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Invasion, Diversification and Extinction of *Scapharca* (Bivalvia: Arcidae) in the Japan Sea Borderland during the Plio-Pleistocene

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Abstract: A semi-enclosed marginal sea such as the Japan Sea was an important locus for species diversification in the benthos, along with climate change. The genus *Scapharca* Gray, 1847 represents an example of such diversification after its first appearance in the Japan Sea in the Late Pliocene (Piacenzian) via the inflow of the Tsushima warm current. In this paper, *S. satowi* Dunker, 1882 is newly recorded and described from the uppermost Lower Pleistocene (Calabrian) Omma Formation in Ishikawa Prefecture. *S. pseudosubcrenata* (Ogasawara, 1977) is redescribed based on newly obtained specimens from the type locality and the Lower Pleistocene (Calabrian) Uonuma Group (Middle Formation) in Niigata Prefecture. By summarizing the geologic range of all Plio-Pleistocene species of *Scapharca* in the Japan Sea, it has been revealed that two latest Early Pleistocene glacial stages (MIS 22 and MIS 20) caused the extinction of *S. ommaensis* (Otuka, 1936) and *S. pseudosubcrenata* respectively. In the glacial-interglacial age of the Middle Pleistocene (Chibanian), *S. akitaensis* (Noda, 1966) appeared and *S. broughtonii* (Schrenck, 1867) also adapted itself to colder conditions. Four Recent species, *S. satowi*, *S. broughtonii*, *S. kagoshimensis* and *S. akitaensis*, also survived the glacial ages since the latest Early Pleistocene (Calabrian) because fossils occur on both the Japan Sea side and the Pacific Ocean side.

Keywords: speciation, marginal sea, Late Pliocene, Early Pleistocene, warm-water current

Introduction

A semi-enclosed marginal sea such as the Japan Sea was important for speciation in the benthos, along with cooling events (*e.g.*, Kamiya, 2003; Amano, 2007). From the Early Pliocene (Zanclean) to Early Pleistocene (Calabrian), the Omma-Manganji fauna (Otuka, 1939) mainly consisting of cold-water and endemic extinct species, flourished in the Japan Sea borderland. For example, *Anadara amicula* (Yokoyama, 1925), a representative arcid species of the fauna, first appeared in the Upper Miocene (Messinian) Ogawa Formation in Nagano Prefecture, central Honshu (Amano & Koike, 1993).

The arcid genus *Scapharca* Gray, 1847 lives in sandy mud bottoms from subtidal to 30 m depth in warm-water areas, except for *S. broughtonii* (Schrenck, 1867) (Higo *et al.*, 1999). When Amano & Komori (2021) described fossil specimens of *S. broughtonii* and *S.* aff. *broughtonii* from the Upper Pliocene (Piacenzian) on the Japan Sea borderland, they pointed out that the extinct species *S. ommaensis* (Otuka, 1936) and the extant *S. satowi* Dunker, 1882 also appeared in the Japan Sea in the Late Pliocene (Piacenzian) because the Tsushima warm current had been flowing into the semi-enclosed sea since about 4 Ma (Amano *et al.*, 2008). The oldest specimen of *S. kagoshimensis* (Tokunaga, 1906) was described from the Upper Pliocene Ogikubo Formation in Nagano Prefectuer by Nagamori (2014). Moreover, *S. akitaensis* (Noda, 1966) (= *S. nopporoensis* Akamatsu, 1980)

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first appeared in the Middle Pleistocene (Chibanian) of central Hokkaido, and might have survived around the Bohai Sea (Amano & Komori, 2021). Based on these data, *Scapharca* invaded the semi-enclosed and relatively cold Japan Sea, and all the Recent species above diversified from the Late Pliocene (Piacenzian) to the Middle Pleistocene (Chibanian).

I have newly found *S. satowi* in the uppermost Lower Pleistocene (Calabrian) Omma Formation (upper part; Kitamura & Kondo, 1990) in Ishikawa Prefecture. I also reexamined the specimens of "*S. subcrenata*" [= *S. kagoshimensis*] from the Lower Pleistocene Uonuma Group, Tokamachi City, Niigata Prefecture that were illustrated by the Molluscan Research Group of the Uonuma Hills Collaborative Research Group (1983), because they have a smaller number of radial ribs than *S. kagoshimensis* and are rather similar to *S. pseudosubcrenata* (Ogasawara, 1977).

In this paper, I describe these two species and discuss the stratigraphic distribution of all species of *Scapharca* in the Japan Sea borderland.

Material and Methods

Fossil specimens of *S. satowi* and *S. pseudosubcrenata* have been collected from the uppermost Lower Pleistocene (Calabrian) Omma Formation (upper part; U4 by Kitamura, 2016) on the bank of the Saikawa River, 450 m upstream of the Okuwa Bridge in Kanazawa City, Ishikawa Prefecture (Loc. 1; 36°32′6″N, 136°40′50″E = Loc. 3 of Amano & Komori, 2021), in association with *S. broughtonii*. Ogasawara (1981) recovered from fine-grained sandstone at this locality some shallow, warm- and open-water molluscan fossils that included no species characteristic of the Omma-Manganji fauna, and named them the "Younger Ommaian Fauna." Based on calcareous nano-fossils, this locality was assigned to Marine Isotope Stage (MIS) 21, by Kitamura & Kawagoe (2006) and Kitamura & Kimoto (2006).

For comparison with *S. satowi*, the extinct species *S. ommaensis* was recovered from the Lower Pleistocene (Calabrian) Omma Formation (middle part; M6 by Kitamura, 2016) on the bank of the Saikawa River, 1 km upstream from the Okuwa Bridge in Kanazawa City, Ishikawa Prefecture (Loc. 2; 36°31′53″N; 136°40′57″E). From this locality, the shallow warm-water molluscan fossils such as *Pecten* (*Pecten*) *byoritsuensis* Nomura, 1933 (*see* Amano & Ohno, 1988) and some characteristic species of the Omma-Manganji fauna occurred in fine-grained sandstone. Based on calcareous nannofossils, this locality was assigned to MIS 39 by Kitamura *et al*. (1999).

"*Scapharca subcrenata* Lischke" identified by the Molluscan Research Group of the Uonuma Hills Collaborative Research Group (1983), was collected from siltstone yielding many plant fragments in the Lower Pleistocene (Calabrian) Uonuma Group (Middle Formation) and just below the tephra SK110 (1.65 Ma, based on correlation with tephra Kd 25 by Kurokawa, 1999), 3 km upstream in the Tobitari River in Tokamachi City, Niigata Prefecture (Loc. 3; 37°10′17″N, 138°48′16″E). All specimens lack shell material and occur as inner casts or external molds. I made silicone rubber casts of two almost perfect mold specimens and counted the radial ribs. As described below, the specimens are here identified as *Scapharca pseudosubcrenata*. From this locality shallow-water and embayment bivalves were collected (Table 1).

The terminology follows Reinhart (1943) and Noda (1966). All collected specimens are housed in the Department of Geology and Paleontology (NMNS PM) of the National Museum of Nature and Science, Tsukuba.

Taxonomy

Family **Arcidae** Lamarck, 1809
Subfamily **Anadarinae** Reinhert, 1935
Genus ***Scapharca*** Gray, 1847

Table 1. Associated fauna with *Scapharca pseudosubcrenata* (Ogasawara) from the Uonuma Group (Middle Formation) at Loc. 2. * Number of individuals.

Species	N*
Arcuatula senhousia (Benson)	2
Pegophysema? *stearnsiana* (Oyama)	1
Raetellops pulchellus (Adams & Reeve)	4
Macoma (*Macoma*) *incongrua* (v. Martens)	1
M. (*M.*) *tokyoensis* (Makiyama)	34
Theora fragilis (A. Adams)	5
Mya (*Arenomya*) *oonogai* (Makiyama)	1
Potamocorbula amurensis (Schrenck)	26

Type species: *Arca inaequivalvis* Bruguière, 1789 (original designation).

Remarks: This genus is characterized by an inequivalve shell, granulate radial ribs, especially in the left valve and partly in the right valve, and a narrow triangular ligament area. Noda (1966) proposed the new subgenus *Hataiarca* based on *Anadara* (*Anadara*) *kakehataensis* Hatai & Nishiyama, 1949, with a flat posterior area, and he placed *Anadara subcrenata* (= *Scapharca kagoshimensis*) in this subgenus. However, the type species of *Scapharca*, *S. inaequivalvis*, also has a flat posterior area. Moreover, based on the molecular data by Feng *et al.* (2015), *S. kagoshimensis* is related to *S. broughtonii*, *S. satowi* and *S. inaequivalvis*. Thus, *Hataiarca* must be synonymized with *Scapharca. Scapharca* can be distinguished from *Anadara* by having no bipartite or tripartite radial ribs and a relatively narrow ligament area.

Scapharca satowi Dunker, 1882

(Figs 2A–F)

Scapharca Satowi Dunker, 1882: 233, pl. 9, figs 1–3.

Arca (*Anomalocardia*) *Satowi* — Kobelt, 1891: 58, pl. 17, figs 1, 2.

Arca nipponensis Pilsbry, 1901: 209, pl. 19, fig. 2.

Arca (*Scapharca*) *satowi* — Yamakawa, 1911: 12, pl. 4, figs 14, 15, pl. 5, figs 5, 6, pl. 7, fig. 6.

Anadara (*Scapharca*) *satowi* — Kawamoto & Tanabe, 1956: pl. 19, fig. 189; Kira, 1959: 87, pl. 43, fig. 13; Hayasaka & Hayasaka, 1960: 265, pl. 31, fig. 2; Hayasaka, 1961: 26, pl. 2, figs 14a, b; Kira, 1962: 122, pl. 44, fig. 13; Noda, 1966: 109; Ohara, 1968: pl. 2, fig. 7; Akamatsu, 1980: 9, pl. 4, figs 3, 8, pl. 5, fig. 1; Ogasawara *et al.*, 1986: pl. 21, fig. 3; Akamatsu, 1987: pl. 1, fig. 9; Ozawa *et al.*, 1998: 89, pl. 16, figs 6a, b.

Scapharca satowi — Habe, 1965: 76, pl. 1, figs 8, 10, pl. 2, fig. 3; Habe & Kosuge, 1967: 125, pl. 46, fig. 5; Kuroda *et al.*, 1971: 529, pl. 68, fig. 1, pl. 69, figs 1, 2, pl. 70, fig. 3; Okumura, 1988: 38, pl. 11, fig. 4; Okutani *et al.*, 1989: 35; Nemoto & Akimoto, 1990: pl. 9, fig. 1; Okumura, 1995: 71, pl. 17, fig. 11; Matsukuma & Okutani, 2000: 853, pl. 424, fig. 37; Min *et al.*, 2004: 387, figs 1242-1, 2; Nakagawa & Fukuoka, 2006: 25, pl. 2, figs 2a, b; Xu & Zhang, 2008: 37, fig. 82; Toba, 2009: 67, fig. 7; Kawase *et al.*, 2015: pl. 21, B18; Matsukuma & Okutani, 2017: 1168, pl. 468, fig. 1.

Anadara satowi — Aoki & Baba, 1987: 77, fig. 4; Baba, 1990: 238, pl. 23, figs 10a, b.

Anadara (*Hataiarca*) *pseudosubcrenata* — Ogasawara, 1981: pl. 1, fig. 13. [*non Scapharca pseudosubcrenata* (Ogasawara, 1977)].

Scapharca broughtonii — Nakagawa *et al.*, 1993: 31, pl. 11, figs 2a, b. [*non Scapharca broughtonii*

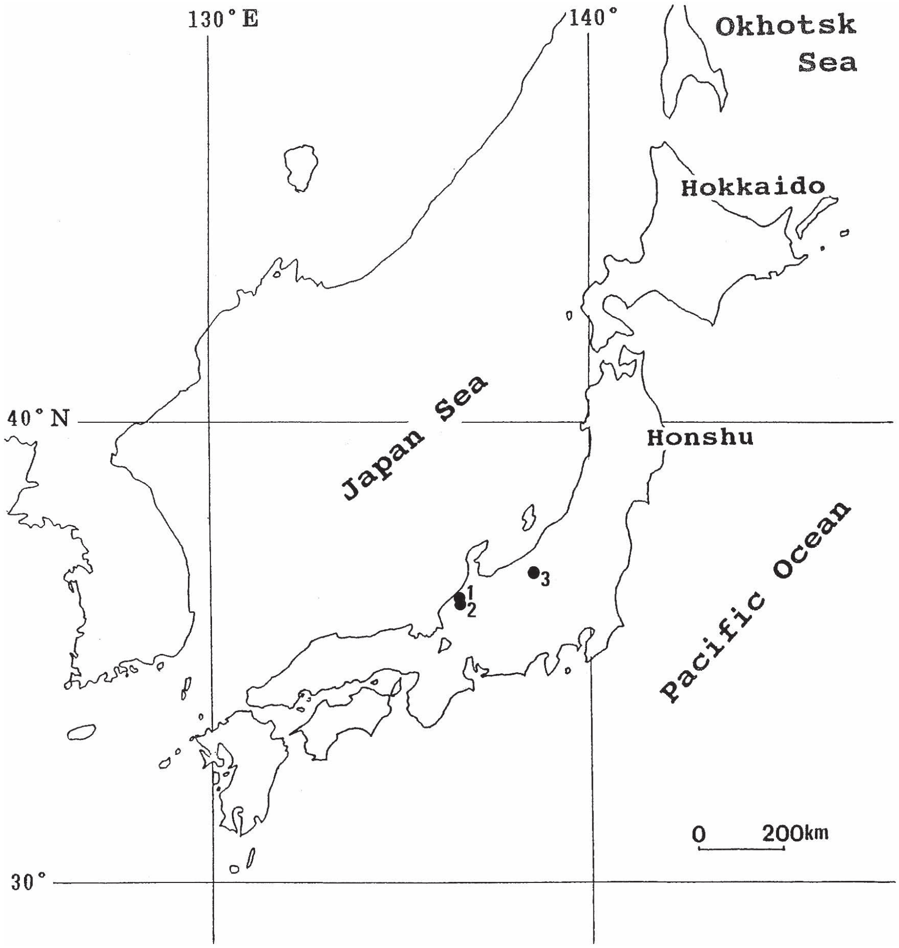

Fig. 1. Locality map of fossil specimens.

(Schrenck, 1867)].

Type locality: Tokio (Jedo).

Material examined: Nineteen specimens including six perfect specimens from Loc. 1.

Measurements: *See* Table 2.

Description: Shell medium for genus, attaining 66.2 mm in length, rather thin, subquadrate (H/L = 0.77 to 0.83) and moderately inflated. Antero-dorsal margin straight, progressing into broadly arched anterior margin; antero-dorsal corner pointed; postero-dorsal margin straight, forming blunt angle with subtruncate posterior margin; uppermost part of posterior margin slightly concave; ventral margin broadly arcuate. Blunt ridge running from beak to postero-ventral angle, forming rather flat area behind ridge. Umbo swollen and protruding above dorsal margin; beak located at anterior one-third of shell length (AL/L = 0.31 to 0.38); beak moderately prosocline. Surface sculpture of 35 to 39 (36 and 37 common) flat-topped radial ribs separated by nearly equal interspaces with many fine growth lines; granules visible at crossing points of radial ribs and growth lines in younger stage of left valve and anterior part of right valve. Ligamental area rather narrow, asymmetrical low triangular, sculptured with two distinct grooves and some weak

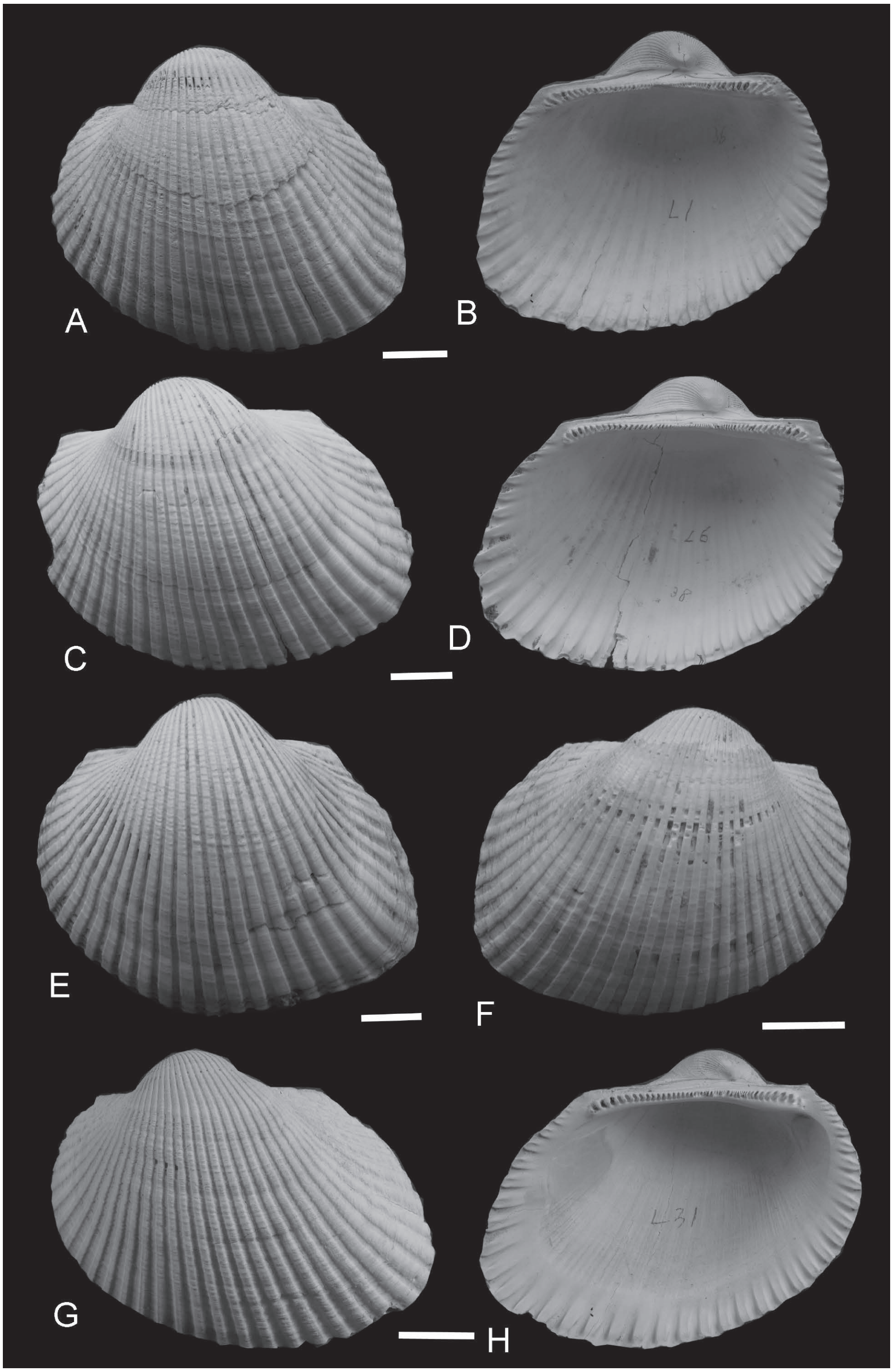

Fig. 2. *Scapharca satowi* Dunker and *S. ommaensis* (Otuka) from the Omma Formation in Ishikawa Prefecture. **A–F.** *Scaphrca satowi* Dunker from Loc. 1; A, B, left valve, NMNS PM 65756; C, D, left valve, NMNS PM 65759; E, left valve, NMNS PM 65760; F, right valve, NMNS PM 65758. **G, H.** *Scapharca ommaensis* (Otuka) from Loc. 2, left valve, NMNS PM 65784. Scale bars = 10 mm.

Table 2. Measurements of *Scapharca satowi* Dunker from the Omma Formation (Loc. 1). * shell length. ** shell height. *** anterior length before beak. **** Number of radial ribs.

Specimens	L (mm)*	H (mm)**	AL (mm)***	NR****	H/L	AL/L	Valve
NMNS PM 65756	55.6	44.9	18.0	37	0.81	0.32	left
NMNS PM 65757	66.2	52.2	23.9	39	0.79	0.36	left
NMNS PM 65758	44.0	36.3	15.0	35	0.83	0.34	right
NMNS PM 65759	61.5	47.2	18.9	39	0.77	0.31	left
NMNS PM 65760	58.2	47.6	22.3	37	0.82	0.38	left
NMNS PM 65761	49.7	40.3	18.1	37	0.81	0.36	left

horizontal grooves. Hinge line straight with 49 to 53 divergent teeth. Pallial line rather shallow. Inner ventral margin crenulate. Anterior adductor muscle ovate; posterior adductor muscle scar subquadrate and larger than anterior one.

Remarks: The Omma specimens share with *Scapharca satowi* Dunker, 1882, a large shell, their ratio of height to length, the position of the beak, the number of radial ribs (36 to 38 in *S. satowi* by Yamakawa, 1911) and many distinct granules on the radial ribs in the anterior part of the right valve (*see* Yamakawa, 1911, pl. 4, figs 14, 15). Although they differ slightly from the Recent *S. satowi* by having a thinner shell and more produced umbo, these differences can be considered as a variation of the species.

Scapharca ommaensis was originally proposed as *Anadara satowi ommaensis* and is closely similar to the present species in having a produced umbo, a narrow ligament area, many nodes on the radial ribs in the left valve and similar number of radial ribs (commonly 36 to 38) (Figs 2G, H). However, it can be distinguished from *S. satowi* by having a more acute postero-ventral angle, more elevated radial ribs and granules over the whole shell.

Ogasawara (1981) illustrated *Anadara* (*Hataiarca*) *pseudosubcrenata* from Loc. 1 of the present paper, where *S. satowi* also occurs. However, one of his figured specimens (pl. 1, fig. 13) has no flat posterior area and at least 37 radial ribs. The shape and number of radial ribs match *S. satowi* as here described.

Many researchers understood incorrectly that this species had been originally described in a different genus, such as *Arca* Linnaeus, 1758 (*e.g.*, Habe, 1965; Kuroda *et al.*, 1971; Ozawa *et al.*, 1998; Matsukuma & Okutani, 2000, 2017). However, *satowi* was originally described in the genus *Scapharca* by Dunker (1882).

Distribution: Late Pliocene (Piacenzian), Tentokuji Formation in Akita Prefecture (Ogasawara *et al.*, 1986); Early Pleistocene (Calabrian) Omma Formation (upper part) in Ishikawa Prefecture (This study), Renkoji Formation in Kanagawa Prefecture (Baba, 1990), Aburayama Formation in Shizuoka Prefecture (Ozawa *et al.*, 1998); ? Early Pleistocene deposit at Tungyüping in Tenghu Islands, Taiwan (Hayasaka & Hayasaka, 1960); Middle Pleistocene (Chibanian), Otoebetsugawa Fomation in central Hokkaido (Akamatsu, 1980, 1987), Mandano Formation in Chiba Prefecture (Baba, 1990), Ninomiya Formation in Kanagawa Prefecture (Okumura, 1988, 1995); Takamatsu Silty Sandstone of Atsumi Group in Aichi Prefecture (Hayasaka, 1961; Kawase *et al.*, 2015); Late Pleistocene Jizodo, Kiyokawa and Narita Formations in Chiba Prefecture (Noda, 1966; Ohara, 1968), Narita Formation in Ibaraki Prefecture (Aoki & Baba, 1987), Tokyo Formation in Tokyo Metropolis (Noda, 1966); Holocene Takahama Shell Bed in Fukui Prefecture (Nakagawa & Fukuoka, 2006); Recent, sandy mud bottom at 10–30 m depth, northeastern Honshu (Iwate Prefecture) and southwards on the Pacific side (Higo *et al.*, 1999; Toba, 2009; Matsukuma & Okutani, 2000, 2017), central Honshu (Niigata Prefecture) and southward on the Japan Sea side (Higo *et al.*, 1999; this study), South Korea (Min *et al.*, 2004), East China Sea and South China

Sea (Xu & Zhang, 2008).

Scapharca pseudosubcrenata (Ogasawara, 1977)
(Figs 3A–H)

Anadara (*Hataiarca*) *pseudosubcrenata* Ogasawara, 1977: 92, pl. 6, figs 1, 2a, b, 5a, b, 6; Ogasawara, 1981: pl. 1, figs 7a, b; Ogasawara, 1982: 316, pl. 158, figs 1483a, b, 1484. Matsuura, 1992: pl. 5-16, fig. 10; Matsuura, 2009: pl. 4-19, fig. 32.

Scapharca subcrenata (Lischke) — Molluscan Research Group of the Uonuma Hills Collaborative Research Group, 1983: pl. 9-I, fig. 3.

non Anadara (*Hataiarca*) *pseudosubcrenata* — Ogasawara, 1981: pl. 1, fig. 13.

Type locality: Saikawa River 450 m upstream of the Okuwa Bridge in Kanazawa City, Ishikawa Prefecture (Loc. 1).

Measurements: *See* Table 3.

Material examined: Thirty-one specimens from the type locality (Loc. 1) and two hundred one specimens from Loc. 3.

Original Description: "Shell medium in size, inequilateral and subequivalve. Anterior margin narrowly rounded and posterior one broadly truncated. Ventral margin smoothly rounded, and shell height rapidly becomes low on anterior side of shell.

External surface of right valve sculptured with 28–29 flat topped, smooth radial ribs squarish in cross section. Interspaces nearly equal to radial ribs in width, and sculptured with concentric growth lines. Posterior depressed area with 7–8 radial ribs.

External surface of left valve sculptured with similar radial ribs to right valve, but radial ribs except on posterior depressed area have five granules on surface. Beak strongly incurved forward, and situated anteriorly on nearly one-third of shell length. Crescent ligamental area with 2 or 3 irregular chevron-like grooves. Small comb-like teeth oblique to straight hinge line, and convergent at both extremities. Inner ventral margin crenulated corresponding to external radial ribs. Inner side with smooth pallial lines, very fine striation and opposite undulation of radial ribs recognized according to external radial ribs." (Ogasawara, 1977).

Supplement description: Shell small to medium in size (*see* Noda, 1966), attaining 45.5 mm (39.0 mm in maximum size measured by Ogasawara, 1977). Beak strongly prosocline and located at anterior one-third of shell length (AL/L = 0.29–0.38). Surface sculptured with 27 to 31 (average 29.0) smooth, flat-topped radial ribs. Granular structure on ribs distinct in younger part of left valve, except for posterior flat area, and also visible in younger part of anterior seven to eight radial ribs of right valve.

Remarks: According to the original description, all the radial ribs of the right valve are smooth. However, based on my observation of topotype specimens, some radial ribs in the anterior part of the younger stage of the right valve have distinct granules. This character, together with fewer radial ribs and smaller shell size, enables me to distinguish this species from the most similar species, *Scapharca kagoshimensis* (= *S. subcrenata* (Lischke, 1869)) commonly living in and around Japan, Korea, the Yellow Sea and the South China Sea (Matsukuma & Okutani, 2017).

The Molluscan Research Group of the Uonuma Hills Collaborative Research Group (1983) illustrated a specimen without shell as *Scapharca subcrenata* from the Lower Pleistocene (Calabrian) Middle Formation of the Uonuma Group at their Loc. 23 (Loc. 3 in this paper). As a result of examination of the silicone rubber cast of fossils from Loc. 3 (Figs 3A, B), the number of radial ribs is 29, which is fewer than *S. kagoshimensis*. Moreover, many small granules are visible on the radial ribs near the umbo in the anterior part of the right valve. Judging from the shell shape, number of radial ribs and sculpture, the Uonuma specimens can be identified as *S.*

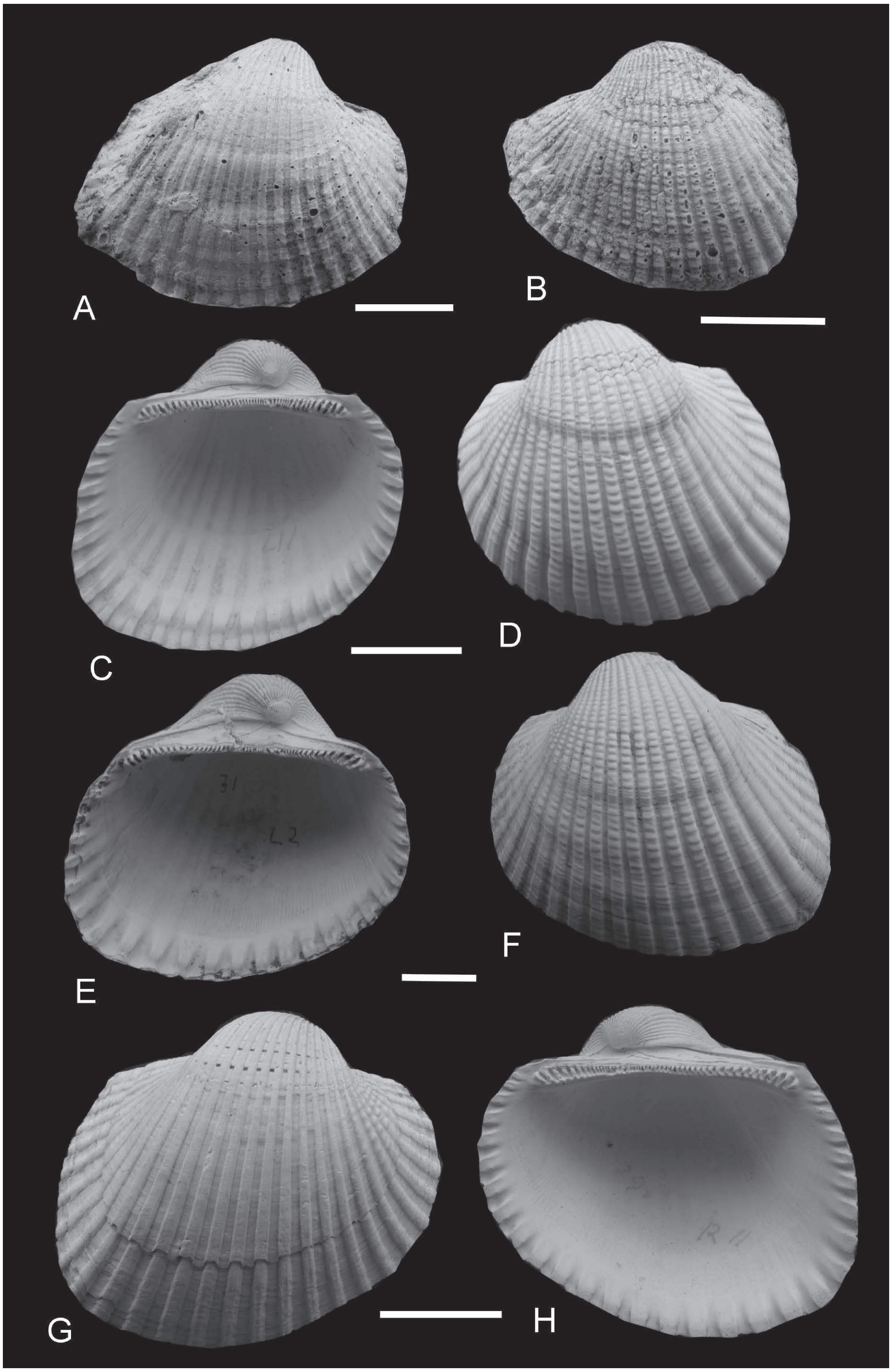

Fig. 3. *Scapharca pseudosubcrenata* (Ogasawara) from the Omma Formation in Ishikawa Prefecture and Uonuma Group (Middle Formation) in Niigata Prefecture. **A, B.** Silicone rubber casts with ammonium chloride from the Uonuma Formation (Loc. 3); A, right valve, NMNS PM 65782; B, left valve, NMNS PM 65783. **C–H.** Topotype shells from the Omma Formation (Loc. 1); C, D, left valve, NMNS PM 65764; E, F, left valve, NMNS PM 65775; G, H. right valve, NMNS PM 65762. Scale bars = 10 mm.

Table 3. Measurements of *Scapharca pseudosubcrenata* (Ogasawara) from the Omma Formation (Loc. 1) * shell length. ** shell height. *** anterior length before beak. **** Number of radial ribs.

Specimens	L (mm)*	H (mm)**	AL (mm)***	H/L	AL/L	NR ****	Valve
NMNS PM 65762	31.9	26.2	11.0	0.82	0.34	29	right
NMNS PM 65763	23.9	21.3	8.6	0.89	0.36	27	right
NMNS PM 65764	30.8	27.7	10.8	0.90	0.35	28	left
NMNS PM 65765	28.7	26.1	10.1	0.91	0.35	28	left
NMNS PM 65766	26.7	23.4	9.3	0.88	0.35	28	left
NMNS PM 65767	24.8	23.0	7.3	0.93	0.29	28	left
NMNS PM 65768	20.3	18.4	6.8	0.91	0.33	30	left
NMNS PM 65769	19.8	16.9	5.8	0.85	0.29	27	left
NMNS PM 65770	39.4	29.8	12.9	0.76	0.33	29	right
NMNS PM 65771	38.2	30.6	14.7	0.80	0.38	28	right
NMNS PM 65772	24.2	21.8	8.0	0.90	0.33	29	left
NMNS PM 65773	33.2	28.7	11.4	0.86	0.34	29	right
NMNS PM 65774	39.2	32.1	12.1	0.82	0.31	29	left
NMNS PM 65775	45.5	40.5	16.1	0.89	0.35	31	left
NMNS PM 65776	31.1	27.5	9.5	0.88	0.31	28	left
NMNS PM 65777	32.5	27.5	9.3	0.85	0.29	30	left
NMNS PM 65778	31.8	26.7	10.3	0.84	0.32	31	right
NMNS PM 65779	35.1	28.8	12.9	0.82	0.37	30	right
NMNS PM 65780	36.5	31.8	11.5	0.87	0.32	30	left
NMNS PM 65781	34.2	28.7	11.6	0.84	0.34	30	left

pseudosubcrenata.

Scapharca kogachiensis (Noda, 1971) from the Lower Pleistocene (Calabrian) Haneji Formation in Okinawa Prefecture is the most similar species to the present one. It shares a similar shell shape and granules in the right valve with *S. pseudosubcrenata*. However, *S. kogachiensis* can be distinguished from *S. peudosubcrenata* by having a larger shell (57.5 mm in length; 45.5 mm in *S. pseudosubcrenata*) and 26 radial ribs.

Distribution: Early Pleistocene (Calabrian) Middle Formation of the Uonuma Group in Niigata Prefecture (this study); latest Early Pleistocene (Calabrian) Omma Formation (upper part) in Ishikawa Prefecture (Ogasawara, 1977, 1981, 1982; Matsuura, 1992, 2009).

Discussion

Scapharca kagoshimensis, *S. satowi* and *S. broughtonii* flourish in the seas around Japan (*e.g.*, Matsukuma & Okutani, 2000, 2017). According to the molecular phylogeny by Feng *et al.* (2015), *S. satowi* is more closely related to *S. broughtonii* than to *S. kagoshimensis*. In this paper, we subdivide four extant species and three extinct species into the *S. satowi* and *S. kagoshimensis* clades. Morphologically, the *S. satowi* clade is characterized by having more than 36 radial ribs, while the species of the *S. kagoshimensis* clade have fewer radial ribs (around 29 and 31) and a flat posterior area. In the Japan Sea borderland, the *S. satowi* clade includes the following five species; *S. satowi*, *S. broughtonii*, *S.* aff. *broughtonii* of Amano & Komori (2021), *S. ommaensis* and *S. akitaensis*. On the other hand, the *S. kagoshimensis* clade includes only two species, *S. kagoshimensis* and *S. pseudosubcrenata*.

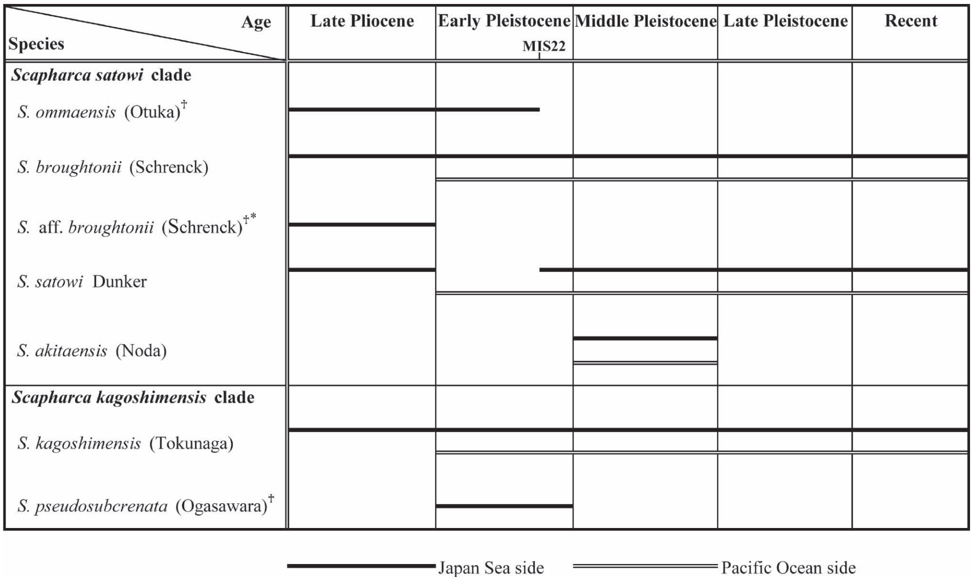

Fig. 4. Chronologic range chart of the *Scapharca satowi* and the *S. kagoshimensis* clades. Solid lines show the occurrence of each species in each age. † = extinct species. *described by Amano & Komori (2021).

As discussed by Amano & Komori (2021), ancestral species of *Scapharca* entered the semi-closed Japan Sea through the Tsushima Strait via the Late Pliocene inflow of the Tsushima warm current. In the Late Pliocene (Piacenzian), five species lived in the Japan Sea; *Scapharca ommaensis*, *S. broughtonii*, *S.* aff. *broughtonii*, *S. satowi* and *S. kagoshimensis* (Fig. 4; Amano & Komori, 2021). Among them, the first four belong to the *S. satowi* clade.

In the end of the Late Pliocene (Piacenzian), *S.* aff. *broughtonii* became extinct. In the Early Pleistocene, earlier than MIS 22 (Calabrian), *S. pseudosubcrenata* first appeared in the innermost part of the bay that existed in the present-day Uonuma Hill in Niigata Prefecture. In the latest Early Pleistocene (MIS 22), many characteristic species of the Omma-Manganji fauna, including *S. ommaensis*, became extinct. According to Kitamura (2016), the sea level during MIS 22 was 20 m lower than during the other previous glacial stages MIS 34 and 26. According to Zhao *et al.* (2022), closure of the Tsushima Strait began in the glacial stage MIS 22.

At that glacial stage, the low sea level caused the enclosure of the Japan Sea, the transition to brackish of the surface water and the extinction of the shallow-water species of the Omma-Manganji fauna (Amano, 2004). At the interglacial stage (MIS 21), after this extinction event, *S. pseudosubcrenata* adapted to an open-water environment following the disappearance of a large bay in and around the Japan Sea shore (Kano *et al*., 1991).

The glacial stage (MIS20) at the end of the Early Pleistocene caused the extinction of *S. psuedosubcrenata*. In the Middle Pleistocene (Chibanian), *S. broughtonii* adapted to colder water and *S. akitaensis* appeared along with the cycles of glaciation and interglaciation (Amano & Komori, 2021). Consequently, *S. satowi*, *S. broughtonii* and *S. kagoshimensis* have survived in the Japan Sea since the Late Pleistocene. *S. akitaensis* might have survived in the Bohai Sea (Amano & Komori, 2021). It is interesting to note that these four species have also been recorded on the Pacific Ocean side of Japan since the Early Pleistocene or the Middle Pleistocene (Fig. 4). Their wide distribution has helped them to survive through the glacial ages since the latest Early Pleistocene (MIS 22).

Scapharca talminensis (Kalishevich, 1976) was originally described from the Holocene

Barabashinskie Bed near Talmi Lagoon in southern Primoriye. At that time, Kalishevich (1976) did not compare his species with similar species *S. inaequivalvis* and *S. kagoshimensis.* Recently, Lutaenko & Noseworthy (2019) postulated that the northeast Asian "*Anadara inaequivalvis* [Japanese name, Kuichigai-sarubo]" is different from *S. inaequivalvis* at its type locality, India (see Lutaenko, 2006) and is a synonym of *S. talmiensis.* Based on this, *S. talmiensis* also lived in the Japan Sea from the Holocene to Recent.

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鮮新世・更新世における日本海沿岸のサルボウガイ属（二枚貝：フネガイ科）の侵入，多様化および絶滅

天野和孝

要　約

日本海のような半閉鎖的な縁海は気候変動に伴い，底生動物の種多様化の重要な役割を果たしてきた。サルボウガイ属は対馬海流の流入により後期鮮新世以降日本海に出現し，多様化した。本研究では，石川県の下部更新統最上部の大桑層から産出したサトウガイ *Scapharca satowi* を記載した。また，模式地および新潟県の下部更新統魚沼層群（中部層）産のサルボウダマシ *S. pseudosubcrenata* について再記載した。日本海のサルボウガイ属の全種の生存期間をまとめると，アカガイの近縁種 *S.* aff. *broughtonii* は後期鮮新世末期，オンマサルボウ *S.ommaensis* は前期更新世末期の氷期（酸素同位体ステージ MIS 22），サルボウダマシは前期更新世末期の氷期（酸素同位体ステージ MIS 20）に絶滅したことが明らかとなった。一方，中期更新世の間氷期にアキタサルボウ（新称）*S. akitaensis* が出現し，アカガイ *S. broughtonii* が寒冷水域に適応した。サトウガイ，アカガイ，サルボウ，アキタサルボウは日本海側と太平洋側に化石記録を持ち，前期更新世以降の氷期を生き残った。