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Dynamics of the lacustrine fauna from the Early Cretaceous Yixian Formation, China: implications of volcanic and climatic factors

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The taphonomy and palaeoecology of the famous Lower Cretaceous Jehol biota of northeastern China are two of its least resolved aspects. The biota occurs in lacustrine sediments characterized by abundant volcanic ash layers. The general view is that these tuff layers correlate strongly with vertebrate mass mortality events. However, though aquatic invertebrates also suffered mass mortality, in the majority of cases individuals tend to occur on bedding planes of finely laminated sediments, suggesting that each mass mortality event is not related to volcanic activity. Based on data collected in the course of two excavations at Zhangjiagou and Erdaougou, the role of volcanic activity and other factors that could have controlled the dynamics of the fauna were investigated. Cluster analyses of fossil assemblages from both localities show similar results, and eight fossil communities are recognized. In the lacustrine Yixian Formation, frequent and often severe volcanic activity represented by the abundant tuff layers influenced the water quality, causing repeated collapse of the aquatic ecosystem. Bedding planes with remains of the eight different communities were analysed, each recording the community dynamics of a shallow eutrophic lake system that was most probably controlled by fluctuations of oxygen level related to climate. A mortality model, in which oxygen-level fluctuations play the decisive role, is proposed to explain the existence and distribution of the fossil communities, as well as the unfossiliferous layers. □ *China, Jehol biota, lacustrine community, mass mortality, palaeoclimate, volcanic activity.*

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The Lower Cretaceous Yixian Formation of western Liaoning, northern Hebei, and adjacent Inner Mongolia, yields a highly diverse, exceptionally well preserved fauna and flora, the 'Jehol Biota', which includes representatives of almost all major clades of Lower Cretaceous terrestrial and freshwater vertebrates, a wide variety of invertebrates and a diverse flora (see Chen & Jin 1999; Chang *et al.* 2001, 2003; Zhou *et al.* 2003; Zhou & Wang 2010). Its species richness and exceptional preservation provides a rare opportunity to address questions about the origin of birds, the evolution of feathers and flight, the early diversification of angiosperms, and the timing of the placental mammal radiation (Zhou *et al.* 2003).

However, the taphonomy and palaeoecology of the Jehol biota are its least resolved aspects. The general view is that the tuff layers are strongly correlated with mass mortality events of the vertebrates (Wang *et al.* 1998, 1999, 2000; Guo & Wang 2002; Guo *et al.* 2003; Zhou *et al.* 2003; Benton *et al.* 2008). Observations show that the most productive horizons of vertebrates are beneath ash tuff falls. The tuffs positively sealed the fossil-rich layers, hereby creating microenvironments around the organisms that promoted anoxia and halted bacterial decay of soft tissues. Moreover, they also prevented bioturbation and scavenging (Zhou *et al.* 2003; Benton *et al.* 2008). Aquatic invertebrates, appear to have also suffered mass mortality, but in the majority of cases individuals tend to occur on bedding planes of finely laminated sediments. Obviously, not every mass mortality event is related to volcanic activity. In this article, therefore, we try to answer the following interrelated questions: is the deposition of tuff the only factor causing the mass

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mortality of aquatic organisms in the Yixian Formation; If not, which other factors could be responsible for it; and, how did these factors control the mass mortality of aquatic organisms?

Geological setting

The Yixian Formation consists of weakly laminated to finely bedded siliciclastic sediments, mainly low-energy sandstones, and shales, intercalated between extrusive basalts and tuffs and cross-cut by occasional dykes and sills (Jiang & Sha 2007; Jiang *et al.* 2011). The Sihetun area is one of the famous fossil localities of western Liaoning, and the outcrops mainly comprise the Lujiatun and Jianshangou units (the first and second members of the formation). The Jianshangou unit (24–112 m thick) is composed of sandstones, siltstones, mudstone, shales and tuffs with intercalations of calcareous shales and gypsum. The unit yields abundant aquatic invertebrate fossils, as well as terrestrial and aquatic vertebrates and plants. Two localities have been excavated within the Jianshangou unit in the Sihetun area in 2006 and 2007 (Fig. 1). At Zhangjiagou (N 41°36′ 13.3′; E 120°49′ 28.7′), the excavation was ca. 3.5 m deep with an area of ca. 9 m^2 at the top, narrowing to ca. 5.5 m^2 at the bottom. Part of the data collected from this excavated section has been studied previously by Fürsich *et al.* (2007). The second excavation at Erdaogou (N 41°31.942′; E 120°47.747′) was ca. 8 m deep, with an area of ca. 30 m^2 near the top, narrowing to ca. 12 m^2 at the bottom. Both localities belong to the Sihetun Lake (‘Zhangjiagou Lake’ of Fürsich *et al.* 2007).

Materials and methods

To obtain a continuous quantitative data set, the rock pile was carefully split, and the fossiliferous levels were identified and excavated (see description in Fürsich *et al.* 2007). The same excavation method was applied in the second excavation at Erdaogou. Levels for quantitative analysis were randomly selected. For each of these levels all faunal elements were recorded in terms of relative abundance. In the present article the faunal elements were not treated at species level, but at genus or group level, e.g. Spinicaudatan (clam shrimps, ‘conchostracans’), *Liaoningogriphus*, *Hexagenites* (mayfly) nymphs. Though these three groups constitute the most abundant faunal elements in the Sihetun palaeolake, usually just one species of each group occurred on a bedding plane (Fürsich *et al.* 2007) (Fig. 2A, B, C). During the Erdaogou excavation, the general faunal occurrences were also recorded for those layers which were not easy to split and therefore were not sampled quantitatively. This had not been done in the case of the Zhangjiagou excavation.

Field observations showed that in most cases fossils were preserved on bedding planes of finely laminated sediments. Besides the thickness and frequency of the tuff layers, the frequency and thickness of

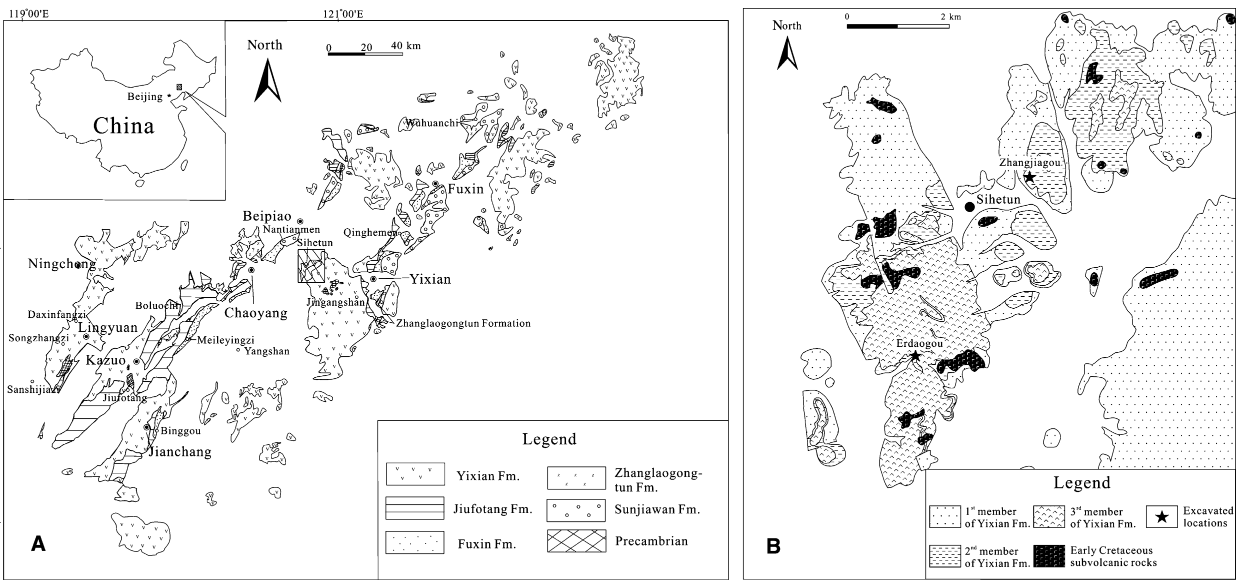

Fig. 1. Location of western Liaoning and the distribution of the Cretaceous formations in western Liaoning (A), and positions of excavations at Zhangjiagou and Erdaogou (B), and (after Jiang & Sha 2007; fig. 1).

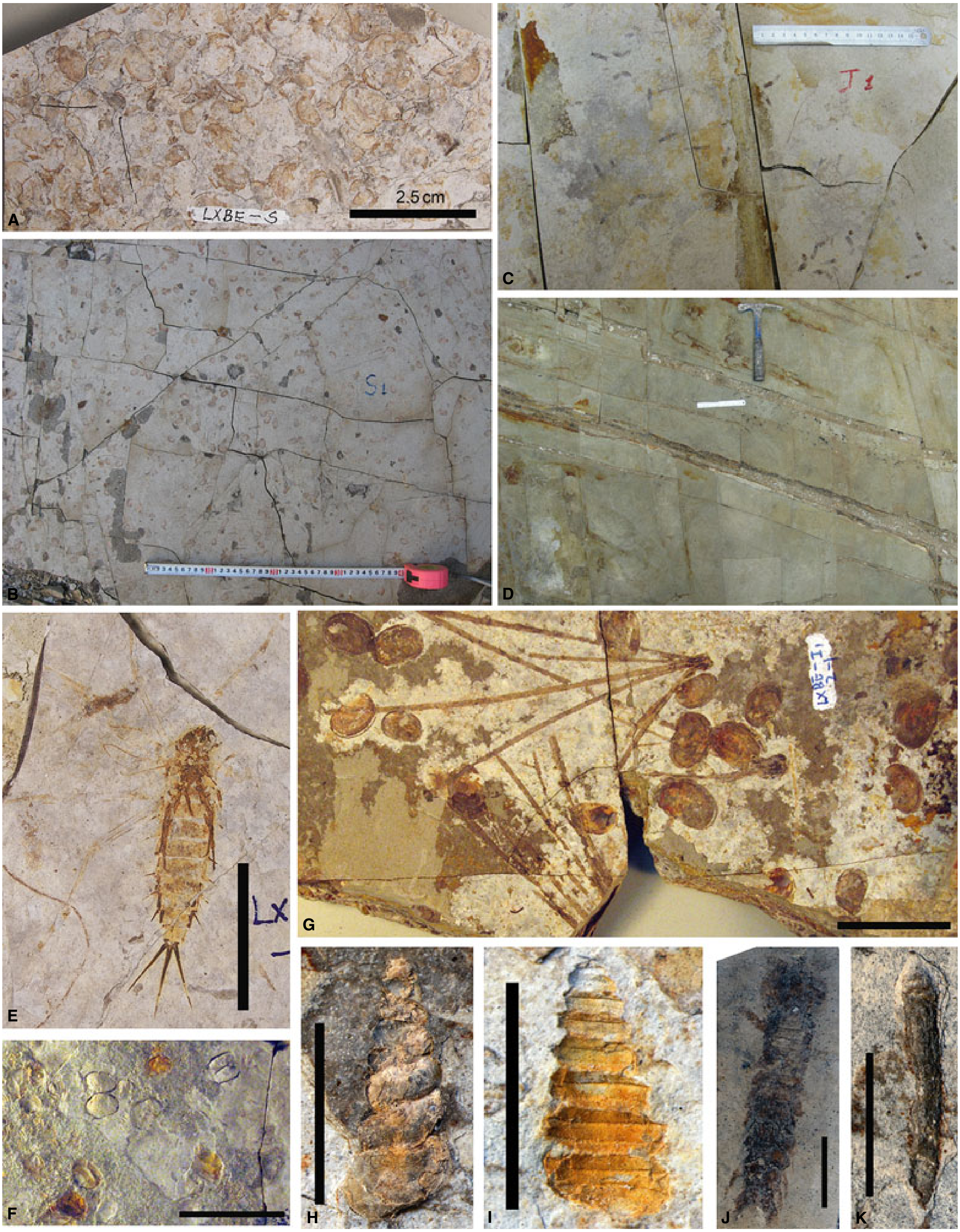

Fig. 2. The fossil densities vary from extremely high (A) to moderate (B), and low (C). Some bedding planes may be devoid of fossils (D). And the most dominant or common members collected from the excavations, *Hexagenites* nymphs (E), bivalves (F), spinicaudatans and plant fragments (G), gastropods (H) and (I), *Liaoningogriphus* (J), fish coprolites (K). Scale bar in E and G is 2.5 cm, F is 2 cm, H-K is 0.5 cm.

laminated units were also carefully recorded. In addition, sedimentological data were recorded. They will be discussed and interpreted in detail in another article.

Each studied fossil assemblage from a single bedding plane was treated as a community relict. To recognize different types of fossil communities in the Sihetun palaeolake, a cluster analysis of datasets, organized into a relative abundance data matrix (Table 1), from the Erdougou and Zhangjiagou localities was conducted using Ward's method and the Euclidean dissimilarity measure. The PAST ver. 2.05 package (Hammer *et al.* 2001) was used for this purpose.

Results

Lithological facies

Four lithofacies were recognized within the excavated strata: (1) grey to dark-grey finely laminated siltstone, silty mudstone and mudstone; (2) grey, dark-grey, or grayish-white, weakly laminated or irregularly laminated siltstone, silty mudstone and fine-grained sandstone; (3) brown, grey, or greyish white sandstone and carbonate without lamination; and (4) yellowish-green tuff. The main features are fine lamination, lack of bioturbation, frequent intercalations of tuff and occasionally coarse sandstone or carbonate units.

Temporal distribution of the fossils

Although the Jianshangou Unit is one of the most fossiliferous parts of the Yixian Formation, the fossils are not evenly distributed throughout the unit. Even within the same package of finely laminated layers, the fossil density may vary from extremely high (Fig. 2A) to moderate (Fig. 2B) or low (Fig. 2C), and some bedding planes may be devoid of fossils (Fig. 2D). Since during the second excavation general information on the faunal occurrences was also recorded for those layers that did not split easily, the analysis in this article is mainly based on the data collected from the second excavation at Erdaogou, supplemented by the data from the Zhangjiagou excavation.

Almost all the fossils were from grey or dark-grey, finely laminated siltstone, silty mudstone and mudstone, corresponding to lithofacies 1 (Figs 3, 4). Rarely, fossils occurred in irregularly laminated siltstone, silty mudstone and mudstone or sandstone (e.g. Fig. 3; Level C, A1, C1). In parts of the section containing abundant tuff layers, which point to very frequent disturbances of the lake environment, hardly any fossils occurred (e.g. Fig. 3, the segments between levels C and D, D and E, F and G, G1 and H1, and between Levels I1 and J1).

Table 1. Values of relative abundance of taxa used.

Relative abundance (n/m^2)	Descriptions in text	values used for cluster analysis
0	–	$2^0 = 1$
≤5	• Rare	$2^1 = 2$
5–25	● Occurring	$2^2 = 4$
25–100	● Common	$2^3 = 8$
>100, but individuals still discernible	● Abundant	$2^4 = 16$
Very high density	● Very abundant	$2^5 = 32$

Abundance and density variations of aquatic organisms

Spinicaudatans (clam shrimps, 'conchostracans'), the small crustacean *Liaoningogriphus*, and nymphs of the mayfly *Hexagenites* are the most abundant fossils occurring in the investigated sections. The densities of 18 fossil assemblages from the Zhangjiagou excavation and 27 fossil assemblages from the Erdaogou excavation were calculated. The density variations of these dominant groups are shown in Figures 5, 6: spinicaudatans display the most severe density fluctuations, then followed by *Liaoningogriphus*, and *Hexagenites* nymphs.

The densities of other aquatic macrofossil groups (bivalves, gastropods and other aquatic insects) were calculated according to the number of individuals in each fossil assemblage (Figs 5, 6). Bivalves are the most common co-occurring fossils, exhibiting relatively high fluctuations, other aquatic insects come second. Gastropods are rare, with no more than five individuals on any bedding plane.

Cluster analysis

The original datasets have been organized into a data matrix based on the relative abundance (Table 1) of each of the 10 taxa collected from the two excavations (spinicaudatans, gastropods, bivalves, ostracods, *Liaoningogriphus*, *Hexagenites* nymphs, other aquatic insects, fish, fish coprolites and plant fragments) (Tables 2, 3; Fig. 2). The cluster analysis of 27 bedding plane samples from Erdaogou (Fig. 3, Table 3) resulted in seven groups based on the distance of 10 (Fig. 7). Fossil density is high on bedding planes of cluster e1, *Liaoningogriphus* is very abundant, spinicaudatans and *Hexagenites* nymphs occur, and other groups are present occasionally (assemblages eH, eJ1, eL1). In cluster e2, fossils are sparse, no taxon dominates, each group occurs either occasionally, rarely or is absent (assemblages eK, eL, eQ, eK1). The fossil

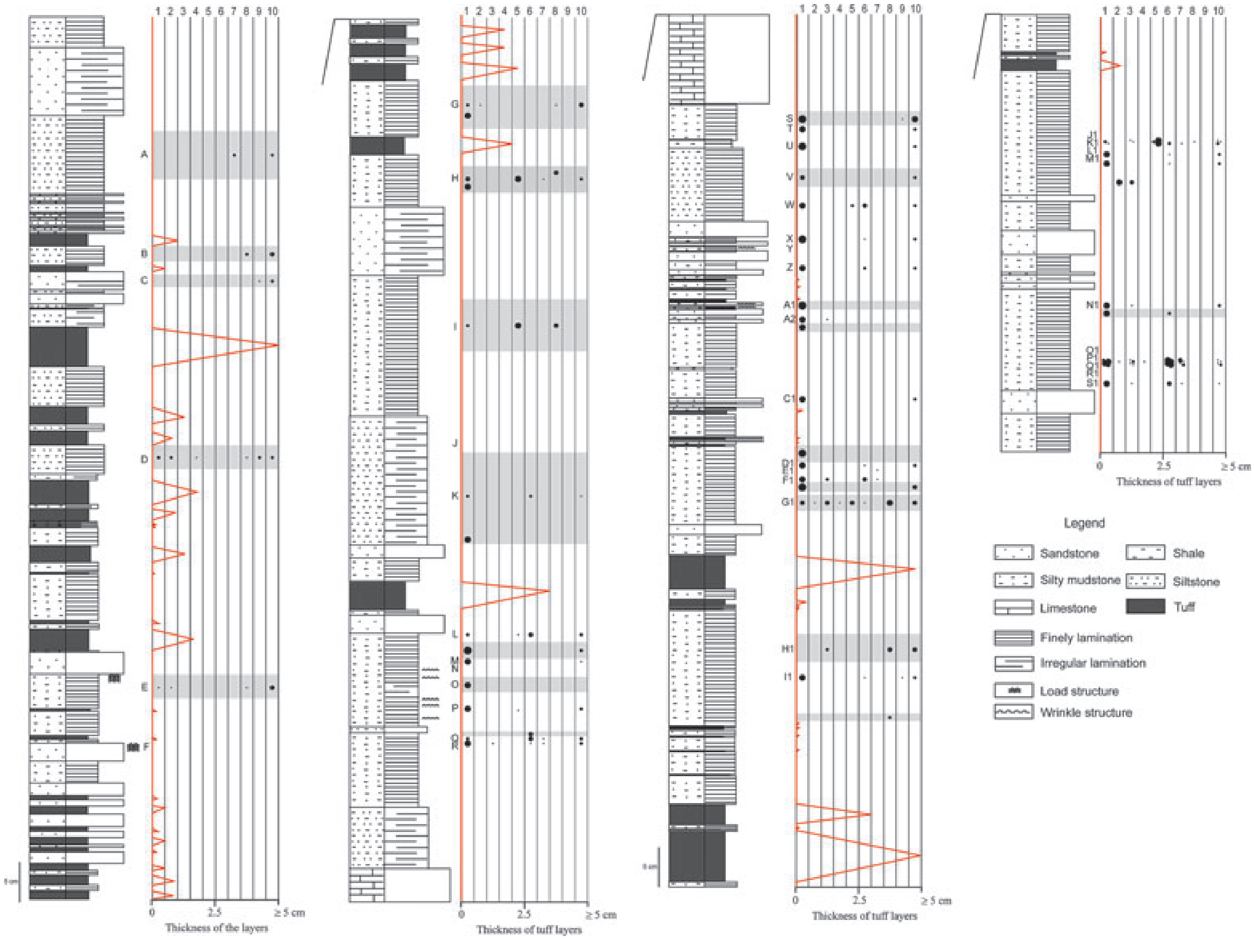

Fig. 3. Excavated section at Erdaougou with positions of investigated bedding planes, main faunal elements and their density were represented by different-sized black circles (see Table 1). Similar fossil assemblages repeatedly occurred within the shaded areas. 1, spinicaudatans; 2, gastropods; 3, bivalves; 4, ostracods; 5, *Liaoningogriphus*; 6, *Hexagenites* nymphs; 7, other aquatic insects; 8, fishes; 9, fish coprolites; 10, plant fragments.

density in cluster e3 is high, and spinicaudatans constitute the most common group, with a reasonable number of *Hexagenites* nymphs. Other groups are quite rare (assemblages eW, eF1, eS1). Cluster e4 is dominated by spinicaudatans and *Hexagenites* nymphs, while other groups are rare or absent (assemblages eQ, eP1). The fossil density in cluster e5 is high, and *Hexagenites* nymphs are dominant. Besides these, spinicaudatans, bivalves and other aquatic insects occasionally occur, while other groups are rare or absent. Cluster e6 is characterized by extremely high density of spinicaudatans, while other groups are rare or absent (assemblages eU, eX). In cluster e7, spinicaudatans clearly dominate, but with a density lower than that in cluster e6, and with other groups rare or absent (assemblages eM, eO, eP, eR, eT, eZ, eA2, eC1, eD1, eM1, eN1).

The cluster analysis of 20 fossil assemblages representing single bedding planes at Zhangjiagou (Fig. 4, Table 2) also produced seven groups (z1–z7) based on a distance value of nine (Fig. 8). According to their composition, these seven groupings correlated very well with e1–e7: cluster z1 with e1 (assemblages zP-zT); cluster z2 with e6 (assemblages zM, zN); cluster z3 with e3 (assemblages zA, zD, zG, zK); cluster z4 with e7 (assemblages zL, zO); cluster z5 with e2 (assemblage zJ); cluster z6 with e4 (assemblages zC, zE); and cluster z7 with e5 (assemblages zB, zF, zH, zI).

Seven different fossil communities could be recognized from the cluster analysis of all 47 fossil assemblages collected from both localities, based on a distance value of 12 (Fig. 9). These seven fossil communities are corresponding to the seven clusters produced from both localities: community 1 including cluster e6 and z2; community 2 including cluster e3 and z3; community 3 including cluster e4 and z6; community 4 including cluster e7 and z4; community 5 including cluster e2 and z5; community 6 including cluster e5 and z7; and community 7 including cluster e1 and z1.

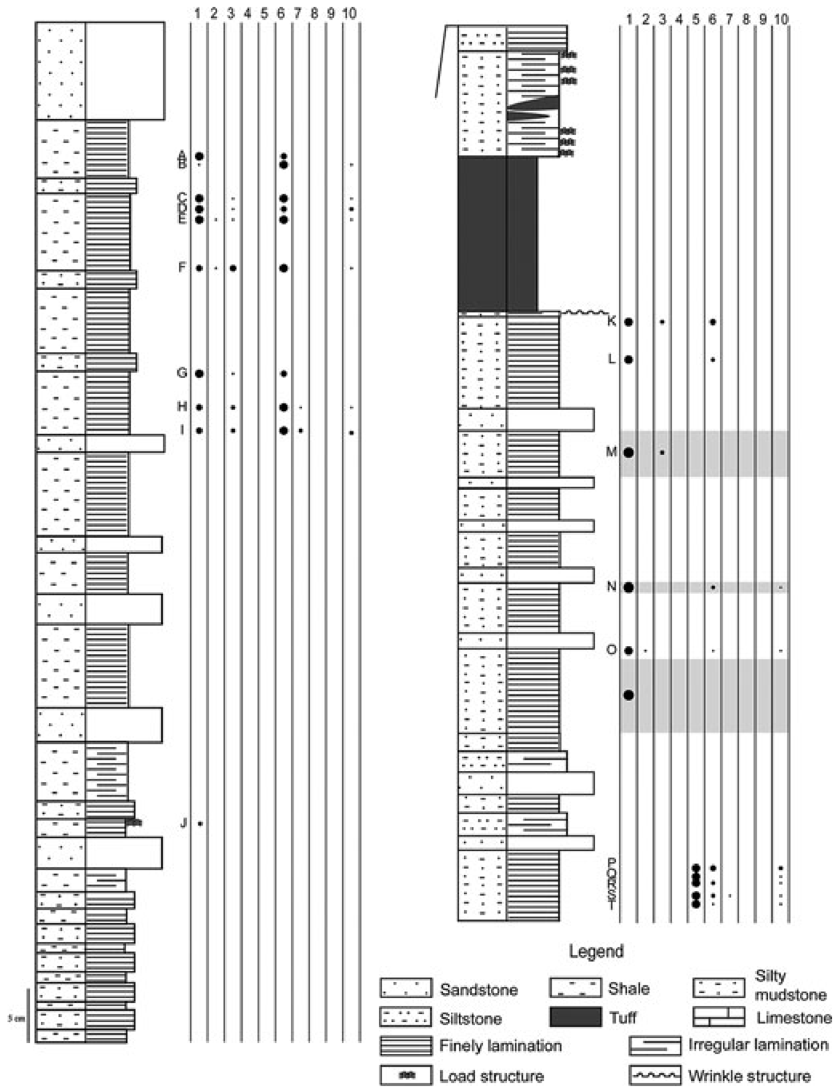

Fig. 4. Excavated section at Zhangjiagou with positions of investigated bedding planes, main faunal elements and their density represented by different-sized black circles (see Table 1). Similar fossil assemblages repeatedly occurred within the shaded areas. Red line shows the frequency and thickness of tuff layers. 1, spinicaudatans; 2, gastropods; 3, bivalves; 4, ostracods; 5, *Liaoningogriphus*; 6, *Hexagenites* nymphs; 7, other aquatic insects; 8, fishes; 9, fish coprolites; 10, plant fragments.

Discussion

Disturbance of the lake ecosystem by volcanic activities

The facies pattern of the detailed sections measured at the two excavation sites can be described by: (1) the variation in thickness and frequency of finely laminated units; (2) the variation in thickness and frequency of the tuff layers; and (3) the variation in thickness and frequency of other sediment types.

The volcanic activities which disturbed the lake ecosystem are documented by the frequency of tuff layers, and the thickness of the tuff layers to some extent reflects the strength of volcanic activities. At the Erdaogou site, 38 assemblages were collected from laminated sediments (including 27 assemblages representing single bedding planes, 11 assemblages from several similar bedding planes), and only levels C, A1 and C1come from thin-bedded sandstone. Thirty-two of the 38 assemblages (84%) were collected from continuously laminated sediments with a thickness of more than 5 cm. Thus, a persistence of the finely laminated facies represents conditions of the lake environment beneficial for the growth and preservation of the lake fauna. In other parts of the section laminated facies is repeatedly disturbed by tuff layers and non-laminated sediments (mainly sandstone). Levels X- Z, A1 and C1 were collected from a part of the section where the lamination was interrupted by sandstone or carbonate beds, and only very rarely by thin tuff layers

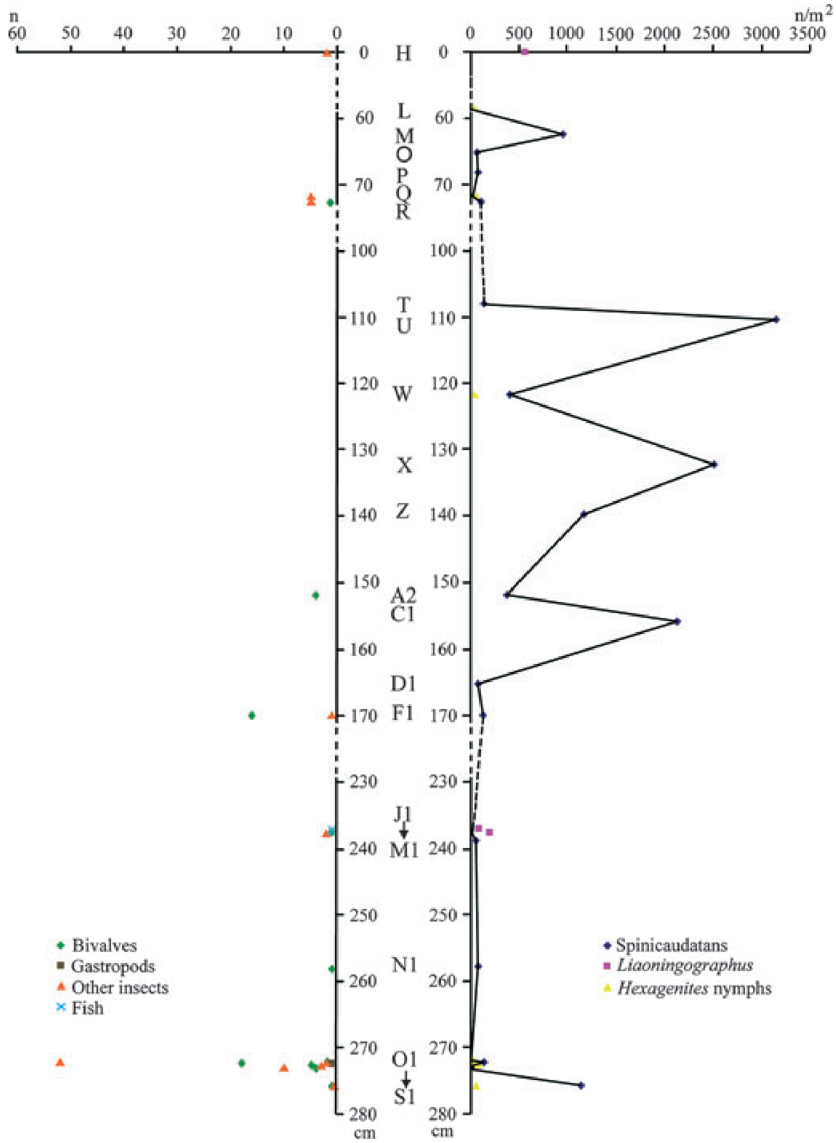

Fig. 5. Variation of the density of the most abundant taxa (spinicaudatans, *Liaoningogriphus*, and *Hexagenites* nymphs) at Erdaougou, calculated as number of specimens per square metre (right column) and the total number of specimens of bivalves, gastropods and other aquatic insects from individual bedding planes (left column).

(Fig. 3). Levels C and E were collected from a part of the section where several centimetre-thick sandstones occur (Fig. 3). Only levels B and D were collected from just between tuff layers (Fig. 3). No assemblages occurred within the segments with frequently developed tuff layers (Fig. 3; e.g. the segments between level C and D, D and E, F and G, G1 and H1, and I1 and J1). Apparently, the frequency of tuff layers and hence the frequency of the volcanic activities directly influenced the occurrence and preservation of the lake fauna.

Population growth

Depending on the available resources, each population has an upper density limit, which is referred to as the carrying capacity of a population. There are two ways to control the population size: one is by density-independent limitations, the other is by density-dependent regulations (Lampert & Sommer 2007). The severe density fluctuations of the three main fossil groups (Figs 5, 6) can be explained in two different ways: (1) the living population was very large; or (2) population growth was frequently interrupted by mass mortality producing high density death assemblages. The trigger of these mass mortalities were more likely catastrophic events caused by density-independent factors rather than density-dependent regulations, because density-dependent factors keep the abundance of a population close to the carrying capacity. They only come into effect when the

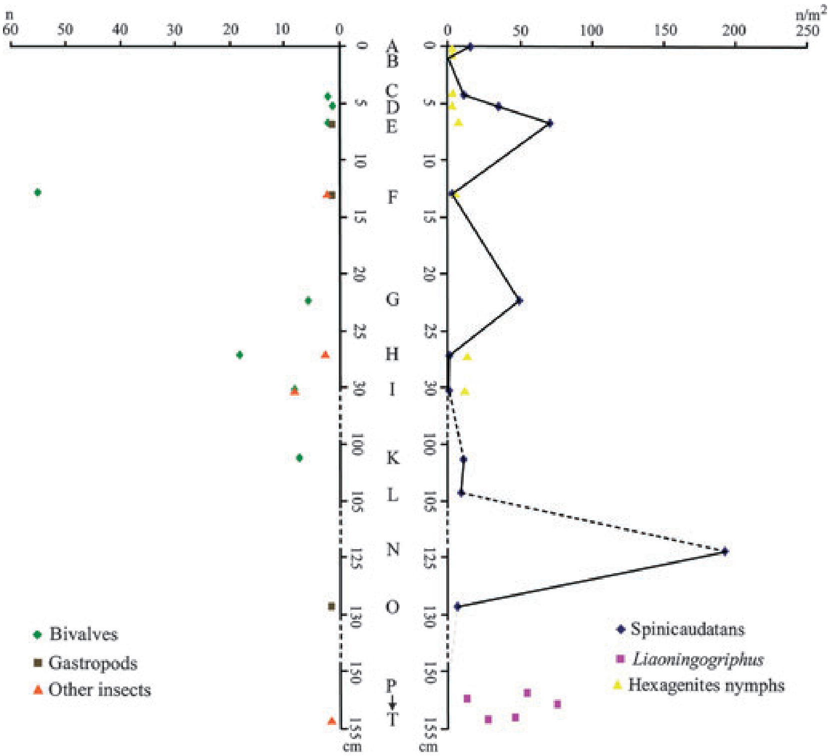

Fig. 6. Variation of the density of the most abundant taxa (spinicaudatans, *Liaoningogriphus*, and *Hexagenites* nymphs) at Zhangjiagou, calculated as number of specimens per square metre (right column) and the total number of specimens of bivalves, gastropods and other aquatic insects from individual bedding planes (left column).

Table 2. Data matrix of the ten taxa encountered in the section of the excavation at Zhanjiagou (assemblages zA-zT) organized as relative abundance data according to Table 1.

Assemblages	Spi.	Gas.	Biv.	Ost.	Liao.	Hex.	OAI	Fis.	Cop.	PF
zA	16	1	1	1	1	8	1	1	1	1
zB	2	1	1	1	1	16	1	1	1	2
zC	16	1	2	1	1	16	1	1	1	2
zD	16	1	2	1	1	8	1	1	1	4
zE	16	2	2	1	1	16	1	1	1	2
zF	8	2	8	1	1	16	1	1	1	2
zG	16	1	2	1	1	8	1	1	1	1
zH	8	1	4	1	1	16	2	1	1	2
zI	8	1	4	1	1	16	4	1	1	4
zJ	4	1	1	1	1	1	1	1	1	1
zK	16	1	4	1	1	8	1	1	1	1
zL	16	1	1	1	1	4	1	1	1	1
zM	32	1	4	1	1	1	1	1	1	1
zN	32	1	1	1	1	4	1	1	1	2
zO	16	2	1	1	1	2	1	1	1	2
zP	1	1	1	1	16	8	1	1	1	4
zQ	1	1	1	1	16	1	1	1	1	2
zR	1	1	1	1	16	4	1	1	1	2
zS	1	1	1	1	16	4	2	1	1	2
zT	1	1	1	1	16	2	1	1	1	2

Spi., spinicaudatans; Gas., gastropods; Biv., bivalves; Ost., ostracods; Liao., *Liaoningogriphus*; Hex., *Hexagenites* nymphs; OAI, other aquatic insects; Fis., fishes; Cop., fish coprolites; PF, plant fragments.

population size exceeds the carrying capacity. Once below the carrying capacity, the growth rate will become positive again and leads to a population increase. The catastrophic events could be sudden changes in physical conditions or rapid changes in the chemistry of the lake waters. The frequent mass

Table 3. Data matrix of the ten taxa encountered in the section of the excavation at Erdaogou (only the data from a single bedding plane are used, including assemblages eH, eK, eL-eM, eO-eR, eT-eU, eW-eX, eZ, eA2, eC1-eD1, eF1, eJ1-eS1) organized as relative abundance data according to Table 1.

Assemblages	Spi.	Gas.	Biv.	Ost.	Liao.	Hex.	OAI	Fis.	Cop.	PF
eH	8	1	1	1	16	1	2	1	1	4
eK	4	1	1	1	1	4	1	1	1	2
eL	4	1	1	1	2	8	1	1	1	4
eM	16	1	1	1	1	1	1	1	1	2
eO	16	1	1	1	1	1	1	1	1	1
eP	16	1	1	1	2	1	1	1	1	4
eQ	4	1	1	1	1	8	2	1	1	4
eR	16	1	2	1	1	2	2	1	1	4
eT	16	1	1	1	1	1	1	1	1	4
eU	32	1	1	1	1	1	1	1	1	4
eW	16	1	1	1	4	8	1	1	1	4
eX	32	1	1	1	1	2	1	1	1	4
eZ	16	1	1	1	1	4	1	1	1	4
eA2	16	1	2	1	1	1	1	1	1	1
eC1	16	1	1	1	1	1	1	1	1	4
eD1	16	1	1	1	1	2	1	1	1	4
eF1	16	1	4	1	1	8	2	1	1	1
eJ1	1	1	2	1	16	1	1	1	1	2
eK1	4	1	2	1	4	1	1	2	1	2
eL1	2	1	1	1	16	4	2	1	1	4
eM1	16	1	1	1	1	2	1	1	1	4
eN1	16	1	2	1	1	1	1	1	1	4
eO1	4	1	2	1	1	16	8	1	1	2
eP1	16	2	4	2	1	16	2	1	1	2
eQ1	16	1	2	1	1	16	2	1	1	2
eR1	8	1	2	1	1	16	4	1	1	4
eS1	16	1	2	1	1	8	2	1	1	2

Spi., spinicaudatans; Gas., gastropods; Biv., bivalves; Ost., ostracods; Liao., *Liaoningogriphus*; Hex., *Hexagenites* nymphs; OAI, other aquatic insects; Fis., fishes; Cop., fish coprolites; PF, plant fragments.

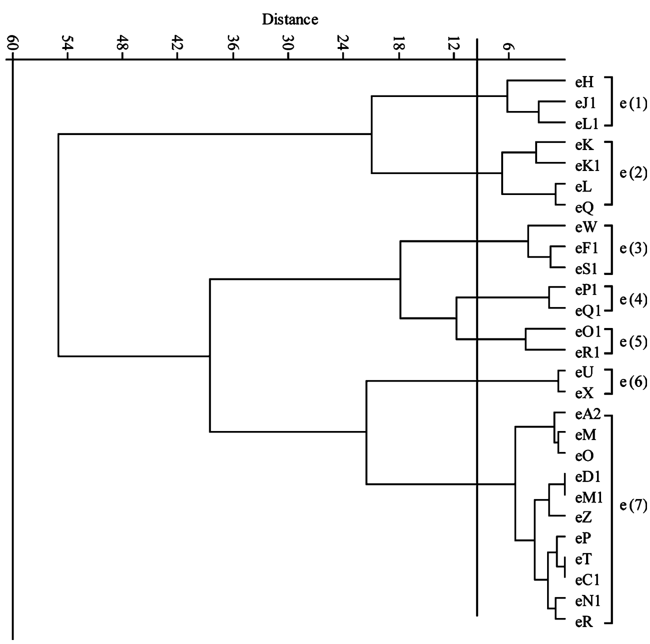

Fig. 7. The cluster analysis (WARD method) of 27 fossil assemblages from single bedding planes at Erdaogou resulted in seven groupings interpreted as relicts of former communities. Stippled line: cut-off point.

mortalities represented by the high density fossil assemblages suggest that the population size of the three main groups was exclusively controlled by density-independent factors, which are indicative of an r-strategy rather than a K-strategy of the faunal elements.

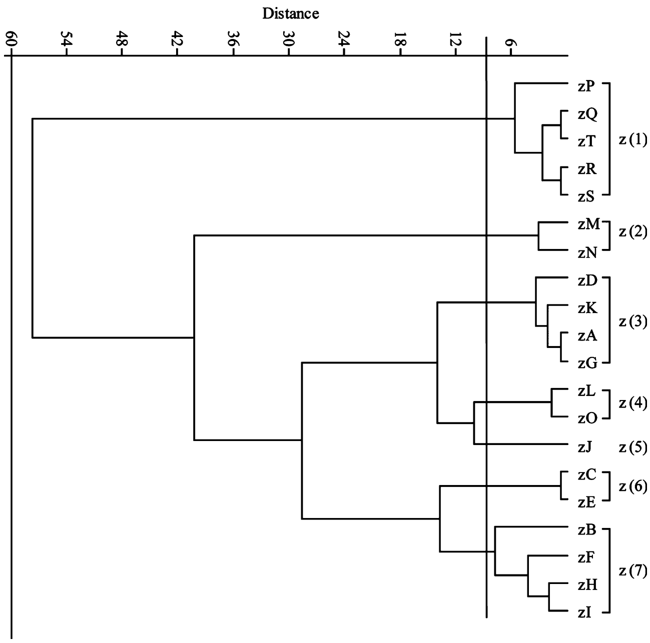

Fig. 8. The cluster analysis (WARD method) of 20 fossil assemblages from single bedding planes at Zhangjiagou resulted in seven groupings interpreted as relicts of former communities. Stippled line: cut-off point.

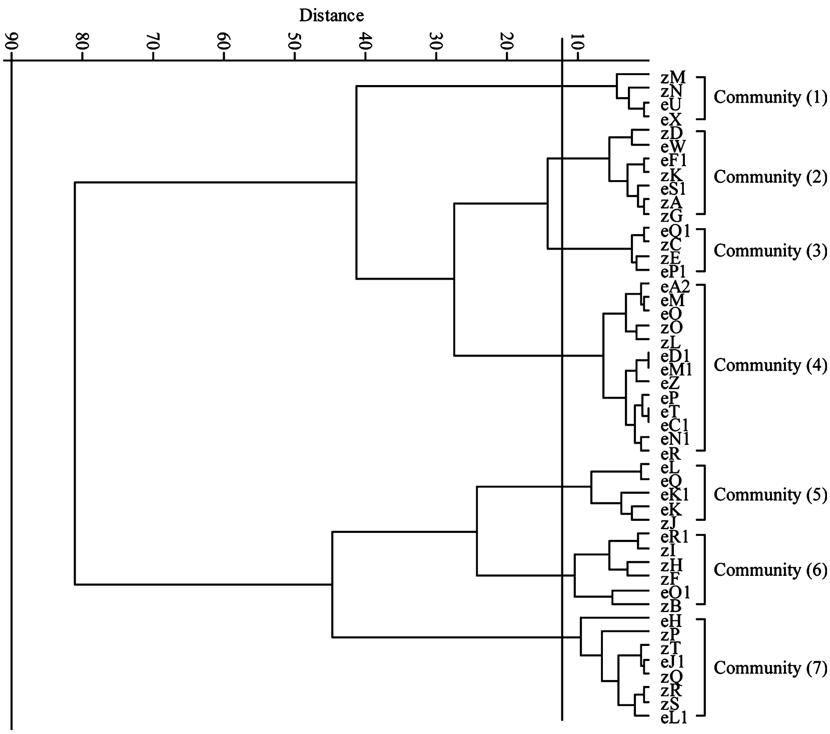

Fig. 9. Result of the cluster analysis of 47 fossil assemblages from single bedding planes at Erdaogou and Zhangjiagou. Seven fossil communities are recognized. Stippled line: cut-off point.

Community dynamics

Apart from the frequently intercalated and often thick tuff layers, also part of the continuously laminated units is devoid of fossil. Examples of these unfossiliferous layers are the part where level I is located, the part below level R, and the part between levels A2 and C1 (Fig. 3). Thus, volcanic activity cannot have been the only reason for the unfossiliferous layers. There must be other factors responsible for some of the unfossiliferous layers, which are either rooted in the original living communities, or are taphonomic processes, or both.

Cluster analyses of the fossil assemblages from single bedding planes at Zhangjiagou and at Erdaogou produced the same cluster pattern, including seven fossil communities (Figs. 7, 8). The combined cluster analyses on all 47 fossil assemblages from both localities also support these seven fossil communities (Fig. 9, Table 4).

No fossil assemblage with abundant fishes on single bedding planes could be defined quantitatively as these layers were not easily split (e.g. Fig. 3; levels H, I, G1, and H1). However, besides the seven fossil communities described above, there is still a fossil community 8, which is characterized by a reasonable number of fishes, while other groups are rare or absent. Thus, altogether eight fossil communities and the unfossiliferous layers document the community dynamics of the Sihetun palaeolake.

Stratification and guild composition of the lake biota

Traditionally, the pelagic zone contains communities composed of two different modes of life: planktonic and nektonic. The distinction is based on the swimming ability of organisms. Nektonic organisms are active swimmers, planktonic organisms, though in some cases capable of swimming (e.g. some elements of the zooplankton, migrate vertically in the water column) are not capable of swimming against strong currents. The lake floor is occupied by the benthos, living either on or in the substrate. In the Sihetun palaeolake, the fishes belong to the nekton. The spinicaudatans, *Hexagenites* nymphs, and *Liaoningogriphus* lived on the surface of the substrate but were also able to swim for short distances (nektobenthic life style). The bivalves, gastropods and ostracods are part of the benthos living on or partly within the substrate. Primary producers form the basis of any lake ecosystem. In the present case, plant fragments are rare. There must have been phytoplankton living in the lake, which is, however, not preserved. In modern lakes, benthic primary producers include cyanobacteria, eukaryotic algae and microphytobenthos, besides macrophytes. The macrophytes of the Yixian Formation are represented by the *Equisetites longevaginatus* – *Beipiaoa spinosa* assemblage, including *Thallities jianshangouensis* Sun & Zheng 2001 (Sun *et al.* 2001), *Th. riccioites* Wu 1999; *Th. dasyphyllus* Wu 1999; *Metzgerites multiramea* Sun & Zheng 2001 (Sun *et al.* 2001), *Muscites tenellus* Wu 1999; *M. drepanophyllus* Wu 1999; *M. meteorioides* Sun & Zheng (Sun *et al.* 2001), *Equisetites longevaginatus* Wu 1999; *E. exiliformis* Sun & Zheng (Sun *et al.* 2001), *Equisetites* spp., *Botrychites reheensis* Wu 1999; *Archaefructus liaoningensis* Sun *et al.* 1998, *Archaefructus* sp., *Beipiaoa parva* Dilcher, Sun & Zheng 2001 (Sun *et al.* 2001), *B. rotunda* Dilcher, Sun & Zheng 2001 (Sun *et al.* 2001), and *B. spinosa* Dilcher, Sun & Zheng 2001 (Sun *et al.* 2001). Most of these taxa formed short herbage at the margin of the lake (Ding *et al.* 2003b). During our excavations, *Equisetites longevaginatus* Wu was the most common plant element, but experienced transportation to some extent (Fürsich *et al.* 2007). Few cyanobacteria, eukaryotic algae and microphytobenthos were recorded (Ding *et al.* 2003b; Fürsich *et al.* 2007).

The fossil biota mainly consisted of epibenthos, rarely of endobenthos, plankton and nekton, with the exceptions of the fish layers. Field observations confirm the presence of high density fish concentrations

Table 4. The seven different fossil communities occurring in the two investigated sections of the Yixian Formation at Zhangjiagou and Erdaogou. The black circles indicate relative abundances of the taxa (see Table 1) are ranked according to the frequency of bedding planes exhibiting a particular abundance pattern of a taxon.

Community	Spi.	Gas.	Biv.	Ost.	Liao.	Hex.	OAI	Fis.	Cop.	PF
1	⬤	-	●,-	-	-	●,•,-	-	-	-	●,•,-
2	⬤	-	●,•,-	-	●,-	⬤	•,-	-	-	●,•,-
3	⬤	•,-	●,•	•,-	-	⬤	•,-	-	-	•
4	⬤	•,-	•,-	-	•,-	●,•,-	•,-	-	-	●,•,-
5	●	-	•,-	-	●,•,-	⬤,●,-	•,-	•,-	-	●,•,-
6	⬤,●,•	•,-	⬤,●,•,-	-	-	⬤	⬤,●,•,-	-	-	●,•,
7	⬤,•,-	-	•,-	-	⬤	⬤,●,•,-	•,-	-	-	●,•

Spi., spinicaudatans; Gas., gastropods; Biv., bivalves; Ost., ostracods; Liao., *Liaoningogriphus*; Hex., *Hexagenites* nymphs; OAI, other aquatic insects; Fis., fishes; Cop., fish coprolites; PF, plant fragments.

in the Yixian Formation, but in the two excavations none of such condensed single bedding planes were excavated as referred above. Still, the high density fossil assemblages provide information on the vertical gradient fluctuations responsible for the different fossil communities.

In modern lakes, there are three major vertical environmental gradients: temperature, light and oxygen. Temperature shows a severe decline in the upper part of the water column. In deeper lakes, temperature at the lake bottom is usually stable and may be as low as 4 °C (Cohen 2003). Thus temperature fluctuations affect mainly shallow-water organisms. Light is the fundamental source of energy and oxygen, and declines with water depth. The supply of oxygen in water comes from exchange with the atmosphere and from photosynthesis, and thus the oxygen content is highest in the upper part of the water column.

The Yixian Formation: a eutrophic shallow lake system

According to Jiang & Sha (2007), the deposits of the Sihetun Lake consist of wave-influenced, suspension-load, hyper-concentrated and concentrated density-flow deposits. The lacustrine succession can be subdivided into beach-near shore, lake floor and fan delta deposits. The two excavations were carried out in the lake floor facies association. There, the dominant facies are finely laminated mudstone and silty mudstone, and normally graded sandstones and tuffs (Jiang & Sha 2007). He *et al.* (1997) studied the alleged 'annual lamination', brownish layers relatively rich in organic material occasionally containing organic filaments and commonly thick wrinkle structures. This facies is usually 2–3 cm thick, occasionally even 20–35 cm. He *et al.* (1997) interpreted these finely laminated, fine-grained sediments, occasionally interrupted by fine-grained sandstones as a shallow, low-energy lake facies of a perennial lake, in which the euphotic zone reached the bottom. The most abundant fossil organisms, e.g. spinicaudatans and *Hexagenites* nymphs, also indicate shallow water depth (Tasch & Zimmerman 1961; Webb 1979; Frank 1988; Wang 1999; Rohn *et al.* 2005). Guo & Wang (2002), carrying out a geological survey of the lacustrine sediments of the Jianshangou Unit of the Yixian Formation in the Sihetun area, suggested that this lake system was about 12–14 km long and 4–5 km wide. Recent studies on hundreds of lakes in Denmark and the Netherlands suggest that small lakes are more likely to be fishless and highly vegetated, even at quite high nutrient concentrations (Van Geest *et al.* 2003; Søndergaard *et al.* 2005). Within the Sihetun Lake at some levels hundreds of fishes occur within an area of less than one square metre. According to Guo *et al.* (2003), fishes were found almost in each layer during their huge excavation in the Sihetun area. In our two much smaller excavations, fish layers were also documented and fishes occasionally occurred also in other layers (Figs 3, 4). Thus, the lake must have been large enough to support fish populations.

The high density of organisms on bedding planes demonstrates that nutrient content was never a limitation for community growth. Besides, stable, nutrient-poor ecosystems are usually characterized by a high diversity and low abundance of individuals, whereas in eutrophic ecosystems species diversity is low, but individuals are abundant (Brenchley & Harper 1998; Hillebrand & Sommer 1999; Kagalou *et al.* 2006; Ansari *et al.* 2010). The lake ecosystem of the Sihetun Lake is characterized by high abundances and low species diversity (e.g. Pan & Zhu 1999; Shen *et al.* 1999; Fürsich *et al.* 2007). McKee & Atkinson (2000) demonstrated that different temperatures did not significantly affect abundances of the mayfly nymphs of *Cloeon dipterum* and only marginally influenced mean nymph body-length. In contrast, nutrient treatment had significant effects on both nymph abundance and size. In other words, the greater numbers of generally larger nymphs occurred in ponds receiving additional nutrients. Thus, the large numbers of large *Hexagenites* nymphs indicate a nutrient-rich environment. The lack of bioturbation (only very rarely tiny horizontal trace fossils have been encountered) and the lack infauna indicate that the oxic–anoxic boundary can hardly have been below the sediment-water interface (Fürsich *et al.* 2007). In most shallow lake systems, the whole water column is oxygenated down to the bottom, and the oxic–anoxic boundary lies within the sediment, except where due to a high primary production or a stagnant water body this boundary is shifted upwards into the water column. Based on the sedimentary evidence (undisturbed lamination), it is herein assumed that the Sihetun Lake was a partially stagnant water body and that oxygen transport took place mainly by molecular diffusion. As long as the oxygen transport is controlled by molecular diffusion, the O_2-H_2S boundary is found at a depth of at least several centimetres below the sediment-water interface in oligotrophic freshwater lakes, whereas in eutrophic lakes, oxygen rarely penetrates more than a few millimetres into the sediment (Brune *et al.* 2000). Frequent nearby volcanic eruptions documented by the abundant tuff layers introduced abundant minerals into the lake waters, which helped to sustain the aquatic ecosystem (Wang 1990, 1999). Thus, we assume that the Sihetun Lake was big, shallow and eutrophic.

Palaeoclimate

Generally, global temperature increased during the Early Cretaceous (Tremolada *et al.* 2006), but did not reach as high values as in the greenhouse stage of the middle Cretaceous (Larson & Erba 1999). The oxygen isotope composition of apatite phosphate ($\delta^{18}O_P$) from various reptile remains indicate a mean air temperature for the period of the Yixian Formation slightly lower than at present at the same latitude (Amiot *et al.* 2011), and most probably distinct seasonal temperature fluctuations existed (Zhou *et al.* 2004; Steuber *et al.* 2005).

The analysis of flora and palynological assemblages from the Yixian Formation suggest a rather warm and humid climate (Li & Liu 1999; Zhu 2000; Ding & Zhang 2004; Zhang *et al.* 2004; Li 2010), perhaps interrupted by seasonal semi-arid periods (Ding *et al.* 2003a; b). Similarly, the analyses of the Jurassic–Cretaceous aquatic insects populations from western Liaoning and northern Hebei demonstrate that the climate was generally rather warm and humid, and also that dry or semi-dry seasons existed (Liu *et al.* 2009a, b)

The size-frequency histograms of *Hexagenites* nymphs, *Liaoningogriphus* and spincaudatans from various bedding planes provide information on the population ecology of these taxa, and the size patterns have been interpreted as representing annual taphocoenoses (Fürsich *et al.* 2007). Modern spinicaudatans prefer shallow rather than deep water (Tasch & Zimmerman 1961; Webb 1979; Frank 1988; Wang 1999; Rohn *et al.* 2005). Mattox & Velardo (1950) tested the reproduction behaviour of spinicaudatans under various water temperatures: at higher temperature, e.g. 28 °C, the population were more active. Wang (1999) also recorded that spinicaudatans are very active when the water is warm, e.g. above 20 °C. The size of the spinicaudatans and the high density indicate that the mass mortality events occurred during a relatively warm season. The repeated densely packed bedding planes suggest repeated mass mortality events, but continuous colonization implies that the palaeoenvironmental fluctuations occurred seasonally or periodically. Seasonal fluctuations of the oxygen level are the most likely factor besides the volcanic activities to govern the dynamics of the aquatic fauna (Fürsich *et al.* 2007). Three possible reasons are proposed for the oxygen-level fluctuations: (1) seasonal precipitation caused fluctuations of the organic input into the lake; (2) seasonal plankton blooms as a result of eutrophication that used up the oxygen in the lake; and (3) the possible existence of microbial mats on the lake bottom. The first two features are strongly correlated to seasonal climate changes. Furthermore, anaerobic conditions favoured fossil preservation, which also enhanced the chances of the vertebrates and plants introduced from the land to become well preserved. The well developed pyrite framboids discovered on plants and vertebrate feathers, led to the 'fossil envelop' model to explain the early fossilization of the Jehol biota (Leng & Yang 2003).

Mortality model

The following mortality model proposes that volcanic activities and anoxic events, the latter related to seasonal climate changes, controlled the dynamics of the lake ecosystem which is documented by the different fossil communities encountered in the investigated sections.

The size-frequency histograms of the spinicaudatans (Fürsich *et al.* 2007) and the high fossil density indicate that the mass mortality events happened during a relative warm season (summer). Thus, the oxic–anoxic boundary was assumed to extend into water column during summer. The populations of spinicaudatans just increased during spring and reached their maximum in summer. This explains why the most abundant spinicaudatans are adults and early juveniles are usually lacking. The density of the death assemblages is controlled by the severity of the anoxic events, producing fossil communities 1 and 4. However, this explanation does not sufficiently explain the distribution pattern of the other fossil groups. Whereas the lake bottom is two-dimensional, the water column is 3-D, and if the temporal scale is added, we deal with at least four dimensions.

Therefore, the niche concept is introduced in the model. Hutchinson (1958) emphasized that organisms have a certain tolerance range for many environmental factors, rather than just for a single factor. Each environmental factor corresponds to an axis in a hypothetical multi-dimensional co-ordinate system. The niche is accordingly an n-dimensional hypervolume within this co-ordinate system. One species occupies a realized niche but there might be an overlap of fundamental niches.

Nymphs of the modern mayflies *Rhithrogena semicolorata* and *Ecdyonurus* sp. gr. *venosus* are quite rare in June and July (Crosa & Buffagni 2002), and the numbers of nymphs of *Cloeon dipterum* also decrease in June (McKee & Atkinson 2000). The reason is because there is a temperature threshold that initiates metamorphosis to the adult stage for mayfly nymphs (Vannote & Sweeney 1980). For example, the peak emergence of the mayfly *Siphlonurus typicus* happens in a very short time; normally 90% emerge within a single day, between June 14 and 15, the remaining ones emerge within less than a week (Kosnicki & Burian 2003). If the emergence of the *Hexagenites* nymphs occurred before the onset of the anoxic event, then it is possible that hardly any *Hexagenites* nymphs accumulated on bedding planes, so that mainly spinicaudatans are present (fossil communities 1 and 4). If the anoxic event had occurred a little earlier, fossil communities 2, 3 and 6 would be recorded on bedding planes.

Fossil community 7 is characterized by the dominance of individuals of *Liaoningogriphus*, which according to its morphological features appears to have been able to swim well (Shen *et al.* 1999). This taxon has very few living relatives, which are only found in caves or underground waters (Gordon 1957, 1960; Pires 1987). One might expect that in most cases they did not suffer from the anoxic event because they could escape to refuge areas due to their swimming ability. This would explain why in 39 of 47 fossil assemblages from single bedding planes *Liaoningogriphus* is rare. In other words, their mass mortality, documented as fossil community 7, records maximum anoxic conditions. This fails, however, to explain the high density fossil assemblage in which *Liaoningogriphus* continuously dominates layer by layer (Figs 3, 4; segments between level H and I, and between J1 and L1 at Erdaogou, and segments between level P and T at Zhanjiagou), without intercalation of any of the other fossil community types. Thus, it seems more likely that *Liaoningogriphus* occupied a niche differing either in time or space from that of the Spinicaudatans and *Hexagenites* nymphs.

Fossil community 5 represents normal mortality with the oxic-anoxic interface close to the sediment-water interface, where fossils are sparse, no taxon dominates, each group occurs either occasionally, or is rare or absent. In contrast, the unfossiliferous layers are interpreted to correspond to frequent and/or severe volcanic activity in some cases. These volcanic activities produced a chemistry of the lake water unsuitable for any aquatic organism (Wang *et al.* 1998, 1999, 2000; Guo & Wang 2002; Guo *et al.* 2003; Zhou *et al.* 2003; Benton *et al.* 2008). Some of these layers, however, may not be completely unfossiliferous but just lack fossils within the excavated area. This would be the case when the fossil density is low, as under normal mortality conditions.

In contrast, fossil community 8 including abundant fishes indicates that anoxia extended almost throughout the whole water column.

Conclusions

In the lacustrine Yixian Formation frequent and/or severe volcanic activity, represented by tuff layers, influenced water quality, which in turn caused the repeated collapse of the aquatic ecosystem. Besides unfossiliferous layers, bedding planes with remains of eight different communities were recognized. They record the community dynamics of a shallow eutrophic lake system. The community dynamics was most probably controlled by climate-related fluctuations of the oxygen level.

In addition, the possible existence of a microbial mat at the bottom of the lake is assumed. Microbial mats commonly define a sharp geochemical boundary. The surface layer of the mat may produce oxygen. Directly below this layer, however, at the level where anaerobic bacteria degrade original mat material, the sediment tends to be strongly reducing (Bauld 1981; Gerdes *et al.* 1985). This would help to understand why the oxic-anoxic interface never extended into the sediment, not even just several centimetres. But more direct evidence is necessary to support the existence of a microbial mat at the bottom of the Sihetun Lake.

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