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DOES THE MONOCOT MODE OF LEAF DEVELOPMENT CHARACTERIZE ALL MONOCOTS?

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ABSTRACT

Patterns of early leaf development in monocots are analyzed in a phylogenetic context. Recent developmental and phylogenetic studies enable this reevaluation of the leaf base model of the developing monocot leaf. Two questions are addressed: a) is the presence of the *Vorläuferspitze* (fore-runner tip) invariably correlated with development of the lamina from the lower leaf zone? and b) was the ancestral monocot characterized by the leaf base mode of development? Scanning electron microscopic observations are made of young primordia using the mold and cast method. These data are combined with data from the literature and examined in a phylogenetic context using parsimony analysis. The results suggest that in some taxa the *Vorläuferspitze* may be associated with a lamina that is derived from the upper leaf zone, and that the ancestral monocot may not have been characterized by the leaf-base mode of development. It is concluded that the leaf-base model, in a strict sense, may apply to a nested subset, but not all, of the monocotyledons.

Key words: development, evolution, leaf, leaf-base model, monocotyledons, morphology, phylogeny, *Vorläuferspitze*.

INTRODUCTION

A key question in the study of monocot leaf morphology has been whether the linear parallel-veined lamina of the monocot leaf is homologous to the broad reticulate-veined leaf of the dicot leaf. Early anatomical and morphological studies suggested that the monocot blade is a bifacially flattened dicot petiole (Arber 1918). Developmental studies revealed differences in the origin of the lamina in the two classes and led to the “leaf base” model of development for the monocot leaf (Troll 1939; Knoll 1948; Kaplan 1970, 1973). Dicots and monocots differ in the origin of the lamina, which develops from the upper leaf zone in dicots and from the lower leaf zone in monocots (Fig. 1). It was shown that the lamina of so-called unifacial leaves of monocots develops from the lower leaf zone, as do the laminae of linear leaves, e.g., *Sansevieria*, and broad leaves, e.g., *Hosta*. Both linear and broad leaves were associated with a unifacial structure at the tip, the *Vorläuferspitze*, that was used as a diagnostic feature for the leaf base mode of development. Since the *Vorläuferspitze* occurs in several monocots it was suggested that the lamina in most monocots is derived from the lower zone and is therefore not homologous to the lamina of dicots (Kaplan 1973). The assumption was that the *Vorläuferspitze* is invariably associated with a lamina that develops from the lower leaf zone. At the same time, Kaplan noted that there exists a wide range of morphological variation

within the monocots that needed to be further studied in order to apply the model more generally.

The conclusion that the laminae in monocots and dicots are not homologous, based on a “biological” concept of homology (e.g., Roth 1988; Wagner 1989), was transferred to the evolutionary realm and taken to also imply “historical” (taxic) nonhomology (e.g., Dahlgren and Clifford 1983; Donoghue and Doyle, 1989). However, the original generalization was based on developmental studies of evolutionarily disparate taxa. Given this data base it is not clear that the “biological” concept can be legitimately converted to the “historical” concept without making major assumptions. One such assumption is that the ancestral monocot had the leaf base mode of development.

Two sets of factors suggest that the time is now ripe for a reevaluation of this model. First, observations on leaf development have been extended into other groups such as the Alismatales (Bloedel and Hirsch 1979), Araceae (Periasamy and Muruganathan 1986), and Cycolanthales (Wilder 1976). These studies reveal a range of variation in the origin of the lamina, as suspected by Kaplan (1973). Second, our understanding of monocot relationships has improved in recent years (Bharathan 1993; Duvall et al. 1993 *a, b*; Bharathan and Zimmer 1995; Stevenson and Loconte 1995; Chase et al. 1995*a, b*). These phylogenetic studies reveal taxa that should be included in an evolutionary study of leaf development, particularly dicot outgroups such as the Piperales, Aristolochiales and Nymphae-

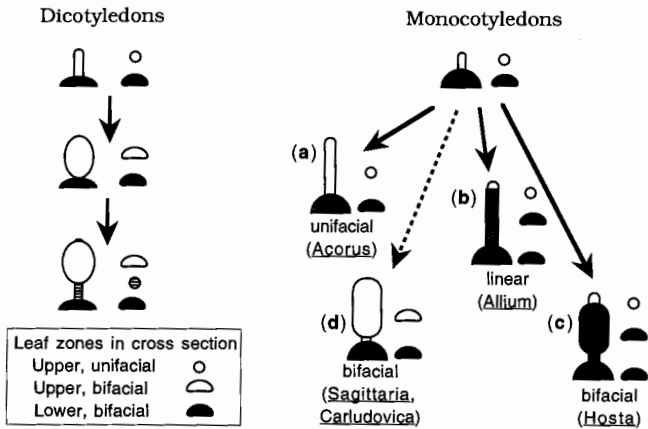


Fig 1. Morphological model of leaf development in monocotyledons. Early primordia consist of an unifacial upper zone (white) and a bifacial lower zone (stippled). In dicotyledons the upper zone differentiates into a lamina, the lower zone differentiates into the leaf base and stipules, and the petiole is intercalated later. In monocots a greater variety of developmental patterns is seen. According to early formulations of the model (a–c) the upper zone differentiated into unifacial laminae and the lower zone differentiated into bifacial laminae. Later formulations also included bifacial forms derived from the upper zone (d).

ales and putative early lineages such as the Dioscoreales that have not so far featured in the discussion.

In this paper I examine two assumptions of the leaf base model of leaf development alluded to above, posing them as two questions:

- 1) Is the Vorläuferspitze invariably correlated with development of the lamina from the lower leaf zone?
- 2) Was the lamina of the ancestral monocot derived from the lower leaf zone?

MATERIALS AND METHODS

Plant Materials

Young shoot apices were obtained from plants growing in the greenhouses of the University of California at Davis. The species sampled were *Aristolochia fimbriata* Cham. (B90.073); *A. labiata* Willd. (B82.152); *Butomus umbellatus* L. (GB127, UA Herbarium); *Calathea lietzi* E. Morr. (B88.033); *Cryptanthus* sp. (B90.051); *Dioscorea discolor* Kunth. (B93.330); *Dioscorea* sp. (B00.069); *Gloriosa superba* L. (B63.339); *Lapageria rosea* Ruiz and Pav. (B63.11); *Philodendron variifolium* Schott (B81.603); *Piper crocatum* Ruiz and Pav. (B89.235); *P. nigrum* L. (B74.003); *P. hispidum* H. B. and K. (B00.604); *Scindapsus pictus* (B00.763). Specimens of all except *Butomus umbellatus* have been deposited at either the John Tucker Herbarium, University of California, Davis, or the herbarium at the University of Arizona, Tucson. Numbers in parentheses are accession numbers of the Botany Collections Greenhouse. Except for *Scindapsus pictus*, whose juvenile stage is the one culti-

vated, plants were mature and the shoots sampled were producing adult leaves. It is assumed that the early stages of development observed here are stages in development of adult leaves. Shoots were dissected under water using a binocular research microscope (Zeiss STEMI V8).

Mold and cast technique.—Molds were made using dental vinyl silicone and casts using epoxy resin (Williams, Vesk and Mullins 1987; Williams and Green 1988; Jernstedt et al. 1992). Impressions were made of successive primordia on the same shoot. Observation of primordial stages at plastochrons one to three (p1–p3) provided the necessary information in most cases. Primordial stages of up to p7 were studied in taxa such as the *Dioscorea* spp. and *Lapageria rosea* in order to determine the origin of the lamina.

Scanning electron microscopy (SEM).—The casts obtained were mounted on stubs, sputter coated with gold, observed with a scanning electron microscope (SEM, Hitachi 450), and digital images captured and stored using the software package SEMICAPS.

Phylogenetic hypotheses.—Topologies used in this study were based on recent morphological and molecular studies (Bharathan 1993; Duvall et al. 1993a, b; Bharathan and Zimmer 1995; Chase et al. 1995a, b). The topologies were pruned to either eliminate taxa for which developmental data are not available, or to accommodate differences in taxon sampling among different phylogenetic studies. Analyses using the *rbcL* topology were done with and without the Cyclanthaceae. The general pattern in all the phylogenetic studies (barring the studies of Chase et al., which had no bootstrap analyses) is one of relatively poor bootstrap support for deeper branches and strong support for nested clades in these studies. The differences between the morphological and molecular data lie largely in the rooting. The exemplar topologies used here may serve to take into account weakly supported branches in the different studies.

Character reconstruction.—Features of leaf primordia were encoded as binary traits. Parsimony reconstruction of these traits was done on topologies of monocot relationships obtained from above using MacClade 3.0 (Maddison and Maddison 1992). Points of agreement between all reconstructions (including differences between topologies and alternative reconstructions on a single topology) provided the basis for conservative conclusions regarding ancestral states. These conclusions were used to infer trends in character evolution.

RESULTS AND DISCUSSION

Variation in Development

There was a wide range of variation in early stages of primordial development (Figs. 2–9). Development

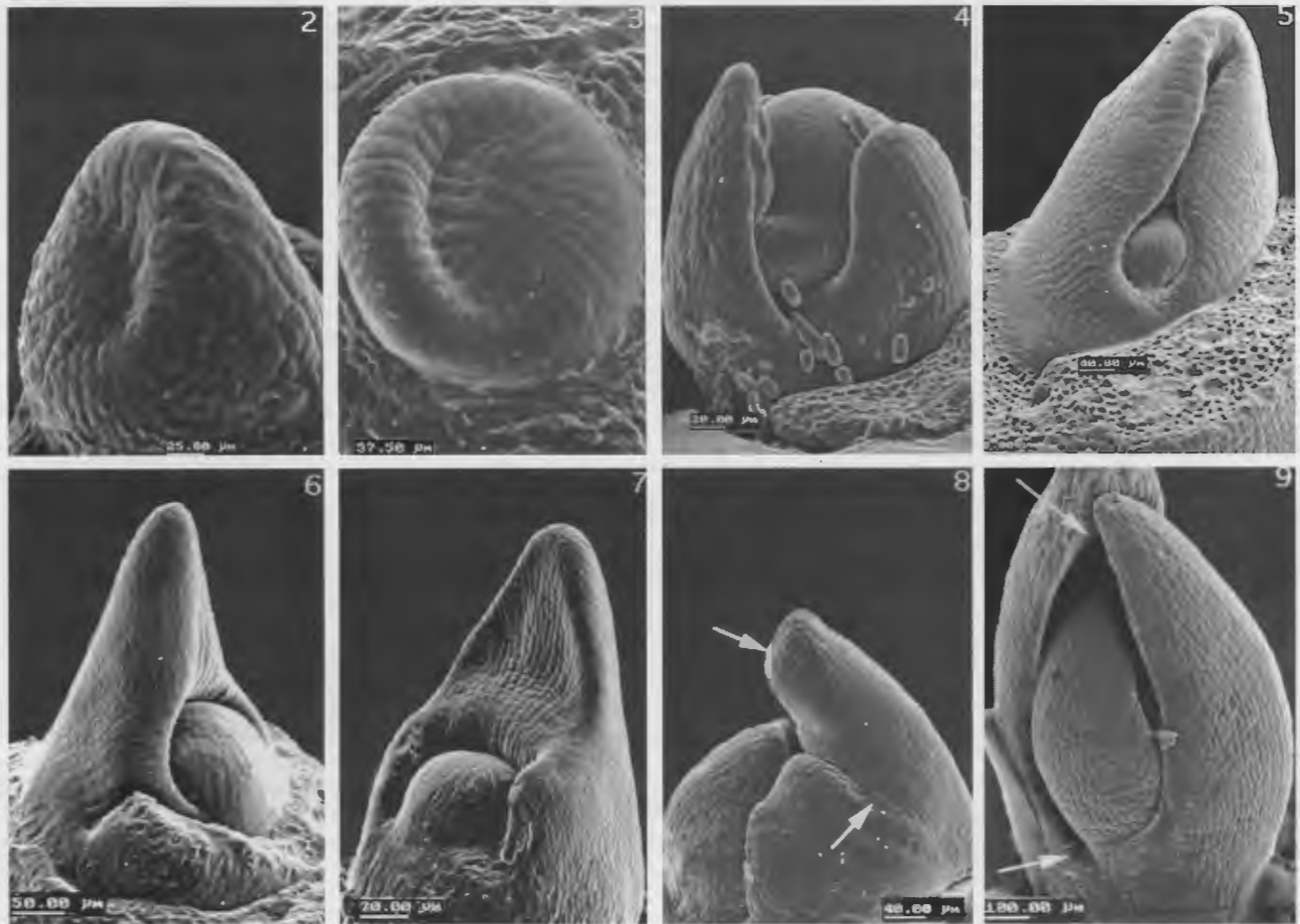


Fig. 2-9. SEM pictures of leaf primordia at plastochrons one through five (p1-p5).—2. *Scindapsus pictus*, p1. "Terminal," massive.—3. *Tradescantia pendula*, p1. Lateral, narrow.—4. *Dioscorea* sp., p1-p4. Base partially sheathing.—5. *Calathea lietzi*, p2. Base completely sheathing.—6. *Cryptanthus* sp., p2. Apex thickened.—7. *Piper crocatum*, p2. Apex not thickened.—8. *Smilax bona-nox*, p3. Lamina develops from upper leaf zone, above tendril-forming leaf base (between arrows).—9. *Lapageria rosea*, p5. Lamina develops from lower zone, below thickened apical portion (between arrows).

of the upper and lower leaf zones may be classified into horizontal and vertical components. The horizontal component describes: a) the position of the primordium—whether lateral (Fig. 3) or nearly terminal (Fig. 2); b) the encirclement of the shoot apex by the lower zone—whether partial (Fig. 4) or complete (Fig. 5); and c) the thickening of the upper leaf zone—whether present, as in unifacial leaves and leaves with a Vorläuferspitze (Fig. 6), or absent (Fig. 7). The vertical component describes a) development of the lower zone—whether it develops into a stipule (Fig. 8), or not, either undergoing limited growth (Fig. 7) or developing into a lamina (Fig. 9), and b) development of the upper zone—whether it develops into a lamina (Fig. 8) or not (Fig. 9).

The data obtained were coded as binary traits. Information on monocotyledons obtained from other studies were similarly coded, and these data are presented as a matrix of 16 taxa and 5 characters (Columns A-E, Table 1).

The lamina develops from the lower leaf zone in most of the monocots studied, as expected from the leaf base model of development. On the other hand, the lamina develops from the upper leaf zone in *Smilax*, *Piper*, *Saururus*, and *Aristolochia*. This pattern is expected for dicots but not for the monocot, *Smilax*. However, this pattern of development has been described previously in some monocots (Wilder, 1976; Bloedel and Hirsch, 1979), and may be inferred for others (*Arisaema*: Figs. 12, 13 in Periasamy and Muruganathan 1986; and *Smilax*: Figs. 5, 6 in Martin and Tucker 1985). The Araceae is apparently variable, as seen from the two modes of development observed in *Scindapsus* and *Arisaema*. However, sampling of this large family is rather limited, and conclusions about the possible ancestral state within the family cannot be made with any certainty at this point.

The further surprising observation is that the pattern of development where lamina is derived from the upper leaf zone is associated with the presence of a Vor-

Table 1. Early development of the leaf in monocotyledons and outgroups. Horizontal growth: A, Position on shoot apex (0 = sub-terminal, 1 = lateral); B, Lower zone, encirclement (0 = partial, 1 = complete); C, Upper zone, thickening of tip (0 = not thickened, 1 = thickened). Vertical growth: D, Lower zone, intrapetiolar stipule (0 = no stipule, 1 = stipule). The "stipular" outgrowth in *Smilax* and *Scindapsus* are coded as ? since their development differs from that of intrapetiolar stipules in the dicots); E, Upper zone, lamina (0 = lamina, 1 = no lamina); Combined characters (see text): F, Leaf tip (combination of characters C, E); G, Primordial type (combination of characters A–E). Superscripts indicate sources: (a) this paper; (b) Bloedel and Hirsch, 1979; (c) Cutter, 1957; (d) Hagemann 1960; (e) Kaplan 1970, 1973; (f) Knoll 1948; (g) Martin and Tucker 1985; (h) Perisamy 1962, 1965; (i) Perisamy and Muruganathan 1986; (j) Rohweder and Endress 1983; (k) Roth 1949; (l) Rudall 1990; (m) Snow 1952; (n) Troll 1955; (o) Thielke 1948; (p) Weberling 1970; (q) Wilder 1976. In some cases a particular point was not discussed in the text, and coding had to be done on the basis of information derived from the figures.

	A	B	C	D	E	F	G
Aristolochiaceae ^a	1	0	0	0	0	"dicot"	0
Ranunculaceae ^{j,k,p}	1	0	0	1	0	"dicot"	1
Nymphaeaceae ^c	1	0	0	1	0	"dicot"	1
Piperales ^{a,d,j,p}	0	1	0	1	0	"dicot"	2
<i>Acorus</i> ^{a,e}	0	1	1	0	0	"mixed"	3
<i>Scindapsus</i> ^a	0	1	1	?	1	"dios"	4
<i>Arisaema</i> ⁱ	0	1	1	1	0	"mixed"	5
<i>Butomus</i> ^a	1	1	0	0	0	"dicot"	6
<i>Sagittaria</i> ^b	1	1	0	0	0	"dicot"	6
<i>Dioscorea</i> ^a	1	0	1	0	1	"dios"	7
<i>Gloriosa</i> ^a	1	0	1	0	1	"dios"	7
<i>Smilax</i> ^{a,g}	1	0	1	?	0	"mixed"	8
Cyclanthaceae ^q	0	1	0	0	0	"dicot"	9
Asparagales ^{a,e,k,n}	1	1	1	0	1	"dios"	10 "monocot"
Arecaceae ^b	1	1	1	0	1	"dios"	10 "monocot"
Zingiberales ^{a,k}	1	1	1	0	1	"dios"	10 "monocot"
Bromeliaceae ^{a,d,c}	1	1	1	0	1	"dios"	10 "monocot"
Commelinaceae ^{a,j,k}	1	1	0	0	1	"comm"	11

läuferspitze. A similar association has been described for juvenile leaves of the Cyclanthaceae (Wilder 1976). Clearly, the Vorläuferspitze may be associated with development from the upper leaf zone. This represents a renewed understanding, if not redefinition, of this structure. The Vorläuferspitze can be considered to represent a combination of two atomized features of the upper leaf zone—vertical and horizontal growth. By treating the two traits of the upper region as a binary coded character four states are obtained that represent all pairwise combinations (Column F, Table 1). In the "dicot" type (0) the upper zone forms the lamina whose tip is not thickened; in the "mixed" type (1 = Vorläuferspitze) the upper zone forms a lamina whose tip is thickened; in the "dios" type (2 = Vorläuferspitze) the upper zone does not form a lamina and is thickened; and finally, in the "comm" type (3) the upper zone neither forms the lamina nor is it thickened. In the past, the term Vorläuferspitze has been applied to leaves developing from both types of primordia, the "mixed" and "dios" types. Although the term was applied first to mature morphological structures without reference to development, in recent years it has usually been assumed that the Vorläuferspitze develops from primordia of the "dios" type. As noted here, this assumption may not hold universally. Given this historical association, and to avoid confusion, it

may be best to apply the term Vorläuferspitze to leaves developing from primordia of the "dios" type.

Character evolution

All five traits were optimized on different topologies and conclusions were drawn about character evolution in the conservative way described above. One trait is discussed in detail below, and general conclusions drawn in other cases.

Vertical growth of the upper leaf zone.—The results of optimization of this character on three topologies are illustrated in Fig. 10. According to the rDNA tree the ancestral leaf in monocots had a lamina that developed from the upper leaf zone (Fig. 10a). The transition to limited growth of the upper zone occurred once, and there were at least two reversals of this trait within monocots (in *Smilax* and unifacial asparagoids, not shown here). A similar pattern of evolution is suggested by the *rbcl* topology (Fig. 10b). However, the morphological topology suggests greater uncertainty (Fig. 10c). According to one reconstruction on this topology the upper zone had limited growth in the ancestral monocot, but this trait was reversed at least once (*Smilax*). An alternative reconstruction suggests that development of the lamina in the ancestral monocot was from the upper leaf zone and that there were

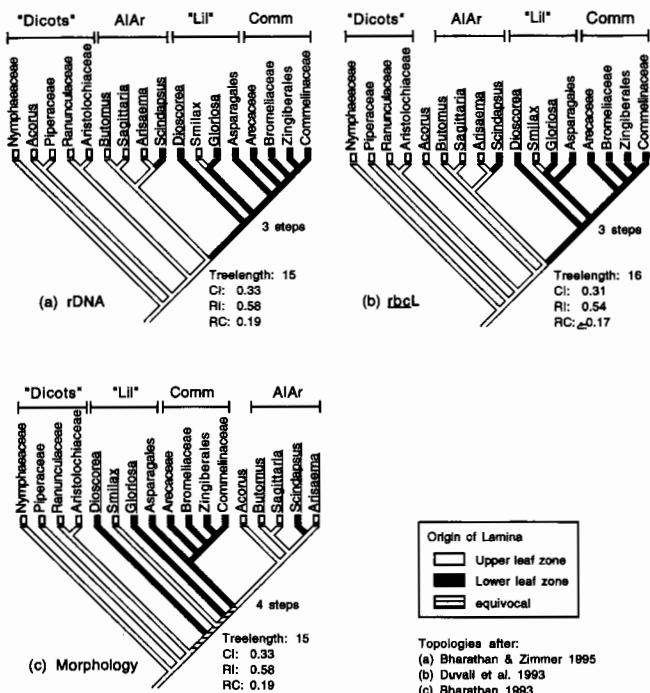


Fig. 10. Parsimony optimization of leaf developmental character, origin of lamina. Reconstructions on topologies from analyses of—(a). rDNA sequences.—(b). *rbcL* sequences.—(c). Morphology. “Lil” = Liliaceae; AIAr = Alismatales-Araceae; Comm = Arecales, Bromeliales, Zingiberales, Commelinales. Tree statistics pertain to all five leaf developmental characters when optimized on the three topologies.

at least two independent origins of limited growth of the upper leaf zone, namely in the Dioscoreaceae, and in the rest of monocots with a reversal in the alismatid-roid clade. According to the second scenario the developmental pattern in *Smilax* is a retained feature of the paleoherb ancestor.

Thus, the ancestral monocot may have had a lamina that developed from the upper leaf zone according to molecular and morphological topologies (equivocal support in the latter case). A difference is that development of the lamina from the upper leaf zone in *Smilax* is a reversal according to the molecular topologies, but a retained ancestral feature according to the morphological topology.

Position of the primordium.—The ancestral monocot had lateral primordia and there were two or three origins of the subterminal position in the Piperales, Araceae, *Acorus* and Cy-clanthaceae depending upon the topology considered.

Stipule.—The evolutionary scenario varies with the coding adopted. If the monocot taxa with “stipules” are coded as being exstipulate or uncertain, the ancestral monocot was not stipulate while the ancestral paleoherb was probably stipulate. On the other hand, if the Araceae, Alismatales, *Smilax*, *Dioscorea*, and Cy-clanthaceae were coded as being stipulate, then the

ancestral monocot was stipulate, and this trait was subsequently lost in the clade consisting of commelinoids and asparagoids.

Horizontal growth of the lower leaf zone.—The leaf base was partially sheathing in the ancestral monocot according to the morphological and rDNA topologies, suggesting that complete sheathing evolved within monocots. However, according to the *rbcL* topology the ancestral monocot may have had a completely sheathing base and there were reversals in the Dioscoreales and Liliales.

Horizontal growth of the upper leaf zone.—The upper zone was thickened in the ancestral monocot according to the morphological and rDNA topologies while the evolutionary trend is more uncertain according to the *rbcL* topology. This feature is the one commonly described as the *Vorläuferspitze*—however, as described above, the *Vorläuferspitze* might be considered to represent the combination of two aspects of the upper leaf zone, and the evolution of such a complex trait is described below.

The *Vorläuferspitze* and origin of the lamina.—This combined trait, coded in column F of Table 1, is optimized on two hypotheses of relationships (Fig. 11). The “dios” type may have arisen either once or twice according to the morphology tree, and at least twice according to the *rbcL* tree. The “mixed” type may have arisen two or three times according to both morphology and *rbcL* trees, there may have been one reversal to the “dicot” type according to the morphology tree. In other words, the association of the thickened tip with lamina development from lower leaf zone evolves few times, but may be lost several times. This latter tendency may lead to the evolution of leaves in which the thickened tip is associated with laminae developing from the upper leaf zone (e.g., *Smilax*, *Arisaema*), or there is no thickened tip associated with laminae developing from the lower leaf zone (e.g., Commelinaceae, unpub.).

The “monocot” primordium.—The set of all five traits may be assembled in a similar way to reconstruct the different types of primordia studied. These combinations yield a total of eleven types of primordia (Column G, Table 1). For example, one of these combinations (11101, character state ten) consists of a lateral primordium (state 1), with a complete sheath (state 1), thickening of the upper zone (state 1), lower zone not forming a stipule (state 0), and upper zone not forming a lamina (state 1). This is the “monocot” primordium as generally understood, and it characterizes a clade that consists of commelinoids and asparagoids. The other combinations are derived in a similar way. The evolution of this complex trait is discussed below.

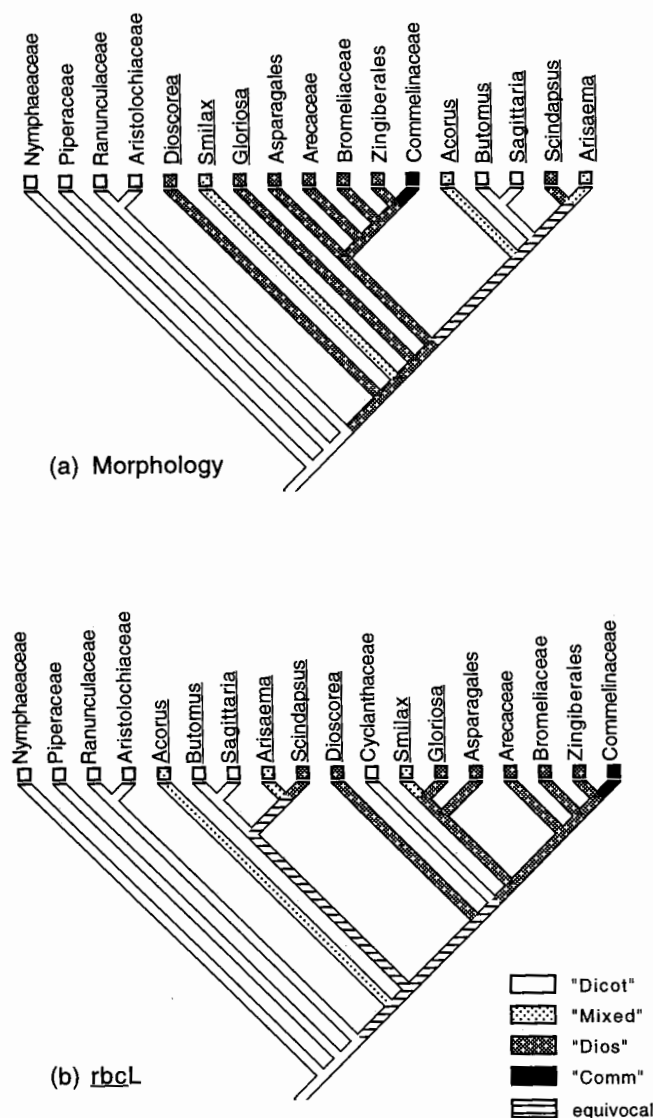


Fig. 11. Parsimony optimization of combined leaf developmental character, Vorläufer Spitze. Reconstructions on topologies.—(a). Morphology.—(b). *rbcL*. Reconstruction on both topologies is compatible with a "Dios" type of Vorläufer Spitze for the ancestral monocot, with thickened upper leaf zone and lamina-forming lower leaf zone; but results for the *rbcL* topology are equivocal.

Taxonomic Scope of the Leaf-base Model

All character reconstructions done on different topologies were examined in order to arrive at a conservative estimate of ancestral states of the five developmental traits in particular clades (Table 2). There are several points of agreement as well as disagreement between the different topologies and reconstructions. The state within the commelinoid ancestor is inferred unambiguously. However, due to uncertainty of early branching order and several alternative optimizations of the characters, no unequivocal statements can be made regarding characteristics of these early branches. Given these uncertainties, and regardless of how narrowly defined the "monocot" primordium is,

Table 2. Leaf developmental characters of ancestors of three monocot clades (Monocots; Commelinoids+"Lilies"; Commelinoids) inferred from parsimony reconstruction on three exemplar topologies. Commelinoids+"Lilies" = monocots on the morphology tree. Characters A to G as in Table 1.

Ancestor	A	B	C	D	E	F	G
MONOCOTS							
Morphology	1	0	1	0/1	0/1	2	7
rRNA	1	0	1	0	1	0/1/2	1-7?
<i>rbcL</i>	1	0/1	1	0	1	0/1	1-7?
COMM+"LIL"							
Morphology	1	0	1	0/1	0/1	2	7
rRNA	1	0	1	0	0	2	7
<i>rbcL</i>	1	0/1	1	0	0	2	7
COMM							
Morphology	1	1	1	0	0	2	10
rRNA	1	1	1	0	0	2	10
<i>rbcL</i>	1	1	1	0	0	2	10

the most conservative conclusion is that the leaf-base model applies universally to just a subset of monocots, the commelinoids.

The "monocot" primordium described above appears first in a group nested within the monocots—in the ancestor of a clade consisting of commelinoids (and asparagoids, according to the molecular topologies). It appears that this type of primordium evolved *within* the monocots and did not characterize the ancestral monocot or all monocots. If we were to redefine the "monocot" primordium to include forms with a partially sheathing base then the most inclusive taxonomic group characterized by the "monocot" primordium would be the clade of commelinoids and "lilies" (=all monocots, with reversals in the ALAR clade on the morphological topology).

The alismatoids and aroids represent a departure from this general pattern of development. The bifacial lamina in alismatoids is clearly derived from the upper leaf zones. The Bloedel and Hirsch (1979) interpretation was that the development of *Sagittaria* conforms to the monocotyledonous leaf-base model. In this taxon the lamina is derived from the upper leaf zone, which is apparently dicot-like. However, the petiole is differentiated early in development (p 3 or p4) from the upper leaf zone, while in dicotyledons it is intercalated later between the upper and lower leaf zones. This difference suggested to the authors an essential departure from the dicot model that led them to expand the leaf-base model for monocots to include the pattern found in *Sagittaria* (Bloedel and Hirsch 1979). It remains to be seen whether this pattern holds for other broad-leaved and petiolate alismatoids and whether this feature represents a basic difference between leaf development in monocots and dicots, or whether the development of the lamina from the upper leaf zone

and absence of a thickened tip suggests a basic similarity of leaf development in alismatoids and dicots as hypothesized here. In the Araceae the lamina develops from either the upper (*Arisaema*) or lower (*Scindapsus*) leaf zones, suggesting that this difference in mode may be more labile than generally considered. Another feature that sets the Araceae apart is the massive, subterminal primordium that it shares with *Acorus* and that is similar to the primordium seen in Piperales. However, the Cyclanthaceae have similar primordia, and this patchy phylogenetic distribution underlines the need to further examine the character in more taxa to get a clearer understanding of its significance.

Decoupling of Venation and Development

It is apparent from this study that mode of early development and origin of the lamina have little to do with the pattern of venation. The Dioscoreales and some Liliales have venation patterns that are very dicotlike, with major venation being reticulate and minor veins ending freely (Conover 1982, 1991); just three traces enter the leaf in *Dioscorea*, a pattern that is typical of dicots (Troll 1939). Arales and Alismatiflorae have major venation that is reticulate, but minor veins that do not end freely; multiple traces enter the leaf forming a midrib from which secondaries arise—a more typically monocot-type pattern (Troll 1939; Dahlgren and Clifford 1983). The typical linear leaf with its all-parallel and closed venation appears only sporadically in early lineages (*Acorus*, *Gymnostachys*, *Butomus*), but is characteristic of the more derived lineage consisting of commelinoids and asparagoids (Bharathan 1993).

Reticulate venation occurs in laminae that originate from either the upper leaf zone (alismatoids, and some aroids) or the lower leaf zone (Dioscoreales, Liliales, some aroids). Similarly, free vein endings occur in laminae that develop from the upper leaf zone (Piperales) or the lower leaf zone (Dioscoreales, some Liliales). There is no correlation between mode of development and venation pattern in these early lineages. It is only in the derived group consisting of commelinoids and asparagoids that the linear leaf with parallel, closed venation cooccurs with the lamina derived from the lower zone, a correlation that may be phylogenetic, rather than developmental.

Phylogenetic Implications

Parsimony analysis was used to assess how well leaf developmental characters “fit” alternative hypotheses of monocot relationships. The characters were optimized on topologies based on other data (rDNA, *rbcL*, morphology), and tree statistics used to assess whether one or other topology was favored by the developmental data (Fig. 10). Low values for these indices are

taken to imply high levels of homoplasy. The indices suggest that there is not much to choose between different topologies as far as leaf developmental characters are concerned, and that homoplasy is rampant among the few developmental traits studied.

Questions

Several questions remain regarding the evolution of leaf development in monocots and I discuss some of these questions. The Melanthiales are an enigmatic group that may be polyphyletic according to *rbcL* data (Duvall et al. 1993a, b; Chase et al. 1995a, b). In *rbcL* analyses *Pleea* (Tofieldiae, Melanthiaceae) is an early branch that is allied with alismatoids-aroids. Since members of Tofieldiae have unifacial leaves, this close proximity to the basal *Acorus* with similar leaves suggests that the unifacial leaf may have been the ancestral condition for monocots. Is the pattern of development in *Pleea* similar to that in *Acorus*? Developmental studies of Melanthiaceae are not yet available to answer this and other questions.

It has been assumed in this study that taxa, other than *Acorus*, in which unifacial/ensiform leaves occur are nested within the tree. The taxa concerned are in the Asparagales (e.g., Iridaceae, Phormiaceae, Alliaceae), Bromeliiflorae (Phylodraceae and Haemodora-ceae) and Commeliniflorae (Xyridaceae, some Junca-ceae, Centrolepidaceae, Anarthiaceae). Recent analyses of the Asparagales suggest that with the possible exception of the Iridaceae the other taxa are nested well within the Asparagales (Chase et al. 1995a). This implies that the basal condition in Asparagales is to have linear leaves whose laminae are derived from the lower leaf zone. Similar assumptions are made with regard to the Bromeliiflorae and Commeliniflorae, but these assumptions remain to be tested explicitly.

Leaf development in the Cyclanthaceae and Pandanaceae is of great interest because their phylogenetic position has been uncertain. A surprising result from the *rbcL* data was that these two groups are closely related to each other and allied with the Dioscoreales, not the Arecales (Duvall et al. 1993a). Analyses of morphological data that included the Cyclanthaceae and Pandanaceae suggested similar relationships (Chase et al., 1995b), while these two taxa were not included in the rDNA study. Data on leaf development reveal that *Carludovica* (Cyclanthaceae) has subterminal primordia (Figs. 9–12 in Wilder 1976) that are similar to those found in the Araceae (Fig 1; Fig. 6 in Periasamy and Muruganathan 1986). Development in *Pandanus*, on the other hand, appears to be similar to that in *Dioscorea* (Kaplan, pers. comm.). This is intriguing, and reinforces the possibility, noted above in the discussion on Araceae, that these features of leaf development are relatively variable. The addition of

developmental and morphological data on a greater range of taxa will permit testing of the hypotheses of character evolution presented above.

Conclusions

The two questions raised at the beginning of the paper may be answered despite uncertainties in the homology of characters and in relationships of monocotyledons. The developmental and phylogenetic analyses suggest that

1) The presence of the Vorläuferspitze does not invariably indicate development of the lamina from the lower leaf zone. In some taxa the upper leaf zone forms both lamina and thickened tip.

2) The lamina of the ancestral monocot may have been derived from the upper leaf zone. Development of the lamina from the lower leaf zone may be a feature that evolved *within* the monocots.

The leaf base model has been an extremely useful heuristic tool. This paper demonstrates that, in a strict sense, it is applicable to a nested subset of the monocots. It is now necessary to develop general versions of the model that apply to all monocots, and studies are in progress on this front. Apparently, the world of "old" morphology has not been fully explored and there are many surprises in store when we examine uncharted areas.

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