HERESY REVIVED: THE MONOCOT THEORY OF ANGIOSPERM ORIGIN

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ABSTRACT: A long-discarded hypothesis, claiming that the earliest angiosperms were small monocot-like plants, is rephrased. Six evolutionary trends are outlined as a basis for developing a framework covering the evolution of the vegetative body of angiosperms. Widely shared character states of the embryo, anatomy, and chemistry are cited to support the thesis that the monocots, as a lineage, are more ancient than the dicots. The monocot hypothesis has been given little credence because it implies that angiosperms evolved the woody habit and dicotyledonous embryos independently of other seed plant lineages. Arguments for such independent origin are given and a hypothesis for the significance of the paired cotyledons is presented. Evidence supporting the Ranalian hypothesis is interpreted to be a product of the origin and diversification of the dicots in the middle Cretaceous; neither contemporary evidence supporting the Ranalian hypothesis nor the radiation event 100 million years ago is thought to be directly associated with the origin of angiosperms from preangiosperms. Vegetative similarities between monocots and pteridophytes suggest an angiosperm origin from very primitive pteridosperms or paedomorphically reduced cycadophytes. A third possibility is the independent origin of the seed habit from a eusporangiate pteridophyte lineage; however, the present paper does not discuss reproductive structures. The Monocot hypothesis makes the general prediction that macromolecules, such as the cytochromes, will show greater similarities between some monocots and some non-angiospermous plants than between any dicots and any other living non-angiospermous taxa.

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INTRODUCTION

The origin of angiosperms is a subject presently dominated by a single theoretical framework. This is a serious shortcoming, for not only does the significance of factual data depend on the conceptual framework within which these data are viewed, but their significance is linked to other data similarly viewed. Together these data tend to support, and in many cases appear to prove, the veracity of the framework. Indeed, a single ruling theoretical framework recognizes only two classes of data: meaningful data and meaningless data; there are no contradictory data. Consider the problem of continental drift. The geometric similarities of the eastern and western continental shelves of the Atlantic Ocean were meaningless: they did not contradict the ruling theory of fixed continental positions. Few geologists viewed the world through two frameworks, fixed versus shifting continents. Rather, most viewed the world through one, and it was only with the influx of dramatic new data, meaningless in terms of the dominant theory, that many geologists finally gave serious attention to an alternative framework. In so doing they found that a great number of previously insignificant facts took on new meaning.

An alternative theoretical framework for the origin of angiosperms presents a similar problem. Workers will be reluctant to set the current theory to one side in order to see what perspectives a very different view provides. The unorthodox theory will be judged in terms of the currently dominant framework and consequently, it will appear quite unconvincing. Facts that are meaningful from one point of view are often unimportant from the other point of view, and vice versa. This also holds true for correlated sets of data which tend to give a theory a sense of confirmation because of hidden circularity that may be part of the correlations. Ideally a scientist should work with several frameworks and, as new data become available, constantly reassess these frameworks. Unfortunately, this is not how we operate. As soon as the data seem to favor one viewpoint, alternatives are abandoned and the "winning"

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viewpoint is adopted, perhaps modified, and refined. This system works well in most cases, but I believe that it has led us into an impasse as regards the origin of flowering plants.

The Ranalian Hypothesis

The Ranalian or Strobilus hypothesis of angiosperm descent has dominated discussions of angiosperm origins for more than half a century. The theory was developed around the turn of the century; important summary statements were presented by Hallier in 1905, Bessey in 1915, and Parkin in 1923. One of its chief theoretical rivals was the notion that the catkin-bearing Amentiferae (oaks and their allies), being similar to conifers in their mode of pollination and having rather simple flower structure, were primitive angiosperms (cf. Wettstein 1908, Strasburger et al. 1912). Data from anatomy, pollen morphology and newly discovered taxa (such as *Degeneria*) confirmed the primitive nature of many ranalian plants (note 1), while the amentiferous taxa were shown to possess relatively specialized anatomy and pollen structure. With increasing evidence that the Ranales, almost alone among dicots, did indeed possess a wide array of primitive character states, the amentiferous theory and all other theories were abandoned by an overwhelming majority of botanists.

Central to the early development of the Ranalian hypothesis was the conviction that the primitive flower was a condensed branch of sterile and fertile (sporangia-bearing) leaves, that is, a strobilus (Arber and Parkin 1907, Eyde 1976). No definitive paleontological evidence supports this view (Dilcher 1979, Doyle 1978a), but there are correlations among certain ranalian plants between leaf-like floral parts and both primitive anatomy and primitive pollen structure. These data have strongly fortified the Ranalian hypothesis and made it so convincing. The strongest evidence for leaf-borne sporangia in angiosperms is the flattened leaf-like stamens of *Austrobaileya* and *Degeneria*, as illustrated in many botany texts. From the point of view of the Ranalian hypothesis, these flat stamens are very significant structures; they further substantiate the primitive nature of ranalian plants. These are indeed the most leaf-like sexual structures in angiosperms, but are they true leaf homologs?

Though the origin and evolution of reproductive parts are not considered in this paper, the general viewpoint developed here interprets the flattened stamens of the woody Ranales as highly modified; they are not leaf homologs and they are not phylogenetically significant. These laminar stamens probably evolved as adaptations to the pollination activities of large and destructive beetles (cf. Carlquist 1969, Gottsberger 1974, Gottsberger et al. 1980, Thien 1980). The fact that *Degeneria* has its microsporangia on the abaxial surface and *Austrobaileya* on the adaxial surface of the so-called sporophyll also argues against the primitive nature of these stamens (Leinfellner 1956, Sauer and Ehrendorfer 1970). However, just as the theory presented here does not attribute significance to certain facts held to be important in the Ranalian framework, it also finds significant data where the currently accepted theory sees none. But why revive an old and discarded theory in the face of one which seems to be supported by good data and is almost universally accepted?

The prime failure of the Ranalian theory is that it suggests no specific relationships with non-angiospermous plants, living or fossil. Thorne (1963, p. 291, 1976, p. 51) has described his perception of a primitive angiosperm, a plant not unlike *Drimys* and clearly a member of the woody Ranales as defined by living taxa. The problem with such a proto-angiosperm is that there is nothing remotely similar outside the angiosperms. This situation should make us suspicious; primitive taxa generally share traits with groups from which they were derived. Ranalian plants suggest no relationships outside the angiosperms. Nevertheless, the Ranalian hypothesis has been very successful in delimiting a number of primitive and correlated character states. The view adopted here is that data supporting the Ranalian hypothesis reflect a secondary stage in angiosperm evolution--that of a successful dicotyledonous diversification about 100 million years ago, and that the Ranalian hypothesis tells us nothing of the critical earlier or pre-angiospermous stages of evolution. In fact, a preangiosperm may have had few of the characters that define a contemporary angiosperm, just as a Triassic cynodont reptile did not possess many of the attributes that we use to characterize a mammal today.

Another important reason for developing an alternative theoretical framework is the equivocal nature of the fossil record (cf. Doyle 1978a). The early Cretaceous leaf remains seem to indicate that pinnate venation is primitive in angiosperms (Hickey 1978), but this could be a product of the early stages of dicot success. If more complete fossil evidence were available, "wild" speculations such as adorn these pages would be unnecessary. One of the main roles of speculation and theories in general is to make meager data produce new insights by looking at the data from new and different perspectives.

The ideas presented here, as well as those of most contemporary angiosperm phylogenists, do have a common base in the conviction that the flowering plants are monophyletic; for some recent polyphyletic views see Krassilov (1977, Meeuse (1975) and Nair (1979). If a majority of distinguishing angiosperm characteristics, such as the flower, did not exist in the earliest angiosperms but evolved in parallel independently, monophyly is not necessarily denied; it may be only set further back in time (cf. Faegri 1980).

In summary, the angiosperms are assumed to be monophyletic and the primitive features of contemporary ranalian plants are thought to be vestiges of an early dicot differentiation that took place in the Middle Cretaceous. The premise adopted here is that the preangiosperms were small stemless plants and that the woody stem evolved independently of woody stems in other living seed plant lineages. The following pages endeavor to build a theoretical framework for the evolution of the vegetative parts of angiosperms based on these premises. The final parts present data and arguments that, I trust, will lend credence to such a framework.

SIX HYPOTHETICAL TRENDS IN THE EARLY EVOLUTION OF ANGIOSPERMS

In the following pages I propose six hypothetical trends regarding the early evolution of leaves and stems in angiosperms. A majority of these trends and their associated primitive states directly contradict the trends enunciated by Bessey in 1915 (dicta numbers 8, 9, 11, and 14) and generally accepted by angiosperm phylogenists over the last half century (cf. Cronquist 1968, 1974, Takhtajan 1959, 1969, 1980, Thorne 1974). While rejecting many of the evolutionary trends accepted by contemporary authors, I have no basic disagreements with their general methodology of phylogenetic analysis, such as the principles enumerated by Thorne (1958, 1963). The following six trends will be used as a basis from which a general framework for the origin and early evolution of vegetative parts of angiosperms can be developed. Hopefully, and at a later date, the framework will be expanded to include the evolution of reproductive structures and more precise cladistic analyses. The following pages outline major trends and are followed by a more general framework with more detailed arguments.

1. SMALL SIMPLE PLANTS PRECEDED LARGE COMPLEX PLANTS IN THE EARLY EVOLUTION OF ANGIOSPERMS

The great evolutionary radiations have generally begun with relatively small organisms; larger organisms have apparently been less adept at moving into new adaptive zones (Raup and Stanley 1971, p. 278). This is often called Cope's Law and is in keeping with Stebbins' (1974b) view that evolutionary trends towards greater complexity of bodily structure and development have often been essential for entering new adaptive zones and initiating major radiations.

A more specific reason for suggesting that angiosperms arose from small plants is that fertilization and seed set in living angiosperms is much more rapid than in living gymnosperms. The rapidity of angiosperm fertilization and seed production is a characteristic that is of great adaptive value to small short-lived plants. It is difficult to understand why such a basic characteristic would have evolved in the earliest angiosperms if they were long-lived Magnolia-like or Drimys-like trees, or even shrubs as Stebbins (1974a) and Doyle and Hickey (1976) have suggested. Likewise, double fertilization and triple fusion, which act to initiate the buildup of food reserves within the seed only after fertilization has taken place, are of particular benefit to small plants that do not have large reserves of energy. It is clearly an advantage over most gymnosperms where food reserves are often built into the seeds whether or not fertilization takes place (Doyle and Hickey 1976). This is a significant energy cost and may be one of the reasons why gymnosperms have not evolved plants with small habit and short life histories.

2. SCATTERED VASCULAR BUNDLES WITHIN THE STEM PRECEDED A TUBULAR VASCULATURE WITH INCLUDED CYLINDRICAL CAMBIUM

It is assumed that the vasculature of the stem in early angiosperms was not clearly organized, having evolved through the buildup of leaf-traces. The cylinder of vascular tissue with its included cambium, producing xylem to the inside and phloem to the outside (the ectophloic siphonostele) is seen here as a very sophisticated and advanced development. Similarities between the vascular systems of modern dicot trees and the trees of living gymnosperms are interpreted to be independent and convergent developments. It was not until the secondary vascular cylinder evolved in dicots that leaf-gaps and branch-gaps (the so-called lacunae) came into being. Theories of leaf-gap and branch-gap formation postulated for the conifers (Namboodri and Beck 1968, Beck 1970) are thought to be inappropriate for angiosperms in this framework. Secondary growth from a cylindrical cambium in a few monocots is an additional independent development; no monocot possesses a radial system in its wood as is found in the wood of dicots and other living seed plants.

3. SIMPLE LEAFY STEMS WITHOUT AERIAL BRANCHING PRECEEDED COMPLEX WOODY GROWTH WITH SEVERAL ORDERS OF BRANCHING

Vigorous and frequent axillary branching on aerial stems is seen here to be a very advanced trait, producing the characteristically broad complex crown found in so many dicot trees and shrubs. The monocots, with little aerial axillary growth and few orders of branching, are assumed to be primitive or directly derived from simple primitive ancestors in this regard (figure 1).

Here we begin to have problems with strong correlations and circularity. The presence of an active cambium and frequent axillary branching are undoubtedly functionally correlated. (The added evaporative surfaces of an axillary shoot place increased demands on the water-conducting tissues of the stem; a tubular cambium can create additional vasculature needed to transport more water.) While these correlations will give our framework a sense of coherence, they also contribute to circular arguments. For example: a tubular vasculature with active secondary growth may be the primary factor facilitating frequent axillary branching in dicots. Conversely, the lack of efficient secondary growth and a tubular cambium may be the primary factor restricting aerial axillary growth in monocots (Tomlinson 1980). Axillary growth in monocots is usually associated with adventitious roots; hence, most axillary growth in monocots is at or near the ground. It may be that many monocots can meet the added demand for water and nutrients imposed by added axillary growth only through adventitious roots (George Wilder, personal communication).

4. SIMPLE UNDIFFERENTIATED LEAVES PRECEDED LEAVES WITH A CLEARLY DIFFERENTIATED PETIOLE AND LAMINA

The division of labor by differentiation of parts is a very general trend in a great many evolutionary advances. The simple leaf, undifferentiated into blade and petiole, is seen in this framework to be a more primitive condition than a leaf with an expanded blade or lamina and a terete narrow petiole (Bessey 1897, Domin 1931). The slender terete petiole permits greater flexibility in the orientation of the broad lamina than does a broad leaf base, either for optimizing exposure to light for photosynthesis or for reducing exposure to maintain heat balance and for reducing wind resistance.

Heteroblastic (juvenile-to-adult) series lend support to this postulated trend. For example, the earliest leaves of Victoria cruziana (Nymphaeaceae) are linear, followed by sagittate, then subcordate and finally peltate leaves (Valla and Martin 1976). The early stages of this sequence, linear to sagittate, are virtually identical to the sequence in Sagittaria latifolia (Bloedel and Hirsch 1979). In addition, the petiole is generally the last part of the leaf to be clearly differentiated in angiosperm leaf ontogeny (Majumdar 1956, Richards 1977), and I suspect that this is because it was the last part of the leaf to have evolved.

5. LEAVES WITH ONE OR A FEW POORLY DIFFERENTIATED ORDERS (RANKS) OF VENATION PRECEDED LEAVES WITH SEVERAL CLEARLY DIFFERENTIATED ORDERS OF VENATION

Fossil evidence supports this postulated trend (Doyle and Hickey 1976, Hickey 1978). Heteroblastic (juvenile-to-adult) series also support the trend; see figure 2. The earliest leaves of the Araceae display a variety of disorganized venation patterns (Ertl 1932) and the cotyledons of Magnolia virginiana have parallel (single ranked) venation (Sugiyama 1976).

According to Hickey (1978), the earliest angiosperm leaves in the Early Cretaceous have pinnate venation with secondary veins clearly distinct from the midvein. I believe that these fossil leaves have nothing to do with the actual origin of angiosperms but rather belonged to early dicot shrubs that may have been weedy streamside colonizers, just as Doyle and Hickey (1976) have hypothesized. The contention here is that the dicot radiation of the Early Cretaceous is a later event in the history of angiosperms and is not closely related to the origin of angiosperms from preangiosperms.

If few orders of venation are primitive, then it is likely that parallel or palmate venation is more primitive than pinnate venation, since pinnate venation has, by definition, two clearly separate major vein orders. Support for the idea that pinnate venation may have arisen from leaves with parallel or palmate venation comes from an ontogenetic study of secondary veins in Populus (Isebrands and Larson 1980). In these leaves the midrib is made up of independent vascular bundles, each of which eventually diverges into the lamina to become a secondary vein. The leaf venation of Chloranthus serratus, a perennial herb, and Sarcandra glabra, a vesselless subshrub, may have evolved from a Plantaginopsis-like precursor of the early Cretaceous (Berry 1911) and, in turn, given rise to the more typical two-trace unilacunar condition found in Ascarina (cf. Nakazawa 1956, Swamy 1953). All three living genera are members of the relictual ranalian family Chloranthaceae (see figure 2).

6. A CLASPING LEAF BASE CONTINUOUS WITH THE TISSUE OF THE STEM PRECEDED A LEAF BASE CLEARLY DIFFERENTIATED FROM THE STEM; DECIDUOUS LEAVES EVOLVED LATER AND WERE A MAJOR INNOVATION

This trend is closely associated with the evolution of the petiole and with the increased efficiency brought about by the division of labor through morphological differentiation. The clasping or sheathing leaf base does not offer the same flexibility in orientation that is afforded a leaf with a narrow leaf base. Evidence for this trend is also found in heteroblastic series. In some species of Piper the first leaves are provided with broadly sheathing leaf bases, while distal leaves associated with the flowering spikes have slender terete petioles lacking basal sheaths (Burger 1972). A similar situation occurs in Philodendron of the Araceae (Ritterbusch 1971). The ontogeny of the typical angiosperm leaf supports the contention that the clasping or sheathing leaf base was the primitive condition. The typical leaf primordium produces two lateral flanges in very early stages before the apical portion expands to develop into the blade and petiole (Bloedel and Hirsch 1979, Hagemann 1970, Ihlenfeldt 1971).

The differentiation of the leaf base to produce an abscission layer coupled with the evolution of the relatively thin and energetically "cheap" but strong reticulately veined lamina that characterizes deciduous dicot trees and shrubs may have been one of the major adaptive advances in the history of angiosperms. I would suggest that it was this development that accounts for the success and diversification of dicots in the Mid-Cretaceous and their present dominance in many parts of the world. Conversely, the difficulty in producing abscission layers may be why monocot trees and shrubs have fared so poorly in seasonally cold and very dry habitats where the deciduous habit is advantageous.

A FRAMEWORK FOR THE EVOLUTION OF THE PLANT BODY IN ANGIOSPERMS

This framework, based on the six evolutionary trends just stated, defines a small monocot-like plant body as the primitive state in early angiosperms. The fact that our hypothesized primitive character states are strongly correlated in a great many small monocots is important but, in itself, proves nothing regarding the validity of the framework. The character states used to develop a theoretical framework can hardly be used to prove the framework correct. Such arguments would be utterly circular, but there is also hidden circularity within the framework because many of the defined primitive traits are functionally interdependent. The following character states probably form a functional and structural continuum: alternate leaves with sheathing leaf bases, sheathing leaf bases with multilacunar nodes, multilacunar nodes with scattered vascular bundles, scattered vascular bundles with the inability to form a tubular cambium and a subsequent inability to produce a secondary growth or frequent axillary branching. The concordance of these character states is interpreted to be the primitive condition because of the framework that we have adopted, and this framework clearly implies that monocots generally represent a more primitive level of development than do dicots (note 2). The following discussions elaborate the framework and cite corroborative evidence. The later sections go beyond the framework to find additional support for the contention that monocots are indeed the living descendants of the earliest angiosperms and not an early side branch that went through an unusual evolutionary bottleneck.

Primitively herbaceous or paedomorphically reduced pteridosperms or cycadophytes that might have been ancestral to early monocot-like angiosperms are unknown. In the following pages comparisons with living eusporangiate pteridophytes are made in order to identify widely shared and primitive character states. It is assumed that the ancestors of angiosperms, whatever their lineage, would have also shared these primitive states. In the primitive living Ophioglossales the persistent shoot of the young sporophyte arises as an adventitious bud on the ephemeral primary root, and the vasculature of the stem is largely, if not entirely, foliar in origin (Campbell 1911, 1930, Mesler et al. 1975). Such a growth form in preangiosperms would be consistent with the framework being developed here and it implies that the superposition of leaves produced the aerial stem in the early evolution of angiosperms. A number of other general observations are consistent with such a hypothesis.

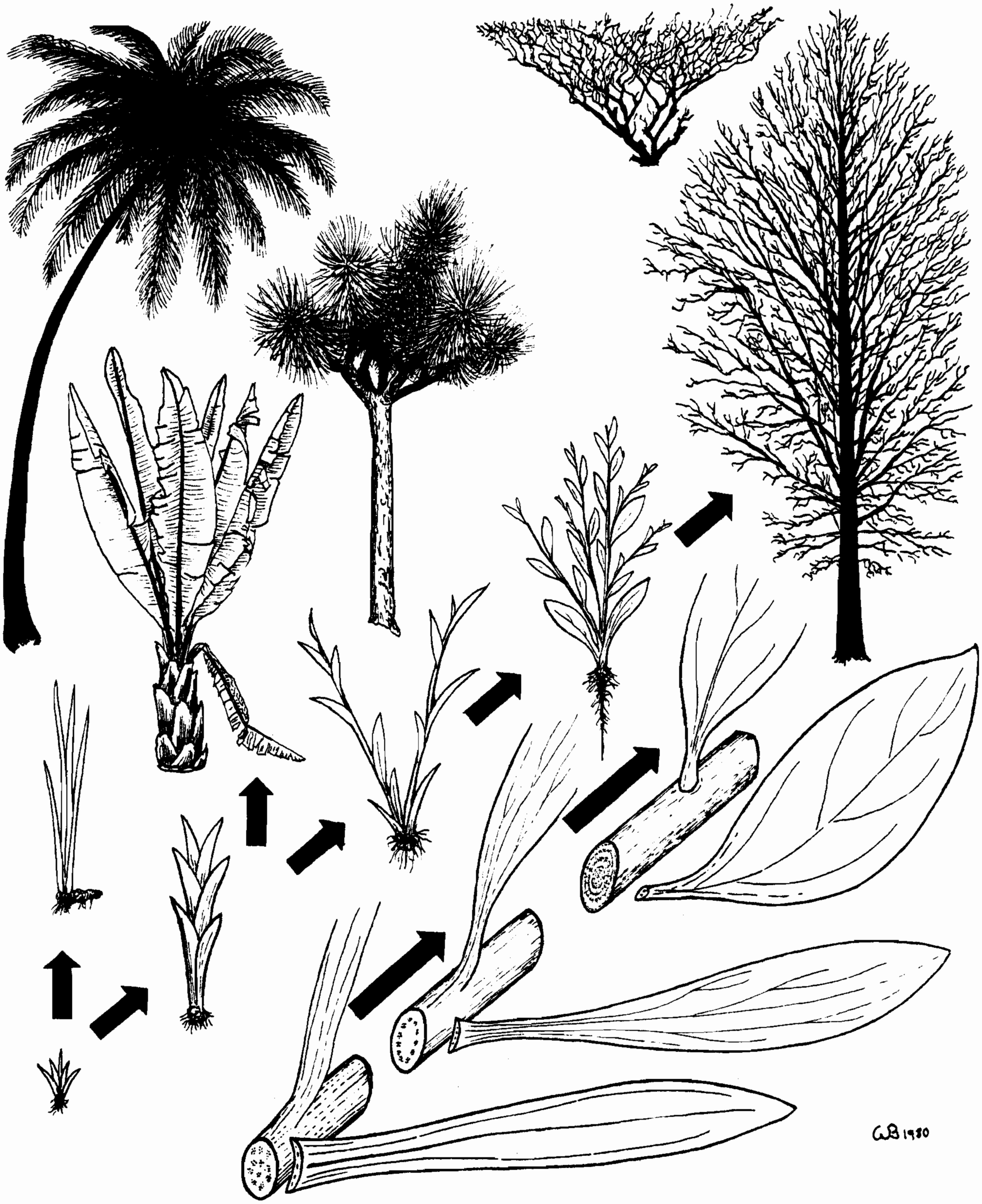

Figure 1. A diagrammatic outline of major trends in the evolution of the angiosperm plant body and leaf.

Carlquist (1975, p. 75) has noted that in ferns all mechanical supporting tissues originate from the primary body and that monocots, characterized by exactly the same basic growth pattern, are limited to a generally similar range of growth form. Carlquist (1975, p. 74) also points out that the occurrence of vessels in ferns, though quite rare, resembles the patterns found in monocots. The direction of xylem specialization in monocots is from roots to the stem to the aerial leaves (Cheadle 1942). A somewhat similar sequence from roots to the rhizome to the leaves is found in the water fern Marsilea (Bhardwaja and Baijal 1977) and in Actiniopteris (Singh et al. 1978). These fundamental similarities between monocots and pteridophytes have received no critical attention in the last half century because they are meaningless data when viewed within the context of the Ranalian framework.

The Monocot framework implies that the large woody habit in angiosperms is an evolutionary development achieved independently of other living seed plant lineages. There is a variety of data to support this view. Surely, palms and pandans evolved their arborescent habit independently of other lineages, no matter which evolutionary framework one adheres to (note 3). More importantly, anatomical diversity in dicots suggests that they may have evolved the woody habit independently in a number of lineages. Gottwald (1977) has identified six structural groups of wood anatomy comprising at least two polyphyletic series in what he calls the ancient dicots: the woody Ranales, Hamamelidales, Dilleniales, and Theales. There is little doubt that vessels are polyphyletic within dicots (Carlquist 1975, p. 167) as well as independently evolved in monocots. In addition, the early protoxylem patterns seen in the woody Ranales are far more diverse than those found in the conifers (Benzing 1967). The occurrence of anomalous patterns of secondary growth in a wide variety of dicot lineages is difficult to understand in the context of the Ranalian hypothesis. Why should some of the most distinctive and taxonomically isolated dicot lineages, such as the Caryophyllales, Piperales, and Polygonales, be characterized by anomalous secondary growth? Our framework suggests a simple answer: these lineages diverged early in the history of dicots, before secondary growth from a tubular cambium had become a general feature of dicot anatomy.

In many monocot stems the leaf traces originate close to the surface of the stem a number of internodes below the node at which the leaf is borne. These leaf traces then become positioned closer to the center of the stem as they travel upward within the stem and finally they bend abruptly, turning outward as they exit into the leaf base (Zimmermann and Tomlinson 1965). This peculiar pattern of vascular anatomy can be interpreted as an ontogenetic recapitulation (frozen within the persisting vasculature of the stem) of how some monocot stems have evolved. Leaves arose on the surface of the stem and hence their vascular bundles begin near the surface. Secondly, the stem was built up by leaf bases and so the vascular bundles move to the interior of the stem. Finally, with the leaf base having contributed to the stem, the vasculature bends abruptly outward to innervate the lamina. The reason that many monocot stems have such a configuration is that they never developed the more highly organized and morphologically more versatile siphonostele.

Vasculature

In the Ophioglossaceae the shoot apex is developed relatively late and the vascular tissue of the stem is largely, if not entirely, foliar in origin (Campbell 1921a, Wardlaw 1955, p. 130). If paedomorphic reduction produced a similar ontogeny in the earliest preangiosperms we would have a basis for the widely held interpretation that the vascular system of angiosperms is of foliar rather than axial origin (Esau 1965, Nast 1944, Philipson and Balfour 1963). In the context of this framework, evolution of the mature vascular cylinder in woody dicots can be outlined in five stages: first, the separate vascular strands of the leaf contributed to the formation of the central stem vasculature; second, these strands were at first poorly organized but later came to form a regular but interrupted cylinder (the eustele or dissected siphonostele); third, this cylinder became sufficiently stabilized to maintain its organization through the nodal plexus; fourth, the cylinder then developed a central tubular and continuous meristem that is the cambium; and finally, the cambium developed the ability to produce a radial system in addition to the axial system (note 4).

Conflict between theories of a foliar versus an axial origin of the vasculature have often focused on the problem of "leaf gaps" or lacunae in the vascular cylinder. Why should the vascular cylinder develop lacunae (areas filled with parenchyma rather than vascular tissue) at nodes where leaves emerge if the system was originally a tubular siphonostele? Proponents of axial theories have had to erect hypotheses of medullation to account for these lacunae, with the central pith or medulla having expanded to cause the formation of lacunae or gaps. There is little question but that such theories of medullation and axial origin cannot be applied to the most primitive (or perhaps reduced) living ferns, the Ophioglossaceae (Campbell 1921a, Stevenson 1980) and, by extension of the present framework, such theories are equally untenable in flowering plants. In angiosperms the vascular system is fundamentally a sympodial arrangement of leaf and root traces.

It may be that the stelar patterns of all living vascular plants have had their ultimate origin from a protostele, as evidenced by the ontogeny of Ophioglossaceae (Fahn 1974, p. 212) and the fossil history of conifers (Namboodri and Beck 1968). Nevertheless, if angiosperms arose from a reduced pteridosperm or herbaceous pteridophytic ancestry, then we should expect that the evolution of their vascular architecture followed a different route than that of the conifers and that ontogeny of living angiosperms and conifers should exhibit fundamental differences. This is what we find. In angiosperm seedlings the early epicotylar protoxylem originates in the base of the leaf primordia and progresses basipetally (downward) to form the central protoxylem of the stem (Benzing 1967, Larson 1976). A similar developmental pattern is characteristic of the stems of grasses (Hitch and Sharman 1971, Patrick 1972, Sharman and Hitch 1967). The pattern of early xylem differentiation is very different in conifer seedlings where the first epicotylar xylem elements are located just above the hypocotyl and mature acropetally toward the expanding primary leaves and basipetally into the hypocotyl (Tilton and Palser 1976). Furthermore, the leaf traces of conifers traverse less than one internode before entering a leaf base, while leaf traces in angiosperms traverse from one to many internodes (Devadas and Beck 1972). This is the reason why angiosperms tend to have many more vascular bundles in stem cross-sections than do conifers. These differences reflect the fact that conifers and angiosperms are very distantly related, and I believe they support the notion that stem structure in angiosperms has had an independent origin. This view also suggests why some angiosperm trees, such as Tetracentron and species of Winteraceae, possess wood more primitive than that of many gymnosperms (Stebbins 1974a, p. 200). In addition, the cellular structure of secondary xylem in angiosperms differs fundamentally from that of all other living woody taxa (cf. Doyle 1978, p. 379); this is additional support for the contention that woody stems in angiosperms are not primitive states widely shared with other living seed plants.

Anomalous secondary growth in angiosperms has been difficult to interpret in the context of an hypothetical ancestry that began with woody stems and tubular cambium. For example, in the Nyctaginaceae a central vascular system supplies the leaves and branches while the outer ring of bundles, similar in position to the vascular system of most dicots, is only indirectly associated with the leaf and branch traces (Zamski 1980). The peculiar internal and external vasculature of the Nyctaginaceae is easily explained in the context of our framework: from an ancestral background of scattered vascular bundles, the Nyctaginaceae have evolved their stem vasculature independently and in an unusual fashion. The Ranalian framework demands a more complex scenario: a woody-stemmed ancestor with tubular cambium evolved into an herbaceous form which lost its highly organized tubular vasculature and then evolved anomalous vasculature when woody stems evolved anew in the Nyctaginaceae, and in related families of the Caryophyllales (cf. Philipson 1975, Philipson et al. 1971, p. 109, Takhtajan 1959, p. 38).

Zimmermann and Tomlinson (1972) claimed that the basic difference between monocots and dicots is the possession of two vascular systems (an outer and an inner) in monocot stems as opposed to a single outer system in the stems of dicots. Their basic premise, however, is that thick-stemmed boles, such as found in palms, dracaenas, and pandans are the primitive condition in monocots. It seems to me that the smaller and simpler stem with a less clearly organized vascular system is a better candidate for the primitive condition in monocots (note 3). From such an origin both thick monocot stems with an inner and outer vasculature and thick dicot stems produced by a tubular cambium are seen as highly evolved character states (figure 1). Similarly, the "double" vascular systems of thick-stemmed monocots and the Nyctaginaceae are independent evolutionary advances from ancestral stocks that were fundamentally herbaceous.

In many monocots the procambium of the stem is discontinuous and open ended. An upwardly developing procambial strand, rather than entering a leaf primordium directly, ends blindly in a meristematic cap just below the apical meristem until the primordium it will enter is formed at the shoot apex (Weidlich 1976, Zimmermann and Tomlinson 1970). This is in contrast to procambial development in dicots which develops acropetally (upwards) and without interruption. I view the monocot pattern as a less efficient and more primitive method of building stem vasculature. Likewise, palms and other large monocots probably have evolved a complex vasculature because their ancestors did not possess the simpler and more efficient siphonostele/eustele which characterizes other seed plant lineages and most woody dicots.

Howard (1974) has suggested that "the multilacunar node of modern plants with a sheathing stipule may well be the residual expression of the primitive nodal plexus." Such a view is consistent with the framework being developed here. We know that the sheathing leaf base is almost always associated with the multilacunar condition in dicots (Majumdar 1956, Majundar and Pal 1961), but few workers have interpreted this condition as primitive since such an interpretation is not consistent with prevailing theory (note 5). The earliest states of leaf ontogeny involve a lateral basal expansion (Hagemann 1970) and this suggests that a clasping or sheathing base was indeed the ancestral state in angiosperms. The large number of traces in the leaf bases of *Magnolia* (Sugiyama 1972, 1976), *Degeneria* (Swamy 1949), *Chloranthus* and *Sarcandra* (Swamy 1953) are consistent with this view and with the general trends of our framework, generalized in figure 2.

In contrast, Jeffrey and Torrey (1921a, 1921b) suggested that an evolutionary increase in the number of foliar traces led to the crowding of strands at the nodes which, in turn, resulted both in the scattered distribution of bundles within the stem and the formation of amphivasal strands in many herbaceous angiosperms. This argument, consistent with the Ranalian framework, is the basis for the general opinion that scattered vascular bundles and many leaf traces are a derived condition. But if scattered vascular bundles or stem cross-sections with both an inner and an outer series of bundles are a derived condition, why do we find them in the central axis of the *Magnolia* flower (Skipworth 1971), in stems and inflorescence axes of *Anemone* (Wordsell 1902) and in the stems and spikes of Piperaceae (Murty 1960, Rousseau 1928)? Jeffrey and Torrey's thesis seems incapable of answering this question. The framework presented here has a simple explanation: scattered vascular bundles are the ancestral condition in angiosperm stems (note 6).

Leaves

In modifying her earlier concepts, Arber (1941) described the leaf of monocots as "*a more or less modified fixation of the whole phyllome at its pre-laminar stage*" (italics hers). She used the term pre-laminar in an ontogenetic sense, but I believe that it reflects historical phylogeny as well. Many monocot leaves may be pre-laminar in the sense that their ancestors never had broadly laminar leaves as do most modern dicots.

Hickey and Doyle (1977) point out that there are three stages of meristematic activity during the ontogeny of the typical dicot leaf: first, a brief apical phase giving rise to the primary venation; second, a brief marginal phase giving rise to the embryonic lamina and the secondary veins; and third, a prolonged phase of diffuse intercalary or plate meristematic activity producing most of the leaf area and all the higher vein orders. They interpret this sequence as a major evolutionary innovation originating from a much reduced gymnospermous leaf; but this unique ontogenetic pattern of leaf formation is also consistent with the trends outlined here and with the suggestion by Arber that the monocot leaf is in a sense pre-laminar. The theory of Doyle and Hickey (1976, Hickey and Doyle 1977) postulated a xeromorphic bottleneck in the evolution of angiosperms to account for the uniqueness of the dicot leaf and its ontogeny; the trends postulated here require no such bottleneck and suggest that some monocots still retain a relatively primitive type of leaf (figure 2).

Just as the diversity of trees and their vasculature suggests polyphyletic development, the diversity of leaves with broad laminae and reticulate venation implies that these too, evolved independently in several major lineages of angiosperms. A complete range, from narrow leaves and angular typically monocot-like fine venation to broad leaves having dicot-like tertiary venation is found in the Liliaceae, Orchidaceae, Potamogetonaceae and Araceae (Schuster 1910). This suggests that each of these families evolved dicot-like tertiary venation independently. The seedling leaves of the Araceae exhibit irregular venation patterns (Ertl 1932) that are reminiscent of the trends seen in early Cretaceous leaves (Doyle and Hickey 1976). Even the very unusual leaves of Palms and Cyclanthaceae appear to have evolved their similar form independently of each other (Wilder 1976).

While the dicot-like leaves of aroids, lilies and orchids and the broad laminae of most dicot lineages are undoubtedly independent and convergent developments, it is unlikely that all monocot and dicot leaves differ in their fundamental ontogeny as Kaplan (1973) has hypothesized. However, analyses of chimaeras by Stewart and Dermen (1979) have shown that early ontogeny in monocots is not as predictable as in the growth of dicot leaves and flowers; different parts of the apical meristem contribute to a greater portion of the developing organs in monocots. This too, suggests that the monocots have a more primitive level of organization and that the dicots are more complex and have a more precisely programmed ontogeny. The phyllode theory, which assumed that the ancestors of monocots had lost the leaf-lamina and subsequently redeveloped the broad distal lamina from the petiole, has proven invalid (Kaplan 1973).

Many herbaceous dicots have leaves with a relatively undifferentiated mesophyll (Esau 1977, p. 355). Additionally, undifferentiated mesophyll is characteristic of early leaves, with later-produced leaves possessing greater differentiation (Schneider 1952). Both this heteroblastic series and the framework developed here suggest that the leaves of many herbaceous dicots may retain primitive characters not shared with their woody relatives. Similarly, it is the herbaceous dicots that so frequently exhibit sheathing leaf bases with multilacunar nodes. These have almost always been interpreted as an evolutionarily advanced condition; but here is another point where the Ranalian hypothesis gives us difficulty. Why should so many different dicot lineages have produced herbs with sheathing leaf bases independently? Dicot herbs with sheathing leaf bases that the Ranalian hypothesis would have us believe evolved independently from woody ancestors without sheathing bases are found in the Compositae, Geraniales, Piperales, Polygonales, Ranunculales, Rosales, Umbellales, and many others.

The clasping leaf base is characteristic of the most primitive living ferns, the Ophioglossaceae, and the Isoetales. It is likely that the narrowly clasping leaf base preceded the broadly sheathing leaf base in angiosperms; the broadly sheathing base serves to protect the emerging apex and basal internodal meristem (note 7). In a similar manner, stipules often serve to protect the young shoot apex in dicots. Weberling (1970 and 1975) has presented considerable evidence indicating that stipules have probably evolved from sheathing leaf bases in the herbaceous Ranales, Compositae and several other dicot lineages. Accordingly, one can postulate three general trends in the evolution of leaf bases among angiosperms: first, from clasping leaf base to broadly sheathing leaf base (as in many modern monocots and dicot herbs); second, from clasping or sheathing leaf base to various stipular developments (as in many dicots); and third, from clasping or sheathing leaf base to a terete leaf base lacking both stipules and lateral extensions of the petiole (as in many dicots).

Dichotomous venation, extremely rare in angiosperms, is found in the fan-shaped leaves of Circaeaster and Kingdonia, genera that have been interpreted as products of extreme reduction from Ranunculus-like ancestors (cf. Foster 1963, Foster and Arnott 1960). The framework developed here views these monotypic little herbs of western China as something much more interesting. The leaves of Circaeaster (figure 2) and Kingdonia may be all that persists of an unsuccessful attempt by an early dicot lineage to produce broad laminae. These isolated relicts of the ranalian alliance may be descendants of very early dicots that had not yet evolved either the woody habit or the typical dicot leaf, though they did reach the stage of having tricolpate pollen. Here again, we find a generally recognized primitive condition linked with herbaceous, rather than woody, Ranales.

THE MONOCOT-TO-DICOT TRANSITION

It seems reasonable that either a simple monocot-like plant or a woody dicot-like plant should have been the life-form from which today's diversity of angiosperm structure evolved. In this framework we begin with a very simple body plan and postulate the progressive development of more elaborate internal and external structure, culminating in the characteristic growth form of dicot trees and shrubs (figure 1). Our framework implies that plants resembling small contemporary monocots gave rise to the great variety of growth forms we see today, both in monocots, whether grasses, orchids or palms, and in dicots. Discussions of the opposing view, the origin of monocots from dicots, have been given by Cronquist (1968, pp. 315-320, 1969, pp. 190-193, 1974), Stebbins (1974, pp. 317-324) and Takhtajan (1969, pp. 108-121) and these discussions should be contrasted with the general trends outlined here.

As their names imply, the single most consistent feature separating monocots and dicots is the possession of one or two cotyledons. The solitary cotyledon of monocots is usually terminal with a lateral shoot apex, while in dicots the shoot apex is terminal with opposing lateral cotyledons. The exceptions to these generalizations are very few and, I believe, minor evolutionary specializations that are trivial from a phylogenetic point of view. Because the embryonic characteristics are so consistent over so many species, and because they divide angiosperms into two unquestionably natural assemblages, these embryonic differences and their evolutionary transition are an essential aspect of any general theory.

The Angiosperm Embryo

Dicots have been assumed to be ancestral to the monocots, and for this reason a large literature has developed attempting to interpret the monocot embryo in terms of the dicot embryo. Numerous studies have argued that the solitary cotyledon of the monocots is not truly terminal, but the result of fusion of two cotyledons or the failure of one or both to develop. The present framework adopts a much simpler story and one that I believe is more coherent. The monocots have a single cotyledon because virtually all monocots have only a single leaf at each node; that is to say, their leaves are all fundamentally alternate (Arber 1925, p. 179, Tomlinson 1970). Their first leaf is terminal because the ancestral preangiosperm lacked a well developed stem. In contrast, the ruling theory for most of this century has dictated that monocots evolved from dicots, and the problem has been how to explain the evolution of the solitary cotyledon.

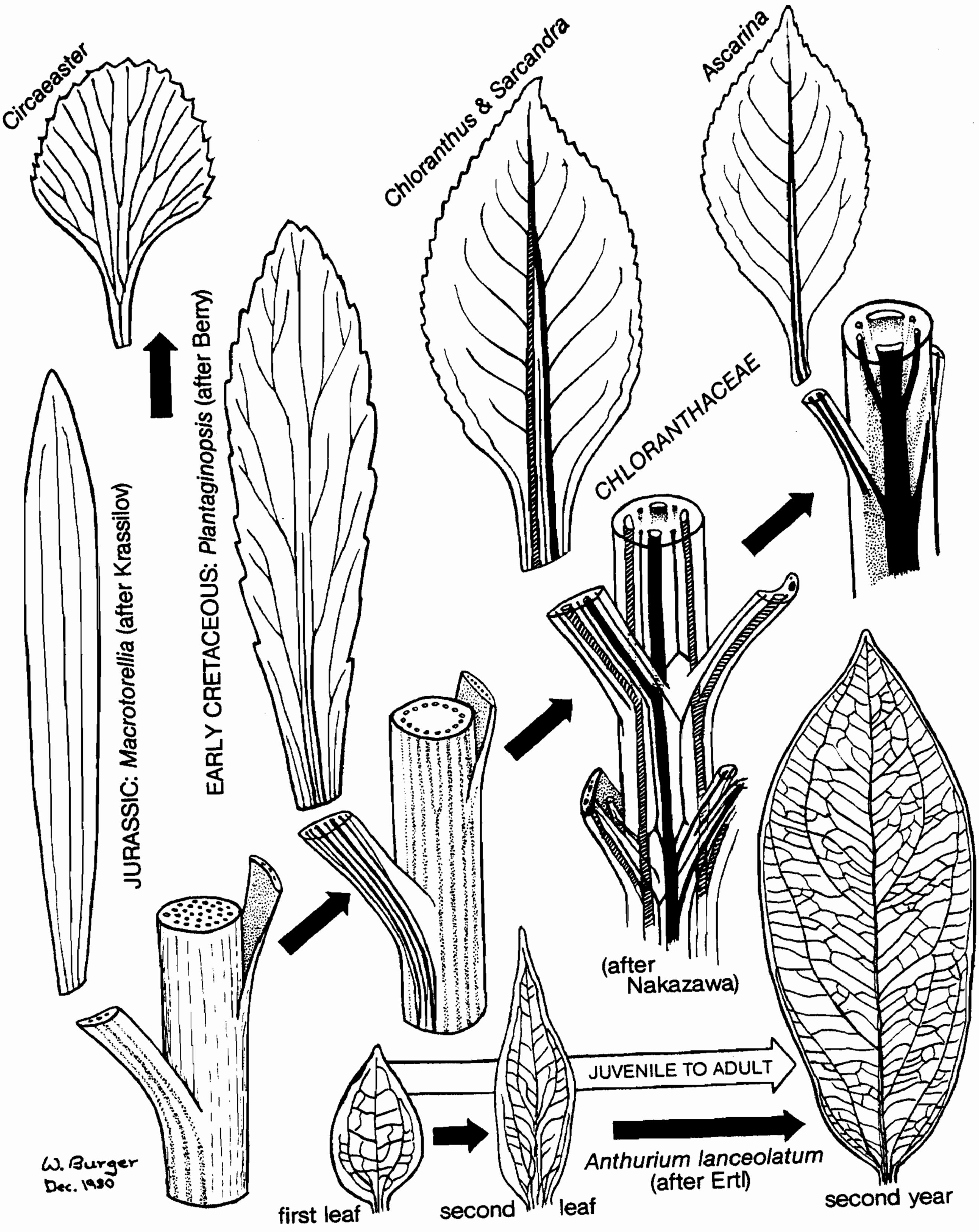

Figure 2. A hypothetical sequence in the evolution of angiosperm leaves and a developmental sequence in a species of Anthurium (Araceae).

There have been a large number of studies that purport to show a lateral origin for the cotyledon in early stages of the proembryo in monocots (e.g. Haccius and Lakshmanan 1966, Guignard 1975, Swamy 1963). These workers have argued that the proembryo of dicots and monocots is identical, that the plumule or shoot apex is terminal on the rounded apex of the proembryo, and that one of the original two lateral cotyledons becomes terminal by active early growth, forcing the shoot apex into a lateral position in the fully developed embryo of most monocots. I believe that these interpretations of weakly differentiated early embryonic stages have been rooted in the conviction that the primitive angiosperm was dicotyledonous and consequently, these studies have found evidence for the assumptions with which they began. Haccius and Lakshmanan (1967) have even gone so far as to claim that certain monocotyledonous dicots represent true intermediates between dicots and monocots as regards embryonic structure. But this seems most unlikely since these are species of Anemone, Ranunculus, Cyclamen, and Pinguicula, with close relatives having perfectly normal dicotyledonous seedlings.

A different explanation for the origin of monocot seedlings has been offered by Kudraishov (1964) who concluded that the third leaf of Nymphaea was the true homolog of the first leaf (cotyledon) of monocots; see figure 3, top center. Thus Kudraishov argued that monocotyledony has originated by the loss of both cotyledons. Since loss is a common evolutionary tendency, Kudraishov (1964) suggested that monocotyledony could have originated repeatedly from dicotyledony. However, the relative uniformity of monocots argues against their polyphyletic origin.

Recently, Haines and Lye (1979) have summarized evidence favoring the syncotylous (fused) nature of the solitary cotyledon in monocots. Stebbins (1974, pp. 325-328) has also argued for the origin of monocotyledony from dicotyledony by the fusion of two original cotyledons. He suggests that the petioles of the two cotyledons have come together to form the cotyledonary tube found in many monocots and supports this view by pointing out that the two vascular strands of the single cotyledon often originate in an opposite configuration at the base of the solitary cotyledon (Sargant 1902). He also stressed the importance of the cotyledonary tube in forcing the hypocotyl and radicle deeper into the ground, thus facilitating survival during dry periods. Stebbins views the origin of the cotyledonary tube in monocots by "intercalary concrescence of the margins of a single remaining cotyledon" as highly unlikely. But in the framework developed here, with the clasping/sheathing leaf base considered to be a primitive condition, the development of cotyledonary tubes would only require the extension and concrescence of the sheathing leaf base. Here too, the cotyledonary tube is seen as an advanced condition, probably playing the adaptive role that Stebbins suggested, forcing the seed deeper into the soil.

Nelumbo is a very unusual dicot genus, formerly placed in the Nymphaeales but differing in having tricolpate pollen and ranalian chemistry, and now placed in its own order. This genus with monocot-like vegetative and anatomical features and typical dicot pollen structure, may be helpful in our understanding the monocot-to dicot transition as regards change in embryonic form. Lyon (1901, 1902) pointed out that the cotyledon of Nelumbo is at first a crescent-shaped mound of tissue encircling the upper surface of the embryo. The shoot apex arises between the points of the crescent and appears to be homologous with a monocot embryo in which the shoot apex is flanked by the stipule-like margins of the sheathing cotyledonary base. The cessation of growth in the center of the crescent produces a bilobed primordium in Nelumbo (Lyon 1901). A shifting of these two growing points to an opposing configuration and to earlier stages of ontogeny would give a typical dicotyledonous embryo with a central terminal shoot apex (figure 3).

Summarizing these developmental trends in terms of the present framework, we can hypothesize that the flanking cotyledonary base evolved to form a ring around the apex of the embryo and that bifurcation of this ring into two (or more) primary growing points produced two (or more) cotyledons. Pelligrini (1957) has interpreted cotyledonary anomalies in Dianthus (Caryophyllaceae) in a similar way. Such a sequence also makes it easier to understand why some very primitive dicots, such as

Degeneria and Idiospermum, have three or four cotyledons rather than two. It goes without saying that the Ranalian hypothesis reads this evolutionary sequence in the opposite direction, with the separate primordia coming together to form a single sheathing cotyledon. Unfortunately, the enigmatic nature of nymphaeaceous embryos and seedlings permits other interpretations and hypotheses, both within the Ranalian framework (cf. Haines and Lye 1975) and from the point of view developed here (note 8).

If monocots were derived from dicots one might expect to find occasional "reversions" to the ancestral dicotyledonous state, but one does not. Reports of four primordia on the embryonic cotyledonary tube in Cyrtanthus (Farrell 1914) and a unique dicotyledonous seedling in Agapanthus, also of the Amaryllidaceae (Coulter and Land 1914), have been cited, but these very rare instances seem to provide evidence for the growth potentials of the cotyledonary ring and not for reversion. There have been other reports of two cotyledons or bilobed cotyledons in a few monocots (Eames 1961, pp. 328, 343, 345, 360) but these are not documented and they do not appear to have been based on careful developmental studies. What appears to be a short second cotyledon or cotyledonary lobe may be a ligule-like development of the basal cotyledonary sheath opposite the cotyledon itself. The coleoptile of grasses may have originated in this way.

Lawton and Lawton (1967) claim to have identified two cotyledons in five species of Dioscorea, but they illustrate two structures which are very different in position and mature sequentially; a simultaneous origin is not at all clear. The situation in Dioscorea seems to be one in which the cotyledon has become an absorptive organ and the following leaf has come to act as the first leaf of the seedling with concomitant changes in growth and development. It seems strange that the putatively primitive condition of two cotyledons (from the Ranalian point of view) would be found in monocots in such a highly modified form as Lawton and Lawton (1967) have suggested. Likewise, Coulter (1915) and Eames (1961, p. 345) interpreted the epiblast of the grass embryo to be a second cotyledon. Here too, the so-called second cotyledon finds itself in a very highly evolved monocot embryo and other interpretations seem preferable (cf. Brown 1960).

Schellenberg (1928) proposed an evolutionary progression of food storage in the seed: from perisperm to endosperm to food storage within the embryo and cotyledons. Following this line of reasoning, a general statistic that supports the claim of monocot embryos being more primitive than those of dicots is the larger percentage of dicots having cotyledons which store food. Additionally, the cotyledons of monocots are generally more similar to the next developed leaves than are the cotyledons of dicots. This lack of differentiation between cotyledons and succeeding leaves in monocots, and the fact that they are often part of the same phyllotactic spiral, also argues for a more primitive condition (Bessey 1897). It is also noteworthy that aberrant embryos are more common in dicots than in monocots (Eames 1961, p. 360, Palser 1975). In addition, it is possible to treat some dicotyledonous embryos with phenylboric acid and produce numerous monocotyledonous embryos (Haccius 1960); I have seen no report of any treatment causing the embryos of monocots to become dicotyledonous.

These various data are consistent with the hypothesis that the monocot embryo is primitively simple and not a reduction product from a dicotyledonous embryo. In dicot seedlings the stem apex is terminal and ready to grow upward rapidly, building stem tissue as it grows; the broad opposite cotyledons offer greater leaf surface for photosynthesis, and their clearly differentiated petioles allow the lamina to be oriented to maximize photosynthesis. The typical monocot seedling, like that of the early sporophyte of pteridophytes, has none of these advanced traits.

Problems of a Hypothetical Dicot-to-Monocot Transition

The prevailing Ranalian hypothesis has pictured monocots as having originated from a primitive dicotyledonous ancestor. This view has necessitated hypothesizing a series of coordinated evolutionary trends that include reduction of the plant body in both size and complexity, loss of a tubular cambium and the potential for typical woody secondary growth, scattering of the vascular bundles within the stem, loss or fusion of a cotyledon, simplification of leaf architecture, and limitation in the diversity of floral morphology and pollen structure. Two general "bottleneck" hypotheses have been developed to explain these coordinated trends. In one group of hypotheses the bottleneck was presumed to have been an adaptation to seasonal drought and the bulbous Liliales were thought to be the primitive type (Sargant 1903, 1904). The other group of hypotheses assumed that adaptation to an aquatic or semi-aquatic habitat was the bottleneck, with plants such as the Alismatales thought to represent primitive monocots (Cronquist 1968, p. 317, 1969, p. 190, Hallier 1903). This latter view is widely held today, in large part because of the many similarities between the Nymphaeales and the Alismatales (Takhtajan 1969, pp. 111-114).

Takhtajan (1976 and earlier) has attempted to explain the prevalence of reduction series in flowering plants in terms of paedomorphic reduction, where early somatic stages are brought forward into the later sexually mature stages of the life cycle with the consequent loss of features that characterized the mature plant of the antecedents. Doyle (1978a) has recently rephrased this theme using ideas developed by Gould (1977) relating progenesis with an adaptive shift to a more "weedy" *r*-selected life style. But is there evidence that might pertain to neoteny or progenesis as an explanation for extensive reduction in the dicot-to-monocot transition required by the Ranalian hypothesis? Evans and Rees (1971) pointed out that the mitotic cycle averages four hours longer in dicots than in monocots. Since the duration of the mitotic cycle is generally thought to be dependent on the amount of DNA carried by the chromosomes, one would conclude that dicots have more DNA than do monocots. This would be consistent with the view that dicots are more complex and more advanced evolutionarily than monocots. The differential in length of the mitotic cycle argues against neotenic reduction, since neoteny does not involve a loss of genetic information, but rather a shift in developmental timing. In fact, neotenic or progenetic reduction probably requires increased genetic information in order to override or accelerate ontogenetic processes. Takhtajan (1976) has also argued that neoteny produces a rich reservoir of hidden potential genetic information that can play a role in later diversification. But here too, the monocots give little support for a neotenic interpretation. In the 100 million years since their separation from dicots (Doyle 1973) they have been very much more restricted in their morphological diversification than dicots. This, as I see it, is a restriction due to a primitive ground plan (*bauplan*) and limited genetic resources; there is no evidence here for neotenic reduction from a once more structurally complex ancestor (note 9).

Why was the Acquisition of Two Opposing Cotyledons so Important?

The framework proposed here implies that the acquisition of two cotyledons was, directly or indirectly, associated with a major adaptive advance in angiosperms. The dramatic mid-Cretaceous diversification of angiosperms now being studied so intensively was almost entirely a dicotyledonous radiation. Moreover, estimated totals of living species number four times as many dicots as monocots. Thus, the success of angiosperms is largely measured by the dicots. The two opposing cotyledons are a virtually invariant characteristic of dicots; the exceptions are clearly derived modifications. But was this character essential to the success of dicots? I believe that it was.

The origin of the two cotyledons at the same level on the plant axis may have made it easier, not only to establish opposite phyllotaxy, but more importantly, to develop a template for reorganization of vascular bundles at the node. The independent leaf traces in the "scattered" vascular configuration characteristic of most stem cross-sections in monocots had to undergo two major changes in order to evolve into the dissected siphonostele of dicots: (1) become arranged in the configuration of an open cylinder and (2) develop a consistent means of retaining this highly organized configuration while traversing the node. The cotyledonary node of the dicots may have been the critical first step in achieving the second change. In this regard it is interesting to note that in the Piperales, including the Chloranthaceae, the nodes are usually conspicuously thicker than the internodes, especially in woody stems of several seasons' growth. I think this is a reflection of the difficulty in maintaining vascular continuity while adding secondary wood at the node in these primitive dicot families. In Piper methysticum the interfascicular cambium develops relatively late in the internodes and even later in the nodes (Hoffstadt 1916). Interestingly, in Lactoris, a relictual monotypic herb of the Piperales, the internodes lack rays (Carlquist 1964). This suggests the further possibility that it was in the organization of the node that dicots solved the problem of creating a tubular cambium capable of producing a radial system as well as an axial system, something never achieved among monocots. Not only did the newly organized dicot vasculature permit the independent evolution of the ectophloic siphonostele with its tubular cambium, but also established the ability to originate additional branch primordia at virtually every node. Dicots can branch and regenerate new aerial axes with a facility matched by no other plant lineage. The ability to branch in diverse ways has produced a great variety of tree architecture among dicots and this in turn has had profound effects on the evolution of arboreal animal life, including our own lineage.

The transitional nature of Nymphaeales (sensu stricto) between monocots and dicots is worthy of further analysis. They seem to be dicotyledonous only as regards the possession of two suctorial organs, which may or may not be true cotyledons. The vegetative morphology, pollen morphology, and the floral structure of Cabomba and Brasenia are very similar to that found in various Alismatales. If my supposition is correct, that the paired cotyledons at the cotyledonary node were an important precursor state in the development of a tubular vasculature, then the fact that cotyledons in Nymphaeales are not really leaf-like and there is no well defined cotyledonary node explains why this lineage has failed to develop a cambium. It was only after the paired cotyledons became leaf-like on a stem-like axis that the stage was set for vascular reorganization.

ARE MONOCOTS MORE ANCIENT THAN DICOTS?

The obvious consequence of the framework developed here is that many monocots are more like the hypothesized angiosperm precursors than are dicots, and that monocots are in fact the direct descendants of the earliest angiosperms. There will be no effort made here to define a particular monocot lineage as being especially primitive; all are modern contemporaries. With well over 100 million years to evolve and differentiate, there is little likelihood that a lineage or taxon has remained relatively unchanged over such a span of time. We see a similar situation in living mammals; there are no therapsid-like or cynodont-like animals alive today. The most primitive living mammals, the Monotremata (platypuses and echidnas) may be an ancient lineage with many primitive traits, but they are also highly specialized and cannot be considered ancestral to any other living mammal lineage. The last time the Monotremata and other living mammals shared a common ancestor was in the Jurassic (cf. articles in Lillegraven et al. 1979). Similarly, we should not expect to find a "pre-angiosperm" hidden within the monocots or that any living monocot represents the kind of plant from which both modern dicots and modern monocots diverged over 100 million years ago. In the same way, though the woody Ranales are an ancient lineage with many primitive traits, chemical evidence suggests that they are descendants of an early side-branch and not the ancestral stock from which all other dicots emanated (Kubitzki 1972). But despite these reservations there should be evidence that the monocots, as a lineage, are older and retain a greater number of primitive traits than dicots.

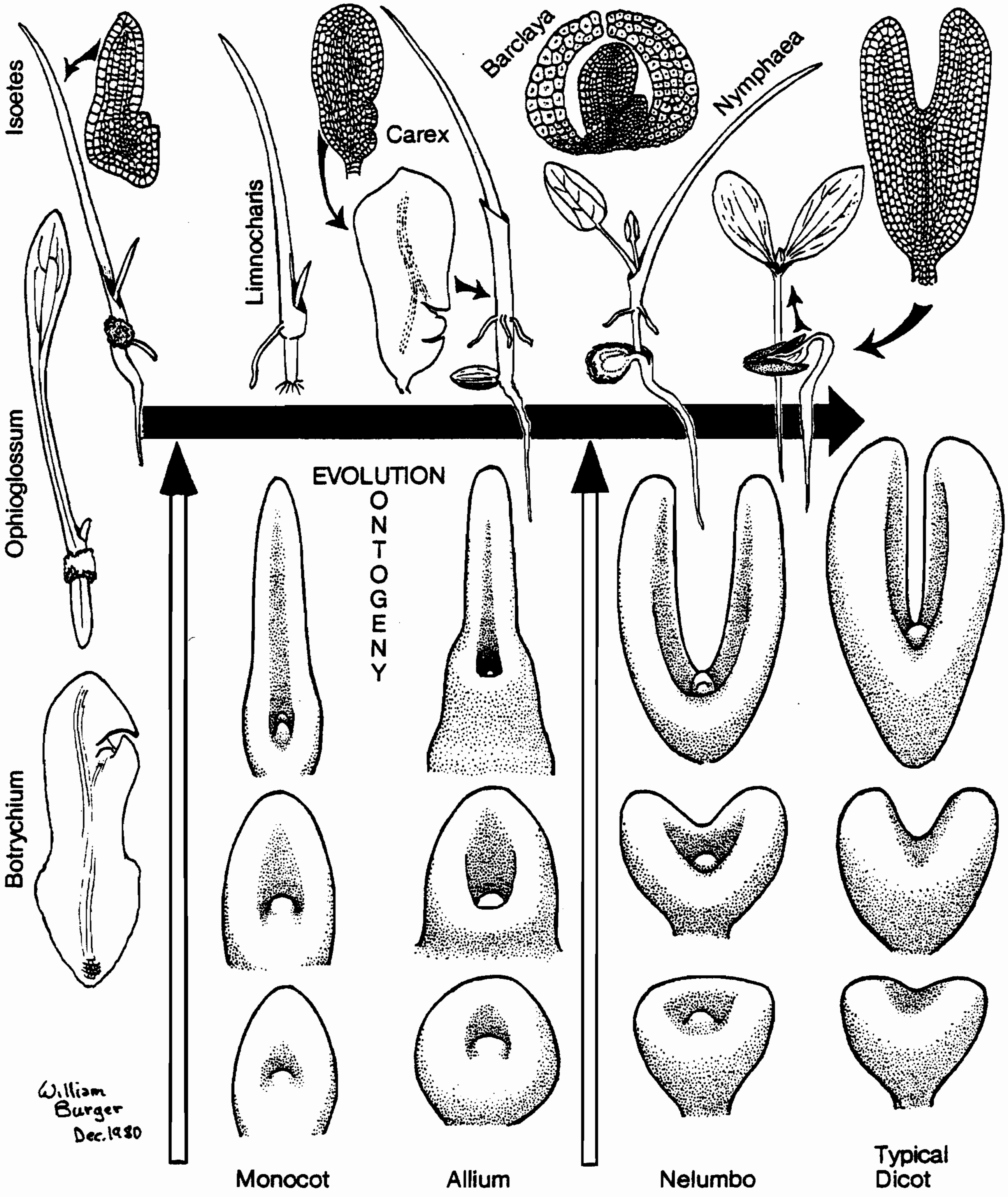

Figure 3. Ontogeny of embryos and hypothesized sequence in the evolution of embryo and seedlings. Pteridophytes are included to suggest homology of widely shared form, not direct ancestry. See note 16 for sources of illustrations.

The more limited diversity of growth habit, leaf form and flower structure in monocots gives the impression that they are a more tightly knit group than are the dicots. Their smaller number of species, and the fact that a great many species are found in a very few large families (such as the Orchidaceae, Gramineae and Cyperaceae), adds to the impression of a phyletic assemblage more uniform than the dicots. However, the higher taxonomic categories are deeply divided in monocots and, unlike dicots, there are few or no connecting links between them (Good 1956, p. 47, Meeuse 1975, Tuzson 1909). The Zingiberales, Alismatales and Hydrocharitales are difficult to link to other groups. The Arales, Palmae, Pandanaceae, Cyclanthaceae, and Typhaceae have often been placed together, but the divisions between them are wide (Clifford and Williams 1980). In contrast, few dicot families and orders seem so isolated from each other. Cronquist in 1978 divided the dicots into six subclasses and the monocots into five subclasses despite the fact that dicots probably outnumber monocots four to one. Takhtajan (1969, p. 121) pointed out that "there is no monocot order that could occupy the place in their family tree that is occupied by the Magnoliales among dicots," and he attempted to explain this curious fact by postulating a faster evolutionary rate in monocots. A simple explanation is that the monocots are an older assemblage than are dicots and that both their common progenitors and ancient intermediates are long extinct.

Stebbins (1975a, p. 315) has noted that the monocot orders with flowers having separate pistils (apocarpy) are not closely related, while the apocarpous orders of dicots form a reasonably close and homogenous group. Apocarpy is generally accepted to be a primitive floral trait, and while rare, its wider taxonomic occurrence in monocots is another data-set consistent with the hypothesis that monocots are an older lineage than the dicots. Stebbins (1974a, p. 317) attempted to explain the taxonomic range of apocarpy in monocots by arguing that the woody Ranales, living in moist evergreen habitats, have had a lower extinction rate than the monocots, many of which live in open seasonal environments. Stebbins' argument was meant to explain why there are more connecting links within the dicots, links largely provided by the Ranales (in a wide sense). But such an argument does not explain the broad taxonomic range of apocarpy in monocots; if we were to lose half the living families of dicots, the range of apocarpous families would not broaden. Apocarpous genera are found in monocots among distantly related aquatics, distantly related saprophytes, and even in the palms (Moore and Uhl 1973). No such range is found in dicots. Again, the simplest explanation of these patterns is that the monocots preceded the dicots in time and for this reason they retain a greater number of primitive features spread over a broader range of their taxa.

Kosakai, Moseley and Cheadle (1970), after noting that the Araceae, Sparganiaceae, and Hypoxidaceae all have decidedly less advanced vessel elements than the herbaceous Ranales (cf. Cheadle 1953), make the remark that it "seems impossible that monocotyledons could be derivatives of even ancestral forms of present herbaceous Ranales." This is another line of evidence suggesting that monocots as a group are more primitive than the dicots. Additionally, just as the herbaceous Ranales have more advanced anatomy, the same holds true for the relative evolutionary status of their pollen grains. Taken together, the anatomical and palynological evidence supports the framework developed here (note 10).

A number of monocot families have become adapted to living as submerged aquatics in a marine environment: the so-called sea grasses. No families, genera, or species of dicots are similarly adapted. In fact, no other land plant lineage has been able to make this return to the sea environment. Yet there is evidence that sea grass communities were already in existence before the end of the Cretaceous, 65 million years ago (Brasier 1975). In addition, both the diversity of floral structure within these marine plants (Cymodoceaceae, Posidoniaceae, Zosteraceae and some Hydrocharitaceae), and the fact that some have flowers very difficult to interpret in terms of what we commonly think of as flowers, suggests great age. The sea grasses, I believe, are further testimony to the antiquity of monocots.

Shared Character States

It is noteworthy that there are no monocots that possess a suite of coordinated dicot-like characteristics. (The Alismatales do not qualify since their embryology, vegetative anatomy, floral ontogeny and morphology and chemistry are typical of monocots). But there are a number of dicot lineages that possess coordinated suites of monocot characteristics; these are found in the Nymphaeales, Piperales and Ranunculales. This is as one would expect if dicots arose from monocot-like ancestors and if the monocots never did possess the later-evolved dicot characteristics. Moreover, the coordinated monocot-like characters in dicots are found in taxa rather tightly clustered within or closely related to those dicots long considered to be the most primitive, the Ranales in a wide sense. But looking at this situation from the perspective of the Ranalian hypothesis one is confronted with the question: why are there no monocots that possess a suite of characteristics derived from their postulated ancestors? Here again, the Monocot hypothesis explains data that the Ranalian hypothesis cannot.

The observation that no monocot taxon possesses a suite of coincident characteristics typical of dicots is further argument that these typical dicot features are unique and derived rather than primitive and widely shared (table 1). Our framework treats similarities in gross structure of dicot and gymnosperm trees and embryos as derived and convergent. I contend that the living gymnosperms are inappropriate for out-group comparisons intending to identify shared primitive states. Because primitive or reduced Pteridosperms are no longer extant, we must use the living primitive pteridophytes as the appropriate out-group for the identification of widely shared primitive states in angiosperms. This brings us to the subject of widely shared character states as a means of determining evolutionary direction in character-state sequences.

Widely shared character states are often primitive, whereas derived character states, especially complex ones, are often very limited in the range of taxa over which they are distributed (Stevens 1980 and included references). This generalization is quite useful in the absence of clear paleontological progressions. The best example of a primitive and widely shared character in monocots probably is the monosulcate nature of their pollen grains and having only pollen types derived directly from a monosulcate condition. The dicots have monosulcate pollen grains restricted to a few families of the ranalian alliance (in a wide sense). Tricolpate grains and their derivatives are characteristic of the vast majority of dicot families. Here, monosulcate grains are the widely shared type, while tricolpate grains are unique to the dicots. Fossil evidence supports the view that tricolpate and their derived types are unique to dicots and, despite some look-alikes (Doyle et al. 1975), did not occur before the latter part of the Early Cretaceous.

The Embryo

The most interesting widely shared similarities of angiosperms are those found in the embryos of monocots and pteridophytes. These similarities include a solitary and terminal first leaf (or cotyledon), a laterally placed shoot apex and unipolar growth. Unlike dicots and all other living seed plants, the primary root cannot continue growing and further root growth is largely by adventitious roots in both monocots and nearly all the living pteridophytes. In both Ophioglossaceae and monocots the earliest leaves are sheathing at the base and root inception and development take place well before the development of the shoot apex. These are fundamental structural and developmental similarities. A lateral origin of the shoot seems to serve no special purpose and together with the general form of the embryos makes a strong argument for a widely shared and primitive state (note 11). The ancestral condition of the early sporophyte may have been very simple, with a basal root and terminal leaf, further growth originating as a bud on the apex of the primary root, just as it does in some species of Ophioglossum (Campbell 1911, p. 42). Such an origin would explain the lateral origin of the shoot apex in virtually all pteridophyte embryos. This is an ancient trait and not a displacement phenomenon (Campbell 1907, Mesler et al. 1975).

The embryos of nearly all seed plants have their distal axis, root and suspensor in a single line, whereas embryos of living pteridophytes are quite variable regarding the orientation of these parts. (Since the function of the angiosperm suspensor is to push the embryo into the food-rich endosperm, it is understandable that the suspensor would be at one pole of a uniaxial embryo.) However, suspensors lateral to the embryonic axis are found in some aquatic monocots (cf. Yamashita 1976). While only trivial aberrations from the Ranalian point of view, these unusual features are further evidence for widely shared and primitive characters when considered within the Monocot framework. The resemblance of monocot embryos to those of primitive living pteridophytes is not an accident of unusual evolutionary convergence.

Here we find the weakest link in the Ranalian hypothesis, for it requires a very unusual transformation in the hypothesized derivation of monocots from a dicot-like (i.e. ranalian) ancestry. Not only does the Ranalian hypothesis demand unusual simplification of the plant body, loss of the tubular cambium and scattering of the vascular bundles, but it also requires that monocot embryos lose their potential for bipolar growth while they independently evolve an embryo that is strikingly similar in basic structure to the embryo of the primitive living pteridophytes. The scenario proposed here gives a much simpler and more reasonable transformation, and it interprets the widely shared similarities of monocot and pteridophyte embryos as shared primitive states of profound phylogenetic significance (figure 3).

Endodermis

The endodermis occurs throughout the entire plant body in pteridophytes and is found in the stems as well as the roots of monocots and many dicot herbs (Eames 1961, p. 4). The presence of endodermis in the embryo also implies that it is a fundamental tissue and a primitive trait. From the point of view of the Monocot hypothesis the absence of endodermis in the stems of most dicots is interpreted as an evolutionary loss related to the vascular reorganization that made possible the evolution of the tubular cambium. The view from our framework is consistent: the presence of endodermis and the absence of cambium in monocot stems are both widely shared and primitive states. The Ranalian hypothesis requires the assumption of discordant trends: monocots retained the endodermis in their stems (a primitive trait) but lost the ability to form a tubular cambium (seen as a derived reduction).

Stomata

Payne (1979) has shown that diameristic mesoperigenous stomata associated with rectate growth are found, with few exceptions, throughout the lower embryophyta. This widely shared character complex is common and basic to the monocots and to the herbaceous Ranales (Payne 1979). The woody Ranales, however, are characterized by paracytic stomata (Baranova 1972) and these are very restricted in their distribution among land plants. Payne points out that rectate growth characterizes virtually all non-angiospermous plants and is a product of intercalary or marginal growth that proceeds in a continuous wave. In contrast, diffuse growth characterizes the leaves of dicots. Here again, the widely shared character states are basic to monocots and the unique states characterize the woody dicots.

Starch Grains

In a comparative study of the starch grains in seeds, Czaja (1978) found pteridophyte-type grains in 14 monocot families but only in Gunneraceae among dicots (note 12). This study revealed a three-step progression within monocots, which Czaja characterized as primary monocots with pteridophyte-type grains (note 13), true monocots, and derived monocots. The derived monocots and a great majority of dicots accumulate fatty oils, proteins or, less often, cellulose in their mature seeds. Among dicots, the Piperales and Nymphaeales resemble Czaja's true monocots as regards the structure and content of their starch grains. Here we find a one-two-three progression where the monocots generally possess the widely shared character, the dicots generally possess the most derived state, and the Piperales and Nymphaeales display an intermediate condition just as they do in many other characteristics (cf. Burger 1977). Czaja (1978) concluded that the prevalence of pteridophyte-type starch grains in the primary monocots proved that they could not have arisen from the dicots--a view that is perfectly consistent with the framework developed here.

Chemistry

In a simple line graph Hegnauer (1962, p. 207) depicts the range of lignin structure in monocots (and Gnetopsida) as covering most of the range of structure found in mosses, pteridophytes and gymnosperms. The range of lignin structure found in dicots does not extend as far into the structural range of lower plants. Here again, the monocots possess the more widely shared character states (note 14).

Parks (in Radford et al. 1974, p. 295) has stated: "Some monocotyledonous families, considered morphologically advanced, have primitive phenolics by analogy to the dicotyledons; and some monocotyledonous families which show generally advanced phenolics have individual genera with phenolics like the primitive dicotyledons." These observations are consistent with the Monocot hypothesis; they are not what we would expect on the basis of the Ranalian hypothesis.

GENERAL EVOLUTIONARY TRENDS AND THE FOSSIL RECORD

The Ranalian hypothesis, beginning with larger complex woody plants bearing large flowers with many parts, cannot help but hypothesize reduction series in both vegetative and reproductive structures. Perhaps it is a consequence of the general acceptance of the Ranalian hypothesis that few recent botanists have addressed the question of progressive evolutionary advance. Fortunately, Stebbins has given this subject considerable thought and I believe that the Monocot hypothesis is consistent with his general views.

Stebbins (1974b) observed that evolutionary trends towards greater complexity of body structure and developmental pattern have often been essential for the entry of a lineage into a new adaptive zone and further adaptive radiation. The general framework proposed here is also consistent with Stebbins' contention (1974b, p. 290) that "the ability to exploit a particular adaptive zone at a higher level of efficiency and organization is rarely or never acquired by an evolutionary line that is occupying continuously the zone in question." The Monocot hypothesis clearly suggests that the earliest angiosperms, like the early mammals, were individually small and played a minor role in the ecology of the early Mesozoic. Nearly all the currently discussed theories of angiosperm origin paint a very different picture, attempting to derive woody angiosperms from previously dominant woody groups, but it is important to remember that in the Mesozoic many Cycadophytes were small slender-stemmed plants (Delevoryas and Hope 1976).

Stebbins (1970, p. 307) has also observed that the origin of most higher categories within angiosperms were associated with changes in reproductive efficiency rather than changes in vegetative morphology. Here again, the Monocot hypothesis agrees with a broad evolutionary generalization. The little monocot-like early angiosperms undoubtedly had evolved characteristic angiosperm reproductive traits <u>before</u> the vegetative innovations leading to the origin and successful diversification of the woody dicots (cf. Doyle 1977, p. 536). Just as the rapid diversification of Paleocene mammals came long after early mammals had differentiated from their reptilian precur-

Table 1.

THE TYPICAL MONOCOT	THE TYPICAL DICOT
Small simple plants with few orders of branching and little aerial axillary growth.	Larger complex plants with several orders of branching and much aerial axillary growth.
Vascular bundles usually scattered, vasculature made up of leaf traces in a loosely organized arrangement. Leaf gaps, branch gaps and nodes poorly defined.	Vascular bundles usually becoming arranged in a highly organized vascular cylinder with internal cambium. Leaf gaps, branch gaps and nodes clearly defined.
Secondary growth lacking or rarely developed and never with a radial system.	Secondary growth frequent, almost always with a well developed radial system.
Prophyll solitary and lateral.	Prophylls usually paired and opposite.
Leaves almost always alternate, not generally differentiated into petiole and lamina; leaf base usually merging without differentiation into the stem.	Leaves alternate, opposite or whorled, usually differentiated into petiole and lamina; leaf base often clearly distinct from the tissues of the stem.
Laminae usually simple and with few ranks of venation, reticulate tertiary veins rare, margins usually entire, trichomes generally rare.	Laminae simple or compound, usually with several clearly defined ranks of venation, tertiary venation usually reticulate, margins various, trichomes common.
Embryo with a single cotyledon and a lateral shoot apex; primary root fails to persist; unipolar growth.	Embryo with opposing paired cotyledons and central terminal shoot apex; primary root continues growth; bipolar growth.
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Many of the above characteristics are shared with primitive pteridophytes.	Many of the above characteristics are shared with gymnosperms.

THE MONOCOT FRAMEWORK

Primitive and widely shared characters.	Advanced, progressive and convergent.
Primitive pteridosperms, reduced cycadophytes or pteridophytes are ancestral; they are the appropriate group for comparisons.	Living gymnosperms are convergent, unrelated and inappropriate for comparisons.

THE RANALIAN FRAMEWORK

Derived by reduction and neoteny.	Primitive and widely shared characters.
Monocots and living pteridophytes are convergent and inappropriate for comparison.	Extinct gymnosperms are ancestral to angiosperms and are the appropriate out-group.

sors, the Mid-Cretaceous radiation of angiosperms probably came long after angiosperms had made the transition from their non-angiospermous predecessors.

Our framework may help explain some of the fossil data now coming to light. Sauropod and stegosaurian dinosaurs became prominent in conifer-dominated forests in the last half of the Jurassic; extinction of this assemblage was followed by the evolution of large low-browsing ornithischian dinosaurs and, a few million years later, the documented radiation of the angiosperms began (Bakker 1978). The Monocot hypothesis fits this scenario very nicely: the earliest angiosperms, small monocot-like plants, may have been the ecological resource responsible for the evolution and radiation of these low-browsing dinosaurs. This proliferation of early herbaceous angiosperms was then followed by the development of dicot shrubs, and it is their radiation which the fossil record documents so vividly (Doyle and Hickey 1976, Hickey and Doyle 1977).

The Monocot hypothesis is also in accord with the conjecture, based on an amino acid divergence rate in Cytochrome C similar to that of vertebrates, that the angiosperms became a distinct lineage about 240 million years ago (Wilson et al. 1977, p. 601). Such an origin, in the latter half of the Permian, predates the documented diversification of the dicots by over 100 million years. Our theory also helps explain why this 100 million-year period has not given us a better clue of angiosperm origin: the earliest angiosperms, like the early Ophioglossales, have left no clearly identifiable fossil record.

The Monocot hypothesis provides a more reasonable scenario for interpreting early monocot-like fossils such as <u>Sanmiguelia</u> with plicate parallel-veined leaves in the Triassic (Tidwell et al. 1977) and <u>Macrotorellia</u> of the Jurassic with a more typical monocot leaf (Krassilov 1977). Early Cretaceous fossils that may be more meaningful in the framework proposed here are <u>Plantaginopsis</u>, perhaps a primitive dicot (Berry 1911, see figure 2), and <u>Palmoidopteris</u> with a stem having both palm-like and fern-like features (Boureau 1954). More importantly, the Monocot hypothesis makes clear why we should not be surprised to find angiosperm-like pollen in the late Triassic (Cornet 1977). The Ranalian hypothesis does not explain why early angiosperm trees and shrubs should have persisted from the Triassic to the early Cretaceous and then, suddenly, diversified. What new adaptive shift explains the mid-Cretaceous diversification? It was the fall of the dinosaurs that preceded the explosive diversification of mammals in the Paleocene, but no such event, physical or biological, preceded angiosperm diversification. The Monocot hypothesis does suggest an adaptive breakthrough: the tubular cambium producing efficient secondary growth coupled with the development of deciduous reticulately veined leaves and tricolpate pollen, superimposed on previously acquired reproductive traits characteristic of all angiosperms. The unexpected diversity of floral structure found in the middle Cretaceous (Dilcher 1979, Basinger and Dilcher 1980) is also in keeping with our framework; the floral parts had evolved much earlier and there was a long period of time during which these various arrangements evolved.

PROBLEMS AND PREDICTIONS

Theories of angiosperm phylogeny have generally concentrated on the reproductive structures, and arguments regarding the nature and evolution of these structures have been central to virtually all discussions of angiosperm origin. In this paper I have deliberately restricted the arguments to vegetative morphology, both to simplify the theoretical framework developed here and because I believe we are in a better position to determine which vegetative structures are homologous and which are convergent. By attacking the problem of angiosperm origin from such a restricted viewpoint, and hopefully making a reasonably strong framework, I believe that we are forced to re-evaluate theories that were rejected primarily on account of highly speculative interpretations of the reproductive parts. Strong support for the Monocot hypothesis is found in shared similarities with primitive living pteridophytes. If these shared character states are indeed homologous, we must consider the premise that the precursors of angiosperms are not closely related to any other living seed-plant lineage. There is supporting data for this point of view. Nearly all gymnosperms (excepting the Gnetopsida) differ from angiosperms in having a free-nuclear stage in early embryonic development (Maheshwari 1950, p. 270, Wardlaw 1955) and their anatomy is quite different. The chemistry of gymnosperms is also quite different, again with the exception of the Gnetopsida (Hegnauer 1962, pp. 441-471). There are also fundamental differences in pollen grains; angiosperms lack the laminated intine of gymnosperms (Doyle 1978b) and gymnosperms lack the characteristic pollenkitt of angiosperm pollen (Hesse 1980). Add to this the uniqueness of the carpel, the simplicity of the ovule, the distinctive embryo sac and double fertilization, and we have ample evidence for the argument that angiosperms are very distantly related to other living gymnosperms, with the probable exception of the Gnetopsida (note 15).

If angiosperms differ so profoundly from other living seed plants and if the original angiosperms were small simple monocot-like plants, we are still left with the abominable mystery: from which lineage did they arise? The Monocot framework seems to imply three general possibilities: (1) a very primitive pteridosperm, (2) a paedomorphically reduced pteridosperm or cycadophyte, or (3) a eusporangiate pteridophyte. The notion that angiosperms evolved a dicotyledonous embryo and the tubular cambium independently of all other living seed plant lineages does not seem very parsimonious and is the primary reason, I believe, that monocots have been given so little consideration in discussions of angiosperm origin. If we go one step further and suggest that the earliest preangiosperms were pteridophytes, with the seed habit having also evolved independently in angiosperms (Campbell 1928, 1930 and earlier), the Monocot hypothesis loses its credibility entirely for most botanists. Why should this be so? We know that seeds have evolved independently and perhaps several times in the pteridosperms (Smith 1964). The gymnosperms, both living and fossil, are a grade and not a monophyletic assemblage. We cannot dismiss the possibility that the uniqueness of angiosperms may be a product of their separate origin from a pteridophytic stock. Proposing so many different seed plant lineages may seem unrealistic, but it was not so long ago that all living things seemed to fit comfortably into only two kingdoms; I believe that the seed plants have been similarly oversimplified in earlier taxonomies. But regardless of which lineage gave rise to angiosperms, is there a way in which we can test the Monocot hypothesis against the ruling Ranalian theory?

Testing the Hypothesis

It has become fashionable to demand that scientific activities produce and test what are called falsifiable hypotheses, and conversely, it has even been suggested that any activity that does not produce and test falsifiable hypotheses is not science. While phrased in the terminology of Karl Popper, philosopher of science, I believe that these attitudes stem from a misunderstanding of Popper's intention. Popper claimed that erecting falsifiable hypotheses distinguishes science from other human endeavors; he did not claim to restrict science to such a definition for he realized that science shares a great many procedures with other non-scientific activities. Moreover, though Popper never defined falsifiability, except in rather general terms (Ackermann 1976), he probably had examples from physics in mind. The simplicity of many physical systems allows the formulation of hypotheses that yield very precise predictions, and it is these predictions that are so readily falsifiable. The complexity of evolutionary biology rarely permits precise prediction; biological hypotheses may even appear to have been falsified when, in fact, extraneous conditions were the determining factors. Regarding questions of how modern lineages separated from each other over 100 million years ago, we are far beyond the realm of precise prediction or its consequence, the possibility of sharp refutation. But is there a way, short of digging up the appropriate fossils, which would allow us to support or refute the Monocot hypothesis?

The Monocot framework states that the woody Ranales were a later evolutionary development than early monocot-like angiosperms; the Ranalian framework states that monocots were the later-evolved group. How might we distinguish between these two views? Out-group comparisons seem to provide the only feasible test regarding living taxa. If monocots are a more ancient lineage than dicots they should share a greater number of traits with the appropriate out-group than dicots. This is based on the assumption that identical and shared innovations (whether by convergence or parallelism) are less common than identical and shared ancestral states. But what new data set might falsify one or the other hypothesis? Probably none, as neither is capable of sharply defined predictions. Nevertheless, large proteinaceous molecules whose amino acid sequences have been used as "evolutionary clocks," such as the cytochromes, should be helpful (cf. Boulter et al. 1972, Wilson et al. 1977). The Monocot hypothesis predicts that the greatest number of cytochrome similarities with an out-group will be found in the monocots, whereas the Ranalian hypothesis predicts that the woody Ranales will have the greatest number of similarities. If some monocots show a greater number of similarities with cycads or gnetopsids than do any dicots, the Monocot hypothesis and a reduced pteridosperm/cycadophyte origin would be supported. If some dicots, especially Ranalian taxa with monosulcate pollen, show stronger similarities with living gymnosperms, then the Ranalian hypothesis would be supported. Finally there is the intriguing possibility that the macromolecules of monocots will be concordant with embryo-form and other pteridophytic features of monocots, favoring a more direct descent from ancient eusporangiate pteridophytes.

A single ruling theory creates an environment inhospitable to the re-examination of basic assumptions, and it discourages the exploration of alternative hypotheses. The strongest form that many scientific questions can take is that of deciding between two competing theories (Brady 1979). Also, new data become much more meaningful in an arena of sharply contrasting hypotheses. It is to this end that these pages have been written, together with the honest conviction that the monocots are the direct descendants of the earliest angiosperms.

Notes

1. I will use the abbreviated terms monocots and dicots for the two major subdivisions of angiosperms. The monocots or monocotyledons have also been called the Liliatae and the dicots or dicotyledons have been called the Magnoliatae (Cronquist 1968, Takhtajan 1969). I will also be using the term Ranales in a traditional sense which is equivalent to the Annoniflorae of Thorne (1974), the Magnoliideae of Cronquist (1968) and the Magnolianae together with the Ranunculanae of Takhtajan (1969). My use of the term 'woody Ranales' is the same as Cronquist's (1968) Magnoliales with the Lactoridaceae removed, Takhtajan's (1969) Magnoliales and Laurales with the Chloranthaceae and Lactoridaceae removed, and Thorne's (1974) Annonales with the Piperineae, Aristolochineae, Chloranthaceae and Lactoridaceae removed.

2. No one should misconstrue these arguments to infer that living monocots should now be considered primitive. Rather, we must view the living taxa as products of long evolutionary lineages; orchids, grasses, and gingers are still among the most highly evolved flowering plants. However, where the Ranalian hypothesis had an implied sequence of Magnolia-like ancestors to Nymphaea-like ancestors to Alismataceae-like ancestors to Liliaceae-like ancestors to orchids or gingers, the Monocot hypothesis has a more direct sequence: pre-angiosperm to primitive monocot to Liliaceae-like ancestors to orchids or gingers. In the case of living dicots, the Monocot hypothesis envisages a sequence of pre-angiosperm to primitive monocot-like flowering plant to primitive dicot to a variety of lineages, most of which have become woody and some of which have undoubtedly reverted to the herbaceous form. In this regard it is interesting to note that while monocots are largely herbaceous, it is in the dicots where one finds the greatest numbers of annuals (Good 1956, p. 38, Tomlinson

1980). The annual habit is apparently a recent innovation; the earliest angiosperms were probably perennial herbs with an underground rootstock.

3. I cannot accept the suggestion that large arborescent monocots are primitive and small herbaceous monocots are the products of evolutionary reduction (Meeuse 1975, Moore and Uhl 1973, Zimmermann and Tomlinson 1972) for the same general reasons as stated under the first hypothetical trend in our framework. The Palmae, Pandanaceae and certain other large monocots may represent very ancient lineages and they do possess some primitive features, but many of their most distinctive traits are not widely shared. The limited success of palms, pandans and other large woody monocots is, I believe, a reflection of their having been unable to evolve an effective tubular cambium and a consequent limitation in the ability to produce new axillary growth and recover from breakage.

4. The rayless condition, often associated with the herbaceous habit and with anomalous secondary growth, has been considered to be a highly specialized condition (Barghoorn 1941). Such an interpretation may be nothing more than a logical consequence of the _a priori_ assumption that the primitive condition in angiosperms included woody growth from a tubular cambium capable of producing specialized radial tissue as well as axial tissue. The Monocot hypothesis requires that we consider two possibilities when confronted with the absence of rays: first, a primitive lack of secondary radial tissue, and second, evolutionary loss in a lineage that did possess rays.

5. Neubauer, working in Caprifoliaceae (1977a), Boraginaceae (1977b), Dipsacaceae and Valerianaceae (1978), has suggested that the multilacunar node may be the primitive condition in all four of these families.

6. Worsdell (1922, p. 658) has remarked, regarding the scattered vascular bundles in the peduncles of _Anemone japonica_ (Ranunculaceae), "if this plant has been derived by reduction from an aerophytic ancestor with an elongated woody stem containing a vascular cylinder with the bundles compactly grouped in one rank, one would think that the elongated peduncle of this species is just the kind of organ in which such a one-ranked vascular cylinder would have been retained, unless one admits the somewhat forced idea that the peduncle has been _redeveloped_ out of a more humble origin" (italics his).

7. The many vascular bundles in the cross-section of a typical modern monocot stem and the broadly sheathing leaf with many parallel veins are probably advanced states. The multiplicity of vascular bundles in stems of modern monocots may be an evolutionary solution for the problem of lateral transport and continued functioning after injury in stems lacking a vascular cylinder (Carlquist 1975, p. 76, Philipson et al. 1971, p. 119).

8. The positional relationship and form of the third leaf and stem apex in the embryo of the Nymphaeaceae is very similar to the form and positional relationship of the first leaf (cotyledon) and shoot apex in the tupical monocot embryo (see figure 3). It was this similarity which led Kudraishov (1964) to postulate that monocots had lost both cotyledons and that they were in fact acotyledonous. It was this same similarity that led Guttenberg and Müller-Schröder (1958) to interpret the embryo of Nymphaeaceae as being monocotyledonous and with a bilobed (dicot-like) development arising from the circumference of the embryo at the top of the hypocotyl.

It is possible that an encircling ring developed and partly enclosed the shoot apex in the embryo of early dicots; this encircling ring then became two-lobed (or more) and eventually gave rise to two (or more) cotyledons. Evidence that supports a _de novo_ origin for the cotyledons of dicots includes the fact that their vascular traces are derived from the hypocotyl and not from the stem as are the traces of other leaves, that their position on the stem is often independent of the phyllotaxy of all succeeding leaves, and that their form is often very different from the form of the succeeding leaves (Eames 1961, p. 364). The development of a thickened ring on the hypocotyl may also have aided the storage of food in the embryo, and this would be consistent with the fact that a great many cotyledons of dicots serve primarily as organs for food storage. In this scenario a leaf-like photosynthetic function may have developed later. Before leaving the subject we might remind ourselves that the dicots may be polyphyletic. Are the bilobed suctorial "cotyledons" of nymphaeaceous embryos and the cotyledons of all other dicots truly homologous, or did different lineages arrive at dicotyledony by different phylogenetic pathways?

9. If Wagner (1964) is correct, then primitive living ferns, such as the Ophioglossales, are the product of evolutionary reduction from larger progenitors with more elaborate stems and leaves. This can be viewed as a reduction bottleneck in the Monocot hypothesis not unlike the dicot-to-monocot reduction bottleneck postulated by the Ranalian hypothesis (Takhtajan 1969, p. 113 and included references) or the gymnosperm-to-xerophytic shrub reduction in the origin of angiosperms as suggested by Stebbins (1974a, p. 205) and by Doyle and Hickey (1976, pp. 183-198).

10. Though Bailey and Swamy (1949) claimed that the secondary phloem of _Austrobaileya scandens_ lacked companion cells, Srivastava (1970) did find primitive companion cells in this isolated woody ranalian taxon. However, primitive phloem is not confined to the magnolialian alliance. Parthasarathy (quoted in Esau 1969, p. 368) found that the roots of palms contained long sieve elements with oblique end-walls similar to those of _Microcycas_, _Cyathea_, _Pteridium_ and to some paleozoic seed ferns.

11. At this point, someone defending the Ranalian hypothesis might argue that we are dealing with convergent similarities and hidden circularity. A great majority of monocot seeds germinate beneath the soil surface (as do a great many primitive ferns) where their narrow terminal cotyledon is well adapted for upward growth through the soil. Most dicots germinate on the soil surface (as do some advanced ferns and most gymnosperms). It could be argued that subterranean germination is correlated with both a single terminal cotyledon and lateral origin of shoot and adventitious roots and consequently, similarities of pteridophyte and monocot embryos are due to convergence. This argument has been further buttressed with the fact that dicotyledonous embryos are widely shared among living seed plants (Eames 1961, p. 363). The Monocot hypothesis views these widely shared dicotyledonous embryos as the result of convergent evolution in independent seed plant lineages.

12. _Gunnera_ is a very isolated genus, not at all related to the genera of Haloragaceae with which it has been placed traditionally (cf. Orchard 1975, 1980). The genus possesses monocot-like vasculature (noted by Van Tiegham almost 100 years ago) which has generally been interpreted as a secondary development (Carlquist 1975, p. 76). In addition, _Gunnera_ possesses very simple flowers lacking a perianth and thought to be highly reduced. I interpret the simple flowers, the monocot-like anatomy, and Czaja's report of pteridophyte-type starch grains as the retention of primitive states in this very isolated herbaceous lineage. Such an interpretation is consistent with reports of _Gunnera_ pollen in the Upper Cretaceous (Jarzen and Norris 1975) and with its very unusual geographic range (Jarzen 1980). A symbiotic relationship with blue-green algae is a very advanced trait that has permitted this genus to develop some huge-leaved species capable of colonizing nitrogen-poor soils on montane landslides.

13. Czaja's primary monocots include the Alismataceae, Aponogetonaceae, Butomaceae, Cyclanthaceae (s. str.), Cyperaceae, Juncaceae, Juncaginaceae, Lemnaceae, Najadaceae, Pandanaceae, Potamogetonaceae, Restionaceae, Scheuchzeriaceae and Sparganiaceae. I consider it very significant that a majority of these families have floral construction which may be primitive among monocots (Burger 1977).

14. In an article on cyanogenic compounds, Hegnauer (1973) points out similarities between monocots and the woody ranales. But while there is no question of the chemical similarities between the two groups, Hegnauer's article does not give evidence for the derivation of monocots from woody ranales as is implied by the article's English abstract. The German abstract of the same article does not mention a derivation of monocots from dicots, nor is such a statement found in the carefully worded German discussion (p. 162).

15. The Gnetopsida differ from all other living gymnosperms in chemistry, chromosome structure, reproductive morphology, embryology and unusual growth forms. They resemble angiosperms in a number of these areas, and it is my belief that they may have evolved as a parallel lineage out of the same stock which gave rise to angiosperms.

16. Embryos and seedlings depicted in figure 3 come from a variety of sources, as follows: *Allium* after Hoffman (1933), *Barclaya* after Schneider (1978), *Botrychium* after Campbell (1921b), *Carex* after Shah (1962), *Isoetes* after LaMotte (1937), *Limnocharis* after Kaul (1978), *Nelumbo* after Lyon (1901), *Nymphaea* after Haines and Lye (1975), and *Ophioglossum* after Campbell (1911, p. 38).

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