

High resolution palaeoecological and taphonomic analysis of Early Cretaceous lake biota, western Liaoning (NE-China)

Franz Theodor Fürsich^{a,b,*}, Jingeng Sha^b, Baoyu Jiang^c, Yanhong Pan^b

^a *Institut für Paläontologie der Universität Würzburg, Pleicherwall 1, D-97070 Würzburg, Germany*

^b *LPS, Nanjing Institute of Geology and Palaeontology, Academia Sinica, 210008, Nanjing, Jiangsu, China*

^c *Department of Earth Sciences, Nanjing University, 210093 Nanjing, Jiangsu, China*

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Abstract

The faunal content of eighteen bedding planes within the Jianshangou Unit of the Lower Cretaceous Yixian Formation of western Liaoning has been analysed in detail in order to understand the environmental and taphonomic framework of this famous lacustrine fossiliferous site. The bedding planes were excavated within a 3 m thick section, which is composed of laminated mudstones, graded sandstones and mudstones, and horizontally stratified structureless sandstones and tuffs. All investigated bedding planes occur within the laminated mudstone facies and contain elements of the so-called Jehol Biota, in particular the conchostracan *Eosesthesia ovata*, the ephemerid nymph *Hexagenites trisetalis* and the crustacean *Liaoningogrampus quadripartitus*. These three faunal elements occur in high abundance, originally possessed chitinous skeletons and are preserved as compressed, faintly mineralized coats or, in the case of *Eosesthesia*, still possess organic material. The specimens do not represent exuviae, but body fossils. The fossils can be grouped into three low diversity associations, each characterized by one of the three taxa. The plan-view orientation of the taxa is invariably random and size frequency histograms are bimodal or polymodal. This indicates that the fauna is autochthonous and that the histograms reflect several recruitment phases. Apparently, the faunal elements suffered seasonal mass mortality caused by anoxic conditions, which became established in the lake during the summer months. Increased humidity during the winter led to mixing of the lake waters, re-establishment of oxic conditions and to deposition of a thin film of sediment. Such environmental conditions were episodically interrupted by flash floods and volcanic ash falls, which may have been responsible for the preservation of the more spectacular elements of the Jehol biota such as birds and feathered dinosaurs.

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1. Introduction

The Lower Cretaceous lacustrine sediments of western Liaoning, north-eastern China, harbour a spectacular biota of mixed terrestrial (e.g., plants, insects, birds, dinosaurs) and lacustrine origin (e.g. fish, crustaceans,

conchostracans, insect larvae), the so-called Jehol Fauna (Grabau, 1928) or, as nowadays known, Jehol Biota (Gu, 1962) (e.g., Chang et al., 2001, 2003; Zhou et al., 2003). Set in a volcanic landscape (Liu et al., 2002), a number of smaller and larger lakes existed, which became filled with sand, silt, volcanic ash, and finely laminated claystone. These lake sediments record volcanic eruptions, catastrophic floods, and tranquil periods during which, as we shall demonstrate, commonly conditions inimical to life

* Corresponding author. Tel.: +49 931 312596; fax: +49 931 312504.

E-mail address: franz.fuersich@mail.uni-wuerzburg.de (F.T. Fürsich).

prevailed. During deposition of the tuffs and finely laminated claystones, the environmental and subsequent diagenetic conditions prevented disintegration of articulated skeletons and favoured preservation of soft parts. Due to the excellent preservation of most organisms and the evolutionary key position of some of the fossils (e.g., early angiosperms, feathered dinosaurs), the Jehol Biota counts as one of the most important Mesozoic fossilagerstätten, rivalling the much longer known Solnhofen Lithographic Limestones and Posidonia Shales from the Jurassic of Germany, which both represent marine environments. Moreover, the lacustrine setting of the Jehol Biota provides us with an opportunity to reconstruct, in detail, the Early Cretaceous freshwater ecosystem that existed in the area. Although a number of large excavations were made in the lake sediments of western Liaoning (e.g., Wang et al., 1998; Chang et al., 2001, 2003), which produced a huge number of fossils, no detailed ecological studies have been undertaken so far, the purpose of these excavations usually being to retrieve the more spectacular elements of the biota such as birds and dinosaurs. Similarly, taphonomic analyses have so far been confined to individual fossils (e.g., Ren et al., 1996; Wang, 1999; Shen et al., 1999). Concerning the lake fauna only very general statements have been made (e.g., Wang et al., 1998, 1999; Zhou et al., 2003).

The present paper is a first contribution to close this gap in our knowledge. In the following we document, in detail, the composition, preservation, and distribution of the organisms that lived in a small area of one of these lakes, henceforth named after our excavation site Zhangjiagou Lake. We are fully aware that our results do not reflect the complexity of the ecosystem of the lake. They are therefore part of a larger project aimed at understanding and reconstructing the Early Cretaceous lake ecosystems of north-eastern China and the taphonomic fate of their organisms.

2. Geological framework

The lacustrine deposits of the excavation site belong to the upper Mesozoic Jehol Group. The Jehol Group is widely distributed in the western Liaoning province (Fig. 1A). It includes (in ascending order) the Yixian, Jiufotang, and Fuxin formations (Jiang and Sha, 2006) (Fig. 2A). The Yixian Formation is composed mainly of volcanic rocks with sedimentary intercalations that contain abundant invertebrate, vertebrate, and plant fossils. It unconformably overlies either the Middle to Upper Jurassic Tuchengzi Formation or Precambrian basement rocks. The Jiufotang Formation overlies the Yixian Formation largely conformably with local

disconformities. The 225–687 m thick formation is composed mainly of tuffaceous shale, mudstone and sandstone. Fossils include gastropods, ostracods, conchostracans, and abundant vertebrates. The Fuxin Formation consists primarily of sandstones and conglomerates alternating with mudstones, sandy shales, and coal beds and contains bivalve, gastropod, and plant fossils. It overlies the Jiufotang Formation conformably and ranges in thickness from 415 to 2344 m (Jiang and Sha, 2006).

We chose the Sihetun area, which is one of the famous fossil localities of western Liaoning, for our study (Fig. 1B). The Jehol Group in the Sihetun area consists only of the Yixian Formation, which comprises four units (Fig. 2B). The lowest unit (12–67 m thick) is mainly composed of volcanic conglomerates, conglomeratic sandstones and sandstones, lapilli-stones and lapilli-tuffs. The succeeding unit is composed of basaltic andesite, disconformably overlying the lower unit. The third unit (24–112 m thick) is made up of volcanic sandstones, siltstones, claystones, shales and tuffs intercalated with calcareous shales and gypsum; the unit contains abundant conchostracan, bivalve, gastropod, ostracod, as well as vertebrate and plant fossils. Most of the well-preserved angiosperms, avifauna, dinosaurs, and other reptilian fossils have been collected from the tuffaceous claystones and shales of this unit, including *Confuciusornis sanctus*, *C. sunae*, *C. sp.*, *Eosipterus yangi*, *Liaoningornis longiditris*, *Lycoptera sinensis*, *Manchurochelys liaoxiensis*, *Peipiaosteus pani*, *Protarchaeopteryx robusta*, *Psittacosaurus sp.*, Sauroptoda indet., *Sinamia sp.*, *Sinosauropteryx prima*, Theropoda indet., and the angiosperm *Archaeofructus liaoningensis* (Wang and Zhou, 2003). The uppermost unit comprises intermediate-basic lava and intrusive rocks, which unconformably overlie or intrude the third unit, also called Jianshangou Unit (Jiang and Sha, 2007).

3. Material and methods

In order to obtain a quantitative data set, a 3.5 m deep hole (Fig. 3A) was excavated using shovels, pick-axes, hammers, and paint scrapers. The area excavated was about 9 m² near the top and narrowed to about 5.5 m² at the bottom of the hole. By carefully probing the rock pile, faunal levels were identified and excavated. As much of the rock (Fig. 3B) was finely laminated (vertically adjacent faunal levels often being less than 1 mm apart) and did not split easily along single bedding planes much care had to be placed on exposing the same bedding plane across the whole excavation area. This was done by applying paint scrapers or, in the case of an

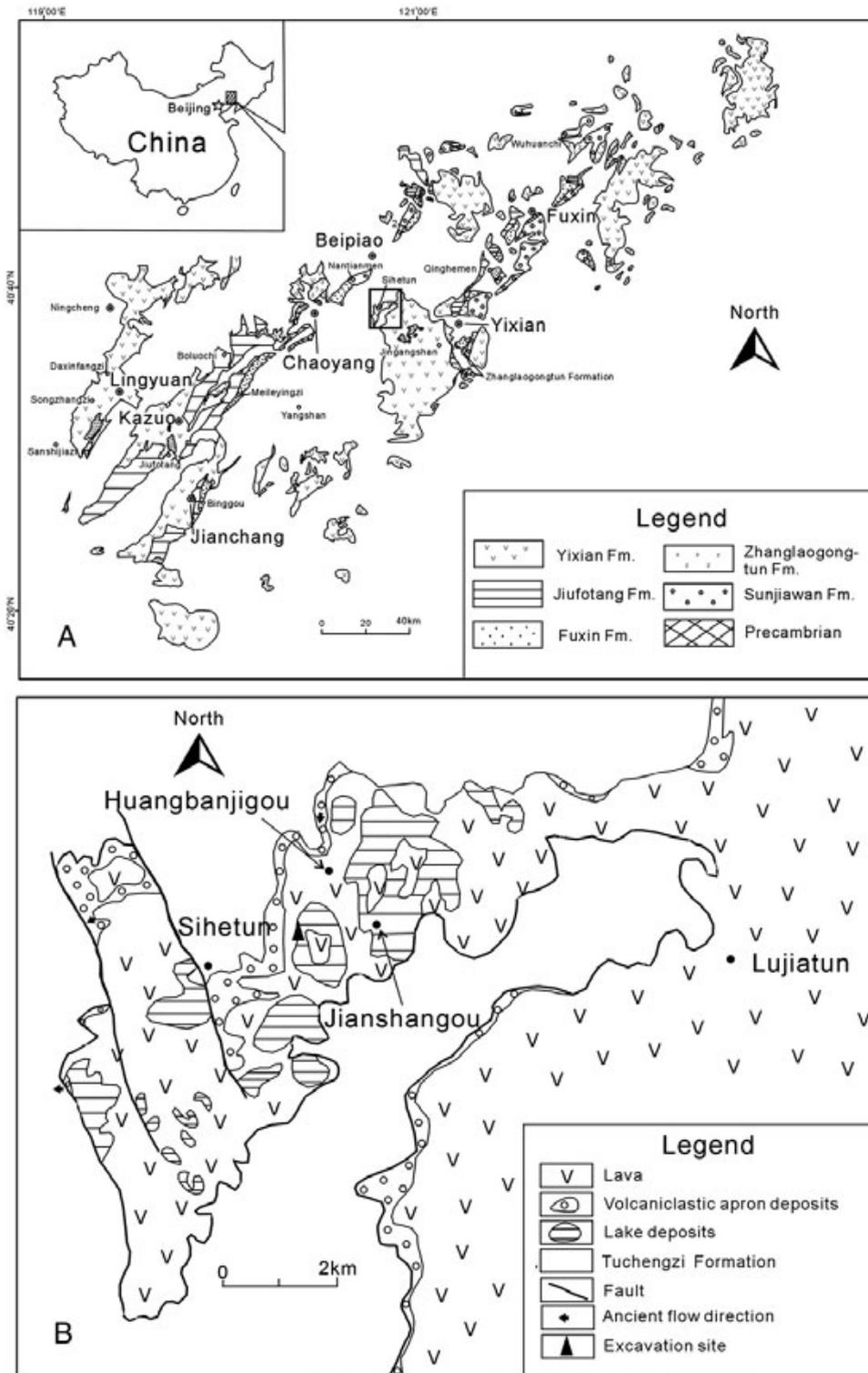


Fig. 1. Distribution of the upper Mesozoic formations in western Liaoning (A) and location of the study area (black triangle) (B). After Jiang and Sha (2007).

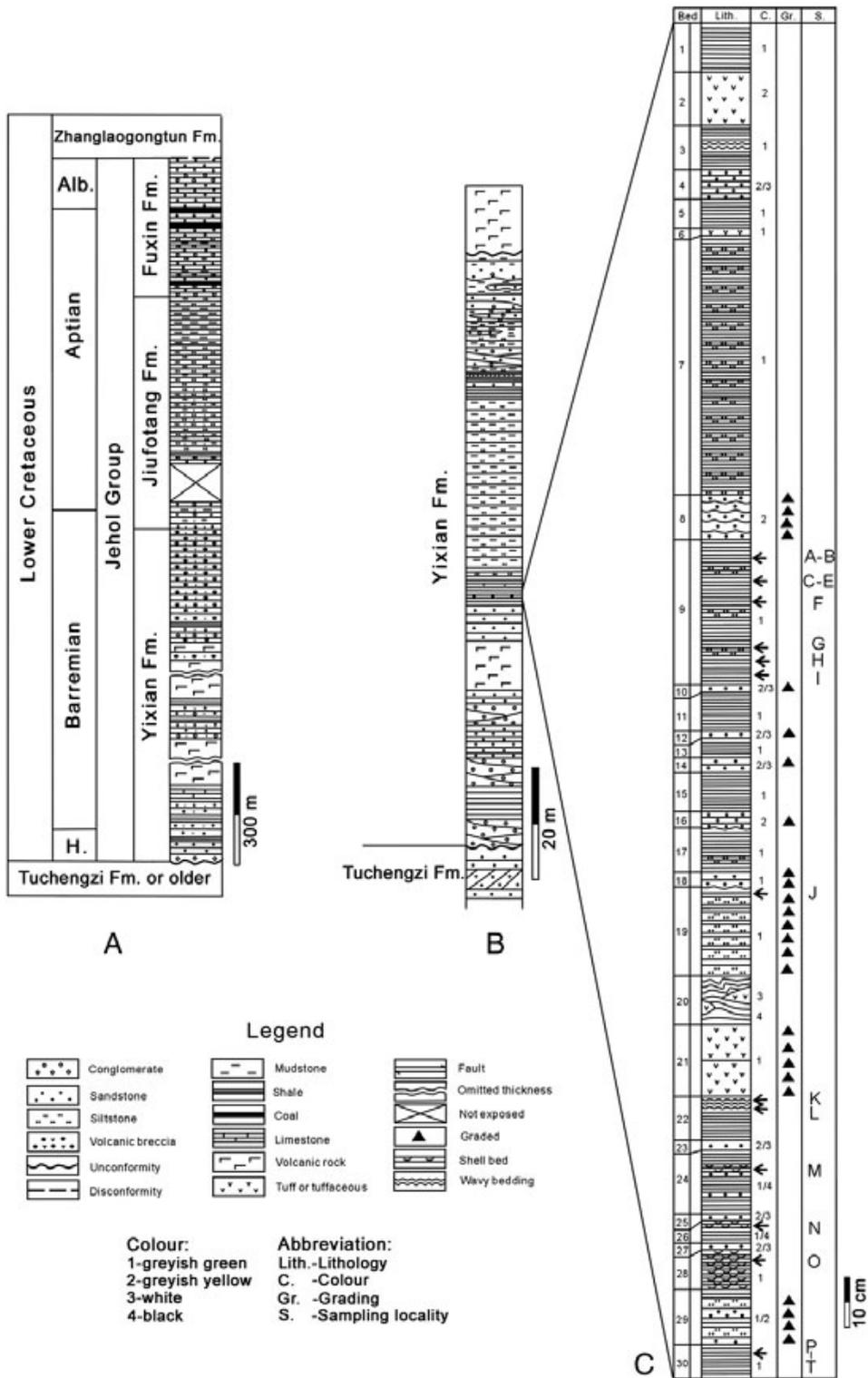


Fig. 2. Composite stratigraphic log of the Jehol Group in western Liaoning (A) and the Sihetun area (B), and details of the excavated section (C). A–T: Bedding planes from which quantitative data were obtained.

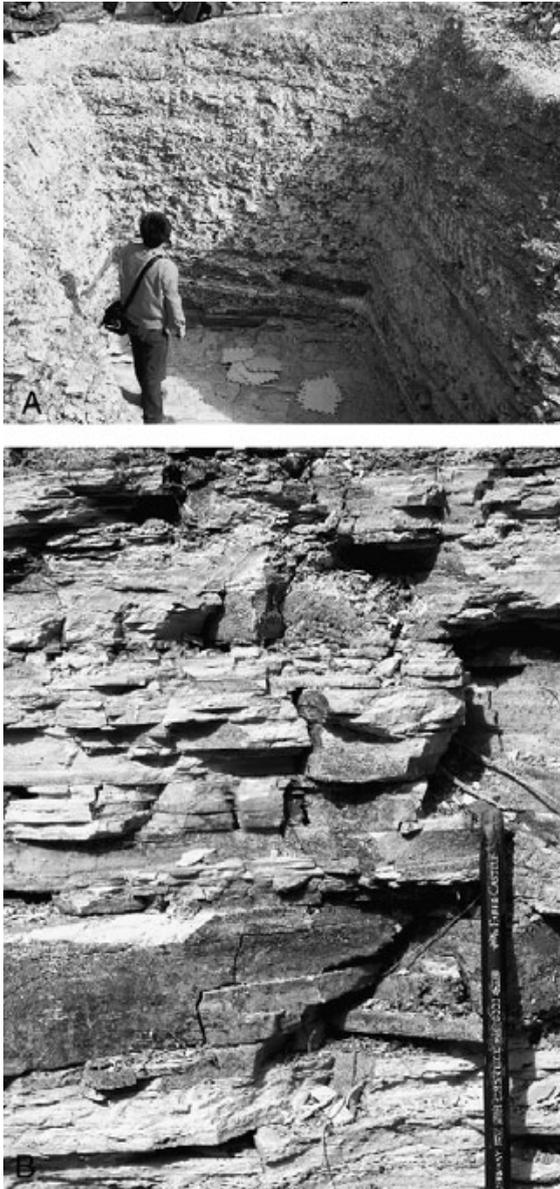


Fig. 3. A. Excavation site. B. Finely laminated sediment, consisting of partly graded mudstones, tuffs, and sandstones.

overlying skin-thin layer, lightly hammering it so that it would crack and become separated from the desired bedding plane. In the case of faunal levels C–E one-and-the-same bedding plane could not be exposed across the whole area and the faunal counts come from several (level C) and two (level D, E) bedding planes, respectively, less than one millimetre apart. As the fossil content of these neighbouring layers proved to be identical, the data of levels C–E have been treated in the same way as the remaining data set.

As the number of fossiliferous layers was fairly high within the investigated section not all of them could be quantitatively analysed. Levels for obtaining quantitative data were selected randomly and according to how easily they could be excavated. Each level selected for counting was divided into several sub-areas (usually three to six) and all faunal elements, plants or fragments thereof were registered to obtain relative abundance data. In addition, size data were obtained for the common faunal elements i.e., *Eosestheria*, *Hexagenites*, and *Liaoningogriphus* at eight of the levels. For the latter three taxa also their plan-view orientation was recorded at 13 levels. In the case of *Hexagenites* and *Liaoningogriphus* this was done by subdividing a circle in 12 segments, whereas in conchostracans the orientation of the hinge line was measured and therefore only six segments were distinguished. Representative, well preserved samples of each taxon were collected for precise identification in the laboratory and for illustrating the variability.

Apart from taphonomic observations, sedimentological data were recorded, in particular bedding plane features. They include the degree of irregularity of the surface and small fold structures, which may represent incipient slumping.

In the laboratory, the taxa were identified and size-frequency histograms and rose diagrams were constructed using PAST (Hammer et al., 2001). Growth lines of conchostracans were checked for crowding and counted in the few cases where this was possible. In addition, observations regarding displacement of the two valves were made. In *Hexagenites* and *Liaoningogriphus* the body orientation (dorsal versus ventral side facing down as opposed to a side orientation) was noted.

4. Section and lithofacies

The section we excavated (Fig. 4) lies in the lower part of the Jianshangou Unit of the Yixian Formation (Fig. 2B). The rocks of the small section correspond to three lithofacies of Jiang and Sha (2007) i.e., (1) laminated mudstones (M2), (2) horizontally stratified homogeneous sandstones and tuffs (S2), and (3) graded sandstones and mudstones (S/M).

4.1. Laminated mudstones (M2) (Fig. 5)

This facies is composed of greyish-green and dark grey, finely laminated, graded siltstones, silty claystones and claystones (shales), occasionally exhibiting convolute bedding. The laminae are 0.1–1 mm thick (Fig. 5). The sediment consists mainly of silt-sized, altered lithic

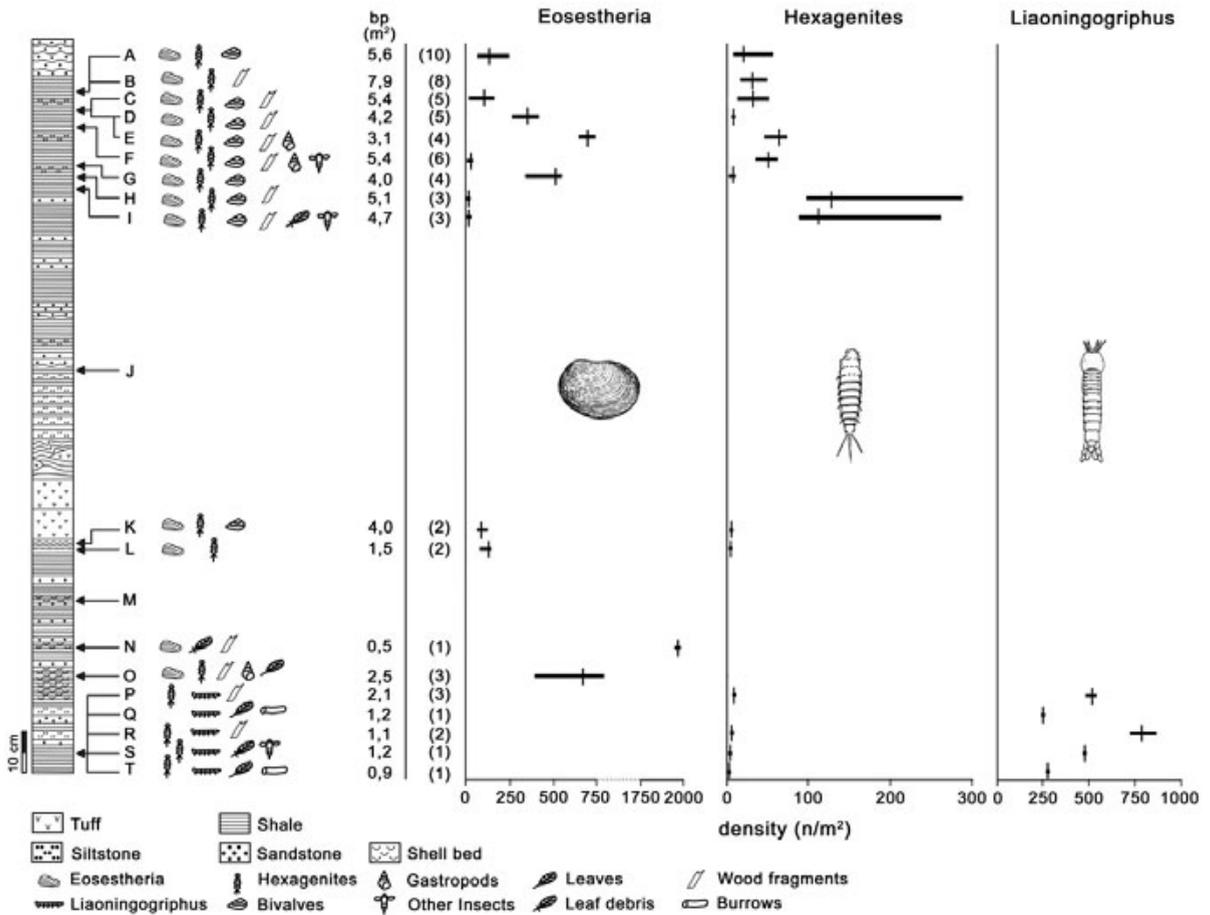


Fig. 4. Excavated section with positions of investigated bedding planes, main macrofaunal elements, size of bedding planes in square metres (bp), and density of the most abundant taxa (*Hexagenites*, *Eosestheria*, and *Liaoningogriphus*). The fossil density has been calculated as number of specimens per square metre. Given is the mean and the range. The number of sub-samples on which the range is based is given in brackets. For additional symbols see Fig. 2.

debris, plagioclase and quartz crystals, and clay minerals. The laminated claystones and silty claystones contain abundant non-marine invertebrate and vertebrate fossils, dominated by conchostracans, insects, fish, shrimps, birds and dinosaurs, with rare gastropods and bivalves.

The highly fossiliferous facies can be interpreted as representing suspension- and low-density turbidity-current deposits (Nelson, 1967; Anderson et al., 1985). The alternating laminae of siltstones and claystones probably result from fluctuations in fluvial discharge (Chun and Chough, 1995), most likely reflecting seasonal changes in precipitation.

In a few cases the sediment surface has been sufficiently cohesive to preserve delicate imprints in the form of tiny dimples and scratch marks, which probably are the result of the feeding and locomotion activity of *Hexagenites*, the dominant faunal element at these levels. The cohesiveness of the fine-grained sediment

may have been caused by the presence of an algal/microbial film.

4.2. Horizontally stratified homogeneous sandstones and tuffs (S2)

The sandstone and tuff beds are horizontally stratified, internally structureless, and several to tens of centimetres thick. Bed boundaries are sharp but non-erosional with underlying and overlying mudstones. In thin-section, the tuffs are poorly sorted, made up of mainly sand-sized pumice, plagioclase and quartz crystals (0.2–2 mm in diameter), randomly oriented in a crystal and vitric matrix. The pumice grains are elongated and irregularly shaped, showing a surface of conchoidal fractures.

The sharp bed boundaries and the lack of grading of the horizontally-stratified sandstones and tuffs resemble hyperconcentrated density flow (grain-flow) deposits (Mulder and Alexander, 2001).

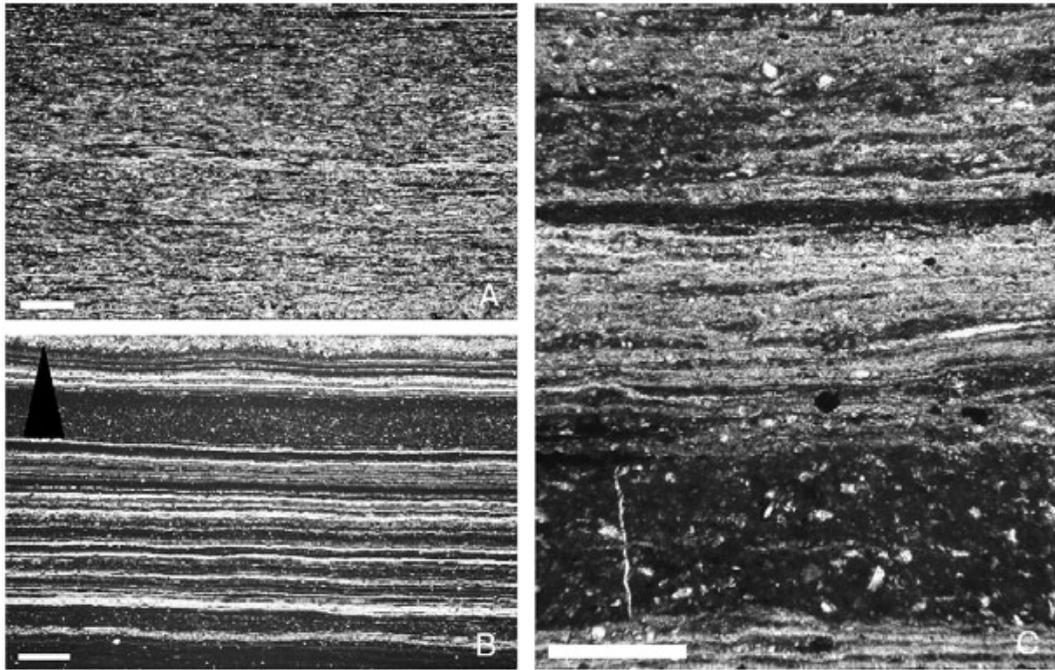


Fig. 5. Variation in microfacies of the laminated mudstone facies. A. Microlaminated shell concentration consisting of numerous valves of the conchostracan *Eosestheria*, most likely deposited by concentrated density flows. This is a rare example of allochthony of the thin-shelled valves. Thin-section through level M (for position of levels see Fig. 4), scale: 1 mm. B. Laminated mudstone and siltstone around bedding plane E. The graded siltstone and overlying wavy lamination in the upper third of the picture (marked by triangle) is interpreted as turbidite. Thin-section, scale: 1 mm. C. A thin tuff layer in the lower third of the cross-section is followed by irregularly microlaminated silt and clay, most likely of microbial origin. Around level K. Thin-section, scale: 0.5 mm.

4.3. Graded sandstones and mudstones (S/M)

These sandstones and mudstones are well sorted, graded, and form laterally persistent beds. The fine-grained sandstone beds are <1 to 5 cm thick. The bedding planes are parallel, with minor load structures at bed bases. The sandstone member of this lithofacies is commonly absent in the excavated section. The mudstones are thinly planar-laminated or convoluted, locally containing abundant conchostracan and insect fossils on the bedding planes.

The graded sandstones and mudstones are comparable to the Tb-e unit of the Bouma sequence, representing turbidity-current deposits (Walker and Mutti, 1973; Ricci-Lucchi, 1975). According to Mulder and Alexander's (2001) classification of sedimentary density flows, the graded sandstones and mudstones reflect surge and surge-like turbidity flow deposits.

4.4. Depositional environment

The lithofacies of the excavated section indicate a lake-floor environment receiving mostly suspension, turbidity current, and hyperconcentrated density flow

deposits. Judging from the numerous horizontally stratified sandstones and tuffs of hyperconcentrated density flow origin, the locality cannot have been far away from the shoreline of the lake. Most likely, the hyperconcentrated density flows were triggered by the rapid input of large quantities of sediment by volcanic activities.

5. Fauna and flora

Altogether, more than 16,000 fossils have been counted. Only 0.07% is non-aquatic in origin being represented by insects such as the dragonfly *Aeschnidium heishankowense* (Hong) (Fig. 6C) and the cupedid beetle *Notocupes laetus* (Lin) (Fig. 8C). The overwhelming majority of the limnic fauna belongs to just three taxa: the conchostracan *Eosestheria ovata* (Chen) (65.2%; Figs. 7E and 12B), the malacostracan crustacean *Liaoningogriphus quadripartitus* Shen, Taylor and Schram (19.6%; Figs. 6D and 12A), and the mayfly nymph *Hexagenites trisetalis* (Eichwald) (14.6%; Fig. 6A and B), in Chinese literature generally called *Ephemeroopsis trisetalis*. The bivalves *Sphaerium anderssoni* (Grabau) (0.1%; Fig. 7A) and *Arguniella ventricosa* (Kolesnikov) (Fig. 7B; 0.6%), and the

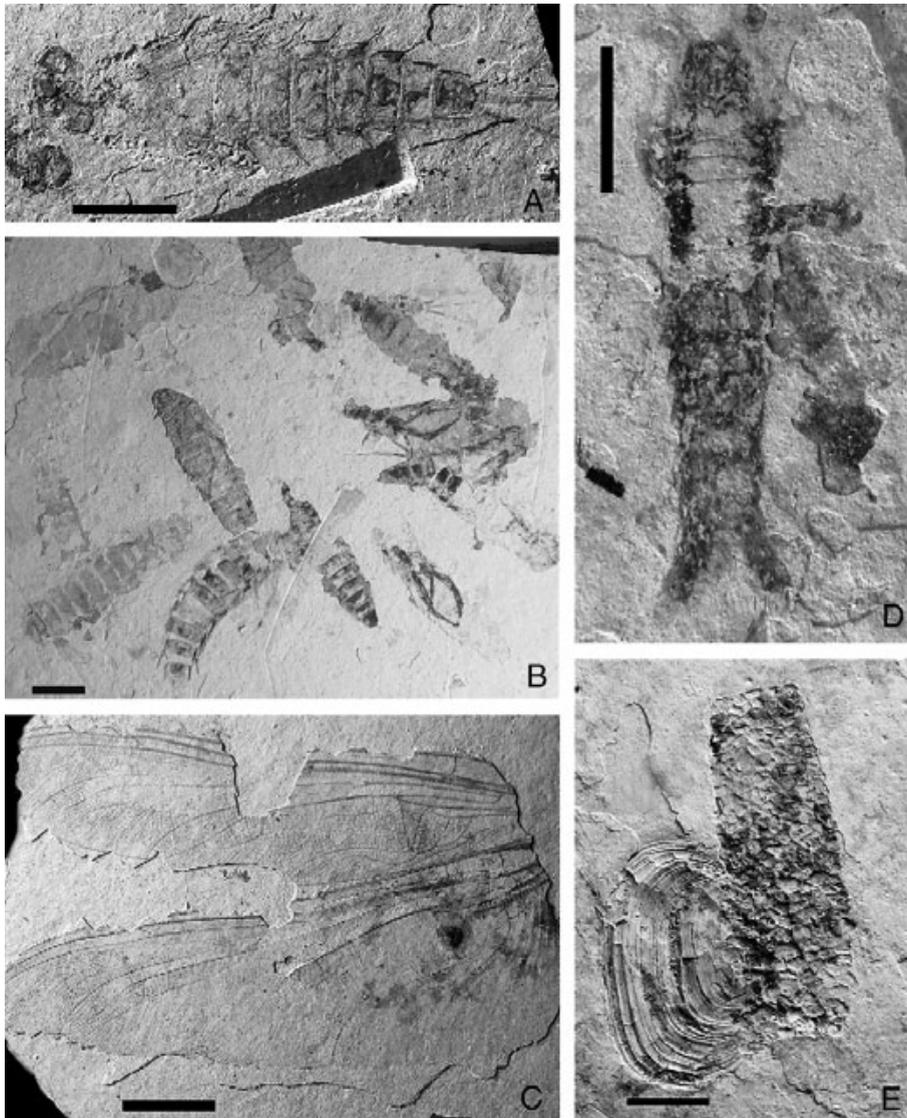


Fig. 6. Characteristic elements of the Jehol Biota in the excavated section of the Zhangjiagou Lake. A. *Hexagenites trisetalis* (Eichwald). Scale: 1 cm. B. Cluster of *Hexagenites trisetalis*. Level H, scale: 1 cm. C. Wings of the dragonfly *Aeschnidium heishankowense* (Hong). Level H, scale: 1 cm. D. The crustacean *Liaoningogriphus quadripartitus* Shen, Taylor, and Schram. Scale: 5 mm. E. Fragment of an agglutinated dwelling tube of a caddisfly larva, composed of small shell fragments, mainly of bivalves. Level H, scale: 5 mm.

gastropod *Probaicalia vitimensis* Martinson (Fig. 7C; 0.01%) complement the faunal spectrum.

The taxonomy of conchostracans relies, apart from outline and position of umbo, on the ornamentation of the shell. Of the various species occurring in the Yixian Formation, we are of the opinion that our specimens most closely resemble *Eosestheria ovata*, because of its widely spaced, slightly irregular, branched radial lirae between successive growth lines.

The density of the various fossils groups, calculated per square metre, greatly varies throughout the section (Fig. 4). Given is the range of variation in density for

each level based on the individual sub-areas as well as the mean value. The density of bivalves is generally below 1 specimen/m², except at levels K–F, where values up to 10.2/m² are reached. In *Hexagenites*, the density varies between zero (levels Q and N) and 129 (level H). For *Liaoningogriphus*, which occurs only in levels T to P, the values range from 259 to 558 specimens/m². These figures are topped by *Eosestheria*, which is conspicuously absent where *Liaoningogriphus* occurs, but highly abundant at most other levels (e.g., Fig. 8A). The conchostracan reaches its greatest density in level N with 1940 specimens/m².

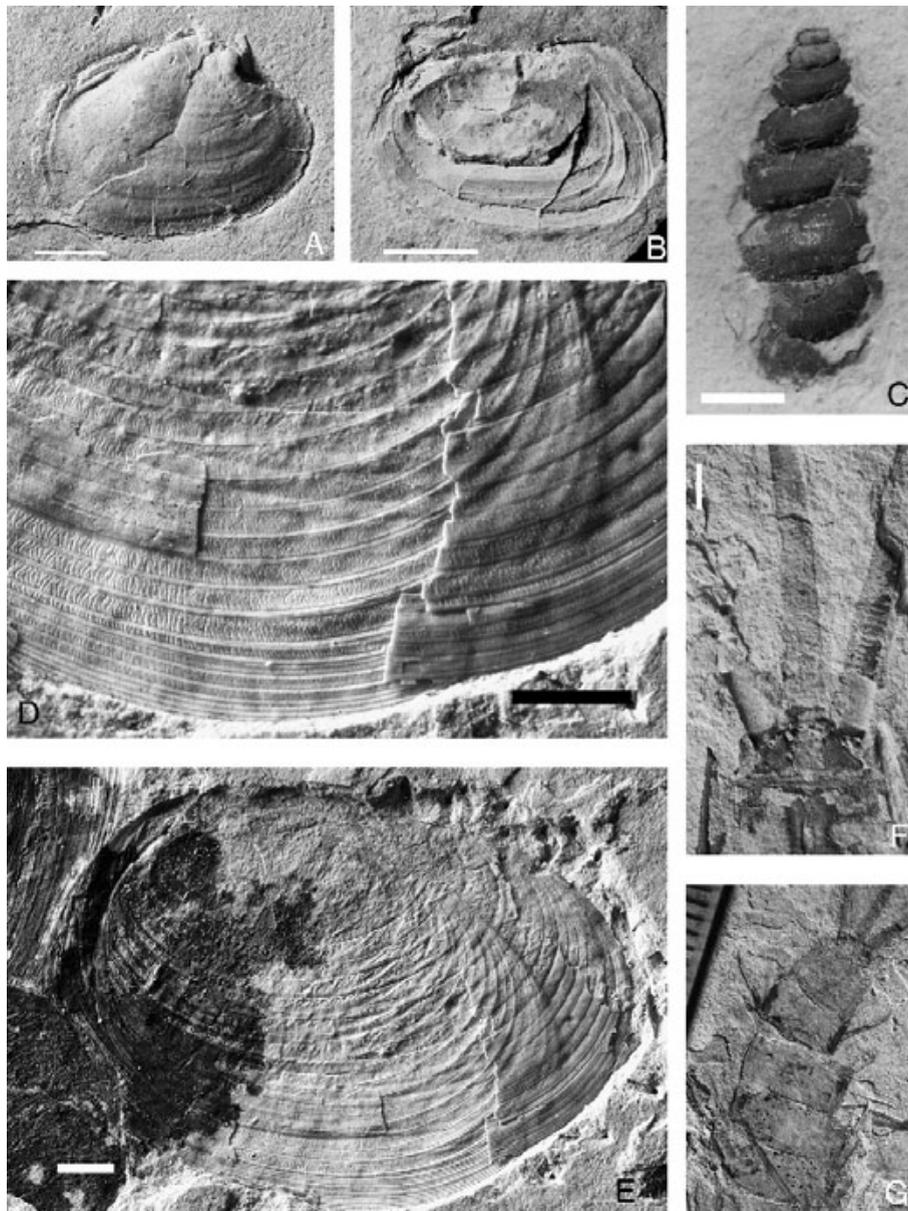


Fig. 7. Characteristic elements (A–E) and some taphonomic features (E–F) of the lake fauna. A. Internal mould of the bivalve *Sphaerium anderssoni* (Grabau); level H, scale: 2 mm. B. The bivalve *Arguniella ventricosa* Kolesnikov; level K, scale: 4 mm. C. Internal mould of the gastropod *Probaicalia vitimensis* Martinson; level F, scale 1 mm. D. Ventral part of the conchostracan *Eosestheria ovata* (Chen) showing the characteristic ornamentation of irregular radial riblets and crowding of growth lines towards the ventral margin. Note that two valves, slightly dislodged, are superimposed. Scale: 2 mm. E. Articulated specimen of *E. ovata* (Chen) with dislodged valves. Scale: 2 mm. F. Comparatively rare three-dimensional preservation of the mayfly nymph *Hexagenites trisetalis* (Eichwald). Shown is here the posterior part of the nymph with the three characteristic setae. The originally circular cross-section of the setae has been distorted by compaction. Level A, scale: 1 mm. G. Dislodged segments in the posterior part of *H. trisetalis*, interpreted as a result of decomposition on the lake floor. Level P, scale in mm.

The taxa change in dominance throughout the section (Fig. 9). In the basal part (levels T–P) *Liaoningogriphus* forms nearly monospecific assemblages accounting for 97–99.7% of the fauna. In levels O–K *Eosestheria* represents between 90 and 99.8% of the fauna (e.g. Fig. 11A),

to be replaced, up-section, by *Hexagenites* (88%) in levels I and H. In levels G, E–C, and A *Eosestheria* again prevails (75–98%), and in the remaining levels (F, B) *Hexagenites* (60–98%) dominates. Only in levels F (13.6%) and H (4.9%) bivalves are of any significance.

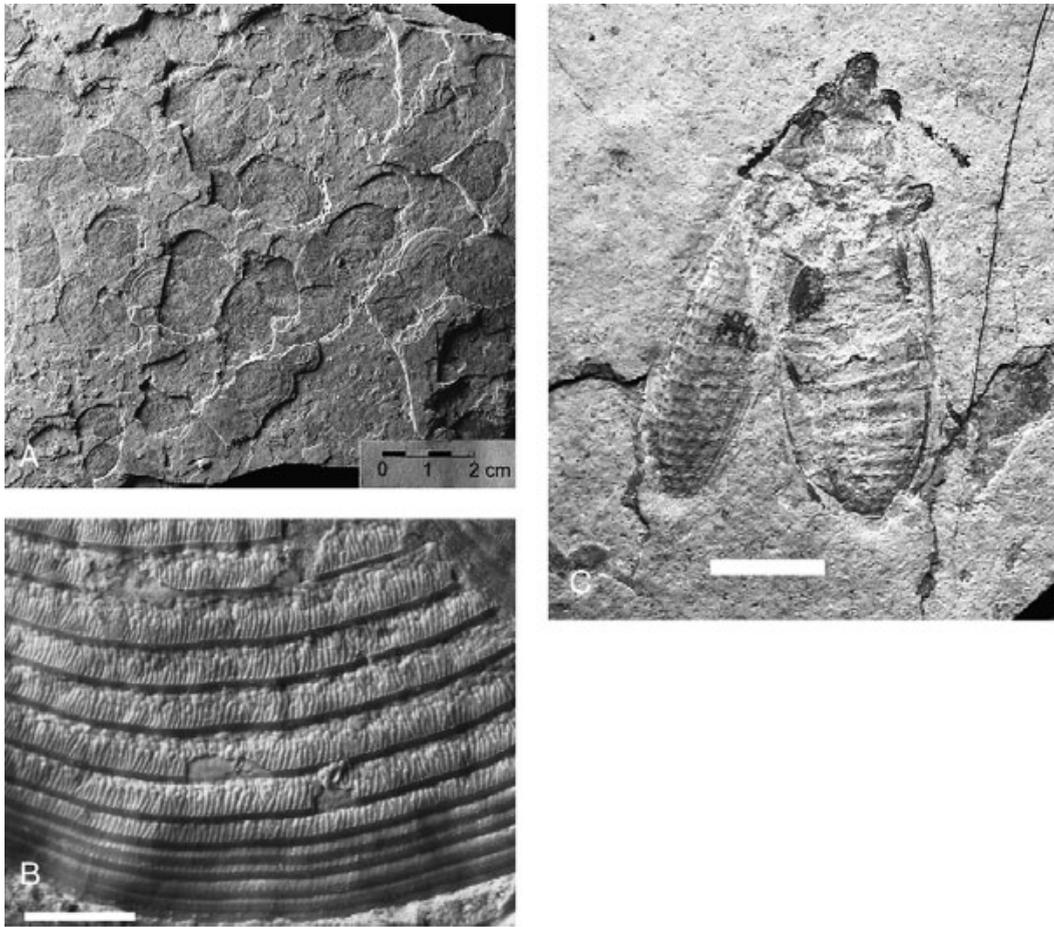


Fig. 8. A. Densely packed valves of articulated *Eosetheria ovata* form closely adjacent levels, often only fractions of a millimetre apart. B. Segment of *E. ovata* with densely crowded growth lines at the ventral margin. Level G, scale: 1 mm. C. The coleopteran *Notocupes laetus* (Lin.). Level E, scale: 3 mm.

Scattered comminuted wood debris (layers D, I) and isolated larger wood fragments (usually a few cm in length; maximum observed length was 15 cm) are found on about half the bedding planes. Identifiable plant remains belong to the horsetail *Equisetites longevaginitus* Wu, the questionable angiosperm *Orchidites linearifolius* Wu, the ginkgophytes *Solenites* sp. (level E) and *Czekanowskia* sp. (level I), and the coniferophyte *Liaoningcladus boii* Sun, Zheng and Mei (level I), the latter three occurring as bundles of leaves.

6. Trace fossils

The finely laminated nature of the sediment indicates that infaunal life was absent or, at least, very scarce. Still, at four horizons evidence of limited bioturbation was found. In level G, irregular elongated concretions, 2–3 mm in diameter form a discontinuous horizontal

network (Fig. 10). Most likely, the concretions trace a network of branched burrows. In levels Q and T sub-vertical to oblique cylindrical burrows with a diameter of 1 mm (level T) and 2 mm (level Q) occur scattered and are filled with coarser tuffitic material. They clearly originated at a stratigraphically higher level. In level S, a thin, horizontal tube (diameter: 1 mm) extends across two specimens of *Liaoningogriphus* and is filled with coarse silt.

In all cases the burrow density was too low to significantly disturb the fine laminations of the sediment. The burrows must have been produced by worm-like organisms, possibly oligochaetes, but no corresponding body fossils were encountered.

In levels E and H each, a fragment of an agglutinated tube with a diameter of 7 mm and 4.5 mm, respectively was found (Fig. 6E). In level H it consists of small shell fragments, mostly of bivalve origin, in level E, the tube is

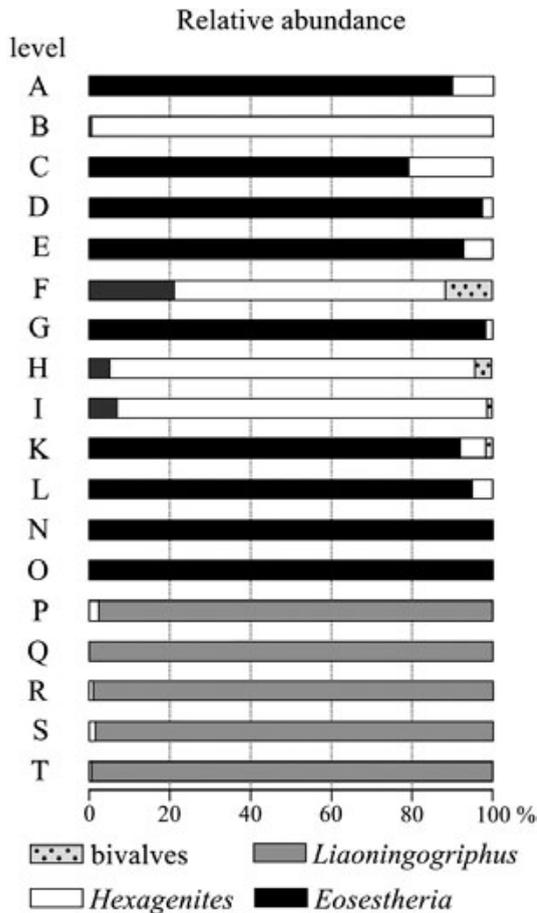


Fig. 9. Changes in the relative abundance of taxa throughout the section. For position of levels A–T see Fig. 4.

built of large sediment grains and shells (?ostracods) which are now dissolved. Both tubes can be interpreted as the dwelling tubes of caddisfly larvae. The two fragments probably are allochthonous. Tiny dimples, imprints, and scratch marks found on the surface of level H probably record the activity of *Hexagenites* and *Eosestheria*.

7. Taphonomic observations

7.1. Preservation

The organisms preserved within the excavated section possessed skeletons of different composition. The bivalves and gastropods had an aragonitic shell, which except for rare cases, has been dissolved during diagenesis. They are therefore represented by internal, external, or composite moulds. The valves of conchostracans are very thin and consist of conchiolin. The skeletal material is commonly preserved and shows the

delicate growth lines and the microstructure, the latter being an important diagnostic feature for separating genera and species (e.g., Chen, 1999). In the dorsal area, however, skeletal material is no longer present in many specimens, which makes it difficult to count growth lines. Although conchostracans molt frequently, they do not shed the carapace. This partly explains the conspicuous absence of smaller, juvenile shells on the investigated bedding planes. The preservation of conchostracans is also clearly related to the grain size of the sediment. When associated with coarser sediment (e.g., coarse silt), the shell material is usually gone except for a thin film.

Hexagenites and *Liaoningogriphus* also possessed an, albeit very thin, skeleton of scleroprotein. The former is characteristically preserved as flattened brownish imprints on bedding planes, mineralized by ferric iron, the skeletal material being gone. In some specimens, skeletal elements such as appendices and the caudal spines are preserved as iron-stained sediment casts (Fig. 7F). *Liaoningogriphus* is preserved as greyish, very faint imprints without any traces of skeletal material on bedding planes P and Q. There *Hexagenites* is preserved in a similar way. In layers R to T, the faint imprint of the crustacean is covered by a brown veneer, but no skeletal material is preserved.

The few insects are also preserved as two-dimensional faint imprints, without skeletal material. In the case of dragon flies usually only isolated wing pairs were found, some of them with beautifully preserved venation (Fig. 6C).

In conclusion, no true soft part preservation can be demonstrated in the investigated section, because all preserved arthropods possessed external skeletons of

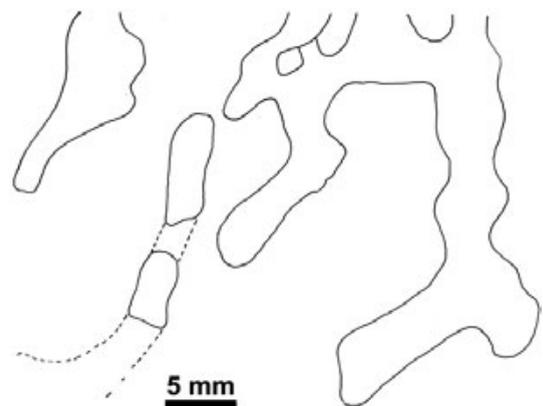


Fig. 10. Burrow system on bedding plane G, preserved as flattened concretions. Dashed line refers to area where the concretion has been removed when splitting the rock. Sketch from photograph.

scleroprotein, even though in some cases (e.g., *Liaoningogriphus*) they appear to have been very thin. The preservation of these forms as articulated imprints, commonly impregnated with iron oxides, testifies that bacterial decay of these skeletons did not take place before burial. Decay of soft parts, in turn, is suggested by the common dislodgement of valves of *Eosestheria*, which is only possible after the ligament and muscles, by which the body was attached to the carapace, have decayed.

Most of the organisms are strongly compacted. This is true of all *Hexagenites* and *Liaoningogriphus*, whereas in bivalves mainly the umbonal areas with the greatest convexity were affected. In conchostracans the degree of compaction differs on different bedding planes. In some cases, only the umbonal area has been affected, in others the total shell has been flattened. Compaction was most likely also responsible for the commonly sheared arrangement of the two valves of *Eosestheria* (Fig. 7E). Kobayashi and Kusumi (1953) noted a similar arrangement of valves when analysing conchostracans from eastern Asia. They explained the dislodgement of the two valves as caused by weak currents. Prerequisite is the partial or complete decay of the soft parts (in particular the ligament and muscles) that keeps the two valves connected during life. However, currents as causative factors can, at least in the present case, be ruled out, because not only are the conchostracan valves randomly

oriented (see below) but also the displacement occurred in all possible directions.

There is little evidence of fragmentation and breakage of shell material, mainly because calcareous skeletons (bivalves, gastropods) were rather rare. The only example of concentration of shell fragments occurs in form of a fragmented agglutinated tube of a caddisfly in level H, which consists of small bivalve fragments. Interestingly, this is the level with the highest proportion of bivalves in the section.

All specimens of *Liaoningogriphus* and nearly all *Ephemeropsis* are well preserved. Only rarely there are signs of disintegration shown by dislodged body segments (Fig. 7G). This suggests that decay processes did not operate on a large scale on the organic skeletons before they became buried.

7.2. Orientation and distribution patterns on bedding planes

In order to obtain information about the autochthonous or allochthonous nature of the fauna and hence their ecological fidelity, the orientation of specimens of *Liaoningogriphus*, *Hexagenites*, and *Eosestheria* was measured at each level, provided the taxa were present in sufficiently large numbers. In the case of *Eosestheria*, this was possible in levels D, E, K, L, and O (Fig. 11). At all five levels, the orientation of the hinge line was

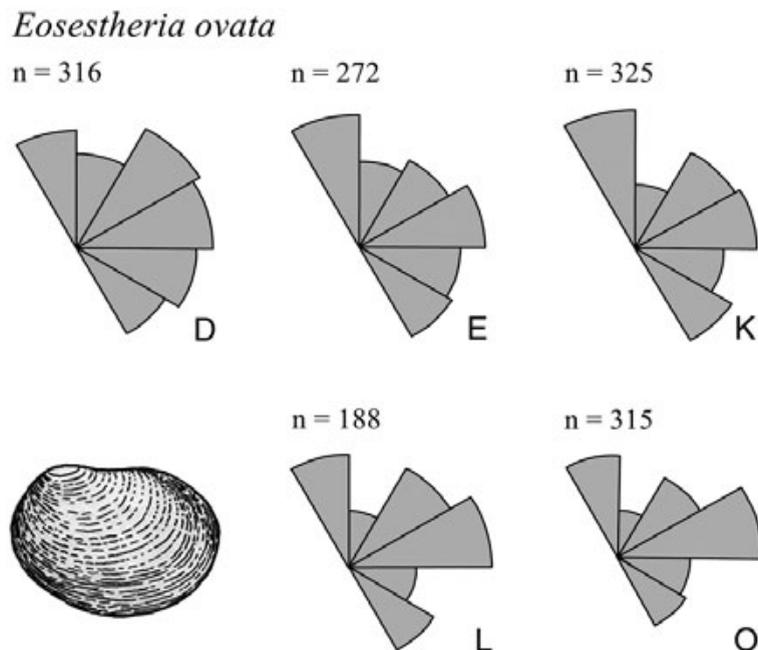


Fig. 11. Plan-view orientation of the conchostracan *Eosestheria ovata* in levels D, E, K, L, and O. For test of the statistical significance see Table 1.

random (see also Fig. 12B), checked by chi square and Raleigh tests (Table 1). The orientation of *Hexagenites* was measured at levels A, E, F, H, and I (Fig. 13). Again, no preferred orientation of the elongated fossil could be detected. The same is true of the equally elongated *Liaoningogrampus* from levels Q to T (Figs. 12A and 14).

The great majority of *Eosestheria* (82%; $n=322$) lie on their side, with the valves slightly sheared. Only in level C, the figure is considerably lower (27%). In rare cases butterfly preservation was encountered. Butterfly preservation occurs also in some bivalves, whereby the valves are convex-down oriented. In a single case the valves gaped with the umbones pointing obliquely upwards.

In *Hexagenites* and *Liaoningogrampus* the body posture was noted. In the material brought back from the field (42 specimens) 61.9% of the *Hexagenites* individuals were resting with the dorsal side facing the bedding plane, 26.2% with the venter, and 11.9% lay sidewise on the surface. In the case of *Liaoningogrampus*

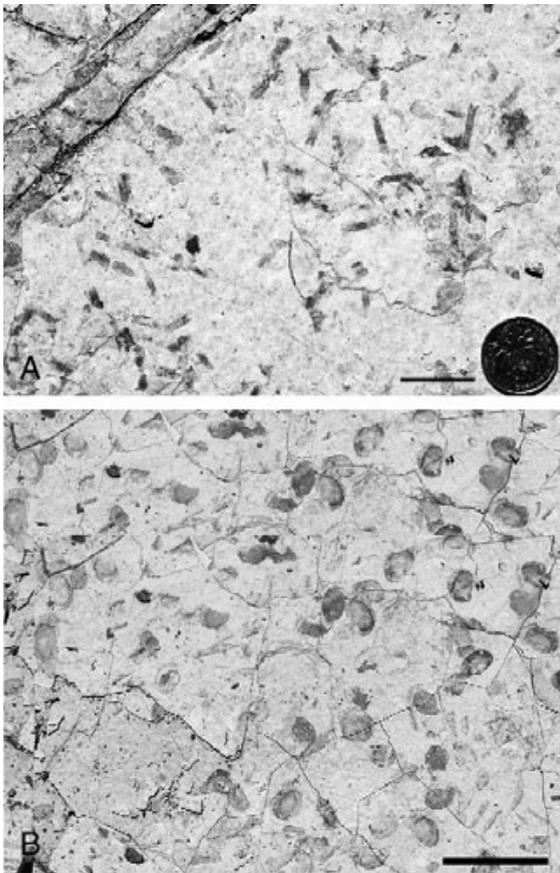


Fig. 12. A. Bedding plane R with randomly oriented *Liaoningogrampus quadripartitus*. Scale: 2 cm. B. Bedding plane with randomly oriented *Eosestheria ovata*. Scale: 5 cm.

Table 1

Results of Raleigh (R) and Chi-square tests of the plan-view orientation patterns of *Eosestheria ovata*, *Hexagenites triserialis*, and *Liaoningogrampus quadripartitus* on various bedding planes

Level	<i>n</i>	Mean	R	<i>P</i> (rand)	χ^2	<i>P</i> (rand)
<i>Eosestheria ovata</i>						
D	316	72.924	0.6887	<0.01	948	0
E	272	69.525	0.6174	<0.01	816	0
K	325	67.326	0.6042	<0.01	975	0
L	188	72.724	0.6790	<0.01	564	0
O	315	74.713	0.6977	<0.01	945	0
<i>Hexagenites triserialis</i>						
B	249	59.884	0.07096	>0.1	747	0
E	100	37.839	0.2933	<0.01	300	0
F	169	71.263	0.1112	0.05	507	0
H	397	162.61	0.06683	0	1191	0
I	412	77.132	0.006623	>0.1	1236	0
<i>Liaoningogrampus quadripartitus</i>						
Q	339	78.139	0.6493	<0.01	1017	
R	284	7.3848	0.02346	0.1<	852	0
S	350	-66.958	0.124	0.025< <i>P</i> <0.05	1050	0
T	254	125.78	0.1551	0.01< <i>P</i> <0.025	762	0

observations were based on 181 specimens (numbers from levels P–T, varying between 27 and 44). About a third (between 32 and 39%) of the specimens rested with their lateral side on the sediment, 0–10% with their dorsal side, the rest with the venter. In a few specimens the body was strongly curved, which naturally resulted in a lateral position on the sediment, but in the overwhelming majority of *Hexagenites* and *Liaoningogrampus* the body was straight.

Hexagenites occurs in clusters of 3–5 individuals in level H (e.g. Fig. 6B). A similar clustering is displayed by *Eosestheria* at level E. The latter taxon also shows a patchy distribution in level G, where the small-scale density of the conchostracan greatly varies. In all other areas, the faunal density is either so high that valves commonly overlap (conchostracans) or else individuals occur randomly scattered (*Hexagenites*, *Liaoningogrampus*).

8. Palaeoecology of the benthic fauna

8.1. Autecology

8.1.1. *Eosestheria*

The biology and ecology of modern conchostracans is well known and has been repeatedly summarized (e.g., Tasch, 1969; Webb, 1979; Chen and Shen, 1985; Frank, 1988; Rohn et al., 2005). Most of them are found in transient water bodies, such as ponds, ditches, transient lakes on flood plains, which they are able to rapidly

Hexagenites trisetalis

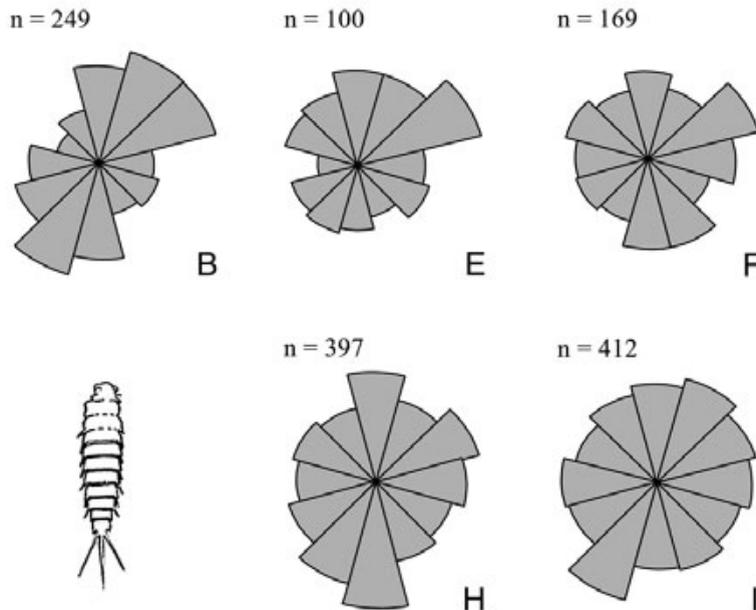


Fig. 13. Plan-view orientation of the ephemerid nymph *Hexagenites trisetalis* in levels B, E, F, H, and I. For test of the statistical significance see Table 1.

Liaoningogrampus quadripartitus

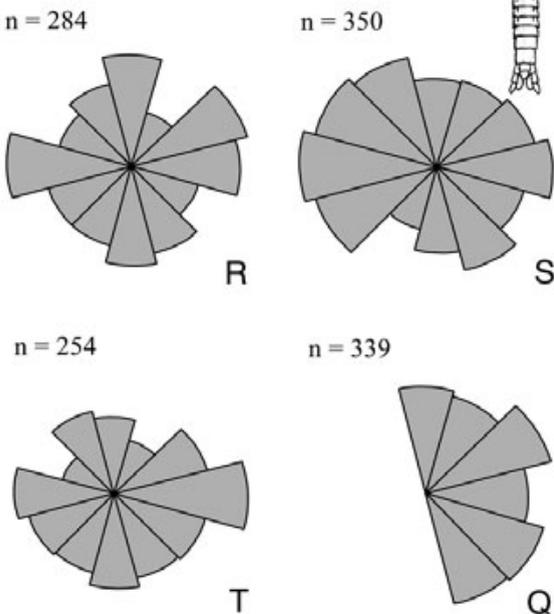


Fig. 14. Plan-view orientation of *Liaoningogrampus quadripartitus* in levels R to T. For test of the statistical significance see Table 1. Note that on bedding plane Q only the orientation of the elongation of the crustacean was measured.

colonize when they become flooded, because their eggs are able to survive for several years under dry conditions. Conchostracans are rare in permanent water bodies, especially when these are populated by fish because the latter prey upon them. If they do occur in perennial lakes, they are confined to very shallow, but quiet marginal areas where they might produce up to four generations per year. Another characteristic feature is that a particular water body usually is inhabited only by a single conchostracan species at a given time. Conchostracans grow very rapidly and may reach maturity after 5–23 days, at that time being about half the adult size. Growth slows down in old age, which is shown by a crowding of growth lines. Some conchostracans are able to stay alive until the pool dries up (in extreme cases eight months), others have a much shorter life span e.g., 14–22 days. In contrast to other crustaceans they do not shed their carapace when molting but add a growth line instead. A great range of variation with respect to life span, growth rate, ecological tolerance, sexual dimorphism, life style (swimming, crawling, burrowing), etc. seems to be characteristic of the group. This makes it extremely difficult to reconstruct the life habits of fossil taxa. Moreover the intraspecific variability, especially with respect to ornamentation, is also considerable.

It is quite clear that the lake, the sediments and biota of which we investigated, was a permanent water body,

because no signs of subaerial exposure such as desiccation cracks are recorded in the sediments. The presence of *Eosestheria* in such high numbers can only be explained by the absence of fish and indeed, not a single fish remain was found on bedding planes dominated by the conchostracan. As the sediment surfaces are generally undisturbed except for rare burrows, it appears that *Eosestheria* did not burrow or disturb the sediment in search of food. More likely the conchostracan rested on the lake floor and, when feeding, swam up to the water surface in search of algae or other suspended organic particles.

8.1.2. *Liaoningogriphus*

Little information is available on the ecology of the malacostracan *L. quadripartitus*, which covers bedding planes in high numbers in the lower fourth of the section. Modern members of the spheleogriphaceans appear to be largely confined to cave systems and ground waters. The well developed pleopods indicate that the shrimp was a very good swimmer (Shen et al., 1999) and probably spent most of the time in the water column. The thinly sclerotized carapace (Shen et al., 1999) probably produced only very thin exuviae which stood no chance to become preserved.

8.1.3. *Hexagenites*

Information on the ecology of the mayfly nymph *Hexagenites*, widespread in the Lower Cretaceous lake sediments, must be deduced from their modern counterparts. The following information is based on a review of the biology of mayflies by Brittain (1982). Modern mayfly nymphs burrow, crawl on the bottom, or swim. Most are herbivores, grazing on algae or plant detritus, whereby food is either scraped from the bottom or taken up by filter-feeding. A predatory habit is relatively uncommon. Growth is mainly regulated by temperature. Several studies (e.g., Fox and Simmonds, 1933; Fox et al., 1935; Eriksen, 1963) have shown that species living in lakes are able to tolerate lowered oxygen levels, and the same appears to have been true of elevated temperatures (e.g., Whitney, 1939). Thus, *Hexagenites trisetalis* from the Early Cretaceous probably was well adapted to life in shallow, marginal parts of lakes, where during the summer partially stagnant conditions and elevated temperatures were common features. In addition, their co-occurrence with *Eosestheria* suggests similar ecological requirements. Populations of present-day mayfly nymphs tend to concentrate in the shallower areas of lakes during the final stages of nymphal life (Swanson, 1967) and this might explain the dominance of large individuals on the investigated bedding planes.

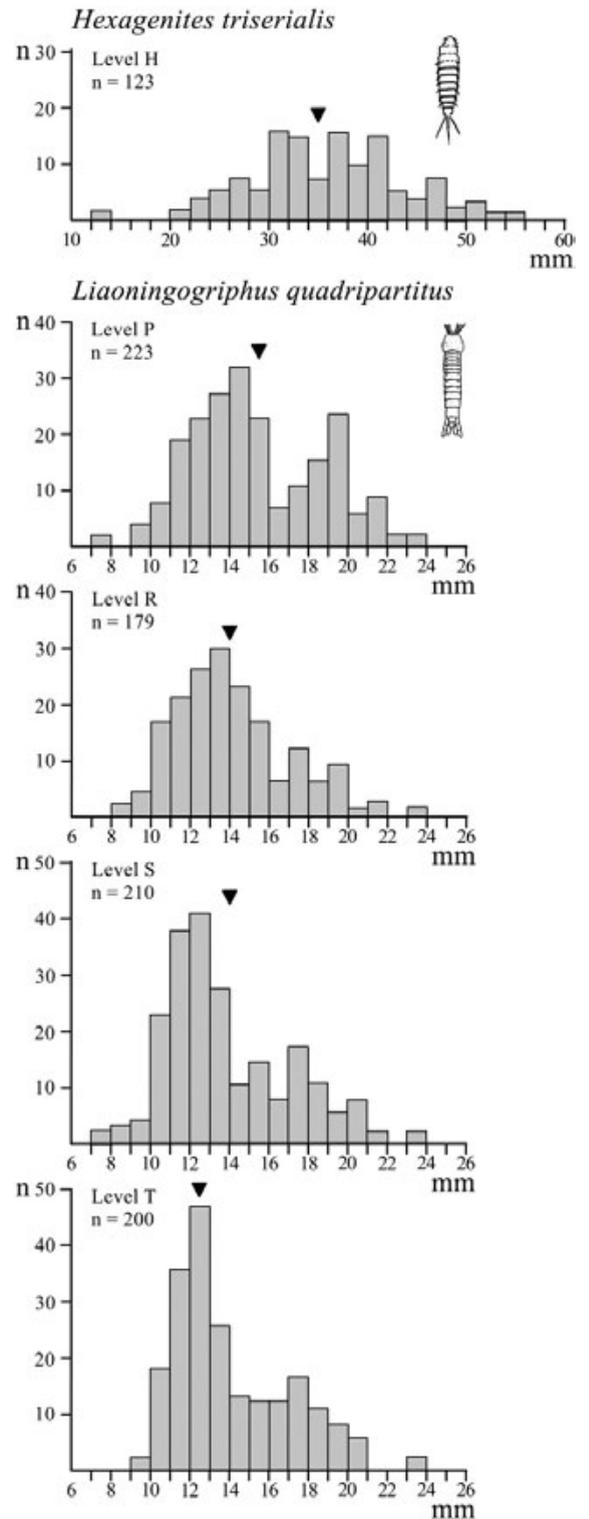


Fig. 15. Size-frequency histograms of *Hexagenites trisetalis* (level H) and *Liaoningogriphus quadripartitus* (levels P, R, S, and T). The triangle indicates the mean value.

8.2. Size-frequency histograms

In order to understand the ecology of the lake system more fully and to obtain additional information on living

conditions of the lake biota the size (length) of *Eos-estheria* and *Liaoningogriphus*, in one case also of *Hexagenites*, were measured at several levels (Figs. 15 and 16). In the case of *Hexagenites* (Fig. 14; level H), the

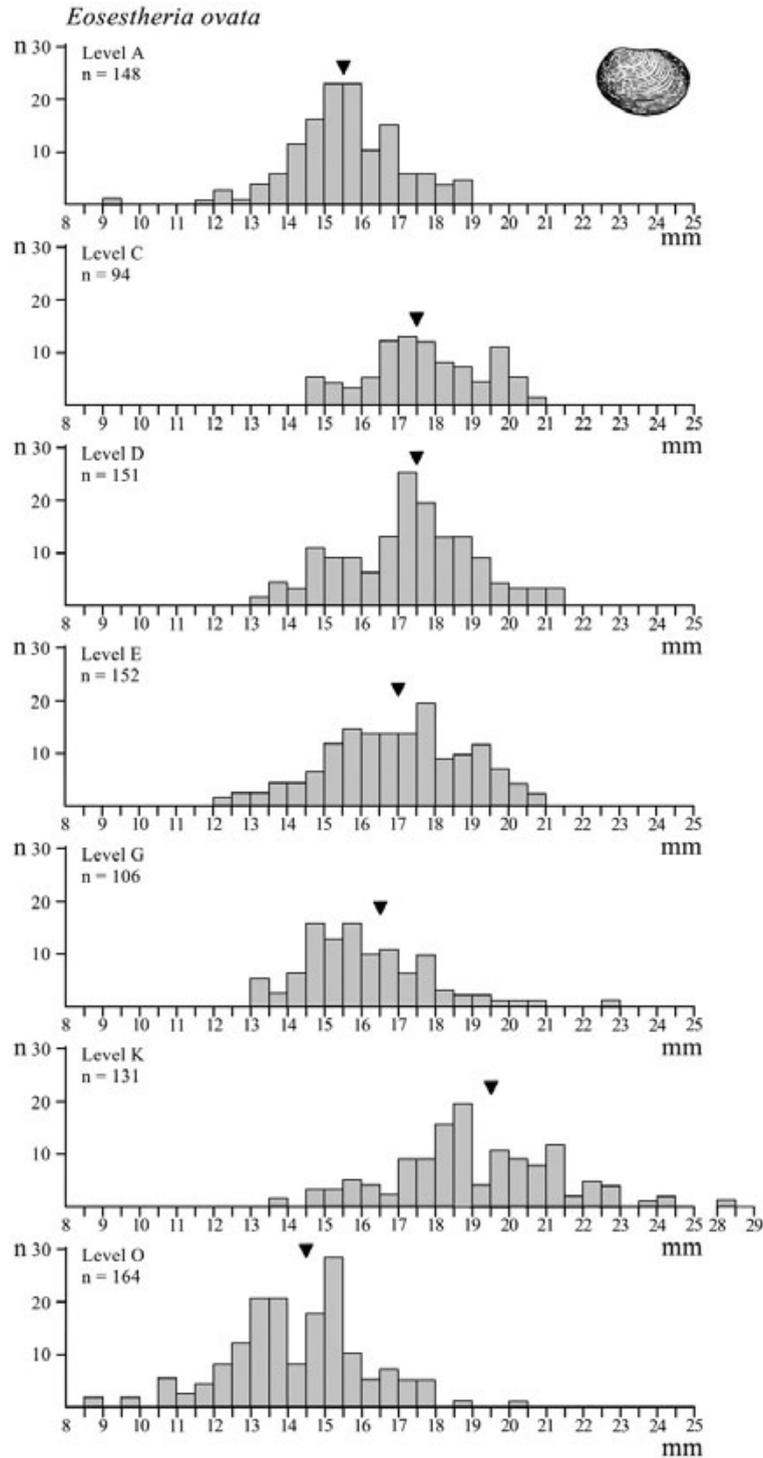


Fig. 16. Size-frequency histograms of *Eos Estheria ovata* from levels A, C–E, G, K, and O. The triangle indicates the mean value.

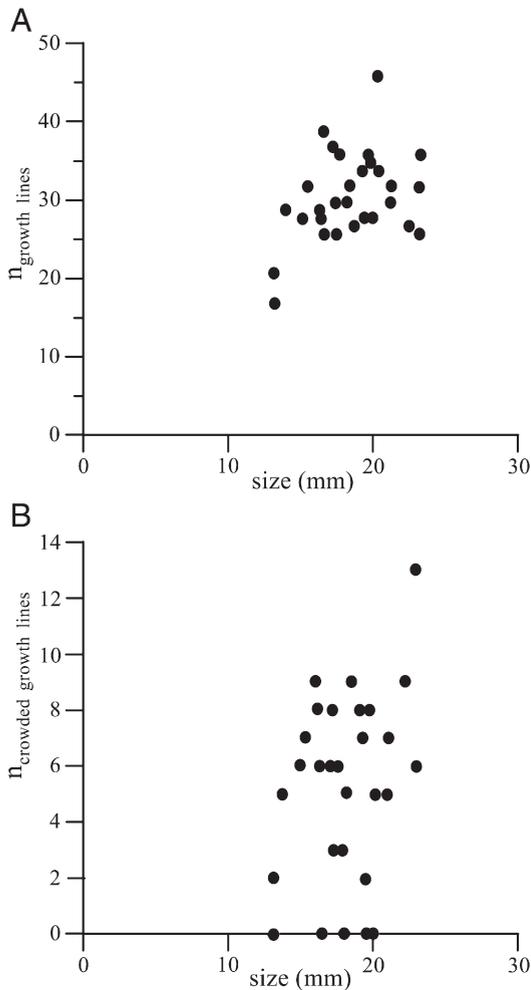


Fig. 17. A. Relationship between size (expressed by length) and number of growth lines in *Eosestheria ovata*. B. Relationship between size (expressed by length) and number of crowded growth lines.

resulting size-frequency histogram is clearly polymodal, but most individuals are between 30 and 42 mm in size. Only a single specimen was smaller than 20 mm.

In *Liaoningogriphus* size-frequency data were obtained from levels P, R, S, and T (Fig. 15). The histograms show a more or less distinct bimodal distribution pattern, in level P possibly even polymodal. The total size range is 7 to 24 mm. A first peak occurs between 13 and 15 mm, a second one between 16 and 19 mm (in one case 19–20 mm). The distance between the peaks appears to be constant at 5–6 mm.

The largest database is provided by *Eosestheria*, where specimens have been measured on seven bedding planes (Fig. 16). All histograms are polymodal, and up to six peaks have been identified (e.g., at level K). Most individuals have a length between 13 and 21 mm, extreme values are 8.5 and 28 mm. The distance between

peaks varies between 1.5 and 3 mm. As in the case in many invertebrates, the histograms are usually positively skewed, mortality decreasing with age. Individuals in levels C, D, E, and G have a mean size of 16.5 to 17.5 mm, individuals in level A and O are, on average, smaller (15.5 and 14.5, respectively), and those in level K distinctly larger (19.5 mm). It should be noted, however, that in finely laminated mudstone facies just above level E the size of conchostracans on several closely adjacent bedding planes is distinctly smaller (there, on average, they are less than 10 mm long). Unfortunately, their preservation is very poor so that

Table 2

Relationship between size of *Eosestheria ovata*, total number of growth lines, and number of crowded growth lines

Bedding plane	Length (in mm)	Total number of growth lines	Number of crowded growth lines
C	15.1	28	5
C	17.6	36	6
C	15.4	32	7
C	13.9	29	5
C	16.5	39	6
C	19.7	35	2
C	16.6	26	0
C	18.3	32	5
C	21.2	32	5
D	20.3	34	5
E	17.1	30	7
E	11.2	26	6
E	10.2	26	6
E	16.1	30	10
E	14.3	32	10
E	14.3	25	4
G	23.2	36	6
G	18.1	30	0
G	23.1	26	6
H	19.6	36	0
H	20.1	46	0
I	16.2	29	9
I	17.4	30	8
I	15.1	28	6
9.8 cm below I	17.2	37	6
9.8 cm below I	17.4	26	3
9.8 cm below I	19.2	34	8
K	21.2	30	7
K	19.4	28	7
K	16.3	28	8
K	23.1	32	13
K	–	26	6
K	19.9	28	8
K	18.6	27	9
K	22.4	27	9
N	13.2	21	0
N	13.2	17	2
N	17.0	21	5
N	17.0	20	6
O	14.5	19	4

Table 3
Percentage of shells of *Eosestheria ovata* that exhibit dense crowding of growth lines at the ventral margin

Bedding plane	Number of specimens	% of specimens with crowded growth lines
C	26	92
D	17	94
E	29	96
G	14	78
I	100	90
N	99	90
O	25	76

growth lines are hardly visible. It looks that many of them show, like the conchostracans on the other bedding planes, crowding of growth lines towards the ventral margin, even though not as pronounced.

8.3. Growth line analysis

Counting the number of growth lines of *Eosestheria ovata* and analysing the spacing between successive growth lines should provide some information on the growth rate of the species, onset of adulthood, and possibly also on the degree of environmental stress. Unfortunately, growth line analysis was possible only in few specimens ($n=39$), because the dorsal area of the conchostracans is usually poorly preserved and growth lines are difficult to make out. For this reason, the number of growth lines presented in Fig. 17 and Tables 2 and 3 may deviate from the real value by one or two.

The number of growth lines was found to vary between 17 and 46, but most values range from 25 to 36. In most shells, growth lines are increasingly more closely spaced towards the ventral margin, and are densely crowded right at the margin, the latter situation being true

in 76 to 96% of the specimens (Table 3). The numbers of densely crowded growth lines vary between 0–13, but in most cases between 5 and 9. There is no relationship between size of the shells and number of total growth lines (Fig. 17A) or between size of shells and number of crowded growth lines (Fig. 17B).

8.4. Benthic associations and their temporal distribution

The aquatic organisms form recurrent assemblages and can be grouped into three associations, each of them strongly dominated by a single taxon (Fig. 18). In the *Eosestheria* association, represented by nine samples and 11,747 specimens, the name-giving species accounts for 94.7% of all individuals, followed by *Hexagenites* with 5.1%. Species richness is low (five taxa) and evenness extremely so. The *Hexagenites* association (4 samples with 1998 individuals) is dominated by *Hexagenites triserialis* (85.3%), followed by *Eosestheria ovata* (9.7%) and the bivalve *Arguniella ventricosa* (4.3%). The bivalve *Sphaerium anderssoni* and the gastropod *Probaicalia vitimensis* each are less than 1%. Species richness is again five taxa, but evenness is slightly higher than in the aforementioned association. Finally, the *Liaoningogriphus* association is nearly monospecific. Apart from *L. quadripartitus* (98.2%) only *Hexagenites triserialis* (1.7%) and *Eosestheria* (0.03%) occur. Here, evenness reaches its lowest value.

The trophic structure of the three associations is relatively simple. The faunal elements can be classified partly as herbivores/detritus feeders, feeding on benthic algae or ingesting plant detritus (?*Eosestheria*, *Hexagenites*, *Liaoningogriphus*, *Probaicalia*), partly as suspension-feeders (?*Eosestheria* and the bivalves *Arguniella* and *Sphaerium*). The rare burrows associated with some of the bedding planes may have been

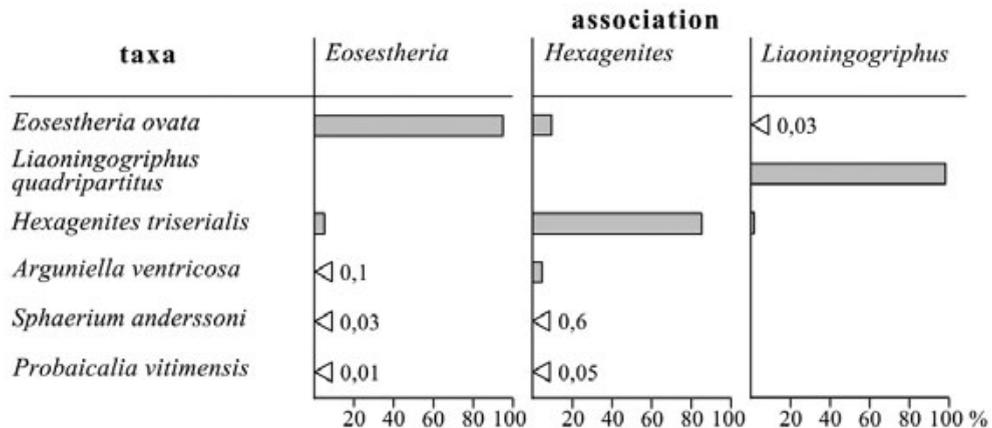


Fig. 18. Composition and relative abundance of species of the three lake associations.

produced by small, soft-bodied deposit-feeders. Diversity values are also low: The number of species present varies between 1 and 4.

The temporal distribution pattern of the associations follows that of the dominant taxa (Fig. 9): The five lowest levels (T to P) are represented by the *Liaoningogriphus* association. Up-section it is replaced by the *Eosestheria* association, except at levels I, H, F and B where the *Hexagenites* association prevails.

9. Discussion

In the following, we try to reconstruct the life conditions of the organisms present in the small segment of the lake investigated by us. Although the statements made below may be valid for much of the lake during the time slice under consideration, they certainly do not apply for the lake as a whole, because the composition and preservation of fossil organisms is known to differ distinctly in other stratigraphic levels (e.g., see excavations nearby, carried out by the Institute of Vertebrate Palaeontology and Palaeoanthropology of the Chinese Academy of Sciences; Wang et al., 1998).

We assume seasonal fluctuations in climate in the area during the Early Cretaceous related mainly to the hydrological cycle that is, a change between a wet and dry season. This assumption is based on the frequent occurrence of comminuted plant debris on the bedding planes and on the occasional occurrence of wood pieces and leaves. Wu (1999) favoured a warm, arid climate, based on the small size of the plants, their robust root system, and the membranous leaves. Li (2003), in contrast, assumed a relatively humid climate for the Yixian Formation of western Liaoning, based on the rarity of arid-tolerating pollen such as *Classopolis*. Combining both arguments we suggest that the climate was semi-arid and that a dry period with little air movements alternated with a stormier wet season.

Three species of invertebrates dominate on the various bedding planes at the excavation site and are regarded as representing three low-diversity associations. We have no satisfying explanation at present why one or the other species dominates on a particular bedding plane. Responsible factors could be subtle differences in lake water chemistry, differences in the trophic state of the lake, or chance repopulation of the lake after mass mortality.

9.1. Autochthonous versus allochthonous nature of the lake fauna

The great density of fossil remains on some bedding planes, in particular the high concentration of conchos-

tracans at some levels suggest that at least some faunal elements might have been concentrated by currents and do not reflect an in-situ accumulation. However, the articulated nature of the conchostracans, the lack of any preferred orientation of the elements (Figs. 11–14), the occasional arrangement in small clusters, and the wide size ranges and bimodal to polymodal size-frequency histograms indicate that the organisms accumulated in-situ, under low energy conditions. (A rare exception is the concentration of *Eosestheria* valves shown in Fig. 5A.) This is corroborated by the finely laminated segments of the section which do not exhibit any sign of current activity. As will be shown below, rather than produced by physical concentration processes, the high faunal density is better explained by the life strategies of the major faunal components.

9.2. Preservational features

The preservation of organisms with organic skeletons (insects and their nymphs, crustaceans), even though partly only as replicas, is the prominent feature of the lake biota. Otherwise the strata would be nearly unfossiliferous, the only other faunal elements being, apart from plant remains, rare internal or external moulds of bivalves and gastropods. The greatly retarded or, in the case of *Eosestheria*, even lack of bacterial decay of organic skeletons can be explained either by anoxic conditions on the lake floor, which greatly slowed down decomposition, or else, by rapid burial. At a first glance, the latter seems perhaps more likely, considering that much of the sediment consists of tuffaceous material. However, in the finely laminated part, each lamina is often just a few 100 µm thick (Fig. 5). A thin algal/bacterial film may have had an additional sealing effect to protect arthropod skeletons from decay.

Soft part preservation cannot be demonstrated within the investigated section, as fish or higher vertebrates with body outlines apparently were not present in this part of the lake, nor were worms or other soft-bodied invertebrates. Moreover the ubiquitous occurrence of dislodged conchostracan valves, which requires loss of the soft parts, speaks for their decomposition.

9.3. Population ecology

The size-frequency histograms of *Hexagenites*, *Liaoningogriphus*, and *Eosestheria* from the various bedding planes are all bi- or polymodal, but in all cases juveniles are conspicuously absent (Figs. 15 and 16). Apart from suggesting autochthony of the faunal elements these distribution patterns offer information on the

population ecology of the species. As will be argued below, the bedding planes contain annual thaphocoenoses, i.e. remains of biocoenoses that lived in the lake during spring and summer, experienced mass mortality, and that were periodically (e.g. during winter months) sealed by a thin film of fine-grained sediment. Especially *Eosestheria* and *Liaoningogriphus* show typical opportunistic behaviour, expressed by the high density in which they commonly occur, their rapid generation turnover, and the population crashes, which are documented by mass mortality.

In the case of *Liaoningogriphus* the bimodal histograms (Fig. 15) can be interpreted to represent two recruitment phases, whereby the second generation with a greater number of individuals was not yet fully grown. The premature death of members of the second generation logically would then indicate mass mortality. The alternative explanation, that the smaller peak represents moult stages is less likely. There are no preservational differences between individuals from the two peaks, which one would expect if one represents only exuviae. Moreover, in this case also smaller specimens, representing earlier moult stages, should be preserved, which is not the case. It has been argued above that the fossilization potential of exuviae of the thinly sclerotized carapace of *Liaoningogriphus* was very low. A third explanation for the two peaks, which cannot be discounted, is that living conditions during growth of the second generation deteriorated. Although being fully grown they did not reach the same size as the earlier generation.

The size of *Hexagenites* was measured only on one bedding plane. The distinctly polymodal histogram (Fig. 15), spanning a wide range of sizes, again suggests several recruitment phases and mass mortality. Mass mortality is supported by the fact that all *Hexagenites* are nymphs and did not develop into imagines. Again, there is no indication that some of the specimens are exuviae.

The largest dataset is available for *Eosestheria* (Fig. 16). As in the two preceding cases, the polymodal size-frequency histograms suggest at least two, if not three recruitment phases and mass mortality. However, due to the great variation in life styles within the conchostracans the interpretation of the pattern is less straightforward. For example, some modern species are known to exhibit sexual dimorphism (Tasch, 1969) including differences in size. However, sexual differences in size do not result in polymodal size-frequency histograms. Up to four generations of conchostracans within a year have been recorded from permanent ponds in modern environments (Webb, 1979) and thus several generations can be expected to have been able to grow in the Zhangjiagou Lake during a single season. However,

consecutive recruitment phases under an identical set of environmental conditions seem unlikely as the various generations should then have reached the same size, except possibly the last one, which was killed by establishment of adverse environmental conditions. The same would be true, if the bedding planes contained generations time-averaged over a period of several years. This is under the premise that all individuals are adults. Indeed, no juveniles have been encountered and nearly invariably all individuals show a characteristic narrowing of growth lines towards, and dense crowding of growth lines at, the ventral margin of the valves which is a characteristic feature of adults (Figs. 7E and 8B). According to Tasch (1969) the number of growth lines may vary considerably within members of a population. Moreover it commonly varies between females and males, the latter having fewer growth lines despite being of the same size. As the number of growth lines is also controlled by age and surely also by environmental factors, the interpretation of growth line patterns of fossil species becomes very complicated.

The important point for our discussion is that adults, identified by the dense crowding of the last growth lines, occur in different sizes. As in the case of *Liaoningogriphus*, this can be explained by variations in environmental conditions, which influenced the growth rate and adult size of the various generations. Obvious reasons for such variations are seasonal or larger-scale differences in food supply or oxygen levels or changes in lake water chemistry due to volcanic activity. The latter factor, however, must have been random and most likely would not have produced the more or less identical pattern found in all size-frequency histogram. The identical patterns strongly suggest that the fluctuations in environmental conditions were seasonal in nature. Differences in environmental conditions also explain the distinctly smaller average size of *Eosestheria* in level O (14.5 mm) and the slightly higher figure in level K (19.5 mm) when compared to the remaining levels, in which the mean size varies between 15.5 and 17.5 mm (Fig. 16).

9.4. Anoxia, the controlling environmental parameter

Having established mass mortality as the main feature controlling life in the Zhangjiagou Lake during the time slice represented by our excavation, we have to look for the responsible environmental parameter(s). Prime candidates are (a) high acidity of the water in connection with deposition of volcanic ash, (b) elevated water temperatures, as a result of deposition of hot ash, and (c) anoxia.

Although the first two features surely affected the lake biota at times, which can be demonstrated by tuff layers and layers of fine-grained ash, they are insufficient to explain regularly re-occurring mass mortality. This identifies anoxia as the most likely culprit. Quite clearly, lake waters at the site must have been oxygenated for much of the time to allow growth of the benthic fauna. Even though the three common taxa were all able to swim, it is highly unlikely that they spent all the time in the water column. For example, according to Frank (1988) a sedentary mode of life is typical of adults of many modern conchostracans. Thus, oxygen conditions probably were also normal or next to normal at the sediment-water interface. This is corroborated by occasional burrows. Moreover both present-day mayfly nymphs and conchostracans are able to tolerate dysoxia to some degree (e.g., Fox et al., 1935; Whitney, 1939). Oxygenated conditions most likely existed from autumn to early summer, when a rich algal flora provided an ample food source for the benthic fauna. Elevated water temperatures during the summer months led to a density stratification of the water column, and decomposition of algal material to depletion of oxygen and the gradual establishment of dysoxic and finally to anoxic conditions also in shallower parts of the lake, which resulted in mass mortality. This mass mortality most likely occurred in mid-Summer, because some of the *Hexagenites* were already quite large and must have reached nearly the end of their larval stage. The anoxic phase may have lasted for a period in the order of a few weeks to a couple of months. The present dataset does not allow to state with certainty how regularly anoxia became established. Correspondingly, the taphocoenoses of some of the bedding planes may represent generations that populated the lake in the course of several years.

9.5. Time frame

Much of the ecological interpretation of the lake biota depends on the time slice represented by individual bedding planes. Three models can be envisaged: In model (1) individual laminae and the corresponding bedding plane represent seasonal cyclicality (see also Liu et al., 2002). The climate of that time would have had to be characterized by a dry season with little sediment input into the lake and growth of the organisms (presumably spring and summer) and a wet season, when increased river discharge produced a sediment lamina. The fauna of each bedding plane, subject to seasonal mass mortality (see above) would then depict in a way the annual production in the lake. Model (2) assumes deposition of the laminae mainly by erratic,

unpredictable processes such as volcanic ash falls or flash floods, which may have occurred several times within a year or only once every few years. According to this model the fauna of a single bedding plane would represent a time span of a few weeks to a few years. Model (3) is a combination of the other two models where a seasonally controlled sedimentation pattern is punctured by episodic sedimentation events.

The sedimentary succession shows quite clearly that episodic sedimentation did take place. The resulting beds are commonly much coarser-grained than the finely laminated sediments and either exhibit a sharp erosional base and/or grading. They are interpreted as the result of flash floods, some finer beds also clearly represent volcanic tuff layers. However, sediments produced by these events are easily recognised by their features and their generally greater thickness compared to that of individual fine laminae. Although model (3) describes the situation in the investigated section most correctly, our faunal data invariably come from the top of fine laminae and thus correspond to the situation sketched in model (1). Model (2) can be refuted by the lack of juveniles in any of the levels. They should have been preserved at least occasionally by mass mortality caused by episodic events.

A predominantly seasonal cyclicality of the fine lamination and repopulation of the lake following mass mortality seem to be the simplest explanation of the various sedimentary and biotic features that we encountered during our study.

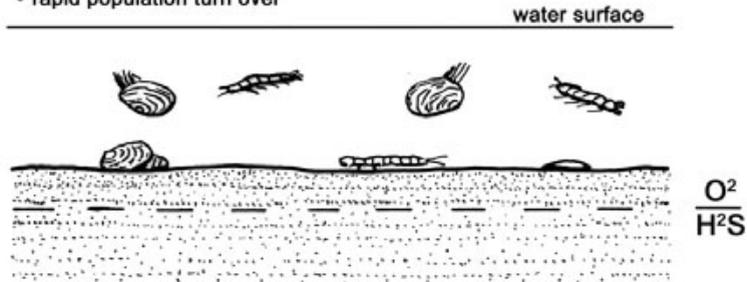
9.6. Environmental model

Based on the arguments presented above, an environmental model for some time segments in the development of the Zhangjiagou Lake is proposed (Fig. 19). We know from the ecology of modern conchostracans that the water depth must have been very small and most likely did not exceed 2 m. The turbulence level similarly must have been very low; otherwise signs of erosion of the lake floor would have been more frequent.

Stage (1). During spring and early summer, the lake waters were well oxygenated. Rich algal growth provided ample food for benthic organisms such as conchostracans, mayfly nymphs and small crustaceans. Due to the opportunistic life strategy of the conchostracans and probably also of *Liaoningogriphus*, their rapid population turnover enabled several successive generations to populate the lake in high numbers. Larger invertebrates and fish, which might have preyed upon the organisms, were absent. Thus, the food web was very

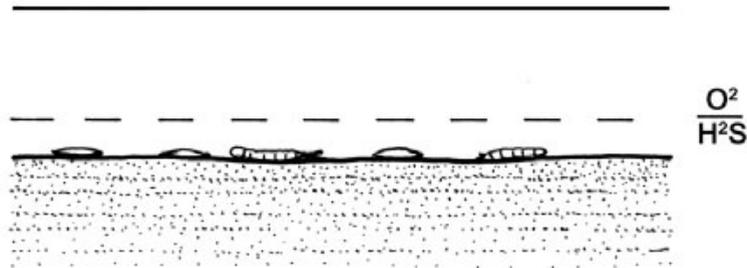
A spring - early summer

- algal growth
- recolonisation of the lake
- rapid population growth
- rapid population turn over



B mid - summer

- gradual establishment of anoxic conditions
- mass mortality



C autumn - winter

- re-establishment of oxygenated conditions at the lake bottom
- deposition of a thin layer of sediment

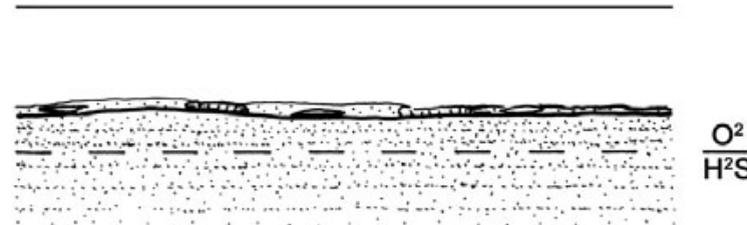


Fig. 19. Model depicting the three environmental modes annually occurring in the Zhangjiagou Lake.

simple and consisted merely of primary producers and primary consumers. Occasionally, elements of the terrestrial biota surrounding the lake, such as insects and plant fragments drifted in and came to rest next to the lake fauna.

Stage (2). The rise in water temperature towards the summer, coupled with consumption of oxygen by respiration processes and bacterial breakdown of algal and plant material, gradually led to the establishment of

dysoxia and a corresponding deterioration of living conditions, which slowed down growth of the organisms. This resulted in adults which did not reach the size of previous generations. Finally, oxygen depletion reached a lethal level for the organisms that populated the lake and mass mortality occurred. The dead bodies accumulated on the lake floor, where gradually the soft parts decayed. However, due to the lack of oxygen, decay was too slow to degrade the organic skeletons as well.

Stage (3). During autumn and winter, an increased precipitation-induced discharge of sediment-laden waters into the lake led to mixing of the water masses, re-established oxic conditions, and deposition of one or several thin layers of sediment. These sediment layers, often merely a veneer, protected the organic skeletons from further decay.

The seasonal phases of anoxia possibly were the reason why no fish population could become established in the lake at that time. An alternative explanation might have been an increased acidity of the lake waters caused by episodic input of volcanic ash. The lack of fish, potential predators of the dominant taxa, in connection with an ample food supply, was responsible for their very high population densities.

In the Cretaceous as today, shallow lakes were usually vegetated by charophyte algae (J.-P. Berger, pers. comm.). Charophytes have been documented in the Jixian Formation of western Liaoning, albeit rarely (Lu and Wang, 1999), but were not found in the part of the lake sediments investigated by us. Their absence might be secondary, caused by dissolution during diagenesis, or primary, caused by the unsuitable water chemistry (see above).

The scenario outlined above characterizes the normal (background) conditions in the lake. They were episodically interrupted by catastrophic events (flash floods, rain of hot ashes), which left a conspicuous record in the sediments and also altered the environmental conditions, in particular the lake water chemistry. To which extent the preservation of the spectacular fossils of the Jehol Biota such as dinosaurs, birds, and fish is tied to such catastrophic events (Wang et al., 1999) future studies at similarly high resolution will have to show.

10. Conclusions

In the Lower Cretaceous lake sediments of western Liaoning different types of environmental conditions are recorded. In an attempt to understand the changes in the ecosystem of these lakes through time we concentrated, in a first step, on the background conditions represented by finely laminated mudstones in a very shallow, marginal part of the lake. The detailed investigation of 18 bedding planes within a 3 m section presented us with a lake biota rich in individuals, but low in diversity. Three species dominated the fauna: the conchostracan *Eosostheria ovata*, the shrimp *Liaoningogriphus quadripartitus*, and the mayfly nymph *Hexagenites tristetalis*. Each of these taxa dominates an association, in which it usually represents between 85 and 98% of all individuals. Remaining elements of the lake fauna (bivalves,

gastropods) are rare. Bimodal to polymodal size-frequency histograms of the faunal elements reflect a recruitment pattern and are interpreted to indicate mass mortality. In the case of the most abundant species, *E. ovata*, growth line analyses showed that individuals were adults, even when they belong to different peaks of the size-frequency histograms. This can only be explained by differing environmental conditions during growth of the various generations, which probably took place within a single season. Considering that mass mortality must have been a regularly re-occurring event, the causative factor most likely was anoxia that seasonally developed in connection with elevated water temperatures and increased oxygen consumption by decaying algae during summer. It is clear that this scenario of a seasonally stratified, eutrophic lake represents only one facet of the ecosystem of the lake. Episodic catastrophic events such as ash falls, produced during eruptions of nearby volcanoes, also must have caused mass mortality, probably causing the concentration of larger land vertebrates (e.g., birds, dinosaurs) in lake sediments. Moreover levels with a rich fish fauna and with other aquatic vertebrates (e.g., turtles, frogs) and invertebrates (e.g., large crustaceans) known from different horizons of the lake succession demonstrate that, during some time slices, conditions were suitable for the development of a more complex ecosystem than the one whose remnants have been described here.

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