ELSEVIER

Cretaceous Research 27 (2006) 262–278

CRETACEOUS RESEARCH

www.elsevier.com/locate/CretRes

Some Lower Cretaceous nonmarine bivalves from fluvio-lacustrine deposits bearing dinosaur fossils in Mongolia and northeast China

Jingeng Sha [a,*], Li Lin [b], Siwei Chen [a], Masaki Matsukawa [c]

[a] *Nanjing Institute of Geology and Palaeontology, Academia Sinica, Chi-Ming-Ssu, Nanjing 210008, China*
[b] *Museum, Chengdu University of Technology, 1 Erxianqiao, Dongsanlu, Chengdu, 610059 Chengdu, China*
[c] *Department of Environmental Sciences, Tokyo Gakugei University, Koganei, Tokyo 184-8501, Japan*

Received 22 February 2004; accepted in revised form 28 November 2005
Available online 10 February 2006

Abstract

One species of *Unio* and three species of *Sphaerium*, the typical nonmarine bivalves in East Asia, from the Lower Cretaceous fluvio-lacustrine deposits of Choyr Basin of southeastern Mongolia and the Beipiao area of Jehol in northeastern China, are described. The assemblage of *Unio longus* (Zhu), *Sphaerium chientaoense* Suzuki, and *S. coreanicum* (Kobayashi and Suzuki) from the Khuren Dukh Formation of the Choyr Basin of southeastern Mongolia can be compared with the *Nakamuranaia-Margaritifera* (*Menyinaia*)-*Neomiodonoides* assemblage in China. The four nonmarine bivalve species described herein are found in numerous formations in East Asia suggesting Valanginian to Albian age.

Keywords: Lower Cretaceous; Nonmarine bivalves; Mongolia; Northeastern China

1. Introduction

Cretaceous nonmarine bivalves are widely distributed in Asia (e.g., Gu et al., 1976; Martinson, 1982) and frequently associated with dinosaurs. Thus, they have often been employed as geological correlation tools for nonmarine strata bearing dinosaurs. However, Matsukawa et al. (2006) pointed out that freshwater molluscan species had many opportunities to change their local habitats on the Cretaceous Asian continent. Likewise, some nonmarine molluscan species from the Cretaceous of Japan had their distribution controlled by the environment. This indicates that Cretaceous nonmarine bivalves cannot always be used as definitive geological correlation tools. Therefore, we must evaluate their occurrences of nonmarine mollusks either controlled by the age of the fauna or the ecological range of species in ancient ecosystem, or both.

Two Lower Cretaceous basins, in Beipiao of the Jehol area of northeast China and the Choyr Basin of southeastern Mongolia, are composed of representative fluvio-lacustrine deposits bearing dinosaurs associated with nonmarine bivalves (Fig. 1, Table 1). In particular, the molluscan assemblage from the Jehol area is classified as the *Nakamuranaia-Margaritifera* (*Mengyinaia*)-*Neomiodonoides* Assemblage, and is correlated to the Berriasian-Barremian as this assemblage is one of the five Cretaceous nonmarine bivalve assemblages recognized in China and is employed as geological correlation tools (Ma, 1994). However, the ecological aspects of these assemblages have not been discussed, although their geographical distributions are readily recognizable.

Based on the geographical distribution of these assemblages in China, the *Nakamuranaia-Margaritifera* (*Mengyinaia*)-*Neomiodonoides* Assemblage, as well as the *Pseudohyria-Sainshandia-Limnocyrena* Assemblage, would be inferred to extend to southern Mongolia. However, the molluscan assemblage from the Lower Cretaceous Choyr Basin of Mongolia has not been studied previously. We thus describe the species comprising this assemblage in the Choyr Basin and discuss

* Corresponding author.
E-mail address: jgsha@nigpas.ac.cn (J. Sha).

0195-6671/$ - see front matter
doi:10.1016/j.cretres.2005.11.002

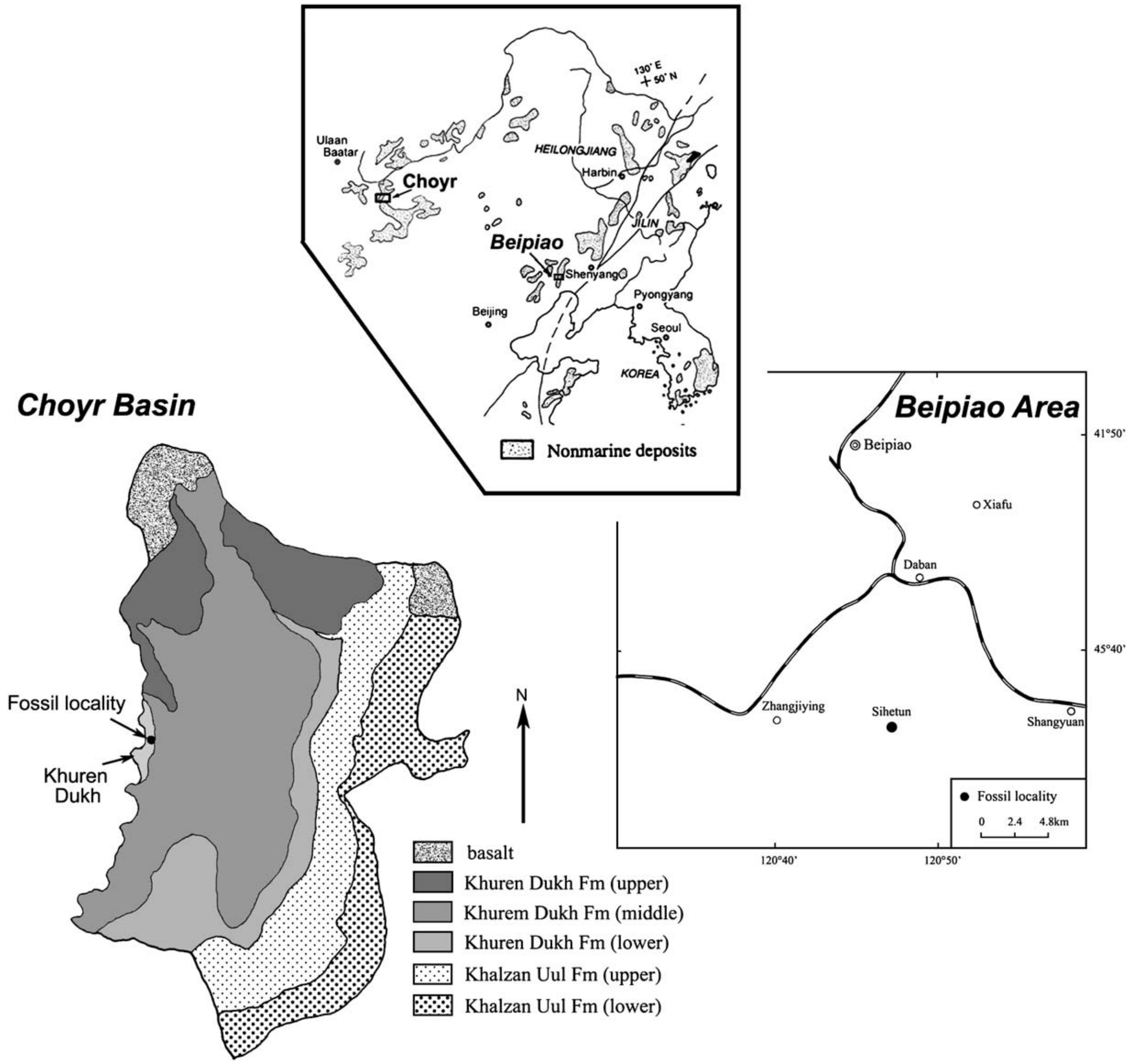

Fig. 1. Map showing nonmarine upper Lower Cretaceous bivalve locality of Choyr Basin, southeastern Mongolia, and Lower Cretaceous bivalve locality of Beipiao area, western Liaoning Province, China.

characteristics of the assemblage in this paper. We then describe the morphologic variation of *Sphaerium* (*S.*) *anderssoni* (Grabau), one of the principal components of the *Nakamuranaia*-*Margaritifera* (*Mengyinaia*)-*Neomiodonoides* Assemblage in the Jehol area, because the species shows variable morphology.

All of illustrated bivalve fossils are deposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGPAS), Nanjing, China.

2. Stratigraphy

2.1. Choyr Basin, southeastern Mongolia

The Lower Cretaceous strata of the Choyr Basin were previously divided into three formations, in ascending stratigraphic order, the Sharilin, Tsagaantsav, and Shinhehudag formations (Matsukawa et al., 1997). Ito et al. (2006) showed that these formations are lateral equivalents of one another that differ only in lithology. In addition, the formation names are misleading in regard to the age of the rocks. Consequently, Ito et al. (2006) proposed the Khalzan Uul and Khuren Dukh formations to replace the earlier names.

The Khalzan Uul Formation is distributed along the eastern margin of the basin. The formation is divided into two members, lower and upper. The lower member is composed principally of poorly sorted and angular conglomerate with sandstone deposits. It is more than 30 m thick and unconformably overlies the granite and metamorphic rocks (e.g., gneiss) constituting the basement of Choyr Basin. The lower member represents alluvial fan deposits (Ito et al., 2006). The upper member consists of well-sorted, fine-grained sandstone beds with terrestrial plant fossils and is more than 17 m thick. Sandy braided and meandering river environments are inferred for the member by Ito et al. (2006).

Table 1
Litho- and biofacies of the Lower Cretaceous in the northern part of the Choyr Basin, southeastern Mongolia (modified from Matsukawa et al., 1997, and Ito et al., 2006)

	Stratigraphic units		Lithology	Sedimentary structures	Main fossils	Environments
	Khuren Dukh Fm	upper mbr	sandstone with mudstone and pebbles	cross stratification, channel structure	dinosaur tracks, bivalves, gastropods	Meandering river and delta
		middle mbr	mudstone	parallel lamination	turtles, insects, ostracodes, plants	Ephemeral lake, flood plain, and swamp
		lower mbr	sandstone with coal seams	cross stratification	dinosaurs, fishes, turtles, crocodiles, plants	Sandy alluvial fan and sandy braided meandering river
	Khalzan Uul Fm	upper mbr	fine-grained sandstone	cross stratification	plants	Sandy delta and meandering river
		lower mbr	conglomerate with sandstone	clast-supported, imbricated gravels		Gravity alluvial fan
Precambrian	Basement rocks (granites, gneiss)					

Solid line, conformity; wavy line, unconformity.

The Khuren Dukh Formation unconformably overlies basement granitic rocks along the western flank of the basin. This formation is informally subdivided into lower, middle, and upper members. The lower member is composed of white quartz-feldspathic sandstone with coal seams. It is 40 m in thickness and yields terrestrial plants, dinosaurs, fish, turtles, and crocodiles. The middle member consists of monotonous mudstone and yields turtles, insects, conchostracans, ostracodes, and terrestrial plant fossils. This member is 5 m in thickness. The upper member, containing abundant bivalves and gastropods, consists of white and yellow quartz-feldspathic sandstone with light and pale grey, thin mudstone and pebble layers. Ito et al. (2006) infer that the lower member reflects sandy alluvial fan and sandy meandering river environments, the middle member represents an ephemeral lake, flood plain and swamp, and the upper member indicates a meandering river and delta. The formation is unconformably overlain by lava flows or terrestrial sediments.

The presence of *Asteropollis asteroides* and pollen of the genus *Tricolpites* suggests that the Khuren Dukh Formation is of Albian age (Hicks et al., 1999; Nichols et al., 2002, 2006; Ichinnorov, 2003). This determination is based on the occurrence of the former species in well-dated mid- to late Albian rocks in western North America (Hedlund and Norris, 1968; Singh, 1975; Wingate, 1980; Nichols and Jacobson, 1982). The co-occurrence of the angiosperm genera confirms the age of the Khuren Dukh Formation as mid- to late Albian.

2.2. Jehol area, northeastern China

The Lower Cretaceous strata of the Jehol area are widely distributed in western Liaoning, northeastern China. They are named as the Jehol Group (Grabau, 1923; Gu, 1962) and are divided into three formations, in ascending order, the Yixian, Jiufotang, and Fuxin formations, although other stratigraphic classifications have been proposed (e.g., Chen et al., 2006). Recently, the Yixian Formation in the Beipiao area has become famous for yielding fossils of feathered dinosaurs such as *Sinosauropteryx*, *Caudipteryx*, and *Protarcheopteryx*, in association with a rich lacustrine fauna and flora including fishes, amphibians, non-dinosaurian reptiles, birds, mammals, many invertebrates including mollusks, and plant species (Chen and Jin, 1999; Chang et al, 2001). Older reports claimed that the Yixian Formation contained a middle ‘‘Jehol’’ fauna that may be as old as Tithonian in age (Chen, 1999). However, more recent interpretations of formation suggest younger dates (136–120 Ma), indicating a late Neocomian (Hauterivian-Aptian) age (Swisher et al., 1999; Zhu et al., 2002).

3. Taphonomic observations

3.1. Choyr Basin, southeastern Mongolia

Unionid bivalve fossils occur in the coarse-grained, quartz-feldspathic sandstone that has been suggested to be a deposit of a meandering river system (Fig. 2) (Ito et al., 2006). They are abundant in quantity and variable in outline (Figs. 3–6). Most specimens are complete or almost complete (e.g., Figs. 3–5). Many are articulated (e.g., Figs. 4A–C, E, 5C); some are represented by single (left or right) valves (e.g., Figs. 4D, F, G, 5A, B, D, E), but fragments are uncommon. These specimens are distributed randomly in sandstone beds and are almost never secondarily deformed (see Fig. 3). Such preservation clearly demonstrates that the unionid bivalves are autochthonous or para-autochthonous, and are randomly oriented in the taphocoenosis.

Bivalves with an elongate elliptical shape and a thin shell but absence of distinct commarginal growth lines are typically rapid burrowers in soft silt-rich sediments. The preservation described above suggests that the dead individuals of unionid bivalves were buried in or near their living place rather than being washed into interchannel areas by floods (Matsukawa et al., 1997). It is likely that the nonmarine bivalves were suddenly buried by sediments that were deposited so quickly that the slow moving and possibly deep-burrowing unionid bivalves could not escape from the rapid and thick accumulations.

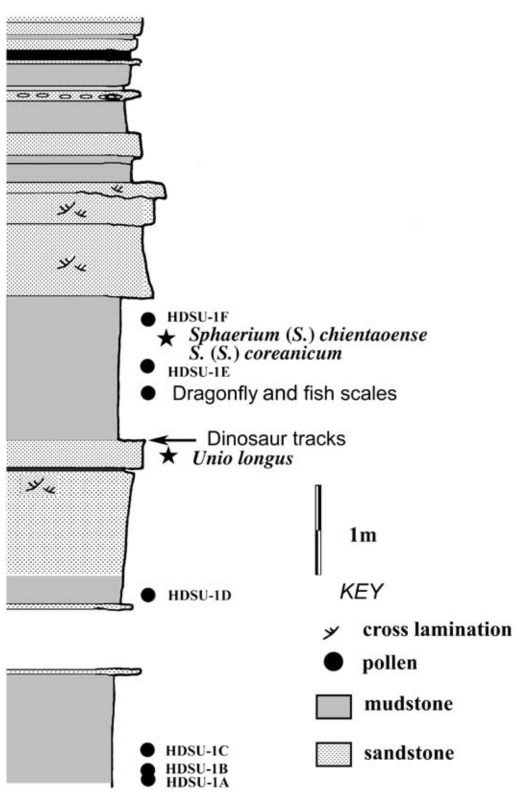

Fig. 2. Horizons of nonmarine bivalve, dragonfly, fish scale, and pollen fossils from the upper member of the Khuren Dukh Formation of Choyr Basin, southeastern Mongolia. HDSU-1A to -1F show pollen horizons.

Sphaerium fossils are also known from the basin from the pale grey mudstone deposited in the flood plain. They were probably carried by storms because the bivalves occur in flood plain mudstone.

3.2. Jehol area, northeastern China

Sphaerium anderssoni comes from tuffaceous sandstone in this basin. Fossil deposits form layered accumulations (Figs. 7, 8), and individuals are preserved mostly as internal and external moulds of single or articulated valves, with occasional whole shells. All specimens are single except for seven articulated valves among more than 400 specimens. Almost all the specimens are complete and fragments are rare. Such preservation implies that *Sphaerium anderssoni* in the basin is para-autochthonous, accumulating near the original living place. The bivalves inhabited the shallow, soft bottom sediments near the lacustrine.

4. Systematic Palaeontology

Class: Bivalvia Linné, 1758
Subclass: Palaeoheterodonta Newell, 1965
Order: Unionoida Stoliczka, 1871
Superfamily: Unionacea Fleming, 1828
Family: Unionidae Fleming, 1828
Genus *Unio* Philipsson, 1788 emended Sha and Fürsich, 1993

Unio longus (Zhu)
Figs. 4, 5A–E

1976 *Pseudelliptio longus* Zhu, p. 23, pl. 1, figs. 5, 7–11 (non fig. 6).
1976 *Protelliptio mongolensis* Martinson; Martinson and Shuvalov, p. 41, pl. 4, figs. 1–2.
1982 *Margaritanopsis elongata* Martinson, p. 56, pl. 13, figs. 5–6.
1982 *Margaritanopsis sainshandensis* Martinson, p. 56, pl. 13, figs. 4–5.
1982 *Oxynaia sainshandica* Barsbold; Martinson, p. 58, pl. 13, fig. 3.
1982 *Rectidens mongolensis* Martinson, p. 58, pl. 14, fig. 3.
1982 *Cuneopsis orientalis* Barsbold; Martinson, p. 60, pl. 14, fig. 4.
1982 *Cuneopsis lanceolata* Martinson, p. 61, pl. 14, figs. 7–8.
1982 *Lanceolaria angustata* Martinson; Martinson, p. 61, pl. 14, figs. 1–2.
1982 *Protelliptio mongolensis* Martinson; Martinson, p. 63, pl. 15, figs. 10–11.
1982 *Protelliptio notabilis* Martinson, Barsbold, and Tolstikowa; Martinson, p. 64, pl. 15, fig. 12.
1991 *Pseudelliptio longa* Zhu; Ma, p. 710, pl. 1, figs. 13, 15–18.
1993 *Unio heilongjiangensis* Sha and Fürsich, p. 157, pl. 1, figs. 1–10; pl. 2, figs. 3, 5–10; pl. 3, figs. 2–3, 5–6, 8–10; text-figs. 11E, 14–15.

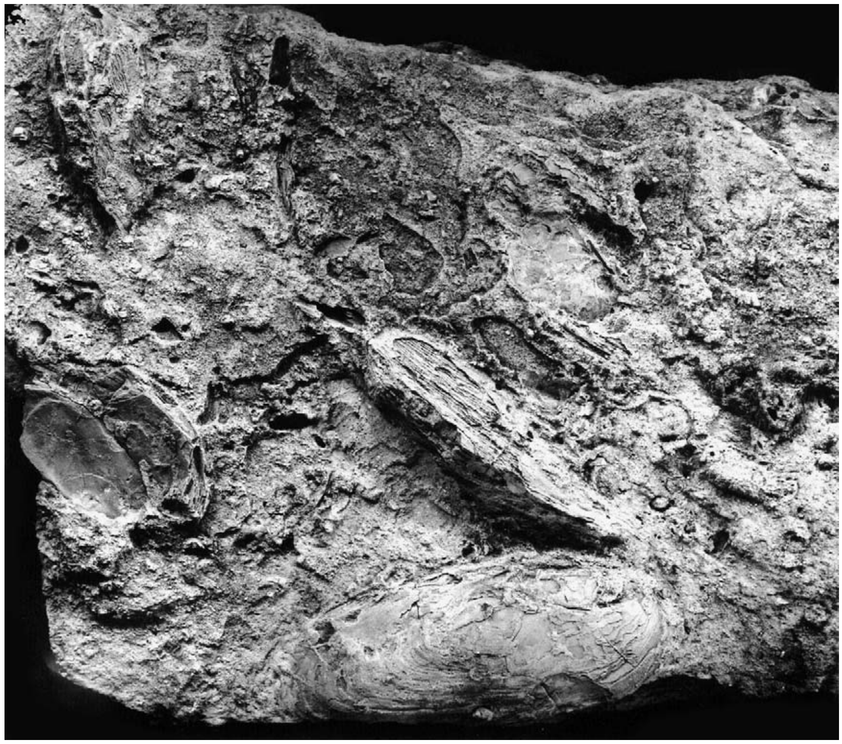

Fig. 3. Randomly orientated *Unio longus* in the upper member of Khuren Dukh Formation of Choyr Basin, southeastern Mongolia.

Holotype. The holotype by original description is the specimen illustrated by Zhu (1976, pl. 1, fig. 7).

Material. Twenty five adult specimens, 13 of them are articulated and most having more or less mineralized shells, but all the hinges are incomplete. Twelve adult specimens (NIGPAS 137057–137064, 137066–137069) are shown in Figs. 4, 5.

Description. Shells fairly large, up to 106 mm in length. Elongated posteriorly, longer than high, height/length ratio less than 1/2. Equivalve but inequilateral. Generally transversely elliptical in outline. Anterior margin rounded, posterior margin rounded to subtruncated. Dorsal margin nearly straight to slightly arcuate, ventral margin broadly convex to slightly concave. Posterodorsal corner broadly rounded and posteroventral corner broadly rounded to narrowly rounded, moderately and evenly inflated. Umbo large, but very low, without distinct boundary between umbo and other part of shell. Beak poorly preserved, placed at about one-third the shell length from the anterior extremity, projecting slightly above the hinge line. Shell thin to at most moderately thick (3 mm at maximum). Posterior slope distinct, posterior umbonal ridge subrounded to subcarinate, running from the umbo to the posteroventral margin. Ligament external and opisthodetic, very long and heavy. Shell surface smooth, except the faint commarginal growth lines and occasional undulating ridges consisting of numerous growth lines. Muscle scars and hinge teeth very poorly preserved, but on the basis of all specimens, two anterior pseudocadinals and two posterior lamellar teeth can be recognized. The pseudocardinals short, but lamellar teeth parallel to the dorsal margin very long.

On the basis of the variation of inflation, convexity of dorsal and ventral margins and the appearance of posterior margins, the shape of the species can be subdivided into five types (Fig. 6): (1) transversely elliptical shape, with subparallel and substraight dorsal and ventral margins; (2) typical transversely elliptical shape, with gently convex dorsal and ventral margins; (3) transversely kidney-shaped shape, with broad curve near the central ventral margin; (4) lance-like shape, with narrowly rounded posterior margin; (5) lance-like shape, with subtruncated posterodorsal margin and curve near the posteroventral margin.

Measurements. See Table 2.

Biometry. The frequency distribution of the characters examined (i.e., length/height) is given in Fig. 9. This clearly shows that the ratio of length/height has an approximately normal distribution although values are skewed to the left. A biometric characters of shell length/height is given in Table 3. Chi-square values (χ^2) generally indicate no significant deviation from the normal distribution (at the 5% confidence level). The null hypothesis, therefore, cannot be rejected, and the specimens examined are judged to represent individuals from a single population. Fig. 9 is a double logarithmic scatter diagram showing the relation between shell length and shell height for all specimens of *Unio longus*. The correlation coefficient (r) is significant at the 5% level (Fig. 10).

Remarks. Specimens of *Unio longus* show various kinds of shapes. Shell outlines include transversely elliptical, lance-like and kidney-shaped; dorsal margins are slightly convex

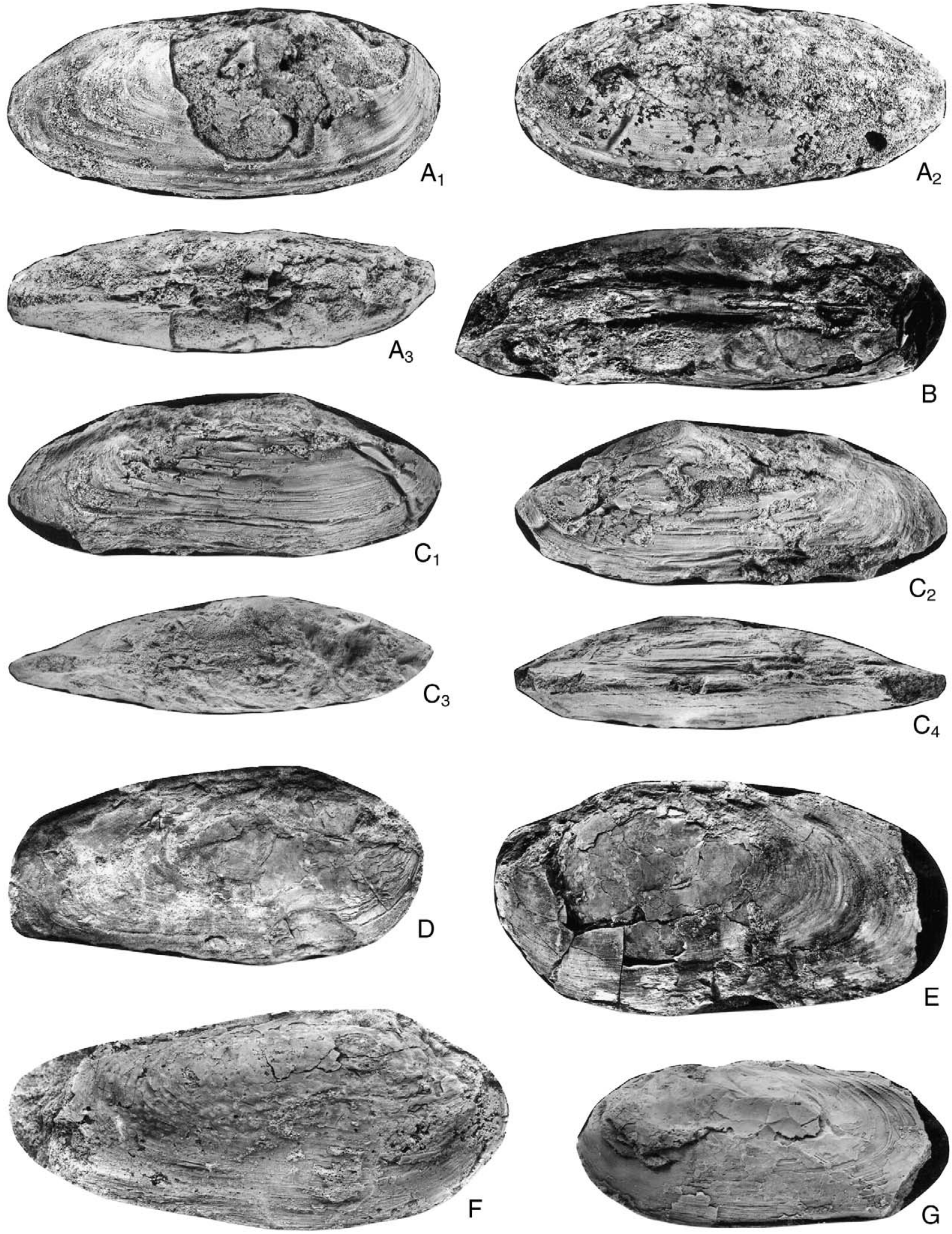

Fig. 4. *Unio longus* (Zhu). A_1, right valve, NIGPAS 137057. A_2, left valve, NIGPAS 137057. A_3, dorsal view of articulated valves, NIGPAS 137057. B, dorsal view of articulated valves, NIGPAS 137066. C_1, right valve, NIGPAS 137062. C_2, left valve, NIGPAS 137062. C_3, dorsal view of articulated valves, NIGPAS 137062. C_4, ventral view of articulated valves, NIGPAS 137062. D, right valve, NIGPAS 137068. E, left valve, NIGPAS 137063. F, right valve, NIGPAS 137069. G, left valve, NIGPAS 137059. All ×1.

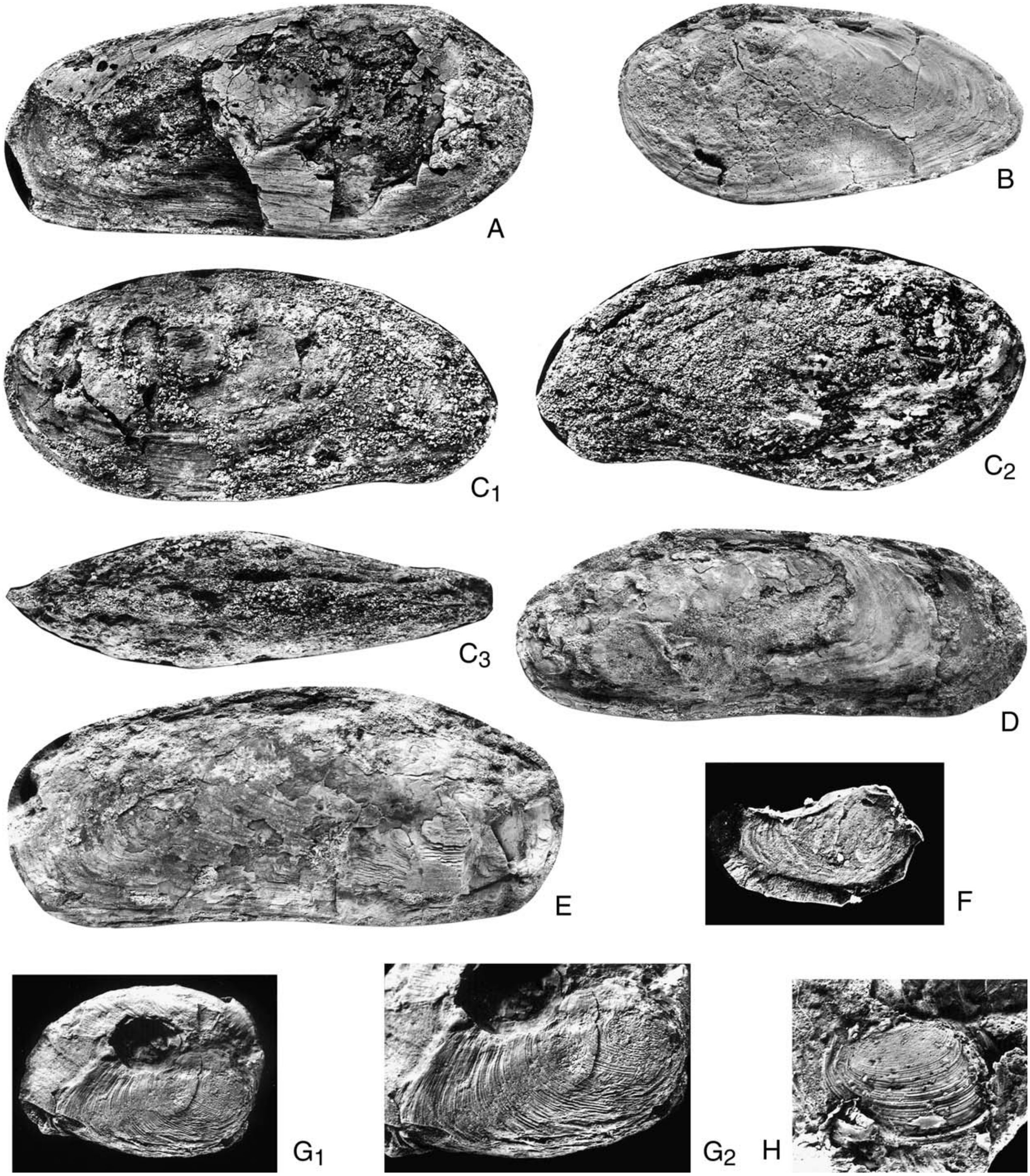

Fig. 5. A–E, *Unio longus* (Zhu); F, G, *Sphaerium coreanicum* (Kobayashi and Suzuki); H, *Sphaerium chientaoense* Suzuki. A, right valve, NIGPAS 137058. B, right valve, NIGPAS 137060. C_1, left valve, NIGPAS 137064. C_2, right valve, NIGPAS 137064. C_3, dorsal view of jointed valves, NIGPAS 137064. D, left valve, NIGPAS 137061. E, right valve, NIGPAS 137067. A–E, all ×1. F, right valve, rubber cast of an external mould, NIGPAS 137065; ×1.5. G_1, dorsal view of articulated valves, NIGPAS 137070; ×2. G_2, right valve, NIGPAS 137070; ×3. H, left valve, rubber cast of an external mould, NIGPAS 137071; ×3.

or substraight; ventral margins are slightly convex or gently concave; and posterior margins are gradational rounded, narrowly rounded or subtruncated. The overall morphological variation is so continuous that it is difficult to find any distinct character to separate these specimens into different taxa (see Fig. 6).

Judging from the overall diagnosis of the elongate shape, moderately thick shell, weak commarginal growth lines and undulating ridge on shell surface, and the thin hinge plate with two opisthocline anterior pseudocardinals and posterior lamellar teeth parallel to the posterodorsal margin, this species belongs to the genus *Unio*. The present specimens are similar to the illustrated specimens of *Pseudelliptio longus* (Zhu, 1976, p. 23, pl. 1, figs. 5, 7–11; non fig. 6) from the Chaganlimennuoer Formation, and to the illustrated specimens of *P. longa* from the Saihantala Formation of Inner Mongolia,

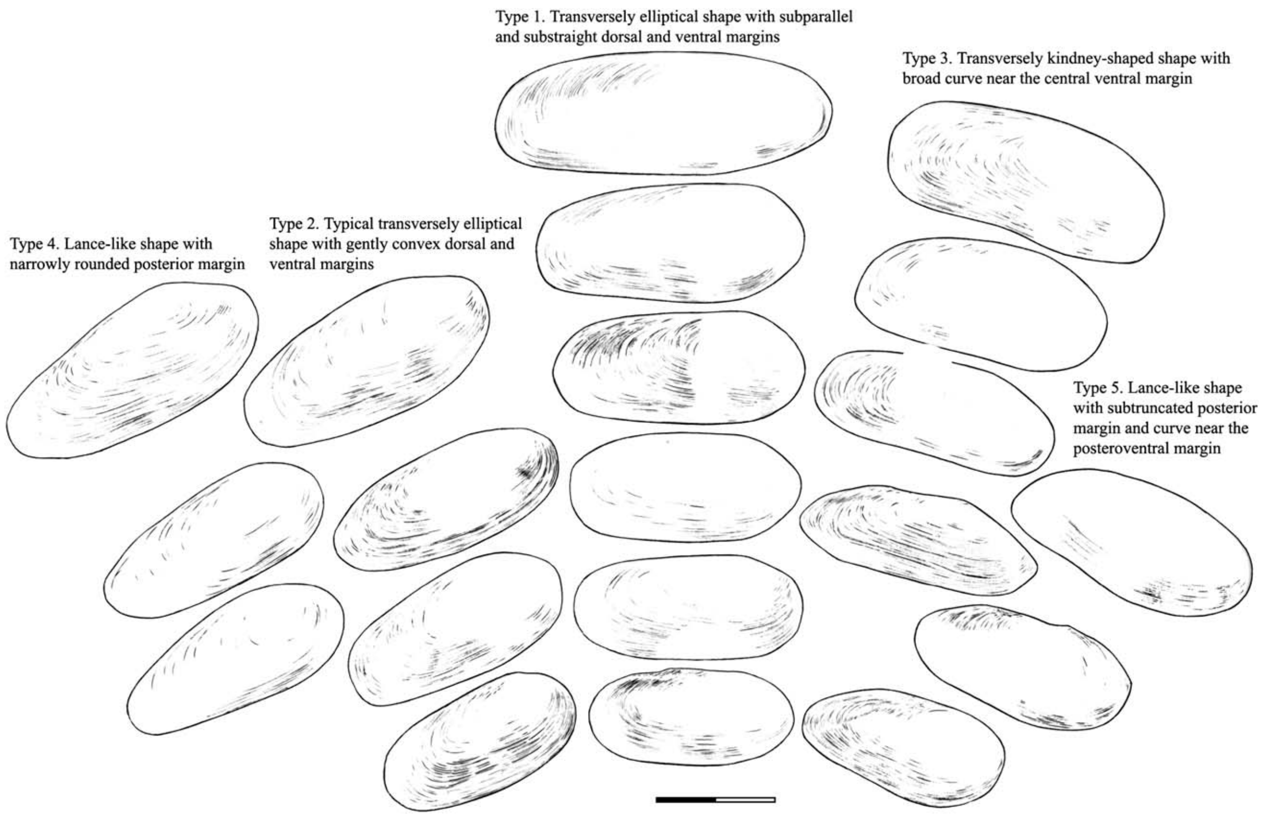

Fig. 6. Variation of the outline of *Unio longus* (Zhu) (left valve) from the upper member of Khuren Dukh Formation of Choyr Basin, southeastern Mongolia. Scale bar represents 40 mm.

northern China (Ma, 1991, p. 710, pl. 1, figs. 13, 15–18), in having a transversely elliptical shape and a small ratio (<0.5) between height and length. However, both the shape and ornamentation of the genus *Pseudelliptio* are similar to those of the genus *Unio*. Zhu (1976) noticed two small unstable submedian teeth beneath the anterior lamellar tooth 3a, and used this feature as criterion of the new genus *Pseudelliptio*. However, such teeth are noted commonly within the genus

Fig. 7. Bedding-plane accumulation and randomly orientated *Sphaerium anderssoni* (Grabau) in the tuffaceous sandstone of the lower Yixian Formation of Sihetun, Beipiao, western Liaoning, northeastern China, showing both the internal and external moulds. Scale bar represents 10 mm.

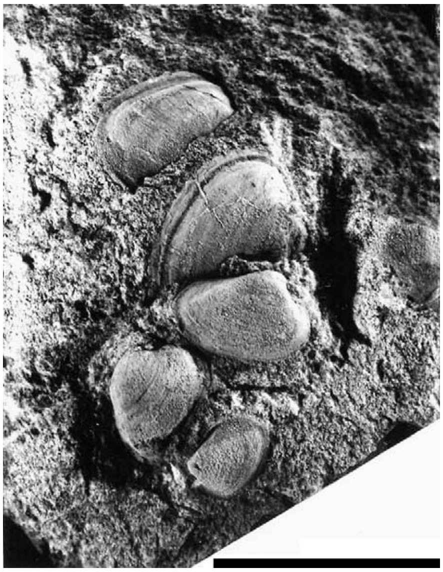

Fig. 8. As for Fig. 7, showing internal moulds only. Scale bar represents 10 mm.

Unio. *Pseudelliptio* should therefore be regarded as a junior synonym of the genus *Unio*.

Morphological features of *Unio longus*, such as the ratio of height to length (<0.5), the commarginal growth lines and inflated undulating ridges, a posterior umbonal ridge, the moderate thickness of the shell, ligament, hinge teeth, and particularly individuals with transversely elliptical shape (Fig. 6, Types 1 and 2; Figs. 4A, D, E, 5A), or lance-like individuals with very slight posteroventral curve (Fig. 6, Type 5; Fig. 5B, C), or transversely kidney-shaped individuals with broad central ventral curve (Fig. 6, Type 2; Figs. 4C, 5D, E), are all features characterizing specimens named as *Unio heilongjiangensis* by Sha and Fürsich (1993, pp. 157–159, text-figs. 11E, 14–15; pl. 1, figs. 1–10; pl. 2, figs. 1–3, 5–10; pl. 3, figs. 2–3, 5–6, 8–10). Although Sha and Fürsich proposed *Unio heilongjiangensis* as a new species, comparing their material only with the recent species *U. douglasiae* (*Unio longus* being ignored), *U. heilongjiangensis* should also be regarded as a junior synonym of *Unio longus*.

The specimen of *Pseudelliptio longus* illustrated by Zhu (1976, p. 23; pl. 1, fig. 6) is classified as *Unio* sp., because its ratio between height and length is greater than that of specimens of *U. longus*.

The ratio of height to length of *Unio hanganensis* Jakushina figured by Martinson (1982, p. 62, pl. 15, fig. 3) from the Upper Cretaceous of Mongolia is greater than 0.5, which is different from the present species but very similar to the specimens named as *Unio* cf. *heilongjiangensis* Sha and Fürsich (1993, p. 159; pl. 4, figs. 2–8) from the Albian Xiachengzi Formation of eastern Heilongjiang, northeastern China.

In outline, the kidney-shaped individuals (Fig. 6, Type 3; Figs. 4C, 5D, E) and some lance-like individuals with subtruncated posterodorsal margin and curve near the posteroventral margin (Fig. 6, Type 5; Fig. 5B, C), are similar to the specimens of *Margaritifera isfarensis* (Chernyshev) from the Mengyin Group of Shandong, northern China; the upper Jehol Group of Liaoning, northeastern China; the Middle Jurassic of Gansu, northwestern China; the Suining Formation of Sichuan, southwestern China; the Shangxiangxi Formation of Hubei, central southern China; and the Yongping Group of Yunnan, southern China (e.g., Gu et al., 1976, p. 354, pl. 98, figs. 17–23; pl. 100, figs. 14–21). They are also similar to

Table 2
Measurements (in mm) of *Unio longus*

	H	L	D	I	H/L	D/L	I/L
N	25	25	18	8	25	18	8
X	34.93	79.47	23.83	19.5	0.441	0.294	0.243
Max	39.25	102.7	36	23	0.517	0.438	0.281
Min	27.4	63.0	15	14	0.357	0.176	0.182
OR	11.85	39.7	21	9	0.160	0.261	0.099
S	4.10	10.38	5.491	3.295	0.042	0.058	0.035

N, number of observations made; X, arithmetic mean; Max, maximum value; Min, minimum value; OR, range; S, standard deviation, which gives a measure of absolute variation of the sample; H, height; L, length; D, umbonal distance from the anterior extremity to umbo; I, inflation; H/L, ratio of height to length; D/L, ratio of umbonal distance to length; I/L, ratio of inflation to length.

Table 3
Biometric characters of *Unio longus*

	Length/Height
N	25
m	2.29
σ	0.22
s	0.23
χ^2	2.55
ν	3

N, sample size; m, mean value; s, standard deviation; χ^2, chi-square (evidently smaller than $\chi^2_{0.05} = 7.81$, which is the 0.05 significance limit; ν, degree of freedom.

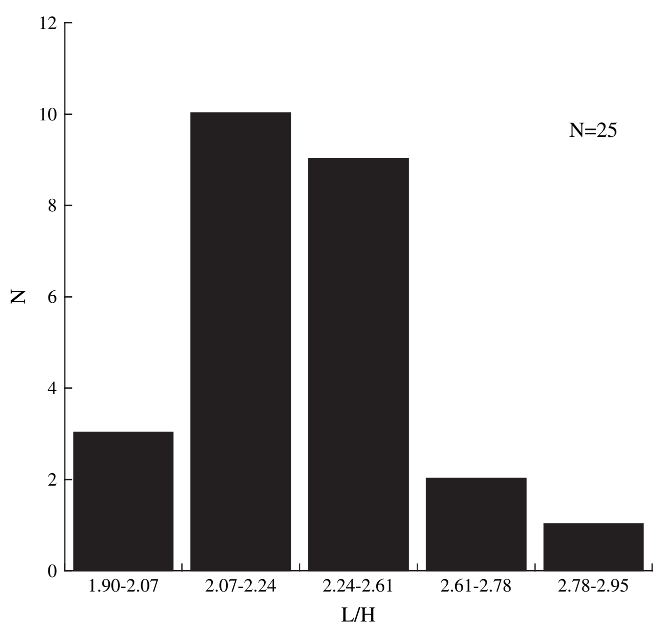

Fig. 9. Size-frequency distribution of shell length/shell height of *Unio longus* (Zhu). Lower cutoff number of column is excepted.

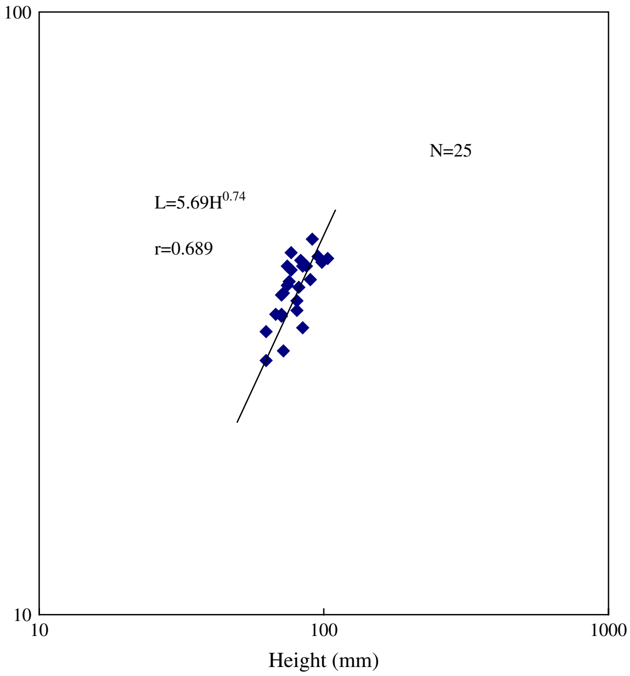

Fig. 10. Diagram showing the average relative growth of *Unio longus* (Zhu).

Margaritifera tugrigensis (Martinson) from the Mengyin Group of Shandong, northern China, and from the Jiufotang Formation of Jehol Group of Liaoning, northeastern China (e.g., Gu et al., 1976, p. 354; pl. 99, figs. 1–4, 15–19). However, all these specimens named as *Margaritifera* have a fairly thick shell, strong hinge, and deep muscle scar, and thus differ from the present specimens.

Morphologically, the lance-shaped individuals with narrowly rounded posterior margin (Fig. 6, Type 4; Fig. 4F) resemble the specimens of *Cuneopsis sakaii* (Suzuki) from the Sifangtai Formation of Heilongjiang and the Nenjiang Formation of Jilin, northeastern China (e.g., Gu et al., 1976, p. 328; pl. 104, figs. 5–13). Nevertheless, these specimens of *Cuneopsis* have a very thick shell, heavy hinge and very impressed muscle scar, and are particularly wedge-like in their shape, flattening and sharpening towards the posterior, all features which prominently distinguish them from the present species.

The specimens of *Protelliptio mongolensis* Martinson figured by Martinson and Shuvalov (1976, p. 41, pl. 4, figs. 1–2), and all the specimens of *Margaritanopsis elongata* Martinson, *M. sainshandensis* Martinson, *Oxynaia sainshandica* Barsbold, *Rectidens mongolensis* Martinson, *Cuneopsis orientalis* Barsbold, *C. lanceolata* Martinson, *Laneceolaria angustata* Martinson, *Protelliptio mongolensis* Martinson and *P. notabilis* Martinson, Barsbold, and Tolstikowa described by Martinson (1982, p. 56, pl. 13, figs. 5–6; p. 56, pl. 13, figs. 4–5; p. 58, pl. 13, fig. 3; p. 58, pl. 14, fig. 3; p. 60, pl. 14, fig. 4; p. 61, pl. 14, figs. 7–8; p. 61, pl. 15, figs. 1–2; p. 63, pl. 15, figs. 10–11; p. 64, pl. 15, fig. 12) from the Cretaceous of southeastern Mongolia do not show any typical features of *Margaritanopsis*, *Oxynaia*, *Rectidens*, *Cuneopsis*, and *Protelliptio*, but rather full within the variation of the genus *Unio*. All of them are longer than high, and the ratio between height and length is less than 0.5. Notably, their shapes vary so continuously that it is difficult to separate them into different taxa at generic or even specific level. All the forms figured by Martinson and Shuvalov (1976) and Martinson (1982) can easily be found in the present population as well.

Locality and horizon. Northern Choyr Basin; Albian sandstone of the upper member of the Khuren Dukh Formation.

Subclass: Heterodonta Neumayr, 1884
Order: Veneroida H. Adams and A. Adams, 1856
Superfamily: Corbiculacea Gray, 1847
Family: Pisidiidae Gray, 1857
Genus *Sphaerium* Scopoli, 1777

Sphaerium chientaoense Suzuki
Fig. 5H

1941 *Sphaerium chientaoense* Suzuki (pars), p. 84, pl. 1, figs. 2, 4, 5 (non figs. 1, 3).
1976 *Sphaerium yanbianense* Gu and Wen in Gu et al., p. 381, pl. 120, figs. 1–11.
1980 *Sphaerium yanbianense* Gu and Wen; Zhu, p. 30, pl. 5, figs. 19–20; pl. 6, figs. 1–2.
? 1982 *Sphaerium albicum* (Martinson); Martinson, p. 65, pl. 13, figs. 7–8.
1984 *Sphaerium yanbianense* Gu and Wen; Gu et al., p. 176, pl. 45, figs. 20–28; pl. 46, figs. 1–6.
1993 *Sphaerium yanbianense* Gu and Wen; Sha and Fürsich, p. 164, pl. 6, figs. 1–13; text-fig. 19.

Holotype. The holotype by original description is the specimen illustrated by Suzuki (1941, pl. 1, fig. 2).

Material. Three external moulds. Only one right external mould (NIGPAS 137071) is relatively complete, but it is compressed.

Description. Shell small, equivalve but inequilateral. Suboval in outline. Anterior margin rounded. Posterior margin subtruncated, dorsal margin slightly arcuate, ventral margin broadly roundly, posteroventral corner subrounded. The relatively complete specimen is about 10 mm long and 7 mm high. Poorly preserved umbo situated at about one-third of shell length from the anterior extremity. Shell surface is covered by the fine, closely and regularly spaced commarginal growth lines.

Remarks. The present specimens are similar to the specimens named as *Sphaerium chientaoense* Suzuki from middle shale member of the Talatzi Series (Suzuki, 1941, p. 84, pl. 1, figs. 2–4) in their outline and commarginal growth lines. Gu and Wen (in Gu et al., 1976) proposed *S. yanbianense* as nomen novum for *S. chientaoense* Suzuki, because the specific name *chientaoense*, which originated from "jiantao," is contrary to Article 5 of the Code of the International Zoological Nomenclature (ICZN). However, the specific name of

Sphaerium chientaoense (Suzuki) should be applied on the basis of Article 18, Inappropriate and Tautonymous Names, of the ICZN.

Sphaerium coreanicum (Kobayashi and Suzuki, 1936, p. 255, pl. 29, figs. 1–10) differs from the present species in having a much larger shell and elongated subtrapezoidal outline.

Sphaerium albicum (Martinson) figured by Martinson (1982, p. 65, pl. 13, figs. 7, 8) from the so-called Upper Cretaceous of Mongolia, looks like the present specimens as well, but its umbo projects more above the hinge line.

Locality and horizon. Northern Choyr Basin; Albian mudstone of the upper member of the Khuren Dukh Formation.

Sphaerium coreanicum (Kobayashi and Suzuki)
Fig. 5F, G

1936 *Corbicula* (*Leptesthes*?) *coreanica* Kobayashi and Suzuki, p. 255, pl. 29, figs. 1–7 (non figs. 8–10).
1941 *Sphaerium chientaoense* Suzuki (pars), p. 84, pl. 1, figs. 1, 3 (non figs. 2, 4, 5).
1976 *Sphaerium* aff. *wiljuicum*; Gu et al., p. 382, pl. 121, figs. 32–35, 37–41.
1980 *Sphaerium coreanicum*; Ma, p. 121, pl. 5, figs. 22–23, 25.
1984 *Sphaerium coreanicum*; Gu et al., p. 177, pl. 45, figs. 18–19 (non fig. 17).
1993 *Sphaerium* (*Sphaerium*) *coreanicum* (Kobayashi and Suzuki); Sha and Fürsich, p. 165, pl. 6, figs. 14–27.

Holotype. The holotype by original description is the specimen illustrated by Kobayashi and Suzuki (1936, pl. 29, fig. 1).

Material. Two specimens (NIGPAS 137065, 137070), one consisting of articulated valves and the other an incomplete right external mould.

Description. Shell large for the genus, 15–21 mm long and 9.5–11 mm high. Elongated subtrapezoidal in outline. Anterior margin obtusely rounded, posterior margin broadly rounded. Posterodorsal corner obtusely angular and posteroventral corner narrowly rounded. Umbo obtuse, projecting slightly above hinge line and placed at about one-eighth to one-third of the shell length from the anterior extremity. Shell thin and shell surface covered by fine, closely and regularly spaced commarginal growth lines.

Remarks. Compared with the specimens of this species from the Tongfosi Formation of Yanji, Jilin (e.g., Gu et al., 1976, pl. 121, figs. 32–35, 37–41), from the Albian Xiachengzi Formation of eastern Heilongjiang, northeast China (e.g., Sha and Fürsich, 1993, pl. 6, figs. 14–27), and the Guantou Formation of Zhejiang, eastern China (Ma, 1980, p. 121, pl. 5, figs. 22–23, 25), the present specimens are larger.

Locality and horizon. Same as that of *Sphaerium chientaoense* above.

Sphaerium anderssoni (Grabau)
Figs. 11–13

1923 *Corbicula anderssoni* Grabau, p. 188, text-fig. 1a–1b.
1923 *Corbicula jeholensis* Grabau, p. 192, text-fig. 1c.
1943 *Sphaerium anderssoni* (Grabau); Suzuki, p. 62, pl. 4, figs. 1–4.
1943 *Sphaerium anderssoni jeholense* (Grabau); Suzuki, pp. 9, 63, pl. 4, figs. 5–13.
1953 *Sphaerium anderssoni* (Grabau); Zhou, p. 171, pl. 1, fig. 7.
1957 *Sphaerium anderssoni* (Grabau); Gu, p. 188, pl. 112, figs. 24–26.
1960 *Sphaerium anderssoni anderssoni* (Grabau); Hase, p. 319, pl. 37, figs. 12–15; pl. 38, figs. 4–8, 9a–b, 10–23, 24a–b; text-fig. 5a–c.
1960 *Sphaerium anderssoni jeholense* (Grabau); Hase, p. 329, pl. 28, figs. 25–30.
1963 *Sphaerium anderssoni* (Grabau); Gu et al., p. 133, pl. 105, fig. 9.
1964 *Sphaerium jeholense* (Grabau); Gu et al., p. 126, pl. 82, fig. 5.
1975 *Sphaerium anderssoni anderssoni* (Grabau); Hayami, p. 143.
1975 *Sphaerium anderssoni jeholense* (Grabau); Hayami, p. 143.
1976 *Sphaerium jeholense* (Grabau); Gu et al., p. 380, pl. 102, figs. 36–45.
1976 *Sphaerium anderssoni* (Grabau); Gu et al., p. 380, pl. 102, figs. 10–17.
1976 *Sphaerium anderssoni* (Grabau); Zhu, p. 32, pl. 4, figs. 5–13.
1976 *Sphaerium jeholense* (Grabau); Zhu, p. 33, pl. 6, figs. 5–16.
1976 *Sphaerium* aff. *jeholense* (Grabau); Zhu, p. 33, pl. 6, figs. 17–19; pl. 7, figs. 1–2.
1976 *Limnocyrena* cf. *anderssoni* (Grabau); Martinson and Shuvalov, p. 43, pl. 4, figs. 8–9.
1980 *Sphaerium jeholense* (Grabau); Zhu, p. 29, pl. 3, figs. 27–31.
1980 *Sphaerium jeholense* (Grabau); Ma, p. 120, pl. 5, figs. 19, 21.
1982 *Sphaerium jeholense* (Grabau); Ding et al., p. 88, pl. 26, figs. 24–25.
1982 *Sphaerium jeholense* (Grabau); Yu, p. 37, pl. 2, figs. 1, 3–6, 7.
1982 *Sphaerium jeholense* (Grabau); Shi, p. 23, pl. 9, fig. 21.
1982 *Sphaerium anderssoni* (Grabau); Shi, p. 23, pl. 9, figs. 14–15.
1982 *Corbicula anderssoni* (Grabau); Martinson, p. 66, pl. 13, figs. 9–10.
1984 *Sphaerium jeholense* (Grabau); Yu et al., p. 60, pl. 14, figs. 15–18, 20–22.
1984 *Sphaerium* cf. *jeholense* (Grabau); Yu et al., p. 60, pl. 15, figs. 9, 12.
1984 *Sphaerium anderssoni* (Grabau); Yu et al., p. 61, pl. 14, fig. 24.

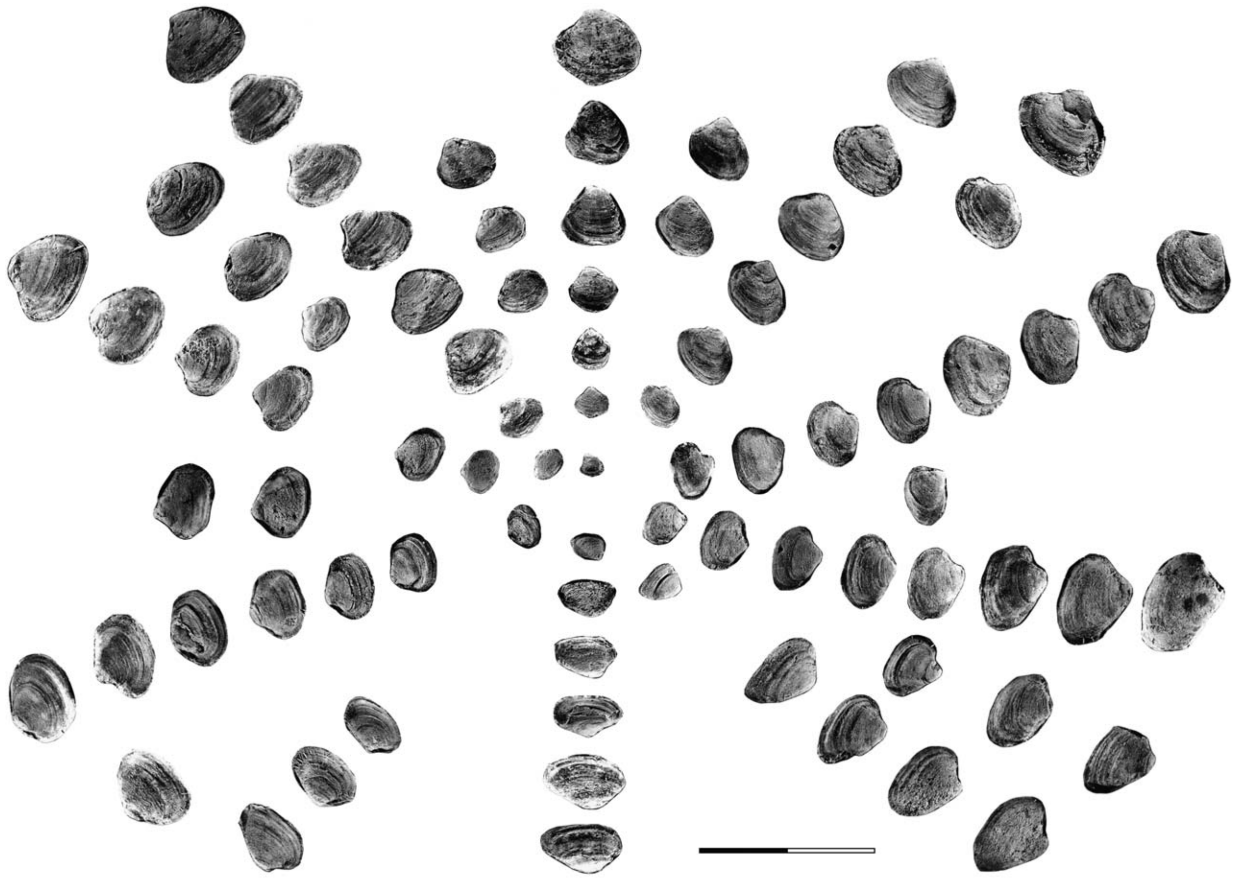

Fig. 11. Variation of the outline of *Sphaerium anderssoni* (Grabau) (left valve) from tuffaceous sandstone of the lower Yixian Formation of Sihetum, Beipiao, western Liaoning. Scale bar represents 20 mm.

1984 *Sphaerium jeholense* (Grabau); Wei, p. 41, pl. 13, figs. 8–9.
1986 *Limnocyrena anderssoni* (Grabau); Ma, p. 197, pl. 6, figs. 18, 20–23.
1986 *Limnocyrena jeholense* (Grabau); Ma, p. 198, pl. 6, figs. 19, 27–30.
1987 *Sphaerium anderssoni* (Grabau); Yu et al., p. 14, pl. 1, figs. 4; pl. 4, figs. 4, 6, 10, 29.
1987 *Sphaerium* cf. *anderssoni* (Grabau); Yu et al., p. 14, pl. 1, figs. 3, 5, 11.
1987 *Sphaerium jeholense* (Grabau); Yu et al., p. 16, pl. 4, figs. 18, 22, 24.
1987 *Sphaerium* cf. *jeholense* (Grabau); Yu et al., p. 16, pl. 3, fig. 15.
1989 *Sphaerium jeholense* (Grabau); Stratigraphical Group, Institute of Geology, Chinese Academy of Geological Sciences, pl. 21, figs. 13–14.
1989 *Sphaerium* cf. *jeholense* (Grabau); Stratigraphical Group, Institute of Geology, Chinese Academy of Geological Sciences, pl. 21, fig. 10.
1999 *Sphaerium jeholense* (Grabau); Chen, p. 103, pl. 2, figs. 1, 8–11, 15; pl. 3, figs. 5–6.
1999 *Sphaerium anderssoni* (Grabau); Chen, p. 103, pl. 2, figs. 5–6, pl. 3, fig. 7.

Syntypes. The syntypes are the specimens illustrated by Grabau (1923, figs. 1a and 1b).

Material. More than 400 specimens that are, except for seven steinkerns, internal and external moulds occasionally associated with shells.

Diagnosis. Small, subtriangular, subquadrate, suboval and subelliptical in outline; umbo fairly remarkable, beaks projecting prominently above hinge line; ornament of commarginal growth lines and rugae.

Description. Shell small for the genus. Usually longer than high but occasionally higher than long. Variable outline of shell, including subtriangular, subquadrate, suboval, and subelliptical forms (Fig. 11). Anterior margin narrowly to well rounded, posterior margin subtruncated to narrowly rounded, dorsal margin obtusely to narrowly angular, ventral margin broadly convex to substraight, posterodorsal angle absent to narrowly rounded. Umbo is fairly remarkable, beaks are short, obtuse and slightly opisthogyrous, and project prominently above hinge line, but their positions are fairly variable, placed at near one-tenth to one-half the shell length from the anterior extremity. Shell surface is covered by commarginal growth

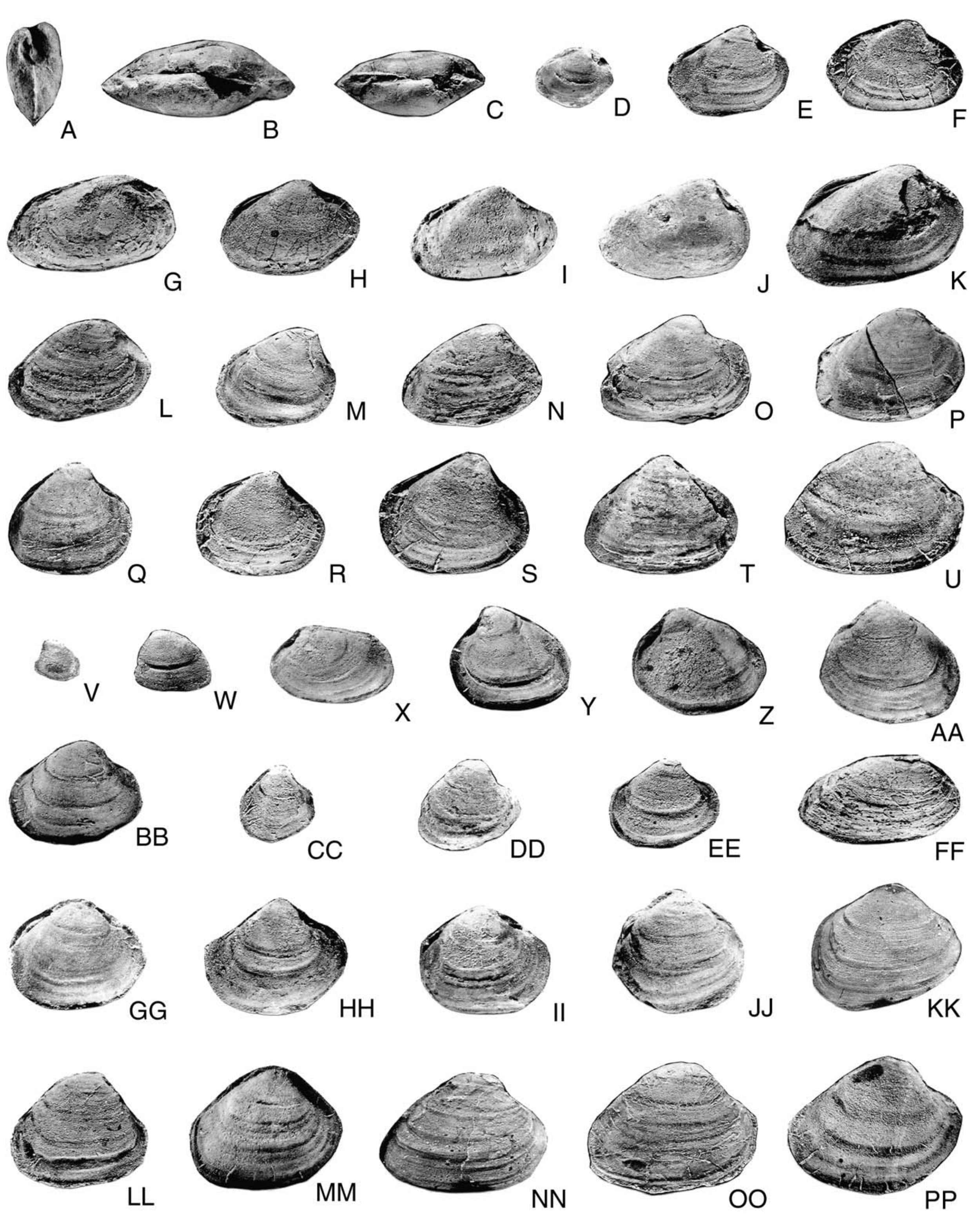

Fig. 12. Some shapes of articulated valves (A−C) and single valves (D−PP), and commarginal growth threads, lines, and rugae of *Sphaerium anderssoni* (Grabau) from the tuffaceous sandstone of the lower Yixian Formation of Sihetun, Beipiao, western Liaoning. A, interior view of articulated valves, NIGPAS 137086. B, C, dorsal view of articulated valves, NIGPAS 137087 and 137088 respectively. D−U, internal moulds of right valve. D, NIGPAS 137089. E, NIGPAS 137090. F, NIGPAS 137091. G, NIGPAS 137092. H, NIGPAS 137093. I, NIGPAS 137094. J, NIGPAS 137095. K, NIGPAS 137096. L, NIGPAS 137097. M, NIGPAS 137098. N, NIGPAS 137099. O, NIGPAS 137088. P, NIGPAS 137100. Q, NIGPAS 137101. R, NIGPAS 137102. S, NIGPAS 137103. T, NIGPAS 137104. U, NIGPAS 137087. V−AA, internal moulds of left valve. V, NIGPAS 137105. W, NIGPAS 137106. X, NIGPAS 137107. Y, NIGPAS 137108. Z, NIGPAS 137109. AA, NIGPAS 137110. BB−JJ internal moulds of right valve. BB, NIGPAS 137111. CC, NIGPAS 137112. DD, NIGPAS 137113. EE, NIGPAS 137114. FF, NIGPAS 137115. GG, NIGPAS 137116. HH, NIGPAS 137117. II, NIGPAS 137118. JJ, NIGPAS 137119. KK, right valve, rubber cast of an external mould NIGPAS 137120. LL, MM, internal moulds of right valve, NIGPAS 137121 and 137122 respectively. NN, right valve, rubber cast of an external mould, NIGPAS 137123. OO, PP, internal moulds of right valve, NIGPAS 137124 and 137125 respectively. Scale bar represents 10 mm.

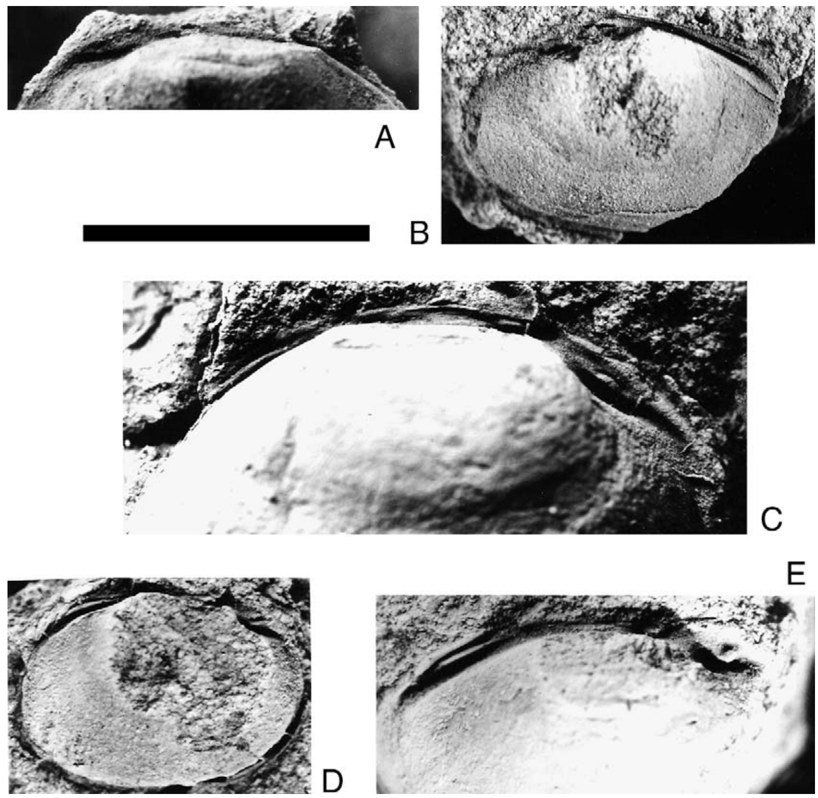

Fig. 13. Photographs showing variations of hinge teeth of *Sphaerium anderssoni* (Grabau). A, B, internal moulds of left valve, NIGPAS 137126 and 137127 respectively. C–E, internal moulds of right valve. C, NIGPAS 137128. D, NIGPAS 137129. E, NIGPAS 137130. Scale bar represents 10 mm.

lines and rugae. Hinge plate moderately long, one cardinal tooth in right valve and two in left valve, two anterior lateral teeth in right valve and one in left, two posterior lateral teeth in right valve and one, occasionally two, in left have been recognized, forming the following formula:

AIII		AI		1		PI		PIII	
	AII		2a		2b		PII		(PIV)

Cardinals are fairly feeble and variable in outline and on the left valve, only one is distinct, but another one indistinct on the internal mould. Anterior lateral teeth are shorter than the posterior ones, and in left valve the ventral laterals are stronger than the dorsal ones. No crenulations are preserved on teeth (e.g., Fig. 13).

Deformation. The specimens are oriented randomly in tuffaceous sandstone layers and are almost never secondarily deformed (see Figs. 7, 8).

Variation. The present species shows some variability in its morphologic characters. For example, shell outline is quite variable: valve shapes include rounded subtriangular, subcircular, rounded subquadrate, rounded subrectangle, suboval, and subelliptical, with intermediate individuals between each shape (Figs. 11, 12D–U). Valve inflation is moderate and even (Fig. 12A–C), but only visible on seven articulated individuals. The strength of the posteroumbonal ridge is fairly variable. Some are quite weak or are even absent (e.g., Fig. 12D, H, V, X), some are fairly prominent (e.g., Fig. 12F, J, K, P–R, T, U, BB, II, JJ, KK, NN), but most are obtuse (e.g., Fig. 12B, C, E, I, L–O, S, W, Y, Z, AA, CC–EE, HH, LL, MM, OO, PP).

Ontogenetic features. Specimens are characterized by numerous, regularly and closely spaced commarginal growth threads and lines, and widely spaced commarginal growth rugae. Between rugae, and between the latest ruga and the ventral margin, there are no commarginal growth threads and lines preserved in the area representing the early growth stage between the beak and the earliest ruga. A maximum of seven growth rugae is found on the largest individuals (e.g., Fig. 12MM–OO), whereas only 3–4 are found on medium- and large-sized individuals (e.g., Fig. 12X, BB, DD–LL, PP), and only one or small individuals (e.g., Fig. 11W, CC). No rugae are preserved on very smallest specimens (e.g., Fig. 12V).

Remarks. Since Grabau (1923) described *Corbicula anderssoni* from the Hunyuan Group of northeastern Shanxi Province of China, which is characterized by a subelliptical-subrectangular shape, and *Corbicula jeholense* from the Jehol Group in western Liaoning Province of China, which is characterized by a suboval-rounded subtriangular shape, the two species have been listed in many papers (see synonymy). The various shapes of these taxa based on about more than 400 specimens (excepting the holotypes and most paratypes of both *C. anderssoni* and *C. jeholense*, because they are missing now), include suboval, rounded subtriangular, subelliptical, subrectangular, and subcircular individuals as well as others.

Their shapes vary continuously and it is difficult to differentiate them as two distinct species. *Sphaerium anderssoni* (Grabau) and *S. jeholense* (Grabau) are, therefore, regarded as one species and *S. anderssoni* must be kept as the senior synonym, although the Jehol Fauna is a well-known late Mesozoic nonmarine fauna in China.

This idea is similar to that of Suzuki (1943): he proposed *Sphaerium anderssoni jeholense* (Grabau) as a new subspecies differing from *Sphaerium anderssoni anderssoni* (Grabau) in having an ovate outline with backwards tapering, far less inequilateral and somewhat more convex outline, and scarcely truncated behind. Suzuki considered the two subspecies of *Sphaerium anderssoni* (Grabau) to be related to different ecological conditions. The specimens classified within these two subspecies, however, are all closely connected by many intermediate forms.

Many specific names of *Sphaerium* have been published by Chinese and Russian authors. Some of these should probably be grouped into *Sphaerium anderssoni*, but this requires further comparison and examination of the Russian literature.

Geographic distribution. *Sphaerium anderssoni* has a wide distribution in East Asia. In Japan it is found in the Sengoku, Nyoraida, Wakamiya, Shiohama, and Inakura formations of the Kwanmon Group of Japan (Suzuki, 1943; Hase, 1960; Hayami, 1975), while in South Korea it is known from Nagdong Group (Suzuki, 1943; Hayami, 1975). In eastern China, it is known from the Shouchang Formation (=Bantou Formation) and the Laocun Formation of the Jiande Group, Jiande, Zhejiang (Gu et al., 1976; Ma, 1980; Ding et al., 1982). It is also known from the Yixian and Jiufotang formations (=Shahai Formation) of the Jehol Group, Luanping, Hebei (Yu et al., 1984), the Hunyuan Group of Hunyuan, Shanxi (Gu et al., 1976; Yu et al., 1984), and the Chaganlimennuoer Formation of Suniteyouqi, Inner Mongolia (Zhu, 1976) in northern China. In central Inner Mongolia, it is known from the Guyang formation of Guyang and Lisangou formations of Wulatqianqi (Yu, 1982) and the Lower Cretaceous of southern Mongolia (Martinson and Shuvalov, 1976; Martinson, 1982). In northwest China, it is known from the Zhonggou, Xiagou and Zhejinbao formations of the Xinmminbao Group, Yumen and Chao Shui (Zhou, 1953; Gu et al., 1976; Ma, 1986), the Huaya and Zhoujiawan formations of the Donghe Group, Wudu and Kangxian (Shi, 1982), and the Gansu, Lianmuqin, and Shengjinkou formations of the Tugulu Group, Changji and Shawan, Xinjiang (Wei, 1984).

Locality and horizon. Sihetun of Beipiao, western Liaoning, northwestern China; Lower Cretaceous tuff sandstone of lower Yixian Formation, Jehol Group.

5. Characterization of bivalve assemblages in the Choyr Basin and evaluation of nonmarine bivalves as index fossils in Asia

In China, *Unio longus* (Zhu) has been reported from the Chaganlimennuoer and Saihantala formations of Inner Mongolia, northern China (Zhu, 1976; Ma, 1991), while *Sphaerium chientaoense* and *Sphaerium coreanicum* have both been reported from the Tongfosi Formation (Gu et al., 1976), and probably also from the Dalatzu Formation (Suzuki, 1941; Zhu, 1980) of Yanji, Jilin, northeastern China. *Sphaerium chientaoense* itself is also known from the Guantou Formation of Zhejiang, eastern China. All the three species have been found in the Xiachengzi Formation of eastern Heilongjiang, northeastern China (Gu et al., 1984, 1997; Sha and Fürsich, 1993). These species are members of the *Nakamuranaia-Margaritifera* (*Mengyinaia*)-*Neomiodonoides* Assemblage (Ma, 1994), widely distributed in southern East Asia. Thus, the bivalve assemblage in the Choyr Basin is a northern extension of this assemblage.

In Korea, *Sphaerium coreanicum* comes from the Gyeongsang Group (Kobayashi and Suzuki, 1936). In Japan, *Sphaerium coreanicum* occurs in the Okurodani Formation in the Tetori area and the Kwanmon Group in the Kitakyushu area (Tamura, 1990; Matsukawa and Nakada, 1999). *Sphaerium anderssoni* is reported from the Sengoku, Nyoraida, Wakamiya, Shiohama, and Inakura formations of the Kwanmon Group (Suzuki, 1943; Hase, 1960; Hayami, 1975). *Sphaerium coreanicum* and *S.* (*S.*) *anderssoni* are also members of the *Nakamuranaia-Margaritifera* (*Mengyinaia*)-*Neomiodonoides* Assemblage. This indicates that the distribution of the assemblage originally extended to Japan through Korea. However, in Korea and Japan, allied species of members of the *Trigonioides* (*T.*)-*Plicatounio* (*P.*)-*Nippononaia* (*N.*) assemblages in China are sometimes associated with *Sphaerium coreanicum* and *S. anderssoni*. This suggests that the five molluscan assemblages recognized in China appear to be strongly diachronous and cannot be used as chronological indices.

All the formations bearing these four species in Asia are different in geological age (e.g., the Okurodani Formation is probably Valanginian–Barremian, the Kwanmon Group is assigned to Hauterivian–Albian, and the Khuren Dukh Formation is correlated to the Albian). Therefore, the four species must have continuously migrated to optimum habitats during the Valanginian–Albian, as such habitats were locally and repeatedly destroyed.

6. Conclusions

1. Freshwater bivalves found in the upper member of the Khuren Dukh Formation of the Choyr Basin include *Unio longus*, *Sphaerium coreanicum*, and *Sphaerium chientaoense*. The assemblage can be compared with the *Nakamuranaia-Margaritifera* (*Mengyinaia*)-*Neomiodonoides* Assemblage in China.
2. Individuals of *Unio longus* are variable in outline and include transversely elliptical, lance-like and kidney-shaped forms, with dorsal margin slightly convex or substraight, ventral margin slightly convex or gently concave, and posterior margin rounded, narrowly rounded, or subtruncated. *Sphaerium anderssoni* is also characterized by variable outline of shell and includes subtriangular, subquadrate, suboval, and subelliptical forms. The morphological variation

within populations of these taxa is strongly continuous, and differentiation of the taxa into separate species or subspecies is therefore unwarranted. Although *Sphaerium anderssoni* and *Sphaerium jeholense* have been differentiated previously, they form end-members of the same population, and *Sphaerium anderssoni*, rather than *Sphaerium jeholense*, must be kept as a senior synonym.

3. The four nonmarine bivalve species described above are found in many formations in East Asia suggesting Valanginian–Albian age. The four species are included in assemblages of both the *Nakamuranaia-Margaritifera* (*Mengyinaia*)-*Neomiodonoides* and *Trigonioides* (*T.*)-*Plicatounio* (*P.*)-*Nippononaia* (*N.*) assemblages of China and demonstrate that these assemblages cannot always be used as chronological indices.

Acknowledgements

We thank M. G. Lockley, I. Obata, and J. W. Haggard for reading the manuscript and suggesting improvements. We are also grateful to I. Hayami and J. H. Hartman for their critical comments and corrections, which led to considerable improvement of the paper. Thanks are extended to R. Barsbold, B. Lauren, P.J. Chen, H.C. Zhang, Q.G. Li, Y.G. Zhang, D.J. Nichols, M. Ito, A. Okubo, K. Hayashi, K. Saiki, K. Kara, and T. Saito for their kind help in the field. This work was financially supported by the National Sciences Foundation of China (40372008), Academia Sinica (KZCX2-SW-129, GJHZ0522), and the Grant-in-Aid for University and Society Collaboration of the Japanese Ministry of Education, Science, Sports and Culture (1179012).

References

Chang, M.M., Chen, P.J., Wang, Y.Q., Wang, Y. (Eds.), 2001. Jehol Biota. Shanghai Science and Technology Publication, Shanghai. 150 pp. (in Chinese).

Chen, J.H., 1999. A study of nonmarine bivalve assemblage succession from the Jehol Group (U. Jurassic and L. Cretaceous). In: Chen, P.J., Jin, F. (Eds.), Jehol Biota. Palaeoworld 11 (Special Issue), 92–109 (in Chinese, English abstract).

Chen, P.J., Jin, F. (Eds.), 1999. Jehol Biota. Palaeoworld 11. Press of University of Science and Technology of China, Beijing, 342 pp. (in Chinese, English abstract).

Chen, P.J., Li, M., Jianjun, Matsukawa, Zhang, M.G., Haichun, Wang, Qifei, Lockley, M.G., 2006. Geological age of the dinosaur tracks bearing formations in China. Cretaceous Research 27 (1), 22–32.

Ding, B.L., Ma, Q.H., Huang, B.Y., 1982. Bivalves (nonmarine). In: Nanjing Institute of Geology and Mineral Resources of the Ministry of Geology and Mineral Resources of the People's Republic of China (Ed.), The Palaeontological Atlas of Eastern China. 3. Mesozoic and Cenozoic Fasicule. Geological Publishing House, Beijing, pp. 53–92. 363–372 (in Chinese).

Grabau, A.W., 1923. Cretaceous Mollusca from north China. Bulletin of the Geological Survey of China 5 (2), 183–198.

Gu, Z.W., 1957. Mollusca. Lamellibranchia. In: Gu, Z.W., Yang, Z.Y., Xu, J., Yin, Z.X., Yu, J.Z., Zhao, J.K., Lu, Y.H., Hou, Y.T. (Eds.), Index Fossils of Invertebrate of China. Geological Publishing House, Beijing, pp. 1–204 (in Chinese).

Gu, Z.W., 1962. Jurassic and Cretaceous of China. Science Press, Beijing, 84 pp. (in Chinese).

Gu, Z.W., Chen, C.Z., Wang, S.M., Huang, Z.Q., 1963. Lamellibrachiata of the Middle Jurassic. In: Zhao, J.K. (Ed.), Handbook of Index Fossils of Northeastern China. Science Press, Beijing, pp. 131–133 (in Chinese).

Gu, Z.W., Chen, C.Z., Wang, S.M., Ma, Q.H., 1964. Lamellibrachiata of the Jurassic. In: Wang, Y. (Ed.), Handbook of Index Fossils of Southern China. Science Press, Beijing, pp. 125–127 (in Chinese).

Gu, Z.W., Huang, B.Y., Chen, C.Z., et al., 1976. Fossil Lamellibranchiata of China. Science Press, Beijing, 522 pp. (in Chinese).

Gu, Z.W., Chen, J.H., Sha, J.G., 1984. Preliminary study on Jurassic and Cretaceous bivalves of eastern Heilongjiang province in China. In: Research Team on the Mesozoic Coal-Bearing Formations in Eastern Heilonjiang (Ed.), Fossils from the Middle-Upper Jurassic and Lower Cretaceous in Eastern Heilongjiang Province, China, 2. Heilongjiang Science and Technology Publishing House, Harbin, pp. 49–220 (in Chinese, English abstract).

Gu, Z.W., Li, Z.S., Yu, X.H., 1997. Lower Cretaceous Bivalves from the Eastern Heilongjiang Province of China. Sciences Press, Beijing, 301 pp.

Hase, A., 1960. The Late Mesozoic formations and their molluscan fossils in west Chugoku and North Kyushu. Journal of Science of the Hiroshima University, Series C 3 (2), 281–342.

Hayami, I., 1975. A systematic survey of the Mesozoic Bivalvia from Japan. Bulletin of the University Museum of Tokyo 10, 1–249.

Hedlund, R.W., Norris, G., 1968. Spores and pollen grains from Fredericksburgian (Albian) strata, Marshall County, Oklahoma. Pollen et Spores 10, 129–159.

Hicks, J.F., Brinkman, D.L., Nichols, D.J., Watabe, M., 1999. Paleomagnetic and palynologic analyses of Albian to Santonian strata at Bayn Shireh, Burkhant, and Khuren Dukh, eastern Gobi Desert, Mongolia. Cretaceous Research 20, 829–850.

Ichinnorov, N., 2003. Palynocomplex of the Lower Cretaceous sediments of the eastern Mongolia. Mongolian Geoscientist 22, 12–16.

Ito, M., Matsukawa, M., Saito, T., Nichols, D.J., 2006. Facies architecture and paleohydrology of a synrift succession in the Early Cretaceous Choyr Basin, southeastern Mongolia. Cretaceous Research 27 (2), 226–240.

Kobayashi, T., Suzuki, K., 1936. Non-marine shells of the Naktong-Wakino series. Japanese Journal of Geology and Geography 13, 234–257, 3 pls.

Ma, Q.H., 1980. Upper Jurassic and Cretaceous bivalve fossils of Zhejiang and southern Anhui. In: Nanjing Institute of Geology and Palaeontology, Academia Sinica (Ed.), Division and Correlation of Mesozoic Volcano-Sedimentary Rocks in Zhejiang and Anhui. Science Press, Beijing, pp. 105–124 (in Chinese).

Ma, Q.H., 1986. Fossil lamellibranchs from the Late Jurassic Xinminpu Group in Western Gansu, NW China. Memoir of the Nanjing Institute of Geology and Palaeontology, Academia Sinica 22, 181–203 (in Chinese, English abstract).

Ma, Q.H., 1991. Some Early Cretaceous unionids from Ningxia and Inner Mongolia, north China. Acta Palaeontologica Sinica 30, 708–713 (in Chinese, English abstract).

Ma, Q.H., 1994. Nonmarine Cretaceous bivalve assemblages in China. Cretaceous Research 15, 271–284.

Martinson, G.G., 1982. Upper Cretaceous mollusks of Mongolia (systematics, stratigraphy, taphonomy). Transactions of the Joint Soviet Mongolian Palaeontological Expedition 17 (Izdatstvo "Nauka", Moscow), 1–82 (in Russian).

Martinson, G.G., Shuvalov, V.F., 1976. Stratigraphy and fresh water Mollusks of Early Cretaceous lake deposits of Gobi outside Altai in Mongolia. In: Martinson, G.G. (Ed.), Fossil Freshwater Mollusks and Their Significance of Limnology. Izdatstvo "Nauka", Leningrad, pp. 20–50 (in Russian).

Matsukawa, M., Nakada, K., 1999. Stratigraphy and sedimentary environment of the Tetori Group in its central distribution based on nonmarine molluscan assemblages. Journal of the Geological Society of Japan 105, 817–835 (in Japanese, English abstract).

Matsukawa, M., Nagata, H., Taketani, Y., Khanda, Y., Khosbajar, P., Badamgarav, D., Obata, I., 1997. Dinosaur bearing Lower Cretaceous deposits in the Choir basin, S.E. Mongolia – stratigraphy and sedimentary environments. Journal of the Geological Society of the Philippines 52, 99−114.

Matsukawa, M., Ito, M., Nishida, N., Koarai, K., Lockley, M.G., Nichols, D.J., 2006. The Cretaceous Tetori biota in Japan and its evolutionary significance for terrestrial ecosystems in Asia. Cretaceous Research 27 (2), 199−225.

Nichols, D.J., Jacobson, S.R., 1982. Palynostratigraphic framework for the Cretaceous (Albian-Maastrichtian) of the overthrust belt of Utah and Wyoming. Palynology 6, 119−147.

Nichols, D.J., Matsukawa, M., Ito, M., 2002. Palynological investigation in the Lower Cretaceous of eastern Asia. Paleoenvironment and age of strata in the Choyr Basin, Mongolia (abstract). Palynology 26, 271−272.

Nichols, D.J., Matsukawa, M., Ito, M., 2006. Palynology and age of some Cretaceous nonmarine deposits in Mongolia and China. Cretaceous Research 27 (2), 241−251.

Sha, J.G., Fürsich, F.T., 1993. Bivalve fauna of eastern Heilongjiang, northeastern China. I. Non-marine bivalves of the Xiachengzi Formation (Lower Cretaceous). Beringaria 8, 139−187.

Shi, B.D., 1982. Bivalvia. In: Xian Institute of Geology and Mineral Resources (Ed.), Palaeontological Atlas of Northwestern China. Fascicule of Shanxi, Gansu and Ningxia. 3. Mesozoic and Cenozoic Volume. Geological Publishing House, Beijing, pp. 3−28 (in Chinese).

Singh, C., 1975. Stratigraphic significance of early angiosperm pollen in the mid-Cretaceous strata of Alberta. Geological Association of Canada, Special Paper 13, 365−389.

Stratigraphical Group, Institute of Geology, Chinese Academy of Geological Sciences (Eds.), 1989. Tectonic-Magmatic Evolution and Metallogeny of Eastern China. No. 2. The Palaeontology and Stratigraphy of the Jurassic and Cretaceous in Eastern China. Geological Publishing House, Beijing, 195 pp. (in Chinese, English abstract).

Suzuki, K., 1941. On some fresh-water shells from the Cretaceous Talatzu series in southeastern Manchoukou. Bulletin of the Geological Institute of Manchoukuo 101, 83−91.

Suzuki, K., 1943. Mesozoic fresh-water shells from the Husin coal-field, southern Manchoukou. Bulletin of the Sigenkagaku Kenkyusho 1 (1), 45−64, pls. 3−4 (in Japanese, English abstract).

Swisher, C.C., Wang, Y.Q., Wang, X.L., Xu, X., Wang, Y., 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. Nature 400, 58−61.

Tamura, M., 1990. Stratigraphic and paleontologic studies on non-marine Cretaceous bivalve fauna in southwest Japan. Kumamoto University Memoirs of the Faculty of Education, Natural Science 39, 1−47 (in Japanese, English abstract).

Wei, Jingming, 1984. Non-marine Bivalvia. In: Section of Geological Survey of Management Bureau of Petroleum of Xinjiang, Party of Regional Geological Survey of Geological Bureau of Xinjiang (Eds.), Palaeontological Atlas of Northwestern China. Fascicule of Xinjiang. 3. Mesozoic and Cenozoic Volume. Geological Publishing House, Beijing, pp. 4−47 (in Chinese).

Wingate, F.H., 1980. Plant microfossils from the Denton Shale Member of the Bokchito Formation (Lower Cretaceous, Albian) in southern Oklahoma. Oklahoma Geological Survey, Bulletin 130. 93 pp.

Yu, J.S., 1982. Lamellibranchia. In: Geological Bureau of Inner Mongolia (Ed.), The Mesozoic Stratigraphy and Palaeotology of Guyang Coal-Bearing Basin Nei Mongol Autonomous Region, China. Geological Publishing House, Beijing, pp. 34−42 (in Chinese).

Yu, J.S., Wang, P., Liu, B.P., et al., 1984. Bivalvia. In: Tianjing Institute of Geology and Mineral Resources, Chinese Academy of Geology Sciences (Eds.), Palaeontological Atlas of Northern China. 2. Mesozoic Fascicule. Geological Publishing House, Beijing, pp. 36−64 (in Chinese).

Yu, J.S., Dong, G.Y., Yao, P.Y., 1987. The distribution and age of bivalves of the Jehol Group. In: Yu, X.H., Wang, W.L., Liu, X.T., Zhang, W., et al. (Eds.). Mesozoic Stratigraphy and Palaeontology of Western Liaoning 3, 1−24. Geological Publishing House, Beijing (in Chinese, English abstract).

Zhou, M.Z., 1953. Mesozoic molluscan fossils from northwestern and Shandong. Acta Palaeontologica Sinica 1, 165−174 (in Chinese).

Zhu, G.X., 1976. Mollusca. In: Bureau of Geology and Mineral Resources of Nei Monggol Province, Northeast Institute of Geology Science (Eds.), Palaeontological Atlas of Northern China, Nei Monggol. 2. Mesozoic and Cenozoic Volume. Geological Publishing House, Beijing, pp. 17−35 (in Chinese).

Zhu, G.X., 1980. Mollusca. In: Shengyang Institute of Geology and Mineral Resources (Ed.), Palaeontological Atlas of Northern China 2. Mesozoic and Cenozoic Volume. Geological Publishing House, Beijing, pp. 8−89 (in Chinese).

Zhu, R.X., Saho, J.A., Pan, Y.X., Shi, R.P., Shai, G.H., Li, D.M., 2002. Paleomagnetic data from Early Cretaceous volcanic rocks of west Liaoning: evidence for intracontinental rotation. Chinese Science Bulletin 47 (21), 1832−1837.