflorescence is developed, though he did not develop a term for this leaf type.

Some workers have used terminology to distinguish foliage leaves from reduced leaves. The widely used German term "Laubblatt"

(Engler, 1877, 1920; Engler and Krause, 1908, 1912; Ritterbusch, 1971) clearly implies foliage leaf. In order to avoid confusing foliage leaves with sylleptic prophylls, Blanc (1977b) clarifies his use of the term leaf (feuille) to refer only to "complete leaves (with reduced sheath, petiole and blade developed)," which specifically describes sympodial leaves. However, he later uses the term to refer to monopodial leaves as well, thus using it more in the sense of Laubblatt. Blanc (1980) used the term "assimilatory leaf" to distinguish foliage leaves from flagellar leaves, and Blanc (1977b) used the term "complete leaf" to distinguish foliage leaves from prophylls and mesophylls.

Reduced leaves have been rather indiscriminately referred to as cataphylls or prophylls, occasionally modified by some kind of reference as to whether the leaf has one or two keels. I will begin by describing the German terminology for reduced leaves. The term "Niederblatt" translates as "cataphyll" and has essentially been used to refer to any kind of reduced leaf. The term "Vorblatt" translates as "prophyll." It has sometimes been used only to refer to sylleptic bracteoles (Engler and Krause, 1912), while at other times it has been used to refer to sylleptic prophylls as well (Engler, 1877, 1920; Ritterbusch, 1971); Rüter (1918) used the term to refer to both sylleptic and proleptic prophylls. The term "Hüllblatt" translates as "spathe" in Engler (1920), but Ritterbusch (1971) uses the term to refer to the sylleptic prophyll. Both Engler and Krause (1912) and Ritterbusch (1971) use the adjective "zweikielige" or "2-keeled" to refer to the sylleptic prophylls. Engler (1877) uses the adjective "einkieliges" or "1-keeled" to refer to the sylleptic mesophylls of *Anthurium*.

I will now list the various terms that have been used to refer to the various types of reduced leaves. Arber (1925) and Tomlinson (1970) used the term "prophyll" to refer to both proleptic and sylleptic prophylls. Engler and Krause (1912) described the proleptic prophyll and proleptic mesophylls as "Niederblättern"; Blanc (1977b) described them as "foliar pieces reduced to scales" and "cataphylls"; and Kaplan (1973) called them "primary, juvenile and scale leaf" interchangeably, but reserved the term "prophyll" to refer specifically to the proleptic prophyll. Blanc (1977b) also used the term "prophyll" to refer to the proleptic prophyll. Although Rüter (1918) used "Vorblatt" to refer to both sylleptic and proleptic prophylls in reference to *Acorus calamus*, she used the compound terms "Laubblatt-Vorblatt" and "Niederblatt-Vorblatt," respectively, to distinguish between them. These terms apparently refer to the difference in size and blade development between the two. Goldberg (1941) referred to both the sylleptic and proleptic prophylls as "two-keeled, acroscopic prophylls."

The sylleptic prophyll has been referred to as a "cataphyll" (Engler and Krause, 1908, 1912; Engler, 1920; Nicolson, 1969, 1982; Blanc, 1977a, b, 1980; Madison, 1977, 1978a, b; Croat and Bunting, 1979; French and Tomlinson, 1981; Croat, 1983a, b, 1984; Croat and Sheffer, 1983; Grayum, 1984; Ray, 1986; Croat and Grayum, unpublished); a "prophyll" (Engler and Krause, 1908; Arber, 1925; Ritterbusch, 1971; Blanc, 1977b, 1980; Galil, 1978; French and Tomlinson, 1980; Croat, 1981; Grayum, 1984); a "bicarinate prophyll" (Croat and Baker, 1978; Madison, 1978a, b; Croat, 1983a); a "2-keeled cataphyll" (Engler, 1877; Engler and Krause, 1912); a "keeled cataphyll" (Grayum, 1984); a "2-keeled prophyll" (Ritterbusch, 1971); a "cataphyll with the value of a prophyll" (Blanc, 1977b); a "scale-like prophyll" (French and Tomlinson, 1980, 1981); a "prophyllar scale leaf" (French and Tomlinson, 1980) and a "Tragblatt" (Engler and Krause, 1912).

References to the sylleptic mesophyll have principally been directed at those occurring in monophyllous sympodial *Anthurium*. They have been referred to as "cataphyll" (Engler and Krause, 1908; Blanc, 1977a, b; Madison, 1978a, b; Croat and Bunting, 1979; Croat, 1983a; Croat and Sheffer, 1983; Grayum, 1984); "single keeled cataphyll" (Engler, 1877; Madison, 1978a, 1978b; Croat, 1983a); "1-ribbed cataphylls" (Croat and Baker, 1978; Croat and Sheffer, 1983); and "second cataphyll" (Blanc, 1977b). Goldberg (1941) referred to the proleptic mesophylls as "bladeless leaves."

Sylleptic bracteoles have been called "prophylls" (Galil, 1978; Croat, 1981); "cataphyll" (Nicolson, 1969); "bicarinate bracts" (Croat, 1981); "prophylls of the inflorescence sympodium" (Engler and Krause, 1912); and "2-keeled prophylls" (Engler and Krause, 1912; Goldberg, 1941).

In the preceding description of flagellar leaves, some of the awkward descriptions of them were mentioned. In addition, they have been called "cataphylls" (Blanc, 1980; Grayum, 1984) and "bracts" (Ray, 1983a). I have seen no reference in the literature to sympodial flagellar leaves.

The stolon cataphyll has been called a "cataphyll" by Blanc (1978, 1980).

The resting cataphylls have been called "cataphylls" (Engler, 1877); "sheath leaves"

(Galil, 1978); and "scale leaves" (Rosendahl, 1911).

The sympodial cataphyll has been referred to by both Madison (1977) and Engler and Krause (1908) as a "cataphyll."

Excluded leaf types—I have described only those leaf types in the Araceae which I have studied closely. I am aware, however, of other leaf types which I have not described. For instance, in some genera, when the seed germinates the first few leaves produced are reduced leaves (Engler, 1920; Hotta, 1971). These could probably be considered to be proleptic prophylls and mesophylls. There may be other kinds of leaves in the Araceae with which I am not sufficiently familiar to comment on. However, I believe that I have given enough examples to make clear how the system of terminology could be extended to new situations.

Summary—Terms used to describe various leaf types observed in the Araceae have been introduced and clarified. In essence, these terms are constructed of the nouns leaf, prophyll, mesophyll, bracteole, mesobracteole, blastophyll, and cataphyll, which are modified by the terms monopodial, sympodial, proleptic, sylleptic, resting, stolon, reduced, foliage, and flagellar. Most of the nouns are already widely used to describe leaves and are not substantially altered from their conventional usage. What is novel is the use of modifiers that do not describe qualities of the leaves, but rather of the stems to which they are attached.

The modifiers chosen are informative because significant aspects of the forms of leaves are a consequence of the type of shoot to which they are attached. Leaves are an integral part of the segments that make up the shoot. It has been shown that the size and shape of monopodial leaves are directly correlated with the size and shape of the internodes to which they are attached (Ray, 1986). In this paper it is shown that the morphology of the many other kinds of leaves found in the Araceae are correlated with the organization of the shoot. To clarify leaf morphology terminology, reference to organization of the shoot is of vital importance. The terminology developed here is intended to facilitate the description of shoot organization in Ray (in press). It is hoped that familiarity with this terminology will help others become more aware of the underlying organization of the shoot in the Araceae.

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