

## ASPECTS OF THE EVOLUTION OF THE MONOCOTYLEDONS

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### SUMMARY

The available evidence, partly laid down in some recent reviews, suggests a morphological and anatomical heterogeneity of the major groups constituting the conventional Monocotyledonae (or Liliatae). A repeatedly signalled connection between certain ranalean forms and some liliate taxa is not unequivocal in that the magnolialean and nymphealean dicots differ from all monocotyledonous orders in some essential, exclusively “dicotyledonous” features whilst, on the other hand, exhibiting some rather convincing “monocotyledonoid” traits. The only interpretation reconcilable with these more or less contradictory deductions is that – unless all features shared by monocots and dicots are explained as the result of convergent evolution – the phylogenetic history of the Liliatae goes back to a pre-angiospermous group of ancestors (or to several such groups), and that this latter taxon (or a part of it) was also progenitorial to the ranalean dicots. This interpretation renders the “derivation” of monocots from (certain types of) dicots, or *vice versa*, inane: the common characteristics of both groups are conceivably inherited from a common, basic group which had not yet attained the level of evolutionary advancement of truly “angiospermous” plant forms. The heterogeneity of the monocots can similarly be explained by an early phylogenetic divergence of lineages sprung from a common stock of pro-angiosperms, which lineages evolved independently for a considerable length of time. Phytochemical evidence somewhat paradoxically suggests a homogeneity of the monocots, however. In spite of the accumulation of a large amount of relevant data, the information is insufficient to permit more definite conclusions apart from the indication of some “impossible”, direct relationships between certain groups. The floral morphology of most, if not of all, liliate taxa must be based on the antheid concept and this at least obviates all attempts to derive monocotyledonous groups directly from a magnolialean type of dicot.

### 1. INTRODUCTION

The Monocotyledonae (or “Liliatae” in some recent taxonomic texts) constitute an assembly which has for a long time been considered to be opposed to the dicots (“Magnoliatae”) and equal-ranked. The interest in the monocots has recently grown (compare, e.g., the symposium papers in *Quart. Rev. Biol.* Vol. 48, nos 2 & 3, June/Sept. 1973), so that an appreciable quantity of information has been surveyed, but one fundamental problem, viz., the phylogenetic origin of the group, remained unsettled.

There are, broadly speaking, three possibilities, namely:

- (a) monocots are derived from a single group of dicotyledonoid progenitors;
- (b) monocots (or promonocots) are ancestral to some or to all of the dicots;
- and
- (c) monocots and dicots have had an independent origin from pre-angiospermous gymnosperms.

Most contemporary phanerogamists would probably accept possibility (a), but their arguments, if not entirely inadequate, are at least not very convincing. It is true that certain magnoliata taxa exhibit characteristics reminiscent of monocotyledonous taxa (such as monocotily, "scattered" vascular strands in the primary stem, trimery of floral parts, monosulcate pollen grains, etc.), but it remains to be seen in how far such a correspondence is contributable to a coincidence (such as convergent evolution) or explicable as being a retained "gymnospermous" (cycadeoid, gnetoid, etc.) character. Monocotily in dicots (as found in, e.g., some Piperales and Ranunculales) is said to be a reduction of one of two "*lateral*" cotyledons, whereas the single cotyledon of the Liliatae originates embryologically as a factually terminal organ as far as can be ascertained. Monosulcate palynomorphs are known from recent and fossil cycadophytinuous gymnosperms, so that conceivably the monosulcate pollen types of monocots and those of some ranalean groups of dicots originated independently. According to WALKER (1974a), the dicotyledonous pollen grains are all basically tectate and originated from progenitorial gymnospermous types by the differentiation of columellae and a tectum in the ectexine. The outer layer of the pollen wall in liliata groups does not exhibit such a texture (at least not in groups considered to be primitive at one time or another), and it follows that when the first monocotyledons appeared, their pollen grains could not possibly have originated from a *tectate* type of grain but only from that of some earlier plant form which was most likely to be still pre-angiospermous. According to DOYLE (1973), the Monocotyledonae (and the Nymphaeales) may be relicts of an *early* radiation of herbaceous and, in part, even aquatic protangiosperms. The present author believes that such an origin may be accepted for some but not necessarily all liliata orders; in any event such herbaceous forms are not likely to be descendants of *woody* magnoliids.

Possibility (b) must, likewise, be queried, because one simply cannot visualise the derivation of the more primitive dicots, almost without exception exhibiting at least a vestigial form of secondary growth in the stem (even in therophytic herbs!), from monocots in which both the stem anatomy and the growth in girth of the stem of arborescent forms are fundamentally different. The arguments mentioned under (a) can be reversed: if monocots cannot be derived from dicots, the origin of the latter from monocots is not very likely either.

Possibility (c) becomes acceptable in the light of recent studies which reveal a rather large number of special "monocotyledonous" traits; compare, e.g., TOMLINSON (1962, 1970, 1972), BEHNKE (1972, 1973), DOYLE (1973, MOORE & UHL (1973), STONE (1972), ZIMMERMANN & TOMLINSON (1972). This idea of a more or less independent evolution of the Liliatae still requires the reconstruction of the most primitive group of monocotyledonous (or protomonocotyledonous) plants, or, conceivably, of several such groups, allowing for a more or less pleiophyletic origin of the liliata assembly.

## 2. SPECULATIONS CONCERNING THE RELATION MAGNOLIATAE – LILIATAE

The current views of most contemporary system-makers (compare TAKHTAJAN 1969, EHRENDORFER 1971, DAHLGREN et al. 1974, etc.) suggest an origin of all Angiosperms inclusive of the monocotyledons from some ranalean stock, and a derivation of the Liliatae from either some ranunculalean archetype (through a “basic” group represented by the early Alismatales or Liliales) or from a nymphaealean type of plant (through a more or less alismatid “connecting” group). These assumptions imply the incidence of a phaneranthous (and even holanthocormoidal) flower type as the original one in the progenitorial group of all Flowering Plants (again including the monocots), and the same holds for a supposedly direct origin of palms from magnoliid ancestors suggested by CORNER (1966). According to the present author (see MEEUSE 1975a and cited papers), true phaneranthy is a derived condition originated as the result of co-evolution of anthophilous insects and early zoophilous flower types; in other words, the magnolialean functional flower is not the most primitive. The latter also represents a holanthocormoid flower type, whereas the functional blossoms of most (if not of *all*) monocots represent anthoids (MEEUSE 1975b). As explained in several contexts (MEEUSE 1975a, 1975b), this precludes the direct derivation of all angiospermous taxa with anthoidal blossoms from magnolioid or nymphaeoid holanthocormoids, but there is another very negative indication, provided by the androecial morphology, and involving the possible progenitorial status of forms close to Magnoliaceae and/or Nymphaeaceae. The polliniferous organs of the large majority (if not of all) monocots are of a meromonandrial nature and provided with a filament (compare, e.g., STONE 1969, MOORE & UHL 1973; the latter workers accept an advanced condition for the “stamens with expanded filaments” of, e.g., Zingiberales and, by inference, consider the thin and terete filament type to be basic in monocotyledons). The anther-bearing floral parts of the water lilies and magnolias are modified and somewhat specialised holomonandra (compare MEEUSE 1974a, 1974b, 1975b), which renders a direct derivation of the meromonandrial androecium members of the monocots from such advanced, ranalean holomonandra altogether unacceptable. The perianth members of all or at least nearly all Liliatae are also meromonandrial elements of androecial derivation, whereas those of the two ranalean groups under discussion represent “sterilised” holomonandra. Phylogenetic connections between the two kinds of androecia and petals can only be indirect: the common archetype of the androecial elements (*cum annexis*) of all groups concerned must be a primitive holomonandron which may have occurred in a presumably still gymnospermous taxon from which, perhaps, both monocotyledonous and dicotyledonous forms descended.

A comparative morphological analysis, following HOLTUM (1955), TOMLINSON (1962, 1970, 1973), STONE (1969, 1972); MOORE & UHL (1973), and others, yields the following list of features which, by consensus of opinion, constitute the most primitive ones in all major monocotyledonous orders:

- *growth habit*: rather large plants with often prostrate or ascending stems which are aerial and almost invariably unbranched, or developed as a system of subterraneous, rhizomatous and simple or variously branched organs; erect stems not very tall;
- *stem structure*: stems devoid of a vascular cambium of the coniferoid-dicotyledonous type, if well-developed (in caulescent taxa) originating from a broad apical growing zone; vascular bundles (in primary stem) arranged in a pattern erroneously called atactostelic (“scattered”); secondary growth of a unique type (compare TOMLINSON & ZIMMERMANN 1969, ZIMMERMANN & TOMLINSON 1972);
- *leaves*: normally single-bladed with a sheathing base, a basal intercalary meristem, and numerous leaf-trace bundles; venation (arcuately) parallel, more rarely (or only postgenitally becoming) pinnate or palmate; nature of “unifacial” leaves undecided, but according to RAVOLOLOMANIRAKA (1972) all monocotyledonous leaves originate in the same way by the action of three growing points and subsequent differential growth (which is denied by KAPLAN (1975), however, who interprets this leaf type as simple and single, and only showing a precocious development of its phyllodic blade);
- *florescences*: complex and polymerous; solitary flowers only in manifestly advanced taxa;
- *functional reproductive units (conventional flowers)*: anthoidal (if not consistently so, at least in the large majority of the families), perianth members not showing a clear difference in colour, shape, or texture as a rule, usually lacking in the female units of diclinous taxa; a single floral prophyll (or none); androecium meromonandrial, *i.e.*, anthers borne on filaments which are usually terete, rarely (secondarily!) expanded and in this case often conspicuous (sema-phyllous); pollen (in all groups?) primarily monosulcate;
- *seed characters*: endosperm abundant; embryo small with one cotyledon; germination hypogeal.

The contrasts with magnoliolate forms, more particularly with taxa which bear holanthocormous reproductive units, are striking. However, there are also some characteristics which are shared by some monocotyledonous forms and some dicotyledonous groups, *viz.*;

- *palynological features*: monosulcate grains (see above);
- *ultrastructural features*: small plastid-like bodies found in the sieve-tubes can be of three types, all of which occur among the dicots and only one (the P-type) in monocots; the latter type is restricted in its occurrence among dicots to some ranalean taxa (compare BEHNKE 1972);
- *phytochemical data*: recently HEGNAUER (1973) pointed out that, as far as can be ascertained, some rather singular (cyanogenetic) compounds are synthesised by means of one of three alternative pathways, with tyrosin as the precursor in monocots and in most of the Magnoliidae (=Magnolianae and Ranunculanae *sensu* Takhtajan = Polycarpicae + Papaveraceae), whereas the other two mechanisms for the biosynthesis of cyanogenic substances are only found scattered among dicotyledonous groups.

HEGNAUER (pers. comm.) believes that the wide-spread occurrence of the substances under discussion among the monocots strongly pleads in favour of the homogeneity of the Liliatae.

It is this controversial evidence which renders any conclusion premature. As stated before, the explanation of the correspondence of characters between a comparatively small and decidedly archaic group of dicots and some of the liliate taxa may rest upon the retention of characteristics from a common progenitorial group of the dicots and monocots in question, but is perhaps (at least partly) attributable to convergent evolution. The unmistakable and cogent intranscendencies between *all* Magnoliatae and *all* Liliatae, such as the lack of the "dicotyledonous" type of secondary growth and tectate pollen grains in the latter, and the differences in development and organisation of the vegetative parts (see, e.g., TOMLINSON 1970, 1973; ZIMMERMANN & TOMLINSON 1972; MOORE & UHL 1973) may outweigh the other arguments. It is noteworthy that all groups of monocots at one time or other considered to be "basic" (Pandanales, Arecales, Liliales, Alismatales) exhibit the singular vegetative and anatomical features of monocotyledonous plants and are in no way "transitional" between monocots and dicots. The Dioscoreaceae have sometimes been reported to show certain "dicotyledonous" traits, but this morphologically rather singular family did not suggest itself as a "link" between the magnoliatae and the liliatae assemblies either. However, the unusual features are not necessarily derived and may reflect an ancient monocotyledonous habit form.

The monocotyledonous floral region differs from that of all but some ranalean dicotyledonous plants in that often trimery prevails, but more significant is that, as pointed out before, most probably all liliate FRUs are anthoidal whereas in the more typical and supposedly basic magnolialean and nymphaealean taxa the reproductive unit represents a whole modified anthocorm. Some of the magnoliids have holomonandrial androecia, whereas all liliate groups apparently have meromonandrial stamens as we have seen. From the rather confusing results of the overall assessment only one conclusion can be safely drawn: some magnoliids are more archaic than the monocotyledons in several respects and exhibit a number of traits and specialisations not encountered in any liliate form (secondary cambial growth; floral polymery; holomonandra; incipiently to fully tectate pollen grains; large embryos; etc.). If one would have to select a "dicotyledonous" (i.e., magnoliid) group as a progenitor of monocotyledonous groups, one would have to pick an archaic type of plant rather than an advanced one, but such reputedly more ancient forms are always "typical" dicots in their growth habit, mode of branching, general organisation, stem anatomy, leaf venation, mode of development of vegetative parts at the shoot apex, etc. The most characteristic features of the monocots which, I believe, are also "primitive" (ancient), are often almost diametrically opposed to those of the magnoliatae plant form: the Liliatae are not or hardly arborescent, do not branch profusely by means of axillary buds produced in the axis of leaves (and tend to be sympodial rather than monopodial) and some groups are often monocaual (and in this case the stems do not have well-differentiated nodes: palms); stem branch-

ing is normally pseudo-dichotomous (or even dichotomous); the apical meristem has a singular organisation and develops a totally different vascular anatomy; the root system is also different; the leaves are stem-sheathing, grow for quite some time by means of a basal, intercalary meristem, are normally not neatly shed, and exhibit a parallel nervation; the seedling develops only one (factually terminal) organ supposed to be the cotyledon; etc. The possible connections with dicots appear to be very remote.

### 3. SECONDARY GROWTH IN MONO- AND IN DICOTYLEDONOUS STEMS

As pointed out by TOMLINSON (1970, 1973), the differences in development and structure of the stems in liliate and in magnoliata forms are fundamental, but in the past not always properly understood. One rather common error was the interpretation of "monocotyledonous" features as modified and derived versions of a "dicotyledonous" condition, so much so that the occurrence of a "vestigial cambium" in the vascular bundles of many monocots was accepted as evidence of the derived nature of their anatomical and other structural (morphological) characteristics: the single cotyledon (regarded as one of a pair, the other one having become reduced, or as a fusion of two, i.e., as the homologue of one or of both of the cotyledons normally found in dicots), the single floral prophyll (by some workers supposed to be of dual origin because there are usually two in dicots), the "loss" of secondary growth, etc.

The secondary growth of a relatively small number of liliata taxa is clearly different from that of coniferopsid gymnosperms and of most dicots in several respects:

- (1) in the initiation of the "nominal" type as found in gymnosperms and woody dicotyledonous forms, all young vascular tissue of the stem is involved and cambium is formed between the protoxylem and protophloem in a zone which includes at least remnants of procambial tissue or is developed as a procambial "ring" as seen in cross section,
- (2) the cambium forms xylem centripetally and phloem centrifugally, and
- (3) the secondary body formed is rather compact (forms a wood cylinder) in most if not all of the more primitive Magnoliatae, whereas in the monocotyledons with secondary growth the cambial zone
  - a) develops towards the periphery of the primary vascular skeleton,
  - b) forms tissues only centripetally, and
  - c) is developed as longitudinal, anastomosing strands embedded in a mass of ground parenchyma.

ZIMMERMANN & TOMLINSON (1972) explain the vascular system of the monocotyledonous ones with secondary growth as a double one, an extensive inner one which is "open-ended" distally in respect of the apical meristem, and an outer one which is "open-ended" at the base and the periphery. The outer complex is said to be frequently represented by cortical bundles of sclerenchyma fibres but sometimes appears as a more fully developed vascular skeleton, and occasionally as secondary vascular tissue. The dicotyledons are supposed to

have only an outer system, and it is suggested that this has a phylogenetic significance. It certainly points to a fundamental intranscendancy between the two groups of Flowering Plants, but in the present author's opinion the peripheral system of the monocots does not resemble the supposedly single vascular complex of the dicotyledonous stem sufficiently to permit a homologisation: the differences may be even greater. It would be highly interesting to study the ontogeny of the vascular system of the nymphaeid forms with a so-called "monocotyledonous" type of stem anatomy in the light of the conclusions drawn by ZIMMERMANN & TOMLINSON.

The secondary growth found in some monocotyledonous taxa is said to be a novel development by TOMLINSON (1970), but, in my opinion, this is by no means a forgone conclusion. The somewhat "scattered" occurrence of secondary growth among the monocots is not necessarily an indication of a novel origin: ancient features may also occur scatteringly in diverse groups. As pointed out before (MEEUSE 1961) the peculiar secondary xylem elements of the monocots with secondary growth (fibre tracheids with a kind of bordered pitting) are unique among the liliate groups and not closely matched by xylem cells of any known dicotyledonous plant, but they are strongly reminiscent of gymnospermous fibre tracheids. They are not very efficient as water-conducting elements and not as mechanical tissue either, so that there is no reason to assume on functional grounds that they are of recent phylogenetic origin. The primary xylem elements of the monocots (thin-walled tracheids and vessels) are much more suited for a water-conducting function, so that the structure of the secondary xylem tracheids can hardly be adaptive but rather reflects a survived, ancient condition.

One must bear in mind, in this context, that plant anatomists are wont to consider the nominal, dicotyledonous (and even the original angiospermous) type of secondary growth as similar to, and probably derived from, some gymnospermous prototype in which only a single vascular system with associated cambium develops and a single solid body of wood is formed centripetally. This type of secondary growth is probably universal among the coniferopsid gymnosperms, but in lower cycadophytinous forms (seed ferns) there are other types of stem structure and even more advanced forms (including the Gnetatae) appear to have forms of secondary growth supposed to be "anomalous". The "nominal" type is obviously used as the basis for comparison, but the question arises whether so-called "anomalous" types of secondary growth in primitive dicots (compare Piperales) are indeed derived from the nominal type. What may appear to be "anomalous" among dicots may well be "ancient" in the sense that most dicots *advanced* towards the "nominal" type (and that the "anomalous" modes of secondary growth are not necessarily secondary modifications of the "nominal" one). It is not even certain whether the "nominal" type of the dicots did not sometimes (or did always?) develop out of some more or less clearly "anomalous" prototype. This problem is closely connected with the probable growth habit of the early angiosperms: lofty trees and therophytes were rare or absent, but various other habit forms must have existed (MEEUSE 1967). The

habit form of the *early* monocots is still a matter of conjecture; as in the case of the early dicots and the early form of secondary growth the ancient type may nowadays be of rather rare occurrence (compare HOLTUM 1955, STONE 1972, MOORE & UHL 1973 for some viewpoints). However, an evaluation must take the secondary growth into account, because all gymnosperms exhibit in principle some form of secondary growth and any group progenitorial to monocotyledonous is not likely to have been exceptional in this respect. The secondary growth exhibited by such premonocots may have soon become obsolete, but has not necessarily disappeared altogether. As intimated before, the more or less "anomalous" (but conceivably archaic) forms of secondary increase in stem girth found in gnetate forms and in some magnoliata groups (Piperales, some Polycarpicae such as Aristolochiaceae, etc.); particularly the early development, should be re-examined in the light of the dual system theory propounded by ZIMMERMANN & TOMLINSON, 1972. Such data may elucidate some points concerning the relation monocots/dicots and also throw some light on the phylogenetic aspects of the special type of secondary growth in monocotyledons.

For the time being the present author accepts the antiquity of the process of secondary growth in girth in monocots. In addition to the above-mentioned anatomical and functional arguments, there is some additional evidence: CROWSON (1970, p. 130) reports that of the group of the phytophagous criorcerinid beetles, frequently associated with liliid taxa, the most primitive representative with known host plant, *Pseudocrioceris*, lives on *Dracaena*, which may be taken as an indication of the relative antiquity of this plant genus (and its relatives such as *Cordyline*) in respect of other liliid taxa. *Dracaena* and *Cordyline* being exceptional in that they exhibit secondary cambial growth, this structural feature is, in the light of the pointer from the host-parasite relationship, more likely to be a retained ancient characteristic than a recent development. It follows that most liliid (or all?) monocotyledonous orders soon "lost" the capacity to produce secondary tissues during their early evolution.

#### 4. THE MONOCOTYLEDONOUS FLORAL "PROPHYLL"

As pointed out by TOMLINSON (1970), who also surveyed the literature on the subject, the so-called "prophyll" of the monocotyledonous "flower" was mostly, but quite erroneously, interpreted as a fusion product of two elements supposed to be morphologically equivalent to the two "prophylls" of the dicotyledonous floral region. Also citing BLASER (1944), Tomlinson concludes that the "prophyll" is "only a leaf" and not a separate morphological category. I would restrict this up to a point: such a prophyll is not usually the full homologue of a trophophyll; and I also have misgivings about the recognition of "prophylls" on vegetative stems, especially when vegetative and reproductive zones of the same plant (or plant family) are compared as HAINES (1966) does in the case of the Cyperaceae. It is quite clear that, among all *recent* monocots at least, never more than one floral prophyll is present (as against two in dicots) *by definition*.



I may add that as far as the supposed identity of "the single (median) monocotyledonous prophyll" with the "paired (transverse) dicotyledonous prophylls" is concerned, the rejection of the silent "classical" tenet of the ubiquity of only one type of "flower" among all Magnoliophyta and its replacement by at least two concepts (viz., holanthocormoidal structures and anthoids, see MEEUSE 1975b) complicate the matter appreciably. A "prophyll" associated with a holanthocormous "flower" cannot possibly be homologous with a "prophyll" associated with an anthoid. The indication "prophyll" thus becomes merely a term of convenience. The monocotyledonous prophyll has an important function in that it ensheathes the young floral buds and a continuity of evolutionary processes suggests a continuity of this function, which means that the monocotyledonous prophylls are probably often homologous organs.

Quite apart from the morphological identity between liliate and magnoliolate floral prophylls, one may still consider a possible phylogenetic dual origin versus a single nature of the monocotyledonous prophyll. TOMLINSON (1970) is quite convinced of the presence of only a single (and mostly adaxial) organ of this kind, but one may also consider the situation in Cyperaceae. In a recent publication the present author has re-considered the so-called florets of the sedge family in the light of the anthoid concept (MEEUSE 1975c). The more primitive mapanioid anthoid has two opposite basal, phyllome-like (bracteoid) organs whereas the more distally situated appendages of the anthoid are helically inserted (or appear di- or tristichously whorled). Any of the basal elements may become a "prophyll", but the *transverse* position of the paired bracteoids is not in agreement with the *adaxial* position of the (often two-keeled) single prophyll as found in most monocotyledonous taxa (including some Cyperaceae!). Other explanations are feasible, but even if a possible dual nature of the liliate prophyll is accepted, there is no reason to assume that there is a homology relation with the prophylls of dicotyledonous anthoids. In other words, irrespective of its single or dual nature, the singular adaxial prophyll of many monocotyledonous taxa emphasises rather than mitigates the contrast between mono- and dicotyledonous forms.

##### 5. GENERAL FLORAL MORPHOLOGY OF THE LILIATAE

The floral morphology of the monocotyledons shows the following characteristics (for details, criteria, and arguments, compare MEEUSE 1974a, 1974b, 1975a, 1975b):

- (a) The functional reproductive units (FRUs), almost always corresponding with the conventional "flowers" or "florets", are anthoidal.
- (b) The androecium is apparently always meromonandrial, each ancient holomonandron having given rise to a perianth member (tepal) and normally only a single meromonandrial stamen with, in primary groups at least, a usually well-developed filament (exceptions: polyandry in some Alismatidae, Velloziaceae, Gramineae-Bambusoideae, and a few arecaceous genera).
- (c) The FRUs (anthoids) are usually cyclic and of a radial symmetry in some

basic groups, but in other ones (Commelinidae) the androecium, although seemingly whorled, may actually well be unilateral (and “belong to different whorls”).

(d) There is only a single “prophyll” as we have seen.

(e) Of the special aspects the sex distribution is noteworthy: some groups are primarily diclinous and anemophilous (Arecidae = Spadiciflorae, with the secondarily zoophilous – but still diclinous – Araceae as a notable exception), and other ones predominantly monoclinal and normally zoophilous (Liliidae, Zingiberales), whereas in some groups both conditions have obtained side by side for a considerable length of time (Commelinales: see Restionaceae, Juncaceae, Cyperaceae, Poaceae, Commelinaceae; Alismatidae: see Alismataceae, Potamogetonaceae, etc.).

The traditional concept of the “basically pentacyclic and trimerous”, monocotyledonous “flower” is in so far misleading that traditionally the archetype is supposed to have been ambisexual and trimerous, and to have possessed five cyclic whorls (which are conventionally also visualised as alternating in the sequence: outer tepals → inner tepals → outer whorl of stamens → inner whorl of stamens → carpels). This starting point has ordained that diclinous taxa, more particularly those with supposedly “reduced” (e.g., “naked” female) FRUs, were supposed to be “derived” (Pandanales, etc.). The interpretation of the Cyperaceae caused some morphological and semantic difficulties which resulted in a controversy regarding the “euanthial” or “pseudanthial” nature of the FRU (KERN 1962, as opposed to, e.g., HAINES 1966; details in MEEUSE 1975c). Such developments render the current interpretation of the liliate FRU rather suspect.

An alternative approach, by assuming an anthoidal architecture of the monocotyledonous FRU (derived from a part of an anthocormoid), avoids several pitfalls. If we start from a semophyletic stage in which the meromonandrial organs had already originated but in which the anthotaxis of the gonoclads and of the monogona was helical to somewhat irregular but not cyclic, a number of divergent trends can be visualised.

As pointed out by TOMLINSON (1970), when he discussed the prophyll, morphogenesis plays an important role. In contrast to the Dicotyledonae, the liliate forms are almost always characterised by the presence of sheath- or glume-like bracteoid organs which surround florets or spikelets, or sometimes (as in palms, etc.) even completely encase a whole inflorescence. Such bracteoid organs exert pressure on the young, developing FRUs and the direction of the pressure is often radial (because the young parts are squeezed between the bracteoid and other parts when the growing reproductive structure expands). Phylogenetically this may have led to a depauperisation or even total reduction of floral parts in (mostly) the median and adaxial zones. The almost magic number of three parts to a “whorl” is not infrequently erroneous, because sometimes the three parts supposed to form a “whorl” are derived from two superimposed whorls whose adaxial parts (1 + 2) are reduced. In some cases a bilateral symmetry occurs

(dimery, as in some Cyperaceae and Poaceae), but it does not follow that this dimery always developed out of cyclic trimery.

As may be expected, monocotyledonous orders in which the ensheathing bracteoids (prophylls) are not large and firm but small or membranous, the FRU is often regularly tri- or tetramerous (Liliales, Alismatales). However, even in such "regular", actinomorphic FRUs the alternation is different from that suggested by most of the published floral diagrams: three (or four) tepal-stamen units alternate with a second whorl of such units. Other special trends not explicable by the conventional rules are: the retention of the original macroblasty of the anthoid (rare: some Cyperaceae) as against the manifestly secondary, but now wide-spread, brachyblasty, the retention of an acyclic anthotaxis in a few taxa (some Arecidae, an occasional cyperaceous taxon such as *Scirpodendron*), retention of a primary polyandry in each tepal-stamen unit as against the oligomerisation of the meromonandra to a single one, and the oligomerisation of the monogona (usually not more than 3 are retained, but only one in Cyperaceae and ? Gramineae).

The question may arise whether polyandry in some graminoid genera, in Velloziaceae, and in some Alismatidae is not due to secondary multiplication. The present author rejects the idea of a "splitting" of primordia (chorisis) and assumes that the incidence of polyandry is a primitive feature and almost always of primary origin. Developmental and anatomical studies (mainly in Alismataceae) do not adduce cogent arguments in favour of a secondary multiplication (compare MEEUSE 1974b and a forthcoming paper on anthotaxis for details).

The gynoecial morphology is in so far adaptive that in the primarily anemophilous groups (Palms, Cyperaceae, most Pandales/Typhales, etc.) the number of ovules in each monogynous is low (they are frequently uniovulate), whereas in the primarily and secondarily zoophilous groups that number may be much higher. This is a matter of efficiency, because an anemophilous FRU is not likely to catch more than a few specific pollen grains, so that the formation of more ovules means a waste of biomass and selective pressure would favour monospermy of the monogyna; zoophilous FRUs may receive an appreciable number of grains by a single visit from a pollinator, so that, even if the frequency of such visits may be low, enough seed is always produced and selective pressure would favour polyspermy. The most interesting cases are provided by more or less closely related taxa with a different pollination syndrome: *Freycinetia* is the only zoophilous representative of the Pandanales-Typhales assembly and is the only one with pluriovulate gynoecia; among the Liliidae the Dioscoreaceae (with pauciovulate FRUs) must be at least partly anemophilous (aphananthly and dicliny prevail) whereas most other groups are zoophilous (with pluri-ovulate gynoecia). The question arises which condition is the more primitive. In the case of *Freycinetia* we can safely assume that it is the most advanced genus of its family, so that the other genera are likely to have a generally more primitive morphology including more or less clearly pauciovulate gynoecia. Dioscoreaceae exhibit several primitive features (see, e.g., HUBER

1969) and it is by no means certain that this family is highly advanced. The very high number of ovules in the Orchidaceae is so unusual that one can hardly maintain that also in this case the rule of thumb of a general oligomerisation of equivalent morphological entities in an evolutionary sequence holds true: there is not a single cogent indication of the presence of hundreds or even thousands of ovules per monogynon in cycadophytic gymnosperms. It is much more likely that the number of ovules was rather appreciable in the cupules (monogyna) of angiosperm progenitors but soon became lower in primary anemophilous taxa and remained fairly high in the zoophilous ones to become very much higher (by intercalation) in some specialised zoophilous forms. The number of ovules is, in any event, not a reliable yardstick of the relative degree of evolutionary progression of related taxa, and pauciovuly is by no means always indicative of an advanced gynoecial morphology (let alone, of a derived status of the corresponding taxon).

#### 6. SPECULATIONS CONCERNING THE PHYLOGENY OF THE LILIATAE

Two conclusions clearly emanate from the above-mentioned considerations, viz., (a) there is a fundamental difference in many essential features between the recent dicots and the recent monocots, and (b) the greatest affinities of at least some liliate groups are with dicots belonging to the Magnoliidae and Ranunculidae (= Polycarpicae). One has to face making a decision which argument or evidence must prevail, i.e., whether the differences between the two large assemblies under discussion outweigh the resemblances, or if the shared features are indicative of a strong and direct connection between at least some liliate taxa and magnoliid-ranunculid forms. In view of the possible origin of the two main groups from a *very ancient* type of progenitor and of the possible incidence of convergences of characters, the resemblances most probably do not carry so much weight in phylogenetic speculations. As an example, cyanogenic compounds are not only scattered among the principal groups of the Magnoliophyta, but their occurrence is manifestly the result of adaptive evolution (repellence of phytophagous animals) and may, therefore, have originated by convergence. Even though HEGNAUER's above-mentioned survey appears to be biochemically well-founded, his deductions are not absolutely water-tight: the precursor (tyrosin) of the cyanogenic compounds of the taxiphyllin/dhurrinrichoglinin group is supposed to be independently synthesised in the plant body (and not derived from phenyl alanine by enzymatic p-hydroxylation), but has the absence of phenyl alanine-p.-hydroxylase in both monocots and (magnoliid/ranunculid) dicots convincingly been demonstrated? Even if this enzyme were consistently lacking, the direct biosynthesis of the key compound (tyrosin) may, at least potentially, have become developed in some gymnospermous group progenitorial to (some) monocots and (some) dicots, and the further synthesis to a cyanogenic glycoside may have originated early or later in such groups. The occurrence of one of these compounds (viz., taxiphyllin) in the isolated, group of the Taxales is clearly indicative of an independent origin of a synthetic mechanism

in *coniferophytin* (*Taxus*) and in *cycadophytin* seed plants. This certainly does not preclude the possible independent origin of the synthetic pathway of the production of cyanogenetic compounds of this kind in two groups of Angiosperms. Considering that the compound trichoglinin (isolated from *Triglochin*) is chemically rather similar to compounds isolated from Ranunculaceae and other herbaceous Polycarpicae, and cyanogenetic compounds are also found in woody ranaleans, a phytochemical relation between the Magnoliidae and Ranunculidae on the one hand, and Poales, Arales, Juncales, Juncaginaceae and presumably other liliate groups on the other, a relation between *ranalean* dicots and some groups of monocots (also suggested by the pollen morphology of some magnoliid forms etc., see above) is at least a possibility. It does not follow that monocots are *derived* from a group of dicots as we have seen, but they may have had common (gymnospermous) progenitors.

The floral architecture and the morphology of the genitalia do not prove any conclusive evidence of a derivation of monocots from dicots either; most probably all monocots have anthoidal FRUs with meromomandrial perianth members and stamens, which precludes any progenitorial archetype of magnolialean affinity (with holanthocormous FRUs and holomonandrial androecial members).

The fossil evidence (DOYLE 1973) may at first sight be suggestive of a rather late appearance of monocotyledonous forms, but the palynological record is very deceptive in that atectate monosulcate palynomorphs of Lower Cretaceous age may represent gymnospermous pollen but may just as well be of some early monocotyledonous type of plant. Fossil leaves and pollen grains referred to some unknown liliate taxon are said to be of possibly Aptian age (DOYLE), and this co-existence of early dicots and early monocots in rocks not very much younger than the strata in which most probably the earliest remnants of true angiosperms have been found is more compatible with an early diversification. As far as the leaf structure is concerned, the peltate-cordate types of liliate leaves may be more ancient than the ligulate ones, and this may render a clear distinction of the early monocotyledonous (protoliliate) and protodicotyledonous leaf types rather difficult. There is a possibility that one may be able to distinguish the structural features. A good many papers dealing with the so-called C-4 metabolism have recently accumulated (biochemical details and references to anatomical papers in LATZKO & KELLY 1974; anatomical details and references in CAROLIN et al. 1973). The interesting part is that apparently this form of photosynthetic activity is located in the chloroplasts of the monocotyledonous leaf bundle sheaths. The foliar vascular bundles of magnoliolate forms apparently do not have such a sheath, so that this combined biochemical and anatomical feature may well be a means to define monocotyledonous leaves and to identify fossil leaves with structure as (early) monocotyledonous. As a taxonomic feature it emphasises the difference between recent monocots and dicots.

## 7. DISCUSSION

Not only is there a manifest intranscendency between monocots and dicots in

most of their essential characteristics, but also an appreciable heterogeneity between the liliate groups themselves. In the light of recently gathered information the relationships of the Cyperaceae, Poaceae, and Juncaceae with most other monocotyledonous groups are remote according to METCALFE 1971, the anatomical differences between the glumiflorous taxa on the one hand, and of, e.g., the Liliales being considerable, so much so that METCALFE stated: "*it appears rather improbable that the sedges, grasses and rushes as we know them today have actually been evolved from the modern Liliaceae. It seems perhaps more likely that they are derived from a proto-monocotyledonous stock without having necessarily passed through a morphological phase that would have justified classifying any of their ancestors as members of the Liliaceae*". Rather similar views have been expressed by TOMLINSON (1962) concerning the Scitamineae (Zingiberales).

The ectetate pollen grains of the Liliatae distinguish them basically from all more advanced dicotyledonous forms as we have seen, so that the derivation of the ectetate grains of monocots from the tectate ones is impossible and, by inference, the descent of monocotyledonous forms from typically dicotyledonous ancestors most improbable. However, both groups may have had a common, pre- or protangiospermous archetype with atectate pollen grains. Chances are that the common progenitorial group was technically still gymnospermous.

The repeatedly suggested origin of monocotyledonous groups from nymphaealean or magnoliacean dicots is precluded by the different nature of the FRUs (anthoids against holanthocormoids, respectively). A ranalean affinity is suggested by the general pollen morphology (the monosulcate type) and phytochemical resemblances, but although certain anatomical and other characters plead against the derivation of monocots from woody ranalean dicots, a common origin from some archaic cycadophytic type of plant is not at all impossible.

The common progenitorial form of (some) dicotyledons and (some) monocotyledons cannot possibly be approximated by the standard recent Liliales and we can only conclude that:

- (1) Not all liliate groups can be derived from a single progenitorial taxon which had already acquired the basic characteristics of such major assemblies as the Alismatidae and Liliidae, and the recent orders apparently constitute a morphologically and anatomically rather heterogeneous assembly (phytochemical evidence is contradictory in this respect).
- (2) It follows from (1) that the phylogeny of the class of the Monocotyledonae must either have been pleiophyletic at the onset or based on a common progenitorial taxon of such a primitive status that it cannot possibly deserve the qualification of having been angiospermous, let alone monocotyledonous, and may not have clearly exhibited the nowadays characteristic liliate traits.
- (3) The more or less alternative conclusions drawn in (2) permit the acceptance of a possible taxonomic relationship between some liliate lineage (or even several such lineages) and (herbaceous) ranalean forms with anthoidal FRUs and meromonandrial androecia, but such a relationship can only be the result

of their descent from a common progenitor still at a primitive level of evolutionary advancement.

- (4) In view of the above-mentioned considerations the question whether “the” monocots are “derived from the dicots” (or *vice versa*) is utterly inane. The evolution of the Angiosperms is the result of the repetitive occurrence of *divergent* (and alternative) traits of semophyletic specialisations and not so much of different degrees of evolutionary progress in one principal lineage: such alternative advancements can only be judged by making reference to a common ancestral stage of both and should not be mutually and directly compared as to their degree of phylogenetic progression.
- (5) More information is required before the phylogeny of the Liliatae can be adequately elucidated, although it is gratifying to see that some broad spectra of features have already contributed valuable taxonomic (and, by inference, phylogenetic) pointers as we have been, and, for instance, render a more or less pleiophyletic ascent more probable than a more strictly monorheithric one.
- (6) For taxonomical purposes it is to be recommended, for pragmatic reasons, to treat the monocots and the dicots as parallel groups “in their own right” without ruling out the possibility of a closer affinity between *some* natural liliate assembly and some (ranalean) magnoliatae taxon than between this particular monocotyledonous group and any other liliatae assembly.

## REFERENCES

- BEHNKE, H.-D. (1972): Sieve-tube plastids in relation to angiosperm systematics – an attempt towards a classification by ultrastructural research. *Bot. Rev.* **38**: 155–197.
- (1973): Plastids in sieve elements and their companion cells. Investigations on Monocotyledons, with special reference to *Smilax* and *Tradescantia*. *Planta* (Berlin) **110**: 321–328.
- BLASER, H. W. (1944): Studies in the morphology of the Cyperaceae. II. The prophyll. *Amer. J. Bot.* **31**: 53–61.
- CAROLIN, R. C., S. W. L. JACOBS & M. VESK (1973): The structure of the cells of the mesophyll and parenchymatous bundle sheath of the Gramineae. *Bot. J. Linn. Soc.* **66**: 259–275.
- CORNER, E. J. H. (1966): *The natural history of palms*. Berkeley.
- CROWSON, R. A. (1970): *Classification and biology*. London.
- DAHLGREN, R. et al. (1974): *Angiospermernes taxonomi*. Copenhagen.
- DOYLE, J. A. (1973): The Monocotyledons: Their evolution and comparative biology. V. Fossil evidence on early evolution of the Monocotyledons. *Quart. Rev. Biol.* **48**: 399–413.
- EHRENDORFER, F. (1971): Systematik und Evolution. In: E. STRASBURGER et al., *Lehrbuch der Botanik für Hochschulen*, 30. Aufl., p. 379–741. Stuttgart.
- HAINES, R. W. (1966): Prophylls and branching in Cyperaceae. *J. E. Africa Nat. Hist. Soc. Nat. Mus.* **26**: 51–70.
- HEGNAUER, R. (1973): Die cyanogenen Verbindungen der Liliatae und Magnoliatae-Magnoliidae: Zur systematischen Bedeutung des Merkmals der Cyanogenese. *Biochem. Syst.* **1**: 191–197.
- HOLTUM, R. E. (1955): Growth-habits of monocotyledons-variations on a theme. *Phytomorphology* **5**: 399–413.
- HUBER, H. (1969): Die Samenmerkmale und Verwandtschaftsverhältnisse der Liliifloren. *Mitt. bot. Staatssamml. München* **8**: 219–538.
- KAPLAN, D. R. (1975): Comparative developmental evaluation of the morphology of unifacial leaves in the monocotyledons. *Bot. Jahrb. Syst.* **95**: 1–105.

- KERN, J. H. (1962): New look at some Cyperaceae mainly from the tropical standpoint. *Adv. Sci.* **19**: 141–148.
- LATZKO, E. E. & G. J. KELLY (1974): Photosynthesis: Carbon Metabolism. *Fortschr. d. Bot. (Progr. in Bot.)* **36**: 77–89.
- MEEUSE, A. D. J. (1961): The Pentoxylales and the origin of the Monocotyledons. *Proc. Koninkl. Akad. Wetensch. Amsterdam Ser. C.* **64**: 543–559.
- (1967): The possible growth habit of the early Angiosperms. *Acta Bot. Neerl.* **16**: 33–41.
- (1974a): The different origins of petaloid semaphylls. *Phytomorphology* **23**: 493–503.
- (1974b): Some fundamental principles in interpretative floral morphology. In: T. M. VARGHESE & R. K. GROVER (eds.), *Vistas in Plant Science*. Vol. 1. Hissar.
- (1975a): Phaneranthy, aphananthy, and floral morphology: Some special aspects of the early evolution of the Angiosperms. *Acta Bot. Indica* **2**: 107–119.
- (1975b): Changing floral concepts: Anthocorms, flowers and antheroids. *Acta Bot. Neerl.* **24**: 23–36.
- (1975c): Interpretative floral morphology of the Cyperaceae on the basis of the antheroid concept. *Acta Bot. Neerl.* **24**: 291–304.
- METCALFE, C. R. (1971): Cyperaceae. In: C. R. METCALFE (ed.), *Anatomy of the Monocotyledons*. Vol. V.
- MOORE, H. E. & N. W. UHL (1973): The Monocotyledons: Their evolution and comparative biology. VI. Palms and the origin and evolution of Monocotyledons. *Quart. Rev. Biol.* **48**: 414–436.
- RAVOLOLOMANIRAKA, D. (1972): Contribution à l'étude de quelques feuilles des monocotylédones. *Bull. Mus. nat. Hist. Nat. sér. III, Bot.* **46**: 29–69.
- STONE, B. C. (1969): Morphological studies in Pandanaceae. I. Staminodia and pistillodia of *Pandanus* and their hypothetical significance. *Phytomorphology* **18**: 498–509.
- (1972): A reconsideration of the evolutionary status of the family Pandanaceae and its significance in Monocotyledon phylogeny. *Quart. Rev. Biol.* **47**: 34–45.
- TAKHTAJAN, A. L. (1969): *Flowering Plants – Origin and Dispersal*. Edinburgh.
- (1973): *Evolution und Ausbreitung der Blütenpflanzen*. Stuttgart.
- TOMLINSON, P. B. (1962): Phylogeny of the Scitamineae – Morphological and anatomical considerations. *Evolution* **16**: 192–213.
- (1970): Monocotyledons – Towards an understanding of their morphology and anatomy. *Advanc. Bot. Res.* (R. D. PRESTON, ed.) **3**: 207–292.
- (1973): The Monocotyledons: Their evolution and comparative biology. VIII. Branching in Monocotyledons. *Quart. Rev. Biol.* **48**: 458–466.
- & M. H. ZIMMERMAN (1969): Vascular anatomy of monocotyledons with secondary growth – An introduction. *J. Arnold Arbor.* **50**: 159–179.
- WALKER, J. W. (1974a): Evolution of exine structure in the pollen of primitive Angiosperms. *Amer. J. Bot.* **61**: 891–902.
- (1974b): Aperture evolution in the pollen of primitive Angiosperms. *Amer. J. Bot.* **61**: 1112–1137.
- ZIMMERMAN, M. H. & P. B. TOMLINSON (1972): The vascular system of monocotyledonous stems. *Bot. Gaz.* **133**: 141–155.