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Mesozoic Lacustrine Biota: Extinction and Persistence of Communities

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Abstract—The hypothetical structure and turnover type of selected Jurassic and Early Cretaceous lentic ecosystems of Siberia and Mongolia are discussed on the basis of paleontological and sedimentological data. The highland lakes were rather similar to the modern oligotrophic mountain ones. The shallow oxbow lakes have no modern analogues having supposedly an unusually low microbial activity rate (the hypotrophic ecosystem type, now extinct). Another peculiar type was represented by large lakes with a very high turnover rate and low saprobity combined with a high rate of primary production (the pseudooligotrophic type). There is some evidence for the existence of eutrophic lentic ecosystems which, however, seem to have been of limited distribution before the angiosperm expansion in the Mid-Cretaceous.

The lacustrine communities are represented in the paleontological record better than any other nonmarine ones providing a good basis for studies in evolutionary ecology. Investigations of representatives of Siberian and Mongolian Mesozoic lacustrine assemblages in the Paleontological Institute during the last two decades have yielded interesting results in this respect. In particular, it emerges that the structure of some lacustrine ecosystems can be interpreted easily by analogy with modern lakes while others have resisted such an interpretation.

Some Mesozoic lakes of Transbaikalia exemplify the former case. Their fossil assemblages are designated here as the Type A (Table 1). Novospasskoe, Ichetui, and Uda in Buryat Republic as well as Unda, Daya, and Shev'ya in the Chita Region are the most representative sites; there are also a number of other localities, either less rich or less studied. Possibly, some Mongolian sites such as Khutel-Khara belong to the same type. The lacustrine sediments forming the lenses within volcanic sequences have been accumulated in deep but not large montane barrier lakes. They are assigned in a broad interval from the latest Early Jurassic up to the Early Cretaceous. When the differences in age are taken into account, it is not surprising that the composition of the biota varies strongly (for data on taxonomic composition and geological age of the selected assemblages, see Zherikhin, 1978 and Rasnitsyn, 1985). However, it is rather uniform ecologically (Table 1). The assemblages are restricted to the finely laminated pelitic sediments. The aquatic vegetation is represented only by semiaquatic horsetails and occasionally by mosses. The aquatic animal diversity is not high. The insects are numerically dominant, first of all the dipterans, stoneflies, and mayflies; some crustaceans and fresh-water bryozoans are common as well. Mollusks and ostracods are infrequent, while fishes are totally absent. A high abundance of oxyphilous benthic

Table 1. Paleoecological characteristics of the Type A lacustrine assemblage

Distribution	Sedimentology	Paleontology
Transbaikalia Uppermost lower Jurassic to Lower Cretaceous	Volcanic-sedementary sequences; coalless, organic matter content very low; lenses of lacustrine sediments, lateral distribution: up to 1–2 km, thickness: hundreds of meters; fossils in finely laminated tuffaceous mudstones and siltstones	Algae unknown; no algal stromatolites; aquatic plant macrofossils scarce (mosses, horsetails); aquatic animal fossils common, dominated with zooplanktonivorous (chaoborids) and detritivorous (stonefly and/or siphlonurid mayfly nymphs) insects and crustaceans (conchostracans, notostracans, or cladocerans), low to moderately diverse (up to 30–40 species); caddis cases absent to uncommon, poor in species; trace fossils rare; oxyphilous taxa well represented; bivalvians and ostracods absent or quite rare; no gastropods; no fishes; minor components of the fauna: water mites, bryozoans; algal grazers uncommon; corixid bugs very rare; zooplanktonivore (chaoborids) moderately abundant; top predators—isophlebiid damselflies and coptoclavid beetles; occasional mass mortality events probably caused by ashfalls; allochthonous plant macrofossils very scarce and poor in species (mostly *Pityospermum* seeds); allochthonous animals uncommon (terrestrial insects, spiders), well preserved, diversity low to moderate

Table 2. Paleoecological characterisnics of the Type B lacustrine assemblage

Distribution	Sedimentology	Paleontology
Southern Siberia, northern Kazakhstan, western Mongolia Uppermost Lower Jurassic; central Transbaikalia, Lower Cretaceous	Fluvial sequences; coal-bearing, organic matter content moderate to high; lenses of lacustrine sediments, lateral distribution up to 100–150 m, thickness up to few meters; fossils mostly in more or less laminated mudstones and siltstones	Xanthophytous and filamentous algae (occasionally common); no algal stromatolites; aquatic plants: horsetails (common), isoetaleans (rare); aquatic animal fossils abundant, dominated by detritivorous (stonefly and siphlonurid mayfly nymphs) and carnivorous (stonefly and *Samarura* damselfly nymphs) insects, moderately diverse (up to 50–-60 species); caddis cases absent to (L. Cret.) common; trace fossils rare; oxyphilous taxa well represented, declining in more coarse-grained sedlments with transported terrestrial fossils; unidentified cladocerans and (in more coarse-grained sediments) small conchostracans common; no other crustaceans; no gastropods; bivalvians rare to common (in more coarse-grained and/or organic-rich sediments); palaeoniscid and pholidophorid fishes common (Jurassic); minor faunal components: bryozoans; algal grazers uncommon; corixid bugs very rare; zooplanktonivorous chaoborids absent; top predators—damselflies and fishes (coptoclavids rare) (Jurassic); no mass mortality events; allochthonous fossils well preserved in fine-grained but mostly fragmented in more coarse-grained layers; allochthonous plant macrofossils highly abundant and diverse; allochthonous animal fossils common (terrestrial insects) but not diverse

insect taxa and predominance of the shredders of allochthonous plant debris are noteworthy. The planktonivorous chaoborids are moderately abundant. Predators are comparatively diverse but represented exclusively by insects; the nymphs of the giant damselflies of the family Isophlebiidae are the largest carnivores.

The ecosystem structure of the Jurassic barrier lakes of the Transbaikal Region has been reconstructed by V.V. Zherikhin and N.S. Kalugina (in Rasnitsyn, 1985). It corresponds well with the present-day montane oligotrophic lakes with cold clear well-oxygenated water, low nutrients, and low primary production (see Table 7).

The Type B assemblages are rather similar in composition to the previous type even including some common species; they are distributed more westwards in southern Siberia and neighboring territories; their main characteristics are presented in Table 2. Chernyi Etap in Kemerovo Region as well as Ust'-Balei and Iya in Irkutsk Region are the most representative sites. The assemblages are described in detail in Rasnitsyn (1985). The most distinct features of Type B are the absence of chaoborids and presence of algal remains, bivalves, and small fish. Probably, these lakes were more productive than in the case of the Type A assemblages. The paleoenvironments differ quite strongly indicating a quite different ecosystem type. The Type B assemblages are restricted to the small lenses of lacustrine origin within coal-bearing fluvial sequences and evidently inhabited shallow oxbow lakes in large river valleys. Because the water would be warmed in this environment, the presence of highly oxyphilous groups is surprising. What is particularly strange, is that their abundance and diversity culminate in the least drained environments, namely in the most fine-grained pelitic deposits lacking any evidence of transportation for terrigenic materials and organic remains. The presence of bivalves predominantly in the coal-bearing layers is also remarkable. We have failed to find an appropriate modern model for this ecosystem type.

A reconstruction of the corresponding ecosystem type called the hypotrophic one has been proposed by Kalugina (1980) and then worked out in detail by Kalugina and Zherikhin (in Rasnitsyn, 1985). It is suggested that the microbial activity was strongly reduced by an antibiotic effect of ginkgoalean and czekanowskialean leaf litter (Table 7). The leaves of the living ginkgo placed into water do not decay at least for a year, and fossil ginkgoalean and czekanowskialean cuticles, as pointed out by Samylina (1988), show virtually no decay even when the conifer remains in the same assemblages demonstrate a high level of decomposition. The oxygen loss level for microbial transpiration and oxidation of microbial metabolites is high, and its decrease can ameliorate the oxygen regime of a water body considerably (Kuznetsov, 1970). A similar situation occurs now in dystrophic peat lakes where bacterial activity is suppressed by water acidity, but the presence of mussels in the B-type assemblages indicates a non- or at most slightly acid environment. Kalugina's (1980) hypothesis explains well the paradoxical effect of increasing flow on the assemblage: the microbial activity would increase when the antibiotic concentration decreased because of dilution. The hypotrophy may be defined as a non-acid dystrophy, a phenomenon unknown in modern hydrobiology. Kalugina (1980) and Zherikhin (1978) suggested that similar assemblages would be found in similar paleoenvironments as well as in younger deposits; this prediction has now been confirmed with the recent discovery by S.M. Sinitsa of a Type B assemblage in the Lower Cretaceous of Chernovskoe in Chita Region. In this most interesting site (its fauna is still undescribed) a rich and peculiar mayfly and stonefly assemblage is found while the dragonfly larvae and the aquatic dipterans are either absent or very rare. This assemblage differs from the

Jurassic ones in the presence of dobsonfly larvae (Megaloptera) and caddis fly cases. There are also some conchostracans, thin shales of mussels, and fragmentary fish remains. The Chernovskoe assemblage is in strong contrast with any faunas previously known from Transbaikal Siberia and Mongolia.

Hence, the apparent similarity of assemblages may be misleading in some cases. The assemblages containing the *Ephemeropsis* mayflies, *Coptoclava* beetles and *Lycoptera* osteoglossomorph fishes provide even more prominent examples. They are widely distributed in the Lower Cretaceous of eastern Asia and at first glance seem to be uniform, but a more detailed study demonstrates sufficient spatial and possibly also temporal differences. We are concerned here with the three different types of those assemblages but there are many localities, especially in Mongolia and China, which can not be classified into any of them, and the total number of the types would be higher.

The Type C assemblages are known from Buryatia, Type D from eastern Transbaikalia, and Type E from Mongolia. The representative sites are correspondingly Baisa and Zaza for Type C, Pavlovka, Serebryanka and Karabon for the Type D, and Shin-Khuduk and Manlai for the Type E. The common features of all three types are as follows (Tables 3–5): aquatic macrophytes are rare or absent, benthic algal grazers are abundant (particularly the mayflies and caddisflies), planktonivorous chaoborids are extremely abundant, large conchostracans *Bairdestheria*, ostracods, molluscs and fishes are present and often abundant. The differences shown in the tables concern the total diversity of the aquatic fauna, and the abundance and diversity of predators, presence or absence of oxyphilous taxa such as corydalid dobsonflies, and the abundance of facultatively algophagous water boatmen and various filter-feeders (mainly ostracods and conchostracans).

All types of lakes with *Ephemeropsis* were rather productive, as indicated by abundant algal grazers and an enormous abundance of the zooplankton feeding chaoborids. The C-type ecosystems seem to be the most productive, and D-type the least productive because of evident differences in the food-web complexity. At the same time, the ecosystem organization was strongly different from the recent eutrophic lakes manifesting a peculiar combination of features of both

Table 3. Paleoecological characteristics of the Type C lacustrine assemblage

Distribution	Sedimentology	Paleontology
Western Transbaikalia, Lower Cretaceous	Thick lacustrine sequences (up to several hundreds of meters), lateral distribution up to few dozens of kilometers; mostly rich in carbonates, occasionally with tuffite layers; coalless, organic matter content from low to high (bituminous paper-shales); fossils mostly in finely laminated marls, also in sandstones, bituminous shales, and other rocks	Algae unknown, algal stromatolites occasionally present; aquatic plant macrofossils virtually absent; aquatic animal fossils abundant, dominated by zooplanktonivorous (chaoborids), algal-grazing (*Ephemeropsis melanurus* mayfly nymphs, caddisworms), and carnivorous (*Hemeroscopus* dragonfly nymphs, *Coptoclava* beetle larvae, *Clypostemma* backswimmer) insects, highly diverse (60–100 species); caddis cases common and diverse; trace fossils uncommon; oxyphilous taxa present; cladocerans occasionally common, large conchostracans (*Bairdestheria*) and small bivalvians (*Limnocyrena*) occasionally abundant (in coastal zone only); the osteoglossomorph fish *Lycoptera fragilis* rather common; the chondrosteid *Stichopterus* presents; minor faunal components: ostracods, gastropods, bryozoans; algal grazers abundant; corixid bugs common to abundant; zooplanktonivorous chaoborids extremely abundant; predators abundant and highly diverse; top predators chondrosteid fishes (*Stichopterus*); no mass mortality events; allochthonous plant macrofossils uncommon but diverse, well preserved; allochthonous animal fossils common (terrestrial insects, spiders, bird feathers), highly diverse, and well preserved

Table 4. Paleoecological characteristics of the Type D lacustrine assemblage

Distribution	Sedimentology	Paleontology
Eastern Transbaikalia, Lower Cretaceous	Volcanic-sedimentary sequences, coalless, organic matter content variable; lenses of lacustrine sediments, lateral distribution: up to 1–2 km, thickness: dozens to hundreds of meters; fossils in finely laminated tuffaceous mudstones and siltstones	Algae unknown, no algal stromatolites; aquatic plant macrofossils virtually absent; aquatic animal fossils abundant, dominated with zooplanktonivorous (chaoborids) and algal-grazing (*Ephemeropsis trisetalis* mayfly nymphs, caddisworms) insects and large conchostracans (*Bairdestheria*), low diverse (20–30 species); caddis cases common, low to moderately diverse; trace fossils uncommon; oxyphilous taxa rarely present; ostracods rare to common; molluscs rare to absent; the osteoglossomorph *Lycoptera* fish common; algal grazers abundant; no corixid bugs; zooplanktonivorous chaoborids extremely abundant; predators rare; no dragonflies and predacious bugs; top predators—osteoglossomorph fishes (*Lycoptera*); no mass mortality events; allochthonous plant macrofossils uncommon, poorly preserved; allochthonous animal fossils uncommon (terrestrial insects, bird feathers), low diverse, and mostly poorly preserved

Table 5. Paleoecological characteristics of the Type E lacustrine assemblage

Distribution	Sedimentology	Paleontology
Mongolia, Lower Cretaceous	Thick lacustrine sequences (up to several hundreds of meters), lateral distribution up to few dozens of kilometers; mostly rich in carbonates; coalless, organic matter content from low to high (bituminous paper-shales); fossils mostly in siltstones, sandstones, and bituminous shales	Charophytes and algal stromatolites often present; aquatic plant macrofossils uncommon(liverworts, horsetails); aquatic animal fossils abundant, dominated by zooplanktonivorous (chaoborids), algal-grazing (*Ephemeropsis* melanurus mayfly nymphs, caddisworms), and carnivorous (*Coptoclava* beetle larvae) insects and large conchostracans (*Bairdestheria*), low to moderately diverse (20–60 species); caddis cases common and diverse; trace fossils uncommon; oxyphilous taxa absent; bivalvians and ostracods common to very abundant; the osteoglossomorph fish *Lycoptera* common to abundant; the chondrosteid *Stichopterus* presents; algal grazers abundant; corixid bugs common to abundant; zooplanktonivorous chaoborids extremely abundant; predators abundant, low to moderately diverse; top predators chondrosteid fishes (*Stichopterus*); mass mortality (probably anoxic) events; allochthonous plant macrofossils uncommon, poorly preserved; allochthonous animal fossils common (terrestrial insects, vertebrates), moderately diverse, mostly poorly preserved

Table 6. Supposed physical and chemical characteristics of selected Mesozoic lacustrine ecosystems

Assemblage type	A	B	C	D	E
Lake type	montane barrier	Oxbow	Intermontane, of tectonic origin	?piedmont, genesis uncertain;	?piedmont and floodplain, genesis uncertain
Surphace area	-10^{5}	-10^{1-2}	-10^{6-7}	$?-10^{2-3}$	$?-10^{2-3}$
Depth, –m	dozens	<1 to few	dozens	few to few dozens?	few to few dozens
Watershed	subhumid forested	wet densely forested	humid to semihumid	humid to semihumid	semiarid strongly eroded
Landscape	volcanic mountain land	floodplain	forested mountain land	forested foothills	low-mountain relief
Water level	stable	stable	stable to moderately oscillated	?variable	unstable
Temperature regime	constantly cold	seasonally warm	cold, with shallow zone seasonal warming	?seasonally warm	seasonally to nearly constantly warm
pH	?slightly acid, with acidification events	nearly neutral	neutral to slightly alkalinic	?slightly acidic, with acidification events	neutral to alkalinic
Dissolved oxygen	constantly high	constantly high	constantly high in epilimnion, no anoxic events	?seasonally low	seasonally low; sufocation events
Mineralization	very low	very low	low	?low	moderate to high
Turbidity	very low	low, increasing during flood events	low	?low	high
Stratification	no	no	constantly stratified, anoxic hypolimnion limit well below wind action limit	?no	stratified, upper limit of anoxic hypolimnion within wind action zone
Nutrients	Very low to low, with occasional ashfall fertilization events	moderate to high	moderate to high	moderate	moderate to high

eutrophy and oligotrophy. It is believed that a high primary production comparable with modern eutrophic systems was combined with a very high rate of grazing and consequently low algal mortmass as in the oligotrophic environments. This type of fresh water ecosystem, which is not represented now, may be designated as pseudooligotrophic.

Each of the three types inhabited a certain type of lake basin (Table 6). The C-type assemblages were restricted to the large and deep intermontane lakes of

Table 7. Supposed biological characteristics of selected Mesozoic lacustrine ecosystems

Assemblage type	A	B	C	D	E
Algal production	low	low	high	?moderate	high
Macrophyte production	very low	moderate	low	low	low
Allochthonous detritus	low	high	low	?low	?variable
Turnover rate	low	high	high	high	high
Microbial activity	low	low, suppressed by antibiotic leaf litter	moderate (high in deep-water zone)	?	?high
Dominating trophic chains	detritic	detritic	grazing	grazing	grazing
Trophic web complexity	low	low	high	low	moderate
Dominating strategy	K	K	?r	?r	r
Shredders	common	common	uncommon	?uncommon	?uncommon
Scrapers	common	common	uncommon	uncommon	uncommon
Grazers	rare	rare	common	common	common
Filtrators	very rare	rare	uncommon	common	common
Planktonivores	moderately common	rare	very abundant	very abundant	very abundant
Predators	common	common	common	rare	common
Modern analogues	cold clear-water oligotrophic lakes	no	no	?	no
Ecosystem type	montane oligotrophic to ultraoligotrophic	hypotrophic (non-acid dystrophic)	pseudooligotrophic (productive non-saprobic)	?mesooligotrophic	?pseudooligotrophic

tectonic origin, the D-type to relatively small piedmont lakes of the humid belt, and the E-type to piedmont and floodplain lakes of the semiarid belt. That basic difference has supposedly determined the main differences in ecosystem organization (Table 7). It is noteworthy, however, that an assemblage similar to the E-type occurs in Anda-Khuduk, Mongolia, in a different paleoenvironment (in floodplain lake deposits).

The model proposed by Ponomarenko and Kalugina (1980) for the Manlai Lake seems to describe well the E-type ecosystems, but its extension to the other types is doubtful. It suggests an unstable hydrological regime, the presence of a thick anoxic hypolimnion, a high turbidity, and weak development of the benthic fauna. Indeed, the E-type assemblages include many supposed r-strategists but the C-type assemblages are rich in slowly developing K-strategists and possess a much more diverse and partially oxyphilous benthic taxa; the D-assemblages seem to be intermediate. The evidence for death from oxygen starvation is restricted to the E-type assemblages. Probably, in the Transbaikalian lakes the water turbidity was much lower, and the lower limit of the well-oxygenated epilimnion was situated well below the wind action zone. The Manlai model describes probably a special case and should not be regarded as a universal one.

The lakes with a constantly high level of organic matter burial in the bottom sediments may be tentatively classified as eutrophic. Their biota is poorly known because the identifiable macrofossils are relatively rarely preserved in highly saprobic environments. Possibly, the Jurassic biota found in Bol'shoi Korui in the Chita Region (Rasnitsyn, 1985) inhabited a eutrophic lake. The faunal remains are restricted to the dark-grey to black siltstones interbedded with sandstone. Aquatic plant remains have not been recorded from Bol'shoi Korui. The invertebrates are represented by abundant thin-shale bivalves of the family Ferganoconchidae, conchostracans, caddis fly cases of the formal genus *Scyphindusia*, and occasionally by water boatmen of the genus *Henbaea* (Hemiptera: Corixidae), that is by filter-feeders and algophages. The vertebrates are not recorded. In general, the eutrophic lakes probably were of rather limited distribution in the Jurassic and Early Cretaceous.

Hence, both modern and extinct types of lacustrine ecosystems existed in the Mesozoic. The existence of hypotrophic lakes became impossible after the great change in leaf litter chemistry caused by the angiosperm expansion, and pseudooligotrophic lakes disappeared when the slowly grazed aquatic macrophytes developed at about the Mid-Cretaceous. Certainly, the above types do not cover the whole diversity of Mesozoic lakes. For instance, there are numerous Jurassic and Lower Cretaceous assemblages with a high abundance of water boatmen (Corixidae). Evidently, they do not form a uniform group. Some assemblages with corixids are connected with brackish lake paleoenvironments as in the well known Late Jurassic locality Karatau in Kazakhstan. However, many of them also contain a great number of other aquatic insects including those sensitive to salinity such as the mayflies (for example, Khoutiin-Khotgor in Mongolia and Bolboi in eastern Transbaikalia). The assemblages with water boatmen are certainly also different with respect to the food-web complexity (the highest consumer level is represented in Bolboi by large damselflies as in the Type A assemblages, and in Khoutiin-Khotgor by paleoniscid fishes).

REFERENCES

Kalugina, N.S., Insects in the Aquatic Ecosystems of the Past, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1980, vol. 175, *Istoricheskoe razvitie klassa nasekomykh* (Historical Development of the Class Insecta), pp. 224–240.

Kuznetsov, S.I., *Mikroflora ozer i ee geokhimicheskaya deyatel'nost'* (The Microflora of Lakes and Its Geochemical Activity), Leningrad: Nauka, 1970.

Ponomarenko, A.G. and Kalugina, N.S., The General Characteristics of Insects from the Manlai Fossil Site, *Tr. Sovm. Soviet-Mongol. Paleont. Exped.* (Moscow), 1980, vol. 13, *Rannemelovoe ozero Manlai* (Early Cretaceous Lake Manlai), pp. 68–81.

Rasnitsyn, A.P., Ed., The Jurassic Non-Marine Biocenoses of Southern Siberia and Adjacent Territories, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1985, vol. 213, pp. 1–199.

Samylina, V.A., *Arkagalinskaya stratoflora Severo-Vostoka Azii* (The Arkagala Stratoflora of North-East Asia), Leningrad: Nauka, 1988.

Zherikhin, V.V., Development and Changes of Cretaceous and Cenozoic Faunal Assemblages (*Tracheata* and *Chelicerata*), *Tr. Paleontol. Inst. Akad. Nauk SSSR*, (Moscow), 1978, vol. 165, pp. 1–200.