Ocean Sci. J. (2016) 51(3):455−463
http://dx.doi.org/10.1007/s12601-016-0041-9
Article
Available online at http://link.springer.com
SpringerLink
Ocean Science Journal
pISSN 1738-5261
eISSN 2005-7172

Temporal Changes in the Geographic Distribution of Two Clam Species *Meretrix lusoria* and *M. petechialis* along the Coast of Japan and South Korea

Shin'ichi Sato[1]*, Yoshitaka Kaneko[2], Hiroshi Torii[3], and Jae-Sang Hong[4]

[1]*Institute of Geosciences, Shizuoka University, Shizuoka 422-8529, Japan*
[2]*Department of Earth Science, Tohoku University, Sendai 980-8578, Japan*
[3]*Planning & Environmental Section, Japan Port Consultants Ltd., Tokyo 141-0031, Japan*
[4]*Department of Ocean Sciences, College of Natural Sciences, Inha University, Incheon 22212, Korea*

Received 27 May 2015; Revised 15 April 2016; Accepted 26 August 2016

Abstract – The objectives of this study were to distinguish fossil specimens of *Meretrix* (Bivalvia, Veneridae) using discriminant score and multivariate analysis, and to examine temporal changes in the geographical distributions of *M. lusoria* and *M. petechialis* in Japan and South Korea. Fossil shells of *Meretrix* were collected from Miyagi, Fukui, Aichi and Kumamoto in Japan, and Gimhae, Seosan, Siheung and Ganghwa-do in South Korea. The outside of the right valve was photographed with a digital camera, and ten characteristics of the shell morphology, such as shell height and shell length, were measured using image analysis software and a digital slide caliper. The discriminant score and multivariate analysis of the shell morphology identified all of the examined fossils as *M. lusoria,* while living individuals collected from the western coast of South Korea were identified as *M. petechialis*. These results suggest that the fossil shells excavated from the western coast of South Korea are a different species from the living individuals collected from the same areas. Radioactive carbon isotopic results revealed that the ages of the four fossil shells collected from tidal flats in Ganghwa-do ranged between 3,270 ± 30 and 1,830 ± 30 Cal BP. These results suggest that *M. lusoria* inhabited the western coast of South Korea until at least 2,000 years ago, but was replaced by *M. petechialis* during the last 2,000 years. Therefore, we propose that either *M. petechialis* spats were introduced artificially, or planktonic larvae migrated naturally from China to the western coast of South Korea during the last 2,000 years.

Key words – extant and fossil shells, Japan, *Meretrix lusoria*, *Meretrix petechialis*, shell morphology, South Korea

*Corresponding author. E-mail: sato.shinichi.c@shizuoka.ac.jp

1. Introduction

The genus *Meretrix* Lamarck, 1799 (Veneridae) is distributed throughout East and Southeast Asia, India, the Persian Gulf and East Africa (Yoosukh and Matsukuma 2001; Martin and Matsukuma 2006; Yamakawa et al. 2008; Henmi 2009). Nine species have been recognized, *Meretrix meretrix* (Linnaeus, 1758), *M. casta* (Gmelin, 1791), *M. lusoria* (Röding, 1798), *M. petechialis* (Lamarck, 1818), *M. ovum* (Hanley, 1845), *M. lyrata* (Sowerby, 1851), *M. planisulcata* (Sowerby, 1851), *M. lamarckii* Gray, 1853 and *M. attenuata* Dunker, 1862 (OBIS Indo-Pacific Molluscan Database 2006; Yamakawa et al. 2008), and other species remain to be described (Henmi 2009). However, these species are difficult to distinguish from one another using morphological features, because the systematic descriptions of *Meretrix* species are very confusing (Yoosukh and Matsukuma 2001; Yamakawa et al. 2008).

Meretrix spp. have been artificially introduced from other countries because of their commercial importance, and many researchers have pointed out that hybrids occur between these species (Kosuge 1995; Kawase 2002; Yamakawa et al. 2008; Torii et al. 2010; Yamakawa and Imai 2012, 2013). Torii et al. (2010) indicated that natural hybridization between *M. lusoria* and *M. petechialis* might have occurred around the southwestern coast of South Korea based on phylogenetic analyses of mitochondrial COI and nuclear ITS sequences. Yamakawa and Imai (2012) reported that exotic individuals of *M. petechialis* and hybrids co-occurred with the local *M. lusoria* in Kanonji, Kagawa Prefecture (Pref.), Japan, based on the combined results of RFLP and *ANT* genotypes.

Fossils of *Meretrix* spp. are abundant in the Pleistocene–Holocene marine deposits of Japanese islands (Oyama 1980; Matsushima 1984) and shell mounds in Japan and the Middle East (Kanamaru 1932; Sakazume 1984; Charpentier et al. 2004; Yamakawa et al. 2008). They have relatively thick and hard shells, and their fossils are usually retained in better condition than other mollusks collected from shell beds and mounds. Therefore, *Meretrix* spp. are more suitable than many other bivalve species for analysis of temporal changes in geographical distribution based on fossil shell morphology.

Torii et al. (2010) established a method to identify *M. lusoria* and *M. petechialis* from the shell morphology, which is a modified discriminant score (*D*) using five selected characteristics: shell length (*L*), shell breadth (*B*), width of the socket (*SW*), length of the posterior-dorsal margin (*LPM*) and height of the posterior-dorsal margin (*HPM*). The discriminant score is expressed as the following equation:

$$D = 110.26 - 61.61(\log B/\log L) + 10.90(\log SW/\log L) - 81.72(\log LPM/\log L) + 27.27(\log HPM/\log L)$$

Using this discriminant score, living individuals of *M. lusoria* and *M. petechialis* can be identified with an accuracy rate of 98.89% (Torii et al. 2010). This method is also applicable to the identification of fossil shells collected from the shell beds and mounds.

The objectives of the present study are: 1) to distinguish the fossil shells of two different *Meretrix* species, *M. lusoria* and *M. petechialis*, using this discriminant score and multivariate analysis, 2) to examine the temporal changes in the geographical distributions of these two species in Japan and South Korea through the comparison of the shell morphologies of fossil specimens and extant ones collected from the twenty different localities in Japan and South Korea, 3) to reveal replacement of *M. lusoria* by *M. petechialis* around the western coast of South Korea, and 4) to discuss the timing and mechanism of the replacement with the results of radioactive carbon isotopic analysis.

2. Materials and Methods

Collection and processing of fossil samples

Fossil shells of *Meretrix* were collected from eight different localities in Japan and South Korea: Satohama Shell Mound, Miyagi Pref. (*MY*, 36 specimens); Takahama Shell Bed, Fukui Pref. (*FK*, 24 specimens); Matsuzaki Shell Mound, Aichi Pref. (*AC*, 43 specimens); and Shirakawa Shell Bed, Kumamoto Pref. (*KM*, 11 specimens) in Japan; and Gimhae Shell Mound, Gimhae City (*GM*, 9 specimens); Daesan Shell Mound, Seosan-gun (*SS*, 18 specimens); Oido Shell Mound, Siheung City (*SH*, 22 specimens); and tidal flats in Ganghwa-do, Incheon Metropolitan City (*IC*, 31 specimens) in South Korea (Fig. 1, Table 1).

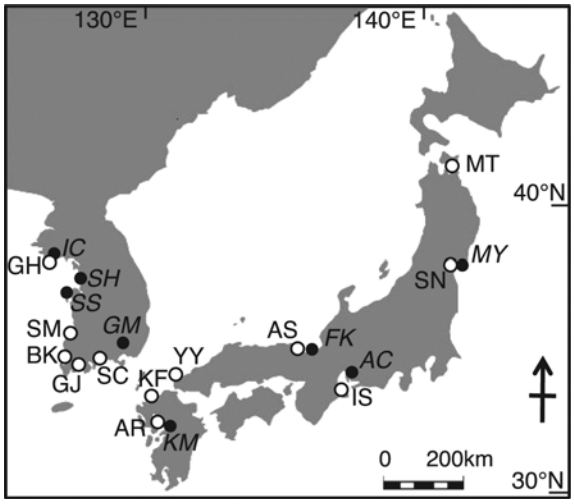

Fig. 1. Sampling localities of *Meretrix lusoria* and *M. petechialis* in Japan and South Korea. Black circles represent fossil shells collected from Satohama Shell Mound, Miyagi Pref. (*MY*), Takahama Shell Bed, Fukui Pref. (*FK*), Matsuzaki Shell Mound, Aichi Pref. (*AC*) and Shirakawa Shell Bed, Kumamoto Pref. (*KM*) in Japan, and Gimhae Shell Mound, Gimhae City (*GM*), Daesan Shell Mound, Seosan-gun (*SS*), Oido Shell Mound, Siheung City (*SH*) and tidal flats in Ganghwa-do, Incheon Metropolitan City (*IC*) in South Korea. Open circles represent living individuals from Mutsu Bay (MT), Sendai Bay (SN), Aso Sea (AS), Ise Bay (IS), Yuya Bay (YY), Kafuri Bay (KF), Ariake Sea (AR) in Japan, and Sacheon Bay (SC), Gangjin Bay (GJ), Baeksu (BK), Saemangeum (SM) (Torii et al. 2010) and tidal flats in Ganghwa-do (GH) in South Korea (this study)

Morphological data of the extant shells of *M. lusoria* and *M. petechialis* from eleven different localities in Japan and South Korea were obtained from Torii et al. (2010). These localities were: Mutsu Bay (MT, 44 individuals); Sendai Bay (SN, 83 individuals); Aso Sea (AS, 34 individuals); Ise Bay (IS, 28 individuals); Yuya Bay (YY, 30 individuals); Kafuri Bay (KF, 72 individuals); and Ariake Bay (AR, 59 individuals) in Japan; and Sacheon Bay (SC, 31 individuals); Gangjin Bay (GJ, 110 individuals); Baeksu (BK, 60

Table 1. Information on locality, number of individuals, age (fossils) or sampling date (living individuals) and references for specimens of *Meretrix lusoria* and *M. petechialis* collected from Japan and South Korea

Locality	Sample point	Latitude and Longitude	No. of indiv.	Age (fossils) or Sampling date (living indiv.)	References
Miyagi (*MY*)	Satohama shell mound, Higashi-Matsushima City, Miyagi Pref., Japan	38°20'15"N, 141°08'27"E	36	6,000–2,000 BP	The Historical Museum of Jomon Villlage Oku-Matsushima coll.
Fukui (*FK*)	Takahama shell bed, Takahama Town, Fukui Pref., Japan	35°29'09"N, 135°33'05"E	24	3,830±90 Cal BP	Nakagawa et al. (1993)
Aichi (*AC*)	Matsuzaki shell mound, Tokai City, Aichi Pref., Japan	35°01'39"N, 136°53'47"E	43	1,333±19–1,256±19 Cal BP	Aichi Archeology Center (2014)
Kumamoto (*KM*)	Shirakawa River, Kumamoto City, Kumamoto Pref., Japan	32°46'00"N, 130°41'12"E	11	5,000–4,000 BP	Kitamura (2004)
Gimhae (*GM*)	Gimhae shell mound, Gimhae City, Gyeongsangnam-do, South Korea	35°13'14"N, 128°52'42"E	9	A.D. 2C–4C	J.S. Hong coll.
Seosan (*SS*)	Daesan shell mound, Seosan-gun, Chungcheongnam-do, South Korea	37°00'23"N, 126°23'23"E	18	4,000 BP	Gunsan National University coll.
Siheung (*SH*)	Oido shell mound, Siheung City, Gyeonggi-do, South Korea	37°20'34"N, 126°41'38"E	22	B.C. 3,500–1,500	J.S. Hong coll.
Incheon (*IC*)	Ganghwa-do tidal flat, Incheon Metropolitan City, South Korea	37°36'06"N, 126°22'55"E	31	3,270±30–1, 830±30 Cal BP	See Table 4
Mutsu Bay (MT)	The mouth of Sin-Tanabe River, Mutsu City, Aomori Pref., Japan	41°16'21"N, 141°11'46"E	44	May 10, 2005	Torii et al. (2010)
Sendai Bay (SN)	The mouth of Nanakita River, Sendai City, Miyagi Pref., Japan	38°15'13"N, 141°00'37"E	83	Feb.-Sep. 2007	Torii et al. (2010)
Aso Sea (AS)	The mouth of Noda River, Yosano Town, Kyoto Pref., Japan	35°33'39"N, 135°09'30"E	34	June 8, 2008	Torii et al. (2010)
Ise Bay (IS)	The mouth of Sakauchi River, Matsuzaka City, Mie Pref., Japan	34°36'30"N, 136°32'54"E	28	Apr. 23, 2005	Torii et al. (2010)
Yuya Bay (YY)	Yuya-igami, Nagato City, Yamaguchi Pref., Japan	34°22'17"N, 131°01'42"E	30	June 28, 2004	Torii et al. (2010)
Kafuri Bay (KF)	The mouth of Izumi River, Itoshima City, Fukuoka Pref., Japan	33°33'10"N, 130°09'40"E	72	Apr. 2005–Aug. 2006	Torii et al. (2010)
Ariake Bay (AR)	The mouth of Shirakawa River, Kumamoto City, Kumamoto Pref., Japan	32°46'54"N, 130°35'17"E	59	Jan. 2005–Jul. 2006	Torii et al. (2010)
Sacheon Bay (SC)	Seonjin-ri, Sacheon City, Gyeongsangnam-do, South Korea	35°02'26"N, 128°02'16"E	31	Apr. 26, 2003	Torii et al. (2010)
Gangjin Bay (GJ)	Guro, Sonro-ri, Gangjin-gun, Jeonllanam-do, South Korea	34°35'28"N, 126°46'50"E	110	Apr. 30, 2003, Apr. 5, 2008	Torii et al. (2010)
Baeksu (BK)	Baekpawi, Duu-ri, Yeonggwang-gun, Jeonllanam-do, South Korea	35°14'23"N, 126°18'30"E	60	May 7, 2003, Apr. 9, 2008,	Torii et al. (2010)
Saemangeum (SM)	Sura, Okbong-ri, Gunsan City, Jeonllabuk-do, South Korea	35°55'43"N, 126°36'05"E	49	Aug. 25, 2007	Torii et al. (2010)
Ganghwado (GH)	Ganghwa-do tidal flat, Incheon Metropolitan City, South Korea	37°36'06"N, 126°22'55"E	31	June 8, 2012	H. Koike coll.

individuals); and Saemangeum (SM, 49 individuals) in South Korea. Living individuals were also collected from tidal flats in Ganghwa-do (GH, 31 individuals) in South Korea, the same place from which the fossil shells were collected (Fig. 1, Table 1).

Radiocarbon age data of fossil shells were obtained from Aichi Archeology Center (2014), Nakagawa et al. (1993) and Kitamura (2004) (Table 1). Four fossil shells collected from tidal flats in Ganghwa-do were analyzed by Beta Analytic Inc. to generate accelerator mass spectrometry (AMS) radiocarbon age data. Calendar calibration of the radiocarbon age was carried out using Intcal13 (Reimer et al. 2013) and Talma and Vogel (1993).

Morphological analysis

The methods used for shell measurements and multivariate analysis followed those of Torii et al. (2010). Ten different shell characteristics (in mm) were measured on each specimen: shell length (*L*), shell height (*H*), shell breadth (*B*), pallial sinus length (*PL*), ligament length (*LL*), width of the socket (*SW*), anterior shell length (*AL*), upper shell height (*UH*), length of posterior-dorsal margin (*LPM*) and height of posterior-dorsal margin (*HPM*) (Fig. 2). For the measurements of *L*, *H*, *AL*, *UH*, *LPM* and *HPM*, the outside of the right shell valve was photographed with a digital camera. Each of these six characteristics was determined from the photograph using image analysis software (Scion Image 1.63 or ImageJ 1.48). The remaining four characteristics (*B*, *PL*, *LL* and *SW*) as well as *L* and *H* were determined directly from the right shell valve using a digital slide caliper (accuracy ± 0.01 mm). The shell breadth (*B*) of a single fossil valve was determined and

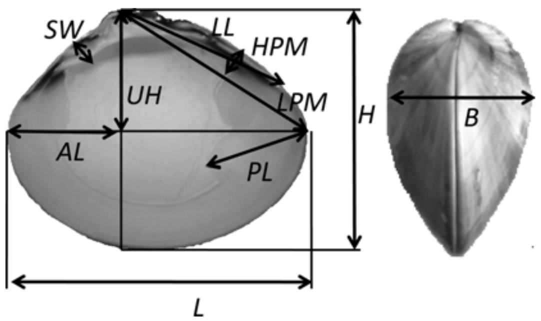

Fig. 2. Nine characteristics of the right shell valve and shell breadth measured on *Meretrix* shell (Torii et al. 2010). Shell length (*L*), shell height (*H*), shell breadth (*B*), pallial sinus length (*PL*), ligament length (*LL*), width of the socket (*SW*), anterior shell length (*AL*), upper shell height (*UH*), length of posterior-dorsal margin (*LPM*), and height of posterior-dorsal margin (*HPM*)

doubled as these individual's *B*. *L* and *H* were measured using both methods. They were analyzed with reduced major axis regression (RMA) and their slopes were compared using the method of significance test at a 95% confidence level (Hayami and Matsukuma 1971), but there were no significant differences between them (Torii et al., 2010).

Using these morphological data, the values of the discriminant score (*D*) proposed by Torii et al. (2010) were examined for the extant and fossil shells, which were identified as *M. lusoria* ($D < 0$) or *M. petechialis* ($D \geq 0$). Canonical discriminant analysis (CDA) was also carried out for all of the extant and fossil shells with the standardized nine characteristics using IBM SPSS Statistics (ver. 22).

3. Results

In living populations, the discriminant score (*D*) revealed that 99.6% (456/458) of the individuals collected from Japan and at Sacheon Bay (SC) and Gangjin Bay (GJ), the southern coast of South Korea, were identified as *M. lusoria*, and 91.1% (92/101) of the individuals collected at Baeksu (BK), Saemangeum (SM) and Ganghwa-do (GH), the western coast of South Korea, were identified as *M. petechialis* (Fig. 3, Table 2). However, the *D* values of all of the 194 fossil specimens collected from the shell beds and mounds in Japan and South Korea were less than zero; they were identified as *M. lusoria* (Fig. 3, Table 2).

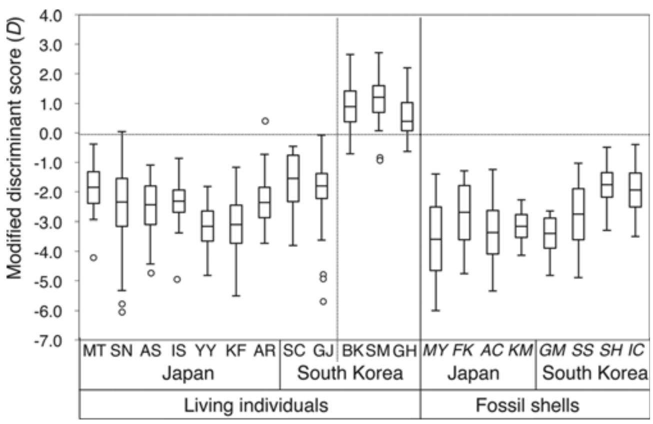

Fig. 3. Distribution of the modified discriminant score (*D* value) for the fossil shells excavated from eight localities and living individuals collected from twelve localities in Japan and South Korea. The horizontal line in the box indicates the mean value of specimens from each locality, and the edges of the box are the upper and lower quartile. The error bar represents the 95% confidence level, and the open circle is the discriminant score for each individual outside the 95% confidence level

Table 2. Number of individuals identified by the modified discriminant score (*D* value) as *M. lusoria* ($D < 0$) and *M. petechialis* ($D \geq 0$) for living individuals collected from twelve localities and the fossil shells excavated from eight localities in Japan and South Korea

	No. of individuals examined	Modified discriminant score		Percent of correct cases (%)
		$D < 0$ (*M. lusoria*)	$D \geq 0$ (*M. petechialis*)	
Living individuals				
Japan				
Mutsu Bay (MT)	28	28	0	100.0
Sendai Bay (SN)	81	80	1	98.8
Aso Sea (AS)	34	34	0	100.0
Ise Bay (IS)	28	28	0	100.0
Yuya Bay (YY)	30	30	0	100.0
Kafuri Bay (KF)	72	72	0	100.0
Ariake Bay (AR)	53	52	1	98.1
Korea				
Sacheon Bay (SC)	22	22	0	100.0
Gangjin Bay (GJ)	110	110	0	100.0
Total (MT–GJ)	458	456	2	99.6
Baeksu (BK)	34	2	32	94.1
Saemangeum (SM)	48	5	46	95.8
Ganghwado (GH)	19	5	14	73.7
Total (BK–GH)	101	12	92	91.1
Fosiil shells				
Japan				
Miyagi (*MY*)	36	36	0	100.0
Fukui (*FK*)	24	24	0	100.0
Aichi (*AC*)	43	43	0	100.0
Kumamoto (*KM*)	11	11	0	100.0
Korea				
Gimhae (*GM*)	9	9	0	100.0
Seosan (*SS*)	18	18	0	100.0
Siheung (*SH*)	22	22	0	100.0
Incheon (*IC*)	31	31	0	100.0
Total (all fossil shells)	194	194	0	100.0

The CDA results indicate clear differences in canonical variate 1 between the living individuals of *M. petechialis* (BK, SM, GH) and the living individuals (MT, SN, AS, IS, YY, KF, AR, SC, GJ) and fossil specimens (*MY*, *FK*, *AC*, *KM*, *GM*) of *M. lusoria* collected from Japan and the southern coast of South Korea, and in canonical variates 1 and 2 between the living ones of *M. lusoria* (MT, SN, AS, IS, YY, KF, AR, SC, GJ) and the fossil specimens (*SS*, *SH*, *IC*) from the western coast of South Korea (Fig. 4). The proportions of canonical variates 1 and 2 were 45.6% and 25.0%, respectively (Table 3). The shell characteristics that principally affected canonical variate 1 were the length and height of the posterior-dorsal margin against the shell length ($\log LPM/\log L = -1.548$ and $\log HPM/\log L = 1.211$, respectively). The values of canonical variate 2 were affected largely by the shell breadth and the pallial sinus length against the shell length ($\log B/\log L = 0.677$ and $\log PL/\log L = -0.958$, respectively) (Table 3). The centroids of the fossil specimens excavated from Miyagi (*MY*) and Fukui (*FK*) were relatively similar (within the range of the standard deviation) to those of living individuals of *M. lusoria* collected from Japan and the southern coast of South Korea (Table 4, Fig. 4). However, the fossil specimens from Aichi (*AC*) and Kumamoto (*KM*) in Japan and Gimhae (*GM*) on the southern coast of South Korea were slightly different (within the range of twice the standard deviation) from the living individuals of *M. lusoria*

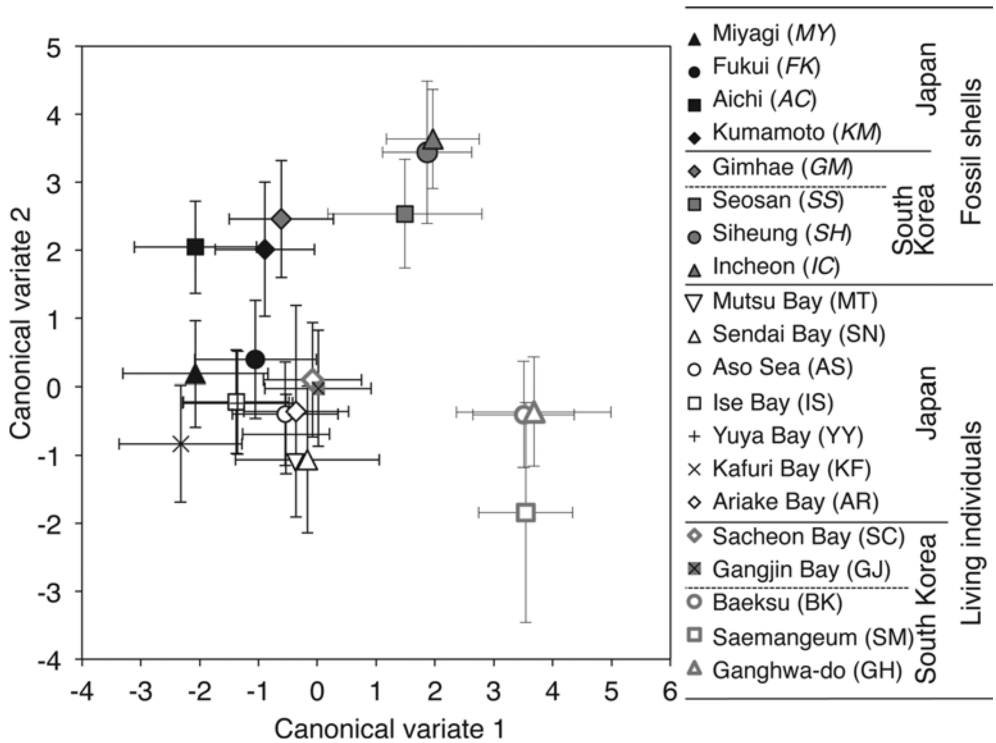

Fig. 4. Two-dimensional scattergrams of *Meretrix lusoria* and *M. petechialis* from twenty localities obtained using canonical discriminant analysis (CDA). The centroid of canonical variates 1 and 2 and the standard deviation for specimens from each locality are shown

Table 3. Standardized coefficients of nine characteristics, eigenvalues and proportions of the canonical variates 1 and 2 for the twenty samples of *Meretrix lusoria* and *M. petechialis*

Characteristics	Standardized coefficients	
	1	2
log *H* / log *L*	0.574	0.412
log *B* / log *L*	-0.675	0.677
log *PL* / log *L*	-0.162	-0.958
log *LL* / log *L*	0.128	0.289
log *SW* / log *L*	0.809	0.454
log *AL* / log *L*	-0.426	0.406
log *UH* / log *L*	0.214	-0.465
log *LPM* / log *L*	-1.548	0.557
log *HPM* / log *L*	1.211	-0.177
Eigenvalue	3.321	1.822
Proportion	45.6	25.0

in the values of canonical variate 2 (Fig. 4). The fossil specimens from the western coast of South Korea (*SS*, *SH*, *IC*) were quite different (outside the range of twice the standard deviation) from the living individuals of *M. lusoria* and *M. petechialis* in canonical variates 1 and 2 (Fig. 4). The morphological characteristics of the shells of living individuals from tidal flats in Ganghwa-do (GH) were also outside the range of twice the standard deviation from those of the fossil shells collected from the same place (*IC*) in the values of canonical variates 1 and 2 (Fig. 4).

The results of the radioactive carbon isotopic analysis revealed that the ages of the four fossil shells collected from tidal flats in Ganghwa-do in South Korea (*IC*) ranged between 3,270 ± 30 and 1,830 ± 30 Cal BP (Table 5). These fossil shells were buried at the depths of 2 to 3 cm of the sediment. Their periostraca were lost as a result of abrasion (Fig. 5).

4. Discussion

Using the discriminant score technique adopted in the present study, all of the fossil shells collected from Japan and South Korea were identified as *M. lusoria*, and 99.6% of the living individuals collected from Japan and at Sacheon Bay and Gangjin Bay, the southern coast of South Korea were also identified as *M. lusoria*, while 91.1% of the individuals collected at Baeksu, Saemangeum and Ganghwa-do, the western coast of South Korea, were *M. petechialis*

Table 4. Centroids of canonical variates 1 and 2 for the living individuals and fossil specimens of *Meretrix lusoria* and *M. petechialis* collected from each locality

Country and kind of samples	Locality	Centroid of canonical variate	
		1	2
Living individuals from Japan	Mutsu Bay (MT)	-0.530	-0.693
	Sendai Bay (SD)	-0.166	-1.068
	Aso Sea (AS)	-0.546	-0.398
	Ise Bay (IS)	-1.381	-0.219
	Yuya Bay (YY)	-1.352	-0.236
	Kahuri Bay (KF)	-2.324	-0.836
	Ariake Bay (AR)	-0.359	-0.360
Living individuals from South Korea	Sacheon Bay (SC)	-0.080	0.100
	Gangjin Bay (GJ)	0.013	-0.024
	Baeksu (BK)	3.506	-0.406
	Saemangeum (SM)	3.539	-1.847
	Ganghwa-do (GH)	3.679	-0.369
Fossil shells from Japan	Miyagi (*MY*)	-2.071	0.187
	Fukui (*FK*)	-1.050	0.398
	Aichi (*AC*)	-2.070	2.044
	Kumamoto (*KM*)	-0.891	2.013
Fossil shells from South Korea	Gimhae (*GM*)	-0.613	2.460
	Seosan (*SS*)	1.486	2.536
	Siheung (*SH*)	1.865	3.441
	Incheon (*IC*)	1.960	3.637

Table 5. ^{14}C ages of four fossil shells of *Meretrix* collected from tidal flats in Ganghwa-do, Incheon Metropolitan City, South Korea

ID No.	$\delta^{13}C$ (‰)	^{14}C age (yrBP ± 1σ)	Calibrated Age	
			1σ	2σ
Beta-374989	+0.6	2660 ± 30	BC 400–370	BC 455–350
Beta-374990	+1.1	1830 ± 30	AD 560–615	AD 535–650
Beta-374991	+1.0	3270 ± 30	BC 1195–1105	BC 1225–1060
Beta-374992	+1.4	2350 ± 30	BC 45–AD 20	BC 95–AD 55

(Fig. 3). The results of genetic studies using mitochondrial COI and nuclear ITS on these two species almost coincide with those of the identification of the living individuals using the discriminant score (Torii et al. 2010). These results suggest that the fossil shells excavated from the western coast of South Korea can be identified as *M. lusoria*, whereas the living individuals collected from the same area are identified as *M. petechialis*.

The results of the canonical discriminant analysis also indicate that the living individuals of *M. petechialis* collected from the western coast of South Korea can be distinguished clearly from both the living and fossil specimens of *M. lusoria* by the values of canonical variate 1 (Fig. 4), and the fossil shells excavated from the western coast of South Korea (*SS*, *SH*, *IC*), which were identified as *M. lusoria*, can be distinguished morphologically from the living individuals of *M. lusoria* using the canonical variates 1 and 2 (Fig. 4). The fossil shells excavated from the western coast of South Korea have: 1) a more rounded shape in the posterior-dorsal margin, 2) a larger shell breadth, and 3) a shorter pallial sinus compared to the living individuals of *M. lusoria*. However, the results of the present study suggest that the fossil shells from the western coast of South Korea can be identified as *M. lusoria*, although they are morphologically different from the living individuals of *M. lusoria*. The fossil remains from the replacement process of *M. lusoria* by *M. petechialis* have a shell morphology markedly different from the living individuals of both *M. lusoria* and *M. petechialis*.

From the results of the radioactive carbon isotopic analysis, the fossil shells collected from the tidal flats in

Fig. 5. *Meretrix lusoria* shell accumulation discovered on the lower tidal flats in Ganghwa-do, South Korea (37°35'14.96"N, 126°21'28.34"E, 16 September 2011, J.S. Hong). The discriminant analysis revealed that this species is *M. lusoria* and the radioactive carbon isotopic analysis indicated that the shells date from more than 2,000 years Cal BP. A: Photograph of accumulated *Meretrix* shell beds in the lower tidal flat, B: Detail of previous shell deposit illustrated in A.

Ganghwa-do (*IC*) had ages between 3,270 ± 30 and 1,830 ± 30 Cal BP (Table 5). The living individuals from the same place (GH) were quite different from the fossil shells in terms of canonical variates 1 and 2 (Fig. 4). These results suggest that *M. lusoria* had inhabited the western coast of South Korea until at least 2,000 years ago. However, this species was replaced by *M. petechialis* in the later years of the time period starting 2,000 years ago. Yamakawa and Imai (2013) mentioned that *M. lusoria* spats were artificially introduced from Japan to Taiwan in the 1920s. Similarly, it is likely that *M. petechialis* spats were also introduced from China to the western coast of South Korea, or planktonic larvae of *M. petechialis* might have arrived naturally on the western coast of South Korea from China during the last 2,000 years. To solve this problem, more data on fossil shells of *Meretrix* from the western coast of South Korea are required.

Acknowledgements

We thank the editors and two anonymous reviewers for their insightful comments that helped to improve the manuscript. We are grateful to Hiroki Sugawara, Masashi Yamaguchi, Junko Anso, Tsuyoshi Kito, Yasuhisa Henmi, Naoshi Kitamura, Hiroko Koike for their help in measuring the fossil and extant shells of *Meretrix* in Japan and South Korea. We also thank Dong-Ki Ryu for his help in measuring the fossil sample from the Daesan shell mound in South Korea, and Kyung-Won Kim, Dong-Pil Oh, Kil-Wook Yoe, Yung-Ki Ju and members of the Japan/Korea Tidal-flats Joint Survey Group for their help in collecting living individuals in South Korea. This work was partly supported by the Toyota Foundation, Takagi Fund for Citizen Science, Kurita Water and Environmental Fundation, JSPS KAKENHI Grant Numbers JP15740308, JP1965021, JP21500861, JP25440229 (for S.S.), the Japanese Association of Benthology (for Y.K. and H.T.), and also supported by the Korea Gyeonggi Sea Grant Program 2016 (for J.S.H.).

References

Aichi Archeology Center (2014) Matsuzaki ruins II, Kami-Hamada ruins. Aichi Archeology Center, Report 182, 300 p (in Japanese) http://www.maibun.com/DownDate/PDFdate/18200.pdf Accessed 3 Apr 2015

Charpentier V, Méry S, Phillips C (2004) Des coquillages … outillages des Ichtyophages? Mise en évidence d'industries sur Veneridae, du Néolithique à l'âge du Fer (Yémen, Oman, E.A.U). Arab Arch Epig **15**:1–10 (in French)

Hayami I, Matsukuma A (1971) Mensuration of fossils and statistics—Analysis of allometry and variation. Mem Fac Sci Kyushu Univ Ser D **10**:135–160 (in Japanese)

Henmi Y (2009) Present situation of the hard clam, Hamaguri in Japan. In: Uchino A (ed) Resource management and branding of Higo Hamaguri. Seibundo, Tokyo, pp 123–152 (in Japanese)

Kanamaru T (1932) Japanese hard clam story in Ise. Venus **3**:144–154 (in Japanese)

Kawase M (2002) Macrobenthic organisms in the estuary of the Yahagi River. Yahagigawakenkyu **6**:81–98 (in Japanese)

Kitamura N (2004) The mollusk corpse crowd of the last jomon transgression excavated by the construction of Kyushu Shinkansenin in Shirakawa, Kumamoto city. Kumamoto Mus Rep **16**:116–126 (in Japanese)

Kosuge T (1995) From the site of fishery resources research 5: how does a clam become? Fish Res **14**:33–37 (in Japanese)

Martin C, Matsukuma A (2006) A new *Meretrix* species from Arabian Sea. Venus **65**:270

Matsushima Y (1984) Shallow marine molluscan assemblages of postglacial period in the Japanese islands - Its historical and geographical changes induced by the environmental changes. Bull Kanagawa Pref Mus **15**:37–109 (in Japanese)

Nakagawa T, Fukuoka O, Fujii S, Chiji M, Nakamura T (1993) Fossil shell assemblages in the Holocene Takahama shell deb discovered at Takahama-Cho, western part of Fukui Prefecture, central Japan. Fukui Nat Mus Rep **1**:1–113 (in Japanese)

OBIS Indo-Pacific Molluscan Database (2006) http://clade.ansp.org/obis/find_mollusk.html Accessed 3 Apr 2015

Oyama K (1980) Revision of Matajiro Yokohama's type mollusca from the Tertiary and Quaternary of the Kanto area. Palaeont Soc Japan Spec Pap **17**:1–148

Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Bronk Ramsey C, Buck CE, Cheng H, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Haflidason H, Hajdas I, Hatté C, Heaton TJ, Hoffmann DL, Hogg AG, Hughen KA, Kaiser KF, Kromer B, Manning SW, Niu M, Reimer RW, Richards DA, Scott EM, Southon JR, Staff RA, Turney CSM, van der Plicht J (2013) Intcal13 and Marine13 radiocarbon age calibration curves 0-50,000 years cal BP. Radiocarbon **55**:1869–1887

Sakazume N (1984) General remarks on food remains from the Jomon Sites in Japan (2nd ed.). Doyokai, Kyoto, 322 p (in Japanese)

Talma AS, Vogel JC (1993) A simplified approach to calibrating ^{14}C dates. Radiocarbon **35**:317–322

Torii H, Sato S, Hamaguchi M, Henmi Y, Yamashita H (2010) The comparison of shell morphology and genetic relationship between *Meretrix lusoria* and *M. petechialis* in Japan and Korea. Plank Benth Res **5**:231–241

Yamakawa YA, Iwai H (2012) Hybridization between *Meretrix lusoria* and the alien congeneric species *M. petechialis* in Japan as demonstrated using DNA markers. Aquat Invasions **7**:327–336

Yamakawa YA, Iwai H (2013) PCR-RFLP typing reveals a new invasion of Taiwanese *Meretrix* (Bivalvia: Veneridae) to Japan. Aquat Invasions **8**:407–415

Yamakawa AY, Yamaguchi M, Iwai H (2008) Genetic relationship among species of *Meretrix* (Mollusca: Veneridae) in the Western Pacific Ocean. Pac Sci **62**:385–394

Yoosukh W, Matsukuma A (2001) Taxonomic study on *Meretrix* (Mollusca: Bivalvia) from Thailand. Phuket Mar Biol Center Spec Pub **25**:451–460