

## CLADISTICS, WOOD ANATOMY AND ANGIOSPERM PHYLOGENY – A CHALLENGE

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### SUMMARY

Conclusions reached by YOUNG (1981) concerning the evolutionary status of homoxyls in woody Angiosperms are biased because the results of his analyses are based upon the silent acceptance of certain postulates and on assumptions emanating from such current but most probably untenable tenets. The phylogenetic history of the Angiosperms, if unravelled by alternative viewpoints and by, *e.g.*, correlation studies yielding an “advancement index” (SPORNE 1982), and as substantiated by recent paleobotanical findings, most probably proceeded pleiorheithrically rather than monophyletically. The construction of cladograms starting from the postulation of a monophyletic ascent of the Magnoliophyta does not necessarily reflect the true evolutionary history of these Flowering Plants. In Young’s cladistic analysis another difference between his adopted conventional viewpoints and alternative, dissentient ideas is that some or all of the supposedly apomorphic (*i.e.* newly acquired) character states need not have originated only once (as accepted and emphasised in his paper), but may well have arisen repeatedly and independently in two or in more parallel evolutionary lineages evolved from technically still gymnospermous ancestral forms and each terminating in some present-day angiospermous assembly.

The principal conclusion attained by Young, *viz.*, that the incidence of homoxyls in arborescent Angiosperms is attributable to a secondary “loss” of the wood vessels by paedogenesis or otherwise, with corollary is partly based on cladistic analyses said to be leading to absurdities concerning wood vessel evolution, can be challenged because alternative starting points render these allegedly unacceptable evolutionary events highly plausible. At least some of the homoxylous primitive angiospermous taxa are early arrivals in the paleontological record, which is more compatible with an ancience (*i.e.*, plesiomorphy) of the character state of homoxyls in these taxa. Most if not all other conclusions emanating from Young’s viewpoints are likewise to be rejected. Since prior to cladistic and other manipulations certain assumptions had been made and conventional ideas adopted as factual data, the ensuing evaluation of features and of character states is at least questionable and the qualifications of such characteristics as plesio- or as apomorphic is decidedly aprioristic. Parallelisms are not accounted for either, which means that the advent of vessel perforations need not have been a single evolutionary event but may have taken place repeatedly, some taxa never evolving beyond the level of homoxyls. For these and for other reasons one need not amend the generally held views concerning the primitive status of certain vessel-less, arborescent Dicotyledons and the pleiomorphy of the character state of homoxyls in these taxa.

This is another example of the inherent handicap in the application of cladistics that the results are to a large extent already aprioristically decided by the acceptance of tenets and “current” ideas and not by the cladistic methodology. One should first attempt to come to agreement as regards the evolutionary polarity of certain conditions and character states (*i.e.*, the direction of phylogenetic advancement) before entering upon any form of cladistic analysis, lest cladistic approaches to Angiosperm phylogeny remain entirely futile because the results may prove to be meaningless.

## 1. INTRODUCTION

An increasing number of botanists advocate the use of cladistics in botany. Upon the whole the results of their mainly Hennigian analyses are anything but epoch-making, nor do they appear to be essential or of any other practical use than a bit of shifting and re-arranging of pre-existing taxa. However, as soon as other aspects become more deeply involved, there is a more than latent danger in that the conclusions reached suggest that some fundamental changes have resulted from such an inquiry. A recent example is a paper by YOUNG (1981) in which not only present-day systematics (as is customary in Hennigian cladistics, presented as phylogeny, in fact nothing but *Alluvialphylogenie* in the sense of W. Zimmerman because it is not based on fossil evidence), but also the evolutionary history of the Angiosperms and of the magnoliophytic wood anatomy are approached by way of cladistics. As stated previously (MEEUSE 1981, 1982a), the acceptance of sometimes far-reaching primary assumptions and of the delimitation of the taxa to be included in the ultimate cladograms always *precedes* the Hennigian analysis. This does not necessarily mean that a cladistic methodology as such would be inadequate or rejectable, but we are always interested in the outcome of such efforts and it seems as if such results do not depend so much on the cladistic evaluation as on the basic data (such as the taxonomic status and supposed relationships of the OTUs, and the plesio- or apomorphy of eclectically selected character states) and on the concepts accepted as factual and valid *before* the analysis is being made. These preconceived notions to a considerable extent decide the outcome aprioristically.

Certain ideas concerning the evolution and the floral morphology of the Angiosperms rest upon basic tenets which have almost become hearsay (compare MEEUSE 1966, 1975a, 1978a, 1979, 1982b). It follows that deductions ensuing from alternative hypotheses may have a considerable bearing upon the outcome of cladistic analyses if applied to the same set of taxa; in other words: the resulting dendrograms will differ to a lesser or greater extent from other ones based on the conventional ideas concerning the taxonomic relationships of angiospermous groups and their probable phylogenetic prehistory. It is doubtful whether workers fiddling with cladistics have any sound ideas about the proper issues involved, let alone acquired a thorough enough knowledge of the pertaining literature. Most, if not all of them pick some existing classification of prefabricated taxa already implying certain phylogenetic relationships, and they take all allegedly supporting arguments, if any, for granted. This applied the more seriously as the subject matter is more complex, of which the above-mentioned paper by Young is a glaring example. One wonders if valuable research time and increasingly scarcer funds had not better be used to try and settle outstanding relevant issues and to decide outstanding controversies. For the time being all attempts at botanical cladistics involving Angiosperms ought to be challenged on account of the rickety fundamentals. The present account may for

that reason also serve as a warning against the uncritical lock, stock and barrel adoption of the so-called current views regarding Angiosperm morphology, taxonomy and evolution usually presented as gospel truth in most text books and manuals.

## 2. SOME FUNDAMENTAL ISSUES AT STAKE

Since Young's paper forms the principal topic, the following disquisitions relate primarily to the – mostly silently made – assumptions and to the issues raised in his contribution.

The first controversy concerns the mode of descent of the Flowering Plants, namely the alternatives of a strictly monophyletic *versus* a more or less pleiophyletic form of evolution. The proper way to put this general question in a more surveyable and more debatable form is to include the definition of "An Angiosperm" in our reasoning. Clearly a higher seed plant exhibiting all characteristics of what is by consensus of opinion a magnoliophyte differs from its ancestor, which is to all intents and purposes classifiable as a gymnosperm and lacks these distinctive, apomorphic character states, all differential features having evolved in the phylogenetic line (genorheithrum) connecting the ancestral taxon in question with its recent derivative (or derivatives, as the case may be). If a number of such genorheithra initially consisting of gymnospermous forms but in the course of time gradually replaced by hemi-angiospermous and, ultimately, by fully angiospermous ones, already existed side by side as independent and co-existent, discrete lines of ascent at a still strictly "gymnospermous" level of the character states, the ultimate ("terminal") angiospermous descendants of such lines are polyphyletic to a greater or lesser extent if cladistically assessed at all levels of the geological time scale after these primarily gymnospermous lineages had become independent. If this can be shown to have indeed been the case, at least some of the "typical" angiospermous features must consequently have arisen independently in two or more such lineages as parallelisms or convergencies (see also DOYLE 1978). MABBERLEY (1982) has gleaned evidence for cases of parallel evolution from various sources exemplified by, *e.g.*, the repetitive incidence of a certain type of tree architecture in unrelated families. In addition, there is a good deal of cumulative, direct and indirect evidence that several evidently hemi-angiospermous or even angiospermous groups occurred side by side at about, or even before the time when, by consensus of opinion, the first full-fledged magnoliophytic plants appeared (see, *e.g.*, RÜFFLE & KNAPPE 1977, DILCHER 1979, FRIIS & SCARBY 1981, MULLER 1981, KRASSILOV 1982, RETALLACK & DILCHER 1981). These finds are only compatible with the presence of already independent evolutionary lineages of pre-angiospermous forms in the Lower Cretaceous.

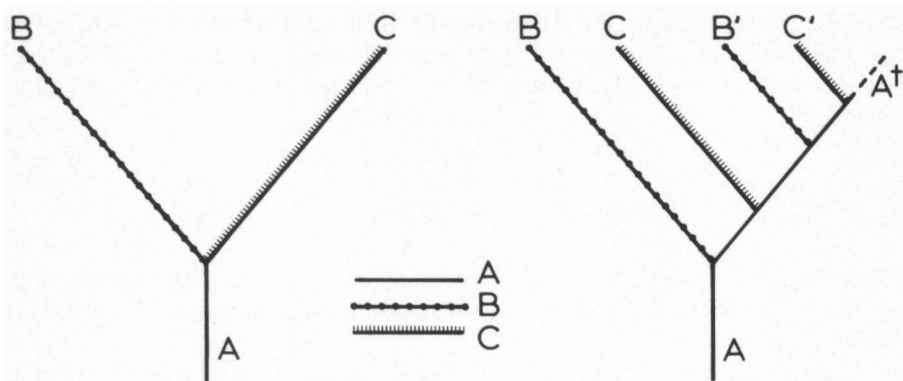


Fig. 1. Left: divergent evolution of character state A into two apomorphic derivative states simultaneously (B and C) by alternative changes. Right: Character state A produces, as an offshoot, character state B and a little later state C. If subsequently A disappears by the extinction of the taxon that exhibited state A, practically the same situation obtains as in the left-hand figure, and in the paleobotanic record at least it would appear like that figure; for practical purposes there is hardly any difference in the ultimate result. A repetition yielded the character states B' and C' as parallelisms of B and of C, respectively.

Now that a polyrheithric form of phylogenetic advancement as defined above has been shown to have been operative, the independent advent of several “magnoliophytic” character states in two or more independently evolved lineages almost becomes a foregone conclusion. One of the characteristic features in question, *viz.*, the acquisition of xylem vessels, is a likely example, which is also relevant to the discussion in the following chapter.

Another aspect of the evolutionary history of the Flowering Plants concerns the floral morphology, in particular when interpreted and assessed in combination with the mode of pollen transfer, because this has a considerable bearing upon the evaluation of character states as more primitive (in the cladistic terminology: plesiomorphic) or as derived (progressed, *i.e.*, apomorphic) in nature. In the present context mainly the following ones included in Table 3 (on p. 320) of Young's paper will be assessed here. Young's qualification “0” is supposed to be indicative of a plesiomorphic state and “1” and “2” represent two degrees of advancement, but both are said to be apomorphic states. At the onset one may stipulate that this is an oversimplification of a much more complicated process of phylogenetic advancement because we now know that parallelism must have been of frequent occurrence (see above). Secondly, it is more than likely that divergent evolution occurred, so that at a certain time level two parallel lines originated (see *fig. 1*: from stage A of a character state two alternative, derivative stages B and C resulted, neither of which is necessarily more primitive or more advanced in respect of the other one. Such divergences and, in particular, parallelisms are not adequately accounted for in Hennigian cladistics (compare also STEVENS 1980).

1. Habit: “scandent shrubs or vines” are not necessarily more advanced in respect of erect arborescent forms (see MEEUSE 1965 for a discussion).

2. In certain groups at least, compound leaves are more primitive and the simple leaf is an apomorphic character state (e.g., in Proto-fagales and Fagales, respectively: RÜFFLE & KNAPPE 1977).
5. Chloranthoid teeth: Chloranthaceae are among the oldest families recognised as such in the fossil record (MULLER 1981) and toothed leaves of a chloranthaceous type may well be ancient in at least some lineages.
9. Stipules: SPORNE (1982) again assesses exstipulate leaves as advanced and he is not the only one who does so; stipulate leaves must be plesiomorphic in at least some lineages.
12. Floral sexuality: SPORNE (1982) has concluded on the basis of correlation features that dicliny is the plesiomorphic state; the present author has pointed at the complexity of the problem but accepts an initial, ancient state of dicliny which persisted in some groups, *i.e.*, unisexuality is primitive in, e.g., Amentiferae, Myristicaceae, Monimiaceae s.s., Arecales and Pandanales (MEEUSE 1978a, 1979, 1982b), whereas an incipient ambisexuality already originated in some still gymnospermous groups (MEEUSE 1978b, c).
13. Divergent evolution led to a plurality of functional reproductive units (FRUs), some appearing as coaxial aggregates ("inflorescences") and others as solitary entities (see MEEUSE 1975b); these character states almost certainly developed more than once and they are phylogenetic alternatives, *i.e.*, the one condition is not necessarily more primitive or more advanced in respect of the other (14 – Flower size –, 15 – perianth – and 16 – petaliferous or apetalous condition – are usually associated with one of the kinds of FRUs).
20. Stamens (and 23. Stamen number, partly): not all so-called "stamens" are homologous morphomes (see MEEUSE 1974: the relations between the various kinds of androecial members are more complex and there are alternative character states).
25. Pollen tetrads: the presence of pollen tetrads in Winteraceae may be a more or less ancient feature (explainable as a case of neoteny or of paedogenesis).
34. (Embryo size) and 35. (Endosperm size) are inversely correlated, in some groups small embryos and copious endosperm are basic features, in other ones large embryos and but little endosperm – these are again alternative features and need not be sequential character states.
37. Fruit type: the primitive fruit was not necessarily always dry and not consistently dehiscent; in some groups fleshy and indehiscent types may be primitive character states instead (compare, e.g., Magnoliaceae with Lauraceae and Piperaceae).
41. Vessel perforations – whether in *all* lineages scalariform pitting of end plates of tracheidal elements was primitive remains to be seen: not all vessel perforations need have originated in the same way.

Especially alternative character states cannot be assessed in a sequential scale 0–1–2– etc., and other features might score "0" instead of "1" or "2" (or *vice*

*versa*). The character state matrix would appear quite differently if the alternative premises were selected for the evaluation, so that Young's Figs. 3 and 4 would also turn out differently, not to mention the monophyletic set-up of these cladograms and of his Fig. 5. As regards the latter figure, the taxonomic relationships of some families are rather arbitrarily chosen; some workers consider the Lactoridaceae and the Chloranthaceae to be more closely related to the Magnoliaceae than is apparent from Young's grouping explained on p. 321–322 of his paper and from the corresponding cladogram (his Fig. 5). Myristicaceae are placed in group B, but many taxonomists would place this taxon next to the Magnoliaceae-Canellaceae-Annonaceae which appear in group A. In group C Monimiaceae are lumped with Piperales, Nymphaeaceae and the Trochodendrales and not placed near the Laurales (with *Amborella*, *Trimeniaceae* etc. classified in group A). The groups A, B and C are manifestly heterogeneous and it is a question whether the Trochodendrales and *Cercidiphyllum* belong to the Magnolioid-Piperoid assembly at all, and some or all of the Nymphaeales may belong to an individual lineage; all these taxa may be more distantly related to the Magnolioid-Piperoid group than the Ranunculoid (Berberoid) taxa which are sometimes included in the Magnoliidae. The arrangement appears to be unnatural owing to the selection of the initial data explained above. There are too many uncertainties to permit the drawing of conclusions and, therefore, the results are by no means convincing. This criticism is partly based on discrete paleobotanic evidence. DILCHER (1979), RETALLACK & DILCHER (1981), SPORNE (1982) and the present author have pointed out that the traditional idea of a phaneranthous, monoclinal and entomophilous protangiosperm still rather closely epitomised by a magnoliaceous plant form is decidedly false. Young was apparently unaware of the fact that cogent evidence is piling up that early and to all intents and purposes angiospermoid forms, some of Lower Cretaceous age, were frequently diclinous, aphananthous and, by inference, anemophilous. This is certainly helpful when it comes to assessing the evolutionary polarity of character states (STEVENS 1980), *i.e.*, the direction of phylogenetic progress from plesiomorphy to apomorphy as pointed out by SPORNE (1982), who feels confident that his advancement index is vindicated and had previously accepted such characters as unisexuality and a haploclamydeous perianth as primitive ones. His assessments are too one-sided because he does not take alternative developments into consideration such as an early divergence of still anemophilous or already entomophilous, diclinous lineages and entomophilous monoclinal ones, but in spite of the shortcomings his above-mentioned findings do not contradict the fossil evidence.

### 3. FUNCTIONAL ASPECTS

The postulation of a retrograde evolution of ecophysiologically important structural elements such as wood vessels must be supported by a plausible explanation of the selective forces responsible for the change. It seems odd that woody plants with an advanced adaptation to water transport would have lost this advantage

over not so well-equipped forms – the “loss” in herbaceous forms is another matter – and one may wonder what they gained by relinquishing a properly functioning system. The more or less primitive angiosperms with homoxylous wood (Trochodendrales, *Sarcandra*, Winteraceae, *Amborella*) are of a modest size (suffrutescent to shrubby, at best small trees usually without a clean bole). It would seem as if their not so efficient form of water transportation may account for their not so impressive biomass formation, conceivably because the available restricted supply of water continued to act as a limiting factor during their evolution. The few monocotyledonous taxa with a special form of secondary growth may also provide a clue. Whether such plants (species of *Dracaena* and some other dracaenoid genera, arborescent species of *Aloë*) have a primitive or a highly advanced stelar anatomy is a moot point, but there is no *a priori* reason to reject the possibility of retention of an ancient xylotomic feature. The till recently held viewpoint that the structures found in some dicotyledonous taxa (such as Piperales, Aristolochiales, and Nymphaeales) and in such monocots as Dioscoreaceae are *per se* anomalous (*i.e.*, derived, apomorphic) is no longer accepted as valid throughout. Some workers have even expressed as their opinion that at least some of the oldest angiospermous taxa and their immediate precursors were plants of small stature and not necessarily arborescent in the sense that they produced boles in the fashion of truly arborescent Dicotyledons. “Polystelic” and other “anomalous” stelar structures may have occurred and they may have persisted in some recent descendants of such early groups. The monocotyledons with secondary growth may, likewise, exhibit an ancient or even archaic condition, in which case their secondary vascular elements may be very primitive. A comparison of the water-conducting elements in their secondary xylem with those in the vascular bundles of their primary stem reveals that the wide and copiously and variously pitted but always rather thin-walled primary tracheids (and vessels) stand in striking contrast with the fibre tracheids making up the bulk if not all of the secondary water-conducting tissue. These tracheids are rather thick-walled and have bordered pits with crossed slit-like openings. They are reminiscent of both the tracheidal elements of fossil gymnosperms such as the Pentoxylales (MEEUSE 1961) and also of certain kinds of tracheids and fibre-tracheids found in some dicotyledonous woods including those of homoxylous taxa. Provided this is an ancient (plesiomorphic) feature which occurred in the common progenitors of (some) monocots and (some) dicots, homoxily is an original feature in the taxa mentioned above, the fibre-tracheids providing mechanical strength as well as, more or less clumsily, water conduction. One can visualise an evolutionary advance from this stage (*e.g.*, by the advent of scalariform pits in the terminal wall parts of the tracheids by a lateral extension of smaller pits, ultimately resulting in perforations) as against an evolutionary stasis, *i.e.*, a retention of the homoxily in several certainly more or less primitive dicotyledonous taxa.

#### 4. DISCUSSION

In view of the many uncertainties and alternatives and of the evaluation of a number of features in the 0–1–2 scale used by Young, the inevitable conclusion is that the outcome of his assessment is of doubtful value to put it mildly. An increasing amount of evidence is only compatible with a pleiorheithric form of evolution as elucidated in Chapter 2, *i.e.*, with the presence of a number of parallel lineages already having become independent at a still gymnospermous level of advancement. The evolving taxa constituting such a phylogenetic sequence may or may not have differed in some essential characteristics from those of other, parallel lineages, so that their ultimate, present-day descendants are not necessarily conformable to a single organisation pattern epitomising a supposedly common ancestral group of *all* living Flowering Plants, but only to that of their own progenitors (compare DILCHER 1979, RETALLACK & DILCHER 1981, SPORNE 1982, MABBERLEY 1982). The pooling of all features of all recent angiospermous groups and their assessment as if they are monophyletic and their features, therefore, consistently homologous (*i.e.*, constitute comparable character states) is to be rejected, not only on account of parallelisms and repeated “parallel” divergencies, but also because certain structures and features (such as those of androecial members) are not necessarily homologous throughout. The evaluation of certain character states as sequential, *e.g.*, feature A evolved into B and B subsequently into C (and assessed as 0, 1 and 2, respectively) thus becomes false. Some groups have always been diclinous and either consistently anemophilous or partly or wholly zoophilous, other ones have been basically monoclinal and zoophilous for an appreciable length of time, and in some major groups such as the magnolioid-ranunculoid assembly and the Rosidae and the Dilleniidae, more than one condition is found (MEEUSE 1978a, 1982b). The associated anthomorphological character states (*e.g.*, anthoids versus holanthocormoids, presence or absence of functional semaphylls) are, likewise, not always sequential but alternative, and the one situation is not necessarily derived in respect of the other; in terms of cladistics: the one is not, or not absolutely, apomorphic and the other one plesiomorphic but they may be either (or occasionally both: there is, *e.g.*, secondary anemophily and entomophily with their respective repetitively acquired morphological syndromes). The parallel evolution of a number of independent lineages starting from a gymnospermous progenitorial group necessitates the postulation of two alternatives, *viz.*, either all supposedly special magnoliophytic characteristics (such as the advent of wood vessels) had already originated *before* the parallel lineages became separated, or they developed more than once in two or more lineages *after* their separation. The main topic of Young’s paper is the question whether the absence of xylem vessels in arborescent angiospermous taxa is derived (apomorphic) or a primitive (original, plesiomorphic) condition. The functional aspect renders a repetitive origin (by analogy or by parallelismic evolution) not at all unlikely.



That the gymnospermous precursors of magnoliophytes were initially homoxylous is a foregone conclusion, so that a hemiangiospermous or full-fledged magnoliophytic group (or several such groups) must have acquired xylem vessels at one time or another. According to Young all primitive angiosperms and conceivably their immediate precursors had acquired xylem vessels only once (monophyletically) and by inference all recent vessel-less woody forms 'lost' them. Leaving all cases of manifestly secondary loss of vessels (in submerged aquatics, certain parasites and saprophytes, true therophytic herbs, etc.) out of consideration, there are a number of by consensus of opinion more or less primitive but not necessarily closely related homoxylous genera. From a functional point of view there can hardly be a reasonable argument why arborescent representatives of such an evolutionary successful plant group as the Magnoliophyta would exhibit any retrograde evolution of that essential, viz., physiologically advantageous, acquisition. The homoxylous Angiosperms are of modest size: small to fairly large suffrutices, or shrubs to small trees. As suggested above, it seems as if it is precisely the absence of wood vessels that accounts for the inexcessive biomass formation among the group under discussion: the non-optimal supply of water would, as a limiting factor, have prevented a more opulent development of boles and major branches. In this context, as shown in chapter 3, the morphology of the secondary tracheidal elements of monocotyledons with a peculiar form of secondary growth may be of special interest. The rate of evolutionary advancement of dicotyledons with homoxylous wood has been assessed in various ways. After a comparative assessment of the xylotomic features of the more primitive angiospermous families GOTTWALD (1977) reached the conclusion that the homoxylous taxa are anatomically less advanced than, e.g., Annonaceae, Magnoliaceae, Monimiaceae and other more or less closely related families with xylem vessels. The present author has pointed out that for various reasons such forms as *Amborella* and Chloranthaceae are in several respects very primitive (MEEUSE 1978a, 1982b; see also YOUNG 1982), so that the incidence of a highly advanced xylem anatomy (as Young has it) in these taxa is incongruous and would, therefore, represent a rather extreme and, hence, most improbable case of heterobathmy. According to MULLER (1981) the fossil record of the Chloranthaceae goes back at least to the Lower Cretaceous (Albian) and this is clearly more indicative of a primitive than of an advanced status of this family.

There is a more than latent danger that practising cladists are getting more credit for their efforts than they deserve. A critical appraisal lays bare some inherent scientific impediments, because even the cladists seem to fail to appreciate the decisive significance of the primarily introduced, aprioristic assumptions. As long as these premises are challengeable, the results of a Hennigian analysis lack conviction because alternative presuppositions would yield different results if the same cladistic methodology is applied (compare also SOLBRIG 1970). The subjective and eclectic element can hardly be eliminated without inquiries into the fundamental issues involved. It follows that because every form of cladistic

evaluation of taxonomic data and of character states must be judged by the non-cladistic apriorisms, and the latter largely decide the outcome of the analysis, all corollaries of a Hennigian analysis of, especially, magnoliophytic groups are rendered of doubtful value. A critical re-appraisal of the basic taxonomic and phylogenetic principles in the light of the now increasingly accruing paleontological evidence of the course of Angiosperm evolution is recommended instead.

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