

Paleobiology of Angiospermization

A. G. Ponomarenko

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow, 117647 Russia

Received December 9, 1996

Abstract—Angiospermization, i.e., the parallel appearance of features, quite variable in plant origins, typical of angiosperms, is characteristic of the Late Mesozoic continental biota. All the most important taxa seem to be derived in a similar way (eucaryotization, metasoziation, arthropodization, spermatophytization, tetrapodization, reptilization, ornithization, angiospermization, etc.), the environmental changes, occurring in this process resulting in the major evolutionary changes.

INTRODUCTION

Krassilov wrote in the beginning of his book (1989), that nearly all eminent botanists considered it their duty to speak on the problem of angiosperm origin. Consequently, as an entomologist, because of the close associations between plants and insects, I have been prompted to contribute to the discussion on this “abominable mystery” as Charles Darwin called it. This work began as a response to Rasnitsyn’s (1988) observation that the beginning of the evolutionary transformations of insects occurred earlier than the distribution of angiosperms. The wide distribution of angiosperm plants caused the Middle Cretaceous biocoenosis crisis, according to Zherikhin (1978).

Studying changes of insect composition during the extinction at the Cretaceous–Paleogene boundary, Zherikhin (1978) found, that the major change of insect composition occurred at the middle, rather than at the end of the Cretaceous. Lyell’s reverse curve, showing a time change of extinct family percentage, served as a formal base. It showed a sharp change in the middle Cretaceous, with the number of extinct families being slightly increased in the Aptian–Albian. The revolutionary changes in the insect composition coincided in time with the range of angiosperms, and Zherikhin formulated the concept of ecological crisis—angiosperms broke the ecological succession characteristic of the Mesozoic, including the pioneer stages. The disappearance of the characteristic Mesozoic ecosystems was associated with the extinction of Mesozoic insects; at the culmination of this process, coenophobes, preserved from older times as relicts, became common among insects, resulting in the development of families, that did not survive to the present. It should be noted, however, that the oryctocoenoses, on which the concept was based, had no fossil angiosperms nor pollen, while in typically Mesophytic oryctocoenoses of the second half of the Lower Cretaceous, fossil angiosperms, particularly pollen, are rather common. The question of how angiosperms managed to occupy the pioneer stages of succession without subsequent

burial remained unsolved. At present, most investigators consider that these localities belong to the late Jurassic, rather than to the middle Cretaceous, while the general curve remains mainly the same.

In 1988, Rasnitsyn attempted a detailed study of this process and found, that the bending of Lyell’s reverse curve indicated that the crisis beginning is much earlier and falls in the Late Jurassic, while angiosperms, according to the then accepted concepts, appeared in the middle of the Early Cretaceous. Angiosperms occurs in considerable numbers in the near-shore terrestrial landscapes in the middle of the Albian, a late stage of the Early Cretaceous. Rasnitsyn concluded that the cause of the Middle Cretaceous ecological crisis was other than that of the appearance of angiosperms. A similar result is shown by the recent analysis of data on the geological occurrence of insect families (based on the data of the Paleontological Laboratory, Paleontological Institute) in the “Treatise of Invertebrate Paleontology” (Carpenter, 1992).

DISCUSSION

The evolution of insects is quite characteristic of the continental biota evolution in general. Their association with plants is close enough to require some specific features of plant evolution to explain the nature of the insect compositional change. The variable ecology and highly specialized way of life made insects a good “touchstone” for determining the state of continental ecosystems. It is in insects that the highest correlation of evolutionary changes in diversity among continental groups is found compared with that of marine faunas. Since their appearance, insects have been closely associated with plants, these associations being mutual. Moreover, Rasnitsyn (1976) managed to convincingly show, that it was feeding on the plant generative organs that led to flight in insects and to their great diversity (ecologically, in particular). Krassilov (1989) considers, that entomophily was characteristic of even the oldest Carboniferous seed plants. From the very begin-

ning, feeding on the plant generative organs was the most common diet of insects. In quite variable tropical Late Carboniferous entomofaunas, most species included forms that sucked unripened seeds. Most of the remaining species fed on pollen, often eating it together with the sporangia. The frequency of pollen-feeding is more difficult to determine because many insects, including those in which pollen was found in the gut (Rasnitsyn and Krassilov, 1996), had no distinct mechanisms for this kind of diet. Insects with a typical anthophilous appearance began to occur from the Late Jurassic, although insects with a quite variable appearance continued to feed on pollen judging from the contents of their gut. It should be noted that this anthophilous appearance is typical of mature insects feeding on the pollen and nectar of open flowers. Insects, the larvae of which develop in the generative organs of plants, generally do not have this typical appearance although they can also participate in pollination. The most common pollen in the feeding of Late Jurassic insects was that of *Classopollis*, belonging to Hirmirellacea (Cheirolepidiaceae). Bennettite "flowers" with larvae-feeding marks are known (Crowson, 1975). At present, parasites of the male strobili are obligate pollinators even of some diclynylian cycads. Hence, these could play an important role in pollinating monoclynylian bennettites.

An interesting specific feature of the history of insect and plant interrelations is noteworthy. Insects did not eat the green parts of plants for almost all the time of their coexistence. They fed upon the generative organs, wood, sucked the vessel contents but, did not actually eat the leaves. Leaf injuries are known only from the Permian; these could well belong to the numerous myriapods of that time that could have fed on fallen leaves. In the Mesozoic up to the Late Cretaceous, neither injuries nor mining-traces within the leaves left by insect larvae are known. Study of the contents of the insects' gut shows only one case in *Brachyphyllum* fossils (Krassilov, 1997). It seems, that the rare utilization of Mesozoic plants by insects (and, most probably by other phytophages) was associated with a characteristic xeromorphic structure showing a great number of skeletal and protective elements and with a low food value. Hughes (1976) related this feature of their structure with the time that the leaves remained on the plant. In this case, eating a considerable amount of the green parts of plants, in contrast to the situation with present angiosperms, would have led to irreversible damage of plants and to their rapid death. Because of the low nourishment value, consumers would have eaten a great amount of vegetable mass per unit of their own mass. This would have increased their destructive effect on plants. The consequences of feeding on the generative organs, plant sap, and wood would have been much less serious. These were the strategies that insects resorted to.

However, the distribution of angiosperms changed everything; partially eaten leaves and mines are known from beds as early as the Cenomanian. A great number

of leaf-eating insects appeared with the angiosperms, and subsequently moved on to the conifers, ferns, and horsetails. At present, there are no primitive leaf-eating insects on these Mesozoic groups of plants. Only relict peloridiids live solely on mosses, and even then these belong to a group, appearing only in the Cretaceous. Indeed, the response of insects to the occurrence of proangiosperms and angiosperms was considerable. In the Cretaceous of Eastern Asia, representatives of groups of insects, living at present on angiosperms, appeared simultaneously with angiosperm pollen and forestalled the occurrence of their leaf litter. Thus, it seems probable that the nature of insect evolution can be used as a very important factor in studying plant evolution, and the above mentioned lack of a time-coincidence of angiosperm occurrence and the insect compositional change actually requires a special explanation.

It seems, that the concept of angiospermization (Krassilov, 1989), similar to that of mammalization, suggested by Tatarinov in 1976 provides a solution to this contradiction. In both cases, the process involved a rather prolonged appearance of features, typical of the descendant taxon, in various representatives of the ancestral taxon. In this sense the process of mammalization is considered to involve the stem-based taxon (de Queiroz and Gauthier, 1990). Particular features of mammals appear both in theromorphic (mammal-like) and sauromorphic reptiles, e.g. pseudosuchian stance changing from sprawling to parasagittal. Similarly, angiospermization involves almost all groups of gymnosperms. Apparently adaptation features have shown that gametophyte reduction and microsporophyll simplification occurred in angiosperms and gnetalians simultaneously (Doyle and Donoghue, 1993). However, such features as the presence of entomophilous "flowers" (*Eoantha*: Krassilov, 1986) in some Early Cretaceous gnetalians, and the affinity between gnetalians and angiosperms in leaf structure (*Drewria*: Crane and Upchurch, 1987), rather than the features of fundamental affinity, seem more essential for the discussion below. In this consideration, the process of angiospermization seems to involve both groups closest to angiosperms, e.g., the *Angiophyta* within the range suggested by Doyle and Donoghue, and the remote groups of gymnosperms and even spore plants, which had features allowing them, to a certain degree, to play an ecological role in the present-day angiosperms. Such mossy plants as *Monsechia* and *Briochoutulinia*, that probably played the role of angiosperm-macrophytes in the Late Mesozoic lakes, and like these, stabilized biogen consumption in the basins, can be taken as an extreme example. The notorious "*Ranunculus*" from the Lower Cretaceous Monsech locality, or the plants recently defined from the Wealdian in Great Britain (Hill, 1996) and Aptian in Australia (Taylor and Hickey, 1990), seemed to be somewhat similar to proangiosperms. Many proangiosperms were aquatic or near-shore terrestrial plants. We cannot but agree with Hughes' statement, that the role of aquatic plants

is much underestimated. It apparently was due to these parallel processes that the possible variability from glossopterids to angiosperms, illustrated in "The Greening of Gondwana" (White, 1993) occurred. It is no mere chance, that the title of our article has something in common with the title of the well known book written by Hughes (1976), in which the author tried to reconstruct the environment in which angiosperms appeared. This article has the same main purpose but the major objective is to show the reasons for the Earth's biota transformation that caused the historical necessity for the appearance of the angiosperms or something similar in the ecological role. This is the main difference in the statements proposed here from Krassilov's ideas (1989). He considers proangiosperms to be related to angiosperms either directly or through virus transduction. According to the proposal here, there is no direct relation between most of proangiosperms and angiosperms; these only formed conditions of life favourable for the evolution towards angiospermization. This path was followed by many groups although only angiosperms appeared to be the best group for playing this ecological role.

The analysis of similar situations shows that all major groups seem to evolve in the same way (eucaryotization, metazoization, arthropodization, spermatophytization, tetrapodization, reptilization, ornithization, angiospermization, etc.). In addition, this approach allows us in my opinion to avoid discussions on the validity of taxonomic and cladistic approaches (rank versus trees: Doyle and Donoghue, 1993).

Until recently, the origin of flowering plants was the subject of impetuous speculations. For Charles Darwin the sudden appearance of angiosperms in the geological record and their wide distribution did not accord with the evolutionary principles suggested by him. The world-wide spread of palynological investigations and the detailed study of macroscopic fossil localities made it possible to radically change the situation. Palynology showed an integral, though not quite detailed, picture of the Earth, leaving no place for conjectures in either geography or the time period for angiosperm origin and occurrences. Of great importance for the latter were findings of pollen in sea deposits. Studying in detail many localities, including those known for a long time and poor in fossils, made it possible to receive both the general data on leaves and woods and numerous flowers and flower-like organs of the direct predecessors of angiosperms. Apparently many groups of gymnosperms, primarily gnetalians and bennettites, simultaneously developed features of flowering plants. There are some serious differences in estimates of the process of angiosperm development although the general data for substantial discussions and scientific investigations are available (Hughes, 1976, 1994; Crane *et al.*, 1995; Doyle and Donoghue, 1993). Thus, the changes of the environment seem to be most important for the evolutionary process involving repeated attempts to find to the best taxon for a particular ecological role in this

environment, the requirements of this taxon change in the course of this process and it should constantly change itself (Van Vallen's Red Queen Hypothesis). The appearance of a new group will not result from one major evolutionary change; it diversifies in the new niche (or license), and some of its features appear in various representatives of the preceding group; it is these new features that make the existence of a new group better adapted to its environment. The role of these processes is determined by the system that accommodates any change in a particular direction and makes further changes in the same direction more reasonable and probable.

The following is a short discussion on the ecological consequences of angiospermization. Examination of the distribution of so-called "proangiosperms" (Krassilov's term for gymnosperms bearing some features of angiosperms) shows that an increase of these findings generally parallels a decrease in the percentage of extinct insect families. As was stated above, insects can be good indicators of the biota state in general. Recently, several studies of insect evolutionary diversity at the family level were made (Labandeira and Sepkoski, 1993; Ross and Jarzembowski, 1993). The results seem to clearly show real processes based on data, including that of paleoentomologists at PIN one of the leading institutes in the world, for the study of Cretaceous insects.

The ecological advantages of angiosperms have been regularly discussed (Stebbins, 1981; Bond, 1989; Marzluff, Dial, 1991; Doyle and Donoghue, 1993). The only essential difference is that of distinguishing the main advantages i.e. the question of what was more essential—a high rate of growth or pollination by insects—seems unimportant. There are apparently three ecological advantages of angiosperms. One is the tendency of neoteny, making angiosperms especially aggressive expellers (grassy dicotyledons) and good suppressors of erosion (monocotyledons). Secondly the production of leaves with a great volume of photosynthesizing parenchyma (among gymnosperms only in gnetalians). And, thirdly, entomophily of flowers (gnetalians and bennettites) and zoochory of seeds (various gymnosperms). The first of these specific features—the ability to derive grassy and annual forms—is actually peculiar to angiosperms, although some fossil forms, very similar to monocotyledons in appearance, were described from the lowermost Cretaceous of the Manlai locality (Krassilov, 1980; Krassilov, 1982). Also important is the ability of gnetalians to exist in the form of liana, which points to the presence of the tendency to neoteny in these. The frequency of gymnosperms with other features also increases in the crisis area. Also more common here are highly-specialized anemochore gymnosperms, e.g., *Problematosperum*, similar to the dandelion flying seeds, and *Basia*, very similar to the aechena-like foetus (bennettites, according to Krassilov). It should be emphasized, that from the point of view of other members of the same ecosystem, these "proangiosperms"

cannot be distinguished from real angiosperms. For a squirrel, hazel and cedar nuts are merely nuts; *Gnetum*, the leaves of which are difficult to distinguish from those of angiosperms, is the only gymnosperm flourishing in a rain tropical forest. Some cycads have weevils, the larvae of which parasitize on male strobili, as their obligate pollinators, that subsequently visit the female strobili (in some yet unknown way) and pollinate them. In botanical gardens, where these specific insects are absent the cycads cannot produce seeds (Norstog and Fawcett, 1989). Their high diversity of angiosperm is made possible by entomophily (Stebbins, 1974, 1981). Hence in some tropical forests, the frequency of trees can be one species per hectare. It would be quite impossible to keep such a low density of population without the help of insects. It is the distribution process of proangiosperms, having features of angiosperms, that seems to create the world in which the appearance of angiosperms or some other ecologically similar group is inevitable. Angiosperms themselves are the result of the process of world angiospermization. If angiosperms had not appeared their role would most probably have been played by gnetalians.

As can be seen, the above concept differs much from the accepted one. Almost all manuals on evolution have a scheme showing the way in which a newly appearing group invades as a "key aromorphosis" a new free adaptive zone. This process seems to be different. Quite different groups of the previous adaptive zone acquire some features, typical of the future dominant group, and each of these forms a new adaptive zone "bulging out" of the previous one. These separate enclaves gradually merge to form one new adaptive zone where both a new assemblage and its new dominant are formed, resulting from the competition between different groups, "proangiosperms" in this case. Naturally, forms closest to the new dominant are displaced by their competitors. The process of angiosperm distribution lead to the gradual extinction of bennettites, chekanowskiales, numerous Mesozoic ginkgoes, and forms close to gnetalians (according to Krassilov). The systematic position of these forms, from an ecological point of view, is not very important. The process of key angiosperm apomorphic appearances, i.e., the process of transition between the *Angiophyta* and *Angiosperma* sensu Doyle and Donoghue, 1993, is not essential, either (the authors themselves felt somewhat uncertain about what this taxon would be—*Angiophyta*, but not quite *Angiosperma*). The world angiospermization does not result from the development of these apomorphs, but it is rather a necessary condition for their appearance and *Angiosperma* taxon formation.

The evolution of insects of the Cretaceous was generally described by Zherikhin (1980) and Kalugina (1980); the description of some groups was given by many authors in the "Continental Cretaceous of the USSR" (1990). We will focus only on the specific features of the evolution of groups not specially mentioned

in the above papers. In the Late Jurassic and Cretaceous, among representatives of hymenopterans, including the most specialized pollinators, bees, a gradual increase of diversity, including facultative anthophiles, occurs. With angiosperm distribution, ants—the most powerful regulating factor for consuming processes in continental ecosystems—appeared. Bees appeared only in the Cenozoic, showing a considerable increase in the diversity of phytocoenoses and decrease in the density of the entomophilous plant population. The evolution of hemipteran—the leading phytophagous group that sucks out vegetable saps, is very interesting. Their replacement at the most valid family level was rather gradual, without any sharp changing at the time of angiosperm distribution. This can be considered as an indication of the gradual replacement of the most common plants rather than catastrophic change. The comparison of the distribution of psyllites and aphides is substantial. Aphides, having a tendency to asexual reproduction and neoteny, are a group most adaptable to living in ecosystems with a much variable phytomass, and poor regulation. It is not without reason that these are the most important pests. Coccids and aleurodids are similar to aphides. Then follow psyllites. Aphides have been in existence since the Triassic; however in the Early and Middle Jurassic they yielded to the prevailing psyllites. In the Late Jurassic they became as numerous as psyllites, and in the Early Cretaceous they were abundant. Coccids joined them in the Early Cretaceous, and aleurodids—in the Late Cretaceous. During this time psyllites are rare; in Neogene, they become abundant again. The ratio changes seem to show a decrease in ecosystem stability during the process of angiospermization, followed by its restoration. Present is a comparison of two groups of plant-eating beetles—xylophagous and phyllophagous. The first group shows the gradual increase in diversity and also the gradual replacing of dominants—from cupedids to buprestids, then to cerambycids. It is important that it is the cupedids, that two oldest of the now existing genera known from Early Jurassic belong to. All the present representatives of these genera live on angiosperms. Hence the considerable ecological change was not associated with any essential morphological change. Leaf-eating beetles were common only since the latest Cretaceous, although some representatives of this family, for which there is reason to suggest a non-leaf-eating mode of life, were known from the Jurassic. Unfortunately, the geological history of insects is not fully known yet, and, considering their great diversity, it is difficult to expect much greater success in terms of financial restrictions. However, these examples, few as they are, show how substantial the use of data on insect evolution can be in studies on the evolution of phytocoenoses.

Describing the process of world angiospermization, we cannot but dwell on Kalugina's hypothesis (1974) about basin eutrophication with the leaf litter of angiosperms as the cause of fresh-water ecosystem reconstruction in the latest Mesozoic. Based on experi-

ments on decomposing leaves of present ginkgoes, araucarians, and cycads, Kalugina drew the conclusion that the Mesozoic gymnosperm leaves that fell into the basins also suppressed microbial activity and consequently were not processed in the detritous food-web for a long time. This resulted in the appearance of specific fresh-water ecosystems with oxyphilous insects living at the bottom, referred to as hypotrophic. With angiosperm distribution, their fast-decomposing leaf litter eutrophicated the basins that led to the disappearance of the hypotrophic ecosystems. However, taphocoenoses, typical of these ecosystems, disappear rather at the beginning, not in the middle of Cretaceous, i.e., if this change occurred, proangiosperms, rather than angiosperms, should have been responsible for it. It is not clear why the microbial activity was not suppressed in the Early Cretaceous, where the same plant groups as those suppressing the microbial activity in the Jurassic prevailed. No fossil angiosperm was reported from oryctocoenoses, which are considered to be typical of the replacement of the Middle Cretaceous ecosystems. How could they eutrophicate basins if there was no litter? If the decomposition was so fast that they did not get into burials, why were fossil insects and crustaceans preserved? If the organic matter was rapidly processed, why did the thin-bedded bottom deposits of the basins have no signs of bioturbation? Ecosystems of huge supereutrophic lakes, having existed since the Late Triassic, formed bottom deposits of such enormous organic matter that they represent rich oil-source rocks that disappeared in the mid Cretaceous. Evidently since no eutrophication occurred there since the ecosystems were already well eutrophicated; moreover, basins with a huge volume of water could not be eutrophicated as a result of leaf litter. The above comments indicate that in the process of proangiosperms and angiosperms proper distribution, basin eutrophication with continental plant leaf litter was no greater than at the present time. On the contrary, the nature of successional changes in the process of angiospermization led to a faster accumulation of organic matter from the soil layer, and a reduction of biogens entering the basins. This process, if it took place, could be responsible for the Late Cretaceous crisis of fresh-water ecosystems and for the influence on the change of marine ecosystems at the Cretaceous–Paleogene boundary.

An inorganic, primarily climatic, background of the angiospermization process should be discussed. It should be noted, however, that, if the above said is true, the angiospermization process, irrespective of the time of the origin of angiosperms, began before the Late Jurassic and became much stronger in the Early Cretaceous. Since the hypothesis of Axelrod (1970) about the origin of angiosperms under the conditions of equable climate with a moderate temperature and low seasonal prevalence, the climatic specific features have always been an essential part. Axelrod suggested, that angiosperms originated long before the Cretaceous time under the high-mountain conditions of low lati-

tudes since he considered moderate latitudes too seasonal and low latitudes too arid. However, it was shown (Vakhrameev, 1970), that the greater part of the Jurassic was characterized by a wide distribution of temperate-mild biomes with extremely low seasonal prevalence. These biomes were marked by a very low diversity of plants, and it is the wide distribution of these biomes in the Early and Middle Jurassic, that the Jurassic decrease in plant diversity seems to be associated with (Niklas *et al.*, 1980). In the Late Jurassic and Early Triassic, the climate did not actually change, although a considerable redistribution of various biomes occurred. The equably damp, moderate-warm biomes were sharply reduced, at least in Laurasia, in favor of the wider distribution of areas with hot, summer-arid climates. Just at that time, the distribution of proangiosperms occurred. Angiosperms appeared and diversified. Thus, angiospermization rather follows the evolutionary scenario of Doyle and Donoghue, than that of Axelrod.

The flat relief, quite typical of the Jurassic, also led to a wide distribution of stable closed forest areas where the highly expellent properties of proangiosperms and angiosperms did not give them considerable advantages. In contrast, a considerable redistribution of biome areas in favor of more open areas and a high increase in faults due to the increase of tectonic activity in the Cretaceous could provoke the development of fast-growing neotenic forms. According to Krassilov's (1989) data on the distribution of angiosperms, these have a distinct desposition for hotter areas with an inequable climate. In the Early Cretaceous, neither proangiosperms nor the oldest angiosperms show any essential climatic preference. It is generally accepted that angiosperm pollen appeared first in low latitudes, and the reports of its finding in the Early Cretaceous of Mongolia were treated with distrust; however, both angiosperm pollen and macrofossils were found in many localities of Transbaikalia, Mongolia, and Northern China, many of these belonging to the lowermost Lower Cretaceous. It should be noted, that these areas were characterized by strong volcanism either when or immediately before the oldest angiosperms were appearing. Thus, with reference to external reasons favourable for the distribution of proangiosperms and the oldest angiosperms, their particular relation to tectonic faults, rather than directly to different climates, can be stated. This influence might be called "lithospheric complexity", if this interpretation (Cracraft, 1982), had not been associated with the appearance of geographical barriers promoting speciation.

Finally, we will discuss the main changes in the biosphere that resulted from angiospermization. Primarily, this is the great increase in continental plant diversity. It should be taken into consideration that the high diversity is both the result and, to a certain degree, the reason for the ecosystem's persistence; thus, the considerable increase in continental ecosystem diversity, due to plants, insects and vertebrates, resulted from angiospermiza-

tion. It should be noted, that, in spite of the extinction in the process of angiospermization of the closest angiosperm equivalents, such as bennettites, chekanowskians, most ginkgoes and gnetalians, the general diversity of spore plants and gymnosperms did not decrease. The ecosystem persistence increased, so that preservation of those plants, which were replaced by angiosperms, appeared possible. Probably, it was the appearance of angiosperms, changing the nature of erosion and transportation of the biomass formed on land, to the sea, that led, on the one hand, to the crisis of marine ecosystems between the Cretaceous and Paleogene, and on the other hand—to the constant increase of marine ecosystem diversity. The latter was not stabilized in the Meso-Cenozoic as it was in the Paleozoic (Sepkoski, 1984).

The second change was in the nature of vegetable food consumption. For all their co-evolution until the appearance of angiosperms, insects rarely ate plant leaves. They fed on only the generative organs or sucked out the vessel contents—phloem and xylem. However, leaves of the oldest angiosperms had minute traces of insect larvae living inside the leaves. Present insects use leaves of both gymnosperms and ferns. Hence the non-use of leaves in the Paleozoic and Mesozoic was probably because the rate of leaf growth in gymnosperms and ferns was too slow for plants not to be affected from losing their leaves. This is in contrast to arguments of some specific digestive biochemistry, making leaf-eating impossible for insects. The feeding mechanisms of herbivorous dinosaurs also changed in the Late Cretaceous as far as we can judge by the appearance of a strong dental system evidently adapted to the grinding of highly abrasive food. The latter is represented by grassy angiosperms, on which mineral particles from the soil inevitably appeared. The appearance of large ceratopses, also having strong dental batteries and adapted to the low plant feeding—low browsing type of Bakker (1978), is also evidence of the above assumption. The appearance of highly productive pasture ecosystems, the evolution of which leads to the appearance of cereal biomes that are able to support a huge biomass of Artiodactyla, is based on angiosperms. It would not be out of place to be reminded that it is these ecosystems with abundant faunal and floral food that appeared to be the most important for man's appearance; such foods are still basic to his diet.

REFERENCES

- Axelrod, D.I., Mesozoic Paleogeography and Early Angiosperm History, *Botan. Rev.*, 1970, vol. 36, pp. 277–319.
- Bakker, R.T., Dinosaur Feeding Behaviour and the Origin of Flowering Plants, *Nature*, 1974, vol. 274, pp. 661–663.
- Bond, W.J., The Tortoise and the Hare: Ecology of Angiosperm Dominance and Gymnosperm Persistence, *J. Linn. Soc.*, 1989, vol. 36, pp. 227–249.
- Carpenter, F.M., Superclass Hexapoda, in *Treatise of Invertebrate Paleontology. Part R, Arthropoda 4*, Univ. Kansas, 1992, vol. 3.4.
- Cracraft, J., A Nonequilibrium Theory for the Rate Control of Speciation and Extinction and the Origin of Macroevolutionary Patterns, *Syst. Zool.*, 1982, vol. 31, pp. 348–365.
- Crane, P.R., Friis, E.M., and Pedersen, K.R., The Origin and Early Diversification of the Angiosperms, *Nature*, 1995, vol. 374, p. 27–33.
- Crane, P.R. and Upchurch, G.R., *Drewria potomacensis* gen. et sp. nov., an Early Cretaceous Gnetales from the Potomac Group of Virginia, *Amer. J. Bot.*, 1987, vol. 74, pp. 1722–1736.
- Crowson, R.A., The Evolutionary History of Coleoptera as Documented by Fossil and Comparative Evidence, *Atti dei X Congresso Nazionale Italiana de Entomologia*, Sassari, 1975, pp. 47–90.
- Doyle, J.A. and Donoghue, M.J., Phylogenies and Angiosperm Diversification, *Paleobiology*, 1993, vol. 19, no. 2, pp. 141–167.
- Hill, C.R., A Plant with Flower-like Organs from the Wealdian of the Weald (Lower Cretaceous), Southern England, *Cretaceous Res.*, 1996, vol. 17, pp. 27–38.
- Hughes, N.F., *Palaeobiology of Angiosperm Origins*, Cambridge Univ. Press, 1976, pp. 1–242.
- Hughes, N.F., *The Enigma of Angiosperm Origins*, Cambridge Univ. Press, 1994, pp. 1–303.
- Jarzewowski, E.A., Time Flies: the Geological Record of Insects, *Geology Today*, 1993, Nov.–Dec., pp. 218–223.
- Jarzewowski, E.A., Early Cretaceous Insect Faunas and Palaeoenvironment, *Cretaceous Res.*, 1995, vol. 16, pp. 681–693.
- Kalugina, N.S., Eutrophication as One of the Possible Reasons for Water Biocoenoses Reconstruction in the late Mesozoic, in *Antropogennoe evtrofirovaniye vodoemov* (Anthropogenic Eutrophication of Basins), (Chernogolovka), 1974, pp. 137–139.
- Kalugina, N.S., Insects in Water Ecosystems of the Past, *Istoricheskoe razvitiye klassa nasekomykh* (Historical Evolution of Insects), Rodendorf, B.B. and Rasnitsyn, A.P., Eds., Moscow: Nauka, 1980, pp. 224–240.
- Kontinental'nyi mel SSSR* (The Continental Cretaceous of the USSR), Krassilov, V.A., Ed., Vladivostok: DVO AN SSSR, 1990, p. 224.
- Krassilov, V.A., Fossil Plants of Manlai, in *Rannemelovoe ozero Manlai* (Early Cretaceous Lake of Manlai), Moscow: Nauka, 1980, pp. 41–43.
- Krassilov, V.A., Early Cretaceous Flora of Mongolia, *Palaeontographica B*, 1982, vol. 181, pp. 1–43.
- Krassilov, V.A., New Floral Structure from the Lower Cretaceous of the Lake Baikal Area, *Rev. Palaeobot. Palynol.*, 1986, vol. 47, pp. 9–16.
- Krassilov, V.A., *Proiskhozhdenie i rannaya evolyutsiya tsvetkovykh rastenii* (Origin and Early Evolution of Flowering Plants), Moscow: Nauka, 1989.
- Krassilov, V.A., The Syngeneses of Xeromorphic Plant Associations in the Paleozoic to Early Cenozoic, *Paleontol. Zh.*, 1997, no. 2, pp. 3–12.
- Krassilov, V.A. and Bugdaeva, E.V., Achene-like Fossils from the Lower Cretaceous of the Lake Baikal Area, *Rev. Palaeobot. Palynol.*, 1982, vol. 36, pp. 279–295.
- Labandeira, C.C. and Sepkoski, J.J., Jr., Insect Diversity in the Fossil Record, *Science*, 1993, vol. 261, pp. 310–315.

- Marzluff, J.M. and Dial, K.P., Life History Correlates of Taxonomic Diversity, *Ecology*, 1991, vol. 72, pp. 428–439.
- Niklas, K.J., Tiffney, B.H., and Knoll, A.H., Apparent Changes in the Diversity of Fossil Plants: a Preliminary Assessment, *Evol. Biol.*, 1980, vol. 12, pp. 1–89.
- Norstog, K.J. and Fawcett, P.K.S., Insect-Cycad Symbiosis and its Relation to the Pollination of *Zamia furfuracea* (Zamiaceae) by *Phopalotria mollis* (Curculionidae), *Amer. J. Bot.*, 1989, vol. 76, no. 9, pp. 1380–1394.
- Queiroz, de, K., Gauthier, J., Phylogeny as a Central Principle in Taxonomy: Phylogenetic Definition of Taxon Names, *Sys. Zool.*, 1990, vol. 39, pp. 307–322.
- Rasnitsyn, A.P., To the Early Evolution of Insects and Pterygota Origin, *Zh. Obshch. Biol.*, 1976, vol. 37, no. 4, pp. 543–555.
- Rasnitsyn, A.P., The Problem of Global Crisis of Continental Biocoenoses in the Middle of the Cretaceous Age, in *Melovoi biotsenoticheskii krizis i evolyutsiya nasekomykh* (Cretaceous Biocoenosis Crisis and the Evolution of Insects), Moscow: Nauka, 1988, pp. 191–207.
- Rasnitsyn, A.P. and Krassilov, V.A., The First Find of Pollen in a Lower Permian Insect Gut, *Paleontol. Zh.*, 1996, no. 3, pp. 119–124.
- Rasnitsyn, A.P. and Krassilov, V.A., Pollen in the Gut Contents of Fossil Insects as Evidence of Coevolution, *Paleontol. J.*, 1996, vol. 30, no. 6, pp. 716–722.
- Ross, A.J. and Jarzembowski, E.A., Arthropoda (Hexapoda: Insecta), in *The Fossil Record 2*, Benton, M.J., Ed., London: Chapman and Hall, 1993, pp. 363–426.
- Sepkoski, J.J., Jr., A Kinetic Model of Phanerozoic Diversity, III. Post-Paleozoic Families and mass extinction, *Paleobiol.*, 1984, vol. 10, no. 2, pp. 246–267.
- Stebbins, G.L., *Flowering Plants: Evolution Above Species Level*, Cambridge: Harvard Univ. Press, 1974.
- Stebbins, G.L., Why are There so Many Species of Plants, *Bioscience*, 1981, vol. 31, pp. 573–577.
- Tatarinov, L.P., *Morfologicheskaya evolyutsiya teriodontov i obshchie voprosy filogenetiki* (Morphological Evolution of Theriodonts and General Problems of Phylogenetics), Moscow: Nauka, 1976.
- Taylor, D.W. and Hickey, L.J., An Aptian Plant with Attached Leaves and Flowers: Implications for Angiosperm Origin, *Science*, 1990, vol. 247, pp. 702–704.
- Vakhrameev, V.A., Jurassic and Early Cretaceous Flora, *Paleozoiskie i mezozoiskie flory Evrazii i fitogeografiya etogo vremeni* (Paleozoic and Mesozoic Flora from Eurasia and Phytogeography of that Time), Moscow: Nauka, 1970, pp. 213–281.
- White, M.E., The Greening of Gondwana, *Reed Publ.*, 1993, p. 256.
- Zherikhin, V.V., The Development and Replacement of Cretaceous and Cainozoic Faunal Assemblages (Tracheophyte and Chelicerate), in *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1978.
- Zherikhin, V.V., Insects in Land Ecosystems, *Istoricheskoe razvitie klassa nasekomykh* (Historical Evolution of Insects), Rodendorf, B.B. and Rasnitsyn, A.P., Eds., Moscow: Nauka, 1980, pp. 189–224.