Giant fossil *Acharax* (Bivalvia: Solemyidae) from the Miocene of Japan

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ABSTRACT

Specimens of *Acharax yokosukensis* recently collected from the upper lower Miocene Kokozura Formation of the Takaku Group in Ibaraki Prefecture, central Japan, served as the basis for a re-description of the species. These specimens include a valve of the largest specimen of this genus known worldwide, exceeding 295.7 mm in length. The occurrences of the giant *Acharax* species in Japan are confined to lower to lower middle Miocene sediments deposited in tropical shallow and deep environments.

Additional keywords: Chemosynthesis, bivalves, deep-sea

INTRODUCTION

Solemyidae is the oldest group of chemosymbiotic bivalves, ranging back to the Ordovician (Taylor and Glover, 2010; Kiel, 2010). Among them, the oldest confirmed member of the extant genus Acharax is known from the early Cretaceous in Hokkaido, northern Japan (Kiel et al., 2008), but there are many unidentified solemyids from the older geological record that may also belong to Acharax. Two species of Acharax are known to live in Japanese waters: A. johnsoni (Dall, 1891) and A. japonicus (Dunker, 1882). The latter species is small and lives in shallow water (0–20 m depth; Habe, 1977) and has been found in settling tanks of sea water at a marine laboratory (Yamanaka et al., 2008). In contrast, A. johnsoni has a large shell attaining 150 mm in length (Kamenev, 2009), similar to other deep-water Acharax species, and lives in deep water (the depth range of A. johnsoni is very wide; according to Kamenev (2009) the species may be found from 100-5379 m. However, 100 m seems to be an exceptional case. Kamenev's data and JAMSTEC data show this species usually lives in deeper than 370 m.) The largest living species of Acharax is A. bartschii described by Dall (1908b) from the Philippines, with a shell length of 191 mm.

Notwithstanding problems with their identification, fossil *Acharax* in Japan are more diverse than extant

species. Eleven species have been recorded from deposits of Cretaceous to Pliocene age (Kanie and Kuramochi, 2002; Kiel et al., 2008). The largest known species is A. gigas from the Miocene Haratajino Formation with a length reaching 264.1 mm (Kanie et al., 1999; Kurihara, 2000). Taylor and Glover (2010) cited a specimen of A. yokosukensis Kanie and Kuramochi, 1995, from the Miocene Hayama Group in Kanagawa Prefecture, central Honshu, as the largest Acharax in the world, refering to "a fossil Acharax from the Miocene [that] measured a massive 300 mm". However, Kanie and Kuramochi (1995) only estimated that, based on a fragment of a shell.

We collected an imperfect specimen of *A. yokosukensis* having a length of 295.7 mm from the Miocene Kokozura Formation of the Takaku Group exposed along Pacific coast in Kitaibaraki City, in the northern part of Ibaraki Prefecture, central Honshu. So far, this specimen is the largest *Acharax* recorded worldwide. In this paper, we describe *A. yokosukensis* and speculate about why it could have evolved to such large size.

MATERIALS AND METHODS

The specimens described herein were collected from boulders present in the uppermost lower Miocene Kokozura Formation that may constitute the base layer under the Izura Kanko Hotel (Figure 1). These boulders with a diameter of around 1 m consist of sandy limestone or calcareous fine-grained sandstone including many shells and trace fossils (Figure 2). Ueda et al. (2005) differentiated these calcareous concretions into six morphological types. Among them, type I concretions (large irregularly shaped carbonates) show negative δ^{13} C value ranging from -29.4 to -20.9%. These values indicate that the carbonates precipitated under the influence of the oxidation of hydrocarbons such as crude oil or methane with an influx of marine bicarbonate (Kiel and Peckmann 2007). The boulders yielding the large Acharax yokosukensis specimens resemble type I concretions in size and shape.

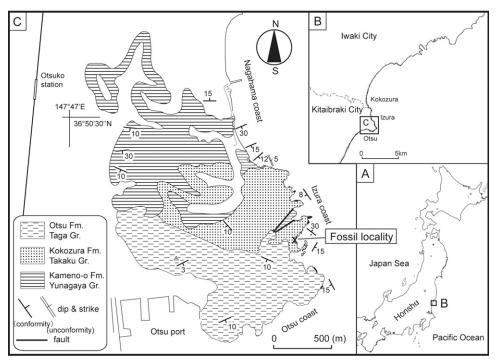


Figure 1. Locality map. Geological map adapted from Ueda et al. (2005).



Figure 2. Occurrence of *Acharax yokosukensis* in a calcareous concretion block.

The age of the Kokozura Formation of the Takaku Group in this area was assigned to the uppermost lower Miocene *Crucidenticula kanayae* zone (NPD 3A zone; NPD = Neogene North Pacific Diatom) by Yanagisawa (1996), based on diatom fossils. From the sedimentary facies and the occurrence of heterotrophic bivalves like *Mizuhopecten kobiyamai* (Kamada) and *Cylocardia siogamensis* (Nomura), these sediments were considered to be deposited on the muddy sand shelf (Ueda et al., 2005).

The fauna associated with *Acharax yokosukensis* is a blend of chemosymbiotic bivalves and predatory gastropods. The chemosymbiotic species include the lucinids

Lucinoma acutilineatum (Conrad) and Nipponothracia? sp., the thyasirid Conchocele bisecta (Conrad), and the vesicomyids Callogonia? sp. and Adulomya sp. The predatory gastropod species are represented by a few specimens of the naticid Cryptonatica clausa (Broderip and Sowerby) and the turrid Megasurcula yokoyamai (Otuka).

For comparing the shell proportion of *Acharax yokosukensis*, some Recent specimens of *A. johnsoni* from northern Pacific, stored at National Science Museum in Tokyo were examined.

Abbreviations used in text: JUE=Joetsu University of Education; YCM-Gp = Yokosuka City Museum.

SYSTEMATICS

Family Solemyidae

Genus Acharax Dall, 1908

Type Species: Solemya johnsoni Dall, 1891

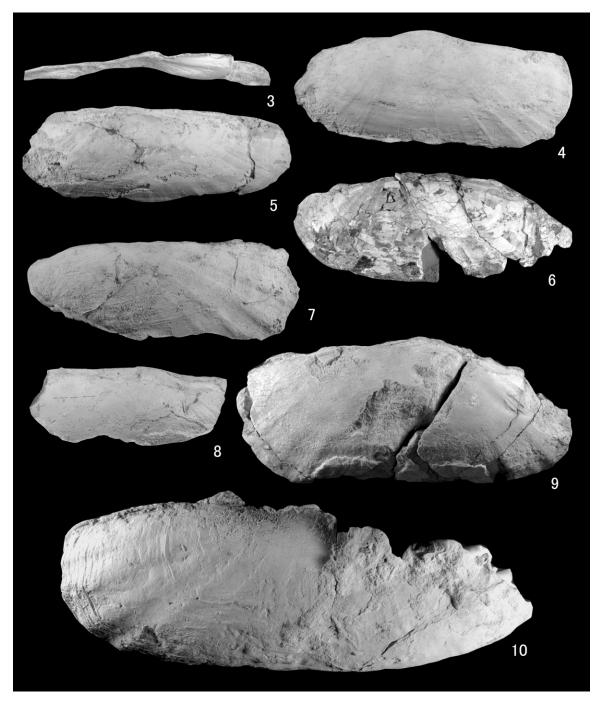
Acharax yokosukensis Kanie and Kuramochi, 1995 (Figures 3–10)

Acharax aff. tokunagai (Yokoyama).—Ogasawara et al., 1994: 34–35, figs. 3-1a-c.

Acharax n. sp. — Kanie et al., 1995: 57–58, figs. 1, 2-1-3, 3-2-4. Acharax yokosukensis Kanie and Kuramochi, 1995: 52, 56, figs. 1–4; Kanie and Kuramochi, 2002: 56, figs. 2–13.

Holotype: YCM-Gp Ig36.

Material Examined: Eight specimens including one almost perfect specimen. JUE nos. 15887-1~8.



Figures 3–10. Acharax yokosukensis (Kanie and Kuramochi). 3–5, 7–10. Specimens from the Kokozura Formation. 3–5. JUE no. 15887-2, right valve. 3. Rubber cast of hinge of the specimen illustrated in Figure 5, hinge length, 82.9 mm. 4. Rubber cast of outer shell surface of the specimen illustrated in Figure 5, length 168.4 mm. 5. Inner mold, length 155.1 mm. 7. Rubber cast of outer shell surface, JUE no. 15887-3, length 195.2+ mm, right valve. Most posterior part and some ventral part are missing. 8. Rubber cast of inner shell surface, JUE no. 15887-4, length 109.9 mm, left valve. 9, 10. JUE no. 15887-1, left valve. 9. Inner mold, length 244.7 mm. 10. Rubber cast of outer shell surface, length 295.7+ mm. 6. Holotype from the Hayama Group. YCM-Gp Ig36, length 144.1 mm, right valve.

Description: Shell exceptionally large for genus, exceeding 295.7 mm in length (Table 1), elongate quadrate, height/length-ratio = 0.40–0.44, equivalve and inequilateral, moderately inflated. Umbo situated nearly

central or slightly posteriorly (anterior length: AL/ shell length-ratio = 0.52–0.61). Anterior margin subtruncate; ventral margin nearly straight; antero-dorsal margin nearly straight; postero-dorsal margin very broadly

Specimens	Length	Height	H/L	AL	AL/L	Valve
IUE no. 15887-1						left
(rubber cast of outer surface)	295.7+	108.5	_	_	_	
(inner mold)	244.7	107.3	0.44	127.6	0.52	
JUE no. 15887-2						right
(rubber cast of outer surface)	168.4	66.7	0.40	102.2	0.61	O
(inner mold)	155.1	60.9	0.39	92.7	0.60	
JUE no. 15887-3						
(rubber cast of outer surface)	195.2+	_	_	_	_	right

Table 1. Measurements (mm) of valves of Acharax yokosukensis.

arched, continuing into well-rounded posterior margin. Hinge edentulous and inner surface of subumbonal part radially grooved. Nymph opisthodetic. Anterior adductor muscle scar indistinct; posterior adductor muscle scar large, quadrate, deeply impressed and crenulated by distinct radial grooves. Surface sculptured by fourteen radial ribs; five distinct, low and wide radial ribs in anterior part; five fine and round-topped radial ribs with very wide interspaces in middle part; four round-topped radial ribs with narrower interspaces in posterior part.

Remarks: As pointed by Kanie and Kuramochi (1995), *Acharax* aff. *tokunagai* (Yokoyama) described by Ogasawara et al. (1994), from the lower Miocene Aokiyama Formation in Chiba Prefecture, is a synonym of *A. yokosukensis*. These authors reached this conclusion because of the species centrally situated beak and similar number of ribs (11 in the Aokiyama specimens).

Comparison: Acharax gigas (Kanno, 1960) from the Miocene Hiranita and Haratajino formations resemble A. yokosukensis in its huge shell size (264.1 mm in length). However, A. gigas can be distinguished from A. yokosukensis in having a smaller height/length-ratio (more elongate shell, H/L = 0.25–0.34), and a more posteriorly situated beak (AL= 0.65–0.78) (Figures 11, 12). The Recent species, Acharax johnsoni (Dall, 1891) differs from A. yokosukensis by its smaller shell and more posteriorly situated beak (AL = 0.70–0.77) (Figures 11, 12).

Distribution: Lower Miocene Aokiyama Formation in Chiba Prefecture; upper lower Miocene Kokozura Formation of Takaku Group in Ibaraki Prefecture; lower middle Miocene Hayama Group in Kanagawa Prefecture.

DISCUSSION

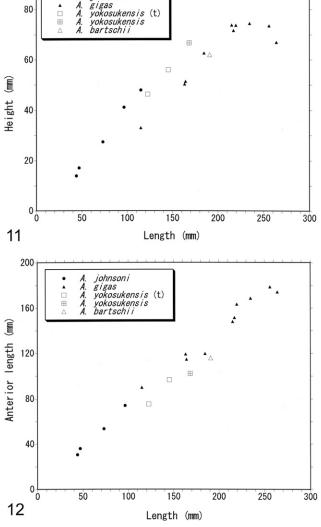
The giant specimens of Acharax yokosukensis reported here were recovered from probable hydrocarbon seep deposits in the lower to lower middle Miocene sediments in the northeastern Kanto District, central Honshu (Figure 13). Another giant Acharax species, A. gigas has also been recorded from ancient seep sites in the Hiranita and Haratajino Formations in the northwestern Kanto District, correlated with zone N8 of Blow (1969)

(latest early to earliest middle Miocene), based on the examination of planktonic foraminiferans (Takahashi, 1992; Oishi and Takahashi, 1990). This Miocene age corresponds to the mid-Neogene Climatic Optimum (Tsuchi, 1987). At that time, a tropical climate prevailed in what is now the Kanto District (Ogasawara, 1994). Other than the occurrence of the Kokozura specimens, these giant *Acharax* were from deep seep sites. Exceptionally, the largest specimen of *A. yokosukensis* was recovered from the shallow seep deposits of the Kokozura Formation. Thus, regardless of depth, the warm climate and methane seep environment might affect the size of fossil *Acharax*.

Like solemyids, lucinid bivalves are chemosymbiotic, deep burrowers, and geologically old members of the seep fauna, which first appeared in the Jurassic (Kiel, 2010). Occurrences of large fossil lucinids were summarized by Taylor and Glover (2009) who described the largest lucinid, Superlucina megameris (Dall) that reached 280 mm in length and 311 mm in height. According to their list, the large lucinids appeared in geological ages with warm climates like the late Jurassicearly Cretaceous, middle Eocene, and middle Miocene. In deposits younger than the early Pliocene, the occurrences are mostly confined to tropical areas like the Philippines and Taiwan. Moreover, large lucinids were recovered from both shallow and deep sites like the giant Acharax.

Generally speaking, the maximum size of largest species of each guild in the coastal marine tropics correlates or correlated with the marine productivity (Vermeij, 2011). Solemyids are well known to have a reduced gut or to lack an alimentary tract, and to depend on their chemoautotrophic symbionts for nutrition (Stewart and Cavanaugh, 2006; Taylor et al., 2008). It seems thus plausible that chemosynthetic species need to take up a lot of sulfide to achieve a large size (Taylor and Glover, 2009). Assuming that warm temperatures facilitate physiological process like sulfide uptake, the warm temperatures of the latest early to earliest middle Miocene might have played a role in the gigantism of the Acharax specimens reported here, although the exact mechanisms are unknown. At modern seeps, Acharax often lives at the periphery away from the highest sulfide concentrations (Sahling et al., 2002). Thus, for obtaining sulfides, the lack of competition might also play a role.

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Figures 11–12. Ontogenetic changes in *Acharax yokosukensis* (t: type material), *A. johnsoni*, *A. gigas*, and *A. bartschii*. The largest shell of *A. yokosukensis* is incomplete and excluded from both graphs. Dimensions of *A. yokosukensis* and the recent specimens of *A. johnsoni* were measured by hand. Data for *A. gigas* and *A. bartschii* respectively from Kanie et al. (1999) and Dall (1908b). 11. Shell length and height. 12. Shell length and anterior length.

ACKNOWLEDGMENTS

We are grateful to Steffen Kiel (University of Göttingen) for his review and useful comments to this paper. We thank two anonymous reviewers for their critical review and many constructive comments. We also thank Kenichiro Shibata (Yokosuka City Museum) and Hiroshi Saito (National Museum of Nature and Science) for examining the fossil and Recent shells of *Acharax*. We acknowledge Akiyoshi Yamashita (Izura Kanko Hotel) for providing some support in the field survey. This

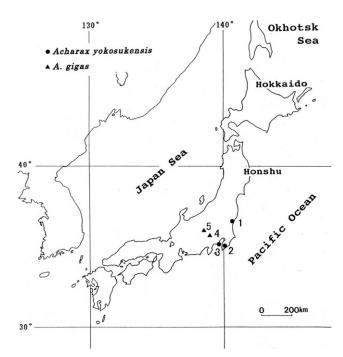


Figure 13. Distribution of *Acharax yokosukensis* and A. *gigas*. 1. Kokozura F.; 2. Aokiyama F.; 3. Hayama G.; 4. Hiranita F.; and 5. Haratajino F.

study was partly supported by a Grant-in-Aid for Scientific Research from the Japan Society for Promotion of Science (C, 20540456, 2008–2010).

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