



## Taphonomy of Early Cretaceous freshwater bivalve concentrations from the Sihetun area, western Liaoning, NE China

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### ABSTRACT

The Early Cretaceous Yixian Formation at Sihetun, Beipiao, western Liaoning, northeastern China, is well-known for yielding diverse and excellently preserved fossils of the Jehol Biota. The lower unit of Yixian Formation, dominated by lacustrine deposits, is rich in concentrations of two freshwater bivalves: *Sphaerium anderssoni* and *Arguniella ventricosa*. These bivalve concentrations can be divided into three types that comprise either paucispecific *A. ventricosa* or *S. anderssoni*, or both bivalves in similar amounts. The lithological, biotic, and taphonomic features of 12 bivalve concentrations are recorded, and the taphonomic signatures (such as shell articulation, size-frequency distribution, and orientation) are analyzed. Autochthonous as opposed to allochthonous bivalve concentrations are discriminated. A very short time-averaging effect is recognized in some concentrations, which was probably caused by seasonal or episodic water-level fluctuations and hypoxia. Three factors operated on the bivalve concentrations before final burial: in-situ reworking, transport, and time-averaging. Although time-averaging of the death assemblages was limited to several years, it is in this way that several generations of the two bivalve species could become preserved together. Reworking of the bivalve concentrations was most likely caused by storm action.

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### 1. Introduction

Shell beds, i.e., dense accumulations of biogenic hard-parts such as bivalve, brachiopod and conchostracan shells, are concentrations formed by physical, chemical or biological processes or by combinations of these (e.g., Fürsich, 1995). In general, fossil concentrations should not be used for ecological studies because they commonly exhibit temporal and spatial mixing. Their sedimentologic and stratigraphic significance has been extensively discussed (e.g., Kidwell, 1986, 1991; Kidwell and Holland, 1991; Fürsich and Oschmann, 1993). The precise analysis of the biofabric and the taphonomic signature of each individual element can be used to reconstruct the palaeoenvironment (e.g., Kidwell et al., 1986; Kidwell, 1991; Fürsich and Oschmann, 1993; Fürsich, 1995; Abbott, 1997). These increasingly refined taphonomic studies make it possible to evaluate the remaining ecological information stored in shell concentrations, including

changes in patterns of dominance and abundance (Li and Droser, 1999; Boyer and Droser, 2003). Hard parts collected from a single bed at one outcrop can be considered to represent a local palaeoecology, if they are within-habitat time-averaged assemblages (Kidwell and Bosence, 1991; Bennington and Bambach, 1996; Etter, 1999).

During the Early Cretaceous, western Liaoning in northeastern China was occupied by lakes of various shapes and sizes. In these lakes, mainly in the Beipiao and Fuxin basins (Fig. 1A, B), the lacustrine Jehol Group yielded the famous fossil-lagerstätten of the Jehol Biota, consisting of various micro- and megaplants, invertebrates and vertebrates, exceptionally well-preserved early birds, feathered dinosaurs, primitive mammals and angiosperms (e.g., Chen and Jin, 1999; Sun et al., 2001; Chang et al., 2003; Ji, 2004). Bivalves are one of the most common fossils in these lake sediments, usually forming shell beds. However, little work has been done so far on the taphonomy and palaeoecology of these shell beds (e.g., Chen, 1999; Sha et al., 2006; Li et al., 2007; Jiang et al., 2007). The present paper provides, for the first time, an analysis of the taphonomic and palaeoecological characteristics of the bivalve shell beds from the Yixian Formation of the Sihetun section in the Beipiao Basin (Fig. 1).

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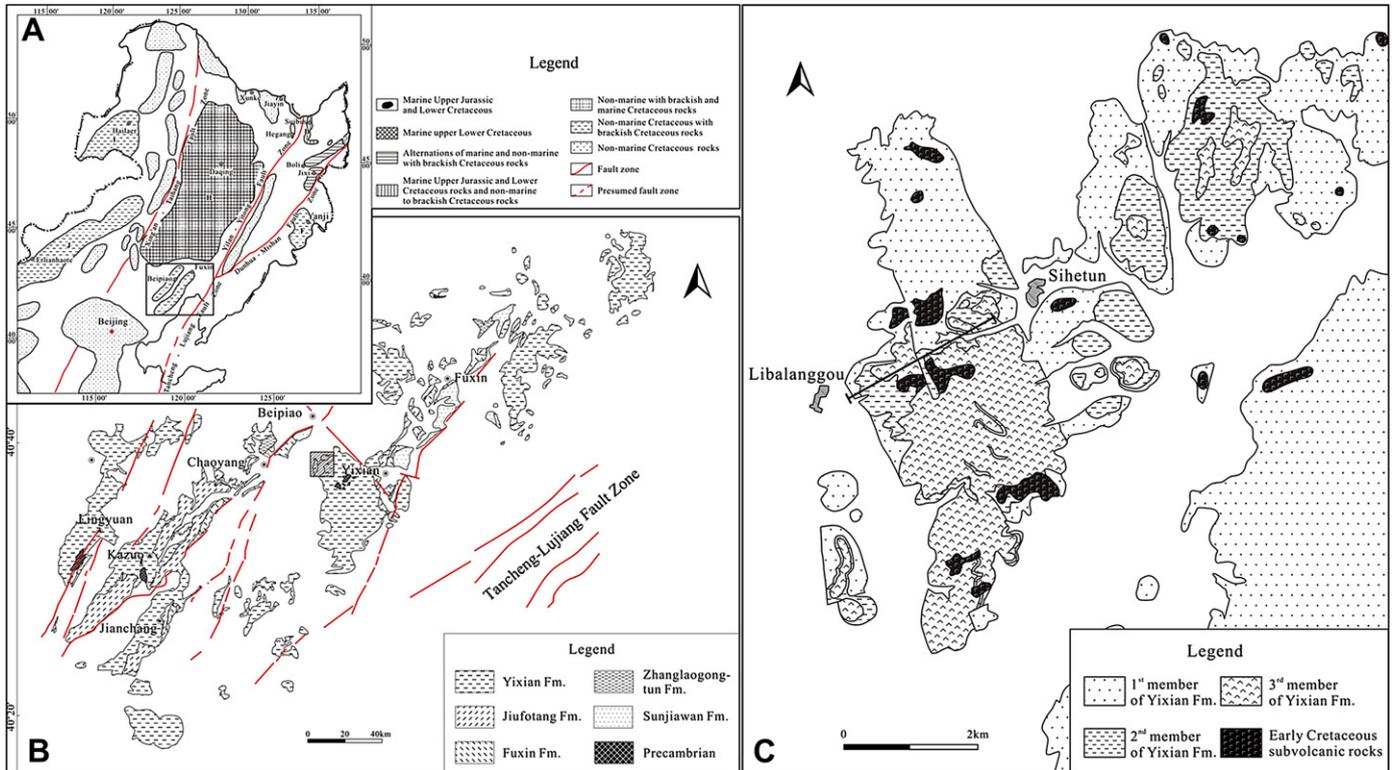


Fig. 1. Location of Beipiao and Fuxin basins (A), study area (C), and distribution of the Cretaceous formations in western Liaoning (B) (after Jiang and Sha, 2007, fig. X).

## 2. Geological setting

During Hauterivian–Albian strike-slip movements, a series of pull-apart basins formed along the NNE-trending Tan–Lu fault zone which branched into the ENE-trending Yanan–Yitong fault zone and NE-trending Dun–Mi fault zone in northeastern China, associated with violent volcanism. The Beipiao and Fuxin basins are situated on the northwestern side of the Tan–Lu fault zone, and south of the Songliao Basin (Fig. 1A; Sha, 2007; Sha et al., 2007), in which the Jehol Group was deposited (Fig. 1A, B).

The Jehol Group consists, in ascending order, of the Yixian, Jiuftotang and Fuxin formations. It rests unconformably on the Tuchengzi Formation and is overlain by the Sunjiawan Formation, mainly ranging from Hauterivian to Aptian in age (Sha, 2007; Sha et al., 2007; Lucas, 2008).

## 3. Material and methods

The fossil materials have been collected from the lower part of the Yixian Formation of the Sihetun–Libalnggou section in the Beipiao Basin within the last few years. It is about 2 km southwest of the village Sihetun (GPS: N 41°35'22.2"; E 120°47'41.6") (Fig. 1C). Twelve shell beds have been investigated, besides YL 28 which is not shown on Fig. 2, since, unlike the other 11, it was not collected successively. Its position is close to YL 27. Fossil specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science (NIGPAS).

Detailed stratigraphic sections of the lower part of the Yixian Formation were logged and multiple samples of each shell bed were collected in the field. Using the methods of investigating shell beds outlined by Kidwell et al. (1986),

Kidwell (1991), and Kidwell and Holland (1991), the features of shell beds were described in both the field and laboratory. In the field, bed thickness, shell orientation, nature of shell preservation, and geometries of shell concentrations were recorded along with the taxonomic composition of each shell bed (Fig. 3A–C). The taphonomic signature of bioclasts and the biofabrics of the shell beds were studied in the laboratory. Specifically, sorting, packing density of the bivalves, plan-view orientation, orientation in cross-section of valves (convex-up and convex-down), the ratio of articulated (closed valves and valves in butterfly position) and disarticulated specimens were calculated whenever available.

There are only two bivalve species, *Sphaerium anderssoni* and *Arguniella ventricosa*, both occurring in high abundance in the concentrations. Usually these two bivalves are preserved in the same bed; hence, their relative abundance was calculated for each assemblage. Besides bivalves, additional organisms preserved in all of the bivalve concentrations were recorded, including gastropods, conchostracans, ostracods, fish fragments and trace fossils.

Compaction is a common feature in these bivalve concentrations, causing various degrees of distortion (Fig. 3D, E). *Sphaerium* valves were hardly affected, exhibiting no or only faint signs of distortion. In contrast, *Arguniella* valves, being much thinner (less than 0.3 mm; Jiang, 2003), were more prone to compaction. So, when shell parameters were measured, the impact of compactional distortion had to be taken into account. In the case of *Sphaerium*, only intact valves lacking compaction were measured (Fig. 3F). As more specimens of *Arguniella* were compacted, those in which the outline remains intact or intact valves lacking compaction were measured (Fig. 3G). In these specimens the length–height ratio remained unchanged. However, the degree of inflation could not be measured.

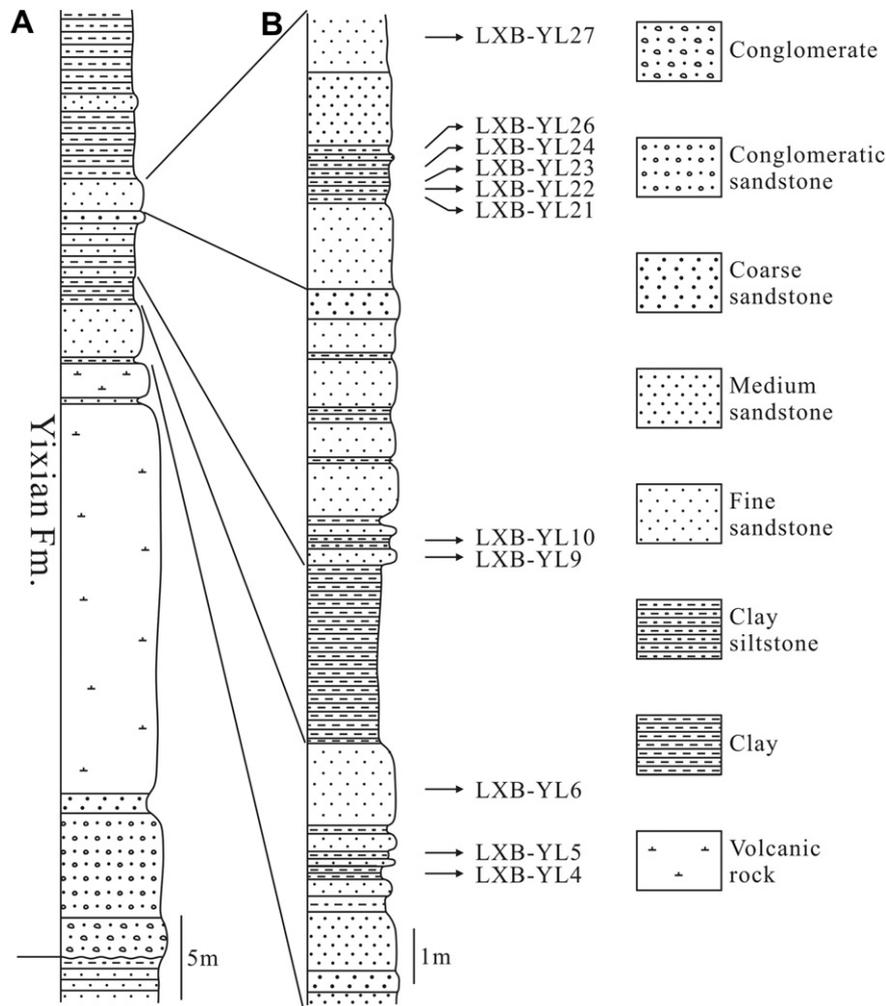


Fig. 2. Composite stratigraphic log of the lower part of Yixian Formation of the Sihetun–Libalangou Section, and the distribution of bivalve concentrations within the section (concentration YL 28 is not included, see text).

## 4. Results

Bivalve concentrations are common in the lower part of Yixian Formation, which represents an environment much closer to the shore than the upper, finely laminated unit (Fig. 2). In the finely laminated rocks, conchostracans and mayfly larvae are very abundant, well-preserved vertebrates (e.g., fishes, birds, dinosaurs) are common, but bivalves are scarce. There are no bivalve concentrations (Chang et al., 2003; Fürsich et al., 2007).

### 4.1. Taphonomic features of the bivalve concentrations

#### 4.1.1. General features

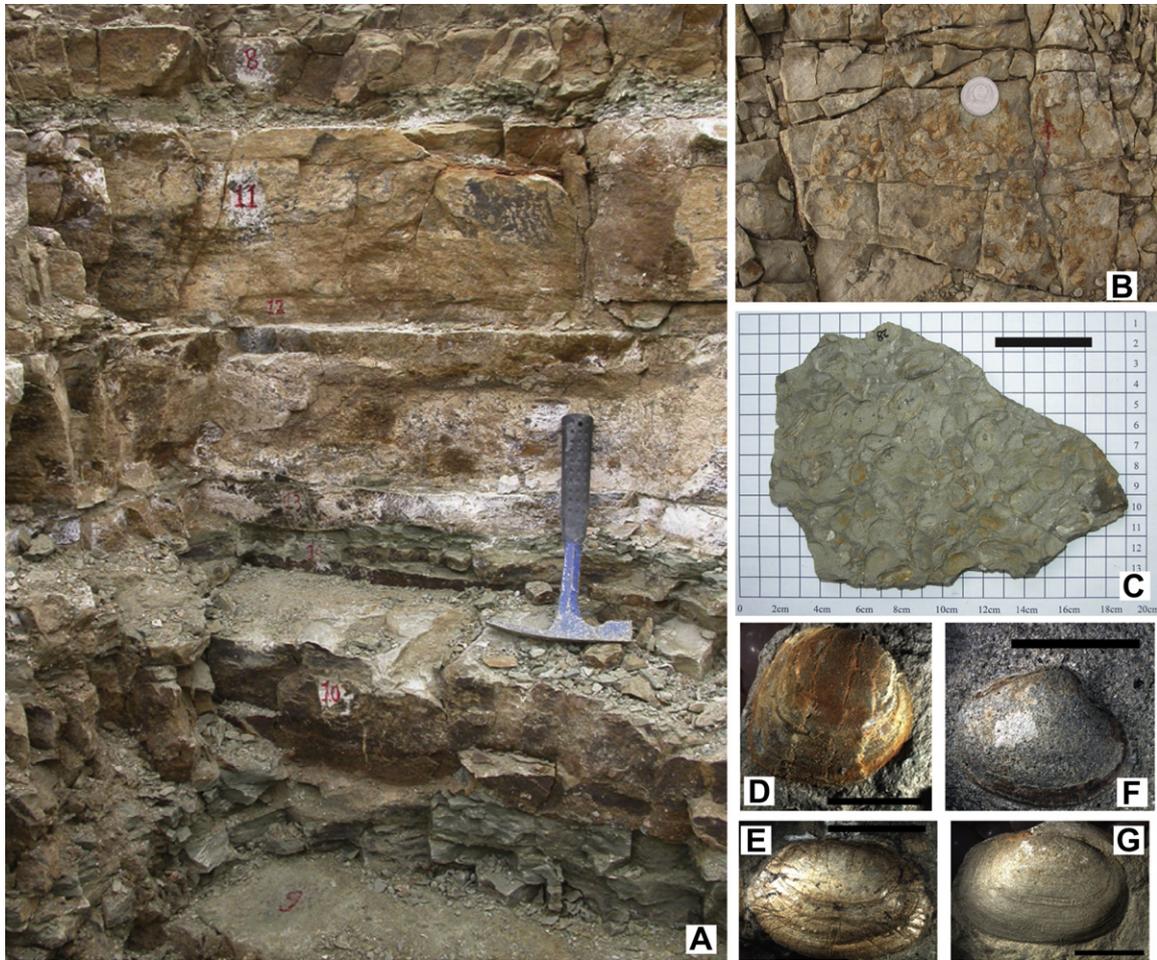
Following the definitions given in Kidwell et al. (1986), shell concentrations with a thickness of no more than one shell layer are referred to as pavements and stringers. Where the thickness exceeds that of one shell, the terms pod, clump, lens, wedge, and bed are applied. For biofabric, the term “densely packed” describes deposits that are bioclast-supported, with finer particles or cement filling the interstices. “Loosely packed” describes deposits that are matrix-supported, but with coarse bioclasts being closely associated. “Dispersed” describes deposits that are

matrix-supported, with sparsely distributed bioclasts (Kidwell and Holland, 1991).

As can be seen in Table 1, the bivalve concentrations are not very thick (mostly around 50 mm, the thickest being no more than 300 mm). Most of the concentrations form beds, but some can be referred to as clumps and lenses. Only concentration YL21 with a thickness of no more than 10 mm forms a pavement. Biofabrics of the concentrations range from dispersed to densely packed, most of them being dispersed or loosely packed, except the densely packed concentrations YL26 and YL28.

#### 4.1.2. Size-frequency distribution pattern of bivalves

Size-frequency distributions are considered to be the most useful criteria for distinguishing between parautochthonous and allochthonous fossil assemblages (e.g., Powell et al., 1989; Kidwell and Bosence, 1991; Tomašových, 2004; Zuschin et al., 2005). The size-frequency histograms of *Sphaerium anderssoni* and *Arguniella ventricosa* demonstrate distribution patterns that remain almost the same, regardless of whether only data of right or left valves or of both are plotted (Fig. 4). However, the two bivalve species differ distinctly in length (around 2–10 mm for *S. anderssoni*, and around 10–20 mm in the case of *A. ventricosa*; Fig. 5). In *A. ventricosa* the length peaks between 15 and 18 mm. In the concentrations YL6, 26



**Fig. 3.** A, excavation site. B, plan-view distribution of fossils in concentration YL 27. C, plan-view distribution of fossils in concentration of YL 28. D, compressed *Sphaerium anderssoni*. E, compressed *Arguniella ventricosa*. F, undistorted *Sphaerium anderssoni*. G, undistorted *Arguniella ventricosa*. Scale bars represent 5 cm in C, 1 cm in D–G.

and 27 (Fig. 5) the size-frequency distribution of *A. ventricosa* is bimodal. The size-frequency distribution of *S. anderssoni* seems even more complex. Concentrations YL21 and 26 have a distinct peak at 7–8 mm, and concentrations YL22, 24 and 27 have three peaks, within a 2–10 mm range. The size-frequency histograms of the 12 shell concentrations (Fig. 5) do not provide any evidence of sorting.

**Table 1**  
Thickness, density, geometries, and plan-view orientation of the 12 bivalve concentrations.

Samples	Thickness (mm)	Geometrics	Orientation	Fabrics
LXB-YL4	32	Beds	No preferred	Loosely packed
LXB-YL5	30	Beds	Preferred	Disperse
LXB-YL6	40	Clumps	Preferred	Loosely packed
LXB-YL9	60	Clumps	No preferred	Disperse
LXB-YL10	40	Clumps	No preferred	Disperse
LXB-YL21	10	Pavements	No preferred	Disperse
LXB-YL22	60	Lens	No preferred	Loosely packed
LXB-YL23	55	Beds	Preferred	Loosely packed
LXB-YL24	22	Beds	No preferred	Disperse
LXB-YL26	100	Lens	No preferred	Densely packed
LXB-YL27	200	Beds	No preferred	Loosely packed
LXB-YL28	30	Beds	Preferred	Densely packed

4.1.3. Articulation ratios and orientation patterns of shells in cross-section

Besides size-frequency distributions, articulation ratios and orientation patterns of shells in cross-section are also very important taphonomic features. The ratios of articulated (closed valves and valves in butterfly position) and disarticulated valves, and the ratios of convex-up and convex-down oriented valves are shown in Fig. 6. Table 2 shows right-valve/left-valve ratios (R/L ratios). In almost all shell concentrations, right valves are slightly more abundant than left valves. Therefore, only right valves were used to calculate the number of disarticulated valves (Fig. 6). In cases where the relative abundance of single valves was less than 50%, the cross-sectional orientation pattern was not recorded. Closed valves predominated in concentrations YL 4, 21 and 28, whereas in YL10, most of the specimens were articulated, preserved either as closed valves or in butterfly position. Single valves are most common in concentrations YL5, 6, 26 and 27. The percentage of single valves exceeds 50% in concentration YL 22, but the ratio of closed valves almost reached 40%. The convex-up/convex-down ratios of concentrations YL5 and 6 (mainly convex-up) differ distinctly from those of concentrations YL22, 26, and 27, in which convex-up and convex-down valves are roughly equally common. Both closed valves and single valves are well represented in concentrations YL23. Concentrations YL 9 and 24 show a slight dominance of

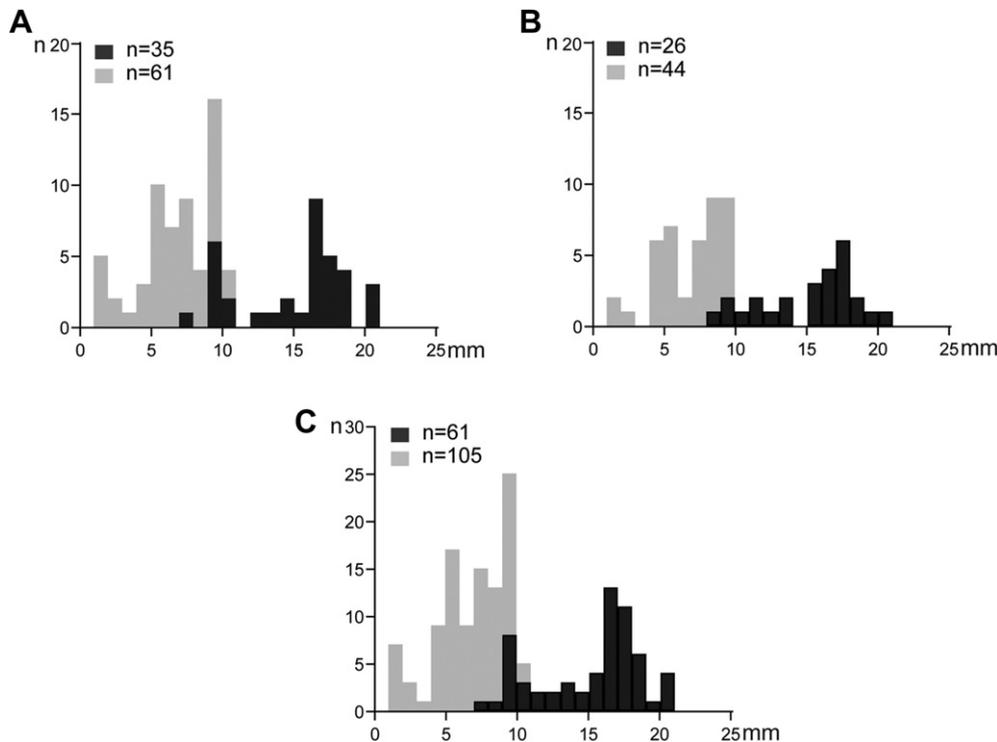


Fig. 4. A, size-frequency distribution of right valves of concentration YL 27. B, size-frequency distribution of left valves of concentration YL 27. C, composite size-frequency distribution of both valves of concentration YL 27.

closed valves with relatively abundant single valves and articulated valves in butterfly position.

#### 4.2. Additional taxa in the bivalve concentrations

The taxonomic composition of each concentration is recorded in Table 3. There is comparatively little variation between concentrations. The most common fossils co-occurring with the bivalves are ostracods and gastropods. Compared to bivalves, gastropods represent only a very small part of the fossil community, except in concentration YL28, in which gastropods are very abundant, with *Probaicalia gerassimovi* being the most common species (Fig. 7A).

Ostracods are quite common in many concentrations, but are generally very poorly preserved (as internal moulds of single valves), making identification difficult (Fig. 7C). Occasionally, fragments of plants, fishes, conchostracans, caddisfly tubes, and burrows were found in some concentrations (Fig. 7B, D and E). Owing to their rarity these fossils make a very limited contribution to the fossil community.

In short, all shell concentrations are dominated by molluscs, chiefly bivalves, apart from YL 28, which consists of gastropods and bivalves (in some parts of the layer the concentration of gastropods higher than bivalves). The relative abundance of the two bivalve species *Arguniella ventricosa* and *Sphaerium anderssoni* varies between concentrations (Table 3).

## 5. Discussion

### 5.1. Taphonomic analysis

#### 5.1.1. Biofabric of the freshwater bivalve concentrations

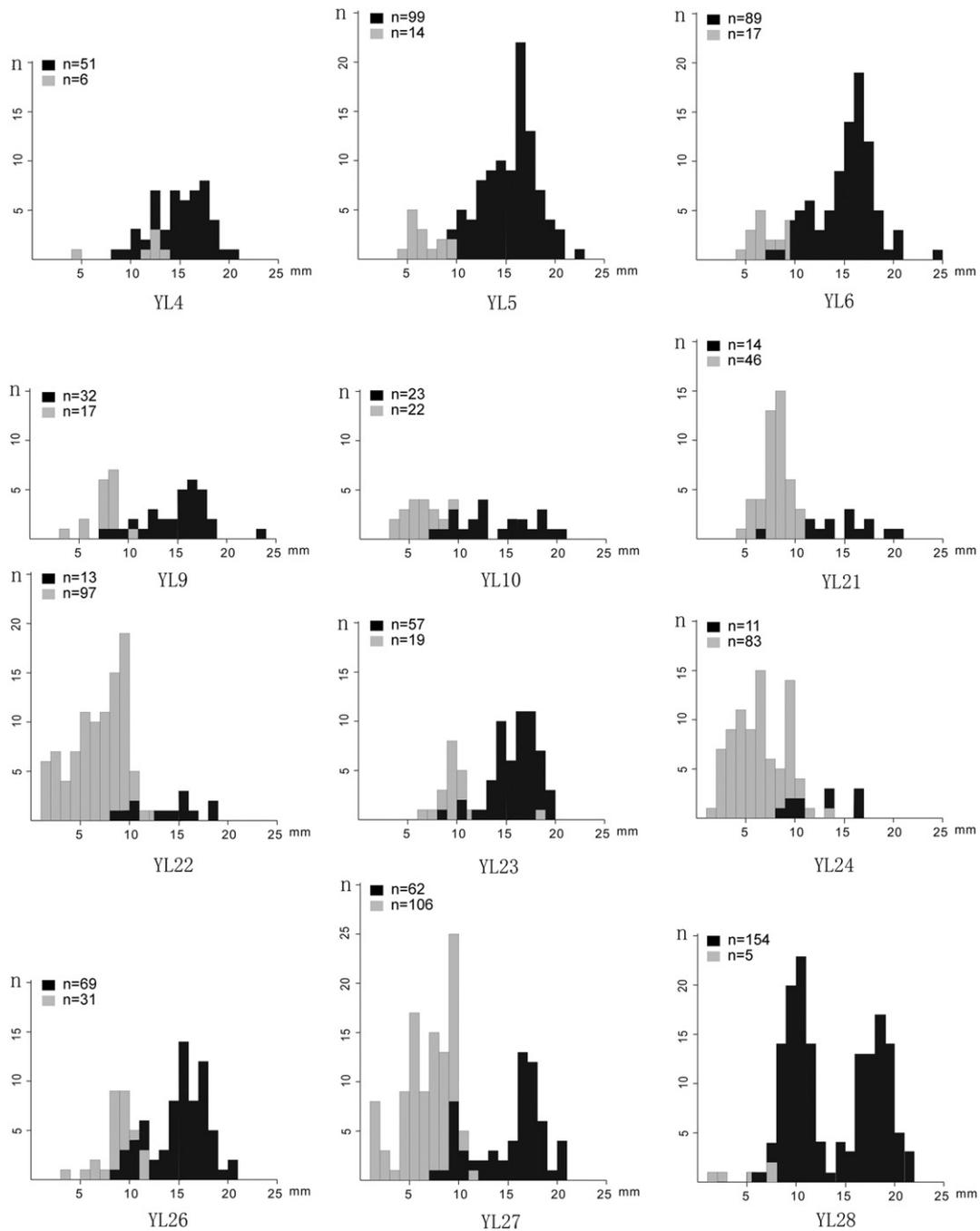
Five types of biofabric of bivalve concentrations are feasible: (1) closed valves in life position; (2) closed valves with the commissure

arranged parallel to bedding; (3) articulated valves either slightly gaping or in butterfly position; (4) randomly oriented single valves; and (5) predominantly convex-up oriented single valves (Fig. 8). In type 1 (Fig. 8), closed valves are oriented with the commissure more or less vertical. Such a position corresponds to the life position of the infaunal bivalves and indicates a lack of reworking. This implies that the bivalves might have been alive when buried. In type 2, closed valves are lying with their commissure parallel to bedding. This suggests that the bivalves were reworked while still alive and died as a result of suffocation due to burial. In type 3, articulated valves, which either slightly gape or are in butterfly position, prevail. The bivalves must have recently died at the time of reworking. The slightly gaping valves suggest that the adductor muscles had not yet decayed, while in valves preserved in butterfly position the adductor muscles had decayed, but the ligament was still intact. In types 4 and 5 single valves dominate. They are either randomly oriented (type 4) or exhibit a preferred convex-up orientation (type 5). In both cases reworking must have taken place after the decay of the ligament either in situ (4) or following transport (5).

#### 5.1.2. Autochthonous versus allochthonous nature of the bivalve concentrations

Concentrations YL4, 21 and 28 are characterized by a dominant bivalve species in which the closed valves are arranged mainly with their commissure parallel to bedding and which occasionally exhibit a preferred plan-view orientation (concentration YL28; Table 1; Figs. 5, 6 and 8). As argued above, the bivalves must have still been alive during transport and died owing to suffocation when buried (see also Fürsich and Oschmann, 1993). Thus, the three concentrations correspond to paraautochthonous assemblages.

Specimens of concentration YL10 with equally abundant *Arguniella ventricosa* and *Sphaerium anderssoni* were mainly

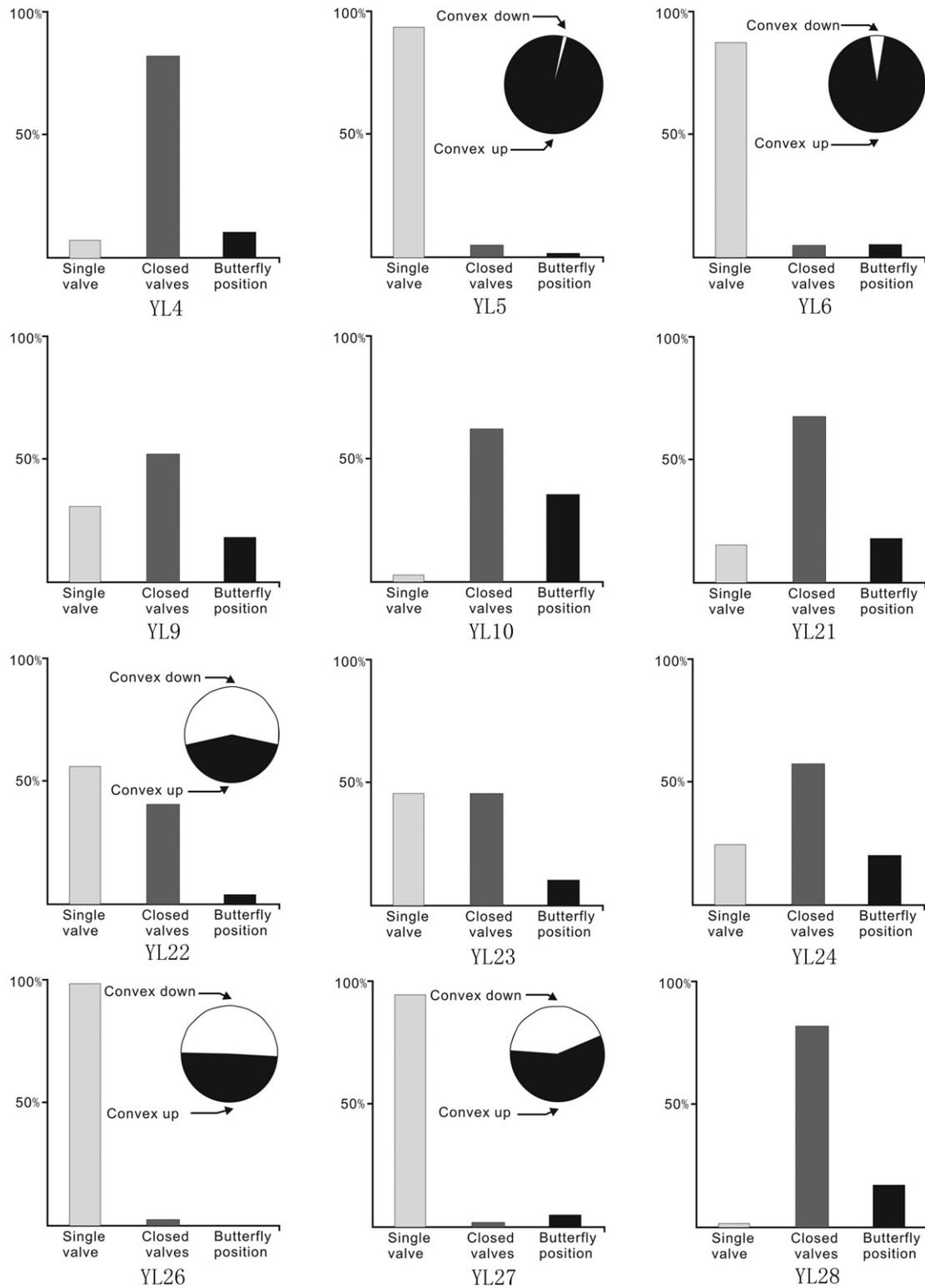


**Fig. 5.** Size-frequency distributions of *Sphaerium anderssoni* and *Arguniella ventricosa* in 12 concentrations (horizontal axis is the length, grey is *Sphaerium anderssoni* and black is *Arguniella ventricosa*).

preserved with closed valves or in butterfly position (Figs. 5 and 6). From field observations, the thickness of this concentration is 40 mm, and the distribution of specimens within the sediment is uneven (Table 1). This concentration is most likely to be biogenic in nature rather than the result of physical controlling factors. Lack of preferred orientation and of sorting also argues against transportation or significant reworking (Fig. 8). Moreover, this concentration exhibits the highest diversity. Therefore, it is here interpreted to be an autochthonous assemblage.

Concentrations YL5, 6, 26 and 27, consist mainly of single valves (Fig. 6). Concentrations YL5 and 6 are dominated by

*A. ventricosa* and show preferred plan-view orientation and a predominance of convex-up oriented valves (Figs. 5 and 6). The bivalves certainly experienced transport before final burial and are therefore clearly allochthonous assemblages (Fig. 8). In contrast, *A. ventricosa* and *S. anderssoni* co-occur in concentrations YL26 and 27 in similar abundances, lack preferred plan-view orientation and have similar proportions of convex-up and convex-down oriented valves (Figs. 5 and 6). In addition, they are five- to six-times thicker than concentrations YL5 and 6 (100 mm and 200 mm as opposed to 30 mm and 40 mm; Table 1). The bivalves most probably experienced in-situ reworking by storm waves rather than transport by currents



**Fig. 6.** Ratios of articulated (closed valves and valves in butterfly position) and disarticulated valves, and ratios of convex-up and convex-down oriented valves in concentrations with predominantly single valves.

before final burial (Fig. 8). Thus, they are most likely to be parautochthonous assemblages.

Concentration YL22, in which disarticulated valves are slightly more abundant than articulated specimens, and the number of

convex-up and convex-down oriented valves is roughly similar (Fig. 6), could also be explained by in-situ reworking, e.g., by weak storm waves. Field observations showed that at the top of the concentration *A. ventricosa* with closed valves dominates, whereas

**Table 2**

Right-/left-valve ratios of concentrations in which single valves dominated.

	Left valves:Right valves
YL4	–
YL5	54/65 = 1.00:1.20
YL6	57/64 = 1.00:1.12
YL9	–
YL10	–
YL21	–
YL22	97/99 = 1.00:1.02
YL23	53/60 = 1.00:1.13
YL24	–
YL26	46/56 = 1.00:1.22
YL27	86/90 = 1.00:1.05
YL28	–

in the rest of the concentration *S. anderssoni* dominates and mainly preserved as single valves. The concentration therefore most likely contains an in-situ death assemblage at the top. Thus, this concentration would be an autochthonous assemblage, although some lateral transport cannot be excluded for the disarticulated valves, which then would be parautochthonous.

In concentration YL9 both *A. ventricosa* and *S. anderssoni* are abundant, lack preferred plan-view orientation, and occur either as closed valves, valves in butterfly position or as single valves; none of these preservational modes dominates (Figs. 5 and 6; Table 1). Based on these features the concentrations can be defined as an autochthonous or parautochthonous assemblage.

Concentration YL24 exhibits similar taphonomic features as YL9 but is dominated by *S. anderssoni* (Figs. 5 and 6). There is no evidence of long-distance transport, and reworking by storm waves probably accounts for the observed features. Again, it

**Table 3**

Taxonomic composition of the studied concentrations.

Samples	Bivalve compositions	<i>Sphaerium/Arguniella</i>	Other organisms
LXB-YL4	<i>S. anderssoni</i> <i>A. ventricosa</i>	6/51 (10.52%:89.47%)	Conchostracans Wood fragments
LXB-YL5	<i>S. anderssoni</i> <i>A. ventricosa</i>	14/99 (12.39%:87.61%)	
LXB-YL6	<i>S. anderssoni</i> <i>A. ventricosa</i>	17/89 (16.04%:83.96%)	Conchostracans
LXB-YL9	<i>S. anderssoni</i> <i>A. ventricosa</i>	17/32 (34.69%:65.31%)	Conchostracans, Fish fragments, Insects tube, Wood fragments
LXB-YL10	<i>S. anderssoni</i> <i>A. ventricosa</i>	22/23 (48.89%:51.11%)	Ostracods, Gastropods, Conchostracans, Fish fragments, Insects tube, Plant fragments
LXB-YL21	<i>S. anderssoni</i> <i>A. ventricosa</i>	46/14 (76.67%:23.33%)	
LXB-YL22	<i>S. anderssoni</i> <i>A. ventricosa</i>	97/13 (88.18%:11.82%)	Ostracods, Gastropods
LXB-YL23	<i>S. anderssoni</i> <i>A. ventricosa</i>	20/57 (25.97%:74.03%)	Ostracods, Gastropods
LXB-YL24	<i>S. anderssoni</i> <i>A. ventricosa</i>	83/11 (88.30%:11.70%)	Ostracods, Gastropods, Conchostracans
LXB-YL26	<i>S. anderssoni</i> <i>A. ventricosa</i>	69/31 (31.00%:69.00%)	Ostracods, Gastropods
LXB-YL27	<i>S. anderssoni</i> <i>A. ventricosa</i>	62/106 (63.10%:36.90%)	Ostracods, Gastropods
LXB-YL28	<i>S. anderssoni</i> <i>A. ventricosa</i>	93/5 (5.10%:94.90%)	Gastropods, Wood fragments

can be defined as an autochthonous or parautochthonous assemblage.

YL23 is the most complex concentration, dominated by *A. ventricosa* but also with common *S. anderssoni*. The preferred plan-view orientation suggests current influence, and the percentage of articulated valves is close to that of disarticulated valves (Figs. 5 and 6). In conclusion, this concentration most likely corresponds to a parautochthonous assemblage.

Hence, among these 12 shell concentrations, YL 5 and 6 correspond to allochthonous assemblages, the other 10 concentrations are autochthonous or parautochthonous assemblages (Table 4).

## 5.2. Bivalve diversity

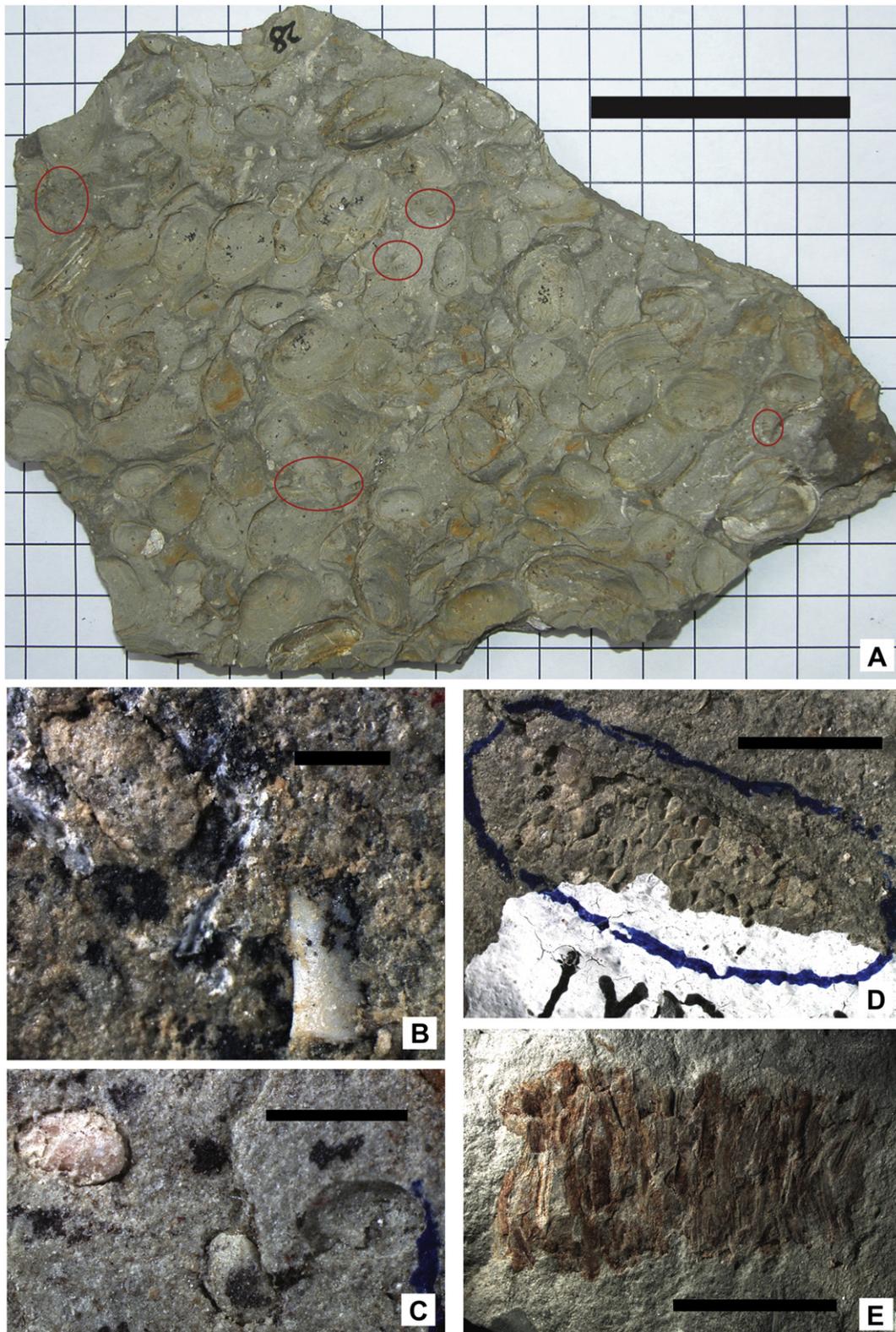
Compared with marine systems, lake systems are temporary, like “islands in a sea of land”. Lacustrine organisms must be well adapted to their fluctuating and unpredictable environments and have strong dispersal ability. In modern lake ecosystems, a number of factors control the species diversity: salinity, pH, temperature, oxygenation, dispersal processes, lake history, stability and size of the lake (Strayer, 1983, 1993). From the exposed sediments, the size of the palaeolake in Beipiao can be estimated to have been about 30 km<sup>2</sup>, and its duration, based on radiometric ages of the volcanic rocks, did not exceed 0.7 myr (Zhu et al., 2007; Sha, 2007). Abundant tuff layers in the sediments indicate that the lake must have been disturbed by volcanic eruptions quite frequently. Still lacking are detailed investigations on salinity, oxygenation, pH, and temperature of the lake (but see Fürsich et al., 2007).

The drainage size proved to be the only useful predictor of modern unionoidean species richness out of six tested factors (i.e., stream size, stream gradient, hydrologic variability, Ca concentrations; physiographic province and presence/absence of tides; Strayer, 1993). Variation in streams, emersion or low oxygen conditions in stagnant pools during dry periods, and bottom scouring and high silt load during floods reduce species richness (Strayer, 1983).

In the concentrations under investigation, there are only two species of bivalves, and when the whole of the Beipiao area is taken into account, only one other bivalve has been recorded (*Mengyinaia mengyinensis*; pers. obs.). This contrasts with the high organism diversity of the Yixian Formation of western Liaoning, from which algae, stoneworts, ostracods, conchostracans, crustaceans, aquatic insects, turtles, amphibians, fishes, gastropods, and bivalves have been recorded. A stressed or repeatedly poisoned lake cannot have supported such a flourishing ecosystem. Furthermore, neither the ecology nor the morphology of the fossils suggests that they lived in a stressed or poisoned lake, because none of these organisms exhibits special adaptations to cope with such environments. One explanation for the low diversity of bivalves is seasonal water-level fluctuation and hypoxia, which also coincides with the ecology of *Sphaerium* (Hornbach et al., 1982; Holopainen and Jonasson, 1983; Burky et al., 1985).

## 5.3. Time-averaging

Information on the ecology of modern *Sphaerium* can be used to infer the ecology of *Sphaerium anderssoni*. Modern *Sphaerium* reaches a peak of density and diversity in fine sandy and silty-clay (McMahon and Bogan, 2001). Almost all of our concentrations were found in such sediment (Fig. 2), which also corroborates the interpretation that most of these bivalve concentrations are more or less parautochthonous to



**Fig. 7.** A, abundant specimens of the gastropod *Probaicalia gerassimovi* in concentration YL 28, indicated by circles. They are small, with a height about 0.3 cm and a width about 0.13 cm (the photograph is the same as Fig. 3C). B, poorly preserved ostracods and fish bones. C, poorly preserved ostracods. D, tube of caddisfly larva composed of sediment grains. E, tube of caddisfly larva composed of plant fragments. Scale bars represent 5 cm in A, 0.1 cm in B, 0.25 cm in C, 0.5 cm in D, 1 cm in E.

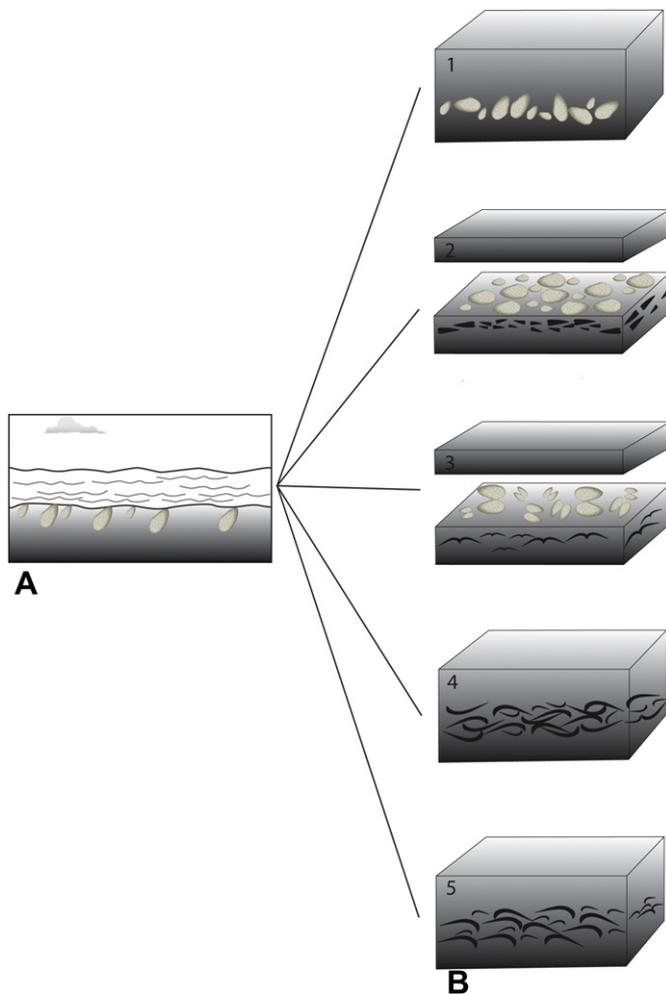


Fig. 8. Five theoretical types of biofabric in bivalve concentrations.

autochthonous assemblages. Almost all modern *Sphaerium* relatives are shallow burrowers, living 1 cm below the sediment–water interface (McCall and Tevesz, 1982). *Arguniella* is an extinct taxon, but its blade-like shape, strong growth lines, relatively thin shell, and equivalved but inequilateral shell with an elongated posterior suggests that it was also a shallow burrower (Stanley, 1970). Since no modern relatives exist, it is hard to say anything else about their life habit. However, shell concentrations YL 4 and 28, dominated by *Arguniella ventricosa* with mainly closed valves and therefore representing parautochthonous assemblages, are found in much coarser substrate than concentration YL 21, dominated by *Sphaerium anderssoni* with also mainly closed valves (Fig. 2). Thus, the habitats of *A. ventricosa* and *S. anderssoni* probably differed only slightly. Besides, *S. anderssoni* and *A. ventricosa* have different shapes: the former is subcircular, the latter elongate-ovate. *Sphaerium anderssoni* is much smaller than *A. ventricosa*, its average length being no more than 10 mm, whereas the average length of *A. ventricosa* is about 20–30 mm.

Two lines of evidence support the interpretation that the bivalve concentrations experienced a very short time-averaging of no more than several years. As argued above, *S. anderssoni* and *A. ventricosa* probably occupied different depth zones but occur together in some concentrations (e.g., concentrations YL9, 10, 21, 26, and 27; Fig. 5). Secondly, three different modes of preservation (closed valves, valves in butterfly position and single valves) representing

Table 4

Autochthonous versus allochthonous nature of the twelve bivalve concentrations.

Bivalve concentrations	Autochthonous versus allochthonous nature
YL4	Parautochthonous Assemblage
YL5	Allochthonous Assemblage
YL6	Allochthonous Assemblage
YL9	Autochthonous or Parautochthonous Assemblage
YL10	Autochthonous Assemblage
YL21	Parautochthonous Assemblage
YL22	Autochthonous or Parautochthonous Assemblage
YL23	Parautochthonous Assemblage
YL24	Autochthonous or Parautochthonous Assemblage
YL26	Parautochthonous Assemblage
YL27	Parautochthonous Assemblage
YL28	Parautochthonous Assemblage

different stages of decay of adductor muscles and ligaments, co-occur in some concentrations (e.g., YL9, 21, 22, and 24, except YL23 with preferred plan-view orientation, indicating transport; Fig. 6).

Apart from transport, the only explanation for similarly large abundances of both bivalves in the same concentration is time-averaging. As has been demonstrated above, there is no evidence of transport in concentrations YL9, 10, 21, 22, 24, 26 and 27 (lack of any preferred plan-view orientation, similar proportions of convex-up and convex-down oriented valves in YL22, 26 and 27; Fig. 6). Any orientation pattern may have been erased by subsequent in-situ reworking, which implies time-averaging. Based on the palaeoecological analysis of the bivalves (Pan, 2009), seasonal or episodic fluctuations in water level might have occurred. Modern lake investigations showed that water levels may vary by an average of 8.2 m between wet and dry seasons (Campbell et al., 2006). Studies on the autoecology of *A. ventricosa* and *S. anderssoni* indicate both preferred to live in predictably fluctuating lacustrine environments, but dominated at different depths (Pan, 2009). Fig. 9 shows how they may occur in roughly equal abundance within the same concentration, owing to short-time fluctuations of the water level. This model does not involve transport, merely a shift of the new population mirroring the change in water level.

However, in order to achieve this, both *A. ventricosa* and *S. anderssoni* must have been able to reproduce quickly. Both are small bivalves, and most modern Pisiidiidae/Sphaeriidae have rapid growth, early maturity, and reduced numbers of reproductive efforts, i.e., 1–3 reproductive efforts within a life span of 1–2 years (Mackie, 1979). Some of the concentrations suffered time-averaging effects, but the duration was very short, no more than several years.

#### 5.4. Formation of the bivalve concentrations

The formation of bivalve concentrations is related to three factors, i.e., production of biogenic hard-parts, their destruction, and accumulation resulting from a low sedimentation rate and/or by physico-chemical processes (e.g., storm events, currents). Based on the analysis presented above, a simple model is proposed that explains formation of the bivalve concentrations in the lacustrine sediments (Fig. 10). In this model, paucispecific concentrations of *Arguniella ventricosa* or *Sphaerium anderssoni* means that the concentrations are composed either of mainly *A. ventricosa* with rare *S. anderssoni* or of *S. anderssoni* with rare *A. ventricosa*, whereas *A. ventricosa* and *S. anderssoni* concentration means that the concentration is composed of similar abundances of both bivalves. As discussed in the palaeoecological analysis (Pan, 2009), *A. yanshanensis* and

*S. anderssoni* flourished at different depths, but their depth ranges overlapped to some extent, leading to the paucispecific *A. ventricosa* and *S. anderssoni* concentrations.

A1 and C1 of Fig. 10 show *A. ventricosa* and *S. anderssoni* concentrations that resulted from a high population density of the bivalves. They therefore correspond to autochthonous biogenic concentrations. None of the concentrations of the Sihetun area exhibits these features, nor have such concentrations been found anywhere else in western Liaoning.

In A2 and C2 of Fig. 10, most of the bivalves were preserved articulated and with a preferred plan-view orientation, when the living community experienced reworking by currents or waves. The point is that reworking took place before death. As a result, parautochthonous assemblages of paucispecific *A. yanshanensis* or *S. anderssoni* were formed (e.g., concentrations YL 4, 21, 24, and 28).

A3 and C3 of Fig. 10 depict the paucispecific *A. ventricosa* and *S. anderssoni* concentrations formed by transport of dead

bivalves. They are interpreted as typical allochthonous storm-flow concentrations (*Arguniella* concentrations YL5 and 6).

B1 and B2 of Fig. 10 show in-situ reworking (e.g., by storms), but no sign of transport, a random plan-view orientation and no preferred taphonomic position, which means that it is chaotic. In some cases the debris is graded upwards. Autochthonous and parautochthonous assemblages of paucispecific *A. ventricosa* and *S. anderssoni* were formed (e.g., concentrations YL 10 and 22).

In Fig. 10, B3 is similar to B1 and B2, but the result of very short time-averaging caused by short-time (seasonal or episodic) fluctuations of the water level. Based on their taphonomic features they correspond to time-averaged parautochthonous storm-wave concentrations. This explains the co-occurrence of similarly large populations of *A. ventricosa* and *S. anderssoni*. Moreover, depending on the relative frequency of storm reworking, the ratio of articulated and disarticulated valves may vary (e.g., concentrations YL 9, 23, 26, and 27).

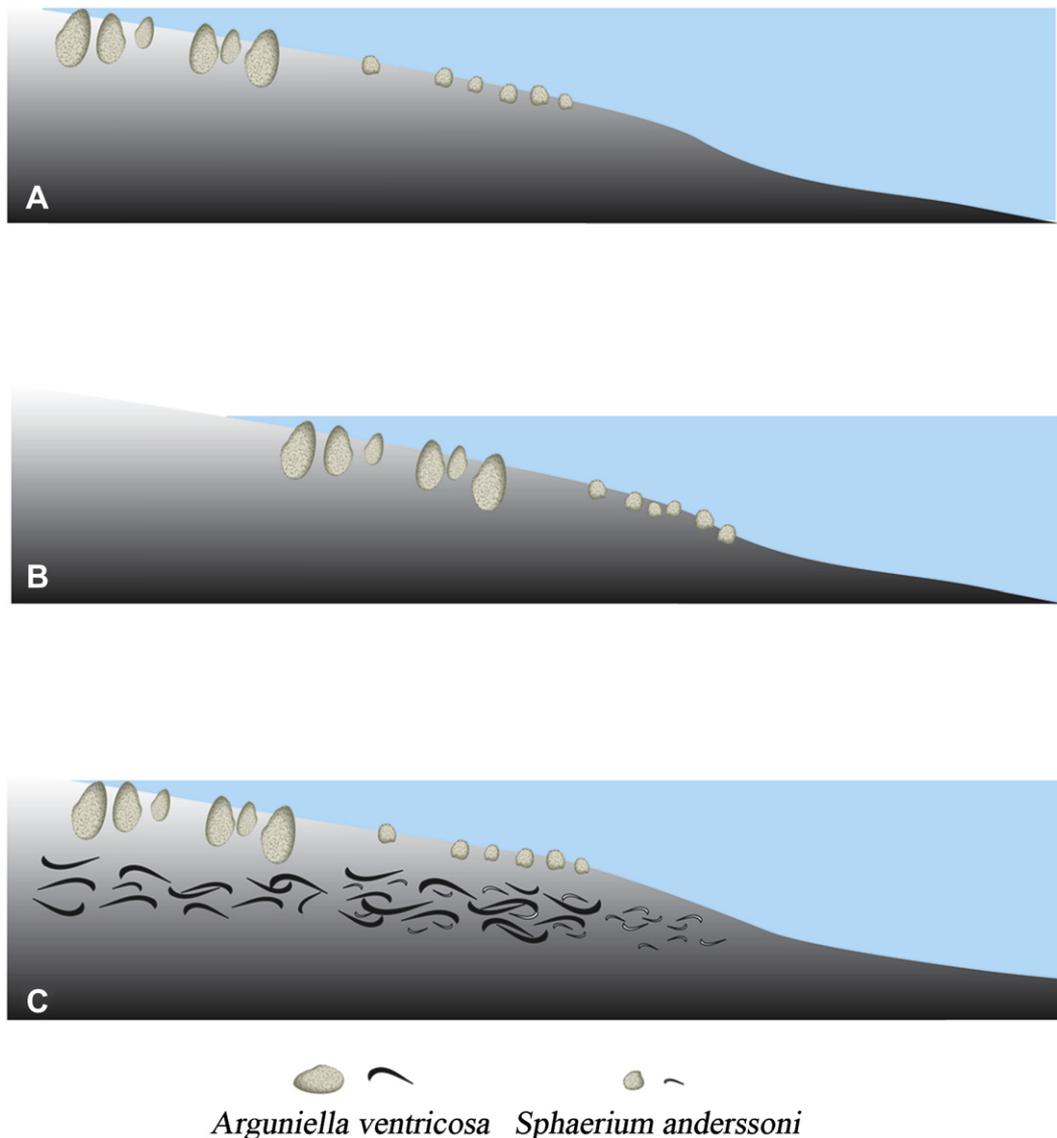


Fig. 9. Model of how *Arguniella ventricosa* and *Sphaerium anderssoni* may occur in roughly equal abundance within the same concentration owing to short-time fluctuations of the water level.

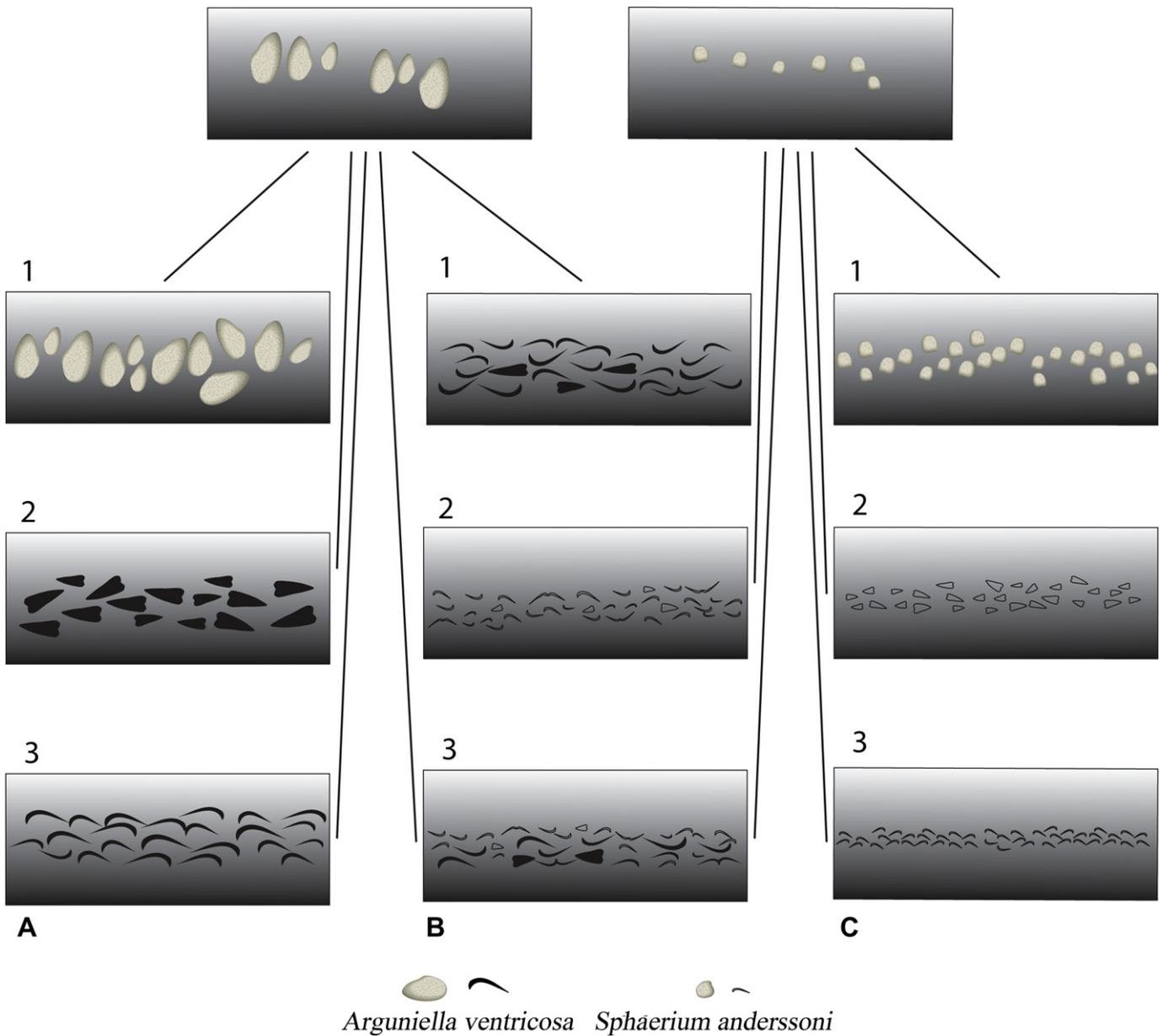


Fig. 10. Model explaining formation of the bivalve concentrations in the lacustrine sediments of the Sihetun area (see text for details).

## 6. Conclusions

Two bivalve species, *Arguniella ventricosa* and *Sphaerium anderssoni*, once lived in the palaeolakes of western Liaoning. Three bivalve concentration types composed of either paucispecific *A. ventricosa* or *S. anderssoni* concentration, or of both bivalves abundant together, occur in the Sihetuan area of western Liaoning.

One autochthonous assemblage, two allochthonous assemblages, six parautochthonous assemblages, and three autochthonous to parautochthonous assemblages were recognized based on a taphonomic analysis of 12 shell beds.

Based on information from modern relatives, *S. anderssoni* lived in environments prone to seasonal or episodic water-level fluctuations and hypoxia. This is supported by autochthonous time-averaged concentrations of the two species, which are explained by episodic fluctuations of the water level. In contrast, seasonal or episodic hypoxia cannot explain time-averaged concentrations comprising similar abundances of *A. ventricosa* and *S. anderssoni* and

even a similar ratio of articulated and disarticulated valves. Consequently, these two bivalve species supposedly flourished in different niches. This is also supported by autochthonous concentrations dominated by just one of the two species (e.g., YL22 and 24).

Three factors operated on the bivalve death assemblages before final burial: in-situ reworking, transport, and time-averaging. Although time-averaging of the death assemblages was very limited, only of the order of several years, in this way the two species could have been preserved together, most of the concentrations representing several generations. The cause of reworking of the bivalve concentrations most likely was storm action.

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