Historical distribution patterns of trigonioidids (non-marine Cretaceous bivalves) in Asia and their palaeogeographic significance

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The non-marine trigonioidid bivalves show five phases of radiation in the Cretaceous of Pal-Asia: pre-Aptian (?Valanginian/Hauterivian–Barremian), Aptian, Albion, Cenomanian and Turonian–Maastrichtian. Their distribution patterns show two distinct palaeo-river systems feeding trigonioidids. Before the Cenomanian, the river system occupied the southwestern–southern–southeastern Pal-Asian continental margin areas. During the Turonian–Maastrichtian, it extended along the line of southcentral China–eastern China–northeast China–northern China and Mongolia–northwestern China–eastern Fergana Basin of Kyrgyzstan–western Tajikistan Basin of Tajikistan–Tashkent area of Kazakhstan–central Kyzylkum of northern Uzbekistan–Aral Sea area of Kazakhstan. Furthermore, the general trigonioidid distribution pattern demonstrates that Japan was probably attached to part of eastern China and/or Korea during the ?Valanginian/Hauterivian–Cenomanian stages.

Keywords: non-marine Bivalvia; Trigonioidacea; Cretaceous; dispersion; biogeography; river system feeding trigonioidids

1. INTRODUCTION

The non-marine trigonioidid bivalves, superfamily Trigonioidacea Cox (1952), are a group of Late Mesozoic Unionoida that are characterized by a minute but very depressed anterior pedal retractor scar, which is distinctly separated from the anterior adductor scar (figure 1; Sha 1990, 1992, 1993, 2007a; Sha & Fürsich 1993). The superfamily can be subdivided into the following four families. Nakamuranaidae Guo (1981): except for commarginal growth lines, shells smooth (e.g. Nakamuranaiia, figure 1a,b). Trigonioididae Cox (1952): shell ornament of V-shaped ribs (e.g. Trigonioides, figure 1c,d). Plicatounionidae Kobayashi (1968): shell ornament of only radial ribs (e.g. Plicatounio, figure 1e,f). Pseudohyriidae Kobayashi (1968): shell with chevron-shaped or reversed V-shaped ribs on the posterior area, but the flank is either smooth or radially ribbed (e.g. Pseudohyria, figure 1g,h; Sha & Fürsich 1993; Sha 2007a).

For the evolutionarily conservative Nakamuranaidae, which shows almost no distinct change throughout its life, trigonioidids varied with the time and even with environment in both ornamentation and hinge structure. They have relatively short geological time ranges and sometimes the trigonioidid-bearing measures are intercalated with marine beds yielding marine fossils including dateable ammonites (e.g. Tamura 1975; Sha & Fürsich 1993; Gu et al. 1997). Also volcanic and tuffaceous rocks can be used to date the rocks radiometrically (e.g. Sha 2007b). Trigonioidids have a wide and abundant distribution in the Cretaceous continental deposits of southern, eastern and middle Pal-Asia and in southern and far eastern Russia (e.g. Yang 1979a; Martinson 1982; Gu 1982; Kobayashi 1984; Ma 1994; Sha 2007a). This specialized group of Cretaceous non-marine bivalves has been studied taxonomically and biostatigraphically for more than 70 years by various authors since trigonioidid forms (Trigonioides and Plicatounio) were first recognized by Kobayashi & Suzuki (1936). The group has been divided into many taxa in numerous individual studies. There are consequently diverging opinions concerning their taxonomy and dating.

Based on the muscle scar diagnosis (at the superfamily level), the general ornament pattern (at the family and subfamily level), the radial ribs—including the VA (angle of V-shaped ribs)—and hinge teeth (at the generic and subgeneric level), Trigonioidacea can be classified into 4 families (see above), 12 subfamilies, 17 genera and 26 subgenera (Sha & Fürsich 1993; Sha 2007a). On the basis of the morphological features, non-marine and marine correlation, as well as a number of the taxonomic revisions at specific level, seven trigonioidid (nakamuranaiid) assemblages, ranging from ?Valanginian/Hauterivian to Maastrichtian, were recognized throughout the region. These seven assemblages appeared in approximately five phases: pre-Aptian (?Valanginian/Hauterivian–Barremian), Aptian, Alban, Cenomanian and Turonian–Maastrichtian stages (see table 1 in Sha 2007a). This implies that trigonioidids underwent five main evolutionary developments during the Cretaceous Period.

The general distribution pattern of trigonioidids have been figured by some authors (e.g. Yang 1979a; Gu 1982; Martinson 1982; Kobayashi 1984; Ma 1994; Sha

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2007a), but their historical biogeographic distribution patterns have not yet been described in detail. This short article mainly tries, by means of historically figuring the spatial distribution patterns of Pal-Asian Trigonioidea excluding Nakamuranaidae, to discuss their palaeogeographic significance. The taxonomic and stratigraphic range schemes of trigonioidids of Sha (2007a) are followed in this work.

2. HISTORICAL DISTRIBUTION PATTERNS OF TRIGONIOIIDS

(a) *Pre-Aptian (?Valanginian/Hauterivian–Barremian) distribution*

Before the Aptian, or during the ?Valanginian/Hauterivian–Barremian interval, the various primitive trigonioidid members, lacking a submedian tooth or crenulation on the hinge teeth (*Pseudohyria* (*Pseudohyrioides*) *cangxiensis* Ma (1982) with a submedian tooth and crenulations on hinge teeth is an unique exception), explosively appeared almost simultaneously in southern, southwestern and eastern Pal-Asia. Phitsanulok Province of northern Thailand, southwestern and central Yunnan, Sichuan, southwestern Qinghai (including Tanggular and southern Hohxil of Qinghai) and Basu of eastern Xizang (Tibet) provinces of southwestern China, Yiyang of northeastern Jiangxi Province of eastern China, Weichang of northeastern Hebei Province of northern China, southern Korea and Tetoiri area of inner side of southwestern Japan, all yield ?Valanginian/Hauterivian–Barremian trigonioidids (figure 2).

In the areas of southwestern China and northern Thailand, a close neighbour of southwestern Yunnan, Sichuan, southwestern Qinghai (including Tanggular and southern Hohxil of Qinghai) and Basu of eastern Xizang (Tibet) provinces of southwestern China, Yiyang of northeastern Jiangxi Province of eastern China, Weichang of northeastern Hebei Province of northern China, southern Korea and Tetoiri area of inner side of southwestern Japan, all yield ?Valanginian/Hauterivian–Barremian trigonioidids (figure 2).
(in Guo 1981) of Plicatounioinidae Kobayashi (1968) and 
_Pseudohyria_ (Pseudohyrioides) cangxensis Ma (1982) of 
Pseudohyrioides Kobayashi (1968) have been reported. 
However, there is only one primitive trigonioidid taxon 
recorded in northeastern Jiangxi Province of eastern 
China (_Koreanaia (Eokoreanaia) cheongi_ Yang (1976) of 
Trigonioididae Cox (1952)), northeastern Hebei Province 
of northern China (Weichangella caelata Yu & Yao (1980) of 
Plicatounioinidae Kobayashi (1968)), southern Korea (_Koreanaia 
(Eokoreanaia) cheongi_ Yang (1976)) and 
Tetori area of inner side of southwestern Japan 
(Nippononaia (Eonipponononaia) tetoriensis Maeda (1962) 
of Trigonioididae Cox (1952)).

(b) Aptian distribution

By the end of the Barremian or during the Aptian time, 
trigonioidids not only thrived in most of their previously 
occupied areas, but also spread rapidly and developed in 
the southern, southeastern and southwestern Pal-Asian 
continent, especially in the continental margin areas 
(figure 3).

In this period, except for a few long-lived forms, all 
the pre-Aptian primitive trigonioidids were extinct or became 
replaced by new forms with submedian tooth (teeth) and/or 
crenulations on hinge teeth and more complicated 
ornamentation at the specific or generic levels (except 
Plicatounio (Plicatounio)). The Aptian stage is characterized 
by the first appearance of _Trigonioides_, and especially 
diversified and abundant _Trigonioides_ and _Plicatounio_. 
The most abundant trigonioidid taxa in this stage were 
_Koreanaia (Koreanaia) bongkyumi_ Yang (1979), _Nippononaia 
(Nippononaia) ryosekiana_ Suzuki (1941), _Nippononaia 
(Nippononaia) sanjienis_ Gu (in Gu et al. 1976), 
_Trigonioides (Wakinoa) wakinoaensis_ Ota (1959), 
_Trigonioides (Trigonioides) kodairai_ Kobayashi & Suzuki (1936), 
_Trigonioides (Trigonioides) quadratus_ Gu & Ma (in Gu et al. 
1976) and _Trigonioides (Trigonioides) kobayashii_ Hoffet 
(1937) of the Trigonioididae; _Plicatounio (Plicatounio) 
naktongensis_ Kobayashi & Suzuki (1936) and _Plicatounio 
(Guangxiconcha) suzukii_ Hoffet (1937) of the 
Plicatounioinidae; and _Pseudohyria (Matsumotoina) matsumotoi_ 
Yang (1979b) of the Pseudohyriidae.

In the south of Pal-Asia, trigonioidids occupied the 
Munong Phalane area of Lower Laos (southern Laos) 
and northeast Khorat Plateau of northern Thailand. In 
thesouthwest, they extended along southwest and central 
Yunnan–eastern Sichuan–Xinaz area of central 
Xizang–Bangongco of western Xizang–eastern Fergana 
Basin of Kyrgyzstan–western Tajikistan Basin of Tajik-
istan. In the southeast, they were distributed from Shiwan-
dashan of southern Guangxi–Luodin, Tengcun and 
Dengta of northern Guangdong–Henyang of southern 
Hunan–Ninghua of western Fujian–Zhejiang–southern 
Anhui–eastern Sandong–western Liaoning–eastern 
Jilin–eastern Heilongjiang–southern Korea–inner side of 
 southwestern Japan and northeastern Japan. Some 
forms extended northwards into Kangxian–Lanzhou 
area of eastern Gansu, even as far as the lower reaches 
of the Lena River, northern Siberia, reaching 60° North 
(figure 3).

(c) Albian distribution

Compared with Aptian and pre-Aptian, Albian trigonioidids 
had a fairly low diversity at both generic and specific levels, 
although some Aptian taxa continued into this stage. They 
are characterized by the first appearance of the forms covered 
with prominent diverse submedian V-shaped ribs (posterior 
branch of submedian V-shaped ribs are very stout and 
widely spaced but anterior ribs fine and densely arranged); 
for example, _Trigonioides (Diverstrigonoides) diversicostatus_ 
Hoffet (1937), _Trigonioides_ (s.s.) bearing multiple 
V-shaped ribs such as _Trigonioides (Trigonioides) 
heilongjiangensis_ Sha & Gu (in Gu et al. 1984; Sha 1992) 
and _Pseudohyria_ (s.s.) such as _Pseudohyria (Pseudohyria) 
subbealis_ Kobayashi (1968). The _Plicatounio_-shaped 
pseudohyriid, _Acinoplicatounio nananensis_ Huang & Ma 
(1979), also appeared during this period.

Albian trigonioidids occur only scattered in the 
Munong Phalane area of Lower Laos (southern Laos), 
the southern part of the northeast Khorat Plateau of 
northern Thailand, Bina area of eastern Xizang

Figure 2. Distribution of pre-Aptian (?Valanginian/Hauterivian–Barremian) trigonioidids (paleocontinental map adapted 
from Smith et al. 1994, map 17).
and Bangongco of western Xizang of southwestern China, Shiwandashan area of southern Guangxi of southern China and southeast Korea, and Zeya-Burein, southern Urgal of Russian Far East (figure 4).

(d) Cenomanian distribution
In Cenomanian time, trigonioidids disappeared from southeast Pal-Asia. They occur only scattered in northeast Khorat Plateau of northern Thailand, Shiwandashan area of southern Guangxi, northeastern China, southeast Korea, and Goshonoura and Mifune areas of southwestern Japan (figure 4).

During the Cenomanian, *Plicatunio* existed with strong and numerous (more than 25) radial ribs on shell surface and dense crenulations on hinge teeth, e.g. *Plicatunio* (*Guangxiconcha*) *tamurai* Guo (1986). Many distinctive taxa appeared in the Cenomanian: *Trigonioides* bearing especially long and/or very strong submedian tooth (teeth), including *Trigonioides* (*Trigonioides*) *paucisulcatus*, *Trigonioides* (*Trigonioides*) *matsumotoi* and *Trigonioides* (*Trigonioides*) *mifunensis*; the forms bearing widely spaced and subequal (no more than eight) radial ribs on shell surface and crenulations on hinges of *Plicatunio*, including *Plicatunio* (*Latiplicatunio*) *latiplicatus* (in Gu et al. 1976; Gu & Yu 1999); and trigonioidids with V-shaped ribs confined on the umbonal area, such as *Martinsonella curta* Hong (in Martinson 1965; Gu & Yu 1999).

(e) Turonian–Maastrichtian distribution
Turonian–Maastrichtian trigonioidids are characterized by the sparsely radially ribbed *Plicatunio*, such as *Plicatunio* (*Plicatunio*) *hunanensis* Zhang (1979), and abundant thick-shelled *Pseudohyria*, including *Pseudohyria* (*Pseudohyria*) *cardiformis* (Martinson 1953), *Pseudohyria* (*Pseudohyria*) *tuberculata* (Martinson 1957) and *Pseudohyria* (*Pseudohyria*) *aralica* (Martinson 1961), and by the lack of *Nippononaia* and *Trigonioides*.

During Turonian–Maastrichtian period, trigonioidids were rare in eastern Pal-Asia, including eastern Hunan of southcentral China, Taizhou of northern Jiangsu and Zhucheng of eastern Shandong of eastern China. However, they are especially abundant along the belt of

Figure 3. Distribution of Aptian trigonioidids (palaeocontinental map adapted from Smith et al. 1994, map 17).

Figure 4. Distribution of Albian trigonioidids (palaeocontinental map adapted from Smith et al. 1994, map 17).
northeastern China including Heilongjiang, Jilin and Liaoning—northern China including Inner Mongolia (including Erlianhaote, Alazuoqi), Shaxi (including Zhuyun), Ningxia (including Alashanzuqi)—Mongolia—northwestern China including Xinjiang (including Kashi)—eastern Fergana Basin of Kyrgyzstan—western Tajikistan Basin of Tajikistan—Tashkent area of Kazakhstan—central Kyzylkum of northern Uzbekistan—the area of Aral Sea of Kazakhstan. They have not been found in southwestern China, southern Korea or Japan (figure 6).

3. PALAEOGEOGRAPHIC SIGNIFICANCE
(a) Palaeo-river system
By plotting the records for Pal-Asia during the Cretaceous it appears that there existed two distinct river systems hosting bivalve trigonioidids.

In Early Cretaceous time (figures 2–4), particularly during the Aptian stage (figure 3), trigonioidid occurrences along the southwestern, southern and southeastern Pal-Asian continent formed a single river system. During the Aptian in the southwest, this river system extended northwards as far as the eastern Fergana Basin of Kyrgyzstan and the western Tajikistan Basin of Tajikistan, in central Pal-Asia (figure 3). In southeast Pal-Asia, rivers extended northeastwards towards the lower reaches of the Lena River, northern Siberia (figure 3). There were numerous branches along the river system, which extended northwards as far as eastern Gansu, southcentral northern China, from southwest, and extended into Hunan and Hubei of southcentral China, from southwest and/or southeast (figure 3).

During the Late Cretaceous, the river system of Pal-Asia changed. In the Cenomanian, the trigonioidids were limited to a river system in the southeastern part but disappeared in southwestern part of Pal-Asia.

However, during the Turonian–Maastrichtian stages, a new distinct wide river system yielding trigonioidids formed. It ran along the line of southcentral China—eastern China—northeastern China—northern China and Mongolia—northwestern China—eastern Fergana Basin of

Figure 5. Distribution of Cenomanian trigonioidids (palaeocontinental map adapted from Smith et al. 1994, map 17).

Figure 6. Distribution of Turonian–Maastrichtian trigonioidids (palaeocontinental map adapted from Smith et al. 1994, map 17).

(b) Palaeogeographic location of Japan
During the ?Valanginian/Hauterivian–Cenomanian stages, Japan was probably attached to part of eastern China and/or Korea, because of the close resemblances between pre-Aptian trigonioidis in these areas and in inner side of southwestern Japan, and these areas were probably occupied by a single fluvial system.

4. DISCUSSION
In this paper, both the taxonomic and stratigraphic schemes for trigonioidis follow the results of Sha (2007a). However, aspects of both the taxonomy and stratigraphy of trigonioidis continue to be discussed. These non-marine trigonioidis are very variable in morphology and occur scattered in both isolated basins and in connected river systems across Pal-Asia (figures 2–6).

The distribution of Pal-Asian Trigonioidis is limited to 15–60° North, with a questionable exception entering 60° North, lower reaches of Lena River Northern Siberia during the Aptian stage (figure 3). Such a general distribution pattern suggests that Cretaceous trigonioidis were controlled by the palaeoclimate/palaeolatitudes and that they were thermophilic molluscs.

There are very wide gaps between some fossil localities of the Albain (figure 4) and the Cenomanian (figure 5). This means that there is a need to find further intermediate trigonioidis localities to help confirm the broad ideas presented here.

In addition to the Asian occurrences of the Trigonioidis, the family is recorded elsewhere globally: ?Picatounio radialis? from the Late Cretaceous of Sudan (Goumard 1956) and ?Picatounio flattersensis? from the Early Cretaceous of Fort-Flatters of Algeria (Mongin 1963), Africa; ?Nippononaiia asinaria? from the Early Cretaceous Burro Canyon Formation of western Colorado, USA (Reeside 1957); ?Pledgia eyensis? from the Cenomanian or latest Albain of Lake Eyre, northern South Australia (Ludbrook 1985); and ?Nippononaiia (Subnippnoraiia) jordi from the Welden Group (Barremian and ?Upper Hauterivan?) of Isle of Wight, southern England (figure 2; Barker et al. 1997).

All the so-called trigonioidis except the English one above were excluded from Trigonioidaceae (Sha 2007a). The English species is without doubt a trigonioidis, although it was merged into ?Koreanaia (Eokoreanaia)? Sha and Fürsich (Sha 2007a). It bears typical trigonioidis anterior pedal retractor scars and submedial V-shaped and anterior and posterior reversed V-shaped ribs. It probably migrated from the Pal-Asian continent. However, the migration or interchange between the English and Pal-Asian Cretaceous trigonioidis remains to be precisely studied, as do the relations between Pal-Asian trigonioidis and the so-called trigonioidis in Africa, North America and Australia.

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