

THE ORIGIN OF ANGIOSPERMS

V. A. KRASSILOV

*Institute of Biology and Pedology
Far-Eastern Scientific Centre
Vladivostok, USSR*

They would never change because they'd given their character too soon.

TRUMAN CAPOTE, *Breakfast at Tiffany's*

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ABSTRACT

The claim of monophyletic origin of angiosperms arose from the confusion of phylogenetic and taxonomic concepts. Unpreconceived studies of extant angiosperms point to more than one archetype. Several lines of angiosperms have simultaneously entered the fossil record; the monocotyledons, proto-Hamamelidales, proto-Laurales and "proteophylls" (possibly ancestral to the Rosidae) are recognized among them. Three groups of Mesozoic seed plants — the Caytoniales, Czekanowskiales and Dirhopalostachyaceae — are distinguished as major sources of angiosperm characters (proangiosperms). Other Mesozoic lineages probably also contributed to the angiosperm character pool. Angiospermization is related to Mammalization and other processes involved in development of the Cenozoic lithosphere and biosphere.

РЕФЕРАТ

Представление о монофилетическом происхождении покрытосеменных сложилось в результате смешения филогенетических и таксономических принципов. Непредвзятый анализ современных цветковых указывает на более чем один архетип. Несколько линий покрытосеменных одновременно появились в палеонтологической летописи, среди них наиболее важны однодольные, прото-гамамелидовые, протолавровые и "протеофиллы" (возможно, предки розоцветных). Главным источником ангиоспермных признаков могли быть три группы мезозойских семенных растений — кейтониевые, чекановские и диропалостахиевые (проангиоспермы). Другие группы также, возможно внесли свой вклад в "фонд признаков". Ангиоспермизация сопряжена с маммализацией и другими процессами, ведущими к формированию литосферы и биосферы.

INTRODUCTION

In the light of recent paleobotanical work, the origin of flowering plants appears not so sudden and less mysterious than only ten years ago. Palynology was especially instrumental in demonstrating steady rise of the early angiosperms from the Barremian to Senonian (115–70 BP) both in abundance and diversity (Hughes, 1961; Kemp, 1968; Doyle, 1969; Muller, 1970; Pačtová, 1970). A parallel trend in the leaf evolution was recognized by Hickey and Doyle (1972). This hand in hand increase in density and diversity leaves little room for the previously widely held view of the angiosperms reaching their nearly present day diversity in small upland populations doomed for oblivion because of imperfect recording.

Another important fact is that the angiosperm density-diversity increase was universally synchronous. No large areas are left unexplored, and still no country can be singled out as the place where flowering plants have matured before conquering the world, though the tropical and southern hemisphere initial records are somewhat earlier than those of the northern hemisphere middle latitudes (Doyle, 1969; Dettmann, 1973).

G. G. Simpson, Teilhard de Chardin and other authors have claimed the automatic truncation of the phylum base because of small initial populations and quantum evolution. However it is more probable that megaevolutionary events occur during a rash-crash-founder cycle in fluctuating populations (Carson, 1975) which are periodically very large and, thus, have a good chance of fossilization. The rash-crash hypothesis is of course only one of several suggested ways out of the allelic space available for microevolutional differentiation up to megaevolution. However, the general situation in genetics at present does not force paleontologists to yield to the claim of particularly small initial populations.

Major contributions to the problem of angiosperm origins (such as the interpretation of *Caytonia* or *Leptostrobus*) were made by paleobotanists who, like T. M. Harris, never undertook the special search for angiosperm ancestors, but thoroughly studied large regional taphofloras. This may witness the perfection of the fossil record. Studies of the Mesozoic gymnosperms have reached the stage when any discoveries of completely unknown extinct groups are unlikely, although further reinterpretations are to be expected.

Thus, imperfection of the fossil record can no longer be the sole excuse for still unsolved problems of the angiosperm ancestry and phylogeny. These problems can be approached from several directions, such as (1) unpreconceived phylogenetic analysis of the living angiosperms, (2) a more realistic estimation of the early angiosperm diversity, not biased by unsound taxonomical practice of "leaf paleobotany", (3) revision of the Mesozoic gymnosperm morphology, (4) clarifying the ecological significance of angiospermy and paleoecology of angiospermization.

EXTANT ANGIOSPERM EVIDENCE

The "law" of irreversibility and the principle of uniquely derived characters are among the most detrimental phylogenetic preconceptions. When Aristotle produced his *scala naturae*, he made an important step toward taxonomic order. But when Lamarck tied taxonomy to phylogeny, this taxonomic design entered phylogeny as the preconception of irreversible progress. Romer (1949) said that "adherence to this creed (i.e., the law of irreversibility) has made it difficult to develop reasonable phylogenies for various groups for which there is an abundance of fossil material, and it has been responsible in many cases for the supposition that successive representatives of a group have not descended one from another but that the known types are a series of side branches from an unknown main line of 'unspecialized' forms".

Similarly, the concept of uniquely derived characters was forced into phylogeny by the taxonomic principle of referring a unit to only one unit of higher order. Parallel acquisition of such angiospermous characters as vessels, closed venation, bisexual floral organs and ovuliferous capsules in different lineages is amply documented, while parallel development of the multiaperturate pollen grains in response to germination on the stigma (Hughes, 1976) or the double fertilization in response to female gametophyte reduction is not inadmissible to the unpreconceived mind.

Pallas (1766) had proposed tree-like classification long before Darwin and with no reference to phylogeny. It is implicit for this type of classification that all basic units are connected via the cladistic member of a group. Thus, when phylogeny is introduced, only monophyletic groups are permitted. However, a classification is natural only when it epitomizes our current understanding of the nature, and the grades are the "facts of nature" (Huxley, 1942) and of the utmost importance for understanding the laws of evolution (not of disguised taxonomy).

Parsimonious grouping can be achieved by using only one set of characters, e.g., floral characters in angiosperms, and the Englerian system or its derivatives are good examples of it. Systems based on different character sets can be tested by the parsimony criterion, which has no reasonable application in phylogeny. In phylogenetic reconstructions, one considers as many morphoclines as possible, and the ancestor-descendant lines are deduced from similar successive relations in the majority of morphoclines. Major splittings in the angiosperms occurred some 65 m.y. BP or earlier, and their phylogenetic relations are obscured by mosaic evolution causing almost inevitable intersection of character clines.

It is often said that, e.g., the vesselless woody forms are primitive. A more correct statement would be that the vesselless condition is marginal in one of numerous character clines, though phylogenetically it may be either ancestral

or derived. In their secondary xylem, the Hamamelididae are more advanced than the Magnoliidae, but phytochemical studies have shown the Hamamelididae to be more primitive (Bate-Smith, 1972). The latter order was believed to be linked to the Magnoliidae via *Trochodendron*, *Tetracentron* and *Euptelea*, all of them having the same basic Caryotype. However, recently corrected chromosome counts no longer bridge the gap between these subclasses (Ratter and Milne, 1973). "Primitive" angiosperms of the Magnolialean plexus are remnants of ancient polyploid complexes. Therefore one may expect them to show some ancestral characters, such as "disorganized" venation in the Winteraceae observed also in some Early Cretaceous leaves (Wolfe in Doyle, 1969). However, the Magnoliidae are highly specialized in respect to pollination ecology (Thien, 1974), display rather advanced chemical composition (Bate-Smith, 1972) and maintain an apical position on the cytochrome *c* tree (Boulter et al., 1972), while the heterogeneity of their Caryotypes, vascular anatomy of stamens and carpels (Bhandari, 1971), sieve-tube plastids (Behnke, 1973) and other characters may evidence very remote common ancestry or more than one archetype.

Blagovestchensky (1975) studied the seed proteins of the Cycadales and angiosperms and recognized several parallel clines from the globulin-poor to globulin-rich taxa. The Laurales and *Liquidambar* are at the globulin-poor end of two separate clines. The Magnoliales are generally globulin-rich.

Meeuse (1970) has concluded that both phytochemical and morphological evidences for angiosperms are in favour of polyphyly. He recently revised the floral morphology of the Polycarpicae and suggested that the Laurales were most primitive, their flowers close to ancestral anthocorm which had been derived directly from the Caytonialean prototype. Khokhrjakov (1975) undertook comprehensive survey of the monocotyledons and furnished convincing evidence of their derivation directly from gymnospermous ancestors instead of early divergence from the dicotyledons.

Other authors (Heslop-Harrison, 1958; Tikhomirov, 1972; Philipson, 1974) have also recognized fairly isolated lines of angiosperms, not easily derived from each other. They followed Heslop-Harrison in suggesting monophyletic origin of angiosperms from progenitors with extremely flexible floral organization. Heslop-Harrison considered also the possibility of pachyphyletic origin, and Cronquist (1968) held that the distinctive syndrome of angiosperm features was acquired by parallel evolution from a set of similar gymnospermous taxa (in the latter case, the angiosperms are polyphyletic by definition, since their most recent common ancestor is not a cladistic member of the group, see Ashlock, 1974). These alternative possibilities are to be tested by estimating the actual diversity and versatility of the early angiosperms.

EARLY ANGIOSPERMS

The Barremian age about 120 m.y. BP is now widely accepted as the starting point of angiosperm evolution, with almost all earlier claims eventually rejected. However, any deadline creates "abominable mystery", and the origin of angiosperms may be viewed as an additive process of "character pool" accumulation rather than an appearance of full-fledged flowering plants. The "character pool" approach encourages further search for angiospermous characters in pre-Barremian plants.

None of the Jurassic or Early Cretaceous angiosperm-like fructifications resemble to any extent the present day "primitive" angiosperms. *Problematospermum* from the Upper Jurassic of Karatau is like the Compositae achene. The Bennettitalean affinities are claimed on the cuticular evidence (Krassilov, 1973a). The *Tyrmia* spiny capsules (*Tyrmocarpus*) are like some fruits in the Proteaceae (Krassilov, 1973b). *Onoana* from the Early Cretaceous of California (Chandler and Axelrod, 1961) is compared to the Icacinaceous fruits, though assignment to this family is premature. No structural details are known for the Jurassic fruit-like *Sogdiania* (Burakova, 1971) or Early Cretaceous *Kenella*, *Nyssidium* and *Ranunculicarpus*, and these fossils may as well be seeds or tubers. The Siberian mid-Jurassic "*Ephedrites*" of Heer (1876) is another overlooked fruit-like body. *Macrotorellia* from the Early Jurassic of Caucasus (Fig. 1) resembles a typical monocotyledonous leaf in the blade plication and apical convergence of the veins. Vakhrameev (1973) depicted a small leaf or leaflet showing angiospermous venation from the Neocomian (?) of the Baikal region. These fossils deserve further study.

The Aptian or early Albian angiosperm-like leaf fossils from the Potomac Group (Arundel-Patuxent: Fontaine, 1889; Doyle and Hickey, 1972; Doyle, 1973) are of very diverse morphology. Doyle postulated monocotyledonous affinities of the *Acaciaephyllum* leafy stems. Other leaves originally described as *Ficophyllum*, *Proteaephyllum* and *Rogersia* are presumably dicotyledonous. The leaf architecture is variable, though the extreme leaf forms, treated as separate genera intergrade and share some "primitive" venation characters.

The Aptian and early Albian angiosperm leaves are known from South Primorye, near Vladivostok (Krassilov, 1967). The age assignments are supported by marine invertebrate evidence. Other presumably Early Cretaceous records from eastern Asia lack rigid stratigraphic control and are at least par-

Figs. 1-3. Enigmatic Mesozoic plants. →

Fig. 1. *Macrotorellia hoshayahiana* Krysh. from the Lower Jurassic of Caucasus, the leaf with monocotyledonous venation. × 1.

Figs. 2 and 3. *Sujfunophyllum dichotomum* Krassil., small leaves of *Scoresbya* group associated with the Albian angiosperms, × 5 (after Krassilov, 1967).



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tially not Albian but Turonian (Krassilov, 1975a). Only two angiosperm fossils are described from the Aptian of South Primorye below *Trigonia* beds. They are monocotyledonous *Pandanophyllum ahnertii* Krysht. (Fig. 9) and dicotyledonous "*Aralia*" *lucifera* Krysht. (Figs. 5, 6). The choice of the generic name is misleading in the latter case, the leaves looking rather like diminutive *Exbucklandia* or *Liquidambar*. "*Aralia*" *lucifera* extends into Albian where it is joined by *Cissites*, "*Sassafras*", *Sapindopsis*, *Laurophyllum* and some other angiosperms. Among them, *Sapindopsis* may be related to the Patuxent angiosperms. Other leaf types are fairly "modern" (percurrent tertiary venation and areolation well developed though partially obliterated: Figs. 7, 8), with no reasonable connections either with "Patuxent angiosperms" or between the Hamamelidalean and Lauralean morphotypes. These early Albian angiosperms associate with *Sujfunophyllum* (Figs. 2, 3)—small leaves showing intricate segmentation characteristic of the *Scoresbya* group (see below under "proteophylls").

The earliest allegedly angiospermous pollen grains appear simultaneously with the leaf megafossils or an age/stage earlier. Doyle (1969, 1973) concluded that total diversity of the Albian angiosperm pollen grains "could probably be accommodated in two or three closely related orders and perhaps five or ten families". He suggested further, that the Albian dicotyledons belonged to the Magnoliidae and lower Hamamelididae. He favoured the monophyletic origin of angiosperms from pre-Albian ancestors producing the monosulcate *Clavatipollenites* pollen grains which gave rise to both tricolpates and monocotyledonous monosulcates. While the latter line from *Clavatipollenites*-*Retimonocolpites* grade to more advanced monocotyledonous *Liliacites* is well documented, any intermediates between *Clavatipollenites* and the Albian tricolpates are lacking. Both monosulcates and tricolpates come from the Aptian of Japan (Takakashi, 1974) and some tricolpate records are even older.

Thus, more than one angiosperm lineage entered geological record in the Aptian and Albian. In the following discussion I would trace these lineages up to the late Maestrichtian when the Betulales, Fagales, Juglandales, Urticales, Salicales and Fabales were raised to dominant status. Here the early angiosperm story ends.

←

Figs. 4-9. Early Cretaceous leaves from Primorye representing three major groups of the early angiosperms.

Figs. 4 and 5. "*Aralia*" *lucifera* Krysht., small leaf showing Hamamelidaceous characters, $\times 2$ and 3.5 .

Fig. 6. *Laurophyllum* sp., the leaf with incurved margins, $\times 1.5$.

Figs. 7 and 8. *Laurophyllum* sp., tertiary venation, $\times 3$ and 8 .

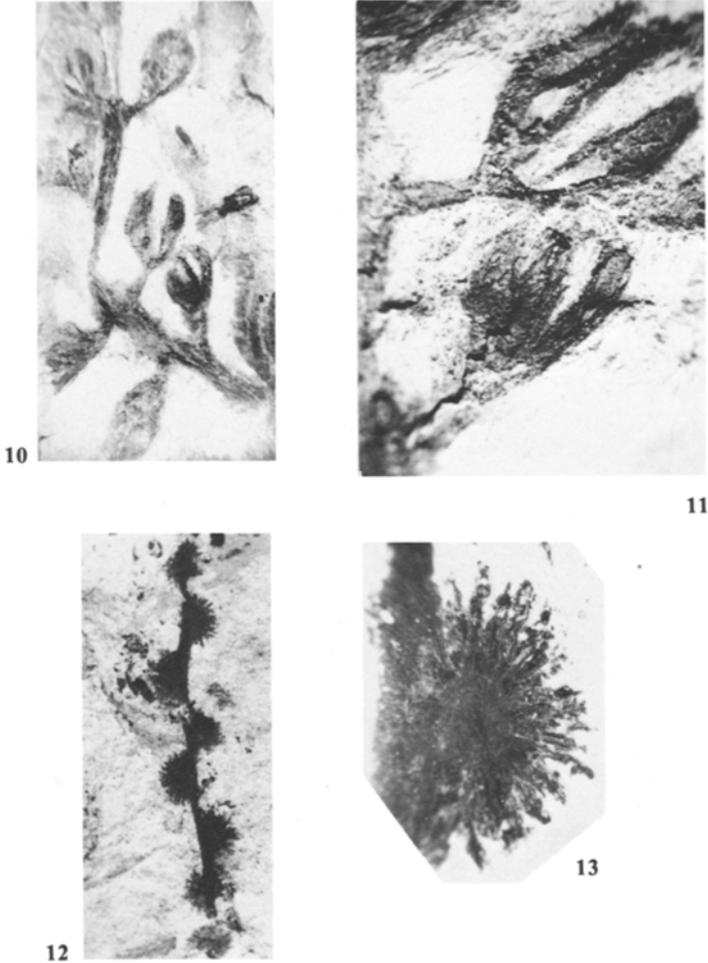
Fig. 9. *Pandanophyllum ahnertii* Krysht., linear leaf showing marginal teeth, $\times 8$.

Hughes (1976) has listed 28 extant angiosperm families which are known from the Cretaceous and have an advancement index of Sporne (1972) below 45. I believe that critical evaluation of Cretaceous records would cause a considerable reduction of this number.

Flowers and fruits are underrepresented in the fossil record and the pollen grains or leaves are more indicative of the early angiosperm diversity. However, the pollen grain taxonomy is suffering from oversplitting and the affinities of the Cretaceous form-genera are mostly uncertain. The diversity of Cretaceous angiosperm leaf types is exaggerated by unfortunate assignments of the same leaf type to various extant genera and substitutions of valid form-generic names in response to subjective taxonomic judgments. Nevertheless, the leaf gross morphology must not be ignored in phylogenetic reconstructions. It appears that fidelity to initial leaf shape is characteristic of many angiosperm lineages. Thus, the following morphological classification is hoped to be not without phylogenetic sense, despite unavoidable lumping of convergent leaf forms. The warning of "backwards systematics" (Hughes, 1976) is fully appreciated, though tracing extant connections is of no minor interest.

1. *Trochodendroides*

The aspen-like leaves had been attributed to *Populus* by classical authors. Berry (1922) had transferred them to *Trochodendroides* implying assignment to the *Trochodendron-Tetracentron-Cercidiphyllum* complex. Subsequent attribution to *Cercidiphyllum* or *Tetracentron* was based on misinterpretation of associated *Trochodendrocarpus* or *Nordenskioldia* fructifications. Smooth-edged specimens were sometimes referred to *Cocculus*, *Paliurus* or even *Smilax*, while minutely serrate ones were described as *Zizyphus*. Several authors have claimed heterogeneity of *Trochodendroides arctica* complex and distinguished the leaves of *Cocculus*, *Cercidiphyllum*, *Tetracentron* and other extant genera by minor venation characters. The preponderance of *Cocculus* has rather odd ecological implication of the Cretaceous vegetation dominated by climbers. In my opinion, *T. arctica* is a fairly natural unit in the sense that it is not easily divisible into two (this practical definition of what is natural in taxonomy belongs to T. M. Harris). In fact, two not sharply delimited blade shapes are distinguishable. They usually go together and possibly represent the long- and short-shoot foliage. Many leaf characters are extremely polymorphic and the "*Cocculus*", "*Cercidiphyllum*", or "*Tetracentron*" specimens can be recognized in any sufficiently large sample from Asiatic or North American localities. Only one type of fructifications, i.e., *Trochodendrocarpus*, repeatedly associates with *T. arctica*. These fructifications are large panicles which have been assigned to Hamamelidaceae on the evidence of fruit pairing and the mode of dehiscence (Krassilov, 1973b). Widely held attribution to *Cercidiphyllum* is unwarranted.



Figs. 10-13. Fructifications of the Late Cretaceous angiosperms.
 Figs. 10 and 11. Fructification of the *Cercidiphyllaceae* affinity from the Senonian of Sakhalin, $\times 2$ and 7.
 Figs. 12 and 13. *Platanus*-like fructification from the Late Cretaceous of the Amur province, $\times 1$ and 7.

Figs. 10-11 show an axis bearing clustered follicles comparable to those of extant *Cercidiphyllum*, though of smaller size. The specimen came from the Santonian of North Sakhalin together with numerous "zizyphoid" leaves of *T. sachalinensis* (Kryshch.) Kryshch. (Kryshchovitch and Baikovskaya, 1960). *Nordenskioldia* fructifications have been attributed to this leaf type by Krysh-

tofovich. My comparison of *Nordenskioldia* with *Trochodendron* (Krassilov, 1971a), though based on fairly representative collection, now appears to be misleading.

2. Platanophylls

Two living species of *Platanus* have elongate leaves rather similar to *Castanea*. It is a more familiar peltate leaf with palinactinodromous venation (terminology after Dilcher, 1974) which stands for comparison in paleobotany. Platanophylls include fossil "*Platanus*", *Platanites*, *Aspidiophyllum*, *Pseudoaspidiophyllum*, *Protophyllum*, *Pseudoprotophyllum*, *Credneria*, *Paracredneria* and *Protoacerophyllum*. Underdeveloped leaves of the same plants were described under *Alnites* (e.g., *A. grandifolius* Newberry, 1898), *Betulites* (*B. westii* Lesquereux, 1892), *Viburnites* (*V. crassus* Lesquereux, 1892), "*Viburnum*", and "*Quercus*" (*Q. viburnifolia* Lesquereux, 1892). The names *Aralia*, *Grewiopsis* and *Pterospermites* were also applied to platanophylls. Figs. 12–13 show pistillate heads comparable to those of extant *Platanus*, though smaller. The heads are borne in a spike as in extant *Platanus orientalis* L. They come from Senonian dinosaur-bearing rocks of the Amur province together with abundant platanoid leaves. Another type of fructifications associated with platanophylls is *Steinhauera* heads of Altingiaceae affinities. Cuticular characters confirm attribution of platanophylls to the ancestral Platanaceae and Altingiaceae (Krassilov, 1973c).

3. Laurophylls

The Cretaceous laurophylls with pinnate venation are placed in *Laurophyllum*, *Magnoliaephyllum* (both names have been originally applied to nearly identical leaves: Göppert, 1854), *Proteoides* (when secondary venation is obliterated) as well as in "*Eucalyptus*", "*Eugenia*" (e.g., *E. tuscaloosensis* Berry, 1919) and "*Ficus*" [e.g., *F. daphnogenoides* (Heer) Berry]. The laurophylls with acrodromous venation are described as *Cinnamomoides*, *Lauraceaephyllum*, *Araliopsoides*, *Araliaephyllum*, "*Sassafras*" and "*Benzoin*". The laurophylls are rather uniform in their cuticular characters which constitute major evidence of their attribution to the Laurales (Krassilov, 1973c). "*Laurus*" *macrocarpa* fruit from the Dakota Sandstones (Lesquereux, 1874) is hardly reliable.

4. Ficophylls

Despite some dubious claims of *Ficus* fruits, the attribution of Cretaceous *Ficus*-like leaves to the Moraceae is very unlikely. The *Artocarpus* "male inflorescence" from Greenland (Nathorst, 1890) and comparable postulose body from Nanaimo Group (Bell, 1957) resemble the Bennettitalean ovuliferous receptacle. The Icacinaceous affinity of ficophylls is suggested by *Phytocrene*

fruit from Kreischerville (Scott and Barghoorn, 1958). M. E. J. Chandler in her masterly treatment of the London Clay flora has initiated the practice of placing any unilocular spiny fruit in the Icacinaceae. All this Icacinaceae story is badly in need of revision (see Hughes, 1976). *Byttneriophyllum tiliaefolium* (Al. Braun) Kn. et Kv. is close morphological ally of the Cretaceous ficophylls (Knobloch und Kvaček, 1965).

5. Proteophylls

The group as here understood is characterised by dichopodial division of the leaf segments. It comprises *Debeya* (*Dewalquea*), *Proteophyllum* of Velenovský and Viniklár (1926–1931), *Araliopsis*, *Manihotites georgiana* Berry, 1914, *Adoxa praeatavia* Saporta, 1894, and some “*Aralia*” (*A. towneri* Saporta, 1876). In the Late Triassic and Early Jurassic time, similar leaf shape occurs in the *Scoresbya-Imania* group of putative Caytonialean affinity (see Krassilov, 1973b). Hughes (1976) considers this leaf comparison unpromising with *Scoresbya* too far separated in time from the early angiosperms to be relevant as an evolutionary succession. It is true that the *Scoresbya-Imania* group is irrelevant as immediate angiosperm ancestors. However, my point is that because evolution is regularly reversible, the peculiar leaf organization once produced would recur in the lineage.

The possibility of ancestral Proteaceae in the Cretaceous cannot be ruled out, the more so as not only proteophylls, but also *Tyrmocarpus*, Bohemian *Banksicarpus* (Velenovský et Viniklár, 1926–1935) and the pollen grains of the *Proteacidites* group display some Proteaceous characters. However, cuticular evidence (Krassilov, 1973c) is rather in favour of a generalized group with no close extant allies. The derivation of both rosiphylls and nymphaephylls (see below) from proteophylls is morphologically conceivable.

6. Rosiphylls

Compound leaves with smooth-edged or serrate leaflets are described as *Sapindopsis*, *Cupanites*, *Koelreuteria*, *Anacardites*, “*Fraxinus*” (e.g., *F. lei* Berry) and “*Rulac*”. Isolated leaflets are often mistaken for simple leaves and some *Celastrinites*, *Celastrophyllum*, *Myriciphyllum* [e.g., *M. yokoyamae* (Krysht.) Krassilov], *Ternstroemites*, *Dryophyllum* (e.g., *D. subfalcatum* Lesquereux, 1876), “*Salix*”, and “*Quercus*” (such as *Q. pseudomarionii* Hollick, 1930, which is hardly distinguishable from “*Rulac*” *quercifolia* Hollick, *ibid.*) may belong in this group. Some cuticular evidence is available for *Myriciphyllum yokoyamae* (Krassilov, 1973c). My suggestion of the Myricaceous affinity is probably premature. *Myrica? trifoliata* (Hollick, 1930), *Juglandiphyllum denticulatum* (Koch, 1963) and some *Dryophyllum* species appear transitional between rosiphylls and *Debeya*-like proteophylls.

7. Legumiphylls

The morphology of *Leguminosites* (e.g., *Leguminosites karatscheensis* Vakhrameev, 1952), *Dalbergites*, *Paleocassia* and *Bauhinites* (or *Liriophyllum*¹) is suggestive of the Fabaceous affinities, though no additional evidence is available. *Papilionaceophyllum kryshstofovichii* Krassil. from Tsagajan beds (Danian) is the earliest record substantiated by cuticular characters and associated legume fossils.

8. Nymphaephylls

Peltate orbicular or reniforme leaves resembling those of the floating living angiosperms are assigned to *Nymphaeites*, *Castallia*, *Nelumbites*, *Menispermities* and *Quereuxia*. The advancement index of the Nymphaeaceae is 34 (Sporne, 1972). Gambarian (1970) adopted a different numerical method of estimating advancement and concluded that Nymphaeales are the most primitive angiosperms. Hughes (1976) has suggested that *Nelumbites* leaf type may represent one of the earliest "experimental" simple shapes rather than an aquatic plant. This may be true for some nymphaephylls, but not for the *Quereuxia* rosette. Kryshstofovich (1958) has assigned to *Quereuxia aculeata* some spicate fructifications from the Anadyr River, but they are neither in organic connection nor even in taphonomic association with the leaves. Vakhrameev (1952) has described under *Cissites* cf. *parvifolius* a shoot bearing ill-preserved nymphaephylls and terminating in paniculate inflorescence. This fossil is of great importance for an understanding of the nymphaephylls and deserves further study.

9. Palmophylls

The palm leaves came from the Late Cretaceous of Maryland (Berry, 1916), Vancouver Island (Bell, 1957), Japan and elsewhere. The occurrence of palms is also confirmed by palynological evidence (Muller, 1970; Doyle, 1973). Moore and Uhl (1973) and Doyle (1973) held that the palms are relatively advanced, while Khokhrjakov (1975) believes them to be almost as primitive as the Xanthorrhoeaceae which he places at the base of the principal monocotyledonous lineages.

Linear leaves showing monocotyledonous characters are common in the Late Cretaceous localities. Their assignment to extant families remains questionable. "*Sparganium*" fruits from Peruč beds, Nanaimo and elsewhere resemble pistillate heads of *Platanus* or *Liquidambar*.

¹D. L. Dilcher has published (Science, 1976, 27: 854-856) the angiosperm axis with carpels associated with *Liriophyllum* leaves. In my opinion, this discovery is not incompatible with the idea of the Leguminosean affinity of *Liriophyllum*.

To summarize, the gross morphology of Cretaceous leaves, supported by some fructification and cuticular evidence, suggests eight major lineages of early dicotyledons. The principal divisions of the Takhtajan (1966) and Cronquist (1968) systems — Hamamelididae, Magnoliidae and Rosidae — can be recognized among them. The dominant Cretaceous dicotyledons belonged in the ancestral Hamamelidales (*Trochodendroides* and platanophylls) and Laurales which were no less distinctly separated from each other than they are today. This may be taken as an evidence of their independent origins. The third dominant group — the proteophylls might give rise to aquatic nymphaephylls of the *Quereuxia* type as well as to the proto-Rosidae stalk which advanced to a dominant position in the Campanian time. No links are conceivable between either of these lineages and the Cretaceous palmophylls.

The fossil record provides no support for the hypothesis of fluid floral organization in early angiosperms (see Philipson, 1974). Such structures as *Trochodendrocarpus* are instead fairly constant throughout their spatial and temporal ranges.

PROANGIOSPERMS

The term “proangiosperms” was informally applied by D. H. Scott, J. Hutchinson and other authors to hypothetical ancestors of flowering plants. I include in the proangiosperms three groups of Mesozoic plants — Caytoniales, Czekanowskiales and Dirhopalostachyaceae. These groups belong in different lineages but in the same grade of angiospermization. Their ovules are enclosed in capsules provided with some devices for pollination and dehiscence (the indehiscent fruits of *Caytonia* were edible as proved by coprolite studies).

1. Caytoniales

Following the pioneer work of Thomas (1925), the morphology of the *Caytonia* capsule was described by Harris (1951a) with recent contributions of Reymanowna (1973) and Krassilov (1976). A thickly cutinized capsule shows a scar-like opening (“mouth”) situated close to the stalk and protected by a valve, or “lip”. On the inner side of the capsule wall, the mouth is bordered by a prominent ridge (Fig. 15). The capsule envelops a thinly cutinized inner sac filled with closely packed ovules facing the mouth. The inner sac occupies about two thirds of the capsule volume. It is connected with the mouth by a cutinized tube (“style”) which is subdivided into a number of “channels”, with occasional pollen grains adhering to their walls (Fig. 16). The mouth was interpreted as a gap between the stalk and the tip of the involuted megasporophyll (the lip). However, I observed the mouth outside the stalk-lip space (Fig. 14) and, thus, concluded that it is independent from



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Figs. 14-15. *Caytonia sewardii* Thomas from the Middle Jurassic of Yorkshire, SEM micrographs.

Fig. 14. Proximal part of the capsule showing the point of attachment to the stalk (perforation at the top) and the lip bulging over the mouth on its distal edge, $\times 100$.

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the stalk. My idea was that the mouth originated from a scar of the inner sac attachment to the capsule wall.

The Caytoniales can be related to the Glossopteridales on the ground of (a) the resemblance of *Sagenopteris* to *Glossopteris*, (b) similar pollen grains, and (c) similar seed structure (Harris, 1954; Pant and Nautiyal, 1960). If the Caytonialean capsule corresponds to the Glossopterid gonophyll (i.e., bract plus epiphyllous fructification), then the mouth might possibly evolve from a scar of an ovuliferous receptacle attached to the midrib of the involuted bract (Fig. 18).



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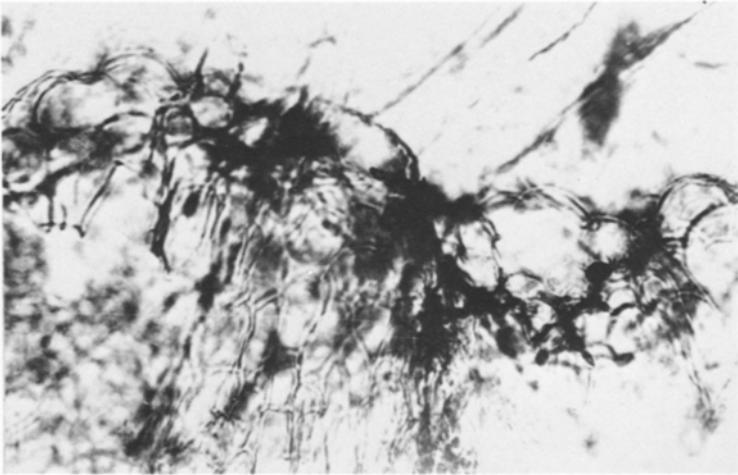
Fig. 15. The same portion of the capsule wall viewed from within. Note the internal ridge bordering the mouth.

The idea of the Lauralean pistil derived from the Caytonialean capsule (Meeuse, 1972) deserves further consideration. The lip and the channelled tube of the Jurassic *Caytonia* surely had not functioned as true stigma and style, but they were preadapted for this function.

The *Caytonialean* pollen grains germinating on the lip would be rather disappointing since these plants would be classified as angiosperms and, thus, excluded from discussion of the angiosperm ancestry. As they are, the Caytoniales are of great evolutionary importance, forming an actual link between gymnosperms and angiosperms.



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Figs. 16-17. *Caytonia seawardii* Thomas from the Middle Jurassic of Yorkshire.
Fig. 16. Part of the pollen-transferring tube showing grooves with arrested pollen grains $\times 166$.
Fig. 17. Two micropyles facing the mouth, $\times 395$.

2. Czekanowskiales

This group is characterized by linear or lenticular leaves with parallel venation clustered on short-shoots. The female fructifications consist of an axis bearing spirally arranged, shortly stalked, many-seeded, bivalved capsules. In the Late Jurassic species from Siberia, the capsule valves are provided with tuberculate and papillate flanges (Figs. 19–22) forming “stigmatic bands”. The marginal flange is expanded inwardly into a thin papillate flap (“inner stigma”) overhanging the ovules (Krassilov, 1968, 1972). The early – and mid – Jurassic fructifications described by Harris (1951b, Harris et al., 1974) from Greenland and Yorkshire showed no stigmatic structures which presumably evolved later. They had also larger seeds than in the younger species. The smallest seeds of the latter are about $250\ \mu$ long which is much below the normal size of gymnospermous seeds.

It is difficult at present to fit the Czekanowskiales in any evolutionary succession. The leaves of *Phoenicopsis* show morphological and cuticular similarity to the Paleozoic *Rufloia* which may belong in the Vojnovskyales (see Maheshwari and Meyen, 1975).

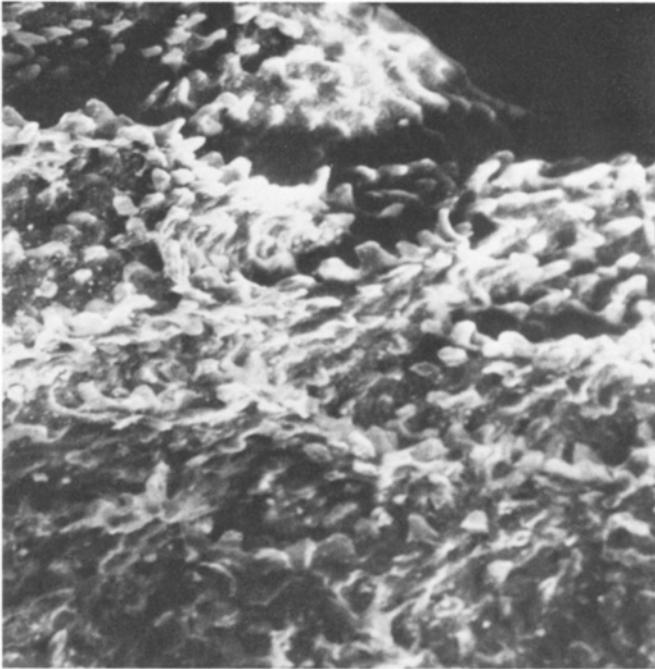
No particular angiosperm group can be traced back to Czekanowskiales with any confidence, though some connexions with monocotyledons are suggested by the leaf gross morphology and cuticular characters.



Fig. 18. The hypothetical transformation of the Glossopteridalean gonophyll into the Caytonialean capsule. The mouth of the latter corresponds to the base of the epiphyllous cupule.



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3. Dirhopalostachyaceae

I proposed this family for the Late Jurassic and Early Cretaceous fructifications with lateral appendages originally described as bracts but later seen to be paired capsules (Krassilov, 1975b). The capsule is single-seeded, beaked, showing a prominent ventral suture. The capsule walls are covered with ribs diverging from the ventral suture. The beak is about three quarters of the capsule length, reflexed, dorsally ribbed. The extension of the ventral suture is evident on the beak as a narrow ridge. The locule occupies the ventral part of the capsule which is dorsally compressed and keeled. In the ripe capsules, the suture is opened, showing the smooth interior of the locule. A few capsules contain intact seeds which are flattened and pointed towards the capsule base (Figs. 23–24).

The compressions have yielded several kinds of cuticles. The nucellus is very thinly cutinized, whereas the outer cuticle of integument is thicker and more resistant. The capsule cuticle is fairly delicate, showing hair base cells. It resembles the adaxial leaf cuticle of *Nilssonia*. This and repeated association suggest attribution of *Dirhopalostachys* to a plant with *Nilssonia* foliage.

The ovuliferous trusses of *Beania* referred to mid-Jurassic European *Nilssonia* (Harris, 1964) resemble *Dirhopalostachys* in gross morphology and seed cuticles, though in *Beania* the paired ovules are exposed on shield-like lateral appendages. This structural similarity as well as the taphonomic association evidence suggests attribution of *Dirhopalostachys* fructifications to a plant with *Nilssonia* foliage.

Nilssonia is one of the most common Mesozoic fossils ranging from the Late Triassic to Maestrichtian. The leaves are ribbon-shaped, entire or segmented, occasionally serrate or spinulose, with fairly constant cuticular characters. The Late Jurassic and Early Cretaceous Siberian *Nilssonia* and the mid-Jurassic species from Yorkshire have nearly identical cuticles, though they are attributed to the plants with different fructifications — *Dirhopalostachys* and *Beania* respectively (Figs. 26–29). These fructifications agree in gross morphology and seed cuticles, though in *Beania* the paired ovules are exposed on shield-like lateral appendages (Harris, 1964). It is assumed that the *Dirhopalostachys* capsule has evolved by involution of the *Beania* ovuliferous shields which was followed by acquiring the beak and ventral dehiscence (Krassilov, 1975b). This being the case, we have an example of rapid evolution of reproductive structures as opposed to constancy of leaf characters.

Dirhopalostachys may belong in the Nilssoniales or constitute an order of its own. The Nilssoniales are putative descendants of the Paleozoic Lyginop-

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Figs. 19–20. *Leptostrobus stigmatoideus* Krassil. from the Upper Jurassic of the Bureja, “stigmatic bands” of the capsule. SEM micrographs, $\times 100$ and 150 .

teridales. They differ from the Cycadales in having their leaves clustered on short shoots, and the outworn comparison of the *Beania* fructifications with *Cycas* has very little ground. *Cycas* appeared in the Late Cretaceous (my unpublished data) just before the final extinction of *Nilssonia*.

Similarity between the paired capsules of *Dirhopalostachys* and paired fruits of the proto-Hamamelidaceous *Trochodendrocarpus* is remarkable (Figs. 30–33). The features of the beak, suture, and external rib pattern match exactly, though in *Trochodendrocarpus* the capsules are many-seeded.

Fig. 34 shows putative relations of proangiosperms to gymnosperms and angiosperms. The Coniferales are removed from the Cordaitales (and the Lebachiaceae which are included in the latter order) and approximated to the other extant gymnosperms by reasons given in Krassilov (1971b). Recent work on the Glossopteridalean fructifications (Surange and Maheshwari, 1970) revealed close similarity between *Scutum* and *Vojnovskya* while the samaras of *Indocarpus* resembled those of Angarian *Sylvella*. Meyen (1971) demonstrated the correspondance between the Angarian and Gondwanian leaf morphotypes. Other relations of gymnospermous lineages would be discussed elsewhere.

ANGIOSPERMIZATION

The above hinted rooting of three major Cretaceous angiosperm lineages, viz., the Hamamelidales, Laurales and monocotyledons in the Dirhopalostachyaceae, Caytoniales and Czekanowskiales respectively is admittedly premature and is not to be explored here. I believe, however, that the occurrence of three separate lineages involved in the process of angiospermization is in accord with the evidence provided by both early and modern angiosperms. The angiosperm characters scattered among proangiosperms and other lineages, such as the Bennettiales, not formally included in this group, have constituted a "character pool" from which the standard angiosperm complement can be drawn. I suggested that some characters appearing in a single lineage might spread over the whole proangiosperm group by means of gene introgression or transduction (Krassilov, 1973b). Understanding of the latter mechanism depends on the studies of "foreign agents" in the genomes of higher plants and animals (Brink, 1973; Peterson, 1970; Rasmusen et al., 1974).

The most advanced proangiosperms come from Siberian localities where they outnumber other fossils. It appears that proangiosperms constituted the dominant element in the Late Mesozoic floras of Siberian realm. They thrived under seasonal climate.

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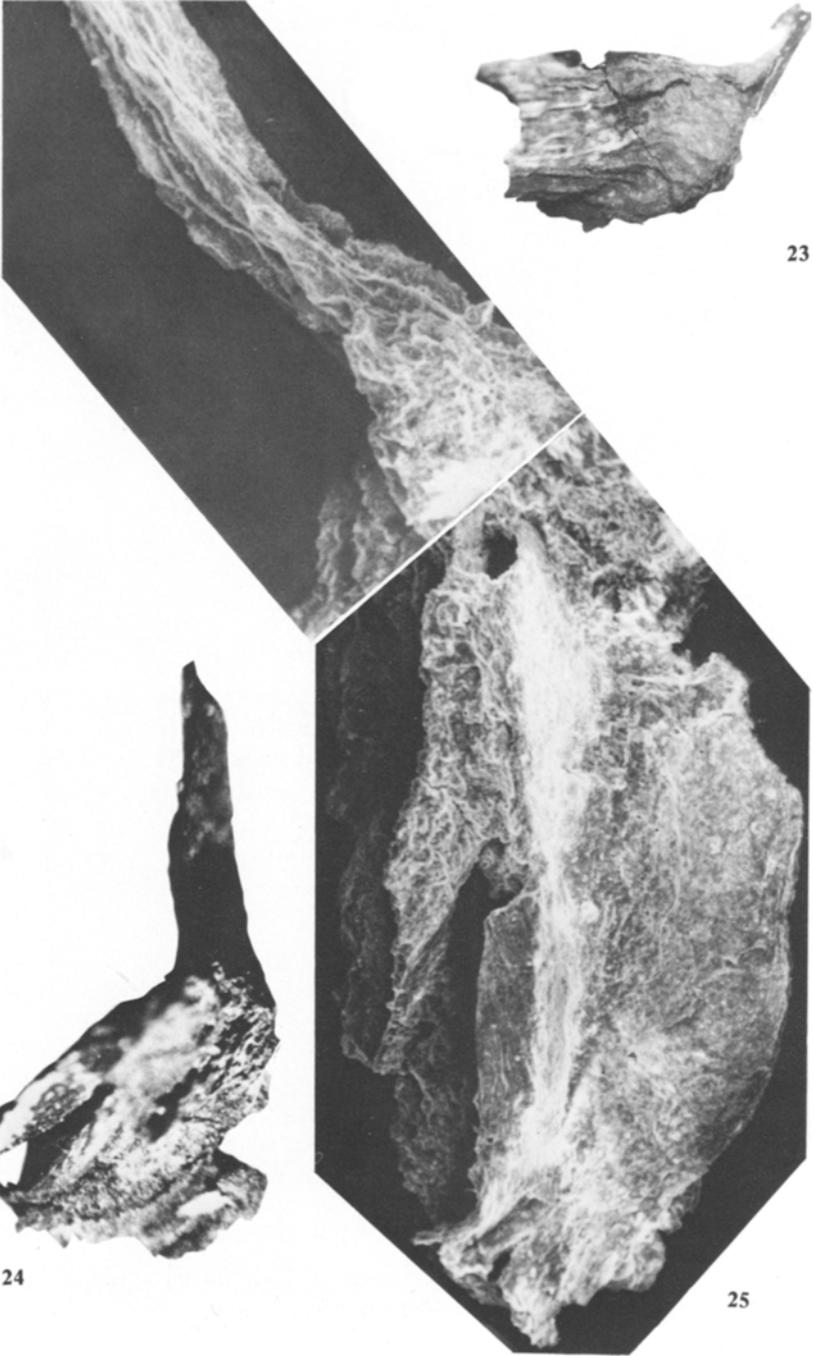
Figs. 21–22. *Leptostrobus stigmatoideus* Krassil., from the Upper Jurassic of the Bureja. Papillae of the "stigmatic bands". SEM micrographs, × 600.



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It is postulated that initial radiation of eutherians occurred in the same general area (Lillegraven, 1974; Trofimov and Reshetov, 1975). The age assignments of critical events in the history of mammals — the first appearance of ancestral therians (*Aegialodon*) in the Wealden, the Albian outburst of radiation (the Trinity therians), the rise to subdominant status in the late Maastrichtian (the Lancian faunas) — are remarkably close to those of angiosperms. These temporal relations suggest coadaptive evolution of the dominant Cenozoic plants and animals.

Tectonic events have affected angiospermization and mammalization by creating environmental instability and, thus, disturbing the balance between K- and r-selection (McArthur and Wilson, 1967) with consequent changes in adaptive strategies of ancestral populations. The appearance of proangiosperms and the first mammals of allegedly prototherian grade in the Late Triassic time coincided with the onset of rifting between Africa and North America and also between the eastern and western Gondwanas (Dingle and Scruton, 1974). There was simultaneous block faulting along the margins of major plates. The subsiding grabens were filled with red and/or coal-bearing beds, such as the Newark series and equivalent sequences in Europe (Bosellini and Hsü, 1973) or the Chinle Formation of western North America and Mongujaj — Khorat series in eastern Asia. Major plant localities were formed in these marginal troughs.

The appearance of the earliest angiosperms and ancestral therians was correlated with a major pulse of tectonic activity manifested in the pre-Barremian spreading between Iberia and Newfoundland (Williams, 1975) and in the western Pacific (Krassilov, 1975d), the separation of southern Africa from South America and the Falkland plateau (Larson and Ladd, 1973) and India from Australia (Veevers et al., 1971). New patterns of plate motions were, thus, established and the process of angiospermization was incorporated in the general development of the Cenozoic world.

CONCLUSIONS

Howells (1950) said that we must not think of the appearance of man “as if he had suddenly been promoted from colonel to brigadier general, and had a date of rank”. But with phylogeny strongly tied to taxonomy this way of thinking is unavoidable irrespective of whether man or angiosperms are

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Figs. 23–25. *Dirhopalostachys rostrata* Krassil. from the Upper Jurassic of the Bureja.

Fig. 23. Capsule, side view, $\times 3$.

Fig. 24. Capsule with broken ventral wall showing distal part of the seed, $\times 10$.

Fig. 25. The same capsule. The ventral wall is removed and the seed is fully exposed. SEM micrograph, $\times 25$.

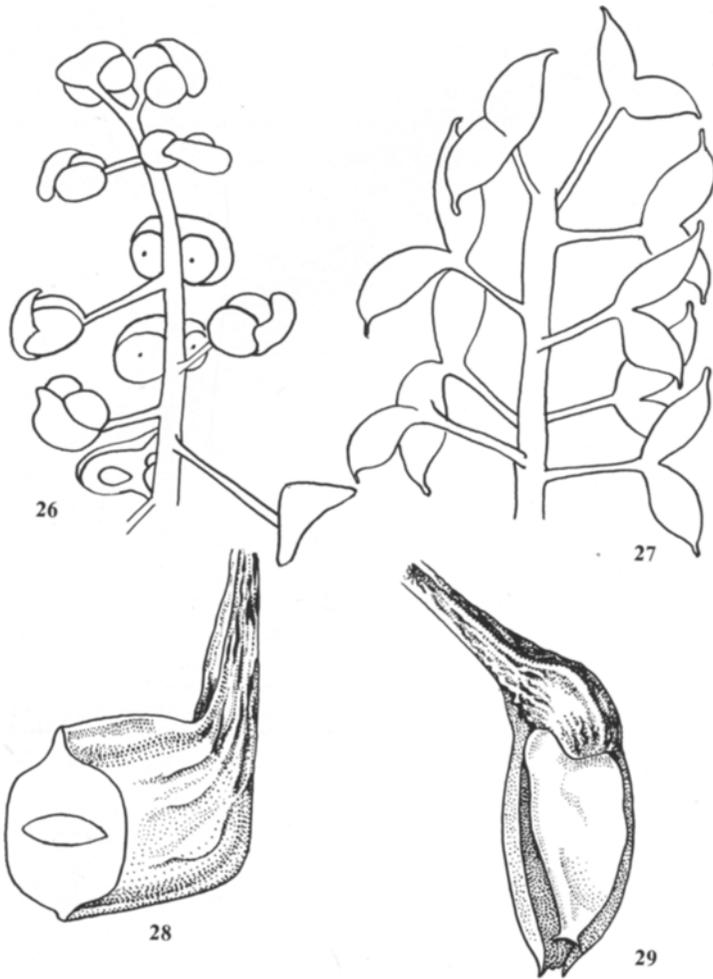
concerned. The paleontologist is expected to hunt for the colonel's dossier. He instead may concentrate on the process of "promotion", that is on tracing the history of biological contrivances bound to particular modes of life embodied in higher taxa. For angiosperms the sources of most successful contrivances are identified above as three groups of proangiosperms. It is postulated that other sources were also involved in completing the basic character pool. Temporal correlation of angiospermization with other processes incorporated in the development of the Cenozoic lithosphere and biosphere is demonstrated and causal relations are suggested. Some lineages of seed plants were less successful in adopting new adaptive strategies and perished or survived as extant gymnosperms. However, living in an angiosperm-dominated world, they might eventually acquire some angiospermous characters. This possibility must not be ignored in comparative morphology.

The basic character pool was explored in different ways by the principal lineages of early angiosperms. Direct indication of specific ancestors cannot be substantiated and is of minor importance for studying evolution (except for drawing diagrams). The studies in paleobotany would result in better understanding and, thus, evaluation of taxonomic characters rather than in correction of putative lines of descent.

The mode of angiosperm origin suggested above does not demand drastic changes of existing classifications. In fact, the validity of grouping in the Takhtajan (1966) and Cronquist (1968) systems is corroborated by the fossil record evidence of very ancient separation of major groups. It must be remembered, however, that a linking of all taxonomic units in an uninterrupted web is an attribute of systematics and not the manifestation of monophyly. Such phylogenetic implications of the angiosperm systems as derivation of the Hamamelididae and monocotyledons from the Magnoliidae must be carefully avoided.

ACKNOWLEDGMENTS

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Figs. 26-29. Middle Jurassic *Beania* (the Nilssoniales) and its putative descendant, the proangiosperm *Dirhopalostachys*.

Fig. 26. *Beania*, reconstruction of Harris, 1964.

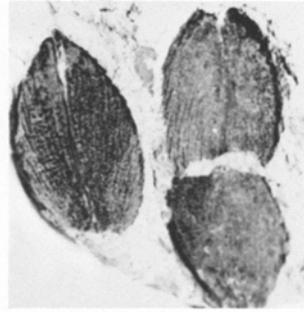
Fig. 27. *Dirhopalostachys*, general aspect of the raceme bearing paired capsules.

Fig. 28. *Dirhopalostachys*, diagrammatic transverse section of the capsule.

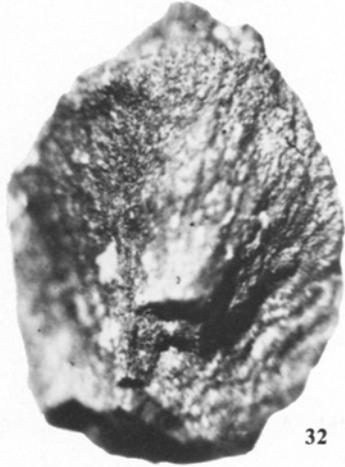
Fig. 29. *Dirhopalostachys*, capsule with ventral wall removed to expose the seed.



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Figs. 30-33. Fructifications of the Late Cretaceous angiosperm *Trochodendrocarpus arcticus* (Heer) Krysht. (Figs. 30-31) and the Late Jurassic-Early Cretaceous proangiosperm *Dirhopalostachys rostrata* (Figs. 32-33). Note the similarity of the arrangement of paired capsules, their shape and the external rib pattern in both species.

Fig. 30. *Trochodendroides* panicle, $\times \frac{2}{3}$.

Fig. 31. *Trochodendroides* pods showing ventral suture and the rib pattern, $\times 1.5$.

Fig. 32. *Dirhopalostachys* capsule showing ventral suture and the rib pattern, $\times 10$.

Fig. 33. *Dirhopalostachys* raceme, $\times 1$.

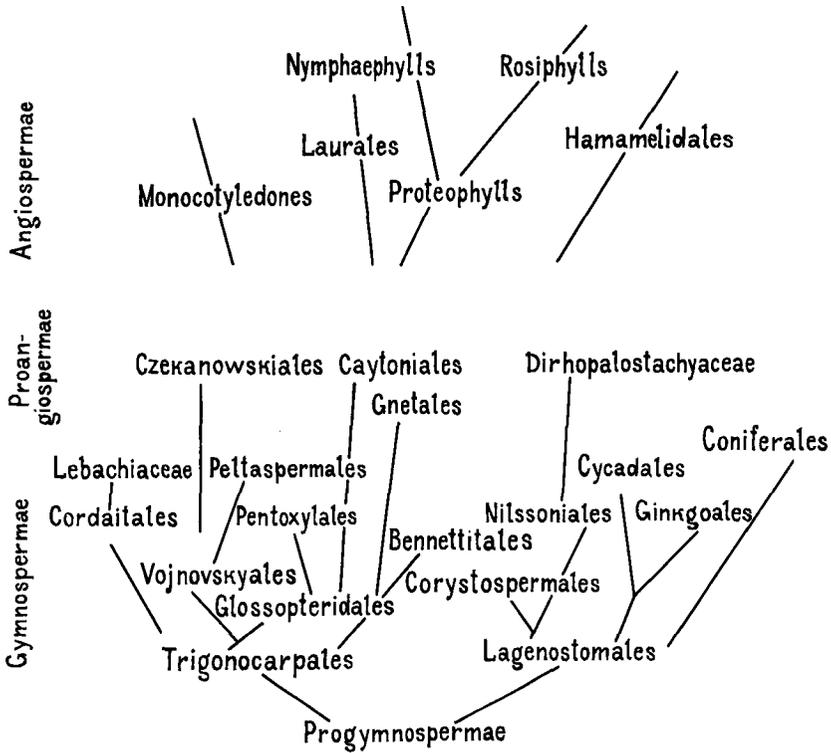


Fig. 34. Putative relations of the proangiosperms to the gymnosperms and angiosperms.

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