

Evolution of Continental Aquatic Ecosystems

A. G. Ponomarenko

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

Received September 30, 1995

Abstract—Algal-bacterial mats retained their ecological significance throughout the whole history of freshwater ecosystems. Geographical distribution of different freshwater ecosystem types was climatically controlled. The modern-type freshwater ecosystems that are, to a considerable extent, regulated by macrophytes, appeared at the end of Paleogene.

Ecosystem evolution still remains the least understood part of evolutionary theory. Discussions of ecosystem evolution almost inevitably digress to biotic components, often to a single group of organisms. Certainly, biotic components evolve with ecosystems, but the focus should not be displaced from ecosystem characters as such, the trophic and, more generally speaking, the information links and internal regulatory interactions. This fully applies to freshwater ecosystems. For instance, the monograph by Gray (1988) describes primarily the geological histories of non-marine organisms. The present work attempts an analysis of the systemic characters of non-marine aquatic ecosystems. While dealing with still poorly studied objects, its propositions are, by necessity, preliminary and sometimes provocative.

Our understanding of ancient ecosystems depends to a considerable extent on our knowledge of ongoing ecosystem processes. However, an uncritical application of the actualistic approach may turn out to be an implicit acceptance of uniformitarian identity of the past and the present. This approach is hardly productive. It seems more expedient to start with an assumption that the biosphere of the past was different from that of the present unless the contrary is established.

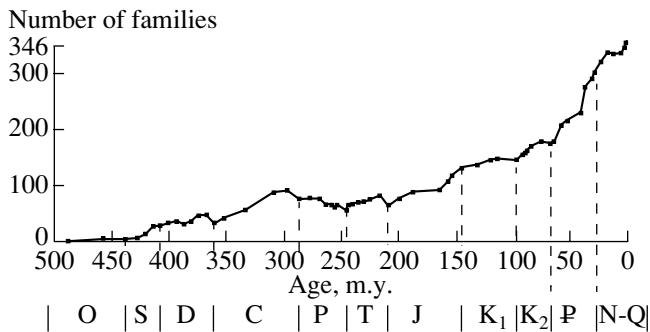
Our idea of freshwater reservoirs are formed under the impression of the present day creeks, rivers swamps and lakes. All these are, in a sense, fast or slow flowing rivers, for they are, to a certain extent, drained, and their major characteristics are defined by this. Limnology was based on observations on the northern European lakes of glacial origin and that had been formed on a tectonically quiescent basement. Deposits of such lakes are infrafacial and are hardly discernible in the fossil record. Reservoirs of the past may have been fairly different from extant ones. They may be comparable with seas rather than rivers. Firstly, the most widespread reservoirs on the continental crust were the epicontinental seas. With a reduction of their oceanic connections (if there were oceans) they often became freshwater. In contrast, lakes of the past, more often than at present,

were non-drained final basins and became salty. The further back in geological history, the more obscure are the distinctions between seas and lakes. That is why the marine or non-marine origin of Paleozoic animals is still an open question despite all of the lengthy discussions.

These complications make the elucidation of the history of continental reservoirs even more problematic. In the following discussion I call these reservoirs freshwater, as tradition has obliged, although they might actually have been hypersaline. The discussion is restricted to lakes, because other types of reservoirs are poorly documented.

In the following analysis it is assumed that, in the course of evolution, the systems capable of a closed recycling of matter and energy are positively selected. While in aquatic systems the deposited organic material was anoxic, a considerable part of this organic material is not recycled and is buried in the bottom sediments. Thus, the preferentially selected systems are those with a more complete utilization of organic matter, that is oligotrophic according to the original definition proposed by Tinnemann.

We use diversity at the family level as a generalized measure of ecosystem stability. The lower taxonomic levels are less reliable because of a strong stochastic component and unequal research allocations. The diversity of the evolution of non-marine biota is considered in more detail elsewhere (Dmitriev *et al.*, 1995). I reproduce the diversity curve from this work (figure) showing that the number of families rapidly increases in the Late Devonian, drops at the beginning of the Carboniferous, then increases again until the major drop in the Permian, rises in the Triassic, drops at the Triassic–Jurassic boundary, strongly rises in the Late Jurassic, and remains nearly constant in the Early Cretaceous, increasing again at the beginning of Late Cretaceous and further in the Cenozoic. A major contribution to the rise of diversity is made by arthropods, especially insects, thus deserving special attention. A comparison of the curves of familial diversity for marine and non-marine reservoirs showed that in both, the most signif-



The numbers of families of freshwater organisms crossing the age/stage boundaries.

icant extinctions coincide in time, but differ in character. In the non-marine reservoirs, extinction usually commenced earlier and was less significant. This was supposedly related to the isolation of non-marine reservoirs and their more immediate response to environmental hazards. The ocean, as a more integrated system, has to respond as a whole, its ecosystem can longer resist changes that results in a more disruptive effect.

It is worth mentioning that aquatic ecosystems are scarcely capable of directing their development by conditioning of their environments in the course of ecogenic succession. The non-marine ecosystems are somewhat more adapted for such conditioning for their water masses and most of the bound energy is their own rather than transitory, as in the seas. At the same time, continental reservoirs are to a much larger extent controlled by tectonic factors and erosion rates on the adjacent land. We have to remember also that, from the point of view of terrestrial successional systems, the aquatic ecosystems represent only one of the initial hydrosere stages and, in this respect, have no evolutionary significance of their own. As will be shown later in the paper, the anti-erosion function of terrestrial vegetation constituted the most important factor in the evolution of continental aquatic ecosystems. But, in the above sense, this factor is a notable one for the whole land system that includes the continental reservoirs as its component.

I use insects for the analysis of aquatic ("freshwater") ecosystem evolution for, as a paleoentomologist, I am better acquainted with the group, and also because insects are almost exclusively non-marine organisms while their diversity dynamics correlates with that of the entire freshwater biota.

The history of continental reservoirs goes back as far as the Precambrian when landscapes structures were considerably different from the extant ones (Kholodov, 1993; Sergeev, 1993; Zavarzin, 1993). Active erosion on land still lacking higher plant cover, peneplated the relief. There were no constant water flows and the existing reservoirs were shallow and saucer-shaped with

unstable coastal lines. Many reservoirs served as final basins and were brackish or hypersaline. Most of them were transient, rapidly filled with the large mass of solid washout. The larger part of yet insignificant continental sediments was deposited as proluvium on the gently tilted coastal plains that did not form a definite coastal line. Just this broad transitional zone between sea and land was colonized by the stromatolites that were thought to be continental (Krylov and Zavarzin, 1988). After peneplation, the erosion slowed down and deposition, spreading over large areas, was shallow.

The earliest ecosystems were benthic and floating algal-bacterial mats preserved as stromatolites. The stromatolites can hardly be conceived of as just "in essence, the byproduct of microbial communities" (Rozanov and Fedonkin, 1994, p. 27). With their appearance several ecological problems were solved. First, they enabled microorganisms to form fixed macroscopic bodies. Second, they directed water flow, supplying nutrients for the colony (in contrast, planktonic organisms rapidly consume all the nutrients in their immediate environments, their further supply being due to a slow process of diffusion).

The role of benthic mats in the primary ecosystems might have been inferior to floating algal-bacterial aggregates. For the latter the mucous sheaths were no less important than for benthic mats. Photosynthesis produced gases that raised the floating mats above water subjecting them to dessication and direct light. Association of producers and reducers in the mats provided for the reduction of organic matter thus stabilizing the biomass and preventing self-poisoning. Extant unicellular algae lose about half of the organic matter produced which is not only wasted in terms of recycling, but also creates anoxic conditions (oxygen is spent on dissolved organic matter without any benefit to the ecosystem). Cooperation in the mats approached the lichen grade, and they functioned as superorganisms.

Although biologically advanced and stable, mats were vulnerable to abiotic impacts. They perished from dessication when stranded by waves and from silt deposition preventing photosynthesis. In effect, the loss of organic matter was considerable, the more so in that reduction of organic substances outside the mats was insignificant. Caustobiolites accumulated at very high rates (Zakrutkin, 1993) because a much larger part of organic production was fossilized than in present day ecosystems. Despite their low biomass, mats effectively oxygenized the atmosphere.

The appearance of eukaryotes and even multicellular plants did not radically change the continental reservoir ecology. Mats remained the major producers, but they now comprised green algae, and grazing was subordinate to detritophagy.

The early evolution of planktonic organisms in continental reservoirs are little studied, but, because the latter resembled marine reservoirs of that time, the evolution patterns might have been similar in both. Marine

planktonic organisms have shown an increase in size since the Middle Riphean (Bursin, 1994) perhaps responding to the appearance of grazing protists. In the Middle Riphean, the largest spiny forms spread among the plankton. This is considered to be a reaction to the appearance of multicellular animals. In the Late Vendian, the diversity of large spiny forms decreased with the appearance of advanced vagile filter-feeders of the copepod size class. Utilization of organic production was still incomplete and the wastes were large resulting in anoxic events and severe density fluctuations in the planktonic populations. Ecosystems remained unstable, with r-selection prevailing.

The appearance of multicellular animals in continental reservoirs is not yet precisely dated, partly because of the shallowness of pre-Devonian continental deposits. They might have existed in the Ordovician: the hydromorphic Ashgillian soles show large burrows made by rather large animals, perhaps arthropods (Retallak, 1985). At that time there could have been arthropods living in mats also, but their fossils, such as euthycarcinoids, first appeared not earlier than the mid-Silurian (McNamara and Trewin, 1993). The mass occurrences of molted skins, previously assigned to myriapods (Schultse, 1972; Tesakov and Alexeev, 1992), might actually belong to euthycarcinoids, as well as the scattered Late Silurian (Jeram *et al.*, 1990; Shear and Selden, 1995) and Early Devonian (Störmer, 1976) remains assigned to a myriapod *Eoarthropleura*. These fossils were found in the deposits containing a large amount of dispersed organic matter that could have been derived from the algal-bacterial mats. Other source beds, the siliceous volcanomictic deposits, do not contradict this suggestion.

With the advent of terrestrial plants in the Devonian, there was a gradual stabilization of continental reservoirs and a slowing down of erosion. The appearance of freshwater mollusks, the long-living organisms intolerant to anoxia and dessication, can be taken as evidence of the stability of Devonian reservoirs. Interestingly, the diversity of freshwater mollusk families remains constant throughout most of their Paleozoic and Mesozoic history indicating the narrow scope of their ecological niches. Another component of the freshwater biota was represented by reptant crustaceans and aquatic chelicerans—eurypterids and scorpions. This was the peak of arthropod diversity (apart from the insects) for the Paleozoic and Mesozoic.

Lengthy discussions on the marine or non-marine habitats of Devonian fish and agnathans pertain to the transitional nature of the respective reservoirs. This problem is not yet resolved, although the antiquity of freshwater vertebrate fauna is beyond any doubt (Graf-fin, 1992).

Fish diversity rapidly increases in the Late Devonian as a result of ecological stability, in turn related to the appearance of forests. This trend is maintained until the end of Carboniferous, when the diversity somewhat

decreases at the Paleozoic–Mesozoic boundary, slightly increases again and remains nearly constant, with a slow rise in the Late Cretaceous and a more conspicuous rise in the Paleogene.

The first appearing Silurian vascular plants were aquatic rather than terrestrial, inhabiting those vast transitional land–water habitats that previously had been occupied by algal-bacterial mats. They had an advantage of three-dimensional bodies for which the silting was not so detrimental and could even have been a source of nutrients.

The so called Carboniferous forests with abundant tall lycopsids and sphenopsids might have been shallow reservoirs filled with organic matter and overgrown by helophytes. They are scarcely comparable to the present day bogs where trees grow on dry turf. In the Carboniferous forests, the root systems, stigmata, occurred below the turf layer giving rise to coal beds when covered with clayey sediments. There were no mangrove analogues that depend on tide action. In the paralic coastal basins, these forested reservoirs were inhabited by marine organisms while in the limnic intracontinental facies specific freshwater groups appeared, at least among mollusks. Among invertebrates, there were surprisingly few active swimmers, most species having walking limbs. The terrestrial groups were adapted to brief submergence: floods might have frequently occurred in these habitats having no close modern analogues except, perhaps, in the north of South America.

The presence of two more invertebrate groups may indicate a considerable distinction of the Paleozoic reservoir environment from the present. They are horseshoe crabs and cirripedes, presently marine organisms that in the late Paleozoic time lived in intracontinental reservoirs and were unknown from marine facies.

Most Triassic reservoirs are like that of the Paleozoic, with similarly alternating sandstones and siltstones and the deeply penetrating mud-flow tongues. However, in the terminal Triassic, there appeared assemblages in which remains of aquatic insects became, for the first time, more numerous than the terrestrial ones. These are assemblages characteristic of the rest of the Mesozoic and supposedly reflecting the structure of typical Mesozoic ecosystems. They are described from the New Arc Group of North America, but are still insufficiently studied. One can assume, however, that we are dealing with lacustrine assemblages dominated by dipterans. The only insect previously indicated for this locality was *Mormolucoides* Hitchcock perhaps including several unrelated taxa. On all slabs that I have seen there are pupae and larvae preserved as faint impressions in coaly shales and indeterminate. Dipteran pupae are perhaps depicted as phyllocarids from the Cow-Branch Locality (Olsen *et al.*, 1978, fig. 4). Specimens figured in Handlirsch (1906–1908, pl. 39, figs. 19–21) resemble characteristic dytiscoid larvae of Coptoclavidae and Colymbothetidae.

If so, then we are dealing with an ecosystem typical of central parts of many Mesozoic lakes with planktonic algae as producers, chaoborid larvae, coptoclid beetle larvae and fish as consumers. Such assemblages often associate with algal carbonate deposition in cyclic finely laminated sequences of marls alternating with organic-rich shales, sometimes containing hydrocarbon accumulations. In the near-shore zones of these reservoirs, there were stromatolites and micritic carbonates of the "lithographic shale" type. Characteristic of such deposits are turbidites, more or less calcitic, penetrating deep into the lake depression despite its gently sloping borders. These lakes often served as final basins and were brackish. Their biotic production was large and was not utilized in grazing whereas a detrital trophic system was mostly lacking because of bottom anoxia. Such ecosystems occurred mostly in the "warm mid-latitude" and "tropical" belts of the "warm" biosphere (so called by Chumakov *et al.*, 1995).

Since the end of the Triassic, there were ecosystems of a different type, designated by Zherikhin and Kalugina (1985) as hypotrophic. These authors suggested that a leaf litter of Mesozoic ginkgoaleans and cze-kanowskialeans had strong bactericidal activity and was not decomposed, thus leaving enough oxygen for oxyphilic benthic insects. This mechanism is, however, unrealistic and the reference to extant ginkgo inconvin-ving, for this relict species is scarcely representative of the dominant Mesozoic ginkgoalean plants. If decomposition was halted in lakes then it would not occur in soil either, while typical forest soil profiles are known in the Mesozoic indicating litter decomposition processes. In addition, abundant insect fossils indicate bottom anoxia or otherwise they would be destroyed.

Actually the aquatic ecosystems considered above seem to have been characterized by low plankton and floating island productivity. They occurred in the temperate humid zone of the warm biosphere with closed vegetation and deep soil concentrating most biogens that did not reach the lakes. Such lakes associated with alluvial deposits, might have developed as oxbow-lakes and were overgrown with helophytes, mostly horse-tails that actively extracted and accumulated biogens. They could even utilize buried biogens returning them to the ecosystem. Heliophytes might support a diverse fauna of dragonflies, stoneflies, and mayflies whose larvae are prominent in such ecosystems.

Former lake ecosystems differ from the extant ones primarily in the absence of submerged macrophytes. Presently, submerged angiosperm macrophytes extract from the water and store huge masses of biogens, thus preventing planktonic blooms. Charophytes, the only Mesozoic submerged plants, consume at least one order less biogens than angiosperms. Mats remained major producers along with plankton. Floating mats on the lycopsid and moss frames gradually gained in importance. A rich invertebrate, primarily insect, fauna lived on such mats. These huge protein rich organic masses

could also be fed upon by vertebrates such as dinosaurs. The lakes had rapidly become eutrophic, with mostly anoxic hypolimnion (Ponomarenko and Kalugina, 1980; Sanz *et al.*, 1988; Fregenal-Martinez *et al.*, 1992).

Comparing the age assignments of both types of Mesozoic aquatic ecosystem, I came to a conclusion that the first type had prevailed in the Late Jurassic and Early Cretaceous, whereas the second type was more common in Early and Mid-Jurassic time. Actually their ages might overlap, but they were confined to different climatic zones. In the Early and Middle Jurassic, almost all lacustrine localities occur in Asia, the larger part of which was encompassed by the extensive temperate zone that spread as far as 30°N. In the Late Jurassic, this boundary shifted far to the north extending at about 60°N, leaving most localities in the warmer zone.

The Early Cretaceous freshwater ecosystems of eastern Asia are characterized by high productivity and low diversity of aquatic insects, their remains being confined to finely laminated deep water deposits that lack traces of bioturbation and have a high content of organic matter. These features suggest bottom anoxia and the absence of benthic organisms. No tracks of heavy sand-built caddis-fly cases are preserved: the larvae did not live on the bottom. The fine-grained deposits suggest low water dynamics, so that insect remains could have scarcely been transported from any remote habitats. Many of the insect fossils are of molted skins that could hardly have been transported intact.

The eastern Asiatic lakes differed considerably from those in other parts of the world. They were inhabited by a specific fish fauna whereas other lakes had the same fish fauna as the sea. They are characterized also by huge masses of buried organic matter as well as by the abundance of remains of chaoborid mosquitoes and coptoclid beetle larvae.

In the Early Cretaceous, there is only one rich limnic locality of temperate aspect, the Koonwarra fossil bed in southeastern Australia. It contains abundant mayfly larvae as well as even more diverse lakefly larvae. This assemblage is comparable with the Jurassic temperate biotas.

The latest Early Cretaceous assemblages are of Aptian age. No Mesozoic-type lacustrine deposits are as yet found in the Late Cretaceous. The Cretaceous-Tertiary mass extinction had little affected the freshwater ecosystems. Dinosaurs alone disappeared while all other groups, including crocodiles, water lizards and turtles, survived. The ostracod and conchostracan assemblages underwent only slight changes indicating insignificant restructuring of aquatic ecosystems.

The first half of the Eocene was fairly warm, with warm-water reservoirs spreading over the globe. Crocodiles occurred even on Ellesmere Land in Arctic Canada. Again widespread were the hypereutrophic reservoirs with huge accumulations of organic matter.

The cooling that commenced in the later half of the Eocene had favorably affected continental reservoirs at

least in two ways. It brought about seasonal water turnovers improving oxygen supply. In addition, the cooler and drier climate promoted the expansion of grasslands that decreased erosion. In effect, the stability of aquatic ecosystems increased as indicated by their rising biological diversity. The diversity rise is apparent in the family curve (figure), but it was even more prominent at lower taxonomic levels. Thus, the species diversity of diving beetles increased almost ten-fold at the beginning of the Oligocene relative to their Eocene numbers. This trend, terminating at the beginning of the Neogene, led to a fairly constant and diverse modern type of aquatic ecosystems with abundant angiosperm macrophytes.

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