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VARIATION OF NUMBER OF PORES ON THE CARAPACES OF GROUP A SPECIES OF THE GENUS *LOXOCONCHA* (CRUSTACEA, OSTRACODA) FOLLOWING THE MOLTING

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Variation of Number of Pores on the Carapaces of Group A Species of the Genus *Loxoconcha* (Crustacea, Ostracoda) Following the Molting. **Le, D. D.** — This study examines the phylogeny of all twenty-eight recent species of Group A of the genus *Loxoconcha* Sars, 1866. Based on the total number of pores on the carapace, three species subgroups of this genus are shown by Differentiation of Distributional pattern of Pore-system (DDP) analysis. All species have the same number and distribution pattern of pores in and before A-4 instar. The difference in the total number of pores on the carapace is found from instar A-3 to adult, and thus three patterns are recognised. In instar A-3 these numbers are 42, 43 and 44 for subgroups A1, A2 and A3 respectively. In addition, the present study shows an identical number of anterior false radial pores among the subgroups at all instars. However, the number of posterior false radial pores is different in three subgroups from instar A-3. In this instar, these numbers of subgroups A1, A2 and A3 are equivalent to 3, 4 and 5. By combining this study with previous studies, the geographical distribution of the three subgroups is shown. Species of subgroup A1 are distributed worldwide, except for the distribution areas of subgroups A2 and A3. Species in subgroups A2 and A3 are restricted to the Atlantic coasts of Europe, North Africa and the Mediterranean.
K e y w o r d s: Crustacea, Ostracoda, *Loxoconcha*, classification, phylogeny, morphology.

Introduction

The genus *Loxoconcha* Sars, 1866 is one of the most diverse recent ostracod taxa. A total of 575 species of the genus *Loxoconcha* have been identified around the World (Brandão et al., 2015). The species of this genus are distributed in low to middle latitude areas in marine and brackish waters. In Japan, the species of this genus are widespread from south to north (Nakao & Tsukagoshi, 2002; Tanaka & Ikeya, 2002; Sato & Kamiya, 2007; Le & Tsukagoshi, 2014).

As for the phylogenetic view of the genus *Loxoconcha*, there are several remarkable papers. Kamiya (1988) described two main life history modes in *Loxoconcha* species, i. e., phytal and bottom-dwelling, and suggested that these modes reflect differences in adaptations for each microhabitat. The clear difference in carapace morphology between species of the two life modes was demonstrated. The phytal species were circular in lateral view and rugby ball shaped in posterior view, whereas the bottom-dwelling species were elongated rectangular in lateral view and triangular in posterior view. Kamiya (1989) interpreted the different distribution patterns of pore systems in adults of the phytal species *L. japonica* Ishizaki, 1968 and the benthic species *L. uranouchiensis* Ishizaki, 1968, especially in the ventral region, as a result of adaptation to their respective microhabitats. Based on carapace morphology, Tanaka & Ikeya (2002) divided the East Asian genus *Loxoconcha* into five species groups. The migration and speciation patterns of four species of the *L. japonica* group were presented. Ishii et al. (2005) studied 17 species of *Loxoconcha* around Japan and concluded that they can be divided into two groups according to the Pore Pattern below Eye tubercle (PPE) analysis. Group A is more diverse, but has fewer pore systems in the ventral area than group B, and this group tends to inhabit normal marine environments, while group B inhabits brackish water. They also showed that the density of pore systems on the ventral surface of *Loxoconcha* species is not determined by habitat adaptation, but by phylogeny. Several papers have been published on the ontogeny of the genus *Loxoconcha* (Smith & Kamiya, 2003; Ishii et al., 2005; Le et al., 2016). Overall, they showed that the ontogeny of species in this genus comprises eight stages, i.e. from instar A-7 to adult.

To date, no study has considered the change in the total pores on the carapace throughout the moult, and then looked at the difference on this change among Group A species of the genus *Loxoconcha*. Therefore, in this study, the total number of pores on the carapace as well as total number of anterior and posterior false radial pores, are shown by instar. Based on these numbers, three subgroups of group A are suggested using DDP analysis. This work will contribute to a more thorough understanding of the phylogeny of the genus *Loxoconcha*, since the detailed taxonomy is essential for the accurate comparisons among species.

Material and Methods

Locations and date of sampling. Material used in this study was collected along the eastern coast of Japan from Obitsu estuary (Chiba Prefecture) to Miyazaky City (Miyazaky Prefecture) and around the Okinawa Islands (fig. 1); the remaining ones were collected in USA (Goodwin Island, York River), Australia

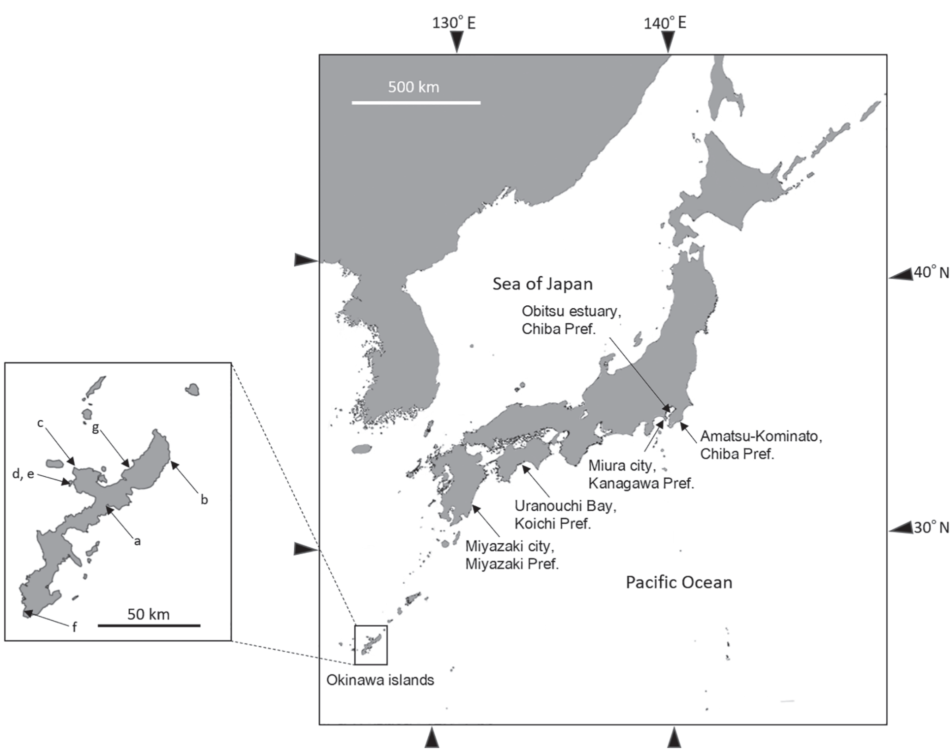

Fig. 1. Maps of Japan showing location of the study areas from 2012 to 2015.

(Stanley, Tasmania; Tweed Head West), Thailand (Satun, Khlong Thom), England (Porth Costell, Holy Island; Beaulieu river), Spain (Torre la sal), Libya (Toripoli) and Italy (Bay of Naples).

Method of sampling and specimen treatment. Samplings were carried out on reef slopes using SCUBA diving, on reef flats, tidal beaches and river mouths during low tide. At each sampling points, the upper layer 5-10mm of sediment, sea grass and sea algae were scooped into a plastic bottle using a spoon (a flat spoon with dimensions of 12 × 15 cm or a rectangular spoon of 4 × 7 cm, depending on the degree of surface irregularity). Then, all of the collected specimens were fixed in 5–10 % formaldehyde that had been neutralised with hexamethylenetetramine before being washed through 16-mesh (# 1 mm) and 250-mesh (# 0.063 mm) sieves. Part of the washed material was fixed with 70–80 % alcohol to observe the appendages, and the remaining material was dried.

Morphological observations and taxonomy. The specimens were dissected under a binocular microscope in the laboratory. For the dissected specimens, soft parts were mounted on a slide glass in the "Neo Sigaral" agent and carapaces were on a cardboard slide with single hole. Dried carapaces and individuals were coated with gold using a quick auto-coater (JFC-1500, Ion Sputtering Device). After coating, the dried samples were used to observe the pores on carapace with a Scanning Electron Microscope (JSM-5600LV, JEOL). SEM photos were subsequently used for estimation of number of normal pores on the carapace, number of anterior and posterior false radial pores using some computer software such as ImageJ, Adobe Photoshop (fig. 2).

Species were classified basing on morphology of carapaces, the chaetotaxy of appendages, muscle scars, hinge elements etc. following Sars (1866) and Yassini & Jones (1995).

Most of the illustrated specimens were deposited in the collection of the Shizuoka University Museum (SUM), identified by numbers with the prefix SUM-CO.

Division of subgroups. Division of subgroups A1, A2 and A3 of group A of the genus *Loxoconcha* and phylogenetic relationship among the species of this genus were estimated by Differentiation of Distributional Pattern of Pore-system (DDP) analysis. This analysis of the carapace pore-systems was first proposed and

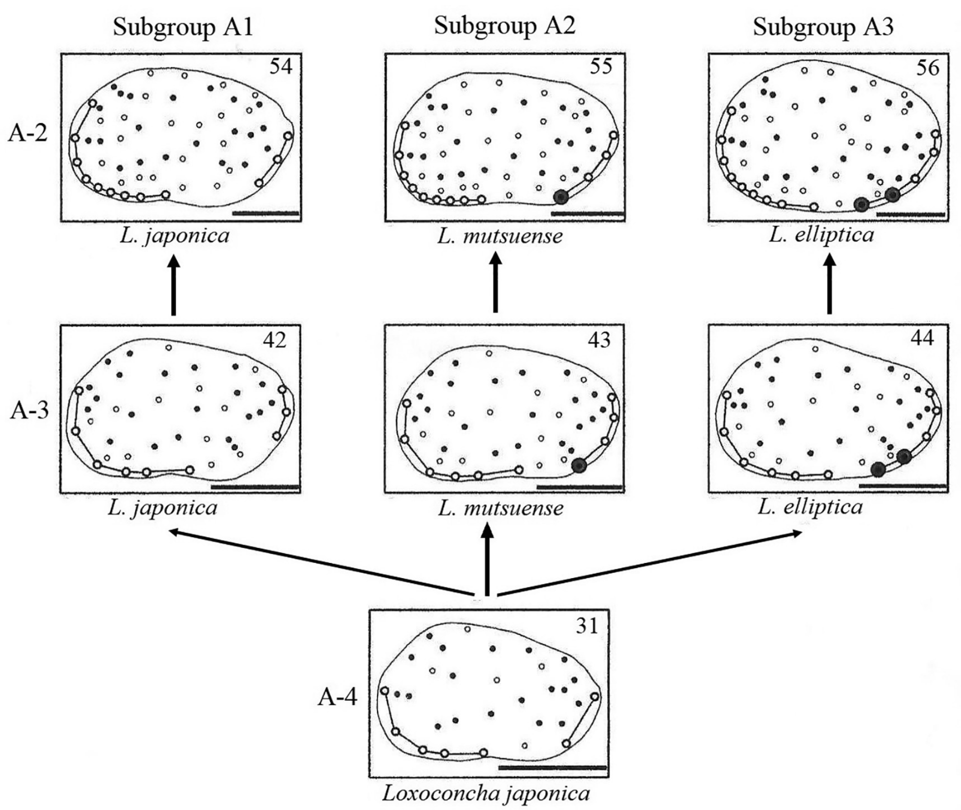

Fig. 2. Sketching of pore patterns of left valve in early diffirentation stage of some species of Group A of the genus *Loxoconcha*, indicating normal pores, anterior and posterior false radial pores on carapace. Pores connected by lines indicate false radial pores. Black solid and open circles mean twisted and smooth type pores, respectively. Double circles for additional pores. Scale 100 μm.

exemplified for the phylogenetic reconstruction of Ostracoda by Tsukagoshi (1990). He examined eleven recent and three extinct species of *Cythere* and concluded that the interspecific differentiation in distributional patterns of pore-systems on the carapace for later instars (A-2, A-1 and adult) reflected the phylogeny of the genus *Cythere*. Then, Kamiya (1997) named the phylogenetic reconstructing method proposed by Tsukagoshi (1990) "DDP analysis", and applied it to determining the phylogenetic relationship among four families (Leptocytheridae, Cytheridae, Loxoconchidae and Xestoleberidae) by the comparison of pores in the early instars (A-6, A-5 and A-4). For the case of the genus *Loxoconcha*, Ishii et al. (2005) applied DDP analysis to find the phylogenetic relationships among twelve species in group A and five species in group B.

Results and Discussions

Results of DDP analysis in phylogeny of Group A based on total pores of carapace

The phylogeny of all twenty-eight recent species of Group A of the genus *Loxoconcha* was examined by the DDP analysis. Figure 3 shows the result of the DDP analysis and table 1 shows total number of pore systems for each species and instar. All species have identical number and same distributional pattern of pore system in and before the fifth instar (A-4). The first differentiation of the pore pattern occurs in the sixth instar (A-3), and three pat-

Table 1. Total number of pore-systems of twenty-eight species of three subgroups of the genus *Loxoconcha* following each species and instar (including anterior and posterior false radial pores)

No.	Sub-group	Species	Molt instars (A-1, A-2, etc., in descending order of size)								Aver-age of adult
			A-7	A-6	A-5	A-4	A-3	A-2	A-1	Adult	
1	A1	*Loxoconcha harimensis* Okubo, 1980[*]	9	13	22	31	42	54	70	82	83.0
2		*L. wilberti* Puri, 1954						54	72	82	
3		*L. variolata* Brady, 1878								82	
4		*L. hattorii* Ishizaki, 1971[*]						54	72	83	
5		*L. kattoi* Ishizaki, 1968[*]						54	72	83	
6		*L. tosaensis* Ishizaki, 1968[*]						54	72	83	
7		*L. epeterseni* Ishizaki, 1981[*]						54	72	83	
8		*L. kitanipponica* Ishizaki, 1971[*]						54	72	83	
9		*L. zamia* Ishizaki, 1968[*]							72	83	
10		*L. prolaeta* Zhou, 1995[*]								83	
11		*L. noharai* Le & Tsukagoshi, 2014				31	42	54	72	83	
12		*L. australis* Brady, 1880				31	42	54	73	82	
13		*Loxoconcha* sp. A					42	54	73	82	
14		*Loxoconcha* sp. B					42	54	73	82	
15		*Loxoconcha* sp. C						54	73	82	
16		*L. japonica* Ishizaki, 1968[*]	9	13	22	31	42	54	73	83	
17		*L. lilljeborgii* Brady, 1868[*]			22	31	42	54	73	83	
18		*L. matagordensis* Swain, 1955				31	42	54	73	83	
19		*Loxoconcha* sp. D							74	85	
20		*L. optima* Ishizaki, 1968[*]			22	31	42	54	74	87	
21	A2	*Loxoconcha* sp. E						55	74	84	87.5
22		*L. tumida* Brady, 1869						55	75	85	
23		*L. mutsuensis* Ishizaki, 1971[*]	9	13	22	31	43	55	75	86	
24		*L. geometrica* Bonaduce et al., 1976							76	87	
25		*L. bairdi* Müller, 1912					43	55	76	89	
26		*L. stellifera* Müller, 1894						55	77	90	
27		*L. rhomboidea* Fischer, 1855				31	43	55	78	91	
28	A3	*L. elliptica* Brady, 1868				31	44	56	77	90	90.0

* Data of these species are after Ishii et al. (2005)

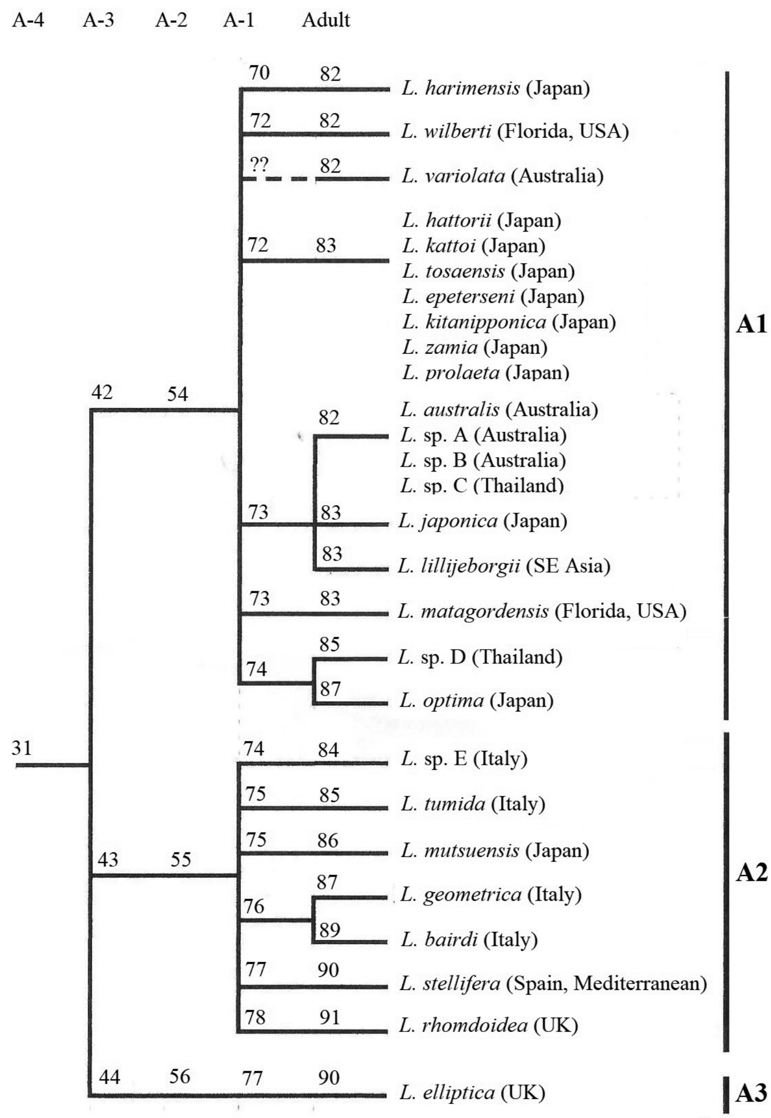

Fig. 3. Phylogenetic relationship between recent twenty-seven species of Group A of the genus *Loxoconcha*, estimated by DDP analysis. Numerals indicate total number of pore system for each lineage and instar.

terns are recognised. The differences among the three patterns are caused by one or two additional pores that discriminate the three pore patterns. In each pattern, there is no further differentiation among species appears at A-2 instar. However, further differentiation branching within each of the three are recognised in the instar A-1 and adult.

The results of the DDP analysis (fig. 3) indicate that there are three phyletic lineages in the recent species of Group A of the genus *Loxoconcha*. The three phyletic lineages are defined in this study as subgroups A1, A2 and A3, respectively. Subgroup A1 contains nineteen species, which have 42 pores in the A-3 instar. Subgroup A2 contains seven species with 43 pores in the A-3 instar. Subgroup A3 includes only one species, *L. elliptica*, which has 44 pores in the A-3 instar.

In A-3 and A-2 instars, there is no difference in normal pores and anterior false radial pores (fig. 2). The difference of one or two pores in total is caused by those in posterior false radial pores (fig. 2). Only a few pores in the restricted area discriminate subgroups A1 from A2 or A2 from A3.

Variation of false radial pores of the three subgroup A1, A2 and A3

Group A species of the genus *Loxoconcha* has unique characters, the false radial pores (Ishii, 2004). Table 2 shows clear number of anterior and posterior false radial pores for each subgroup from instar A-3 to adult. There is no difference in number of anterior false radial pores among all thirty species for each stage, e.g., six in A-3 instar, nine in A-2 instar, ten in A-1 instar and eleven in adult. Each subgroup possesses a certain number of posterior false radial pores in A-3 and A-2 instars. Subgroup A1 has three, A2 has four and A3 has five posterior false radial pores in the instar A-3 as well as in the instar A-2. In the next A-1 instar and adult, some varieties within each subgroup and the overlap between subgroups are found, although each subgroup possesses almost common numbers in posterior false radial pores; in adult, subgroup A1 has five or six; A2 has six, seven or eight; A3 has eight. No increase through A-3/A-2 instar and A-1 instar/adult molting is found in all species in number of posterior false radial pores.

Table 2. Number of anterior and posterior false radial pores of thirty species belonging to three subgroups of the genus *Loxoconcha*

No.	Subgroup	Species	A-3 instar		A-2 instar		A-1 instar		Adult	
			An.	Po.	An.	Po.	An.	Po.	An.	Po.
1	A1	*Loxoconcha harimensis*	6	3	9	3	10	5	11	5
2		*L. wilberti*	6	3	9	3	10	5	11	5
3		*L. variolata*							11	5
4		*L. hattorii*			9	3	10	5	11	5
5		*L. kattoi*			9	3	10	5	11	5
6		*L. tosaensis*			9	3	10	5	11	5
7		*L. epeterseni*			9	3	10	5	11	5
8		*L. kitanipponica*			9	3	10	5	11	5
9		*L. zamia*					10	5	11	5
10		*L. prolaeta*							11	5
11		*L. noharai*	6	3	9	3	10	5	11	5
12		*L. australis*	6	3	9	3	10	5	11	5
13		*Loxoconcha* sp. A	6	3	9	3	10	5	11	5
14		*Loxoconcha* sp. B	6	3	9	3	10	5	11	5
15		*Loxoconcha* sp. C			9	3	10	5	11	5
16		*L. cumulus*							11	5
17		*L. variolata*							11	5
18		*L. japonica*	6	3	9	3	10	5	11	5
19		*L. lilljeborgii*	6	3	9	3	10	5	11	5
20		*L. matagordensis*	6	3	9	3	10	6	11	6
21		*Loxoconcha* sp. D					10	6	11	6
22		*L. optima*	6	3	9	3	10	6	11	6
23	A2	*Loxoconcha* sp. E			9	4	10	6	11	6
24		*L. tumida*			9	4	10	7	11	7
25		*L. mutsuensis*	6	4	9	4	10	7	11	7
26		*L. geometrica*					10	8	11	8
27		*L. bairdi*	6	4	9	4	10	8	11	8
28		*L. stellifera*			9	4	10	8	11	8
29		*L. rhomboidea*	6	4	9	4	10	8	11	8
30	A3	*L. elliptica*	6	5	9	5	10	8	11	8

Abbreviations: An. — Anterior false radial pore; Po. — Posterior false radial pore.

Most species of subgroup A2 have higher total number of the pore-system than the species of subgroup A1 in the A-1 instar and adults (tables 1 and 2). Not only additional posterior false radial pores but also additional normal pores cause clear differences between subgroup A1 and A2 in the last two stages (A-1 instar and adult).

Interspecific relationships within Group A of the genus *Loxoconcha* and their geographical distributions

The geographical distribution of the twenty-eight recent species of Group A of *Loxoconcha* examined by the DDP analysis was compiled in this study (table 3). Species of subgroups A2 and A3 occur mainly along the Atlantic coasts of Europe, North Africa and the

Table 3. Distributional areas of twenty-eight recent species of three subgroups of the genus *Loxoconcha* in Japan and other areas

No.	Sub-group	Species name	Recent distributional areas	Source
1	A1	*Loxoconcha harimensis*	Japan coast (except for Hokkaido and Ryukyu Islands)	1
2		*L. hattorii*	Japan coast (except for Ryukyu Islands)	1
3		*L. kattoi*	Japan coast (except for Hokkaido and Ryukyu Islands)	1
4		*L. tosaensis*	Japan coast (Eastern coast of Hokkaido in the northern end and excepts for Ryukyu Islands)	1
5		L. epeterseni	Japan coast (except for Hokkaido and Ryukyu Islands)	1
6		*L. kitanipponica*	Japan coast (except for Hokkaido and Ryukyu Islands)	1
7		*L. zamia*	Japan coast (except for Hokkaido and Ryukyu Islands)	1
8		*L. prolaeta*	Tsukumo Bay, Japan	2
9		L. japonica	Japan coast (this study), southern part of Korean Peninsula (including Cheju island) and Hong Kong	1 & 3
10		*L. optima*	Japan coast (except for Ryukyu Islands)	1
11		*L. noharai*	Okinawa Islands, Southern Japan	1
12		*L. lilljeborgii*	Japan coast, Philippines, Thailand and northern part of Australia, Nha Trang MPA of central Vietnam, throughout the Indian Ocean	1 & 3
13		*Loxoconcha* sp. C	Khlong Thom and Satun in the west coast Thailand	2
14		*Loxoconcha* sp. D	Khlong Thom and Satun in the west coast Thailand	2
15		*L. variolata*	Port Phillip Bay, Victoria, Australia, Common in Bass strait, Australia	4 & 5
16		*L. australia*	Australian Coast	6
17		*Loxoconcha* sp. A	Stanley, Tasmania, Australia	2
18		*Loxoconcha* sp. B	Cowell Bay, Supencer Gulf, South Australia	2
19		*L. wilberti*	West coast of Florida, Belize, southwestern coast of Panama	7–9
20		*L. matagordensis*	Mexico, Texas and Florida in the gulf of Mexico; on the Atlantic coast of north Carolina, Varginia and New Jersey	10
21	A2	*Loxoconcha* sp. E	Toripoli, Lybya	2
22		*L. tumida*	Common throughout the Mediterranean	11
23		*L. mutsuensis*	Japan coast (except for Hokkaido and Ryukyu Islands)	1
24		*L. geometrica*	Toripoli, Libya; Adriatic Sea	11
25		*L. bairdi*	Adriatic Sea, Tunisian Shelf	11
26		*L. stellifera*	Common throughout the Mediterranean	11
27		*L. rhomboidea*	Carary Island in the south of the Atlantic, Adriatic Sea and Tuunisian Shelf in the Mediterranean	11, 12
28	A3	*L. elliptica*	Northwest Europe and whole of the Mediterranean	12

Note. 1 — this study; 2 — Ishii (2004); 3 — Tanaka & Ikeya (2002); 4 — McKenzie (1967); 5 — Yassini & Jones (1995); 6 — Ikeya (1997); 7 — Puri (1960); 8 — Teeter (1975); 9 — Puri & Hulings (1957); 10 — Garbett & Maddocks (1979); 11 — Bonaduce et al. (1992); 12 — Athersuch et al. (1989).

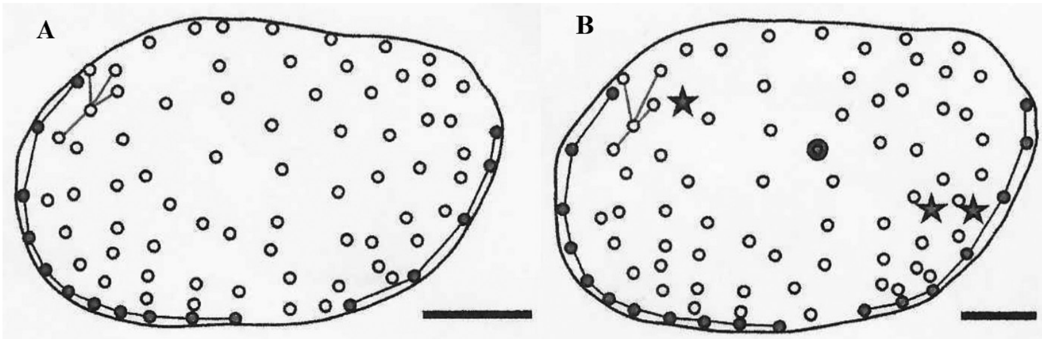

Fig. 4. Distributional patterns of pore-systems of left valve in adult: A — *L. nozokiensis*, B — *L. hastata*. Pores connected by lines indicate false radial pores. Scale 100 μm.

Mediterranean. The only exception is *Loxoconcha mutsuensis* Ishizaki, 1971, which also occurs along the coasts around Japan. Subgroup A1 species are distributed along the Atlantic coasts of Northern and Central America, the coasts of East and Southeast Asia, and the coasts around Australia. Therefore, the probable geographical distribution of subgroup A1 by bridging the gaps between the confirmed distribution ranges of the Pan-Indian area, the Pan-Pacific area (except for South America) and the Atlantic coasts of North and Central America (Ishii, 2004; Ishii et al., 2005). In particular, species of subgroup A1 of the genus *Loxoconcha* can be distributed all over the World except for the distribution areas of subgroups A2 and A3 of this genus. There are no data for all coasts of South America and most coasts of Africa due to lack of specimens from these areas.

Hypothesis of origin of subgroup A

Data from the table 1 and table 2 show that total number of pores on carapace as well as total number of posterior false radial pores are highest in the subgroup A3, median in the subgroup A2 and lowest in the subgroup A1.

Loxoconcha nozokiensis Ishizaki, 1963 has five posterior false pores in aldult (fig. 4), thus this species proved to belong to subgroup A1 and has been known as one of the oldest *Loxoconcha* species in Japan. The oldest records of *L. nozokiensis* are from the early Miocene Akeyo Formation, Mizunmani Group and Toyama Formation, Iwamura Group, central Japan (ca. 18 Ma) (Ishizaki, 1963; Ishii, 2004; Irizuki et al., 2004; Le, 2015).

Loxoconcha hastata Brady, 1869 has seven posterior false radial pores (fig. 4), this species is classified in subgroup A2. Up to now, the oldest fossil record of the subgroup A2 has belonged to *L. hastata*, this specimen is from the Early Middle Miocene (Langhian), Czech Republic (ca. 16 to 16.5 Ma) (Ishii, 2004). The lack of specimen before this age as well as the lack of fossil specimens of the subgroup A3 hindered further research. However, from the trend of the total number of pores of the three subgroups (tables 1 and 2) and the fossil record, the geological age of subgroup A1 is the oldest, followed by subgroups A2 and A3. Due to the lack of fossil species of the subgroup A3, the following hypothesis has been made concerning origin of subgroup A2. Subgroup A2 may be established after the appearance of the Paleo-Mediterranean Sea resulted from the plate-tectonic event that caused the continent of Africa continent to converge with the continent of Eurasia (Early Miocene) (Ishii, 2004). The distribution of subgroup A2 species concentrated in Europe and the Mediterranean coasts and the oldest age datum (16 to 16.5 Ma) clarified in this study support the hypothesis (Ishii, 2004; Ishii et al., 2005). The hypothesis suggests that subgroup A2 may be possibly derived from subgroup A1.

Conclusion

This study focused on examining the phylogeny of all twenty-eight existing species within Group A of the genus *Loxoconcha*. These specimens were collected from various locations, including the east coast of Japan spanning from the Obitsu estuary in Chiba Prefecture to Miyazaky City in Miyazaky Prefecture, around the Okinawa Islands; Goodwin Island, York river in the USA; Stanley, Tasmania, Tweed Head West in Australia; Satun, Khlong Thom in Thailand; Porth Costell, Holy Island; Beaulieu River in England; Torre La Sal in Spain; Toripoli in Libya and the Bay of Naples in Italy. Based on the total number of pores on the carapace, three subgroups A1, A2 and A3 of Group A were introduced by using DDP analysis. The clear difference in the total number of pores on carapaces among the three subgroups is established from A-3 instar to adult. In the instar A-3, these numbers of subgroup A1, A2 and A3 are 42, 43 and 44 respectively.

There is an identical number of anterior false radial pores among the subgroups in all instars. However, the difference in the number of posterior false radial pores among three subgroups is found from instar A-3. In this instar, these numbers of subgroups A1, A2 and A3 are equal to 3, 4 and 5.

Species of subgroup A1 are distributed throughout the World except the distributional areas of subgroups A2 and A3. Meanwhile, the species of subgroups A2 and A3 live mainly in Atlantic coasts of Europe, North Africa and the Mediterranean.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could appear to have influenced the work reported in this paper.

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