

Early Albian *Mytiloides* (Inoceramidae, Bivalvia) from the Northwest Pacific: a pioneering species for Late Cretaceous inoceramid diversification

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Abstract. The inoceramid bivalve *Mytiloides ipuanus* (Wellman, 1959) from the Lower Albian is reported for the first time in the Northwest Pacific and described in detail. This is the oldest record of a Cretaceous inoceramid in this region. It is possible that the present study documents the origin of the extreme diversification and abundance of inoceramid bivalves in the Late Cretaceous of the Northwest Pacific. The beginning of inoceramid diversification in the Late Cretaceous is seen during the latest Early Cretaceous, which suggests that *M. ipuanus* is an important species for inferring the causes of the Late Cretaceous flourishing of inoceramids.

Key words: Albian, Cretaceous, diversity, inoceramid, Japan, *Mytiloides*

Introduction

Inoceramid bivalves originated in the Permian (Waterhouse, 1970) and flourished worldwide in the Late Cretaceous (e.g., Tröger, 1989; Dhondt, 1992; Voigt, 1995; MacLeod *et al.*, 2000). The inference that most inoceramid adults were epibyssate or endobyssate benthos (e.g., Stanley, 1972; Harries and Crampton, 1998) implies that they should have been strongly affected by marine environmental changes. As a result, inoceramids are presumably suitable for investigating the relationships between diversity changes and submarine environmental changes. Furthermore, the fact that inoceramids evolved rapidly means that their stratigraphic distributions are short, so they are an important intrabasinal correlation tool, occasionally even an interbasinal correlation tool, for the Cretaceous. Accordingly, numerous studies of inoceramid biostratigraphy and systematic palaeontology have been conducted since the last century.

Inoceramids thrived in the North Pacific in Japan, Far East Russia, Alaska, and the West Coast of North America during the Late Cretaceous. For example, Takahashi (2005a) documented inoceramid species-diversity changes in Japan during Albian to Maastrichtian time, and observed many species. Inoceramid diversification in the Late Cretaceous of the Northwest Pacific began in the Albian (Dhondt, 1992; Voigt, 1995;

MacLeod *et al.*, 2000; Takahashi, 2005a). Therefore, in order to investigate the causes of the flourishing and diversification of inoceramids in the Late Cretaceous, it is important to study the pioneering species, namely those in the early Albian. Takahashi (2005a) verified that Albian (Early Cretaceous) inoceramid occurrences in Japan are very scarce compared with Late Cretaceous occurrences. Recently, however, we discovered in Japan the Early Albian inoceramid *Mytiloides ipuanus* (Wellman, 1959). Previous reports of *M. ipuanus* have been restricted to New Zealand, where it ranges from the early to late Albian (Crampton *et al.*, 2004) and was once thought to be endemic, and Antarctica (Crame, 1985).

The present study documents the origin of inoceramids in the Late Cretaceous Northwest Pacific, and the morphological characters of the pioneering Early Albian species. We report the first occurrence of the important species *M. ipuanus* in Japan, and describe it in detail. We consider *M. ipuanus* to be the pioneering species that gave rise to Late Cretaceous inoceramid abundance and diversification in the Northwest Pacific.

Geological setting

The Yezo Group (= Yezo Supergroup of Okada, 1983; see Takahashi *et al.*, 2004) is represented by a thick sequence

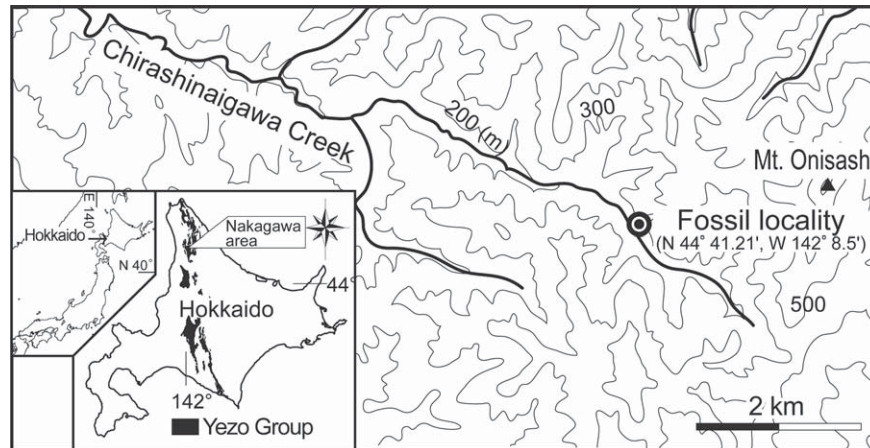


Figure 1. Map showing the locality of inoceramid fossils. The Yezo Group on central Hokkaido Island is also shown.

of clastic sediments about 8,000 m thick, which was deposited in the Aptian–Paleocene forearc basin of the East Asian active margin that extended from southern Hokkaido north to Sakhalin Island (Far East Russia) (e.g., Okada, 1982; Takashima *et al.*, 2004). The Upper Cretaceous strata of this group on Hokkaido Island, northern Japan, yield abundant and diverse ammonoids, inoceramids and other molluscan taxa at various horizons. The Upper Cretaceous in Japan has been established as a bio- and lithostratigraphic standard for the Northwest Pacific region (Toshimitsu *et al.*, 1995), and provides important data on Cretaceous molluscan evolution and diversity changes. In contrast to the Upper Cretaceous, the Lower Cretaceous part of the Yezo Group yields extremely scarce molluscan fossils.

The Yezo Group in the Nakagawa area (= Teshionakagawa area of Takahashi *et al.*, 2003, 2007), northern Hokkaido is subdivided into ten formations: the Kamiji, Moehoro, Shirataki, Sakotandake, Sakugawa, Saku, Nishichirashinai, Omagari, Osoushinai and Hokobuchi formations, in ascending stratigraphic order (Kawaguchi, 1997; Takahashi *et al.*, 2003). The Kamiji Formation represents the lowest portion of the Yezo Group in this area. It consists mainly of mudstone and alternating beds of sandstone and mudstone, and has been subdivided into eight lithostratigraphic units (Kj1 to Kj8, in ascending order) by Hashimoto *et al.* (1967). Inoceramid specimens reported in the present paper were recovered from mudstone of the Kj5 unit of the Kamiji Formation in the Nakagawa area, northern Hokkaido, at an exposure along Chirashinaigawa Creek (Figure 1, identical to the Chirashinai “River” of Takahashi *et al.*, 2003, 2007, etc.). The Kj5 unit is more than 200 m thick in this section and consists of sandy mudstone and alternating beds of sandstone and mudstone. The sandstone beds represent a fine-grained turbidite facies. Macrofossils are very rare in this lithostratigraphic unit. The Early Albian ammonite *Archtoplites* (*Sub-*

archtoplites) sp. has been reported (Iba, 2008) from the same horizon as the inoceramids.

Systematic Palaeontology

Family Inoceramidae Giebel, 1852
Genus *Mytiloides* Brongniart, 1822
Mytiloides ipuanus (Wellman, 1959)

Figures 2A, 2B and 2C

Inoceramus ipuanus n. sp. Wellman, 1959, p. 157, pl. 11, fig. 6.
Inoceramus kapuus n. sp. Wellman, 1959, p. 159–160, pl. 12, fig. 11.
Inoceramus urius n. sp. Wellman, 1959, p. 157–158, pl. 11, fig. 7.
Inoceramus kapuus Wellman. Stevens, 1978, p. 365, fig. 6. 3–11.
Inoceramus ipuanus Wellman. Stevens, 1978, p. 365, fig. 6. 3–15.
Inoceramus ipuanus Wellman. Raine *et al.*, 1981, p. 240, pl. 1, fig. 3.
Inoceramus kapuus Wellman. Raine *et al.*, 1981, p. 240, pl. 1, figs. 7, 8.
Inoceramus urius Wellman. Crame, 1985, p. 493, pl. 56, fig. 2.
Mytiloides ipuanus (Wellman). Crampton, 2004, p. 1093, fig. 3: 1–8.

Type.—Holotype: TM2115, collection GS5830, locality O31/f8516, Split Rock Formation, Seymour Stream, Clarence Valley, Marlborough, New Zealand. Right valve. Preserved in poorly sorted, calcareous, coarse-grained sandstone. Latex cast of complex composite external mold preserving features of the external surface, shell interface (between internal nacreous and outer prismatic layers) and, presumably, internal surface; features of shell interface dominant (Wellman, 1959; Crampton, 2004).

Material.—Three specimens, UMUT MM30052 to 30054 (Figure 2), which were recovered from the Kamiji Formation of the Yezo Group in the Nakagawa area (Figures 1 and 2; see below (*Occurrence*)).

Diagnosis.—Adult shell moderate, elongate, mytiliform, inequilateral, with growth axis fairly to weakly convex towards posterior margin. Anterior margin straight to slightly concave, passing into fairly convex ventral margin. Ven-

tral region broad. Posteroventral margin straight to convex, passing into elongated nearly straight to slightly convex posterodorsal margin. Umbo with beak pointed and finely curved anteriorly. Sculpture on juvenile outer shell surface consists of relatively acute, moderately close, irregularly to relatively regularly spaced ribs. External shell surface of middle to adult growth stage, with irregular to relatively regular, and relatively wide-spaced, nearly round-topped ribs. There are some variations in the shell ornamentation, and in the strength and regularity of the ribs.

Description.—Shell small to moderate (left valve, maximum 73.20 mm high, 35.80 mm long), prosocline, elongate, mytiliform, with growth axis fairly convex towards posterior margin, and extremely inequilateral outline. Anterior margin slightly concave, long (equal to nearly 50 per cent of the corresponding axial length), passing into a moderately long, convex anteroventral margin. Ventral region broad, ventral margin fairly convex, rounded. Posteroventral margin convex, then nearly straight, passing into elongated posterodorsal margin. Posterodorsal margin slightly convex and long. Hinge line missing in available material. Umbo with beak pointed and finely curved anteriorly. Anterior and posterior auricle not well enough preserved to see. Shell very weakly inflated, with maximum inflation in posterodorsal area and secondary inflation in anterodorsal region.

Sculpture on juvenile outer shell surface consists of relatively acute, moderately close, irregularly spaced ribs. Middle to adult growth stage of shell interface (between internal nacreous and outer prismatic layers, sensu Crampton, 2004) usually with irregularly and relatively widely spaced, nearly flat- to round-topped ribs (folds). The shell typically is rather thin.

Occurrence.—Lower Albian Substage, in which it occurs with the ammonite *Archthoplites* (*Subarchthoplites*) sp. (Iba, 2008) in the K_j5 unit of the Kamiji Formation (Yezo Group) in the Nakagawa area, northern Hokkaido, Northern Japan (Figure 1).

Remarks.—We were able to observe only three specimens, including two juvenile individuals (UMUT MM30053 and 30054); the above shell characters are based mainly on specimens UMUT MM30052 and 30053 (Figures 2A and 2B), which are left valves. The right valve (UMUT MM30054) may have a narrow posterior wing, shown in Figure 2C, which gradually changes along the shell disk. The shell form may be slightly inequivalve to subequivalve, as shown in Figure 2. There are some variations in the strength and regularity of the ribs, shell ornamentation and shell form.

Comparison.—The *Inoceramus carsoni* group (Crame, 1985), including *I. carsoni* McCoy and *I. sutherlandi* McCoy from the Upper Albian of Northeast Australia (Crame, 1985; Henderson, 2004), southernmost Argentina (Olivero and Martinioni, 1996) and Antarctica (Kelly and Moncrieff, 1992) morphologically resembles *M. ipuanus*. However, *M.*

ipuanus as described herein occurred in the Lower Albian and is distinguished from the *Inoceramus carsoni* group by its lesser valve inflation. In addition, the form of the growth axis of the figured *M. ipuanus* specimens, especially Figure 2A (UMUT MM30052), is more convex toward the posterior margin than seen in the *I. carsoni* group (Crame, 1985; Olivero and Martinioni, 1996).

The concentric ribs on the holotype of “*Inoceramus ipuanus*” seen in Wellman (1959) and Crampton (2004) are finer and more regular than those of our three specimens. The holotype of “*I. ipuanus*” is similar in the overall elongate outline and mytiliform appearance to UMUT MM30052 (Figure 2A), and the form (curves) of the growth axis of the holotype somewhat resembles our three specimens. Although the outline of the holotype of “*I. kapuus*” is partly unclear, especially the posterior margin, the specimen is very similar in the curves of the concentric ribs, convexity of the growth axis and elongate outline to our UMUT MM30052 (Figure 2A). The concentric ribs on the holotype of “*I. urius*” are much weaker than those of our material (Figure 2), because the former specimen comprises a composite internal mold of a juvenile of *M. ipuanus* (see below (*Discussion.*)). However, the elongate outline and acute umbo of the holotype of “*I. urius*” bear an extreme resemblance to our available material.

Discussion.—Crampton (2004) and Crampton *et al.* (2004) have synonymized three nominal species of Wellman (1959), “*Inoceramus ipuanus*”, “*I. kapuus*” and “*I. urius*.” Crampton (2004) claimed that the holotype of “*I. kapuus*” is a subadult external shell surface of *M. ipuanus*, while the holotype of “*I. urius*” is a composite internal mold of a juvenile of *M. ipuanus*. The present study follows this concept. Thus, inoceramid bivalves as well as *M. ipuanus* may be seen as different species on the basis of different taphomorphs (the term following Crampton, 2004), including the internal mold, shell interface and external shell surface.

Repository.—The abbreviation UMUT indicates that the repository of the specimens described herein is the University Museum, the University of Tokyo.

Importance of *Mytiloides ipuanus* as a pioneering species for Late Cretaceous inoceramid diversification in the Northwest Pacific

Takahashi (2005a) documented inoceramid species-diversity changes in Japan during the late Albian to Maastrichtian, and observed that 94 described species and ten genera occur only in Japan. Since Japanese Cretaceous strata are widely distributed, they contain a continuous and abundant record of inoceramids. As a result, the Northwest Pacific region is an appropriate area to investigate and elucidate inoceramid-diversity changes, including their extinction and origination rates. In the Northwest Pacific,

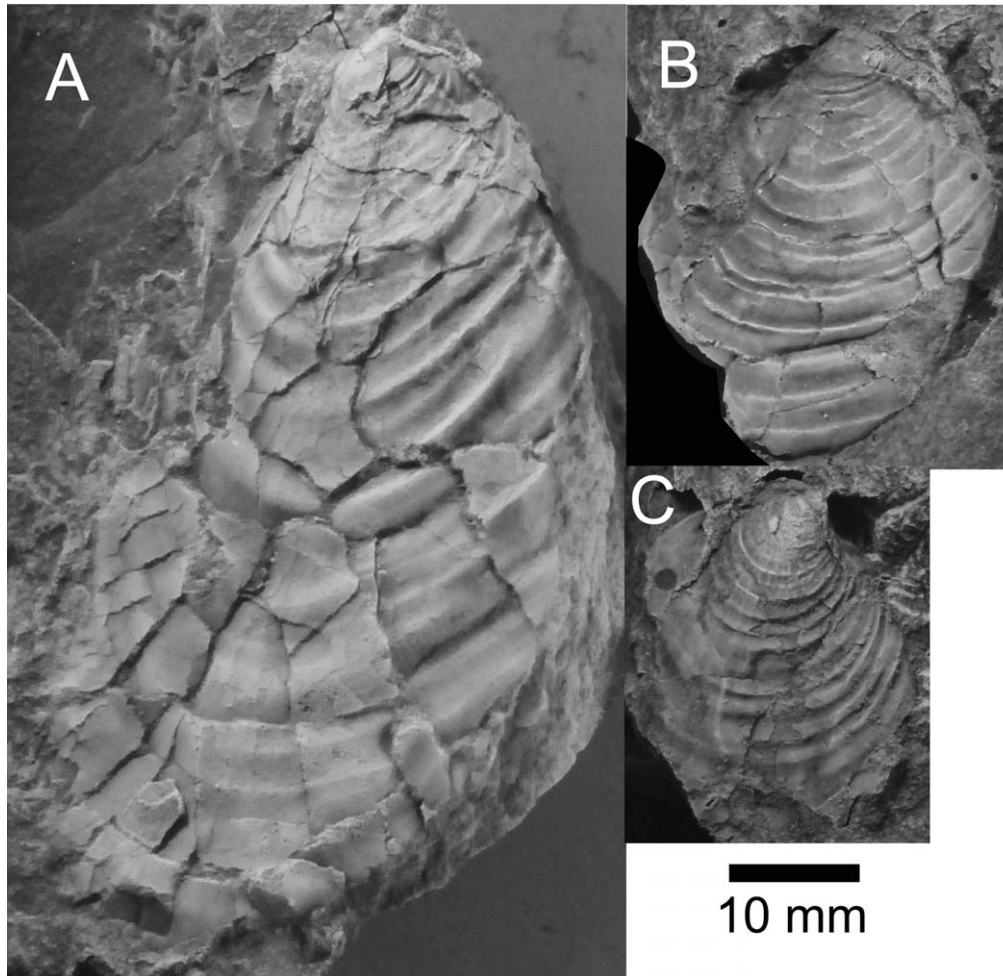


Figure 2. Photographs of inoceramid (*Mytiloides*) specimens. **A.** *Mytiloides ipuanus* (Wellman). UMUT MM30052, left valve, shell interface (between internal nacreous and outer prismatic layers). **B.** *Mytiloides ipuanus*. UMUT MM30053, left valve, external shell surface. **C.** *Mytiloides* cf. *ipuanus*. UMUT MM30054, right valve, internal mold.

inoceramid bivalves were extremely diverse and abundant during the Late Cretaceous (Figure 3; Takahashi, 2005a). Although pre-Albian Lower Cretaceous fossiliferous marine deposits containing abundant molluscan fossils are widely distributed in Japan (e.g., Hayami, 1975), there have been no reports of inoceramids in this time period. This suggests that the absence of inoceramids was not the result of depositional facies effects and/or lack of Lower Cretaceous marine strata. Diversity increased gradually during the Cenomanian to Campanian and reached a maximum in the Early Campanian, and then suddenly dropped in the Late Campanian (Figure 3). Inoceramid diversity and abundance are inferred to have been sensitive to marine environmental changes (Takahashi, 2005a, b). For example, Takahashi (2005a, b) verified that changes in inoceramid species-diversity, as well as extinction and origination rates, were strongly affected by sea-level changes and oceanic anoxic events. Accordingly,

studying inoceramid diversity is important for inferring marine conditions and environments during the Cretaceous.

It has been demonstrated that Cretaceous inoceramids began to diversify and become abundant during the Albian Stage in the Northwest Pacific (e.g., Tröger, 1989; Dhondt, 1992; Voigt, 1995; MacLeod *et al.*, 2000; Takahashi, 2005a). In particular, Takahashi (2005a) reported that Cretaceous Japanese (Northwest Pacific) inoceramids appeared during the Late Albian Substage (Figure 3). Five species of Albian inoceramids have been reported in Japan (e.g., Takahashi, 2005a), namely *Actinoceramus concentricus* (Parkinson), *A. sulcatus* (Parkinson) (including the synonymous species *A. subsulcatus* (Wiltshire) sensu Crampton, 1996; Crampton in Kennedy *et al.*, 1999; Crampton and Gale, 2009), *Inoceramus anglicus* Woods, *I. aff. reachensis* Etheridge, and *I. virgatus* Schlüter. However, all five species are also known in the Upper Albian (partly known in the Cenomanian). Be-

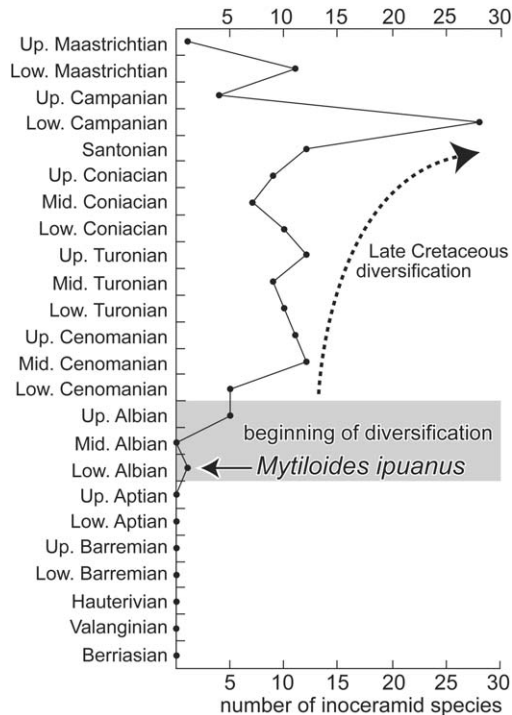


Figure 3. Species-diversity changes in inoceramid bivalves of Japan. The data are revised after Takahashi (2005a). New data (occurrences of *Mytiloides ipuanus*) are added to the Early Albian of Takahashi (2005a).

cause of the difficulty in recognizing the Middle Albian Substage in the Northwest Pacific region due to the paucity of index fossils (Iba and Sano, 2008), we cannot discuss the existence of Middle Albian inoceramids in this region. *Mytiloides ipuanus* of the present study occurred only in the Lower Albian, and is the oldest Cretaceous inoceramid in Japan (with the possible exception of *Inoceramus maedae* Hayami in the Mitarai Formation of the Tetori Group, because the age of the formation is currently uncertain (see Matsukawa *et al.*, 2006; Goto, 2007; Sano *et al.*, 2008; Sato *et al.*, 2008)).

A. concentricus and *A. sulcatus* occur worldwide, including Europe, the Mediterranean, the Western Interior Seaway, the North and South Pacific, the South Atlantic, and Antarctica (Crame, 1985; Marcinowski and Radwan-ski, 1989; Dhondt, 1992; Crampton, 1996; Kennedy *et al.*, 1999; Fenner, 2001a, b; Prokoph and Thurow, 2001; Wiedmann and Owen, 2001; Crampton and Gale, 2005; Lazo, 2006; Lehmann *et al.*, 2007). *I. anglicus* and *I. virgatus* also have widespread distributions, though the latter species occurs mainly in the Cenomanian (Crame, 1985; Matsumoto *et al.*, 1987; Marcinowski and Radwan-ski, 1989; Dhondt, 1992; Gale *et al.*, 1996; Gallemí *et al.*, 1997; Prokoph and Thurow, 2001; Wilmsen and Niebuhr, 2002; Kozai *et al.*, 2005). Thus,

the general appearance of the Albian inoceramids from Japan is widespread palaeobiogeographic distribution. Although *M. ipuanus* has been considered endemic to New Zealand (Wellman, 1959; Stevens, 1978; Raine *et al.*, 1981; Crampton, 2004; Crampton *et al.*, 2004) and Antarctica (Crame, 1985), our study shows that it also lived in Japan of the North Pacific. *M. ipuanus* evidently was a common Albian inoceramid that was widely distributed in both the North and South Pacific.

M. ipuanus as described herein first appeared and is likely the pioneering species for inoceramid diversification in the Northwest Pacific (e.g., Figure 3; Takahashi, 2005a). Inoceramids in other regions also began to diversify, mainly in the Albian Stage (e.g., Dhondt, 1992; fig. 1 in Voigt, 1995; fig. 6 in Gradstein *et al.*, 1999). The eventual cosmopolitan inoceramid diversification of the Late Cretaceous started in the latest Early Cretaceous, namely the Albian Stage, which implies that *M. ipuanus* would be an important species for elucidating the causes of the great Late Cretaceous inoceramid explosion.

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