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

Jingeng Sha*

LPS, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

The non-marine trigonioidid bivalves show five phases of radiation in the Cretaceous of Pal-Asia: pre-Aptian (?Valanginian/Hauterivian–Barremian), Aptian, Albian, 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–northeastern 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; Trigonoidacea; Cretaceous; dispersion; biogeography; river system feeding trigonioidids

1. INTRODUCTION

The non-marine trigonioidid bivalves, superfamily Trigonoidacea 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. Nakamuranaiidae Guo (1981): except for commarginal growth lines, shells smooth (e.g. *Nakamuranaia*, figure 1a,b). Trigonoididae 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).

Except for the evolutionarily conservative Nakamuranaiidae, 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). Trigonoidids 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 biostratigraphically 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), Trigonoidacea 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 (nakamuranaiids are excluded because of their morphology having no clear change in their history, as mentioned above) 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, Albian, 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

* jgsha@nigpas.ac.cn

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Figure 1. Morphological characteristics of Trigonioidea. (a–d,f) Right valve, (e,g,h) left valve, (a,c,e,g) external view and (b,d,f,h) internal view. Scale bar, 1 cm (adapted from Sha 2007a, fig. 1). aa, anterior adductor scar; aarv, angle of anterior revised V-shaped ribs; aprv, angle of posterior revised V-shaped ribs; arvr, anterior reversed V-shaped ribs; asmv, angle of submedian V-shaped radial ribs; cgl, commarginal (concentric) growth line; hcr, hinge crenulation; imcr, internal marginal crenulation; pa, posterior adductor scar; pl, pallial line; plt, posterior lamellar tooth (teeth); prvr, posterior reversed V-shaped ribs; rr, radial rib; smvr, submedian V-shaped radial ribs; smt, submedian tooth (teeth).

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 Nakamuraniidae, 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 TRIGONIOIDIDS

(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 Tetori 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, the primitive representatives of all trigonioidid families, such as *Cyotrigonioides yunnanensis* Guo (1981), *Danlengiconcha elongata* Liu (in Cai & Liu 1978), *Koreanaia* (*Eokoreanaia*) *cheongi* Yang (1976), *Koreanaia* (*Eokoreanaia*) *antiqua* Gu & Ma (in Ma *et al.* 1976), *Koreanaia* (*Eokoreanaia*) *qinghaiensis* (Sha 1995; Sha & Grant-Mackie 1996) and *Peregrinoconcha yunnanensis* Chen & Lan (in Gu *et al.* 1976), all of Trigonioidea Cox (1952), *Plicatunio* (*Plicatunio*) *rostratus* Guo & Zhang

Figure 2. Distribution of pre-Aptian (?Valanginian/Hauterivian–Barremian) trigoniodids (palaeogeographical map adapted from Smith *et al.* 1994, map 17).

(in Guo 1981) of Plicatounioididae Kobayashi (1968) and *Pseudohyria* (*Pseudohyrioides*) *cangxiensis* Ma (1982) of Pseudohyriidae Kobayashi (1968) have been reported. However, there is only one primitive trigoniodid taxon recorded in northeastern Jiangxi Province of eastern China (*Koreanaia* (*Eokoreanaia*) *cheongi* Yang (1976) of Trigoniodidae Cox (1952)), northeastern Hebei Province of northern China (*Weichangella caelata* Yu & Yao (1980) of Plicatounioididae Kobayashi (1968)), southern Korea (*Koreanaia* (*Eokoreanaia*) *cheongi* Yang (1976)) and Tetori area of inner side of southwestern Japan (*Nippononaia* (*Eonippononaia*) *tetoriensis* Maeda (1962) of Trigoniodidae Cox (1952)).

(b) Aptian distribution

By the end of the Barremian or during the Aptian time, trigoniodids 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 trigoniodids 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 trigoniodid taxa in this stage were *Koreanaia* (*Koreanaia*) *bongkyuni* Yang (1979b), *Nippononaia* (*Nippononaia*) *ryosekiana* Suzuki (1941), *Nippononaia* (*Nippononaia*) *yanjiensis* Gu (in Gu *et al.* 1976), *Trigonioides* (*Wakinoa*) *wakinoensis* (Ota 1959), *Trigonioides* (*Trigonioides*) *kodairai* Kobayashi & Suzuki (1936), *Trigonioides* (*Trigonioides*) *quadratus* Gu & Ma (in Gu *et al.* 1976) and *Trigonioides* (*Trigonioides*) *kobayashi* Hoffet (1937) of the Trigoniodidae; *Plicatounio* (*Plicatounio*) *naklongensis* Kobayashi & Suzuki (1936) and *Plicatounio* (*Guangxiconcha*) *suzukii* Hoffet (1937) of the

Plicatounioididae; and *Pseudohyria* (*Matsumotoina*) *matsumotoi* Yang (1979b) of the Pseudohyriidae.

In the south of Pal-Asia, trigoniodids occupied the Munong Phalane area of Lower Laos (southern Laos) and northeast Khorat Plateau of northern Thailand. In the southwest, they extended along southwest and central Yunnan–eastern Sichuan–Xainza area of central Xizang–Bangongco of western Xizang–eastern Fergana Basin of Kyrgyzstan–western Tajikistan Basin of Tajikistan. In the southeast, they were distributed from Shiwandashan of southern Guangxi–Luodin, Tangcun and Dengta of northern Guangdong–Henyang of southern Hunan–Ninghua of western Fujian–Zhejiang–southern Anhui–eastern Shandong–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 trigoniodids 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* (*Diversitrigonioides*) *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*) *subovalis* Kobayashi (1968). The *Plicatounio*-shaped pseudohyriid, *Acclinoplicatounio nananensis* Huang & Ma (1979), also appeared during this period.

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

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

Figure 4. Distribution of Albian trigonoioidids (palaeocontinental 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, trigonoioidids 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 5).

During the Cenomanian, *Plicatounio* existed with strong and numerous (more than 25) radial ribs on shell surface and dense crenulations on hinge teeth, e.g. *Plicatounio* (*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 *Plicatounio*, including *Plicatounio* (*Latiplicatounio*) *latiplicatus* (in Gu *et al.* 1976; Gu & Yu 1999); and trigonoioidids 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 trigonoioidids are characterized by the sparsely radially ribbed *Plicatounio*, such as *Plicatounio* (*Plicatounio*) *hunanensis* Zhang (1979), and abundant thick-shelled *Pseudohyria*, including *Pseudohyria* (*Pseudohyria*) *cardiiformis* (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, trigonoioidids 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 5. Distribution of Cenomanian trigonioidids (palaeogeographic map adapted from Smith *et al.* 1994, map 17).

Figure 6. Distribution of Turonian–Maastrichtian trigonioidids (palaeogeographic 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 northwestwards 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

Kyrgyzstan–western Tajikistan Basin of Tajikistan–Tashkent area of Kazakhstan–central Kyzylkum of northern Uzbekistan–Aral Sea area of Kazakhstan.

(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 trigonioidids 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 trigonioidids follow the results of Sha (2007a). However, aspects of both the taxonomy and stratigraphy of trigonioidids continue to be discussed. These non-marine trigonioidids 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 Trigonoidids 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 trigonioidids were controlled by the palaeoclimate/paleolatitudes and that they were thermophilic molluscs.

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

In addition to the Asian occurrences of the Trigonoididae, the family is recorded elsewhere globally: *Plicatounio radiei* from the Late Cretaceous of Sudan (Goumard 1956) and *Plicatounio flattersensis* from the Early Cretaceous of Fort-Flatters of Algeria (Mongin 1963), Africa; *Nippononaia asinairia* from the Early Cretaceous Burro Canyon Formation of western Colorado, USA (Reeside 1957); *Pledgia eyensis* from the Cenomanian or latest Albian of Lake Eyre, northern South Australia (Ludbrook 1985); and *Nippononaia* (*Subnippononaia*) *fordi* from the Wealden Group (Barremian and ?Upper Hauterivian) of Isle of Wight, southern England (figure 2; Barker *et al.* 1997).

All the so-called trigonioidids except the English one above were excluded from Trigonoidacea (Sha 2007a). The English species is without doubt a trigonioidid, although it was merged into *Koreanaia* (*Eokoreanaia*) Sha and Fürsich (Sha 2007a). It bears typical trigonioidid 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 trigonioidids remains to be precisely studied, as do the relations between Pal-Asian trigonioidids and the so-called trigonioidids in Africa, North America and Australia.

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