

AGAIN: THE GROWTH HABIT OF THE EARLY ANGIOSPERMS

A. D. J. MEEUSE

Hugo de Vries-laboratorium, Amsterdam

SUMMARY

The question of the putative growth habit of early angiospermous plants, recently brought to the fore again by STEBBINS (1965), is not a simple problem, it being complicated by, *e.g.*, the alternative hypotheses of a single or a multiple descent of the Flowering Plants. A reconsideration based upon palaeobotanic, comparative morphological, and other evidence reveals that, in contradistinction to current views, the probable growth habit of pre- and proto-angiosperms was not of a single (uniform) type, but varied and included nearly all types exhibited by the various, recent dicotyledonous and monocotyledonous groups except the truly therophytic life form. Among the arborescent life forms represented at an early stage, the lofty dicotyledonous tree habit, though presumably present, was comparatively rare.

1. INTRODUCTION AND PRELIMINARY CONSIDERATIONS

Recently the probable growth habit of the early Angiosperms has been discussed by STEBBINS (1965). His contribution invites some comment, not only because several alternative, contemporary views (CORNER 1949, 1954; TAKHTAJAN 1959) were not cited, but also because some of Stebbins' suppositions are disputable.

It is quite true, as Stebbins points out once more, that a great deal of attention was paid to the problem by such workers as E. C. Jeffrey, Sinnott and I. W. Bailey, but it is a serious omission that the rather exhaustive reviews by TAKHTAJAN (1959: 32-34) and ZIMMERMANN (1959: 492) were not taken into account. Stebbins was not the first to suggest that the putative, early angiospermous growth habit was that of a diminutive woody plant or a "shrub". As early as 1912 HALLIER expressed the opinion that the first flowering plants and their immediate precursors were not lofty trees, but more probably weakly branched, small and perhaps rather soft-stemmed shrubby to small arboreous plants with leaves borne in terminal tufts. TAKHTAJAN (1959) adopted this idea almost unchanged, mentioning the "shrubby" species of *Paeonia* and *Illicium* as surviving, representative examples of this type of life form. CORNER'S (1954) somewhat similar suggestion of a monocaul and pachycaul (soft-stemmed) group of angiosperm progenitors apparently emanated from other premises and considerations than Hallier's and was, as far as can be ascertained, independently conceived. At any rate, the postulation of smallish, "shrubby" rather than tall, tree-like protangiosperms antedates Stebbins' proposal by many years.

Another reason to re-open the discussion is an unwarranted trend towards generalisation resulting from the silent acceptance of a number of precon-

ceived, conventional doctrines or "dicta" regarding the origin of the Flowering Plants, which was for a long time considered to be a monophyletic evolutionary event primarily giving rise to forms which were, essentially, early Dicots and from which subsequently both the recent Dicots and the Monocots descended. I have repeatedly pointed out that the problem of Flowering Plant evolution is a very complex one involving a considerable number of questionable or debatable aspects, each of which must be dealt with separately in the proper order, and, later on, considered in conjunction with the other facets of the problem, before one can discuss such rather secondary features as early growth habit in a sensible way (see MEEUSE 1962, 1965: especially Chapters I-IV and XIII-XIV, 1966: especially Chapters 6 and 20). All authors on the subject of early angiospermous life forms, from Hallier and Jeffrey to Takhtajan and Stebbins, take far too many things for granted, the most important being:

- a. a monophyletic descent of all Flowering Plants;
- b. an evolutionary antecedence of early Dicots in respect of the first Monocots (*i.e.*, Monocots descended from an essentially dicotyledonous type of plant), so that
- c. as a consequence of b., the growth habit of every angiospermous group is presumed to be derived from the (supposedly invariable) life form of the postulated (single) ancestral group of dicotyledonoid affinity, in other words, the various habit forms of the living angiospermous taxa are all derived from a *single* prototype.

As a prerequisite for this third postulate a silent but decidedly biased addition to the first (concerning the supposed monophyly of all Flowering Plants) was made, *viz.*, the assumption that *all* immediate angiosperm progenitors were of one life form: trees (or non-climbing shrubs, or suffrutices, as the case may be) with a "dicotyledonous" stelar anatomy and showing a development of secondary vascular tissues considered to be "normal" among the *recent* woody Dicots. All three fundamental premises are preconceived, because the fossil evidence is inadequate (or at least not unequivocal) and a retroactive reconstruction of extinct, precursory forms from the morphologically so diversified, recent Flowering Plants is a rather hazardous procedure.

I am of the opinion that, all things considered, the following alternative postulates provide a much better foundation of a hypothesis explaining Angiosperm phylogeny and the associated semophyletic processes including the evolution of the habit forms:

- a. Angiosperms descended *polyphyletically* from Mesozoic cycadopsid precursors;
- b. Monocots descended from gymnospermous protomonocots, *independently of the dicotyledonous groups* (MEEUSE 1961 *et seq.*) and are, therefore, not secondarily derived from some early dicotyledonoid taxon (nor are the Dicots derived from protomonocots, for that matter);
- c. Consequently, certain principal angiospermous groups (such as Monocots) descended from cycadopsid progenitors which already differed morphologi-

cally from other and partly coetaneous (e.g., *predicotyledonous*), angiospermoid Gymnosperms, so that the habit form of each independently evolved angiospermous group reflects the growth habit of its specific group of gymnospermous precursors and need not closely correspond with the life form of the ancestral prototaxon of a different angiospermous group;

d. Accordingly, the ancestral stelar structure and mode of secondary growth of a group of recent Flowering Plants (such as Monocots) need not necessarily have been of the so-called "normal" (dicotyledonous!) type in an anatomical sense, but may have been fundamentally different.

Irrespective of any corroborative palaeobotanic information, we may conclude that as likely as not the growth habit of an early angiospermous form may have been one of several possible life forms which include trees, smaller, sparingly branched and more or less pachycaul arborescent plants, soft shrubs, almost stemless plants with a thick and almost completely subterranean caudex, or a subherbaceous geophytic type with rhizomatous or creeping aerial stems, and even woody climbers (all these life forms being represented in the various angiospermous taxa that have, at one time or other, been considered to be primitive and, consequently, may have retained an ancient growth habit). For the same reason, the stelar structure, the form of secondary growth in girth (if any), the nodal anatomy, the number of leaf gaps and leaf trace bundles (in addition to such features as foliar morphology: simple or compound, entire, dentate or dissected leaves; as monoclinal or diclinal; as anemophily or zoophily, etc.) need not inevitably have been of only one kind. This must be the starting-point of all discussions pertinent to the question what the earliest Angiosperms and their immediate precursors looked like.

2. SOME RELEVANT PALAEOBOTANIC AND COMPARATIVE-MORPHOLOGICAL EVIDENCE

The idea is rapidly gaining ground (BECK 1960, 1966; MEEUSE 1963 *et seq.*; CARLUCCIO *c.s.* 1966; BANKS 1967) that all spermatophytic groups are the descendants of a Devonian group of vascular plants, the Progymnospermopsida. One of the most characteristic features of these progenitors of the seed plants is their secondary growth by means of a vascular cambium. The presence of secondary xylem is apparently a very ancient feature of the Spermatophyta, but it does not necessarily follow that the degree of secondary growth and the structure of the secondary tissues has remained the same ever since its initiation in, presumably, the Lower Devonian. Ecological adaptations and re-adaptations, associated, among other things, with the relative importance and the morphology of the foliar organs (affecting leaf gaps, nodal anatomy, etc.) may have changed the morphology and anatomy of the cauline organs in various ways. Important in this connection is the conclusion that the prototypes of the earliest Coniferophytina (or Pinicae) and the precursors of the first Cycadophytina (or Cycadicae) were already evolved as separate groups in Late Devonian times (MEEUSE 1963 *et seq.*; BECK 1966), so that the morphology of the

fossil and the recent Conifers has hardly any direct bearing on the question of the early angiospermous growth habit. The precursors of the cycadopsid seed plants were presumably plants of a much more modest stature than the already tree-like, coetaneous preconifers (the Archaeopteridales). The early cycadopsid evolutionary line of the seed ferns already exhibits a number of habit forms: both rather freely branching and erect representatives of Lyginopterid groups and supposedly rambling types such as certain Neuropteridales (Medullosae) are known. There is as yet no unanimity regarding the probable growth habit of the glossopterid line of pteridosperms. The interpretation of the form genus *Vertebraria* as a glossopterid rhizomatous (subterranean) or creeping stem sending up the leaves or dwarf shoots is opposed by the suggestion that the glossopterid fronds were borne in terminal tufts on erect, not or sparingly branched stems. In any event, and this is essential in the present argument, the glossopterid seed ferns were certainly not tall, arboreous plants.

The anatomy of the Mesozoic cycadopsid groups of which the stem structure is preserved (such as the Pentoxylales and certain Cycadeoidales) and the structure of their recent descendents (such as cycads and chlamydosperms) does not show a great deal of uniformity of structural organisation either, but it is noteworthy that there are few tall trees with solid boles among them, if any. There are not only examples with slender (leptocaul) and possibly sometimes twining woody stems (Pentoxylales; *Gnetum*), and forms with pachycaul and sometimes also monocaule stems (such as some Cycadales and Cycadeoidales), but also almost stemless plants with a partly or wholly subterranean, massive caudex bearing a kind of rosette of leaves (some Cycadales such as *Zamia*, *Stangeria* and *Bowenia*; *Welwitschia*; but, in my opinion, this was also the predominant growth habit of such forms as Nilssoniales, Caytoniales, and Corystospermaceae). The presence of several, rather fundamentally different types of stelar structures is also indicative of a divergent adaptive evolution. "Homoxyllic" woods of Mesozoic age resembling those of certain arborescent Ranalians are known, but there are also examples of an "anomalous" cambial growth (e.g., in certain species of *Gnetum* and in some Cycads); and schizo-, meri- or "poly"-steles occur apart from the so-called "normal" siphono- or eustelic type (a divided stelar system is, for instance, characteristic of Medullosae and Pentoxylales). Also conceivable is that forms existed which had altogether lost the capacity of producing secondary growth and assumed the habit of a geophytic herb with a perennial rootstock or a creeping rhizome. If this is taken for granted, there is hardly any (terrestrial) angiospermous life form which was not already extant in Mesozoic eras with the possible exception of the (probably much more recent) therophytic growth habit of the "modern" angiospermous herbs. Conversely, the Cretaceous fossil records of early angiospermous plants include such diverse forms as Piperiales, Urticales, Nymphaeales, *Nelumbo*, Pandanales (Typhaceae and Sparganiaceae), Arecales, and Liliales, apart from several arborescent groups such as Magnoliales s.s., Laurales, and Amentiferae (ZIMMERMANN 1959: 480); in other words: the habit forms of early angiospermous plants were as diversified as those of

their putative Mesozoic precursors. *The obvious and logical preliminary conclusion is that the different growth habits of the Flowering Plants (the therophytic life form excepted) were inherited from those of their already diversified pre-genitors of Mesozoic age, so that, from the very beginning, the Angiosperms exhibited a variety of growth forms.*

3. SPECULATIONS AND DEDUCTIONS

One of the reasons why fossils are (or were) not recognized as potential pre-angiosperms, and, to my mind, probably the principal reason, is the simple consideration that they do not come up to expectation and look rather different from the mental picture most contemporary botanists have made of these "elusive" forms (MELVILLE 1960, quoted by STEBBINS 1965: 458). An illustration of this prejudice, but in an altogether different context, is given by STEBBINS (l. c.; 457): "... some angiosperms, such as *Kingdonia* and *Circeaster* (Foster 1959, 1963), have leaves with such an anomalous venation pattern that if they were found as fossils, unaccompanied by reproductive structures, they would not be recognized as angiosperms at all". Such leaves (of which *Nelumbo* provides another example, incidentally) would, in the form of detached fossil specimens, indeed be taken for the foliage of some cycadopsid gymnosperm rather than that of a truly angiospermous plant, but is only the relative scarcity of these *ancient* types of foliar organs among the *recent* Angiosperms that renders them conspicuous and suggests that they are "aberrant". They simply represent one of the forms of leaves common to both protangiosperms and angiosperms, of which the pinnatisect leaves of certain Myricaceae provide another example (MEEUSE 1966: 50-51, fig. 3), the digitately compound leaves of *Akebia* a third etc. The known Mesozoic fossil cycadopsids simply *must* include some protangiosperms or at least forms closely related to protangiosperms and exhibiting a number of budding angiosperm characters (MEEUSE 1962 *et seq.*). It is highly significant in this connection that, as we have seen, the growth habits of these Mesozoic forms are so diverse that all but one of the principal growth forms of the recent flowering plants were already represented among the known Mesozoic fossil plants (some of which were, as I see it, potential angiosperm progenitors) and by the recent chlamydosperms. It is certainly rewarding to follow up this supposition whilst disregarding the still highly controversial issue of the interpretation (and homology) of the respective reproductive organs, especially if one does not fall into the traditional error of considering every rare, unusual or seemingly bizarre plant form as secondarily derived from some "standard" archetype such as the stereotyped "woody ranalean". This approach to the problem of the origin of the Angiosperms also does away with such absurd implications of a postulated monophyletic descent as the derivation of a nymphaeid, or of an arborescent liliaceous form with secondary growth (such as *Dracaena*), from a magnoliaceous tree. The very presence of a variety of habit forms, stelar types, leaf shapes, types of secondary growth, etc. among the Mesozoic cycadopsid groups, which features

are all "duplicated" in a number of angiospermous taxa and are, moreover, so diversified among the few surviving hemiangiospermous chlamydosperms, leaves no option but to accept a "broad", polyrheithric evolution as the most plausible explanation of the rapid rise of the Flowering Plants. One had in the past been obsessed by such things as angiospermy and the process of double fertilisation, thus clouding the issue and failing to see the forest for the trees. It was mainly on the ground of typological traditions that "generalised" primitive angiosperms were being postulated, be it a woody magnoliaceous or amentiferous, or a more herbaceous, ranunculaceous or piperalean form or group.

One might raise the objection to my point of view that there are so many indications of the primitive status of the woody Ranales (such as wood anatomy: some are primarily vessel-less, other forms show the supposedly only primitive, scalariform type of vessel perforation; also: nodal anatomy, leaf traces) that they must represent an ancient prototype and are still a close approximation of the early angiospermous plants. This way of reasoning is quite fallacious, because the so-called "primitive" anatomical features are perhaps the retained ancient features of, say, the progenitors of the Magnoliales s.s., but they need not necessarily have occurred in *all* early Flowering Plants. Scalariform pitting in the end plates of tracheids and the resulting scalariform perforation in vessel members, for instance, never developed in the evolutionary line of the Monocotyledons: the only water-conducting *secondary* xylem elements occurring in this group are the fibre tracheids with bordered pits found in the secondary vascular tissue of the, mainly liliiflorous, arborescent forms with a special type of cambial growth (such as *Dracaena*, *Cordyline*, caulescent species of *Aloë*, etc.). It is inconceivable that this ancient "gymnospermous" type of tracheid could have originated from a "ranalean" type of tracheid with scalariform end plates. BAILEY (1957) found a very poor correlation between the distribution of anatomical features currently supposed to be primitive and the occurrence of the "more primitive" types of reproductive organs of the ranalean Angiosperms. It all boils down to the same thing: there are several and alternative ancient characteristics and the presence or absence of, e.g., scalariform or simple vessel perforations has only a restricted phylogenetic significance. Elaborate discussions of the question whether the two-, the three-, or the multi-trace leaf gap is the original (most ancient) type are equally futile. Monocots and Pro-Monocots almost invariably have, or had, numerous leaf-trace bundles, some Pro-Dicots had two, others three or more, or perhaps only a single one. Possibly secondary adaptive changes increased the original diversity of the early angiospermous characters to such an extent that the present-day picture became very complicated and even confusing (BAILEY 1957!). In the Piperales and the related Lactoridaceae the number of habit forms varies from erect shrubs or small trees and lianas (Piperaceae, Chloranthaceae) to soft-stemmed suffrutices (Saururaceae) and even to herbs (*Peperomia*), some with perennial subterranean organs. There are two possibilities: one could either assume that the order is derived from a single group of woody

ranalean progenitors and assumed many adaptive forms (which inevitably implies that the group is an ancient offshoot), or that the group is not so very much advanced as compared to its progenitors but, rather, "reduced" in some respects whilst retaining many ancient features. The second alternative seems to me to be the more plausible of the two. This natural order is, in my opinion, even an illustrative example of a group which not only still resembles its group of progenitors in many respects, but is, at the same time, also fairly representative of the ancient hemi-angiosperms as a whole. The observation that both Piperales and Chlamydospermae exhibit a variety of habit forms must have a considerable bearing on our phylogenetic and semophyletic speculations. The presence of such diversified and presumably ancient groups is a great advantage, because there is no need to derive, e.g., such reputedly "advanced" habit forms as the aristolochiaceae, or dioscoreaceae (climbing or geophytic herbaceous ones) from a magnoliaceous arborescent form (which possesses only scalariform tracheid pitting and vessel perforations, penninerved leaves, showy flowers, follicular fruits, etc.).

I may recall that the piperalean alliance exhibits a number of primitive features (there is at least one vessel-less form: *Sarcandra*; several genera have perisperm; the pollen morphology is probably of an old type now mainly superseded by the tricolpate dicotyledonous pollen, to mention only a few) which would agree with the relict status of the group. The evidence is, to my mind, so consistent and convincing if one disregards the (conventionally very much derived) floral morphology of the piperalean alliance and similar taxa, that one should not let the preconceived classical floral theory outweigh all other indications and accept the resemblance between *certain* protangiospermous taxa and the recent Piperales and Chlamydosperms. Other protangiosperms must have resembled Nymphaeales or *Nelumbo* and still others *Casuarina*, etc. The diverse growth habits, leaf shapes, floral morphology and vegetative anatomy are consistent with this idea as we have seen.

4. CONCLUSIONS

A discussion of "*the* probable growth habit of *the* early Angiosperms" can not be separated from other important questions concerning the origin of the Flowering Plants, such as their possible mono- or polyrheitic descent. An appraisal of the available evidence must take such questions thoroughly into account.

It is quite clear that the various opinions regarding the early angiospermous habit form all contain an element of truth but none of them is quite compatible with the relevant evidence from palaeobotanic sources and from the comparative anatomy and morphology of recent taxa. A number of data suggest that the early Angiosperms and their immediate precursors were perennials almost always producing secondary conductive tissues by means of the activity of a vascular cambium, but they were certainly not all proper trees (as postulated in several older publications) and usually of a much more modest stature, but not so frequently of the dwarfed shrubby to suffruticose, "leptocaul" type sug-

gested by Stebbins (examples: *Ephedra*, *Chloranthus*); they not infrequently had rather massive perennial axes and (or) rootstocks, but were most definitely not all monocaule and pachycaule trees as Corner has it; possibly they were, in the dicotyledonous line of descent at least, quite often of the low, more or less soft-stemmed and sparingly branched type postulated by Hallier, Takhtajan, and others, but not invariably of this habit. All "modern" angiospermous habit forms, the therophytic annuals excepted, were already represented in the Mesozoic era, but tall hardwood trees were certainly not so common as they are to-day. Some rather unusual habit forms, such as those of Aristolochiaceae, Casuarinaceae, Dioscoreaceae, Nymphaeaceae, several Piperales, Berberidales-Ranunculales (*Podophyllum*, *Nandina*), including stemless geophytes with a perennial rootstock or rhizome, plants with suffruticose climbing stems from a perennial base, ramblers, and woody vines, are not all derived from the same hemi-angiospermous prototype, but mostly as old as the Angiosperms. One can safely assume that the stemless geophytic type of Nymphaeales, "herbaceous" Paeoniaceae, *Podophyllum*, some Araceae, etc., the small-sized and sparingly branched dicotyledonous treelet ("shrubby" peonies, *Nandina*, and others) and, also, the "arborescent" growth forms of palms, pandans and dracaenoid monocots, may, in the past, have been relatively more common than some of the other growth forms.

The "secondary" diversification within a recent, subordinate taxonomic group may render the recognition of the "original" (*i.e.*, the ancestral) habit form (or forms!) among the various growth habits within that group rather difficult. Apart from the order of the Piperales, the Dilleniaceae provide a case in point. Each of the habit forms, the acaulescent one of the Acrotremeae, the erect or rambling one of *Dillenia*, the suffruticose one of some species of *Hibbertia*, etc. may qualify, but also two or all of them. One should try to keep an open mind in these things, because it is not so important if the earliest representatives of each of the habitually diversified assemblies such as Piperales, Dilleniales, Ranunculales (Berberidales) – Papaverales, and Magnoliales (Annonales) exhibited only one growth form of more than one, as long as one agrees to the only possible alternatives of: (1) one characteristic early habit form per group (*what* form it is depending on the taxon in question), and (2) two or more different growth habits per group, often still represented by some recent taxa descended from that group. However, one should exercise a good deal of caution before accepting the occurrence of the so-called "secondary" arborescent habit supposed to be derived from a truly herbaceous (therophytic) condition. The example mentioned by Stebbins, *viz.*, the shrubby to tree-like and usually more or less pachycaule centrospermous growth form, for instance, is highly suspect, because there is no cogent reason to accept a herbaceous habit form as the prototype. Cactaceae (*cf.* *Pereskia*), Didieriaceae, and some Portulacaceae, Nyctaginaceae and Phytolaccaceae are shrubby to arboreous, other, presumably more advanced, forms, are frequently suffruticose (Chenopodiaceae, Amaranthaceae). The centrospermous alliance is possibly one of the few taxa descended from a pachycaule (but not always monocaule) tree-like form

as postulated in Corner's Durian Theory. The incidence of "anomalous" forms of secondary growth in girth of several centrosperous taxa, adduced as an ancillary, or sometime even as the principal argument pleading in favour of a "secondary" advent of the tree habit in forms with truly herbaceous progenitors, is not necessarily relevant, because, as I have mentioned before, the early angiosperous plants may already have had more than one form of cambial activity and the rather "isolated" Centrospermae may have exhibited an "anomalous" stem anatomy from the very beginning.

REFERENCES

- BAILEY, I. W. (1957): The potentialities and limitations of wood anatomy in the study of the phylogeny and classification of Angiosperms. *J. Arnold Arbor.* **38**: 243-254.
- BANKS, H. P. (1967). (in the press)
- BECK, C. B. (1960): The identity of Archaeopteris and Callixylon. *Brittonia* **12**: 351-368.
(1966): On the origin of gymnosperms. *Taxon* **15**: 337-339.
- CARLUCCIO, L. M., F. M. HUEBER & H. P. BANKS (1966): Archaeopteris macilenta, anatomy and morphology of its frond. *Amer. J. Bot.* **53**: 719-730.
- CORNER, E. J. H. (1949): The Durian Theory or the origin of the modern tree. *Ann. Bot. (N.S.)* **13**: 367-414.
(1954): The Durian Theory extended. III. Pachycauly and megaspermy. *Phytomorphology* **4**: 263-274.
- HALLIER, H. (1912): L'origine et le système phylétique des Angiospermes exposés à l'aide de leur arbre généalogique. *Arch. néerl. Sci. Exact. Natur., Sér. III B*, **1**: 146-234.
- MEEUSE, A. D. J. (1961): The Pentoxylales and the origin of the Monocotyledons. *Proc. Kon. Akad. Wetensch. Amsterdam, C*, **64**: 543-559.
(1962): The multiple origin of the Angiosperms. *Advancing Front. Pl. Sci.* **1**: 105-127.
(1963): From ovule to ovary: A contribution to the phylogeny of the megasporangium. *Acta Biotheor. (Leyden)* **16**: 127-182.
(1965): Angiosperms - Past and Present. *Advancing Front. Pl. Sci. (Spec. Vol.)* **11**: 1-228.
(1966): *Fundamentals of Phytomorphology*. New York.
- MELVILLE, R. (1960): A new theory of the Angiosperm flower. *Nature* **188** (no. 4744): 14-18.
- STEBBINS, G. L. (1965): The probable growth habit of the earliest Flowering Plants. *Ann. Missouri Bot. Gard.* **52**: 457-468.
- TAKHTAJAN, A. L. (1959): *Die Evolution der Angiospermen*. Jena.
- ZIMMERMAN, W. (1959): *Die Phylogenie der Pflanzen*. (2nd. Ed.). Stuttgart.