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Recent palaeobotanical discoveries assisted by the thorough morphological analysis of 'living fossils' – archaic extant plants – have brought to light many unexpected features of the early angiosperms and their immediate precursors, while studies in palaeoecology have provided a basis for deciphering the chronology of evolutionary events and their environmental forcing. Our previous ideas of what is primitive and what angiosperm ancestors looked like are presently under revision. We now have a clearer picture of how macroevolution proceeds and how a large taxon could come into being.

Angiosperms pose evolutionary problems fascinating both by themselves and in a wider macroevolutionary context. For centuries their origins remained, as Darwin said, abominably mysterious. In effect, their phylogeny and systematics had a vanishingly thin historical foundation while morphological concepts remained arbitrary and often confused. We know what a flower is in the functional sense, but it is difficult to define it morphologically. Furthermore, the whole problem of evolutionary origin was reduced to 'when, where and from what', which are but minor components of the larger questions of 'how' and 'why'.

Comparative morphology and systematics seek to discover order in the immense diversity of angiosperms. It was tempting to reduce the diversity to a single archetypal (ancestral) structure or taxon. Morphological concepts of this kind were based on occasional similarities between organs of different categories (such as tepals and stamens) which, as we now know,

can simply be due to homeotic mutations¹.

The 18th century paradigm of plant morphology (the Goethe–De Candolle foliar concept) was that all organs are modifications of leaves – specifically, fern leaves, either sterile or fertile (sporophylls). Before the end of the 19th century the paradigmatic concept of the angiosperm organs was *sui generis* (or having no direct precursors); simple flowers as in Amentiferae were claimed to be primitive, and Gnetales were proposed as the nearest outgroup and probable ancestors (the Engler–Wettsteinian concept).

In the early part of the 20th century a rival theory of morphological evolution by reduction from a ranalean* flower of many parts to the simpler amentiferous one (Hallier–Bessey) came to the fore, reviving some of the 18th century concepts. Several systems appeared, invariably placing ranaleans (Polycarpicae, magnoliids) at the base as ancestral stock. Polyphyletic origins have been proposed from time to time but remained outside the mainstream of morphological thought.

These conceptual revolutions were guided by the comparative morphology of extant plants, or so it seemed. Palaeobotany was expected to provide hard facts, but most palaeobotanical facts were re-

jected as irrelevant. This attitude has persisted to this day in the writings of some influential botanists, due to a failure to recognize the intellectual impact of such palaeobotanical discoveries as:

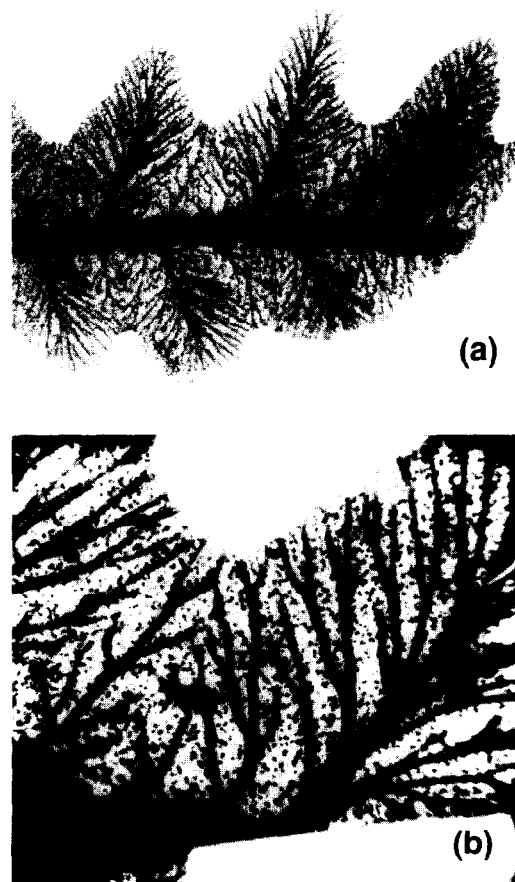


Fig. 1. Leaf of the peltasperm *Scytophyllum* (an extinct group of gymnosperms) showing: (a) fusion of pinnules; (b) incipient reticulation of veins in the coherent portion of the blade.

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*See Box 1 for definitions of this and other specialist terms used in this article.

Box 1. Editor's glossary

The field of angiosperm evolution is fraught with its own specialized but necessary terminology. The following brief definitions of terms used in this article are offered to assist the general reader.

Amentiferae: catkin-bearing angiosperms
asciform: pitcher-shaped
Bennettitales: an extinct gymnosperm order based on leaf fossils
biternic: of ovules with two outer coats (integuments)
Caytoniales: an order of mesozoic seed plants, intermediate between seed ferns and gymnosperms
chloranthoid: having affinity to the primitive dicot family Chloranthaceae
colpi: the apertures (pores, grooves or furrows) in the surface of a pollen grain
conduplicate: folded lengthways
cupule: a cup-shaped structure surrounding the fruit
cyperoid: having affinity to the sedge family, Cyperaceae
Czekanowskiales: an extinct order of pro-angiospermous woody plants with *Leptostrobus*-type cupules
ectexine: the outer layer of the coat of the pollen grain
endozoochorous: having seeds dispersed via animal guts
fasciculate: in a bundle, the members arising from the same point
gigantopterids: Lower Permian vascular plants with ribbon-like fronds

globose: globe-like or spherical
Gnetales: an order of gymnosperms (descended from the gnetophytes), whose extant genera are *Gnetum*, *Welwitschia* and *Ephedra*
gynoeceal valve: a segment of the gynoecium
Hamamelididae: a major and disparate subclass of angiosperms, containing orders such as Fagales, Urticales and Juglandales
interseminal bracts: bracts between or amongst the seeds
involute: with margins inrolled
macrosporophylls (= megasporophylls): the 'leaves' bearing the megaspores, which develop into female gametophytes in heterosporous plants
marginal meristems: the dividing cells at the leaf margin, which give rise to the plate meristem
microsporophylls: the 'leaves' bearing the microspores, which develop into male gametophytes in heterosporous plants (e.g. pollen grains in angiosperms)
monosulcate: of pollen grains with a single groove or furrow at the distal end
Neocomian: the first epoch of the Cretaceous
paeonoid: having affinity to the paeony family, Paeoniaceae
peltasperms: a seed-fern family from the Triassic
phyllome: any leaf or leaf-like organ
platanoid: having affinity to the plane family, Platanaceae
plate meristems: the dividing cells extending from the midrib to the margin of the

developing leaf, which give rise to the layered leaf tissues
plicate: with fan-like folds
proangiosperm: an early angiosperm in the process of evolving from some ancestral form
psilophytes: a primitive (Devonian) ancestral stock of vascular plants
racemose: having the form of a raceme – a kind of inflorescence with a central axis bearing flowers along its length
ranalean: belonging to the complex of primitive angiosperm orders that includes Magnoliales, Laurales, Piperales, etc.
ranunculoid: having affinity to the angiosperm family Ranunculaceae
seed ferns: a palaeozoic group of seed-bearing but otherwise fern-like plants
spicate: spike-like
syncarpy: condition in which the carpels are united
telome concept: a theory of how branching patterns and the disposition of organs evolved in vascular plants, based on morphological units or 'telomes'
tetrad: the body formed of four cells, originating by meiosis, from which the pollen grain is derived
triaperturate: of pollen grains with three apertures
tricolpate: of pollen grains with three furrows in the surface layer
triporate: of pollen grains with three pores in the surface layer
trochodendrids: members of the angiosperm family Trochodendraceae

(1) psilophytes, which inspired the telome concept as a viable alternative to the now obsolete foliar theory; (2) seed ferns, which replaced ferns in the models of angiosperm origin; (3) bennettitaleans, which promoted the ranalean concept of a primitive angiosperm; and (4) caytonialeans, which can be used as an outgroup in phylogenetic analysis of angiosperm traits.

At present, palaeobotany is taking the lead in the development of a new paradigm. New fossil plants with angiospermoid characters have helped in formulating the pro-angiosperm concept² (see below). Studies of mid-Cretaceous flowers have shown what the primitive flowers were like². Angiosperm entry into the fossil record has been documented by palynological analysis^{3,4}. Due attention has been paid to the palaeoecology of early angiosperms^{5,6}. These results have been augmented by painstaking morphological analysis of the supposedly primitive extant angiosperms⁶⁻⁹, as well as by cladistic analysis of gymnosperm-angiosperm relationships^{10,11}. In effect, the factual and conceptual bases of a new paradigm have been laid

down, although a consensus has not yet been reached on many essential issues.

Morphological evolution

Because fossil plants are usually preserved as separated organs, palaeobotanical data are better suited for historical analysis of different traits than of whole-plant evolution. In addition, separate evolutionary histories of different organs are justified by the fact that organs in plants are less developmentally correlated than they are in animals.

In the following examples, the fossil record suggests some hitherto unconventional homologies between ancestral and descendant organs.

Leaf

The typical angiosperm leaf is broad with reticulate venation showing several orders of meshes. Superficially similar leaves occur in ferns, but here they grow by a marginal meristem while in angiosperms there are two kinds – marginal and plate meristems. Extant gymnosperm leaves are entirely different (except in *Gnetum*), but

in the extinct gymnosperm groups of gigantopterids and peltasperms entire or lobed angiosperm-like leaves had evolved by parallel evolution from the fern-like precursors.

Fortunately, various evolutionary stages are preserved showing how the angiosperm leaf might have arisen. Initially, the original segmentation is evident in the entire blade because venation remains as it was in the ancestral bipinnate leaves. Obviously, the segments fuse marginally and the fusion meristem, while incorporated in the blade, still retains the marginal developmental program of not producing veins (which normally develop from submarginal initials). It is known, however, that fusion meristems readily change their developmental programs and even acquire new functions. Actually, more advanced stages of leaf fusion show reticulations in the zones of former fusion, suggesting that the fusion meristem evolved in the direction of what is now plate meristem in angiosperm leaves. Ultimate stages are not unlike the early angiosperm 'disorganized' reticulate venation (Fig. 1).

This example illustrates what may

be very typical for angiosperms: their superficially simple organs are condensed systems of ancestral organs (incidentally, leaves could be condensed fronds or leafy shoots) containing fusion meristems which made them developmentally plastic.

Flower

In a typical flower, the floral apex produces fertile organs – pistils and (or) stamens surrounded by sterile tepals. Some flowers, however, have sterile appendages – inner phyllomes – between stamens and pistils. These occur mostly in primitive magnoliids and hamamelids such as *Liquidambar*. Actually, such flowers are slightly modified dwarf shoots with fertile and sterile organs mixed in the apical zone, as in *Ginkgo* or Bennettitales. On the other hand, a fertile shoot of *Irania*, a Jurassic proangiosperm¹², can be reduced to a flower without inner phyllomes. Thus, in support of theoretical postulates by Meeuse¹³, prototypes for at least two types of flower can be found among Mesozoic gymnosperms.

Stamen

Though traditionally seen as derived from microsporophylls, stamens (or at least some of them) show anatomical features of axial rather than foliar organs. Moreover, in some families there are fasciculate stamens arising from a common primordial knob. Their prototype could be a profusely branched sporangial system. Recently, a Cretaceous pollen organ was discovered that appears as an ideal prototype for a fasciculate stamen¹⁴. It is an axis bearing lateral branches, some of which are sterile, while the others give off a pair of stalked subapical sporangial heads with a scaly sterile apex between them (Fig. 2). When their stalks are reduced, the sporangial heads appear not unlike the thecae of a typical angiosperm anther, with the sterile apex as a protruding connective. Thus, a stamen fascicle could be a condensed shoot of coaxial sporangial systems, with stamens – its lateral branching systems, and thecae – the ultimate branches.

Pollen

While monosulcate angiosperm pollen grains are obviously related

to gymnosperm pollen of the same apertural type, the tricolpate and triporate grains that appeared slightly later are not readily derivable from any pre-existing pollen morphologies.

A solution could be a derivation of the triaperturate type not from a single prototypal grain but from a permanent tetrad¹⁵. Early Cretaceous tricolpate grains are similar to early monosulcates in exinal structure. Each lateral face of such tricolpates showing one of the colpi resembles the distal face of a monosulcate grain. Permanent tetrads occur in angiospermoid plant groups such as Hirmeriaceae (*Classopollis*). Moreover, permanent tetrads with common ectoexine have been found in the Lower Cretaceous deposits¹⁶. While this

condition was achieved that early, it is conceivable that a final step in turning such tetrads into grains was made by pushing meiosis one cell cycle backwards.

Pistil

In the face of terminological confusion, it seems necessary to define pistils as gynoecial organs containing ovules and providing structures for extraovular pollination, while carpels are structural units of pistils. A pistil can be formed by one or several carpels, while a gynoecium consists of one to many pistils.

Current interpretations of carpels as involute, conduplicate or ascidiform macrosporophylls are remnants of the classical foliar theory created at the time when neither ontogeny nor relevant fos-

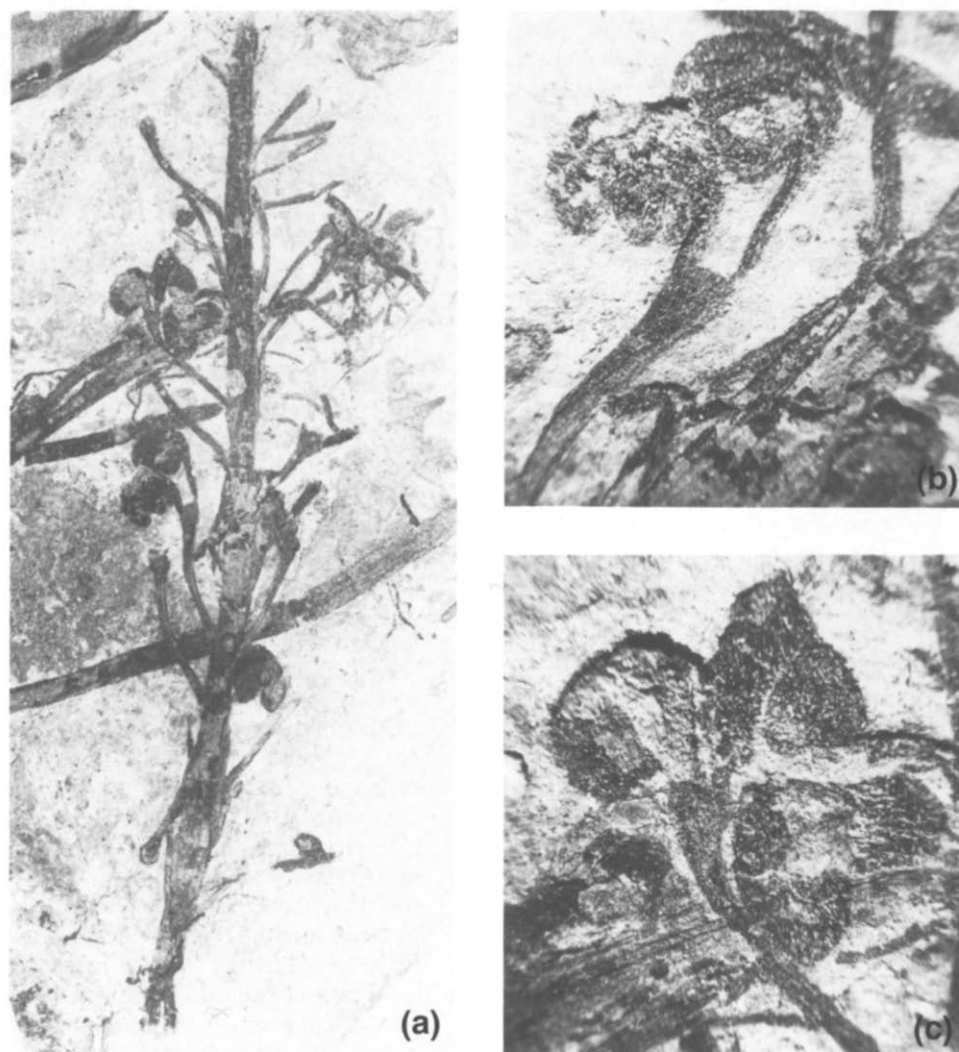


Fig. 2. *Meeusella*, a possible prototype of a stamen fascicle. (a) Branching staminate shoot. (b) Lateral branch with a pair of stalked subapical sporangial heads. (c) Another branch with the subapical sporangial heads condensed in an anther-like structure¹⁴.

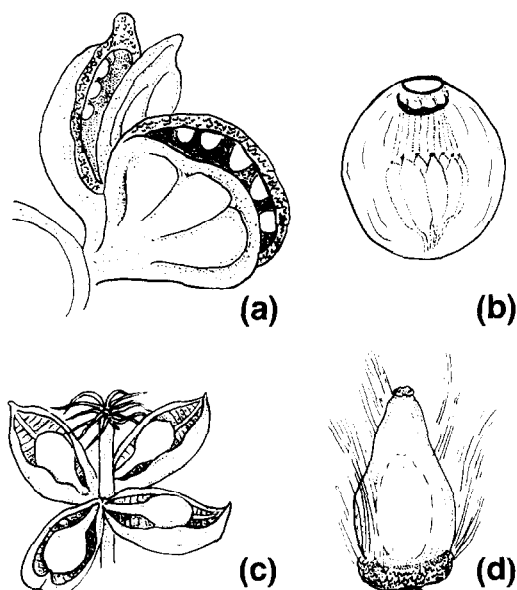


Fig. 3. Possible prototypes of pistils and stigmas. (a) *Leptostrobus*, showing bivalved cupules with stigmatic crests. (b) *Caytonia*, showing a globose cupule with a slit-like mouth covered with a vestigial supporting bract ('lip'). (c) *Eoantha*, showing a four-valved gynoecium with protruding axis and a fascicle of slender bracts on top of it. (d) *Baisia*, showing a flask-like cupule with apical 'corona'^{15,20}.

sils were known. Now we know several types of pistil-like cupule produced by Jurassic and Early Cretaceous proangiosperms. Among them, *Caytonia* (a globose cupule with a slit-like opening and many anatropous ovules) resembles the ascidiform dorsally plicate carpel as in Ranunculaceae¹⁷, while *Leptostrobus* (a bivalved cupule with papillate marginal crests and submarginal ovules) looks not unlike the carpels of primitive extant Winteraceae once considered paradigmatically conduplicate (Fig. 3). *Leptostrobus* valves are fused open cupules and the stigmatic crests seemingly evolved from their fusion meristem.

At the same time, bennettitaleans and gnetophytes produced cupules of fused interseminal or subtending bracts containing basal orthotropous ovules (Box 2). In *Eoantha* (of gnetalean affinity)¹⁸ there were four gynoecial valves with an orthotropous ovule each, crowned

by a fascicle of slender bracts – a possible precursor of a bushy stigma.

Thus, syncupuly – cupule fusion – preceded syncarpy, which appeared as early as the mid-Cretaceous as a second round of fusion, and there was more than one prototype of stigmas.

Double fertilization

Whether double fertilization is a unique character of angiosperms or whether it is shared with gnetophytes (and supposedly other proangiosperms of the same evolutionary grade) depends on the homology of the embryo sac nuclei. In angiosperms, double fertilization involves egg and polar nucleus (or nuclei) while in *Ephedra* it is egg and ventral canal cell¹⁶. However, the polar nuclei may correspond to gymnosperm eggs, while the angiosperm egg could be a sexualized ventral canal nucleus¹⁹. The double fertilizations in *Ephedra* and angiosperms would then be strictly homologous.

To conclude, not a single angiosperm character is unique to the group. Absolute boundaries, cherished by typological thinking, just do not exist. Most typical angiosperm structures have obvious precursors (and sometimes more than one) among gymnosperms. As in the case of stigmas and double fertilization, the structures were ready; angiosperms had only to find a new function for them. When there is a structural gap, some radical restructuring can be suspected. More often than not it was a condensation of developmental processes. Multiple fusion meristems with their readily changeable genetic programs could in turn add to the structural plasticity of angiosperms.

Phylogeny

Phylogenetics seeks to reproduce historical relationships between taxa. Though much attention has been paid recently to the methods of constructing phylogenetic trees, phylogenetics depends primarily on ideas of homology (above) and actual chronology of evolutionary events as represented in the fossil record.

Among the early angiosperm records, flowers (though infrequent) provide phylogenetic information of

primary importance, augmented by subordinate evidence from fruits, wood, leaves and pollen grains. Lower Cretaceous floral organs indicate lineages of chloranthoid, ranunculoid, paeonioid and platanoid affinities^{20–23} (Fig. 4). Most Lower Cretaceous leaves with cuticles are assignable to these groups²⁴, while a few more dicot and some unassigned monocot groups are suggested by leaf impression and pollen records.

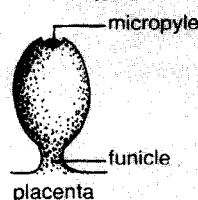
In the late Albian and early Cenomanian, about 100–95 million years ago, angiosperms underwent explosive evolution, which produced inflorescences and single large flowers showing generalized magnoliid, hamamelid and rosoid characters^{25–30}. The dominant group – *Normapollis*, pollen-producing plants of diverse floral morphology – might comprise ancestral forms of the Myricales, Juglandales and Fagales³¹.

Basic differentiation of the major angiosperm groups was thus accomplished. Such mid-Cretaceous forms as *Asterocelastrus* (Fig. 5), with a syncarpous ovary fused to a calyx cup³⁰, look quite modern and by conventional standards even more advanced than many extant rosids. Previously there was a tendency to lump the earliest chloranthoid, platanoid and paeonioid angiosperms with some later-appearing stocks. Systematists have now to reconsider their ideas of both the primitive–advanced character polarities and the basic taxon.

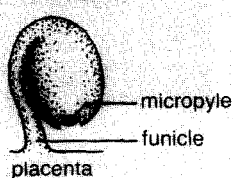
Strikingly, the mid-Cretaceous representatives of the major angiosperm stocks are morphologically no less distant from each other than they are from their extant descendants. Floral organization could be initially more 'open' (plastic, capable of producing extreme variations)³². No transitional forms are known, however, between gynoecia with a single basal orthotropous ovule developing from the floral apex, as in Myricales, and carpels bearing several to many anatropous ovules. Moreover, similar differentiation existed among Mesozoic proangiosperms, gnetaleans and bennettitaleans with cupules containing a single basal orthotropous ovule on the one hand, and the caytonialean–czekanowskialeans with cupules bearing many anatropous ovules on the other.

Box 2. Types of ovule

Orthotropous



Anatropous



Among the early angiosperms, the 'orthotropous' group includes platanoid, chloranthoid, cyperoid and somewhat later-arising myrioid forms, each of which can stem from different ancestors within the bennettitalean–gnetalean grade, while the 'anatropous' stock is represented by ranunculids, magnoliids, hamamelids and *Cercidiphyllum*-like trochodendrids. The anatropous group can be further subdivided into magnoliids–hamamelids with intrafloral phyllomes, and ranunculids–trochodendrids without them. While this distinction points to different flower prototypes, the monosulcate/tricolpate dichotomy marks out magnoliids from both hamamelids and such forms as *Illicium* or *Schizandra*, sometimes erroneously included in the Magnoliales but more convincingly assignable to the ranunculid–trochodendrid group.

Historical analysis thus provides a few distinctive characters that go back to the base of angiosperm phylogeny and even further down the proangiosperm level. They define lineages fairly distinct at the time of their first appearance, which hence were probably related to different groups of proangiosperms, as shown in Fig. 6.

Exact rooting of the basic angiosperm stocks can be accomplished after the remaining larger gaps in the fossil record (and the conceptual biases) have been removed. At present it appears that the long-neglected polyphyletic model is in the ascendant. It reconciles the Englerian and Hallierian concepts, which were seen as mutually exclusive for almost a century. It is for palaeoecology to explain why angiosperm characters appeared in more than one lineage.

Palaeoecology

Early angiosperms are almost universally conceived now as weedy *r*-strategists^{33,34}. However, the pre-Albian records are very rare, even though weedy plants tend to be abundant in the vicinity of the frequently flooded areas favourable for deposition of plant remains. During the Mesozoic era, such areas were occupied by horsetail (*Equisetum*) fern marshes, czezanowskias, swamp conifer forests and cycadophyte shrublands that ex-

tended into mesic ginkgo–conifer upland forests. Recent findings add gnetophytes as important components of both cycadophyte and czezanowskialean shrublands that occupied stream-side and seashore habitats.

In the beginning of the Cretaceous period, fern marshes were drastically reduced in northern hemisphere middle-latitude temperate–subtropical ecotonal areas such as Mongolia³⁵. They were replaced by some vanguard members of the shrubland cycadophyte–gnetophyte community. The first mid-Neocomian angiosperm fossils appeared at this stage of ecological evolution.

The second mid-Cretaceous stage coincided with the rapid decline of czezanowskialeans and bennettitaleans as dominant members of the middle-latitude shrubland communities. Immediately after that there was a steady increase in abundance and diversity of angiosperms.

Early angiosperm evolution may thus have been episodic, and closely linked with the history of certain gymnosperm communities. A notion of gymnosperms being out-competed by angiosperms is unlikely because angiosperms were far too rare before the bennettitalean extinction, which obviously correlated with the mid-Cretaceous environmental crisis³⁶. In disturbed environments, former dominants were replaced by some minor species in which condensed development was combined with more effective reproductive systems. Innovations included pollen with the exinal features of self-incompatibility syndrome³⁷ and stigmas as counterparts of the same mechanism. Both features could develop from different gymnosperm precursory structures³⁸.

Lower Cretaceous angiosperms had small inconspicuous flowers clustered in spicate, racemose or globose inflorescences. They could be pollinated by wind, dipteran insects or both. Larger pollinators, such as beetles, might have preferred the sturdy flower-like cones of bennettitaleans. It is hardly a coincidence that single large flowers of many parts, resembling bennettitalean cones (hence rendered primitive), appeared soon after the extinction of bennettitaleans, which

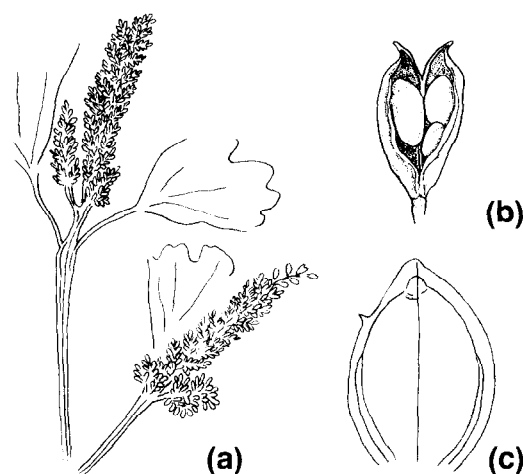


Fig. 4. *Caspiocarpus*, an Early Cretaceous angiosperm. (a) Shoot bearing paniculate inflorescences. (b) Dehiscent follicle. (c) Bitegmic ovule²⁰.

emptied the reproductive niche of beetle pollination.

The advent of comparatively small-leaved early angiosperms would have reduced total leaf mass, thus imposing dietary and related dental changes in dinosaurs. New groups with beaks and strong dental batteries, such as ceratopsids or hadrosaurs, were able to consume whole twigs with leaves and fruits. They in turn created a selective pressure in favour of endozoochorous seeds and fruits such as those recently found in coprolites³⁹.

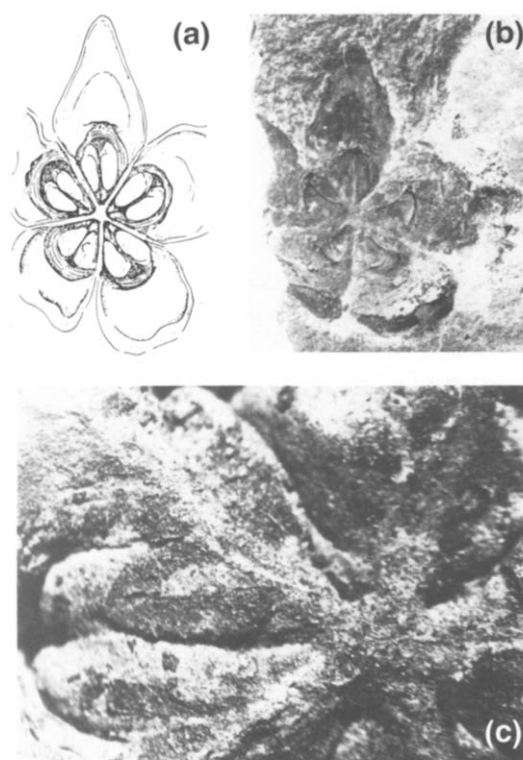


Fig. 5. *Asterocelastrus*, a mid-Cretaceous rosoid flower showing 'advanced' features of syncarpy and calyx to ovary fusion. (a) Dehiscent five-loculate capsule, drawn from (b). (c) Basal anatropous ovules³⁰.

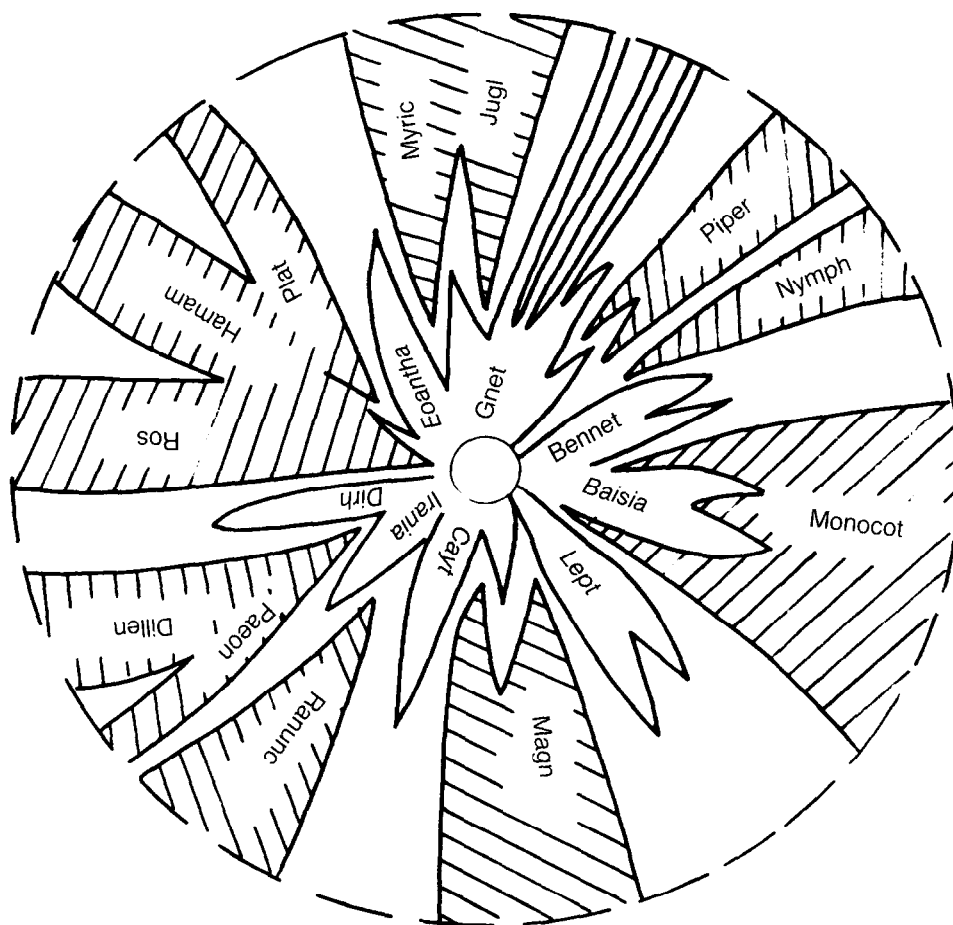


Fig. 6. Schematic phylogenetic relationships of the early angiosperms (Hamamelidales, Juglandales, Magnoliales, Myricales, Nymphaeales, Paeoniales, Piperales, Dilleniaceae, Rosales) to proangiosperms (*Baisia*, Bennettitales, *Caytonia*, *Dirhopalostachys*, *Eoantha*, Gnetales, *Irania*, *Leptostrobis*).

To conclude, successive global environmental crises of the mid-Neocomian and Albian-Cenomanian times may have selected plants with condensed life histories capable of filling empty ecological niches. Each adaptive innovation appearing in a single lineage opened a new ecological niche, thus promoting similar innovations in other preadapted lineages. Evolutionary 'fashions', such as angiospermy, could arise in this way. From what is now known of viral gene transfer mediated by fungi and bacteria⁴⁰, one can speculate that 'horizontal' spread of a new trait among coevolving lineages could be facilitated by this mechanism. Parallel evolution could be seen then as a joint effect of the 'fashion-monger chase' and non-sexual gene delivery. These hypotheses need now to be tested from palaeobotanical, morphological and genetical points of view.

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