VENUS 65 (4): 299–317, 2007

Phylogeny of the Genus *Volachlamys* (Bivalvia: Pectinidae) from Japan

Kōji Yokogawa[1] and Ken-ichi Nakao[2]

[1] *13-5 Higashihama, Tadotsu-cho, Nakatado-gun, Kagawa 764-0016, Japan; gargariscus@ybb.ne.jp*

[2] *Tokushima Prefectural Museum, Bunka-no-mori Park, Hachiman-cho, Tokushima 770-8070, Japan*

Abstract: Following analytical studies on the two forms (Japanese names: Awaji-chihiro and Yami-no-nishiki) of *Volachlamys hirasei*, fossil specimens in genus *Volachlamys* from Japan were examined. The fossil specimens were from the Kazusa Formation (1.7 Ma), the Kitaarima Formation (0.9 Ma), the "Maiko Shell-Beds" (Early-Middle Pleistocene), the Takatsukayama Formation (0.41 Ma), the Atsumi Group (0.44 Ma), the Kioroshi Formation (0.125 Ma) and a seaside alluvium in Takamatsu (0.006 Ma). In addition to these, Recent specimens collected from the Seto Inland Sea were examined. Shells of the specimens were measured, and growth was analyzed by observing the annuli on the shell surfaces. In the fossil specimens, the Yami-no-nishiki form was detected in the Atsumi, Kioroshi and Takamatsu samples; it appeared in 1 of 44 individuals in the Atsumi sample, 1 of 2 individuals in the Kioroshi sample, and 17 of 39 individuals in the Takamatsu sample. The remaining specimens were comprised entirely of the Awaji-chihiro form, suggesting that the Yami-no-nishiki form first appeared around the middle Pleistocene. Morphologically, although shell proportions and costae number were unique by locality, there were no samples that were particularly specialized. On the other hand, the shell weight index (SWI) of the Maiko sample was prominently lower, indicating that these shells were much thinner and lighter than the other specimens. The growth analysis revealed distinctly greater growth in the Maiko specimens, although the other specimens (including the Recent ones) showed similar growth rates to one another. These results suggest that only the Maiko specimens were genealogically distinct from the others. The fossil specimens of *Volachlamys* from Japan were generally supposed to be *Volachlamys yagurai*, being treated as a species distinct from *V. hirasei*. The specimens from the "Maiko Shell-Beds", which is the type locality of *V. yagurai*, have biological characteristics so different from those of the Recent specimens that they are treated as a distinct species; however, in the other fossil specimens, significant characteristics that differ from those of the Recent specimens of *V. hirasei* could not be detected. These results indicate that only the fossil individuals from the "Maiko Shell-Beds" are referable to *Volachlamys yagurai*, and those from all other localities should be assigned to *Volachlamys hirasei*, which is common to the Recent specimens.

Keywords: Phylogeny, *Volachlamys*, fossil, morphology, growth

Introduction

Hirase's scallop, *Volachlamys hirasei* (Bavay, 1904) (Bivalvia: Pectinidae), has a strongly costate form (Awaji-chihiro) and a weakly costate form (Yami-no-nishiki). These forms have been regarded as subspecies by some researchers (Habe & Kosuge, 1967; Kira, 1959; Habe, 1977; Habe & Okutani, 1985). Hayami (1985) preliminarily examined the two forms and suggested that the differences between them were merely discontinuous variations within a single population. Thereafter, Yokogawa (1997a, 1997b, 1998a, 1998b) examined the relationship between the two forms using morphological, ecological and genetic techniques, concluding that they represent intraspecific morphological variations, and proposed to unify the specific name (Yokogawa, 1998b).

This study examines the morphology and growth of fossil specimens of the genus *Volachlamys* collected from various Japanese localities, in order to carry out a phylogenetic study of the genus, elaborate further on their evolutionary history and discuss taxonomic treatment.

Materials and Methods

The fossil specimens examined were collected from the Kazusa Formation, Nagasaki Prefecture (1.7 Ma: Otsuka & Furukawa, 1988; Otsuka *et al*., 1995), the Kitaarima Formation, Nagasaki Prefecture (0.9 Ma: Otsuka & Furukawa, 1988; Otsuka *et al*., 1995), the "Maiko Shell-Beds", Hyogo Prefecture (the Early-Middle Pleistocene: Matsubara, personal communication), the Takatsukayama Formation, Hyogo Prefecture (0.41 Ma: Kato *et al*., 1999), the Atsumi Group, Aichi Prefecture (Takamatsu silt facies, 0.44 Ma: Shimamoto *et al*., 1994), the Kioroshi Formation, located between Chiba and Ibaraki Prefectures (0.125 Ma: Omori *et al*., 1986; Koike & Machida, 2001), and a coastal alluvium in Takamatsu, Kagawa Prefecture (0.006 Ma: Kawamura, 1988) (Fig.1). In addition, the Recent *Volachlamys hirasei* was included in the study via 270 specimens that were collected in May, 1989 and examined in a former report (Yokogawa, 1997a). Data from the examined specimens are shown in Table 1; some of the specimens have been deposited in the Tokushima Prefectural Museum (TKPM), Osaka Museum of Natural History (OMNH) and the University Museum of the University of Tokyo (UMUT).

The shells were measured following the methods described by Yokogawa (1997a), providing

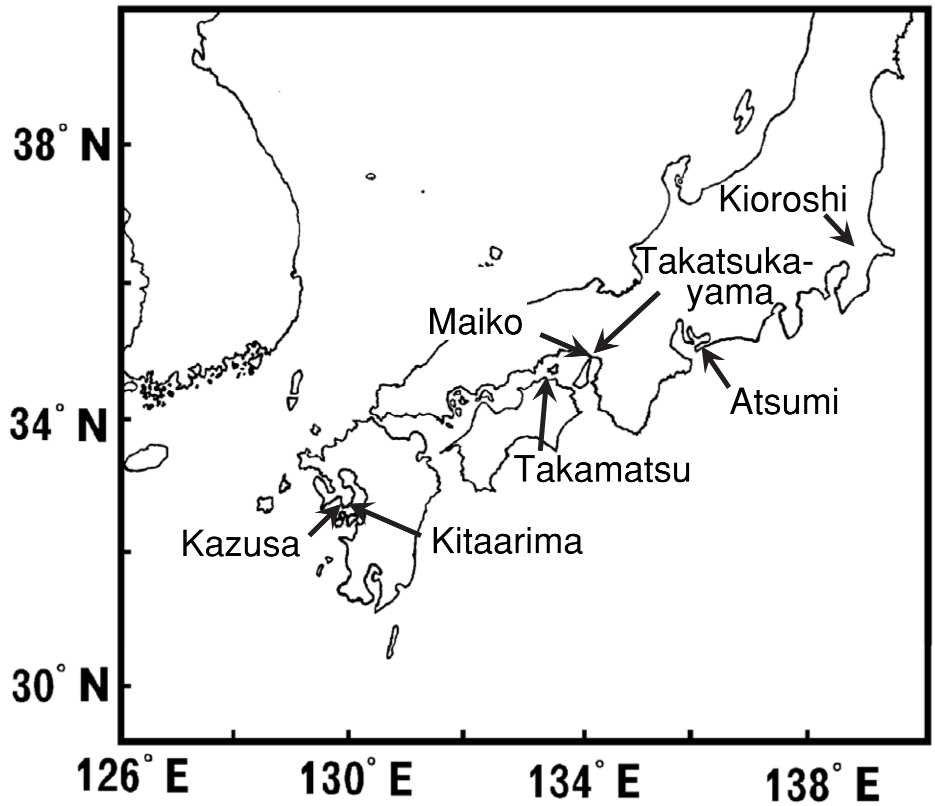

Fig. 1. Localities where fossil specimens were collected.

Table 1. Data from specimens examined.

Sample lot Form	Age (Ma)	Left valve N	Left valve Shell length Average	Left valve Shell length Range	Right valve N	Right valve Shell length Average	Right valve Shell length Range	Catalog No.
Kazusa	1.7							
Awajichihiro		30	38.0	14.6 – 51.3	35	38.8	19.0 – 53.3	TKPM-GFI3801
Kitaarima	0.9							
Awajichihiro		65	40.2	18.0 – 59.2	64	40.2	17.3 – 58.8	TKPM-GFI3802
Maiko	Early-Middle Pleistocene							
Awajichihiro		46	56.2	23.0 – 70.8	40	47.5	18.3 – 71.7	OMNH-QM3870
Atsumi	0.44							
Awajichihiro		18	32.0	16.1 – 55.2	25	31.4	9.1 – 56.5	TKPM-GFI4493 (17 of 43)
Yaminonishiki					1	29.0		TKPM-GFI4494
Takatsukayama	0.41							
Awajichihiro		18	31.1	12.9 – 64.9	33	35.2	16.3 – 71.5	UMUT CM-16777
Kioroshi	0.125							
Awajichihiro		1	54.4					TKPM-GFI4269
Yaminonishiki					1	45.2		TKPM-GFI4586
Takamatsu	0.006							
Awajichihiro		11	29.0	17.1 – 39.2	11	25.8	16.7 – 41.9	
Yaminonishiki		7	34.1	23.0 – 41.9	10	23.2	12.3 – 34.5	
Recent specimens								
Awajichihiro		221	43.8	30.5 – 59.2	221	43.6	30.4 – 59.9	
Yaminonishiki		49	45.8	33.9 – 53.1	49	45.4	30.2 – 52.6	

data on shell length, shell height, valve convexity, auricle width, shell weight, and the number of radial costae. In the former report, although the valve convexity and shell weight were measured for paired valves, this study measured these for single valves, as it is very rare to obtain conjoined valves in the case of fossil specimens. For the same reason, the radial costae number was counted for each single valve, even though the left valve of each pair only were measured in the former report. The formula defining shell weight index (SWI) in the former report was for paired shells, so in an effort to standardize the shell weight, this study redefined it for single shells, using the new formula:

$$SWI = SW/(SL \times SH \times VC) \times 10^5$$

where SW: shell weight (g); SL: shell length (mm); SH: shell height (mm); VC: valve convexity (mm)

For Recent specimens, these parameters were remeasured for the single valves and SWI was recalculated.

To compare the morphology of the specimens analytically, principal component analysis (PCA) by the usual method (Arima & Ishimura, 1997) was carried out. For the analysis, specimens were deleted that lacked some of the measured items because of incomplete shells. Auricle width, radial costae number and SWI were adopted as variates for the analysis. Shell length and valve convexity were deleted to avoid factor overlap, since those factors were used to calculate SWI.

Because the annuli observed in the shell surface have been found to be yearly rings (Yokogawa, 1998a), the annulus diameters were measured and the growth was analyzed with the methods described by Yokogawa (1998a). For the Recent specimens, the results of the growth analysis done on 929 Awaji-chihiro and 258 Yami-no-nishiki forms and described in the former report (Yokogawa, 1998a), were used.

Results

Shell morphology

Among the fossil specimens, samples from Kazusa, Kitaarima, Maiko and Takatsukayama comprised only the Awaji-chihiro form, whereas those from the remaining localities included the Yami-no-nishiki form. The Yami-no-nishiki form appeared in 1 of 44 individuals in the Atsumi sample, 1 of 2 individuals in the Kioroshi sample and 17 of 39 individuals in the Takamatsu sample (Table 1).

Table 2 summarizes average values of characters in the shells, and Figs. 2 and 3 illustrate general aspects of typical individuals from each sample lot. Regarding the general morphology of the shells, it is notable that individuals from the Maiko sample particularly have very little angular expansion at the anterior and posterior margins of the shell, and their shell shape is thus almost rounded (Figs. 2C, 3C). Also, the Maiko individuals have narrower radial costae and consequently the radial grooves become broader (Figs. 2C, 3C).

Figures 4 and 5 illustrate relationships between shell length and relative shell height ([shell height]/[shell length]), and between shell length and relative auricle width ([auricle width]/[shell length]) of the samples examined, respectively. Because the relative shell height and relative auricle width tended to diminish with growth in most of the samples, linear regression lines between shell

Table 2. Average values of shell characteristics in each sample lot.

	Left valve					Right valve				
Sample lot Form	Shell height*	Valve convexity*	Auricle width*	SWI	Costae number	Shell height*	Valve convexity*	Auricle width*	SWI	Costae number
Kazusa										
Awajichihiro	100.8	17.4	62.2	27.1	18.1	101.0	18.4	57.6	26.6	18.3
Kitaarima										
Awajichihiro	101.4	15.4	68.8	32.5	21.4	101.3	17.9	68.0	27.2	21.1
Maiko										
Awajichihiro	97.6	15.0	55.6	20.9	22.4	98.8	16.7	61.1	20.1	22.1
Atsumi										
Awajichihiro	101.3	15.0	75.6	32.6	17.1	102.9	16.4	79.5	26.8	16.8
Yaminonishiki						104.5	17.2	75.5	27.1	16.0
Takatsukayama										
Awajichihiro	101.1	14.9	80.9	28.9	18.2	100.1	16.3	79.1	28.5	18.8
Kioroshi										
Awajichihiro	98.0	15.8		27.1	17.0					
Yaminonishiki						92.3	14.2	75.2	24.0	
Takamatsu										
Awajichihiro	102.8	17.2	73.5	33.5	16.6	104.4	19.5	78.7	32.7	16.7
Yaminonishiki	105.9	16.9	71.9	34.3	15.5	106.8	18.0	77.3	28.5	15.1
Recent specimens										
Awajichihiro	97.6	15.7	64.9	31.6	16.7	97.8	18.4	64.7	28.1	16.9
Yaminonishiki	99.1	14.4	63.3	30.7	15.8	99.7	17.2	63.8	27.8	15.1

* Percentage of shell length.

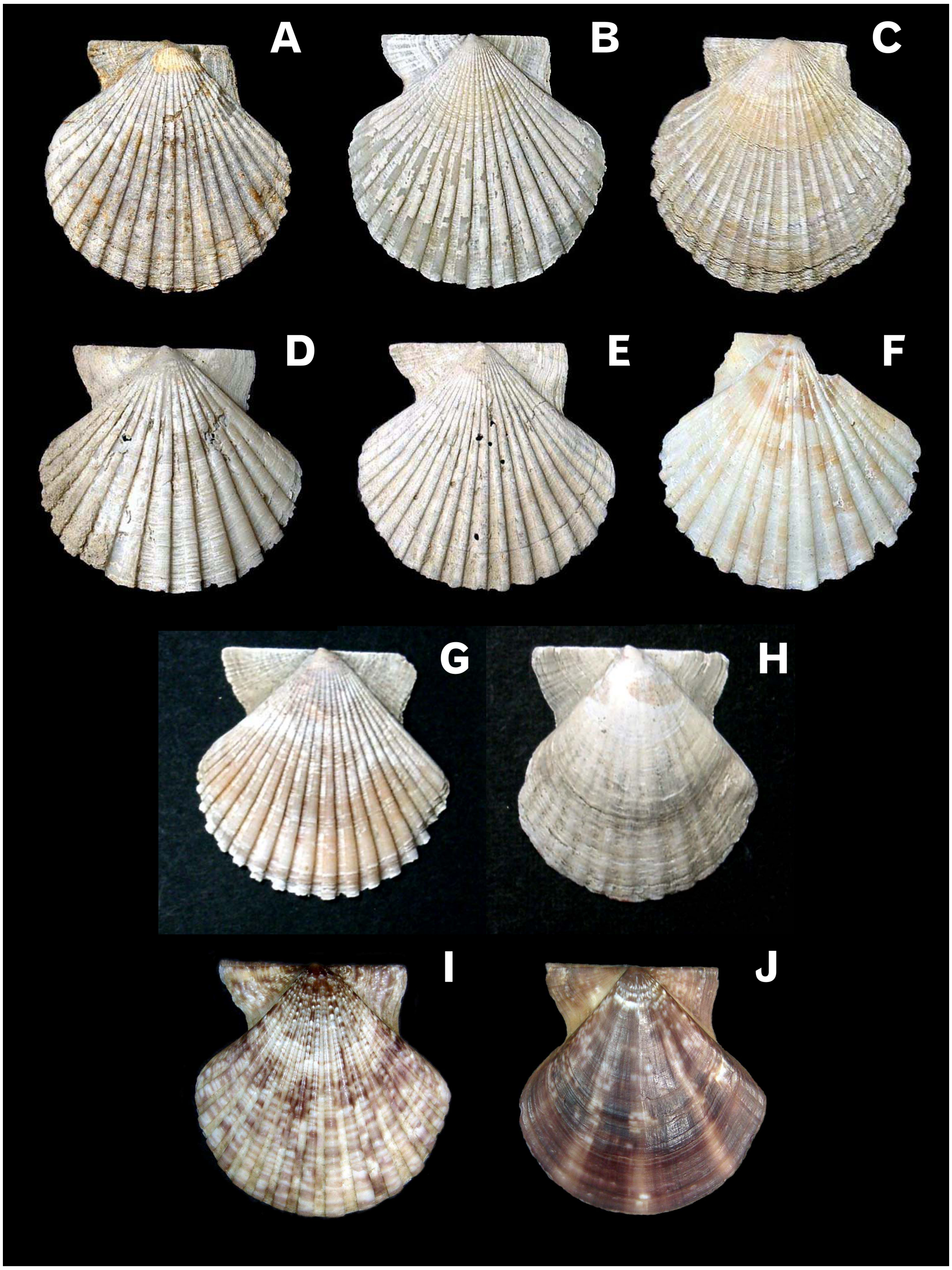

Fig. 2. Exterior views of typical left valves from each sample lot. **A.** Kazusa (SL 46.2 mm, SH 48.2 mm, collected by K. Nakao). **B.** Kitaarima (SL 46.1 mm, SH 45.6 mm, collected by K. Nakao). **C.** Maiko (SL 53.7 mm, SH 53.0 mm). **D.** Atsumi (Awaji-chihiro form) (SL 40.2 mm, SH 38.4 mm, collected by T. Moriwaki). **E.** Takatsukayama (SL 62.0 mm, SH 60.6 mm, collected by Y. Maeda, T. Ozawa and I. Hayami). **F.** Kioroshi (Awaji-chihiro form) (SL 54.4 mm, SH 53.3 mm, collected by K. Yoshida and K. Nakao). **G.** Takamatsu (Awaji-chihiro form) (SL 34.5 mm, SH 34.8 mm, collected by N. Kawamura). **H.** Takamatsu (Yami-no-nishiki form) (SL 22.9 mm, SH 24.6 mm, collected by N. Kawamura). **I.** Recent specimen (Awaji-chihiro form) (SL 38.1 mm, SH 37.8 mm). **J.** Recent specimen (Yami-no-nishiki form) (SL 37.7 mm, SH 38.1 mm).

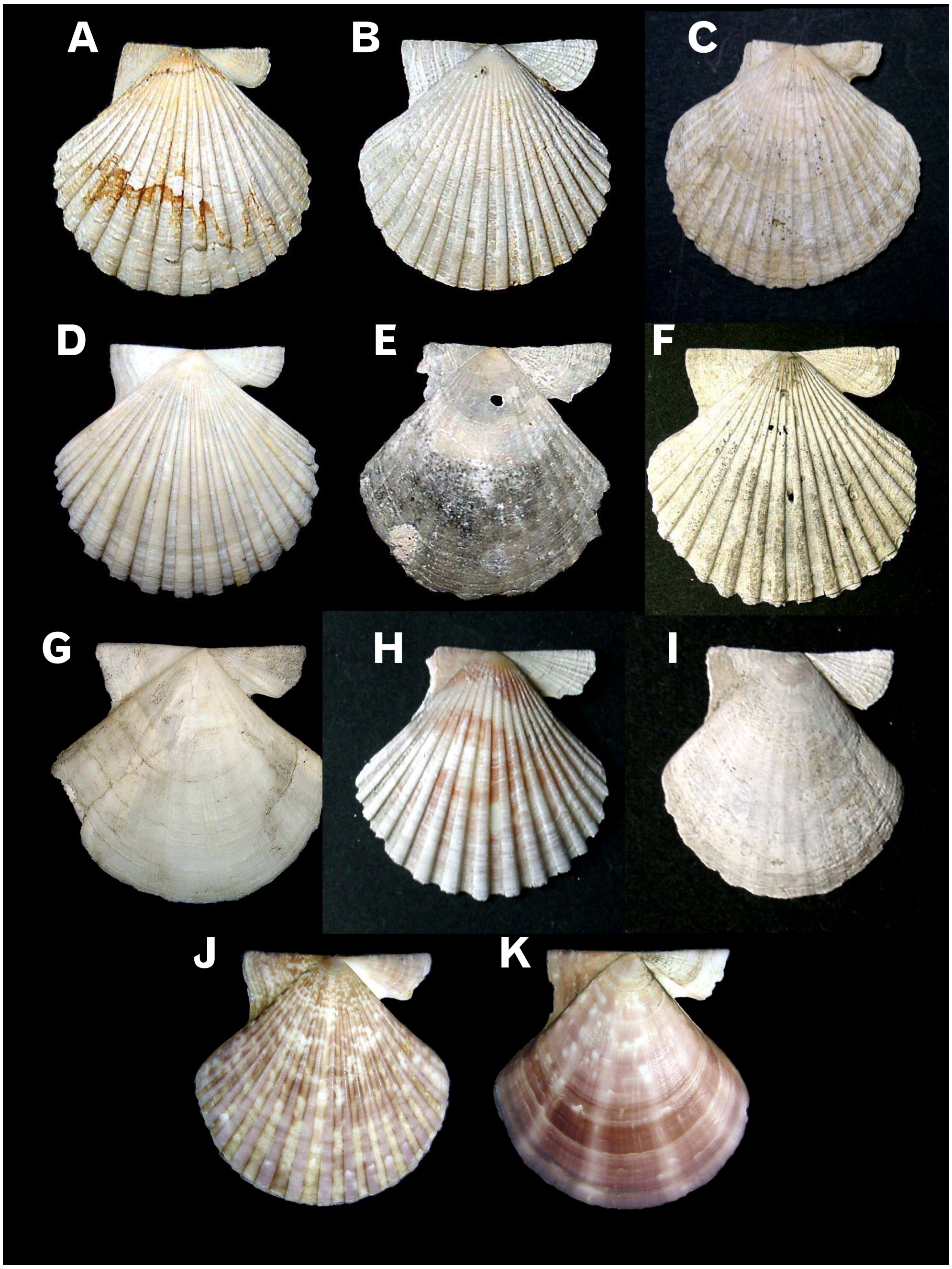

Fig. 3. Exterior views of typical right valves from each sample lot. **A.** Kazusa (SL 35.6 mm, SH 35.2 mm, collected by K. Nakao). **B.** Kitaarima (SL 35.2 mm, SH 35.4 mm, collected by K. Nakao). **C.** Maiko (SL 59.5 mm, SH 58.5 mm). **D.** Atsumi (Awaji-chihiro form) (SL 49.3 mm, SH 47.7 mm, collected by M. Kawase). **E.** Atsumi (Yami-no-nishiki form) (SL 29.0 mm, SH 30.3 mm, collected by M. Kawase). **F.** Takatsukayama (SL 50.2 mm, SH 48.5 mm, collected by Y. Maeda, T. Ozawa and I. Hayami). **G.** Kioroshi (Yami-no-nishiki form) (SL 45.2 mm, SH 41.7 mm, collected by K. Yoshida). **H.** Takamatsu (Awaji-chihiro form) (SL 34.4 mm, SH 34.6 mm, collected by N. Kawamura). **I.** Takamatsu (Yami-no-nishiki form) (SL 20.7 mm, SH 22.0 mm, collected by N. Kawamura. **J.** Recent specimen (Awaji-chihiro form) (SL 38.1 mm, SH 37.8 mm). **K.** Recent specimen (Yami-no-nishiki form) (SL 37.7 mm, SH 38.1 mm).

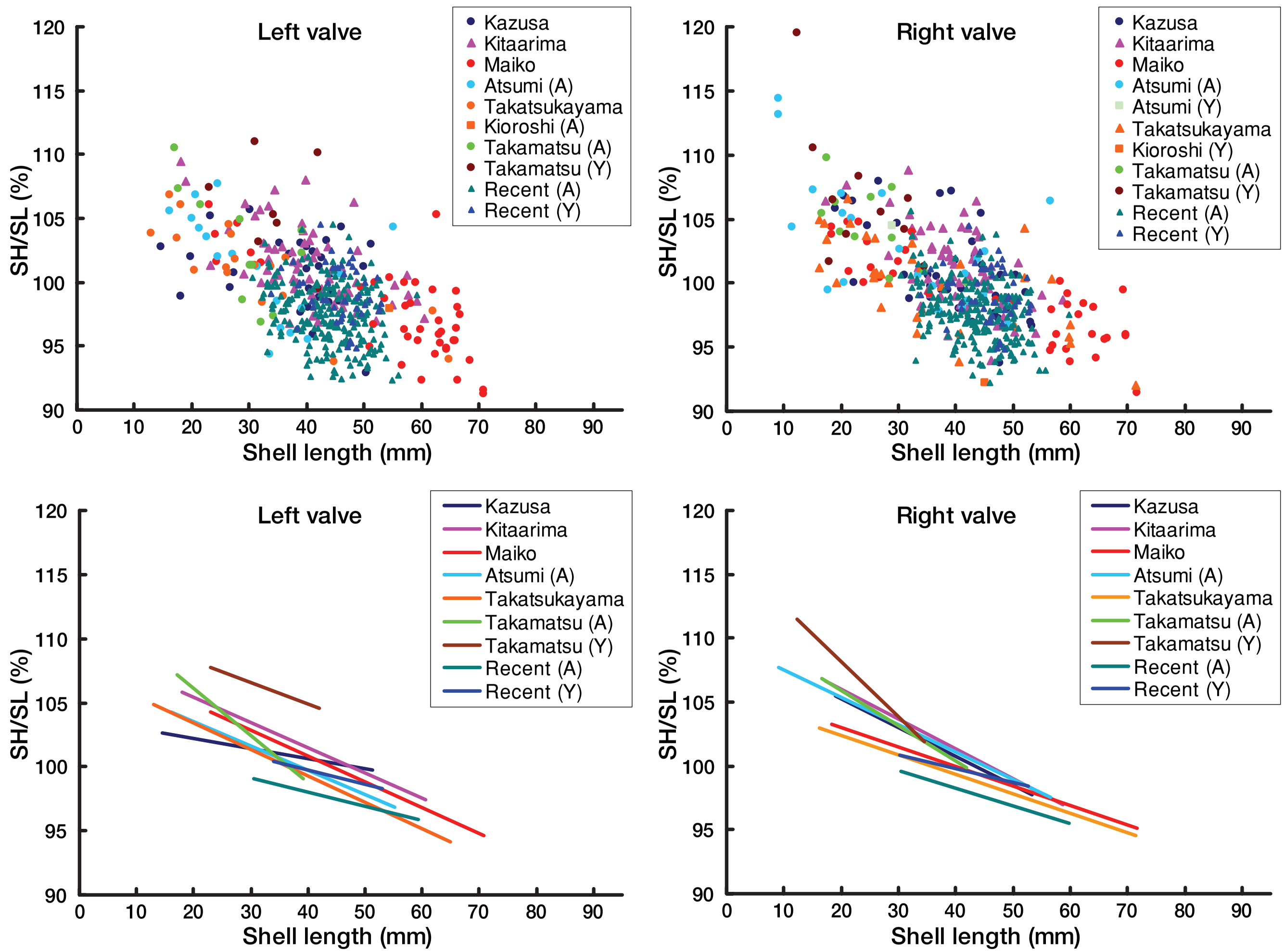

Fig. 4. Relationship between shell length and (shell height)/(shell length) (SH/SL) of the sample lots examined. Upper graphs illustrate plain plotting and lower graphs illustrate linear regression lines of the samples. Upper case letters in parentheses represent forms; A: Awaji-chihiro form, Y: Yami-no-nishiki form.

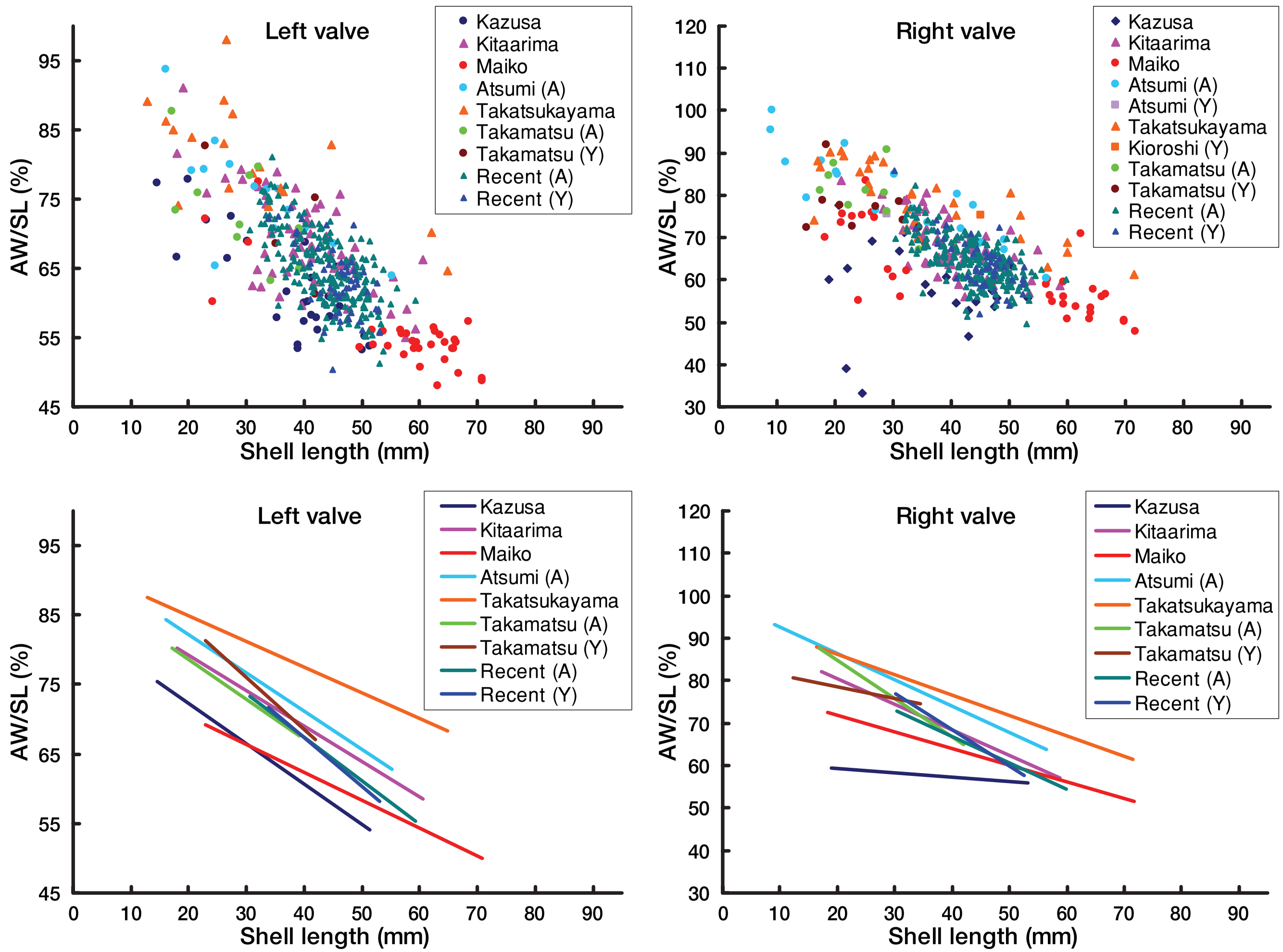

Fig. 5. Relationship between shell length and (auricle width)/(shell length) (AW/SL) of the sample lots examined. Upper graphs illustrate plain plotting and lower graphs illustrate linear regression lines of the samples. Upper case letters in parentheses represent forms; A: Awaji-chihiro form, Y: Yami-no-nishiki form.

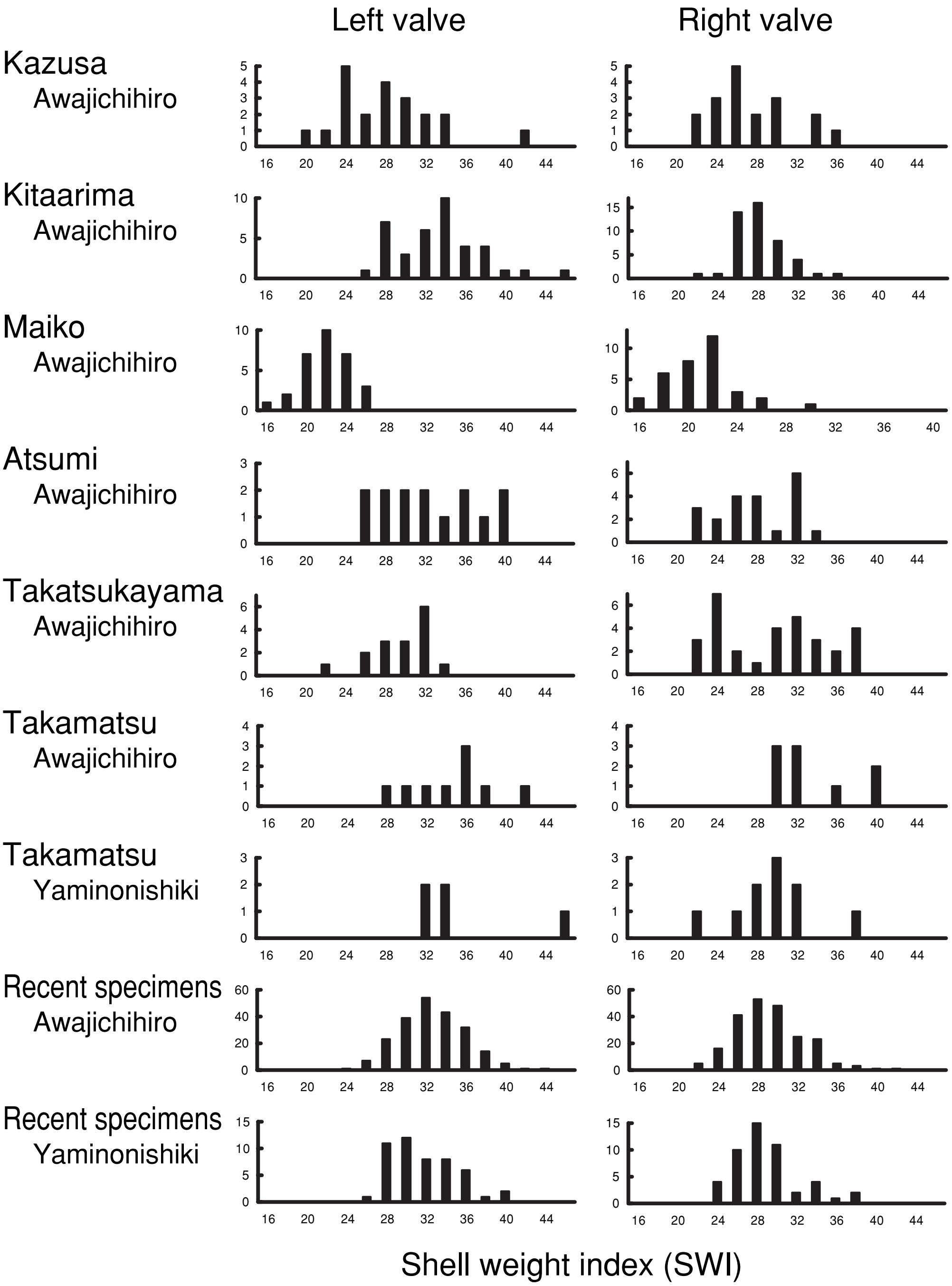

Fig. 6. Frequency distributions of shell weight index (SWI) of some sample lots. Longitudinal axes indicate numbers of individuals.

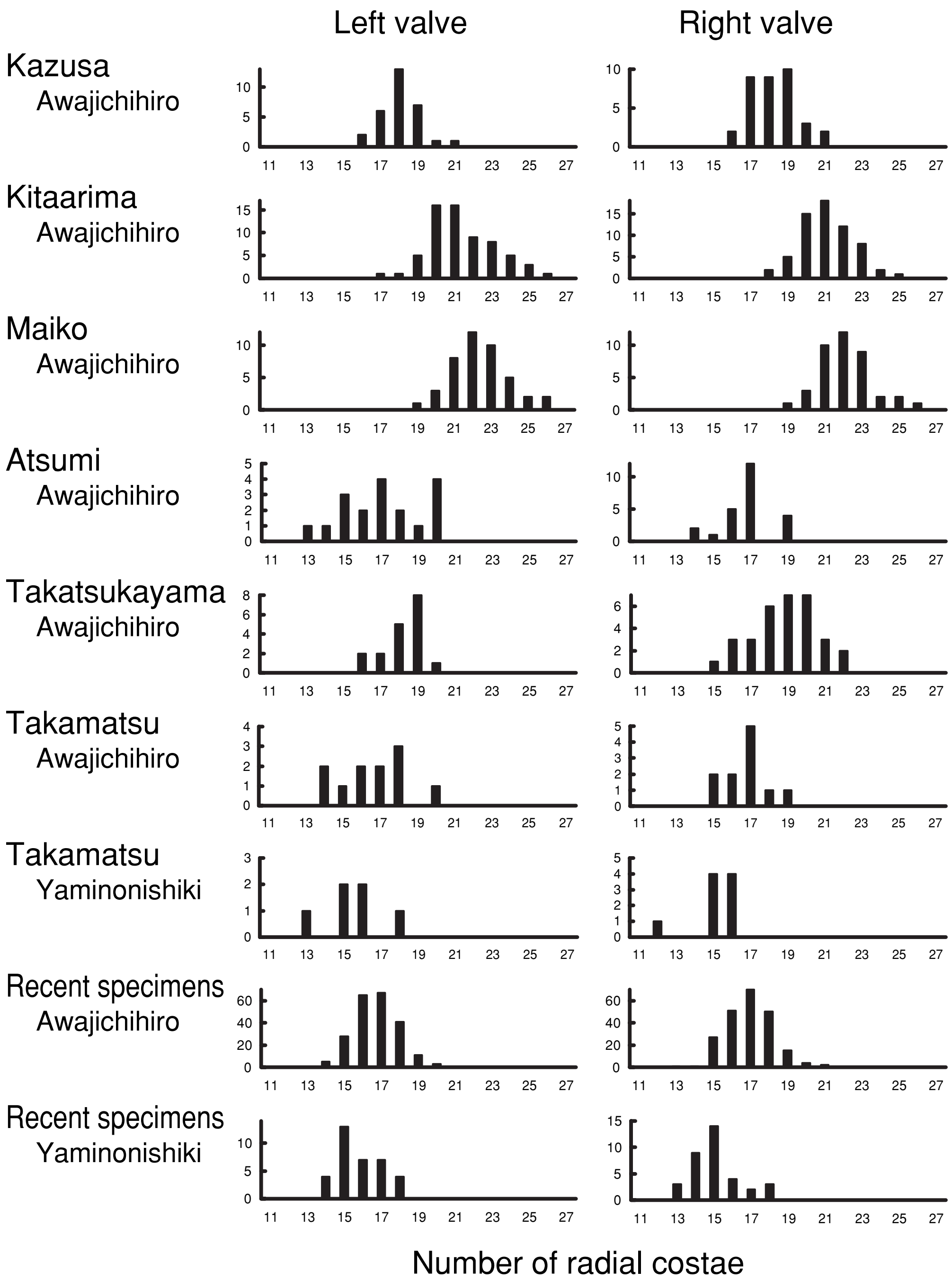

Fig. 7. Frequency distributions of radial costae numbers of some sample lots. Longitudinal axes indicate numbers of individuals.

length and those items were computed and are added in the lower part of the figures.

Regarding shell height, plotting points of the individuals from the Takamatsu sample (some of Awaji-chihiro and many of Yami-no-nishiki forms) are distributed in the higher zone of the graphs (Fig. 4), indicating markedly greater shell height. This is in contrast to the fact that the

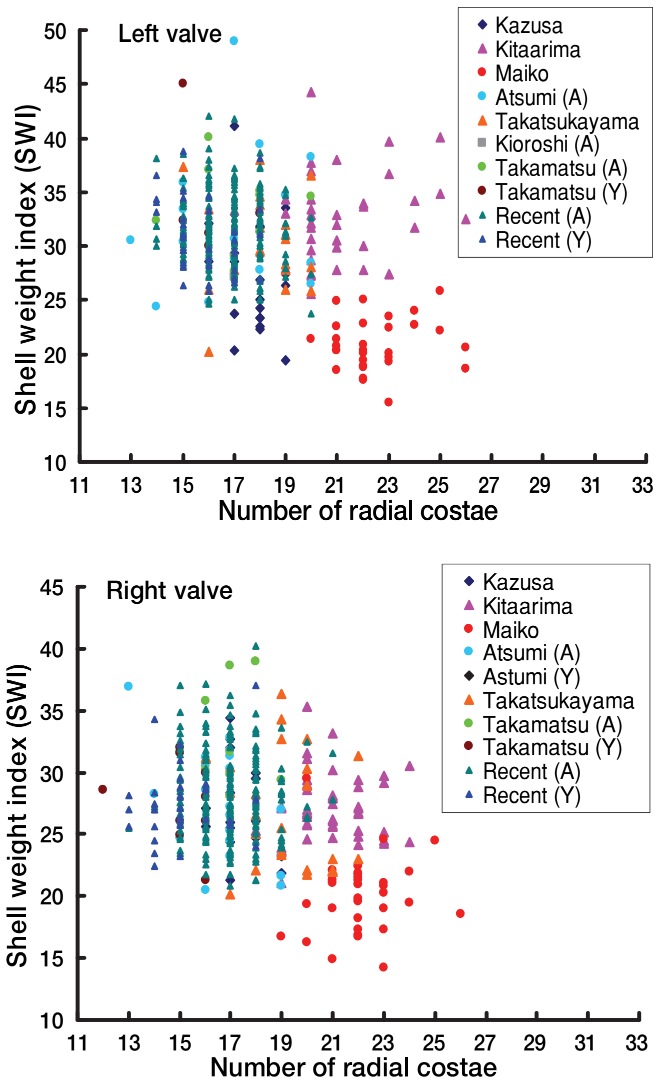

Fig. 8. Relationship between radial costae number and shell weight index (SWI). Upper case letters in parentheses following the sample names represent forms; A: Awaji-chihiro form, Y: Yami-no-nishiki form.

Recent specimens, which is very close both chronologically and geographically to the Takamatsu sample, tends to have a lower relative shell height (Fig. 4). In particular, the regression lines of the Takamatsu sample (Awaji-chihiro form) are located in the lowermost zone (Fig. 4). Among the remainder, the regression lines of the Kitaarima sample are located somewhat upwardly and those of the Takatsukayama sample are located somewhat downwardly (Fig. 4).

Regarding the auricle width, the regression lines represent well the tendencies of the samples examined (Fig. 5). The regression lines of the Takatsukayama sample are located distinctly upwardly (Fig. 5), indicating large auricles, while the regression lines of the Kazusa and Maiko samples are located downwardly (Fig. 5), inferring that the two samples have smaller auricles. The smaller auricle is recognizable also by appearance (Figs. 2A, 2C, 3A, 3C). Regression lines of the remaining samples are roughly concentrated (Fig. 5), indicating similarity.

The convexity of the right valve tended to be greater than that of the left valve in all the samples

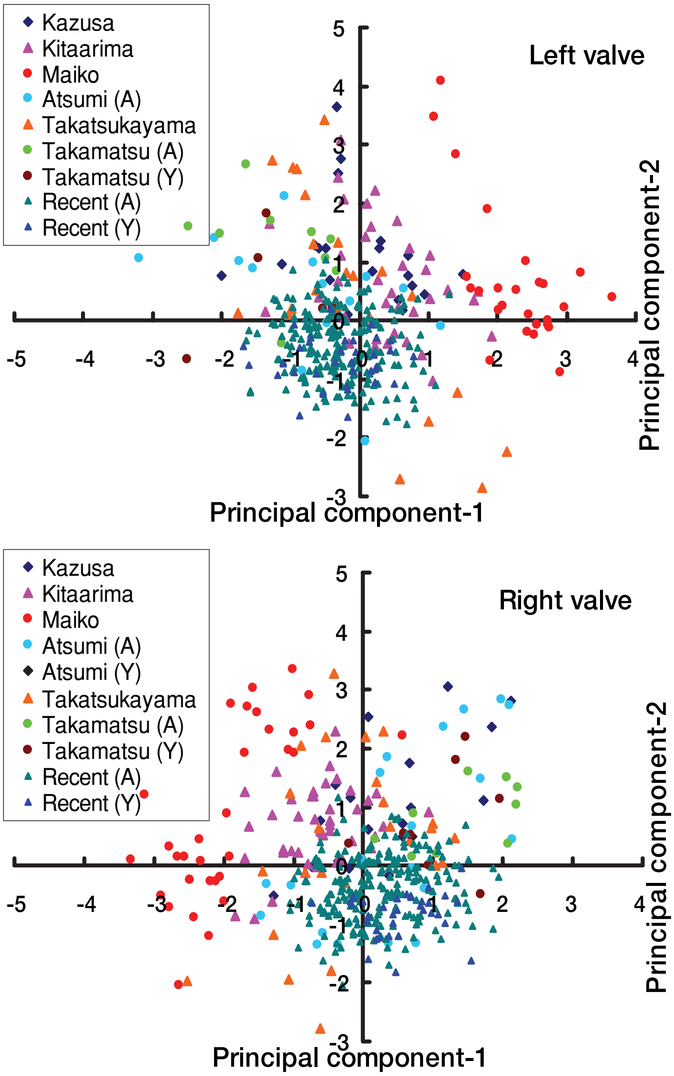

Fig. 9. Principal component analysis for the specimens examined. Upper case letters in parentheses following the sample names represent forms; A: Awaji-chihiro form, Y: Yami-no-nishiki form.

(Table 2). The convexity of both valves is significantly greater in the Kazusa and Takamatsu samples (Table 2). Of the samples examined, the Yami-no-nishiki form of the Recent specimens had the highest value for the difference between left and right valve convexities (Table 2).

Figures 6 and 7 illustrate frequency distribution histograms of SWI and the number of radial costae respectively. Regarding the shell weight index (SWI), it was significant that that of the Maiko sample was considerably lower (Fig. 6, Table 2). Among the others, SWI values of the Kazusa and Takatsukayama samples tended to be lower than those of the remainder (Fig. 5, Table 2).

The number of radial costae was greatest in the Maiko sample; the average values were 22.4 and 22.1 in the left and right valves, respectively (Table 2), and the ranges were 17–26 and 18–25 in the left and right valves, respectively (Fig. 7). The Kazusa and Takatsukayama samples followed the Maiko sample; the average values were between 18 and 19 in both valves (Table 2). The average values of the other samples were between 16 and 17 in general, while those of the Yami-no-nishiki

Table 3. Average values of estimated shell lengths in each annulus group in each sample lot.

	r_1	r_2	r_3	r_4	r_5	r_6	r_7	r_8	r_9	r_{10}	r_{11}
Kazusa											
Awajichihiro	12.78	22.18	29.85	36.83	41.93	46.62	50.76				
Kitaarima											
Awajichihiro	11.14	20.25	28.66	34.89	40.09	44.75	49.76	52.86			
Maiko											
Awajichihiro	17.37	29.34	40.54	48.87	55.17	59.37	63.77				
Atsumi											
Awajichihiro	11.73	20.88	28.55	34.76	40.00	44.95	49.07	56.68			
Yaminonishiki	10.80	22.23	28.40								
Takatsukayama											
Awajichihiro	8.79	17.13	24.57	31.17	37.70	43.36	49.60	53.37	57.29	61.22	64.50
Kioroshi											
Awajichihiro	10.40	16.70	25.40	35.10	42.20	47.80	51.20				
Yaminonishiki	13.55	24.61	33.17	40.65							
Takamatsu											
Awajichihiro	12.35	21.50	29.53	36.70	39.89						
Yaminonishiki	11.76	20.56	26.88	31.32	37.27						
Recent specimens											
Awajichihiro	16.53	25.13	32.12	37.46	41.61	45.01	48.08	51.46			
Yaminonishiki	15.85	24.46	32.00	37.80	42.27	45.73	48.43	51.60	48.15		

Table 4. Parameters of Walford growth transformation and von Bertalanffy growth formulae.

	Walford parameter [1]		von Bertalanffy paramter [2]		
	α	β	k	L_∞	t_o
Kazusa					
Awajichihiro	0.831	11.67	0.185	68.98	− 0.106
Kitaarima					
Awajichihiro	0.844	11.07	0.170	70.78	− 0.007
Maiko					
Awajichihiro	0.817	15.65	0.202	85.66	− 0.123
Atsumi					
Awajichihiro	0.835	10.96	0.181	66.30	− 0.084
Yaminonishiki	0.540	15.84	0.617	34.41	0.381
Takatsukayama					
Awajichihiro	0.895	9.27	0.111	87.90	0.055
Kioroshi					
Awajichihiro	0.905	9.82	0.100	102.90	− 0.085
Yaminonishiki	0.816	13.42	0.204	72.77	− 0.011
Takamatsu					
Awajichihiro	0.808	11.80	0.214	61.30	− 0.053
Yaminonishiki	0.778	11.37	0.251	51.20	− 0.039
Recent specimens					
Awajichihiro	0.783	12.34	0.244	56.95	− 0.404
Yaminonishiki	0.806	11.96	0.216	61.64	− 0.378

[1] $L_{t+1} = \alpha L_t + \beta$ [2] $L_t = L_\infty (1 - e^{-k(t - t_o)})$

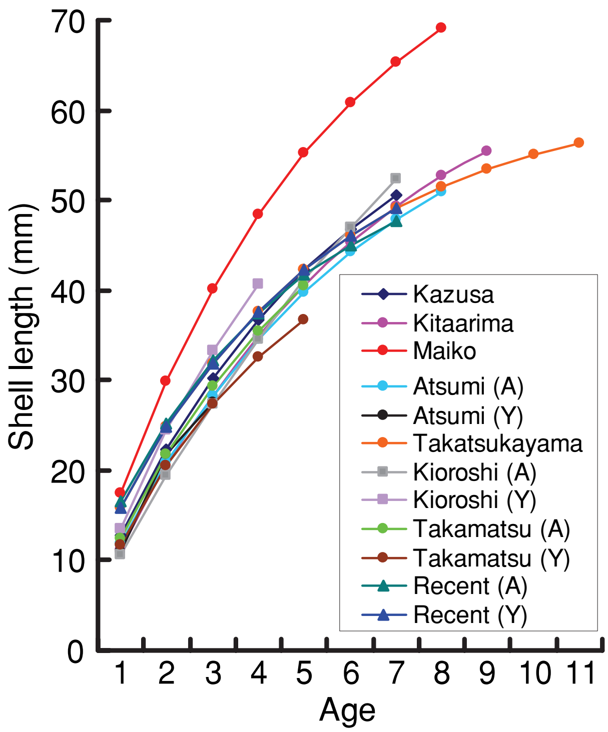

Fig. 10. Growth patterns of the sample lots by von Bertalanffy growth formulae. Upper case letters in parentheses following the sample names represent forms; A: Awaji-chihiro form, Y: Yami-no-nishiki form.

forms from the Takamatsu and Recent species were lower than 16 (Table 2).

The relationship between the radial costae number and shell weight index (SWI) is illustrated in Fig. 8. When these two characters are combined, the individuals from the Maiko sample separate from the others almost completely. Also, the individuals from the Kitaarima sample are well converged, though they do not separate completely from the others (Fig. 8).

Figure 9 shows results of principal component analysis (PCA) indicated by plots of individual principal component scores. These show the individuals from the Maiko sample significantly separated from the others, while the individuals from the other samples were almost randomly distributed, although some samples showed a certain convergence in individuals. This implies morphological peculiarity of the Maiko sample.

Age and growth

Initially, Walford growth transformation formulae were applied to the left and right valve groups in each sample, and differences between the parameters of the two formulae were examined with *t* test. From the results, no significant differences were recognized in any of the samples, and thus the growth analysis was performed with the pooled data of the left and right valves.

For each sample, the correlation formula of the shell height with shell length was calculated. Subsequently, the shell lengths at the annulus formation were estimated with the formulae, and average values of each annulus group were calculated (Table 3). In addition, the parameters of the Walford growth transformation and von Bertalanffy growth formulae are summarized in Table 4. Further, Fig. 10 shows growth curves of the samples expressed using the von Bertalanffy growth formulae. All the fossil samples except Maiko indicated rates of growth similar to those of the

Recent Awaji-chihiro and Yami-no-nishiki forms; however, the Maiko sample clearly showed the highest growth rate (Fig. 10, Table 3).

Discussion

The results of the present study reveal that the Maiko sample is morphologically different from the other samples (Fig. 9) and that its growth rate is notably higher (Fig. 10, Table 3). Of the morphological differences, it is significant that the shell weight index (SWI) of the Maiko sample is rather smaller than that of the other samples (Fig. 6, Table 2). Low SWI can indicate that shells of the Maiko individuals are thin, and this may be related to a higher growth rate. Yokogawa (1998a) examined growth of the Recent Awaji-chihiro and Yami-no-nishiki forms, and revealed that growth of the Yami-no-nishiki form is greater than that of the Awaji-chihiro form. The reason for this phenomenon is thought to be that the Yami-no-nishiki form can conserve calcium carbonate for shell formation and subsequently use the surplus calcium carbonate for additional shell growth, resulting in greater growth than in the other form. A very similar phenomenon is reported for two forms of the blistered scallop, *Cryptopecten vesiculosus* (strongly and weakly costate forms) (Hayami, 1984). The unusual growth of the Maiko sample also can be explained by this hypothesis. The Maiko individuals were able to conserve the calcium carbonate for shell formation because their shells are thin; subsequently, the surplus calcium carbonate was used for additional shell growth, resulting in the unusual growth.

The biological characteristics of the Maiko sample obviously indicate that it is a systematically distinct population from the other samples. This may explain the other morphological characteristics of smaller auricle width and greater radial costae number in the Maiko sample. Because the Maiko individuals are almost completely separated from the others with respect to the radial costae number and SWI (Fig. 8), they should be treated as an independent species.

As for the remaining samples, although values for morphological characters including the radial costae number are unique to individuals, examples with extremely specialized morphology were not recognized, including among the Recent species (Figs. 4–7, Table 2). The growth patterns of those samples are similar to one another (Fig. 10, Table 3), implying monophyly of all the material other than the Maiko sample. But even if those samples are monophyletic, considerable biological (ecological and genetic) differences can be expected among the samples, between which a time gap of hundreds of thousands of years exists. Therefore, within the concept of the biological species proposed by Wiley (1991), the other samples might also be independent species. However, given what presently is known about their morphological characteristics, there is no choice but to regard them as one species because they cannot be completely distinguished. The individuals from the Takamatsu sample, which are very close to the Recent specimens chronologically and geographically, differ considerably morphologically from the Recent specimens (Figs. 4, 5; Table 2). This suggests the possibility that morphological changes occurred within a very short span of geological time. This could support the treatment of the samples other than the Maiko sample as a single species.

Fossil bivalves of the genus *Volachlamys* are generally treated as *Volachlamys yagurai* (Japanese name: Mukashi-chihiro, also called Yagura-nishiki), and are regarded as a distinct species from the Recent *V. hirasei* (Hayami, 1985; Fujiyama, 1986; Kaneko & Kajiyama, 1993). Nomenclaturally, the valid name *V. yagurai* had generally been attributed to Makiyama (1923) in literature, but it was shown to be preceded by Yagura (1922) (see Yokokawa *et al.* (2007) for discussion). Both *V. yagurai* Yagura, 1922 and *V. yagurai* Makiyama, 1923 were described from the "Maiko Shell-Beds".

Although populations of the weak costae form (Yami-no-nishiki form) may be regarded as *V. hirasei*, it is difficult to identify whether a population is *V. yagurai* or *V. hirasei* when the entire sample consists of just a few individuals of the Awaji-chihiro form. Individuals of the Yami-no-nishiki form could potentially appear thereafter. Thus, the taxonomic treatment concluded that the individuals from the "Maiko Shell-Beds" are *Volachlamys yagurai* (Japanese name: Mukashi-chihiro), while for the other fossil specimens, the oldest specific name (Bavay, 1904) for the Japanese *Volachlamys* bivalves is adopted; that is, they are *Volachlamys hirasei* (Japanese name: Awaji-chihiro). The Japanese name "Awaji-chihiro" is appropriate because most of the fossil specimens are of the Awaji-chihiro form (Table 1).

Although the samples other than the Maiko sample are here all treated as *Volachlamys hirasei*, some of them, such as the Kitaarima sample, have somewhat peculiar morphological characteristics. Therefore, it may be reasonable to establish some subspecies for the fossil samples. This should be considered carefully with further examination of the other fossil specimens of the genus *Volachlamys* from the various localities, including any newly discovered ones hereafter.

Tokunaga (1906) described the new fossil species, *Pecten pulchellimus* from Oji, Tokyo, but Hayami (1985) regarded it to be identical with *Volachlamys hirasei* owing to morphological similarity. Consequently, *P. pulchellimus* is here treated as a junior synonym of *V. hirasei*. Thereafter Yokoyama (1926) described *Pecten atsumiensis* from the Atsumi Group. That species also was regarded to be identical with *V. hirasei* (Kuroda, 1932; Hayami, 1985). Since the photographs in the original description were very similar to *V. hirasei* and the Atsumi Group deposits contain *V. hirasei*, *P. atsumiensis* is also here considered a junior synonym of *V. hirasei*.

Hayami (1985) considered the phylogeny of the Japanese *Volachlamys* bivalves. He hypothesized that the population from the "Maiko Shell-Beds", which have many radial costae, chronologically transited into the populations from the Takatsukayama and Kazusa Formations, which have somewhat fewer radial costae. Subsequently, the radial costae number further decreased chronologically, and they transited into the Recent population monophyletically as a consequence. However, a possible contradiction to his hypothesis is that the radial costae reduced chronologically because the radial costae number of the individuals from the Kazusa Formation (1.7 Ma) was fewer than that of the individuals from the Kitaarima Formation (0.9 Ma). Although he hypothesized that the Japanese *Volachlamys* bivalves are monophyletic, the present study revealed that at least two strains once existed in Japanese waters.

Hashimoto & Maeda (1989) considered the chronological order of the Takatsukayama Formation and "Maiko Shell-Beds" based on the hypothesis of Hayami (1985). They proposed that the Takatsukayama Formation is younger because the radial costae number of so-called "*Volachlamys yagurai*" from the Takatsukayama Formation is lower than those from the "Maiko Shell-Beds". However, Hayami's hypothesis is invalidated by the present study. Moreover, comparison of the specimens from the Takatsukayama Formation and "Maiko Shell-Beds" is not pertinent because the specimens represent distinct species; consequently, Hashimoto and Maeda's opinion is baseless. Ando (1953) examined the fossil shells of the genus *Volachlamys* from the "Maiko Shell-Beds" and Takatsukayama Formation, and regarded the two samples both to be *Volachlamys yagurai*, owing to similarity of the radial costae number; however, his opinion is here rejected for the same reason.

The present study determined that the fossil *Volachlamys* bivalves (except those from the "Maiko Shell-Beds") are monophyletic; among those, the weakly costate form (Yami-no-nishiki form) appeared in 1 of 44 individuals in the Atsumi sample, 1 of 2 individuals in the Kioroshi sample and 18 of 39 individuals in the Takamatsu sample (Table 1). This suggests that the Yami-no-nishiki form, which is an intrapopulational morphological variation, first appeared in the middle Pleistocene. Thereafter, its frequency increased chronologically, and transited into that in the Recent population. The fact that fossils of the Yami-no-nishiki form appear in the Kanto and Tokai regions in addition to the Seto Inland Sea and Ariake Sea, where the Recent populations dwell, implies that a common population inhabited a broad area when the fossils lived, or that environmental factors, such as elevation of sea level during the inter-glacial epochs, expanded the distribution easily. Thereafter, the shallow and closed sea areas inhabitable for the population decreased, and consequently the Recent population has a restricted distribution at present.

Many of the problems concerning the genus *Volachlamys* have been resolved by previous analytical studies (Yokogawa, 1997a; 1997b; 1998a; 1998b) and the present study; however, there still are some problems to be examined, such as related *Volachlamys* species in China and the establishment of subspecies among the fossil samples. Hereafter, the taxonomy and phylogeny of the genus *Volachlamys*, including species from India, Pakistan, South Africa, Papua New Guinea, and Indonesia, should be reviewed.

Acknowledgements

The present study could not have been carried out without the willing help of people noted below in obtaining the fossil shell specimens. Mr. Hisao Ishii, Osaka Museum of Natural History, loaned. Dr. Itaru Hayami, ex-professor of Faculty of Science, Kanagawa University, loaned the Takatsukayama sample, Mr. Toru Moriwaki, Okazaki City, Aichi Prefecture, Mr. Motohiro Kawase, Faculty of Human Science, Aichi Mizuho University, and Mr. Kazuo Yano, Nagoya City, Aichi Prefecture, loaned part of the Atsumi sample, and Mr. Norihito Kawamura, Marugame High School, loaned the Takamatsu sample.

Dr. Yasuo Kondo, Faculty of Science, Kochi University, gave some support and advice in creating the present paper. Also, we wish to thank Elizabeth Paxton, ScratchCat LLC, Alpharetta, Georgia, US, for checking the manuscript.

References

Ando, Y. 1953. Molluscan fossils from Maiko and Takatsukayama. *Hyogo Biology* 2: 141–144, 140. (in Japanese)

Arima, S. & Ishimura, S. 1997. *A Story of Multivariate Analysis*. ix+320 pp. Tokyo-tosho Co., Tokyo. (in Japanese)

Bavay, A. 1904. Descriptions de quelques nouvelles espèces du genre *Pecten* et retifications. *Journal de Conchyliologie* 52: 197–206, pl. 6.

Fujiyama, I. 1986. The Cenozoic Quaternary, Shells (1-13). *In*: Fujiyama, I., Hamada, T. & Yamagiwa, N. (eds.), *Illustrated Guide of Japanese Ancient Livings for Students*, 2nd ed., pp. 338–363. Hokuryukan, Tokyo. (in Japanese)

Habe, T. 1977. *Systematics of Mollusca in Japan, Bivalvia and Scaphopoda*. xiii+372 pp. Zukan-no-Hokuryukan, Tokyo. (in Japanese)

Habe, T. & Kosuge, S. 1967. *Common Shells of Japan in Color*. 223 pp., 64 pls., Hoikusha Publ. Co., Osaka. (in Japanese)

Habe, T. & Okutani, T. 1985. "*Compendium of Seashells*" by Abbott, R. T. & Dance, S. P. (Japanese edition). 443 pp. Heibonsha, Tokyo. (in Japanese)

Hashimoto, I. & Maeda, H. 1989. *Reading Strata in Kobe 2, Natural History for the Past Two Million Years in Kobe*. 119+12 pp., 1 foldout. Nature of Kobe 17, Kobe Shizen Shuppankai, Kobe. (in Japanese)

Hayami, I. 1984. Natural history and evolution of *Cryptopecten* (a Cenozoic-Recent pecitinid genus). *The University Museum, the University of Tokyo, Bulletin* (24): i–ix, 1–149, pls. 1–13.

Hayami, I. 1985. Systematics and evolution of *Volachlamys* from Japan (Preliminary notes). *Venus (Japanese Journal of Malacology)* 44: 3–14. (in Japanese with English abstract)

Kaneko, S. & Kajiyama, H. 1993. Molluscan fossils from the Osaka Group, Pre-Lake Biwa Group and terrace sedimentation, and crab fossils in alluvia. *In*: Itihara, M. (eds.), *The Osaka Group*, 1st ed., pp. 203–215. Sogensha, Osaka. (in Japanese)

Kato, S., Sato, H., Matsubara, T., Hyodo, M. & Danhara, T. 1999. Fission-track age and correlation of the Takatsukayama volcanic ash layer distributed at the western foothills of the Rokko Mountains, western Japan. *The Quaternary Research* 38: 411–417. (in Japanese with English summary)

Kawamura, N. 1998. Paleoenvironmental analysis of the Takamatsu plain, Kagawa pref. based on Holocene molluscan association and ^{14}C dating. *Kagawa Seibutsu* (25): 31–42. (in Japanese)

Kira, T. 1959. *Coloured Illustrations of the Shells of Japan, Enlarged & Revised Edition* (*1st Printing*). ix+240 pp., 71 pls. Hoikusha Publ. Co., Osaka. (in Japanese)

Koike, K. & Machida, H. (eds.) 2001. *Atlas of Quaternary Marine Terraces in the Japanese Islands*. pp. 6–7. Tokyo University Press, Tokyo. (in Japanese)

Kuroda, T. 1932. An illustrated catalogue of the Japanese shells. *The Venus* (*Organ of the Malacological*

Society of Japan) 3(2): appendix 87–102. (in Japanese)
Makiyama, J. 1923. Some Pliocene mollusks from Maiko, near Kobe. *Japanese Journal of Geology and Geography* 2: 19–26, pl. IV.
Omori, M., Hayama, Y. & Horiguchi, M. (eds.) 1986. *Geology of Japan 3, Kanto Region*. xiv+355 pp. Kyoritsu Publishing, Tokyo. (in Japanese)
Otsuka, H. & Furukawa, H. 1988. Early and middle Pleistocene stratigraphy in Kyushu and Ryukyu, Japan. *The Memoirs of the Geological Society of Japan* 30: 155–168. (in Japanese with English abstract)
Otsuka, H., Hokama, K., Tanaka, T., Atomura, N., Takenouchi, T. & Ueno, H. 1995. Re-examination on the geology of the southern part of the Shimabara Peninsula, west Kyushu, Japan. *Report of the Faculty of Science, Kagoshima University, Earth Sciences and Biology* 28: 181–241. (in Japanese with English abstract)
Shimamoto, M., Higashino, H., Suzuki, H. & Tanaka, Y. 1994. Geological age and correlation of the Pleistocene Atsumi Group in Atsumi Peninsula, Aichi Prefecture, Japan. *The Journal of the Geological Society of Japan* 100: 618–630. (in Japanese with English abstract)
Tokunaga, S. 1906. Fossils from the environs of Tokyo. *Journal of College of Science, the Imperial University of Tokyo*, 21 (Part 2): 1–96, pls. 1–6.
Wiley, E. O. 1991. *Phylogenetics*. (Translated from English by Miya, M., Nishida, S. and Okiyama, M.). xxii+528 pp. Bun-ich-Sogo-Shuppan, Tokyo. (in Japanese)
Yagura, W. 1922. *Shumi Kenkyu, Kairui Sowa* [*Hobby study on shells*]. [8]+403+16+[5], 33 pls. Maiko Kairui-kan, Tarumi. (in Japanese)
Yokogawa, K. 1997a. Characteristics in two forms of Hirase's scallop *Volachlamys hirasei* - 1. Shell morphology. *Venus (Japanese Journal of Malacology)* 56: 319–329. (in Japanese with English abstract)
Yokogawa, K. 1997b. Characteristics in two forms of Hirase's scallop *Volachlamys hirasei* - 2. Soft part morphology and its seasonal changes. *Venus (Japanese Journal of Malacology)* 56: 330–339. (in Japanese with English abstract)
Yokogawa, K. 1998a. Characteristics in two forms of Hirase's scallop *Volachlamys hirasei* - 3. Age and growth. *Venus (Japanese Journal of Malacology)* 57: 49–56. (in Japanese with English abstract)
Yokogawa, K. 1998b. Characteristics in two forms of Hirase's scallop *Volachlamys hirasei* - 4. Genetic characters. *Venus (Japanese Journal of Malacology)* 57: 57–71. (in Japanese with English abstract)
Yokogawa, K., Nakao, K. & Matsubara, T. 2007. Precedence of *Pecten yagurai* Yagura, 1922 (Bivalvia: Pectinidae), over *Pecten yagurai* Makiyama, 1923, with lectotype designation of both taxa. *Venus* 65: 375–378.
Yokoyama, M. 1926. Fossil shells from the Atsumi Peninsula, Mikawa. *Journal of Faculty of Science, the Imperial University of Tokyo, ser. 2,* 1, (pt. 9): 369–375, pl. 43.

(Received October 27, 2005 / Accepted March 31, 2006)

日本産アワジチヒロ属貝類の系統進化

横川浩治・中尾賢一

要　約

既報では，アワジチヒロ 2 型（アワジチヒロ型，ヤミノニシキ型）の差異について形態的，生態的，遺伝的に総合的研究を行ない，両型は同一種内の形態的多型であることを明らかにして，種名を *Volachlamys hirasei* に統一すべきとした。今回はその続報として日本産アワジチヒロ属 *Volachlamys* 貝類の化石標本を調べ，その系統進化と分類学的扱いについて考察した。

調べた化石標本は，長崎県の加津佐層（1.7 Ma）と北有馬層（0.9 Ma），兵庫県の舞子層（更新世前期〜中期）と高塚山層（0.49 Ma），愛知県の渥美層（0.45 Ma），千葉県と茨城県にまたがる木下（きおろし）層（0.125 Ma），および香川県高松市の臨海沖積層（0.006 Ma）から産出したものである。これらに加えて香川県沖で得られた現生のアワジチヒロの標本も併せて研究に用いた。標本は殻の計測を行ない，殻の重量を相対的に表わすために殻重量指数（SWI）を計算した。また，殻表にみられる成長輪から既報の方法によって成長を解析した。

化石標本群中でヤミノニシキ型が出現したのは，渥美層で 44 個体中 1 個体，木下層で 2 個体中 1 個体，高松市の沖積層で 39 個体中 17 個体で，その他の産地のものはアワジチヒロ型のみの組成であり，このことから更新世中期頃からヤミノニシキ型が出現し始めたものと思われた。形態的に，殻のプロポーションや放射肋数は産地ごとにそれぞれ独特ではあるものの，著しく特殊な形態の個体群はみられなかった。一方 SWI は，舞子層の個体群が顕著に小さく，他の産地ものに比べて殻が薄質で軽いものと思われた。また成長解析の結果，舞子層のものだけが著しく卓越した成長度を示し，現生種を含めた他の産地の標本群はかなり類似した成長度であった。これらのことから，舞子層の個体群だけが他の産地のものと生物学的に明らかに別系統であると思われた。日本産アワジチヒロ属の化石は一般にムカシチヒロ（ヤグラニシキ）*Volachlamys yagurai* とされ，現生の *V. hirasei* と別種とされている。*V. yagurai* のタイプ産地である舞子層産の個体群は明らかに現生種と別種とすべき生物学的特徴を有するが，しかし他の産地の化石個体群は現生種と明確に区別される特徴は見いだせなかった。これらのことから，舞子層産の個体には *V. yagurai*，その他の産地の個体には現生種と同じ *V. hirasei* の学名を適用するのが妥当と考えられた。