

Mesozoic plants and the problem of angiosperm ancestry

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Trends leading to the foliar and floral structures of angiosperms may be deduced by comparison with Mesozoic gymnosperms. The *Debeya-Fontainea* group of Cretaceous angiosperms closely resembles the Early Mesozoic *Scoresbya* group of pteridosperms with regard to leaf characters. The bivalved capsules of Jurassic *Leptostrobus*, with stigmatic bands, are regarded as the forerunners of certain types of angiosperm carpels. The angiospermous characters arose in several lineages of gymnosperms and were probably accumulated by non-sexual transfer of genetic material. The earliest angiosperm mega- and microfossils have been reported from the Middle and Upper Jurassic of the northern hemisphere. Most of these angiosperms were confined to chaparral-like communities dominated by shrubby conifers and cycadophytes. The rise of angiosperms was promoted by the climatic changes and the simultaneous rise of mammals.

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It has been suggested that fossils have no or negligible bearing on the theory of angiosperm evolution because the angiosperms were 'ready-made' when they arrived in the geological record, their early history being hidden from us by the gaps in record. Darwin suggested that the angiosperms had arrived from the vicinity of the South Pole, where no fossil plant localities were known in his time. Bailey, Croizat, Plumstead, Melville, and others developed the theory of a southern origin of the angiosperms as an alternative to the boreal origin advocated by Heer, Engler, Seward, and others. Neither theory has been substantiated in the rapidly accumulating fossil record. Furthermore, the concept of submerged land masses (the Arctic Land, or parts of Gondwana), which might have been the original home of angiosperms, is no longer popular among earth scientists.

Another escape from Darwin's 'abominable mystery' is the theory of an upland origin of angiosperms. Their ancestors are then claimed to have been upland plants as well and not preserved in the fossil record (Axelrod 1960). This is the best way to make the problem unsolvable *ab initio*. However, the fossil record of plants is by no means restricted to the lowland vegetation. Moreover, the changes of climate bring about altitudinal migrations (upland-lowland). Chaney (1936) emphasized the role of altitudinal migrations in the history of the Tertiary vegetation. There are also several examples of syndynamic changes of Mesozoic communities. The dominant lowland type of Late

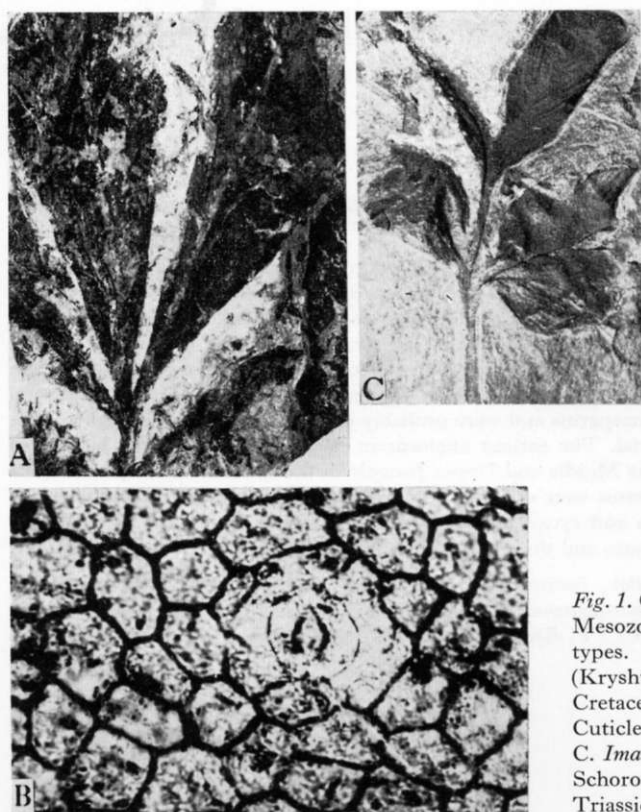


Fig. 1. Comparison between Early Mesozoic and Late Cretaceous leaf types. A. *Debeya tikhonovichii* (Krysht.) Krassil. from the Upper Cretaceous of Sakhalin, $\times 1$. B. Cuticle of the same leaf, $\times 395$. C. *Imania heterophylla* Krassil. & Schorochova from the Upper Triassic of Primorye, $\times 1$.

Jurassic vegetation of East Siberia was the *Czekanowskia-Pseudotorellia* forest. Remains of these gymnosperms prevailed in most autochthonous deposits of fossils (Krassilov 1971). A *Ginkgoites*-dominated type of upland vegetation is represented in exceptional localities and restricted to allochthonous (or drifted) facies of the same age. Due to the Early Cretaceous (Barremian to Aptian) deterioration of climate, the *Czekanowskia-Pseudotorellia* lowland forest was replaced by the *Ginkgoites* forest, which became the principal source of fossil material. Certain groups of modern conifers entered the fossil record due to altitudinal migration induced by the mid-Jurassic cooling. If the angiosperms had been in the uplands at that time, they would inevitably have been brought to the lowlands along with the conifers. Hence we may conclude with Simpson (1965:19) that 'first appearances in the known record are accepted as more nearly objective and basic than opinions as to the time when each group really originated'. The beginning of the geological record of the angiosperms was hardly separated by any considerable time interval from their actual appearance.

If the origin of angiosperms is still a mystery, the explanation should be found not in the gaps of geological record but in the deficiencies of our evolutionary concepts. It was assumed that Mesozoic gymnosperms were too specialized to be the angiosperm ancestors. However, all living beings are spe-

cialized, and it is rather the despecialized than the unspecialized organism which gives way to a new adaptive type. Evolutionary trends leading to foliar and floral angiosperm structures should be revealed by careful examination of Mesozoic gymnosperms.

Trends of evolution of angiosperm characters

The leaves. – Many authors have discussed the problem of simple versus compound ancestral leaf form, and it has been realized that modifications from simple to compound as well as from compound to simple leaves occur in certain angiosperm lineages (Eames 1961). The majority of Mesozoic angiosperm leaves resemble (at least externally) those of *Laurus*, *Magnolia*, *Quercus*, *Platanus*, and other familiar trees. But against them stand out peculiar leaves named *Debeya* Miquel, *Dewalquea* Saporta & Marion, *Proteophyllum* Velenovsky, *Fontainea* Newberry, *Manihotites* Berry, and some others. They have the same basic type of sympodial branching of segments resulting in a palmate

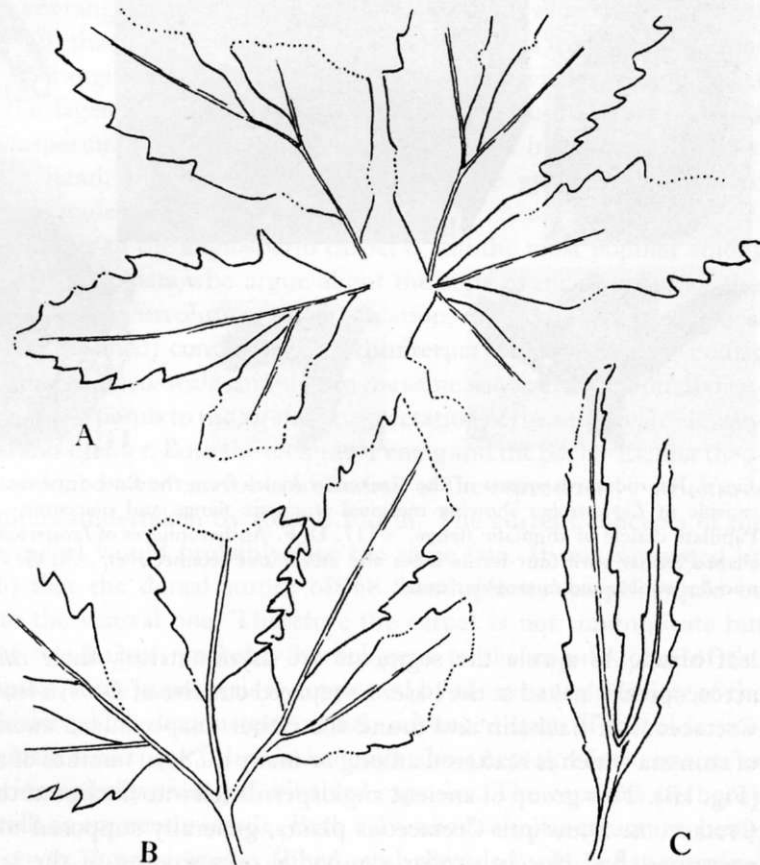


Fig. 2. Leaf morphology of *Scoresbya* from the Lower Jurassic (A, after Harris, 1932, $\times 1$) and *Proteophyllum* from the Upper Cretaceous (B-C, after Viniklar, 1931, $\times 1$).

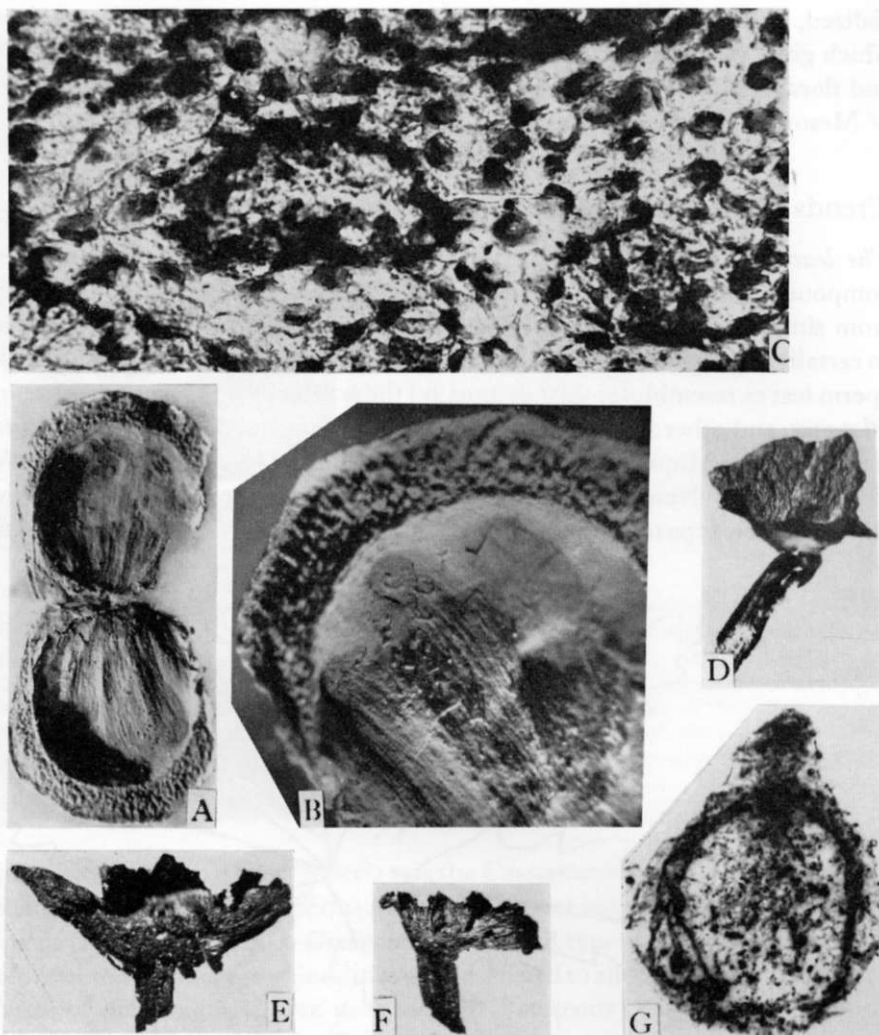


Fig. 3. Reproductive organs of the Czekanowskiales from the Late Jurassic. A-B. Opened capsule of *Leptostrobus* showing marginal stigmatic flange and placentae, $\times 3$ and 6 . C. Papillate cuticle of stigmatic flange, $\times 117$. D-F. Antherophores of *Ixostrobus* showing cup-shaped anther with four fertile lobes and sterile one (connective), $\times 8$. G. Ovule showing nucellar cuticle and micropylar canal, $\times 146$.

leaf blade. As a rule the segments are asymmetrical, their midribs being acroscopically naked at the base. I prepared cuticles of *Debeya* leaves from the Cretaceous of Sakhalin and found the rather unspecialized anomocytic type of stomata which is scattered among so many modern families of angiosperms (Fig. 1B). This group of ancient angiosperms fell into decline at the end of the Cretaceous. Some pre-Cretaceous plants, generally supposed to be gymnospermous, had closely similar sympodial organization of the leaf segments (Figs. 2 A-C). The Late Triassic - Early Liassic leaf-genus *Scoresbya* (Harris 1932; Kräusel & Schaarschmidt 1968) agrees in shape and venation with

'*Proteophyllum*' from the Cenomanian of Czechoslovakia (Viniklar 1931). The leaf-genus *Imania* Krassilov & Schorochova (1970) from the Late Triassic of Primorye (USSR) illustrates the transition from monochasial to dichasial segmentation and is intermediate between *Scoresbya* and *Sagenopteris* (the latter is attributed to *Caytonia* fructifications). Yet another *Scoresbya*-like leaf-genus, *Suffunophyllum* (Krassilov 1967), was found in association with the Early Cretaceous angiosperms.

Pinnate-compound, lobed and even entire angiospermous leaves may be easily derived from the *Scoresbya-Proteophyllum* prototype by a short series of elementary morphogenic processes. The *Scoresbya*-like plants ranged from East Greenland and Central Europe to Central and Eastern Asia. This broad area might be a stage of formation of certain angiosperm groups.

The reproductive structures. – Some authors believe that the angiosperms are not closely related to gymnosperms: the gymnospermous ovule is composed of the sporangium protected by one or more envelopes, whereas the angiospermous ovule arises as a carpel emergent, and its nucellus is not homologous to a sporangium (Eames 1961). I tried to show in another paper (Krassilov 1970) that the nucellus of the gymnospermous ovule is not homologous to a sporangium either. The pollen-catching devices of the nucellar apex, i. e. the lagenostome, salpynx, and the micropyle-like nucellar beaks of the pteridosperms, the *Gnetales* etc., are certainly of integumental origin. On the other hand, the corresponding parts of the gymnospermous and angiospermous ovules are strictly homologous.

The foliar theory of the angiosperm carpel is still the most popular among those plant morphologists who argue about the style of modification of this originally flat organ by involution, conduplication, or peltation. This classical (or rather old-fashioned) concept has its counterpart in the Delpino-Penzig theory of the conifer seed-scale complex, in the same way as the gonophyll theory of Melville corresponds to the ligular interpretation of the seed-scale, developed by Sachs and Eichler. Both the Delpino-Penzig and the Sachs-Eichler theories were abandoned after careful examination of the reproductive structures of fossil conifers undertaken by Rudolf Florin. The current concepts of the angiosperm carpel would probably face the same fate. It was suggested by Long (1966) that the dorsal suture of the 'conduplicate' carpel would be equivalent to the ventral one. Therefore the carpel is not conduplicate but composed of two halves, probably homologous to the cupule lobes of the Paleozoic ovules. This hypothesis is supported by the recent discovery of the Czekanowskiales which demonstrate a fairly advanced stage of carpel formation. The female structure of the Czekanowskiales (*Leptostrobus*) consists of an axis, bearing spirally arranged, bivalved capsules. The capsules are borne on a short stalk or are nearly sessile. Both valves have similar structure, being externally convex, longitudinally ribbed, and provided with a flat marginal flange (Figs. 3A–C). The internal surface of the flange is microtuberculate, densely papillate, forming stigmatic bands. The marginal flange is expanded

inward into a thin papillose flap ('inner stigma') overhanging the ovules. The ovules are arranged in a single row along the margin. These characters have been observed in the *Leptostrobus* remains obtained from the Upper Jurassic (Krassilov 1968, 1969). The Early and Middle Jurassic *Leptostrobus* fructifications described by Harris (1951) did not show specialized stigmatic structures. Presumably these structures evolved during the Jurassic. The episporangiate sporangiophores of the Czekanowskiales (*Ixostrobus*) with their downward-pointing, finger-like connectives (Figs. 3 D-F) seem to be the nearest approach to the angiospermous type of stamen.

The ontogeny of 'conduplicate' carpels of some extant angiosperms gives some indications of the evolution from the bivalved structures of *Leptostrobus* type. For example, the carpel of *Drimys* initiates from two parallel primordial ridges (Tucker & Gifford 1966). It grows upward as a tube. The two dorsal carpellary bundles arise from two different vascular sympodia. Tucker & Gifford conclude that 'the use of the term "conduplicate" for *Drimys* carpels is an oversimplification which emphasizes the similarity to a foliar structure'. The tube-like growth of carpel of *Drimys* is an example of 'zonal' or 'toral' growth of adnated organs (Stebbins 1950).

It is not certain whether the Czekanowskiales were the immediate predecessors of some groups of the angiosperms, but they clearly demonstrate the possibility of evolution from the pteridospermous level of floral organization to the angiospermous one. The subsequent evolution of the angiospermous pistil was evidently influenced by the interaction with the insect pollinators. There were probably other lines of carpel development, starting from the Caytoniales or the Bennettiales-Gnetales plexus. The ovule of *Gnetum* is similar to the trigonocarpalean ovule (Rodin & Kapil 1969). If the cupule of Trigonocarpaceae were homologous to the carpel, then the same might be true for the gnetalean cupule.

The similarity between Gnetales and Bennettiales has been recognized by Lignier, Thoday, and others. The comparison between them was influenced by different interpretations of bennettitalean interseminal scales. In my opinion, the interseminal scales are homologous to perianth lobes of Gnetales (alternative interpretation of interseminal scales as abortive ovules seems to me less probable). In *Ephedra* and *Gnetum* the perianth lobes are fused into continuous envelopes (abnormal envelopes, split nearly to the base). The fusion is congenital and the cupule grows as a tube (Lehmann-Baerts 1967), whereas in the Bennettiales the perianth lobes are free, forming interseminal scales. Thus the 'hemiangiosperms' of Arber and Parkin had already produced the closed or semiclosed carpels.

The megagametophyte organization of *Gnetales* provides valuable information on the origin of the angiosperm embryo sac. In *Gnetum*, 32 free nuclei are present before pollination. One or several egg nuclei arise. In the latter case, both male gametes may be functional, i.e. two eggs undergo fertilization (Maheshwari & Vasil 1961). A number of nuclear fusions accompanies the formation of the cell wall. The angiospermous condition was probably achieved

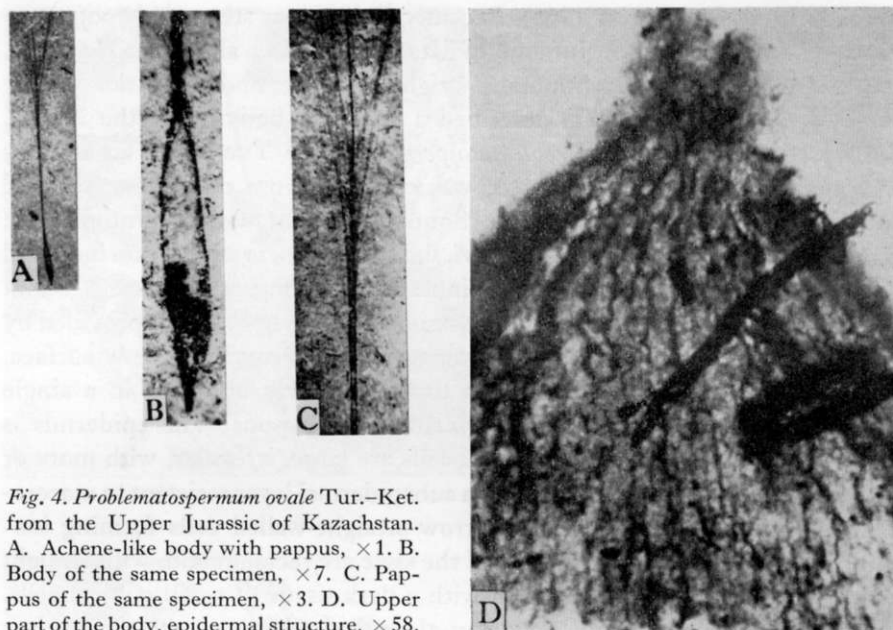


Fig. 4. *Problematospermum ovale* Tur.-Ket. from the Upper Jurassic of Kazakhstan. A. Achene-like body with pappus, $\times 1$. B. Body of the same specimen, $\times 7$. C. Pappus of the same specimen, $\times 3$. D. Upper part of the body, epidermal structure, $\times 58$.

by reduction and telescoping of developmental stages (Takhtajan 1970). We have no chance of proving the double fertilization in extinct plants, but some inferences may be drawn from the seed size. This feature is influenced mainly by ecological factors. However, the lower limit of seed size is much higher in the modern gymnosperms than in the angiosperms. It is of interest that the seeds in the Mesozoic gymnosperm orders Caytoniales and Czekanowskiales were much smaller than those of modern gymnosperms. I obtained a number of minute ovules from Czekanowskia beds of the Late Jurassic age. The ovules with completely developed micropyle and pollen chamber were only 250–270 μ in length (Fig. 3G).

It may be concluded from these examples that the angiosperm characters evolved independently in different lineages of Mesozoic gymnosperms. I agree with Lam (1936:189) that 'the solution of this enigmatical condition [the absence of definite ancestors] is to be found in the acceptance of a very large ancestral group of plants in which features of recent angiosperms, eventually in primitive phase, are much more widely scattered than they are at present'. In Heslop-Harrison's (1958) words the angiosperms are 'pachyphyletic' (see also Meeuse 1967, etc.). The familiar adaptive type of flowering plant developed by accumulation of independently arising characters, probably by transduction of genes by viruses or other means of non-sexual transfer of genetic material (Ravin 1955).

Early evolution of angiosperms

Several reports on Precretaceous findings of the angiosperms have been proved to be in error (Harris 1960; Hughes 1961; Kräusel 1956; Stockmans &

Willière 1962; Delevoryas 1968). Recently *Palmoxylon* stems and roots were reported from the Upper Jurassic of Utah (Tidwell et al. 1970). However, the suspicion of an allochthonous origin of these finds was not wholly eliminated. Burakova (1971) described a fruit-like body from the Middle Jurassic of Central Asia. *Problematospermum ovale* Tur.-Ket., an achene-like fossil with capillary pappus, was collected from the Upper Jurassic fossiliferous shales of Karatau (South Kazakhstan) by Antonina I. Turutanova-Ketova and recently by M. P. Doludenko, to whom I am indebted for the loan of specimens. The disseminule body is elongate-elliptical, 5–8 mm long and 1.5–1.8 mm wide, apically passing into a style-like tube provided by few longitudinal ribs. Small hairs arranged in rows cover the body surface. The enlargement of apical hairs up to 0.3 mm was observed in a single specimen. Such hairs probably augmented the pappus. The epidermis is devoid of stomata, and the epidermal cells are large, irregular, with more or less sinuous walls (Fig. 4D). There is a subepidermal layer resistant to maceration. This layer is composed of narrow straight-walled cells forming longitudinal files. The epidermal cells of the style are rectanguloid, with straight or curved walls. The tube is filled with a dark tissue of small cubical cells. The pappus bristles arise directly from the apical tube, or in some cases they are fused proximally into a single thread up to 20 mm long, and a plumose pappus is produced by pinnate branching of the thread (Figs. 4A–C). Pollen grains have been observed on the tube.

Although hairy seeds date back to Devonian (*Archaeosperma*, *Thysanosperra*, etc.) the parachute apparatus of the pappus type is entirely alien to gymnosperms. It is characteristic of some families of flowering plants. The Jurassic *Problematospermum* shows bennettitalean cuticular characters and at the same time resembles the achenes of such *Compositae* genera as *Taraxacum* or *Hieracium*. The pappus of *Compositae* is derived from calyx although it may be augmented by enlargement of the uppermost hairs of the achene (Cronquist 1955). The *Compositae* is believed to be a highly advanced family. However, *Palaeanthus problematicus* Newberry from the Upper Cretaceous is assigned by Stebbins and Cronquist to the *Heliantheae* tribe of *Compositae*.

I collected fruit-like capsules provided with glochids from the Tithonian-Berriasian deposits of Tyrma River (far east in the USSR). Twelve capsules occurred on a single hand-specimen. The capsules were rounded elliptical, up to 6 mm long, sculptured with longitudinal ribs and conical protuberances (glochids). Internal surface smooth. Seed-like body 3.2 mm long was observed inside one of the capsules (Fig. 5E). Some of capsules were transferred to balsam and the whole mounts of cuticular coats of protuberances were obtained (Figs. 5F–H). This fossil is reminiscent of the *Hakea* (*Proteaceae*) fruits which are dehiscent into valves and have characteristic surface sculpturing.

The fossil fruits resembling those of *Icacinaeae* have been described from the Valanginian of France and Hauterivian of California (Chandler & Axelrod 1961). From the Aptian of Primorye (Far East of the USSR) I have recorded fruits comparable with the Californian ones and referred them to the same

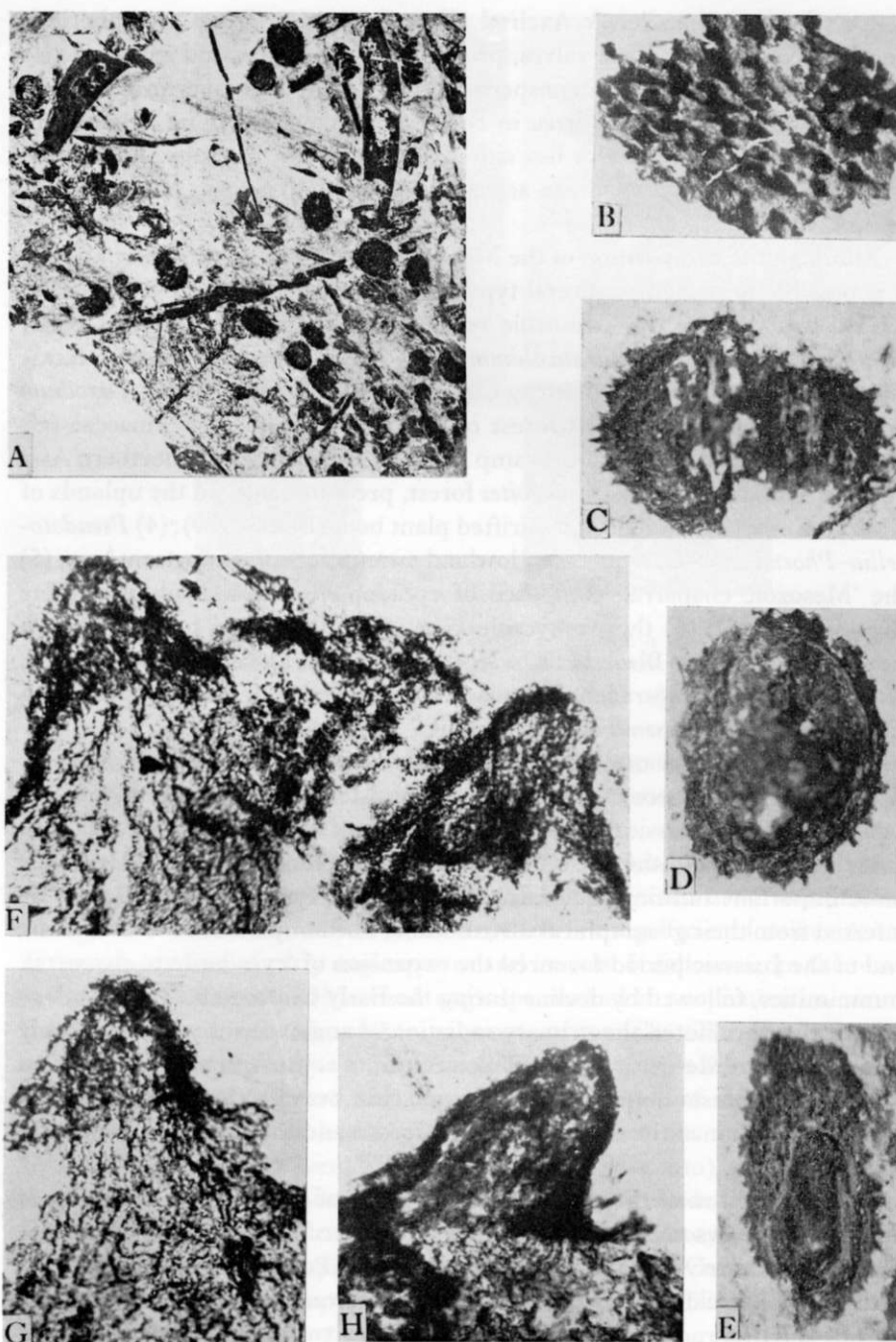


Fig. 5. Fruit-like capsules from the Tithonian-Berriasian of Tyrma River, Far East. A. Several capsules in association with fern and conifer leaf remains, $\times 1$. B. Capsule surface with protuberances, balsam transfer, $\times 12$. C-E. Capsules, $\times 7$. F-H. Cuticular coats of protuberances, $\times 146$.

genus, *Onoana* Chandler & Axelrod (Krassilov 1967). They are spherical, one-loculed, dehiscent into valves, probably many-seeded, and spiny.

It is interesting that the angiosperm (or at least the angiosperm-like) fruits preceded the angiosperm leaves in the geological record. The angiosperm pollen grains arrived more or less simultaneously with the fruits. All records from the Jurassic or Neocomian are confined to the gymnosperm dominated assemblages.

Although the composition of the Mesozoic vegetation is but poorly known, it is possible to recognize several types of plant communities (see Krassilov, 1971). They are (1) the 'Mesozoic redwood', dominated by *Elatides* Heer, *Athrotaxis* Fontaine, *Parataxodium* Arnold & Lowther, *Parasequoia* Krassilov, and other precursors of living *Cunninghamia*, *Sequoiadendron*, *Taxodium* and *Sequoia*; (2) the upland forest of Europe dominated by Pinaceae (cf. Stopes 1915) and the lowland swamp forest of *Pityophyllum* in northern Asia and the Arctic Islands; (3) *Ginkgoites* forest, predominantly in the uplands of western Europe as evidenced by drifted plant beds (Black 1929); (4) *Pseudotorellia-Phoenicopsis-Czekanowskia* lowland swamp forests of northern Asia; (5) the 'Mesozoic chaparral' composed of cycadophytes and shrubby conifers (Krassilov 1967); (6) the pachycaule vegetation dominated by *Cycadeoidea* e. g., localities in the Black Hills in North America). The earliest angiosperm records (*Prolematospermum*, Tyrrean capsules, *Onoana*) are associated with assemblages of 'Mesozoic chaparral' type.

These associations occupied the dry sites of mesophytic forest regions. They were much more characteristic of the Mesozoic floras of subtropical aspect (e.g., the Jurassic flora of Yorkshire) than of the temperate '*Phoenicopsis* floras' of Siberia and the Arctic Islands. The temperature conditions were the most important limiting factor to the Mesozoic cycadophytes, as may be inferred from their geographical distribution. The temperature increase at the end of the Jurassic period favoured the expansion of 'cycadophyte chaparral' communities, followed by decline during the Early Cretaceous. The cycadophyte decline promoted the primary radiation of angiosperms which probably penetrated the 'Mesozoic redwood' communities at the Aptian or early Albian time. These forests dominated by Taxodiaceae became the most important type of vegetation at the end of Early Cretaceous and through the Late Cretaceous epoch.

The comparison of the early evolution record of angiosperms with that of mammals reveals some interesting coincidences. According to Simpson (1965) true mammals arrived at the middle of the Jurassic Period. Primitive mammals with tribosphenic dentition have been described from the Wealden of Western Europe and more advanced members of the same stock appeared at the Albian stage (Clemens 1968). The proportion of mammals in the reptilian-dominated Late Cretaceous faunas (e.g. Lance fauna of North America) was approximately equal to that of angiosperms in the floras of the same age.

The simultaneous rise of mammals and angiosperms through the Cretaceous hints at the functional relation between these two phenomena. Some of the

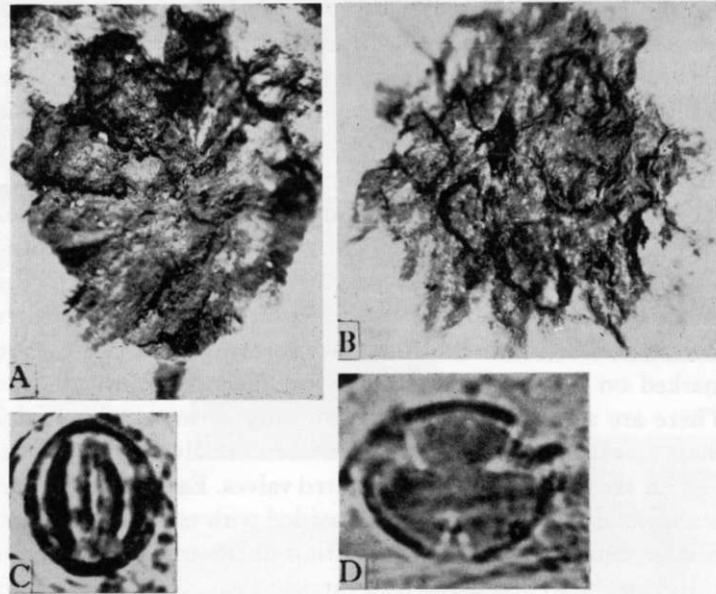


Fig. 6. Staminate heads from the Upper Cretaceous of the Amur basin. A. Split head showing stamens, $\times 7$. B. Head showing distal expansions of stamens, $\times 7$. C-D. Pollen grains, $\times 1000$.

earliest angiosperm fruits are provided with glochids, and it could be suggested that adaptations to zoochory acquired a highly selective value at the beginning of the Cretaceous.

It has been recognized by many authors (e.g. Stebbins 1947) that the rapid evolution of *Hymenoptera* during the Cretaceous promoted the diversification of angiosperm floral structures. However, there is not sufficient fossil evidence of the coevolution of early angiosperms and insects. It follows from the fossil record that the majority of Mesozoic angiosperms had inconspicuous unisexual flowers arranged in heads, spikes, racemes, or panicles. The occurrence of numerous fruits of *Onoana* (Krassilov 1967) and capsules from Tyrma on a single slab of rock suggests their aggregation in a sort of infructescence. I described the staminate heads with pollen grains *in situ* from the Upper Cretaceous of Bureja River. The heads are small (7–8 mm), globular, borne singly, or in spikes. Stamens with massive, distally expanded connective and long pollen sacs. The pollen grains are of *Tricolpopollenites* type (Figs. 6A–D).

The most common reproductive structures of Late Cretaceous age are *Nordenskioldia* Heer (compound fruits resembling those of living *Trochodendron*) and *Trochodendrocarpus* Kryzstofovich (previously referred to *Nyssa*, *Leguminosites*, *Berrya*, *Cercidiphyllum*, etc.). The following interpretation of the latter is based on new findings from the Upper Cretaceous of the Amur basin. The fruits are borne in pleiochasial panicles (Fig. 7A) up to 30 cm long. The axis, about 2.5 to 4 mm thick, bears alternating lateral branches at intervals of 30–50 mm. Each lateral branch is a raceme up to 100 mm long,

bearing from 8 to 14 more or less crowded fruits. It ends in a fruit. Short branches with crowded pods are probably underdeveloped. The elongation of the branch axis is evidently continued up to the fruit dehiscence; the raceme is gradually becoming more and more loose. The pods are spirally arranged, borne in pairs or singly on short, longitudinally striated stalks. The pod is elliptical, suborbicular in transverse section, up to 30 mm long. The style is about 3 mm long, straight or slightly curved, reflexed. The dorsal face shows a median groove and subparallel longitudinal ridges. The ventral face has more prominent suture and ridges, diverging obliquely. The ridges are often obliterated near the suture. The surface is irregularly pitted. Internal casts show fine transverse striation of the inner surface (Fig. FG). The ventral suture is marked on the internal cast as a conspicuous groove, flanked with ridges. There are series of fruits demonstrating various stages of dehiscence: from short apical split to complete separation of valves. The valves are persistent. Fig. 7F shows two partially separated valves. Each of them bears an elongated, convex body, 2–2.5 mm wide, provided with transverse striations. This body is interpreted here as an incrustation of the row of overlapping seeds.

Brown (1939) investigated an extensive collection of similar fruits and chose *Cercidiphyllum* as a proper name for them. Many authors adopted his view, but it was opposed by Mädler (1939), Kirchheimer (1957), and Kryshtofovich & Chandler. Mädler and Kirchheimer stated that the fossil fruits differed from *Cercidiphyllum* in splitting into valves. May (1963) suggested that the splitting would be only occasional. Kryshtofovich & Chandler opposed Brown's view with respect to inflorescence morphology. Chandler (1961) described similar fructifications from the Lower Tertiary as *Carpolithes gardneri*. According to her, the fruits were in a raceme, singly or occasionally in pairs, follicular, not split along the dorsal edge. My specimens show rather frequent pairing of fruits, and they split more or less deeply along the dorsal suture. *Jenkinsella* is a closely comparable fruit, but it is smaller, with conspicuous rows of placenta bordering the ventral suture. *Trochodendrocarpus* and *Jenkinsella* resemble fruits of Hamamelidaceae more than those of any other family. The seeds of *Trochodendrocarpus* are winged, bowed, crescent-shaped, scythe-shaped or horse-shoe shaped. The wing is curved, clasping the seed body, with maximum width about the middle, gradually narrowed into an apex. The wing surface is covered with very fine, crossed striations. The seed body is elongate-elliptical to narrowly lanceolate, 2–3 mm long, with longitudinally striated surface. Hilum and micropyle are on small protuberances of the free end (Fig. 7H).

According to Boothroyd (1930), the inflorescence of *Platanus*, with one or several heads, is fundamentally a panicle. The hypothetical primitive form, suggested by Boothroyd, is closely similar to *Trochodendrocarpus*. Discussing the relationship of the Platanaceae to the Hamamelidaceae, this author considered that 'the heads of the Hamamelidaceae seem to have been derived from simple spikes, and as far as the writer can determine, compound racemes of the hypothetical type from which the *Platanus* head might have been derived

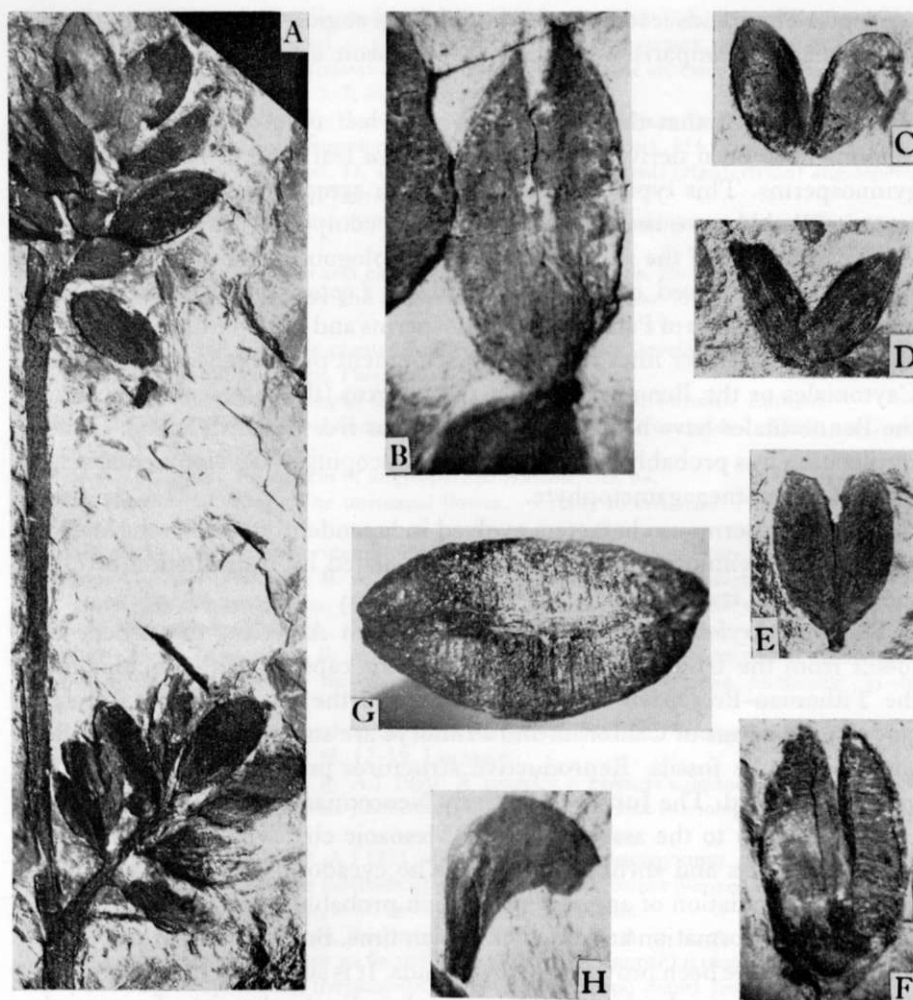


Fig. 7. *Trochodendrocarpus arcticus* (Heer) Krysht. from the Upper Cretaceous of the Amur Basin. A. Panicle, $\times 1$. B. Split pod, $\times 3$. C-E. Paired pods, $\times 1$. F. Split pod showing seed rows, $\times 3$. G. Internal cast, $\times 3$. H. Seed, $\times 7$.

do not occur in the Hamamelidaceae'. However, *Trochodendrocarpus* is more closely related to the latter group on account of carpel pairing, splitting into valves and anatropous ovules. Therefore, the *Trochodendrocarpus* panicle is probably the nearest approach to the primitive ancestral form of inflorescence, common to the Hamamelidaceae, the Altingiaceae, the Platanaceae, the Rosaceae, and some other families.

Conclusions. – The beginning of the geological record of angiosperms was not separated by any considerable time interval from their actual appearance. If the origin of angiosperms is still a mystery, the explanation should be found not in the gaps of the record but in the deficiencies of current evolutionary

concepts. The trends leading to foliar and floral angiosperm structures should be revealed by comparison between the Mesozoic angiosperms and gymnosperms.

It is suggested that the *Debeya-Fontainea* leaf type of Cretaceous angiosperms have been derived from the *Scoresbya* leaf type of Early Mesozoic gymnosperms. This type of palmate leaf with sympodial branching of segments probably gave rise to both simple and compound leaves.

The seed coats of the angiosperms are homologous to those of the gymnosperms. The bivalved capsules of Mesozoic *Leptostrobus* are intermediate between the cupules of Palaeozoic pteridosperms and the 'conduplicate' angiosperm carpels. Other lines of carpel development probably started from the Caytoniales or the Bennettitales-Gnetales plexus (the interseminal scales of the Bennettitales have been interpreted here as free perianth lobes). Double fertilization was probably achieved by the telescoping of developmental stages of the *Gnetum* megagametophyte.

The angiospermous characters evolved independently in different lineages of Mesozoic gymnosperms and were accumulated by transduction or other means of gene transfer.

The *Palmoxylon* from the Jurassic of North America, the achene-like fossils from the Upper Jurassic of Karatau, the capsules with glochids from the Tithonian-Berriasian of Tyrma River, and the *Onoana* fruits from the Lower Cretaceous of California and Primorye are supposed to be the earliest angiosperm-like fossils. Reproductive structures preceded the leaves in the geological record. The Jurassic and Early Neocomian angiosperms have been confined mostly to the assemblages of 'Mesozoic chaparral' type dominated by cycadophytes and shrubby conifers. The cycadophyte decline promoted the primary radiation of angiosperms which probably penetrated the 'Mesozoic redwood' formation at Aptian or Albian time. Some of the earliest angiosperm fruits have been provided with glochids. It is suggested that adaptations to zoochory acquired a highly selective value due to the rise of mammals.

The majority of Mesozoic angiosperms had inconspicuous unisexual flowers arranged in heads, spikes, racemes or panicles. The *Trochodendrocarpus* panicle is to be considered as the nearest approach to ancestral form of inflorescence, common to the *Hamamelidaceae*, *Platanaceae*, *Altingiaceae*, and other families.

REFERENCES

- Axelrod, D. I. 1960: The evolution of flowering plants. In S. Tax [ed.] *Evolution after Darwin 1*, 227-305. Univ. Chicago Press. Chicago.
- Black, M. 1929: Drifted plant-beds of the Upper Estuarine Series of Yorkshire. *Quart. Journ. Geol. Soc.* 85.
- Boothroyd, L. E. 1930: The morphology and anatomy of the inflorescence and flowers of the Platanaceae. *Amer. Journ. Bot.* 17, 678-693.
- Brown, R. W. 1939: Fossil leaves, fruits, and seeds of *Cercidiphyllum*. *Journ. Paleontol.* 13, 485-499.

- Burakova, Aleksandra T. (Буракова, А. Т.) 1971: *Sogdiana abdiata* из среднеюрских отложений Средней Азии – возможный предок цветковых растений. [*Sogdiana abdiata* from the Middle Jurassic of Central Asia – a probable ancestor of flowering plants.] *Вопросы палеонтологии* 4, 3–7, Ленинград.
- Chandler, M. E. J. 1961: The Lower Tertiary flora of Southern England (1). Palaeocene floras. London Clay flora (Supplement). Brit. Mus. (Nat. Hist). 354 pp. London.
- Chandler, M. E. J. & Axelrod, D. I. 1961: An Early Cretaceous (Hauterivian) angiosperm fruit from California. *Amer. Journ. Sci.* 259.
- Chaney, R. W. 1936: Plant distribution as a guide to age determination. *Journ. Wash. Acad. Sci.* 26, 313–329.
- Clemens, W. A. 1968: Origin and early evolution of marsupials. *Evolution* 22, 1–18.
- Cronquist, A. 1955: Phylogeny and taxonomy of the Compositae. *Amer. Midland Natur.* 53, 478–511.
- Delevoryas, T. 1968: Jurassic plants. In R. C. Moore et al.: Developments, trends and outlooks in paleontology. *Journ. Paleontol.* 42, 1357.
- Eames, A. J. 1961: Morphology of the angiosperms. New York, Toronto, London.
- Harris, T. M. 1932: The fossil flora of Scoresby sound, East Greenland, 2. *Medd. om Grønland* 85, 1–112. København.
- Harris, T. M. 1960: The origin of angiosperms. *Advanc. Sci.* 64.
- Heslop-Harrison, J. 1958: The unisexual flower – a reply to criticism. *Phytomorphology* 8, 177–184. Lucknow.
- Hughes, N. F. 1961: Fossil evidence and angiosperm ancestry. *Sci. Progr.* 49, 84–102.
- Krassilov, V. A. (Красилов, В. А.) 1967: Раннемеловая флора Южного Приморья и ее значение для стратиграфии. [Early Cretaceous flora of South Primorye and its bearing on the stratigraphy.] 248 pp. «Наука», Москва.
- Krassilov, V. A. (Красилов, В. А.) 1968: К изучению ископаемых растений из группы Czekanowskiales [Studies on the Czekanowskiales.] *Мезозойские растения*, 31–40 «Наука», Москва.
- Krassilov, V. A. 1969: Approach to the classification of Mesozoic 'Ginkgoalean' plants from Siberia. *The Palaeobotanist* 18, 12–19. Lucknow.
- Krassilov, V. A. (Красилов, В. А.) 1970: К вопросу о происхождении и гомологии репродуктивных органов цветковых растений [On the origin and homology of reproductive organs of angiosperms.]
- Krassilov, V. A. (Красилов В. А.) 1971: К методике реконструкции древних растительных сообществ. [On the methods of reconstruction of extinct plant communities.] *Бюл. Моск. общ. испыт. природы, отд. геол.* 46, 87–105. Москва.
- Krassilov, V. A. & Schorochova, Svetlana A. (Красилов В. А. и С. А. Шорохова) 1970: Новые триасовые растения из бассейна р. Имана (Приморье) и некоторые проблемы морфогении мезозойских птеридофиллов. [New Triassic plants from the Iman basin (Primorye) with some comments on the Mesozoic pteridophyll morphogeny.] *Триасовые беспозвоночные и растения востока СССР*, 98–121. Владивосток.
- Kräusel, R. 1956: Zur Geschichte der Angiospermen. *Bot. Mag. Tokyo* 69, 537–544.
- Kräusel, R. & F. Schaarschmidt. 1968: *Scoresbya* Harris (Dipteridaceae?) aus dem Unteren Jura von Sassendorf. *Palaeontographica* 123B, 124–131. Stuttgart.
- Lam, H. J. 1936: Phylogenetic symbols, past and present. *Acta Biotheoretica* 2A, 152–194.
- Lehman-Baerts, M. 1967: Ontogenese ovulaire chez *Gnetum africanum* et *Ephedra distachya*. *La Cellule* 66, 313–327.
- Long, A. G. 1966: Some Lower Carboniferous fructifications from Berwickshire, together with a theoretical account of the evolution of ovules, cupules, and carpels. *Trans. Royal Soc. Edinburgh* 66, 345–373.
- Mädler, K. 1939: Die pliozäne Flora von Frankfurt am Main. *Abh. Senckenberg. Naturforsch. Ges.* 446, 1–202. Frankfurt am Main.
- Maheshwari, P. and Vasil, V. 1961: *Gnetum*. 142 pp. New Delhi.
- May, D. H. 1963: Beiträge zur Kenntnis der Tertiärflora von Seifhennersdorf (Sachsen). *Jb. Staatl. Mus. Mineral. Geol.*, 39–114. Dresden.
- Meeuse, A. D. J. 1967: Again: the growth habit of the early angiosperms. *Acta Bot. Neerl.* 16 (2), 33–41.
- Ravin, A. W. 1955: Infection by viruses and genes. *Amer. Scientist* 43, 468–478.
- Rodin, R. J. & Kapil, R. N. 1969: Comparative anatomy of the seed coats of the *Gnetum* and their probable evolution. *Amer. Journ. Bot.* 56, 420–431.

- Simpson, G. G. 1965: *The Geography of Evolution*, 249 pp. Philadelphia, New York.
- Stebbins, G. L. 1947: Evidence in rates of evolution from the distribution of existing and fossil plant species. *Ecol. Monogr.* 17, 149-158. Durham.
- Stebbins, G. L. 1950: *Variation and Evolution in Plants*. 643 pp., New York, London.
- Stockmans, F. & Willière, Y. 1962: Que sait-on de l'apparition des Angiospermes? *Natur. Belg.* 43, 237-256.
- Stopes, M. C. 1915: Catalogue of the Mesozoic plants in the British Museum - The Cretaceous flora, 2. Lower Greensand (Aptian) plants of Britain. *British Mus. Nat. History*. 360 pp. London.
- Takhtajan, A. L. (Тахтаджян, А. Л.) 1970: *Происхождение и расселение цветковых растений*. [Flowering plants: origin and dispersal.] 145 pp., «Наука». Ленинград.
- Tidwell, W. D., Rushforth S. R. & Simper, A. D. 1970: Pre-Cretaceous flowering plants: further evidence from Utah. *Science* 170, 547-548.
- Tucker, S. C. & Gifford, E. M. 1966: Carpel development in *Drimys lanceolata*. *Amer. Journ. Bot.* 53, 671-678.
- Viniklar, L. 1931: K vyskytu Proteacei v českém útvaru kridovem. *Preslia* 10, 167-172.