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Larval ecology of Cretaceous inoceramid bivalves from northwestern Hokkaido, Japan

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Abstract. Larval shell morphology of four Cretaceous inoceramid species, *Inoceramus tenuistriatus*, *Inoceramus hobetsensis*, *Inoceramus amakusensis* and *Sphenoceramus naumanni* was examined on the basis of well-preserved specimens from the Yezo Group in the Tappu area, northwestern Hokkaido. SEM observations reveal that all of the four species possess large prodissoconchs with a similar shape. Relatively small prodissoconch I and large prodissoconch II indicate that they all underwent a long planktotrophic larval stage. This result as well as the available biogeographic data in the north Pacific Bioprovince suggest that these four species had a high dispersal capability in the larval stage.

Key words: dispersal capability, inoceramid bivalves, larval ecology, prodissoconch, Upper Cretaceous

Introduction

Inoceramid bivalves have long been used as good indices for Upper Cretaceous biochronology because of their wide biogeographic distributions and relatively short species longevities (Kauffman, 1977; Dhondt, 1992). On the other hand, only a few authors have focused on the ecological aspect of inoceramids (Hayami, 1969; Stanley, 1972; Tanabe, 1973). It has long been postulated that the worldwide distribution of some inoceramids (e.g., *Mytiloides labiatus*) was achieved by their planktotrophic larval ecology (Kauffman, 1975). However, this assumption has not been based on any direct evidence.

Larval ecology of an invertebrate determines the dispersal capability of the animal, and this, in turn, affects the geographic distribution of the species. In bivalve molluscs, larval shell morphology can be utilized as a reliable basis for larval ecology (Ockelmann, 1965; Jablonski and Lutz, 1980; Waller, 1981; Palmer, 1989). Recently, Knight and Morris (1996) for the first time reported larval shells of inoceramids from the Albian of southern England and showed that some inoceramids had a long-lived planktotrophic larval stage. In Knight and Morris (1996), however, taxonomic positions of the larval shells were inferred from the adult specimens of some coexistent species and were not determined convincingly. As pointed out by Gili and Martinell (1994), the duration of the planktotrophic

stage is variable among species belonging to the same genus. Therefore, larval ecology and dispersal capability should be studied in each species.

I have attempted to observe the early shell portion of a juvenile individual the taxonomic relationship of which can be determined. This paper reports the larval shell morphology in a total of four Upper Cretaceous species and evaluates the dispersal capability of these species.

Notes on larval development of Bivalvia

Among the Bivalvia, in the early growth stage a larva develops from a fertilized egg via the nonfeeding trochophore stage into the feeding veliger stage with a velum (Waller, 1981; Palmer, 1989). The entire shell which is formed prior to metamorphosis is called a prodissoconch. The prodissoconch is divided into two stages, namely prodissoconch I (pd. I) and prodissoconch II (pd. II). Pd. I is secreted by the shell gland and poorly differentiated mantle epithelium in the early veliger stage (Carriker and Palmer, 1979). It has a D-shaped outline with straight hinge line possessing a micropunctate texture, but lacks growth lines. On the other hand, pd. II is secreted mainly at the mantle edge along the shell margin and inside the pd. I in the late veliger stage (Carriker and Palmer, 1979). Pd. II has well-developed commarginal growth lines on its external surface, which distinguish pd. II from pd. I (Waller, 1981).

Table 1. List of materials examined and summary of biometric data of prodossoconchs. For localities of samples, see Tanaka (1963). The locality numbers in parenthesis indicate the locality from which the calcareous concretions in the river gravel were obtained. Horizons are indicated with members based on Tsushima *et al.* (1958). LV: left valve, RV: right valve, pd I L.: length of prodossoconch I (μm), pd II L.: length of prodossoconch II (μm).

Species	registered no.	LV/RV	locality	horizon	age	pd. I L.	pd. II L.
<i>Inoceramus tenuistriatus</i> Nagao and Matsumoto	SUM-MM-B0253	RV	NH285	Mm-o	Turonian	<210	630
<i>I. hobetsensis</i> Nagao and Matsumoto	SUM-MM-B0254	LV	NH285	Mm-o	Turonian	<240	>530
<i>I. amakusensis</i> Nagao and Matsumoto	SUM-MM-B0255	RV	NH490	Uf	Santonian	<180	>480
	SUM-MM-B0256	RV	NH490	Uf	Santonian		
	SUM-MM-B0257	RV	NH490	Uf	Santonian	120	640
	SUM-MM-B0258	LV	NH490	Uf	Santonian		680
	SUM-MM-B0259	LV	(NH485)				650
<i>Sphenoceras naumanni</i> (Yokoyama)	SUM-MM-B0260	RV	NH485	Uf	Santonian		620
	SUM-MM-B0260	LV	NH485	Uf	Santonian		700
	SUM-MM-B0262	LV	NH490	Uf	Santonian		610
	SUM-MM-B0263	RV	NH490	Uf	Santonian		>600
	SUM-MM-B0264	LV	NH490	Uf	Santonian		500
	SUM-MM-B0265	LV	NH490	Uf	Santonian		600
	SUM-MM-B0266	RV	NH490	Uf	Santonian		680
	SUM-MM-B0267	LV	NH490	Uf	Santonian		540
	SUM-MM-B0268	LV	NH490	Uf	Santonian		810
	SUM-MM-B0269	LV	NH490	Uf	Santonian		550
	SUM-MM-B0270	RV	NH490	Uf	Santonian		700
	SUM-MM-B0271	LV	NH490	Uf	Santonian	< 80	>560
	SUM-MM-B0272	LV	(NH490)				680

After settlement onto the seafloor, a larva begins to form the adult shell, or dissoconch (d), with a clear constriction at the pd. II-d boundary. The dissoconch grows additionally around the periphery of the prodossoconch. In inoceramids, the boundary between prodossoconch and dissoconch is distinct in a well-preserved specimen, since the dissoconch consists of prismatic calcite while the prodossoconch has a granular texture (Knight and Morris, 1996).

Materials and methods

A total of 20 inoceramid larval shells belonging to four species, *Inoceramus tenuistriatus* Nagao and Matsumoto, 1939, *I. hobetsensis* Nagao and Matsumoto, 1939, *I. amakusensis* Nagao and Matsumoto, 1940 and *Sphenoceras naumanni* (Yokoyama, 1890) were studied (Table 1). They were preserved in calcareous concretions from the Upper Cretaceous along the Obirashibe River and its branches in the Tappu area, northwestern Hokkaido, Japan (Figure 1). Specimens of *I. tenuistriatus* and *I. hobetsensis* were obtained from the Turonian, and *I. amakusensis* and *S. naumanni* from the Santonian. All the specimens examined are housed in Shizuoka University (SUM).

Shells of inoceramids were exposed by carefully removing the muddy matrix of calcareous concretions using a small cutting knife. They were distinguished from the matrix under a binocular microscope by their brownish color,

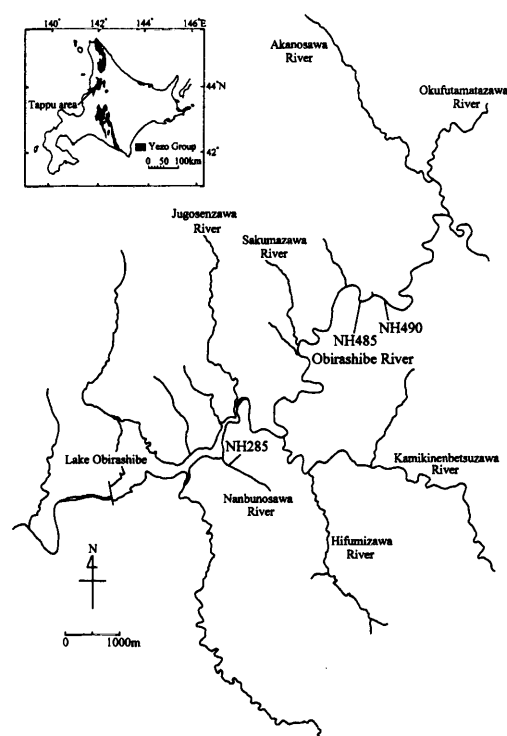


Figure 1. Index map of the Tappu area. For locality of samples, refer to Tanaka (1963).

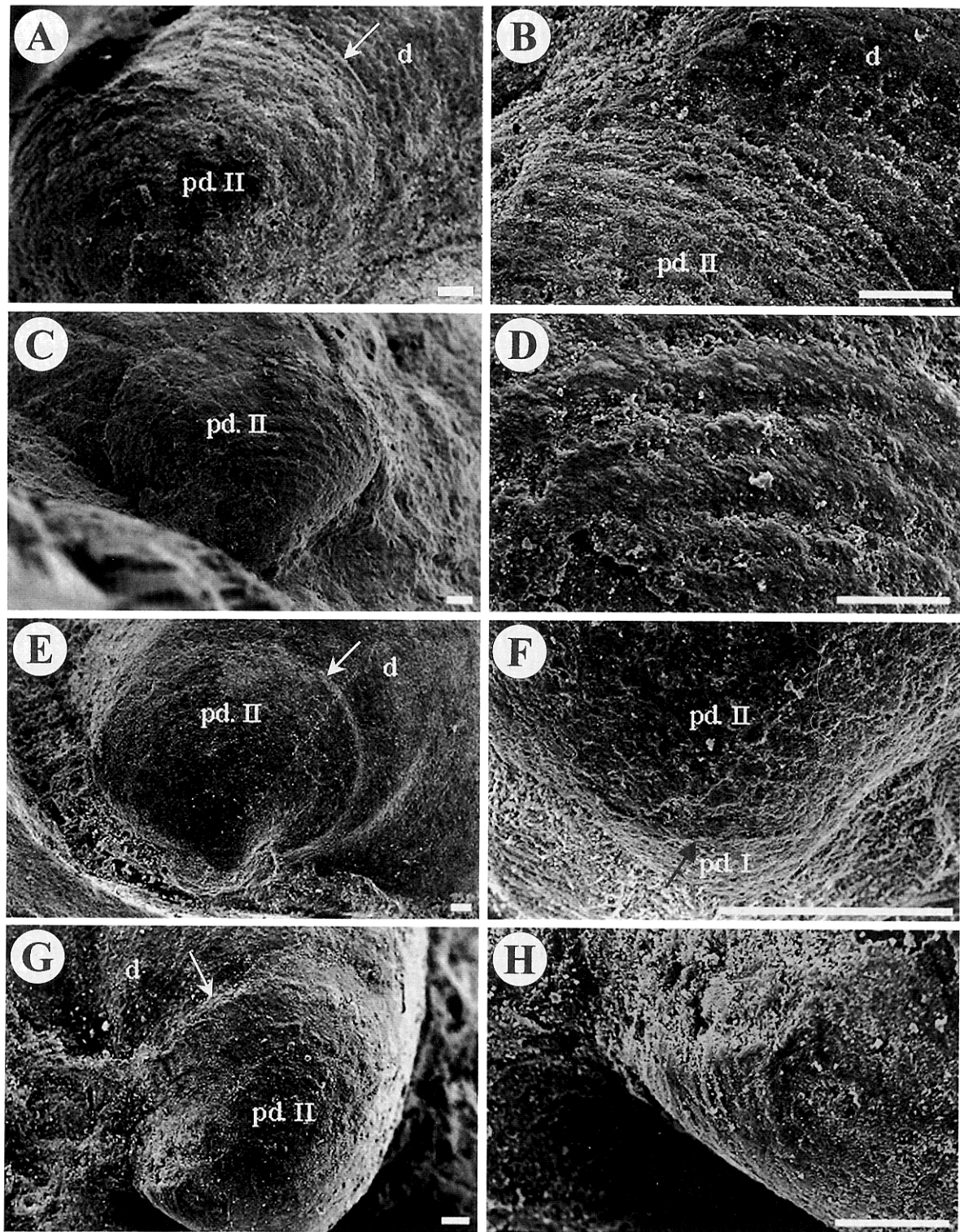


Figure 2. Prodissoconchs of inoceramid bivalves from the Tappu area. **A, B.** *Inoceramus tenuistriatus* Nagao and Matsumoto. SUM-MM-B0253. Mm-o. Right valve. **C, D.** *I. hobetsensis* Nagao and Matsumoto. SUM-MM-B0254. Mm-o. Left valve. **E, F.** *I. amakusensis* Nagao and Matsumoto. SUM-MM-B0257. Uf. Right valve. **G, H.** *Sphenoceramus naumanni* (Yokoyama). SUM-MM-B0271. Uf. Left valve. pd. I: prodissoconch I, pd. II: prodissoconch II, d: dissoconch. White arrows in A, E, and G indicate the pd. II-d boundary and black arrow in F indicates the pd. I-pd. II boundary. Scale bars: 50 µm.

while the muddy matrix is rather gray. Then, each specimen was coated with gold using a JEOL JFC-1500 ion coater, and examined with a JEOL JSM-5800LV scanning electron microscope (SEM) operated at 15kV and interfaced to a computer (Dell Optiplex Gxa EM). The external shell surface of the umbonal region was studied. In the present study, the taxonomic position of each juvenile specimen was determined by the shell sculpture compared with that of the coexistent adult specimens.

Results

As a result of SEM observation, prodissococonchs were distinguished in *Inoceramus tenuistriatus*, *I. hobetsensis*, *I. amakusensis* and *Sphenoceramus naumanni* (Table 1). Prodissococonchs in these species have a homogeneous microstructure and sometimes look like the matrix of calcareous concretions under the SEM, but have a smoother surface than that of the matrix. Prodissococonchs of all specimens are longer than high.

In *I. tenuistriatus*, the prodissococonch was observed in a single specimen (Figure 2A, B). This specimen had a prodissococonch with clear growth lines on the external surface (Figure 2B), which was identified with pd. II. The pd. II in this specimen was 630 μm in length. Although pd. I was not discerned, it was smaller than 210 μm in length because of the extent of the area on the prodissococonch without growth lines (Figure 2A).

Although *I. hobetsensis* occurs commonly in the Middle Turonian of the Tappu area, only one specimen of this species retaining a well-preserved prodissococonch was found (Figure 2C). Distinct growth lines that are characteristic of pd. II were recognized on the external surface of the prodissococonch (Figure 2D). Although the ventral margin of this prodissococonch was not preserved, the pd. II was at least 530 μm in length. The portion of the prodissococonch lacking growth lines was smaller than 240 μm in length so that pd. I is less than this length (Figure 2C).

In *I. amakusensis*, prodissococonchs were observed in five specimens and their length can be estimated in two of them (Figure 2E, F). Since the umbonal region of the prodissococonch is well preserved in one specimen, the initial growth line, which is identical to the pd. I-pd. II boundary, was clearly recognized (Figure 2F). In this individual, pd. I was 120 μm and pd. II 640 μm in length, while the other had a pd. II with a length of 650 μm .

S. naumanni is the most abundant inoceramid species in the Coniacian-Lower Campanian sequence of the Tappu area, and a total of 11 specimens with prodissococonchs were found. Pd. II of this species was 640 ± 90 μm in length (Figure 2G). Among them, growth lines were particularly well preserved in the specimen shown in Figure 2H. In this specimen, growth lines were found around a small tip

area lacking growth lines. Consequently, pd. I of this specimen may be smaller than 80 μm in length, although the pd. I-pd. II boundary is obscure.

Discussion

According to Jablonski and Lutz (1980), bivalve larvae can be distinguished into two developmental types, *i.e.*, planktotrophic and nonplanktotrophic. This dichotomy in feeding type can be recognized based on early shell morphology, which allows us to ascertain the larval ecology of fossil bivalves.

Planktotrophic larvae feed on smaller plankton during the long pelagic stage as free-swimming veligers (Jablonski and Lutz, 1980). Species having a planktotrophic stage tend to have a relatively small pd. I and a large pd. II (Ockelmann, 1965). Nonplanktotrophic larvae are either pelagic, oviparous or brooded, and feed on yolk reserves as their source of nutrients. They have a relatively large pd. I and an undeveloped pd. II. Planktotrophic larvae tend to have a higher dispersal capability than nonplanktotrophic larvae because the lack of dependence on yolk supply allows a longer pelagic larval duration (Jablonski and Lutz, 1980).

In all four species examined, prodissococonchs consisted probably of small pd. I (smaller than 240 μm in length) and large pd. II (500 to 810 μm in length), although the boundary between them was not clear except in one specimen of *I. amakusensis* (Figure 3). The sizes of pd. II observed in this study were rather large compared to those reported in other studies (Ockelmann, 1965; LaBarbera, 1974; Waller, 1981; Tanabe and Zushi, 1988; Palmer, 1989). Regarding the unusually large size of pd. II and relatively small size of pd. I, all of the four inoceramids must have had a planktotrophic larval stage. As a result, they had a high dispersal capability. Scheltema (1977) estimated that two to four months of pelagic life of planktonic larvae is long enough for trans-Atlantic dispersal. If the four inoceramid species had a duration of pelagic larval stage of several months, it could be possible for a larva to cross the Pacific Ocean, and the species might achieve a wide distribution in a few generations. This inference is supported by biogeographic data. The four inoceramids are known to occur in the North Pacific Bioprovince including Hokkaido-Sakhalin (Nagao and Matsumoto, 1939-1940), Kamchatka (Pergament, 1961), California-Oregon (Matsumoto, 1960; Popenoe *et al.*, 1960).

Meanwhile, Knight and Morris (1996) reported "giant" prodissococonchs of inoceramids from the Middle Albian in England, the average length of which is 1080 μm . The pd. II sizes estimated in the present study were smaller than those they report. Such difference of pd. II among species suggests that the duration of the pelagic stage was variable

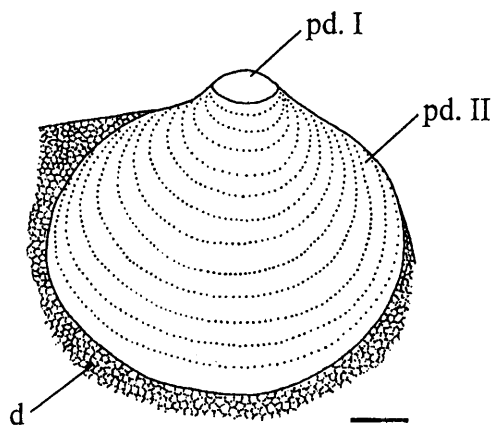


Figure 3. *Inoceramus amakusensis* Nagao and Matsumoto. SUM-MM-B0257. pd. I: prodissococonch I, pd. II: prodissococonch II, d: dissoconch. Scale bar: 100 μ m

within the Inoceramidae, although the duration of the pelagic stage cannot exactly be determined just from the size of prodissococonchs.

Conclusion

As a result of the SEM observation of prodissococonchs, it became clear that each of the four examined inoceramids shows a planktotrophic development characterized by a long pelagic stage and high dispersal capability as inferred from their shell morphology. Many previous studies have dealt with the stratigraphic and geographic distributions of inoceramid species (Popenoe *et al.*, 1960; Kauffman, 1977; Dhondt, 1992), but have offered little explanation of how such wide distribution patterns were established. Studies on the larval morphology of inoceramids create a basis for comprehending their biogeography and biostratigraphy. Although little is known about the biological aspects of inoceramids, this study should facilitate the solution of biological problems posed by these enigmatic bivalves. If the taxonomic confusion surrounding inoceramid bivalves is resolved, the intercontinental or pandemic distribution of each species will be recognized more clearly.

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