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Taxonomic revision of genus *Loxoconcha* in Japan and Vietnam and its origin

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ABSTRACT

In preceding the study, 30 species of the genus *Loxoconcha*, which were collected on reef slopes, reef flats, tidal beaches, and river mouths in Japan and Vietnam from 2012 to 2015, are reviewed taxonomically. Based on carapace characteristics, such as hinge, fulcral point, muscle scars, and frontal scars, the results show that 27 species still prove to be the genus *Loxoconcha*. However, two species are assigned to *Bonnyannella* and one to *Sagmatocythere* and re-described. In addition, this research also initially reveals the origin and distribution in the Atlantic Ocean of the genus *Loxoconcha* which is considered as one of the most diversified recent genera in marine ostracods. Fossil records of *Loxoconcha* species worldwide show that the origination of the genus *Loxoconcha* may be in Indo-West Pacific Region and by the Late Oligocene (possibly the Late Eocene). To this day, most fossil records of the genus *Loxoconcha* belong to group A. Among the three subgroups of group A, species subgroup A1 is distributed widely in Indo-West Pacific Region, and therefore, subgroup A1 may be an origin group of the genus *Loxoconcha*. The geographical distribution of subgroups A2 and A3 mainly restricted within European marine water, including the Mediterranean Sea, meanwhile subgroup A1 lives around the World except for the distributional areas of subgroups A2 and A3, suggesting that the Atlantic Ocean may be a barrier to dispersing subgroups A1 and A2 (and A3).

Keywords: Taxonomy, *Loxoconcha*, *Bonnyannella*, origin, *Sagmatocythere*.

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INTRODUCTION

The genus *Loxoconcha* was established by Sars (1866) [1] with type-species, and Brady & Norman (1889) [2] subsequently designated *Cythere rhomboidea* Fischer, 1855 [3] as type-species of *Loxoconcha*. *Loxoconcha* is one of the most diverse extant ostracod genera, with 224 living and 351 fossil species described worldwide [4]. The species of this genus are distributed in low-to-middle-latitude areas in marine and brackish waters. This genus also shows a high species diversity around Japan, with more than 23 living species [5–10] and approximately 41 fossil species [11] have been reported. In Vietnam, more than 30 species of this genus of both living and fossil species have been classified by Tanaka et al., (2009) [12] and Le (2019) [13]. Over the World, the genus *Loxoconcha* is currently considered to have originated in the late Paleogene and radiated during the Neogene [7]. The oldest records of *Loxoconcha* in Japan are from the early Miocene (approximately 18 Ma) (e.g., [14, 15]).

After the 1970s, the genus *Loxoconcha* definition started to reconsider in Europe. *Sagmatocythere* [16] and *Bonnyannella* [17] were proposed to separate from *Loxoconcha*. *Palmoconcha* was proposed by Swain & Gilby (1974) [18] based on the specimen from Baja California, Mexico, and Horne & Whatley (1985) [19] applied the genus European *Loxoconchidae* taxonomy. Athersuch & Horne (1984) [20] and Athersuch et al., (1989) [21] reviewed European genera of *Loxoconchidae* and indicated that their genera are discriminated by detailed morphology of carapace and appendages. In Japan, many works in which *Loxoconcha* was identified have neglected to examine the characters that discriminate *Loxoconcha* from other genera by Athersuch's standard. Japanese *Loxoconcha* could include the genera, which could be assigned to other genera according to European standards. Therefore, at the beginning of this study, *Loxoconcha* of Japan and Vietnam were reviewed based on the standard of Athersuch's work. The main of the present study is to reveal the history and the evolution of the genus *Loxoconcha*.

MATERIALS AND METHODS

Sampling and specimen treatment

Locations and date of sampling

Investigations were conducted along the coasts of Japan, the Okinawa Islands, Okinawa Prefecture; Miura City, Kanagawa Prefecture; Kisarazu City, Chiba Prefecture; Uranouchi Bay, Kochi Prefecture, and Miyazaki, Miyazaki Prefecture (Japan) from 2012 to 2015 (Fig. 1). In Vietnam, of two surveys conducted in 2013 and 2014, the first was at the coast of Ha Long Bay and Cat Ba Island in December 2013. The second was at Nha Trang Bay Marine Protected Area and Phu Quoc Marine Protected Area in November 2014. Addition, a lot of specimens collected in Japan and other areas by our colleagues were used in this study.

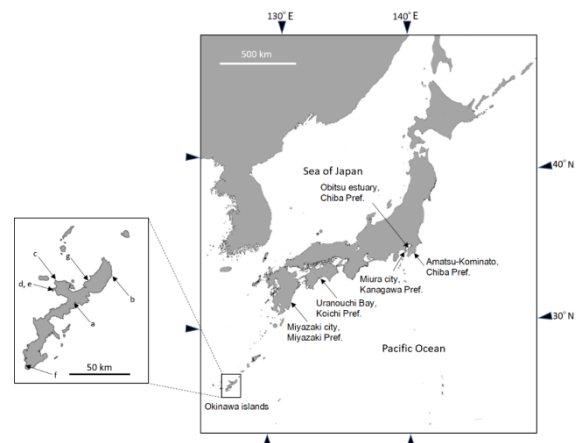


Figure 1. Maps of Japan showing location of the study areas from 2012 to 2015

Method of sampling and specimen treatment

Samplings were conducted on reef slopes using SCUBA diving, reef flats, tidal beaches, and river mouths during low tide. At each sampling point, the upper layer 5–10 mm of sediment, sea grass, and sea algae was 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 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. Carapaces were then observed and sketched using a differential interference contrast microscope with a camera lucida (BX-50, OLYMPUS) for illustration photos. 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 the carapace with a Scanning Electron Microscope (JSM-5600LV, JEOL) (SEM). SEM photos were subsequently used to observe hingement, anterior and posterior element of hinge, frontal, adductor muscle, and mandibular scars (Fig. 2).

Species were classified based on morphology of carapaces, the chaetotaxy of appendages, muscle scars, hinge elements following Sars (1866) [1], Yassini & Jones (1995) [22].

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

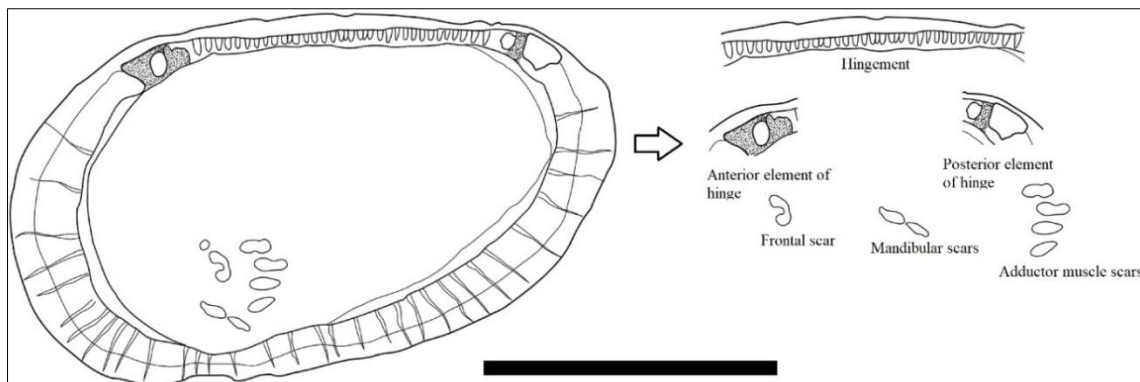


Figure 2. Internal lateral view of female right valve of *Loxoconcha yoshidai* Le et al., (2016) [23]. Scale: 200 μ m

RESULTS AND DISCUSSION

Taxonomic revision of *Loxoconcha* in Japan and Vietnam

Twenty-nine recent species of *Loxoconcha* and one extinct species *L. nozukiensis*, including 8 undescribed species, were reviewed to determine their generic position in this study based on the criterion of Athersuch & Horne (1984) [20]. Among these species, 25 were collected in Japan, and five were in Vietnam (Table 1, Fig. 3). The present study shows three species *L. subkotoriforma* Ishizaki, 1966; *Loxoconcha* sp. H and *Loxoconcha* sp. (from 351 m depth in the Japan Sea) [24] do not

possess the internal valve characteristics of the genus *Loxoconcha*, and the rest of species possess those of *Loxoconcha*.

L. subkotoriforma and *Loxoconcha* sp. H should be called a *Bonnyannella* species based on the following reasons: Internal valve characters, the smooth median element, the comma-shaped posterior element of hinge, and the V-shaped frontal scar of the two species (Table 2, Figs. 4 and 5) are identical with those of *Bonnyannella*. External valve characters, the outline of carapace and surface ornament of the two species are very similar to *B. robertsoni* [25], which is the type species of *Bonnyannella*, having two or three horizontally running ridges in the anterior area, a horizontally running ridge

in the mid-posterior area and a protuberance in the posteroventral area. Therefore, in this study, *L. subkotoriforma* and *Loxoconcha* sp. H were systematically replaced in the genus *Bonnyannella* and called *B. subkotoriforma* n. sp. and *Bonnyannella* sp. hereafter (Table 1).

Table 1. Sampling data of Loxoconchidae species of Japan and Vietnam examined in this study

No.	Species name	Sampling location	Sampling date	Number of specimens
1	<i>Loxoconcha japonica</i> Ishizaki, 1968 [5]	Sesoko Island, Okinawa Islands, Japan	10/5/2013	5
2	<i>L. shanhaiensis</i> Hu, 1981 [26]	Sesoko Island, Okinawa Islands, Japan	10/5/2013	5
3	<i>L. lilljeborgii</i> Brady, 1868 [4]	Sesoko Island, Okinawa Islands, Japan	1/6/2014	3
4	<i>L. tumulosa</i> Hu, 1979 [4]	Okinawa islands, Japan	30/5/2014	4
5	<i>Loxoconcha</i> sp.1	Sesoko Island, Okinawa Islands, Japan	10/5/2013	3
6	<i>Loxoconcha</i> sp.7	Sesoko Island, Okinawa Islands, Japan	10/5/2013	6
7	<i>L. mutsuensis</i> Ishizaki, 1971 [4]	Miyazaki Pref., Japan	22/2/2014	3
8	<i>L. harimensis</i> Okubo, 1980 [6]	Aburatsubo cove, Kanagawa Pref., Japan	11/8/2014	4
9	<i>L. tosaensis</i> Ishizaki, 1968 [5]	Miura City, Kanagawa Pref., Japan	11/8/2014	3
10	<i>L. modesta</i> Ishizaki, 1968 [5]	Miura City, Kanagawa Pref., Japan	11/8/2014	3
11	<i>Loxoconcha</i> sp. 8	Sesoko Island, Okinawa Islands, Japan	1/6/2014	5
12	<i>L. damensis</i> Le & Tsukagoshi, 2018 [27]	Dam Ngoai Island, Phu Quoc MPA, Phu Quoc Island, Kien Giang Pro., Southern Vietnam	21/11/2014	5
13	<i>L. noharai</i> Le & Tsukagoshi, 2014 [9]	Ohura River Estuary, Okinawa Islands, Japan	11/5/2013	5
14	<i>L. santosai</i> Le & Tsukagoshi, 2014 [9]	Ada River Estuary, Okinawa Islands, Japan	11/5/2013	4
15	<i>L. pulchra</i> Ishizaki, 1968 [5]	Kisarazu City, Chiba Pref., Japan	18/11/2012	3
16	<i>L. kosugii</i> Nakao & Tsukagoshi, 2002 [28]	Kisarazu City, Chiba Pref., Japan	18/11/2012	3
17	<i>L. uranouchiensis</i> Ishizaki, 1968 [5]	Obitsu River Estuary, Chiba Pref., Japan	18/11/2012	4
18	<i>Loxoconcha</i> sp. 5	Obitsu River Estuary, Chiba Pref., Japan	18/11/2012	5
19	<i>L. ocellata</i> Bold, 1973 [29]	Thien Cung cave, Ha Long Bay, Ha Long City, Quang Ninh Pro., Northern Vietnam	19/12/2013	4
20	<i>Loxoconcha</i> sp. 4	Miura City, Kanagawa Pref., Japan	11/8/2014	4
21	<i>L. yoshidai</i> Le et al., 2016 [23]	Bise beach, Motobu town, Okinawa Islands, Japan	7/9/2013	6
22	<i>Loxoconcha</i> sp. 3	Sesoko Island, Okinawa Islands, Japan	1/6/2014	3
23	<i>L. sesokoensis</i> Le & Tsukagoshi, 2014 [9]	Sesoko Island, Okinawa Islands, Japan	10/5/2013	6
24	<i>L. vietnamensis</i> Tanaka et al., 2009 [12]	Van Don Island, Quang Ninh Pro., Northern Vietnam	20/12/2013	6
25	<i>Loxoconcha</i> sp. 26	Saraku resort, Nha Trang City, Central Vietnam	24/11/2014	3
26	<i>Loxoconcha</i> sp. 11	Soi Sim Island, Ha Long Bay, Quang Ninh Pro., Northern Vietnam	18/12/2013	4
27	<i>L. subkotoriforma</i> Ishizaki, 1966 [4] (as <i>Bonnyannella subkotoriforma</i> n. sp.)	Akkeshi bay, Eastern Hokkaido, Japan	30/6/1992	3

No.	Species name	Sampling location	Sampling date	Number of specimens
28	<i>Loxoconcha</i> sp. H (as <i>Bonnyannella</i> sp.)	Otsuchi Bay, Iwate Pref., Japan	24/10/1991	3
29	<i>Loxoconcha</i> sp. (as <i>Sagmatocythere japonica</i> n. sp)	About 25 km off Tugaru Peninsula, Japan sea (351 m depth)	12/9/1997	4
30	<i>L. nozokiensis</i> Ishizaki, 1963* [30]	Early Miocene deposits, Sunakozaka Fm., Ishikawa Pref., Japan	-	2

Note: * - extinct species.

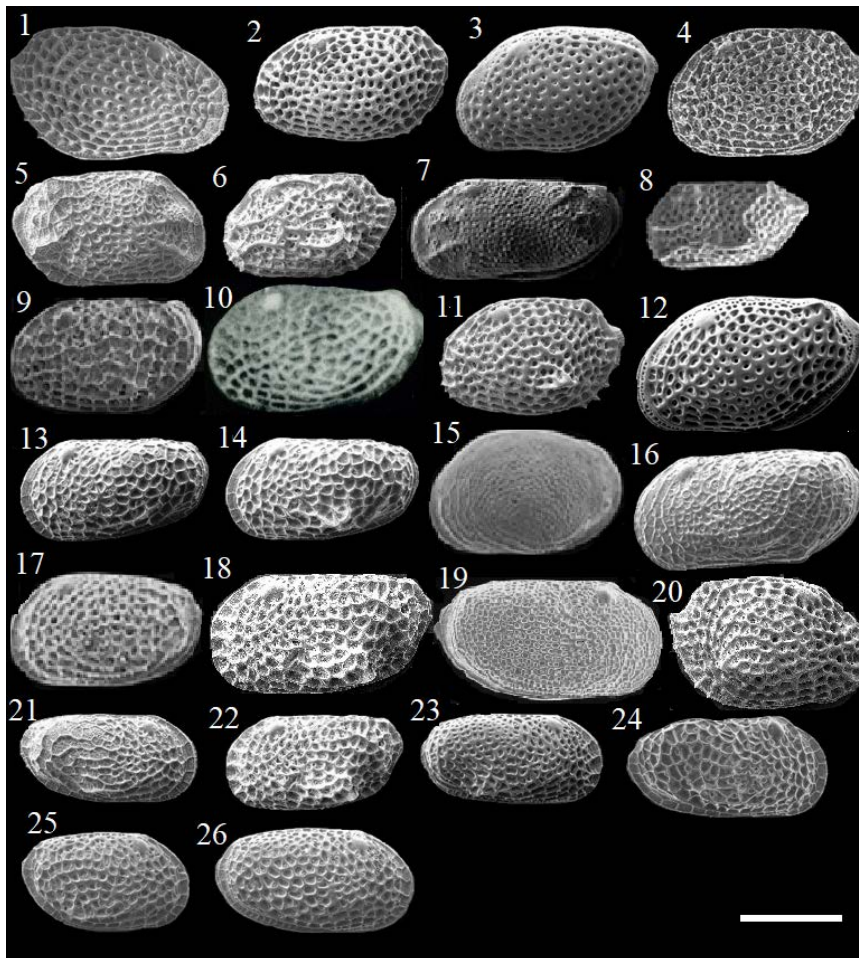


Figure 3. External view of examined species of *Loxoconcha* from Japan and Vietnam: 1) *L. japonica* (male, RV); 2) *L. shanhaiensis* (male, LV); 3) *L. lilljeborgii* (male, LV); 4) *L. tumulosa* (male, LV); 5) *Loxoconcha* sp. 1 (female, RV); 6) *Loxoconcha* sp. 7 (LV); 7) *L. mutsuensis* (male, LV); 8) *L. harimensis* (LV); 9) *L. tosaensis* (male, LV); 10) *L. modesta* (male, LV); 11) *Loxoconcha* sp. 8 (male, LV); 12) *L. damensis* (male, LV); 13) *L. noharai* (male, LV); 14) *L. santosi* (male, LV); 15) *L. pulchra* (male, LV); 16) *L. kosugii* (male, LV); 17) *L. uranouchiensis* (male, LV); 18) *Loxoconcha* sp. 5 (female, LV); 19) *L. ocellata* (male, LV); 20) *Loxoconcha* sp. 4 (LV); 21) *L. yoshidai* (male, LV); 22) *Loxoconcha* sp. 3 (male, LV); 23) *L. sesokoensis* (male, LV); 24) *L. vietnamensis* (male, LV); 25) *Loxoconcha* sp. 26 (male, LV); 26) *Loxoconcha* sp. 11 (male, RV). Scale: 200 μ m.
Abbreviations: LV: left valve; RV: right valve

Table 2. The main characters of six European genera of the family Loxoconchidae, after [20, 21]

Genus	Hinge	Fulcral point	Frontal scar	Surface ornament	Number of podomeres of antenna
Loxoconcha	Gongylodont, crenulate median element	Absent or present	C-shape	Smooth to coarsely pitted or reticulate	5
Bonnyannella	Gongylodont, smooth median element, posterior tooth comma-shaped	Present	V-shape	Pitted to reticulate	6
Sagmatocythere	Gongylodont, smooth median element, posterior tooth comma-shaped and lobate	Present	V-shape	Pitted or reticulate	6
Palmoconcha	Gongylodont, smooth median element	Present	Y-shape	Smooth to pitted or reticulate	6

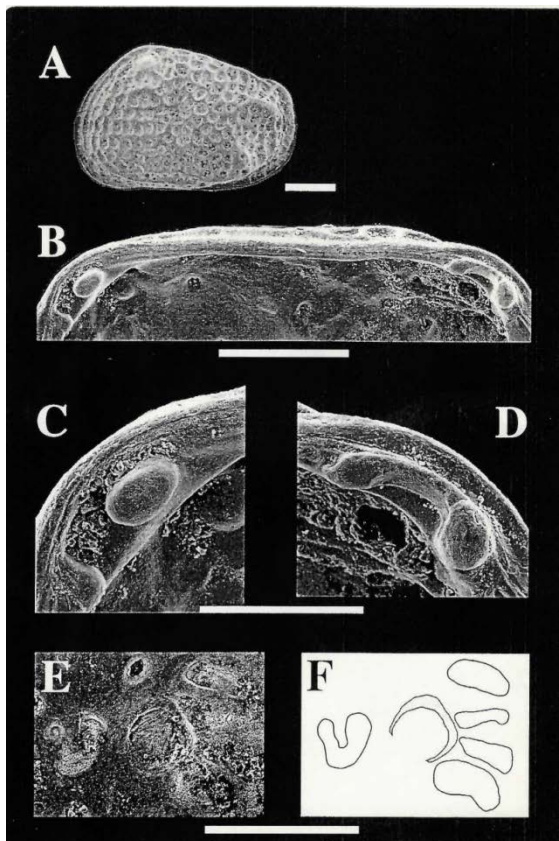


Figure 4. Carapace characters of *Bonnyannella subkotoriforma*: A) External view of valve; B) Hingement; C) Anterior element of hinge; D) Posterior element of hinge; E) Frontal and adductor muscle scars and fulcral point; F) Sketch of E. Scale: 100 μ m for A & B; 50 μ m for C, D, E & F, respectively

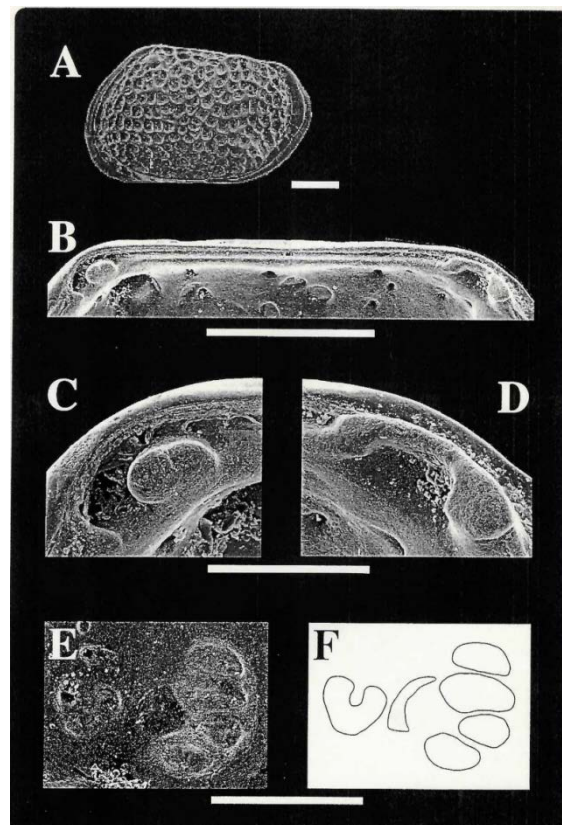


Figure 5. Carapace characters of *Bonnyannella* sp.: A) External view of valve; B) Hingement; C) Anterior element of hinge; D) Posterior element of hinge; E) Frontal and adductor muscle scars and fulcral point; F) Sketch of E. Scale: 100 μ m for A & B; 50 μ m for C, D, E & F, respectively

Loxoconcha sp. was collected from 351 m depth in the Japan Sea (Fig. 6) and is similar to *Sagmatocythere* in possessing a V-shaped frontal scar, the smooth median element, the comma-shaped and lobate posterior element of hinge in the right valve (Table 2), but the posterior element of hinge of the species is less lobate than that of *Sagmatocythere*. External valve characters, especially the surface ornament of this species, are quite different from those of *S. napoliana* [31], a type species of *Sagmatocythere*. Therefore, *Loxoconcha* sp. was placed in the genus *Sagmatocythere* in this study, and this species was described as a new species, *S. japonica* n. sp.

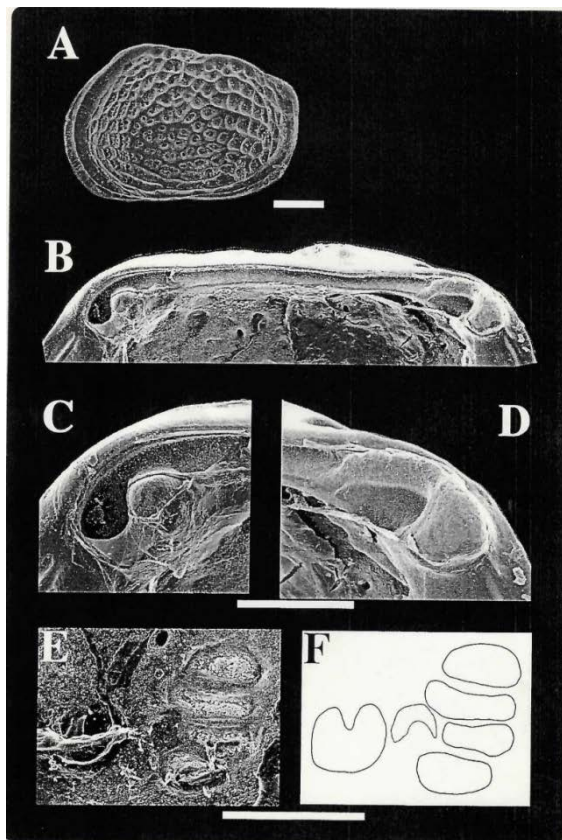


Figure 6. Carapace characters of *Sagmatocythere japonica* n. sp.: A) External view of valve; B) Hingement; C) Anterior element of hinge; D) Posterior element of hinge; E) Frontal and adductor muscle scars and fulcral point; F) Sketch of E. Scale: 100 µm for A & B; 50 µm for C, D, E & F, respectively

The following three species also changed their attached genera because of the review of the original description of previous papers. *Loxoconcha ozawai* Tabuki, 1986 [32] is presently assigned to *Bonnyannella ozawai*, whose morphology is similar to *B. subkotoriforma* and *Bonnyannella* sp. *Loxoconcha parapontica* Zhou, 1995 [33], whose internal and external valve characters are similar to *Sagmatocythere japonica* n. sp., should be switched to *S. parapontica*. *L. propontica* Hu (1983) [34] to *Palmococoncha propontica* for the same reasons.

Where and when: the origin of *Loxoconcha*

Paleogene Ostracoda, including *Loxoconcha*, has been reported from four continents: North America (e.g. [35, 36]), Australia (e.g. [37, 38]), Africa (e.g. [39, 40]), and Europe (e.g. [41]). Many *Loxoconcha* species were described from the Paleogene and Late Cretaceous. However, based on their external carapace morphology, most are not *Loxoconcha*, but *Palmococoncha* and *Sagmatocythere*. Although most of the Paleogene species were described in the previous works without detailed descriptions of the morphology of the hinge and shape of the frontal scar, a review of previous studies still found some *Loxoconcha* species from the Paleogene, as follows: *Loxoconcha punctabella* McKenzie et al., 1991 was described from the Late Oligocene, Victoria Australia [37] and possesses typical phyltal carapace shape of recent group A species in lateral view; *Loxoconcha (Loxocorniculum) cf. longispina* Keij, 1953 occurred from the Middle Oligocene, Tanzania [40]. These two species from the Oligocene possess internal valve characters of *Loxoconcha*. In the Early Miocene, *Loxoconcha (Loxocorniculum) tricornis* Ahmad et al., 1991 from Tanzania also possesses internal valve characteristics of *Loxoconcha* [40].

Some *Loxoconcha* species are contained in the Paleogene and Early Miocene species described without internal valve characters. Following four species probably belong to the genus *Loxoconcha*: *Loxoconcha* sp. from the Late Eocene to Late Oligocene, Australia [40, 41], *L. punctata* Thomson, 1878 from the Late Eocene, New Zealand [42] that resembles

L. punctabella in external carapace morphology except for surface ornament; *Loxoconcha (Loxocorniculum) postnodosa* Ahmad et al., 1991 from the Middle Oligocene to Early Miocene, Tanzania [40] that highly resembles *L. lilljeborgii* from the Late Miocene to Recent; *L. mbanjaensis* Ahmad et al., 1991 from the Early Miocene, Tanzania [40] whose male carapace shape in lateral view resembles typical phytal species of recent Group A species (e. g. *L. japonica* and *L. rhomboidea*).

Up to now, no species of *Loxoconcha* have occurred in Paleogene Europe and North America. To sum up, the origination of the genus *Loxoconcha* may have been in the Indo-West Pacific Region and by the Late Oligocene (possibly the Late Eocene). Because species subgroup A1 distributes widely in Indo-West Pacific Region [43, 44], subgroup A1 may be an origin group of the genus *Loxoconcha* [44].

Atlantic Ocean is a barrier to deep sea of *Loxoconcha*

There may be two types of barriers to preventing *Loxoconcha* species from migration and dispersal. One may be in the deep sea, and another may be an arctic area because *Loxoconcha* species live in shallow marine and brackish water from tropical to subarctic areas [43]. The Pacific and Atlantic Oceans have been known as barriers of deep sea against many shallow marine organisms [43]. In the Pacific Ocean, species of subgroup A1 inhabit both western and eastern coasts, and dispersals have happened between both sides [43, 44]. Possible dispersal route may be from the Kamchatka Peninsula through the Aleutian Islands to Alaska. Some tropical organisms that cannot use the possible Aleutian route succeed in dispersal to another side of the Pacific [45]. Shallow marine fishes [46] and prosobranch gastropods [47] were reported to migrate over the East Pacific Barrier that lies between Polynesia and America. It is only natural that dispersal over the East Pacific Barrier has occurred in subgroup A1 of *Loxoconcha*. Briggs (1995) [45] noted an interesting phenomenon: successful migration (invasion followed by colonization) of shallow marine species takes

place in one direction only, from east to west. Supposed the hypothesis that the origin of *Loxoconcha* is in the Indo West Pacific Region is true. In this case, the same argued by Briggs (1995) [45] occurred in this genus.

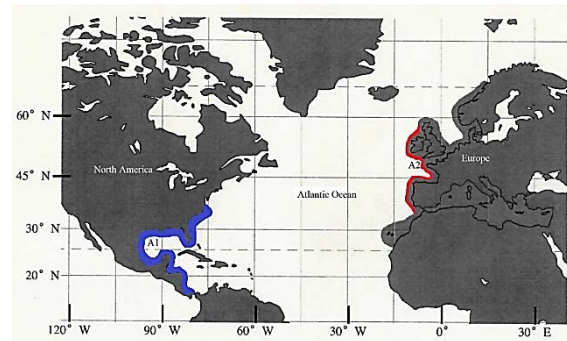


Figure 7. Distributional areas of subgroups A1 (blue) and A2 (red) of the genus *Loxoconcha* in the Atlantic coasts

Based on the total number of pores on the carapace, three subgroups A1, A2, and A3 of group A species of the genus *Loxoconcha* were showed by Differentiation of Distributional pattern of Pore-system analysis [10, 48, 49]. In the Atlantic Ocean, distributional areas are distinct between subgroups A1 and A2 [10, 43, 44]. Species of subgroup A1 live on the western coasts (American coasts) of the Atlantic, and species of subgroup A2 live on the eastern coasts (European coasts including the Mediterranean Sea) (Fig. 7) [44]. No successful migration was found, and species of subgroup A1 cross over the Atlantic Ocean to Europe, and species of subgroup A2 was introduced to America. This fact means the Atlantic Ocean operates as a deep sea barrier for group A species of the genus *Loxoconcha*. Pan-Atlantic shallow marine species were reported in fishes and some invertebrates [45]. It becomes clear that the distributional area of shallow marine ostracod species represents strong endemism, resulting from the comparison between Titterton & Whatley (1988) [50], who researched the endemism of shallow marine ostracod species (podocopid and platycopid species) and Briggs (1995) [45] who studied the endemism of shallow marine fishes and invertebrates. It may cause shallow marine

ostracod species do not have planktonic larvae stages through ontogeny [43]. This factor prevents shallow marine ostracod species from frequent and long-distance migration and may prevent subgroups A1 and A2 of *Loxoconcha* from successful migration to another side of the Atlantic.

CONCLUSION

Thirty species of the genus *Loxoconcha* distributed along the coasts of Japan and Vietnam were reviewed, especially in detail in the morphology of hinge and shape of scars of carapace in this study. *L. subkotoriforma* Ishizaki, 1966 and *Loxoconcha* sp. H were redescribed as *Bonnyannella subkotoriforma* n. comb and *Bonnyannella* sp. *Loxoconcha* sp. from deep sea deposits of the Japan Sea was placed as a new species *Sagmatocythere japonica* n. sp. *L. ozawai* Tabuki, 1986 was suggested to be *Bonnyannella ozawai*, *L. parapontica* Zhou, 1995 to be *S. parapontica*. This finding is the first of *Bonnyannella* species outside of Europe.

Fossil records of *Loxoconcha* species around the World show that the genus *Loxoconcha* originated in the Indo-West Pacific Region and by the Late Oligocene (possibly the Late Eocene). Because species subgroup A1 distributes widely the in Indo-West Pacific Region, subgroup A1 may be an origin group of the genus *Loxoconcha*.

The geographical distribution of species of the genus *Loxoconcha* differs between subgroups A1 and A2 (and A3). Distribution of subgroups A2 and A3 is mainly restricted within European marine water including the Mediterranean Sea, and subgroup A1 inhabits throughout the World except for the distribution areas of subgroups A2 and A3 of this genus. For this evidence, the Atlantic Ocean may be a barrier dispersing subgroups A1 and A2 (and A3).

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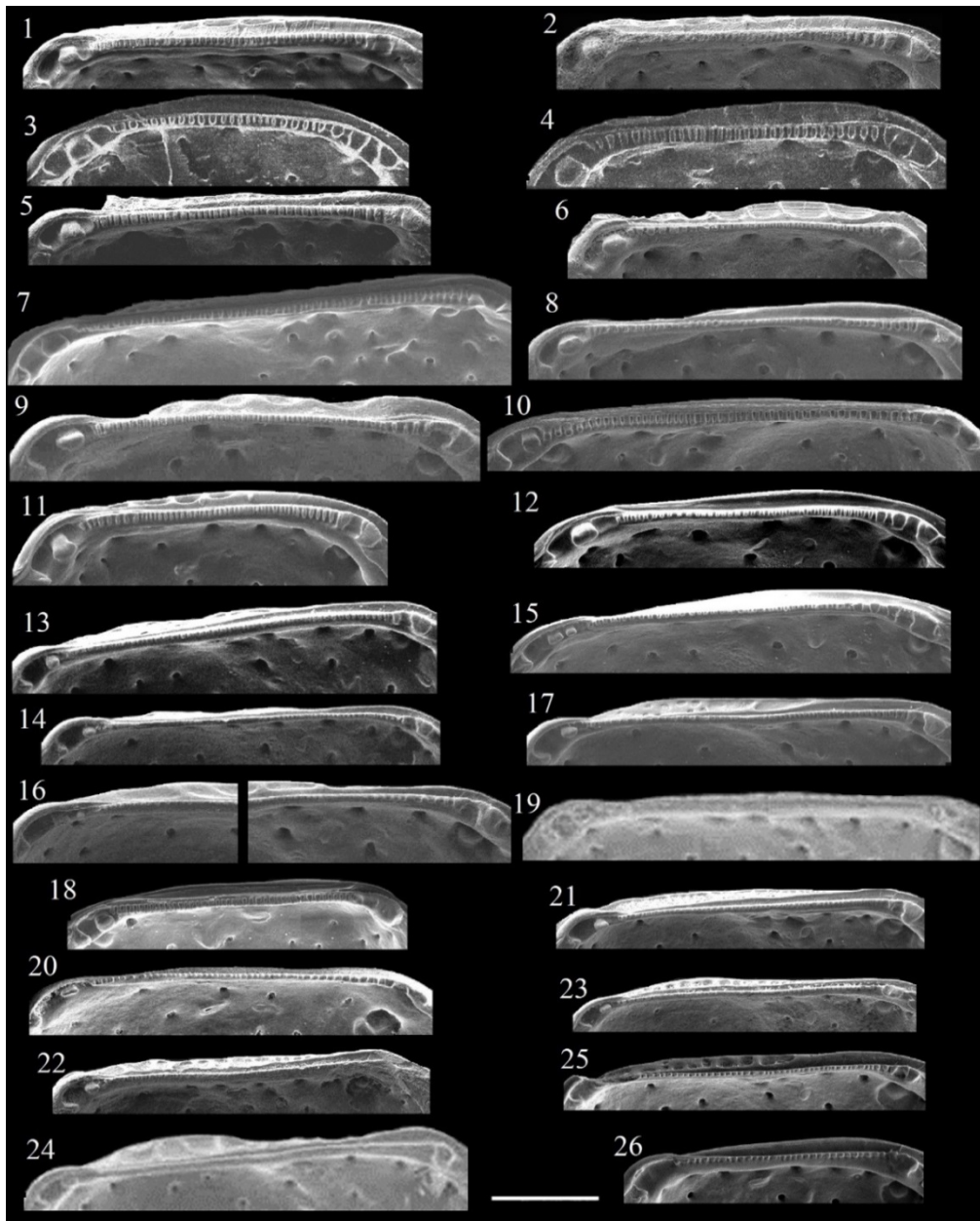
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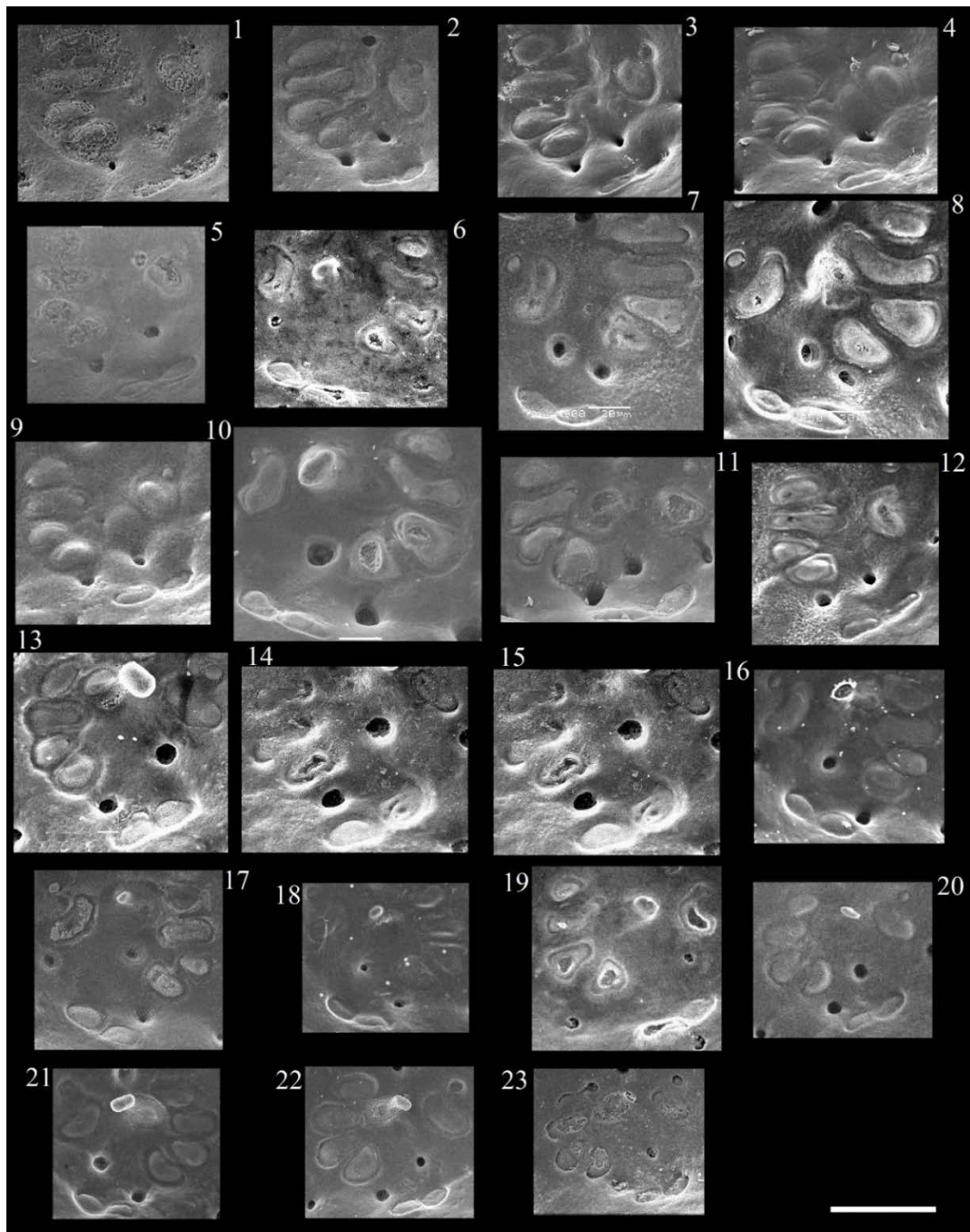
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Appendix



Appendix 1. Internal view of hingement of 26 species in the genus *Loxoconcha*. 1, *L. japonica* (male, LV); 2, *L. shanhaiensis* (male, LV); 3, *L. lilljeborgii* (female, LV); 4, *L. tumulosa* (female, LV); 5, *Loxoconcha* sp. 1 (male, LV); 6, *Loxoconcha* sp. 7 (LV); 7, *L. mutsuensis* (male, LV); 8, *L. harimensis* (LV); 9, *L. tosaensis* (male, LV); 10, *L. modesta* (male, RV); 11, *Loxoconcha* sp. 8 (female, LV); 12, *L. damensis* (male, LV); 13, *L. noharai* (male, LV); 14, *L. santosi* (male, LV); 15, *L. pulchra* (male, LV); 16, *L. kosugii* (male, LV); 17, *L. uranouchiensis* (male, LV); 18, *Loxoconcha* sp. 5 (female, LV); 19, *L. ocellata* (male, LV); 20, *Loxoconcha* sp. 4 (LV); 21, *L. yoshidai* (male, LV); 22, *Loxoconcha* sp. 3 (male, LV); 23, *L. sesokoensis* (male, LV); 24, *L. vietnamensis* (male, LV); 25, *Loxoconcha* sp. 26 (male, LV); 26, *Loxoconcha* sp.11 (female, LV). Scale: 100 μm. Abbreviations: LV, left valve; RV, right valve



Appendix 2. Muscle scars of 23 species of the genus *Loxoconcha*. 1, *L. shanhaiensis* (male, LV); 2, *Loxoconcha* sp. 1 (male, LV); 3, *L. japonica* (male, LV); 4, *Loxoconcha* sp. 9 (LV); 5, *Loxoconcha* sp. 10 (LV); 6, *Loxoconcha* sp. 30 (RV); 7, *L. mutsuensis* (male, RV); 8, *L. modesta* (male, RV); 9, *L. tosaensis* (male, RV); 10, *L. harimensis* (LV); 11, *Loxoconcha* sp. 8 (female, LV); 12, *L. damensis* (male, LV); 13, *L. pulchra* (male, LV); 14, *L. kosugii* (male, LV); 15, *L. uranouchiensis* (male, LV); 16, *L. noharai* (male, RV); 17, *L. santosi* (male, RV); 18, *Loxoconcha* sp. 5 (female, RV); 19, *Loxoconcha* sp. 4 (LV); 20, *Loxoconcha* sp. 26 (male, LV); 21, *L. sesokoensis* (male, RV); 22, *L. yoshidai* (male, LV); 23, *Loxoconcha* sp. 3 (male, LV). Scale: 100 μ m. Abbreviations: LV, left valve; RV, right valve