VENUS 79 (1–4): 15–28, 2021
DOI: http://doi.org/10.18941/venus.79.1-4_15

June 11, 2021

Origin and Biogeographic History of *Scapharca broughtonii* (Schrenck, 1867) (Bivalvia: Arcidae) and Its Related Species

Kazutaka Amano[1*] and Kanae Komori[2]

[1]*Department of Geoscience, Joetsu University of Education, 1 Yamayashiki, Joetsu, Niigata 943-8512, Japan*
[2]*Ii Elementary School, 1946 Ii, Joetsu, Niigata 943-0896, Japan*

Abstract: *Scapharca broughtonii* (Schrenck, 1867) and *S.* aff. *broughtonii* have been recovered for the first time from the upper Pliocene (Piacenzian) deposits on the Japan Sea side of Honshu. This is the oldest record of *S. broughtonii* and its related species. *S. satowi* is known from the same locality as *S. broughtonii* in the upper Pliocene Tentokuji Formation in Akita Prefecture, Japan Sea side of northern Honshu. These fossils suggest that the genetically similar ark shells speciated near the northern limit of the warm-water current in the semi-enclosed Japan Sea by the late Pliocene. In the middle Pleistocene (Chibanian), *S. broughtonii* first adapted to cold-temperate water, being known from the Dateyama Formation on the Japan Sea side of central Hokkaido and associated with many cold-water and a few temperate-water species.

Keywords: late Pliocene, Tentokuji Formation, warm-water current, cold-water adaptation

Introduction

The red ark shell, *Scapharca broughtonii* (Schrenck, 1867), lives in sandy and muddy bottoms from subtidal to 60 m in depth and is widely distributed from the southern Primorie and southern Sakhalin areas of Russia through Hokkaido to Kyushu, Korea, the Bohai Sea, Yellow Sea and East China Sea (Akamatsu, 1992; Higo *et al.*, 1999; Scarlato, 1981; Qi *et al.*, 1989; Li, 2004; Matsukuma & Okutani, 2000, 2017; Xu & Zang, 2008; Lutaenko & Noseworthy, 2012; Zhang *et al.*, 2016). This is one of the more important bivalves in fisheries in Japan and adjacent countries (*e.g.*, Tamura, 1960). Its type locality is Hakodate in southern Hokkaido, northern Japan (Schrenck, 1867). Most species of *Scapharca* live in mild-temperate areas (Nishimura, 1981) and southwards (*e.g.*, Higo *et al.*, 1999) but *S. broughtonii* is unusual in also inhabiting cool-temperate and subarctic areas (Nishimura, 1981) such as the Bohai Sea and the southern Primorie Region of Russia. However, it is uncertain when and where the species first appeared and adapted to cold-water areas.

Yokogawa (1997) noted that the Chinese population from Dalian identified as *S. broughtonii* has more numerous radial ribs, ranging from 43 to 50 (average 45.83), whereas the number in the Japanese population ranges from 39 to 44 (average 41.25) including the type specimens (42 to 43). He also recognized a genetic difference between two forms. Based on examination of the mt DNA COI, Cho *et al.* (2007) confirmed that the Korean and Russian red ark shells are genetically different from the Chinese (Shandong) population. Tanaka & Aranishi (2016) separated two lineages, the Korean and Japanese Lineage A and Chinese (Dalian) Lineage B. From these results, *S. broughtonii* can be separated into two species or subspecies as claimed by Yokogawa (1997).

Fossil records of *S. broughtonii* are common from the Pleistocene of the Pacific side of central

* Corresponding author: amano@juen.ac.jp

Honshu (Baba, 1990). Ozawa *et al.* (1998) described this species from the lower Pleistocene (Gelasian) Dainichi Formation (2–1.9 Ma) and lower Pleistocene (Calabrian) Aburayama Formation in Shizuoka Prefecture. Jimbo *et al.* (2017) illustrated *S. broughtonii* from the lower Pleistocene (Gelasian) Imaizumi Sandstone and Conglomerate Member of the Nojima Formation in Kanagawa Prefecture whose age has been established as 2.5–1.97 Ma based on magnetostratigraphy. These early Pleistocene occurrences were associated with the warm-water Kakegawa fauna (Otuka, 1939b). On the Japan Sea side of Honshu, on the other hand, fossils of this species are not so common. The oldest specimen on the Japan Sea side was reported from the lowermost Pleistocene (Gelasian) part (dated at around 2.4 Ma by Yanagisawa & Amano, 2003) of the Nadachi Formation at Osuga in Joetsu City, Niigata Prefecture by Amano *et al.* (1988). From this locality, the Omma-Manganji fauna was collected (Otuka, 1939a), consisting of some cold-water and extinct endemic species with fewer warm-water species.

Scapharca broughtonii and *S.* aff. *broughtonii* were recovered for the first time from upper Pliocene deposits on the Japan Sea side of Honshu that are older than the Nadachi Formation and the Nojima Formation. In this paper, we describe these late Pliocene specimens and discuss the biogeographic history of this species by considering climatic change and the geohistory of the Japan Sea.

Material and Methods

Scapharca broughtonii has been newly recovered from the following three localities (Locs. 1–3; Fig. 1); three specimens from the upper Pliocene (Piacenzian) Tentokuji Formation at a large cliff along Yodo River, Awasegai in Daisen City, Akita Prefecture, northern Honshu (Loc. 1 = Loc. 21 of Amano *et al.*, 2000; 39°37′14″N, 140°18′41″E), one specimen from the lowermost Pleistocene (Gelasian) Nadachi Formation (uppermost part) at the river bed of the Nadachi River near Osuga Bridge in Joetsu City, Niigata Prefecture, central Honshu (Loc. 2; 37°8′46″N, 138°6′20″E) and two specimens from the uppermost lower Pleistocene (Calabrian) part of the Omma Formation (upper part of the formation *sensu* Kitamura & Kondo, 1990) at 450 m upstream from Okuwa (formally called Omma) Bridge in Kanazawa City, Ishikawa Prefecture (Loc. 3; 36°32′6″N, 136°40′50″E). The molluscan fossils from the last locality correspond with the Younger Ommaian fauna (Ogasawara, 1981).

Two specimens of *S.* aff. *broughtonii* were collected from the upper Pliocene (Piacenzian) Higashigawa Formation exposed along the Shibumi River between Tazawa and Inubushi in Tokamachi City, Niigata Prefecture, central Honshu (Loc. 4; 37°8′22″N, 138°38′23″E).

For comparison we examined 56 specimens of *Scapharca ommaensis* (Otuka, 1936) from the lower Pleistocene (Calabrian) part of the Omma Formation on the bank of the Saikawa River, 1 km upstream of Okuwa Bridge in Kanazawa City, Ishikawa Prefecture (Loc. 5; 36°31′51″N, 136°40′59″E) and 31 Recent specimens of *Scapharca satowi* Dunker, 1882 collected from the Kakizaki coast in Joetsu City, Niigata Prefecture (Loc. 6; 37°16′55″N, 138°23′21″E). The terminology follows Reinhart (1943) and Noda (1966). All specimens treated herein are stored in the Department of Geology and Paleontology (NMNS PM) of the National Museum of Nature and Science, Tsukuba.

Description of the Pliocene species

Family **Arcidae** Lamarck, 1809
Subfamily **Anadarinae** Reinhart, 1935

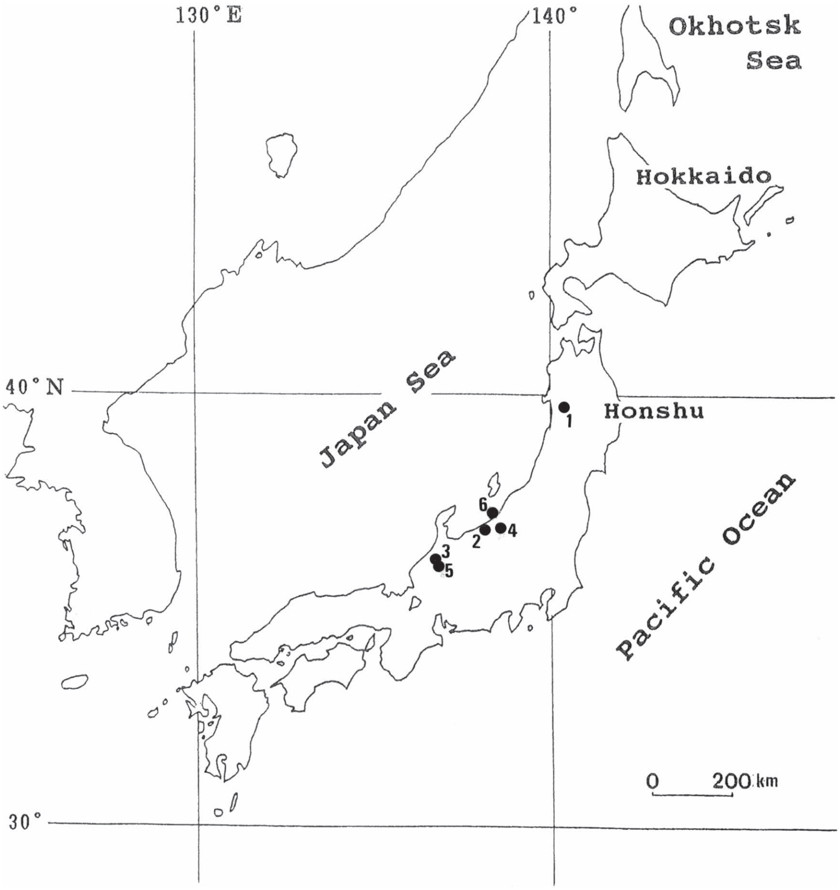

Fig. 1. Locality map of fossils and Recent specimens. See the text on the information of localities.

Genus ***Scapharca*** Gray, 1847
Type species: *Arca inaequivalvis* Bruguière, 1837 (original designation)

Scapharca broughtonii **(Schrenck, 1867)**
(Fig. 2)

Arca inflata Reeve, 1844: *Arca* sp. 30; Tokunaga, 1906: 57, pl. 3, fig. 19; Yokoyama, 1920: 167, pl. 17, fig. 9; Kinoshita & Isahaya, 1934: 12, pl. 9, fig. 65.
Arca reeveana Nyst, 1848: 60.
Arca broughtonii Schrenck, 1867: 578, pl. 24, figs 1–3.
Arca (*Anomalocardia*) *inflata* — Kobelt, 1891: 30, pl. 10, figs 1, 2; Yokoyama, 1922: 187, pl. 15, fig. 9.
Arca tenuis Tokunaga, 1906: 58, pl. 4, fig. 1.
Arca (*Scapharca*) *inflata* — Yamakawa, 1911: 17, pl. 4, fig. 13, pl. 5, figs 1–4, pl. 6, figs 1–6, pl. 7, figs 1–5.
Anadara (*Scapharca*) *inflata* — Kuroda, 1930: 32.
Anadara (*Scapharca*) *broughtonii* — Fujie, 1958: 666, pl. 28, fig. 26; Kira, 1959: 112, pl. 43, fig. 14; Kira, 1962: 124, pl. 4, fig. 14; Noda, 1966: 107; Kobayashi, 1976: pl. 1, figs 1–4; Matsuura,

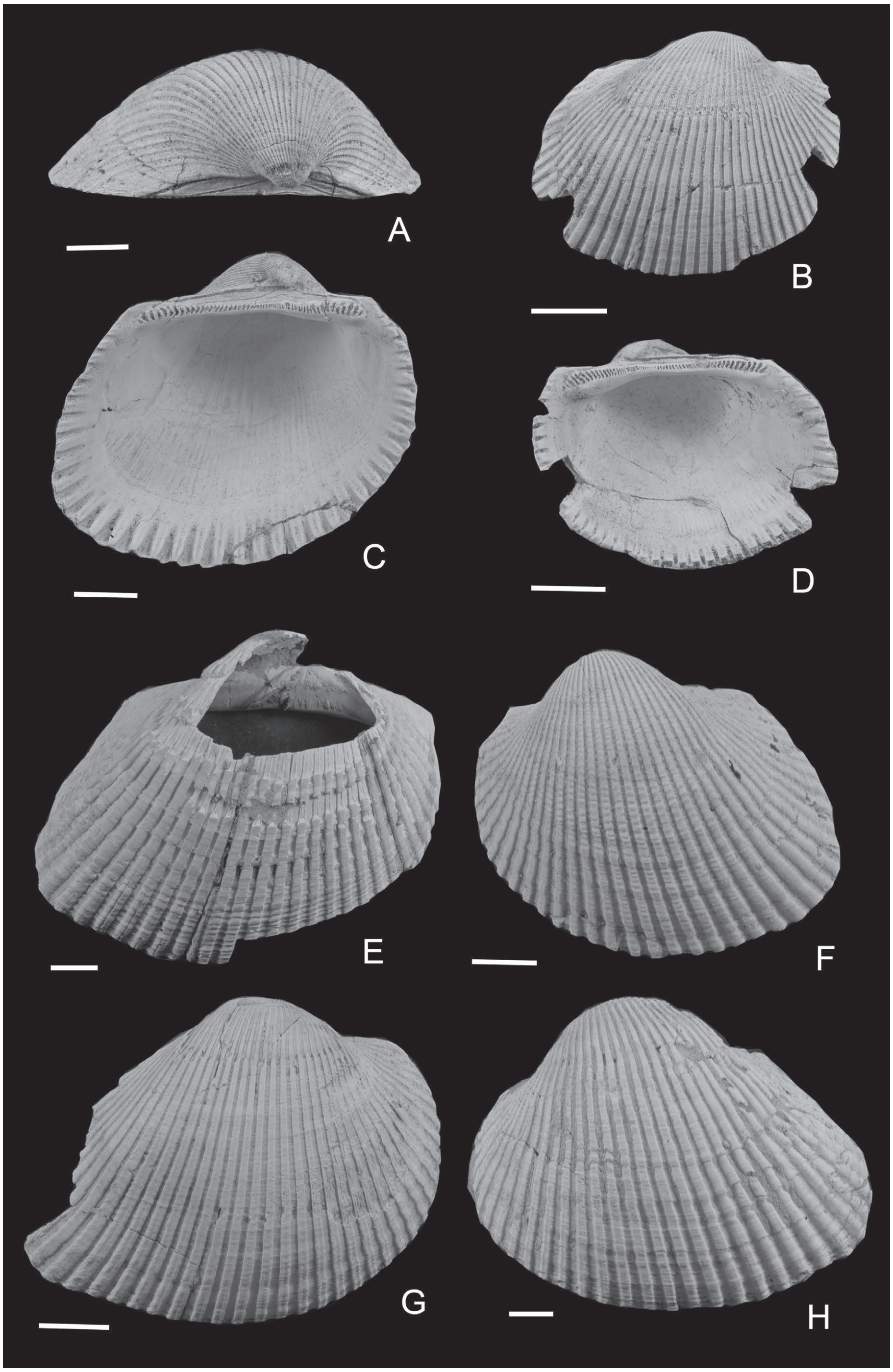

Fig. 2. *Scapharca broughtonii* from the upper Pliocene to lower Pleistocene deposits in the Japan Sea side of Honshu. **A–D, F, G.** Fossils from the upper Pliocene (Piacenzian) Tentokuji Formation at Loc. 1; A, C, F, NMNS PM 65051-1, left valve; B, D, NMNS PM 65051-2, right valve; G, NMNS PM 65051-3, right valve. **E.** Fossil from the uppermost lower Pleistocene (Calabrian) Omma Formation (upper part) at Loc. 3, NMNS PM 65053, right valve. **H.** Fossil from the lowermost lower Pleistocene (Gelasian) Nadachi Formation (uppermost part) at Loc. 2, NMNS PM 65052, left valve. Scale bars = 10 mm.

1977: pl. 10, fig. 16, pl. 15, fig. 4; Fujiyama, 1982: 338, pl. 189, fig. 1633; Masuda *et al.*, 1983: 9, pl. 1, figs 11a, b, 12; Matsuura, 1985: pl. 32, fig. 17; Amano *et al.*, 1988: 68, pl. 1, fig. 7; Ozawa *et al.*, 1998: 89, pl. 16, figs 6a, b; Huber, 2010: 137; Lutaenko & Noseworthy, 2012: 29, pl. 4, figs A–H, text-fig. 10; Lutaenko *et al.*, 2019: 174, pl. 4, figs A, B.

Anadara (*Scapharca*) *broughtoni* — Taki & Oyama, 1954: 32, pl. 18, fig. 9, pl. 35, fig. 9; Ozaki *et al.*, 1957: 167, pl. 29, fig. 18; Ozaki, 1958: 112, pl. 21, fig. 8; Ohara, 1968: 56, pl. 2, fig. 8; Ando, 1971: pl. Q-11, fig. 2; Oyama, 1973: 79, pl. 26, fig. 8; Kanno *et al.*, 1978, pl. 1, fig. 8.

Scapharca broughtoni — Habe, 1965: 75, pl. 1, figs 6, 11; Habe & Ito, 1965: 111, pl. 36, fig. 1; Ishii, 1987: 6, pl. 2, figs 1a, b.

Scapharca broughtonii — Habe & Kosuge, 1967: 125, pl. 46, fig. 6; Kuroda *et al.*, 1971: 334, pl. 68, figs 2, 3; Habe, 1977: 36, pl. 8, fig. 2; Akamatsu, 1980: 9, pl. 4, figs 2, 4, 7, pl. 5, fig. 2; Zhao *et al.*, 1982: 88, pl. 11, fig. 8; Akamatsu, 1987: pl. 1, figs 7, 8; Qi *et al.*, 1989: 157, pl. 10, fig. 3; Okutani *et al.*, 1989: 34; Akamatsu & Suzuki, 1990: pl. 4, fig. 7; Nemoto & Akimoto, 1990: pl. 8, fig. 13; Akamatsu & Suzuki, 1992: pl. 4, fig. 6; Akamatsu, 1992: pl. 1, fig. 1; Tsuchida & Kurozumi, 1993: 7, pl. 2, fig. 4; Nakagawa *et al.*, 1993: 31, pl. 11, figs 2a, b; Matsukuma & Okutani, 2000: 853, pl. 424, fig. 36; Min, 2004: 387, figs 1241-1, 2; Nobuhara, 2003, pl. 1, fig. 10; Li, 2004: 218, pl. 115, fig. K; Xu & Zhang, 2008: 35, fig. 74; Toba, 2009, 67, fig. 6; Jimbo *et al.*, 2017: figs 3Da, b; Kawase *et al.*, 2015: pl. 21, fig. B17; Matsukuma & Okutani, 2017: 1168, pl. 467, fig. 15.

? *Anadara* (*Scapharca*) *satowi* (Dunker) — Omori, 1971: Q-15, fig. 6.

Anadara broughtoni — Scarlato, 1981: 251, fig. 166; Evseev, 1981: 122, pl. 3, fig. 3; Baba, 1990: 237, pl. 23, fig. 8; Lutaenko, 1993: 27, pl. 1, fig. 5.

Anadara broughtonii — Zhang *et al.*, 2016: 243, fig. 303; Lutaenko & Noseworthy, 2019: fig. 2D.

non Scapharca broughtonii — Okumura, 1994: 46, pl. 8, fig. 20 [= *Scapharca akitaensis* (Noda, 1966)?]

Material examined: Three specimens from Loc. 1.

Description: Shell small for species, attaining more than 60.0 mm in length, rather thin for genus, subquadrate (H/L = 0.78 and 0.85), moderately inflated and inequilateral. Antero-dorsal margin straight, forming right angle with broadly arched anterior margin; postero-dorsal margin straight, forming blunt angle with subtruncate posterior margin; ventral margin broadly arcuate. Blunt ridge running from beak to postero-ventral corner. Umbo swollen and protruding above dorsal margin; beak located at anterior one-third of shell length (AL/L = 0.30 and 0.33); beak prominent prosocline. Surface sculptured by 42 and 44 narrowly elevated, flat-topped radial ribs separated by nearly equal interspaces with many fine growth lines; some nodes recognized at crossing points of radial ribs and growth lines in left valve. Ligamental area rather wide, crescent shaped and sculptured with three distinct grooves and some weak horizontal grooves. Hinge line straight, with 52 and 54 small vertical teeth to hinge base. Pallial line rather deep. Inner ventral margin crenulate. Anterior adductor muscle ovate; posterior adductor muscle scar subquadrate and larger than anterior one.

Remarks: The Tentokuji species has a smaller shell with less inflated ventral margin than the Recent specimens, which attain 150 mm (Habe, 1965). However, it can be confidently identified as *Scapharca broughtonii* because it has the same or a similar number of radial ribs (42 and 44) as the type specimens and similar ratio of shell height to length (H/L = 0.78 and 0.85; 0.78 Liang *et al.*, 2011, for Korean population). Moreover, the shell outline of *S. broughtonii* has a wide range of variation (Ando, 1971).

The Tsunozu Research Group (1983) recorded the occurrences of "Akagai" (the Japanese name of *S. broughtonii*) without any illustrations from the marine clay M1 of the upper Pliocene (Piacenzian) part (Kano *et al.*, 2001) and M4 clay of the lower Pleistocene (Gelasian) part (Kano *et al.*, 2001) of the Tsunozu Formation in Shimane Prefecture on the Japan Sea side of western

Honshu. Takao (1996) illustrated the outer molds of shells (pl. 1, figs 1, 2 in Takao, 1996) from the M1 clay of the Tsunozu at Ushiroji-cho, Gotsu City, Shimane Prefecture. These fossils have very few radial ribs (about 22 ribs counted from his figures) and smaller shells. We also examined four ill-preserved fossils from the upper Pliocene (Piacenzian) M1 clay of the Tsunozu Formation at Ushiroji-cho, stored at the Tokushima Prefectural Museum (TKPM-GFI6285) and identified them as probably *Scapharca kagoshimensis* (Tokunaga, 1906) because of their small shell size (43 mm) and 32 radial ribs.

Scapharca akitaensis (Noda, 1966) from the upper middle Pleistocene (Chibanian) Shibikawa Formation at Tayasawa in Akita Prefecture, northeast Honshu is similar to a juvenile shell of *S. broughtonii*. However, *S. akitaensis* has a small shell (21.7 mm in length) and larger number of radial ribs (48 in the left valve, 47 in the right valve) like the Chinese population of *S. broughtonii* from the Bohai Sea. *Scapharca nopporoensis* Akamatsu, 1980 from the upper middle Pleistocene (Chibanian) Otoebatsugawa Formation in central Hokkaido has a very similar shell and size (92 mm in length) to *S. broughtonii*. Like *S. akitaensis*, *S. nopporoensis* has more numerous radial ribs (46 in the left valve, 45 in the right valve) than *S. broughtonii*. Although Akamatsu (1980) did not compare his species with *S. akitaensis*, it is plausible that *S. nopporoensis* is a junior synonym of *S. akitaensis*. Okumura (1994) described *S. broughtonii* from the upper middle Pleistocene (Chibanian) Ninomiya Formation in Kanagawa Prefecture, central Honshu. According to his description, the species has a medium-sized right valve (65.5 mm) and 48 radial ribs as in *S. akitaensis*. It is possible that Okumura's species is *S. akitaensis* because of the number of radial ribs.

Scapharca ommaensis is the characteristic species of the Omma-Manganji fauna (Otuka, 1939a) which flourished in the Japan Sea side of Honshu and southwestern Hokkaido during the Pliocene to early Pleistocene. *S. ommaensis* resembles *S. broughtonii* in having narrowly elevated radial ribs separated by nearly equal interspaces. Unfortunately, there are few descriptions or measurements of this species. Our examination of the species from the Omma Formation (Loc. 5) shows that *S. ommaensis* differs from *S. broughtonii* by having more centrally situated beak (average of AL/L = 0.34), lower shell (average of H/L = 0.78) and fewer numerous radial ribs (35–40, average 37.2).

Scapharca satowi from Loc. 6 can be easily distinguished from *S. broughtonii* by having a thick shell, more centrally situated beak (average of AL/L = 0.37) and fewer radial ribs (35–40, average, 37.4). Moreover, *S. satowi* has wider and smooth radial ribs with no nodes in the left valve.

Measurements: NMNS PM 65051-1 (left valve): Length (L) 56.7 mm, Height (H) 48.1 mm, Anterior length (AL) 17.2 mm, Number of ribs (NR) 42. NMNS PM 65051-2 (right valve): L 39.4 mm, H 30.9 mm, AL 13.2 mm, NR 44. NMNS PM 65051-3 (right valve): L 60.0 mm+, H 48.1, AL 25.4 mm, NR 39+.

Distribution: Late Pliocene (Piacenzian), Tentokuji Formation in Akita Prefecture (this study); earliest Pleistocene (Gelasian), Nadachi Formation in Niigata Prefecture (Amano *et al.*, 1988; this study); early Pleistocene (Gelasian), Nojima Formation (Imaizumi Member), Renkoji and Iimuro Formations in Kanagawa Prefecture (Baba, 1990; Jimbo *et al.*, 2017); late early Pleistocene (Calabrian), Aburayama Formation in Shizuoka Prefecture (Ozawa *et al.*, 1998), Omma Formation (upper part) in Ishikawa Prefecture (this study); middle Pleistocene (Chibanian), Dateyama, Otoebetsugawa and Umaoi Formations in central Hokkaido (Fujie, 1958; Akamatsu, 1980, 1987; Akamatsu & Suzuki, 1990, 1992; Oka, 1992), Kiyokawa, Mandano and Sanuki Formations in Chiba Prefecture (Noda, 1966; Baba, 1990), Naganuma Formation in Kanagawa Prefecture (Yokoyama, 1920, 1922; Baba, 1990), Hamamatsu Formation in Shizuoka Prefecture (Nobuhara, 2003); Takamatsu Silty Sandstone of Atsumi Group (Hayasaka, 1961; Kawase *et al.*, 2015); late Pleistocene, Tsukabara Formation in Fukushima Prefecture (Noda, 1966), Narita Formation in Ibaraki Prefecture (Kanno *et al.*, 1978), Katori and Narita Formations in Chiba Prefecture (Yamakawa, 1911; Ozaki, 1958; Ohara, 1968), Tokyo Formation in Tokyo Metropolis

(Tokunaga, 1906; Yamakawa, 1911; Ozaki *et al.*, 1957; Ando, 1971), Hiradoko Lower Shell bed, Wakura-eki Shell Bed and Ushima Shell Bed in Ishikawa Prefecture (Matsuura, 1977, 1985); Holocene, Post-glacial deposits from off Primorie (44°N; Evseev, 1981), Yurakucho Formation in Tokyo Metropolis, Nanba Formation in Osaka Prefecture (Ishii, 1987), Takahama Shell Bed in Fukui Prefecture (Nakagawa, 1993); Recent, Peter the Great Bay, Busse Lake in southern Sakhalin (empty shell; Akamatsu, 1992), southern Hokkaido to Kyushu, Japan Sea, Korea, Yellow Sea and Bohai Sea (Higo *et al.*, 1999; Scarlato, 1981; Zhao *et al.*, 1982; Matsukuma & Okutani, 2000, 2017; Li, 2004; Xu & Zhang, 2008; Min, 2004; Lutaenko & Noseworthy, 2012, 2019; Zhang *et al.*, 2016).

Scapharca aff. broughtonii (Schrenck, 1867)
(Fig. 3)

Material examined: Two specimens from Loc. 4.

Description: Shell very small for genus, attaining 34.4 mm in length, quadrate (H/L = 0.78, 0.82), well inflated and inequilateral. Antero-dorsal margin straight, forming blunt angle with broadly arched anterior margin; postero-dorsal margin straight, forming blunt angle with obliquely truncated posterior margin; ventral margin broadly arcuate. Blunt ridge running from beak to postero-ventral corner. Umbo well inflated and protruding above dorsal margin; beak located at anterior one-third of shell length (AL/L = 0.28, 0.30); beak prominent prosocline. Surface sculptured by 41 and 42 narrowly elevated, flat-topped radial ribs separated by nearly equal interspaces with many fine growth lines; some nodes at crossing points with radial ribs and growth lines in anterior half of both valves. Ligament and inner structure unknown.

Remarks: The present species is very similar to the adult shell of *Scapharca broughtonii* in having a subquadrate outline and 41 or 42 radial ribs despite its small size, but young specimens of *S. broughtonii* have generally less inflated and elongate shells. Moreover, it is difficult to examine the inner structure. Therefore, we treat it as an uncertain species, *S.* aff. *broughtonii.*

Measurements: NMNS PM 65054-1 (right valve): Length (L) 32.5 mm, Height (H) 25.2 mm, Anterior length (AL) 9.2 mm, Number of ribs (NR) 41. NMNS PM 65054-2: (left valve): L 34.4 mm, H 28.1 mm, AL 10.4 mm, NR 42.

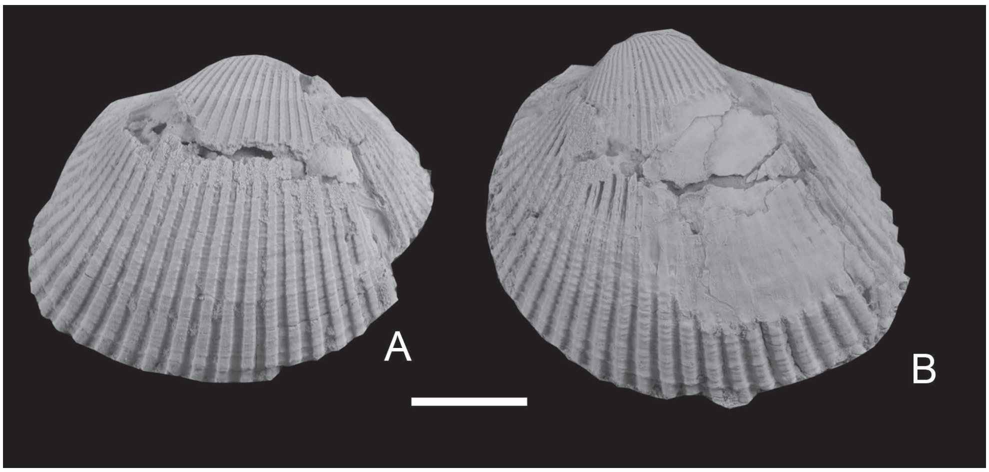

Fig. 3. *Scapharca* aff. *broughtonii* from the upper Pliocene (Piacenzian) Higashigawa Formation at Loc. 4. **A.** NMNS PM 65054-2, right valve. **B.** NMNS PM 65054-1, left valve. Scale bar = 10 mm.

Distribution: Late Pliocene (Piacenzian), Higashigawa Formation in Niigata Prefecture.

Discussion

The Japan Sea was semi-enclosed in the early Pliocene, opening through the northern straits (Ogasawara, 1994). From the early Pliocene to early Pleistocene, the Omma-Manganji fauna mainly consisting of cold-water and endemic species flourished in the semi-enclosed sea (Ogasawara, 1986; Amano, 2001, 2007). The oldest warm-water species have been recognized from the lower Pliocene part (*ca.* 4 Ma) of the Mita Formation in Toyama Prefecture, central Honshu (Amano *et al.*, 2008). However, the Tsushima warm current reached northern Honshu around 3.5 Ma and several warm-water species invaded the cold sea (Gallapher *et al.*, 2015; Itaki, 2016; Amano, 2019a, b; Amano, 2020).

Anadara amicula (Yokoyama, 1925) is the best known Anadarinae of the Omma-Manganji fauna and first appeared in the late Miocene (Amano, 2001). *Scapharca ommaensis*, *S. satowi* and *S. kagoshimensis* occurred in the Japan Sea borderland beginning in the late Pliocene (Ogasawara *et al.*, 1986; Nagamori, 1998; Amano, 2001, 2007). As a result of this study, it has been revealed that *S. broughtonii* from the Tentokuji Formation in Akita Prefecture is the oldest known record of this species. The age of the formation was assessed to about 3.5 Ma, based on the calcareous nannofossils and diatom fossils (Amano *et al.*, 2000). Moreover, *S.* aff. *broughtonii* was recovered from the upper Pliocene Higashigawa Formation in Niigata Prefecture whose age was assessed as older than 3.3 Ma by fission track dating method (Amano, 1994). The oldest known record of *S. satowi* is from the Tentokuji Formation at Awasegai (Loc. 1 in this study) in association with *S. ommaensis* (Ogasawara *et al.*, 1986). Consequently, *S. broughtonii* and *S. satowi* first appeared in the upper Pliocene Tentokuji Formation at Awasegai of Akita Prefecture. According to the molecular phylogeny, *S. broughtonii* and *S. satowi* are more closely related than other *Scapharca* species (Matsumoto & Hayami, 2001; Feng *et al.*, 2015). The oldest known *S. ommaensis*, which was proposed as a subspecies of *S. satowi* by Otuka (1936), has been recorded from Loc. 7 of the Mita Formation (Amano *et al.*, 2008), slightly lower than MT1 Tuff (3.4–3.5 Ma by the fission-track dating method; Goto *et al*., 2014). There is no Pliocene record of *S. broughtonii* or *S. satowi* from the Pacific side. In the late Pliocene, the Tsushima warm current reached the southwestern part of Aomori Prefecture, northernmost Honshu (Amano, 2020). In the late Pliocene, the shallow warm current affected about 50 m of the water column and sea surface temperature was 4°C higher than today (Kitamura & Kimoto, 2006; Amano, 2019a). During this time, the warm current carried the ancestral species of *S. broughtonii*, *S. satowi* and *S. ommaensis* into the originally cold-water Japan Sea where the characteristic species of the Omma-Manganji fauna lived. The genetically closely related *S. broughtonii* and *S. satowi* speciated near thenorthernmost limit of the warm current in the semi-enclosed Japan Sea. During this time, *Scapharca castellata* (Yokoyama, 1923) and *Diluvarca suzukii* (Yokoyama, 1926) dominated the warm-water Kakegawa fauna on the Pacific side of southwestern Japan (*see* Noda, 1966).

In the early Pleistocene, *S. broughtonii* occurred in the mild-temperate areas on the Japan Sea side while it was distributed in the subtropical to mild-temperate area on the Pacific side (*see* Ogasawara, 1994). The size of the shell increased in the Pleistocene. For example, the shell length of the specimen collected from the lowermost lower Pleistocene Nadachi Formation at Loc. 2 is 80.8 mm and that from the uppermost lower Pleistocene Omma Formation (upper part) at Loc. 3 is 89.0 mm.

In the middle Pleistocene, *S. broughtonii* reached the Japan Sea side of central Hokkaido. According to Fujie (1958) and Akamatsu (1984), *S. broughtonii* is associated with many cold-water species and a few temperate species such as *S. kagoshimensis* and *Phacosoma japonicum* (Reeve, 1850) from the lower part of the Dateyama Formation which corresponds to the higher terrace deposits (Oka, 1992). Judging from the stratigraphic position and correlation with the deposits around the Ishikari Lowland, the formation can be assigned to the middle Pleistocene (Oka, 1992; Ozaki & Komatsubara, 2014). This was the earliest appearance of this species in cold-temperate water. It has been revealed that *Saxidomus purpurata* (Sowerby) adapted to the cold-temperate water in the end of the Miocene to the early Pliocene along the global climatic cooling (Amano & Nemoto, 2020). Probably there were many more cases of temperate species adapting to cold-water environments as *S. broughtonii* and *S. purpurata* did.

It is interesting to note that *Scapharca akitaensis* and *S. nopporoensis*, which resemble *S. broughtonii* but have more numerous radial ribs (45–48), occurred with warm-water species from the middle Pleistocene Otoebaetsugawa Formation in Hokkaido (around 0.4 Ma; Akamatsu & Suzuki, 1990), the Ninomiya Formation in Kanagawa Prefecture (0.451–0.265 Ma; Yano, 1986) and the Shikikawa Formation in Akita Prefecture (0.451–0.265 Ma; Sato *et al*., 2012). In having 45 to 48 radial ribs, *S. akitaensis* and *S. nopporoensis* are similar to the Recent population of "*S. broughtonii*" in the Bohai Sea recognized by Yokogawa (1997) and Tanaka & Aranishi (2016) as a separate species or subspecies. If the Chinese population can be identified as *S. akitaensis* or *S. nopporoensis*, which appeared during the interglacial period of the middle Pleistocene in Japan, then the species would have migrated through the Japan Sea to the Bohai Sea (*see* Amano, 2005).

Acknowledgements

We thank Geerat J. Vermeij (University of California at Davis) for his critical reading of the manuscript, Yasuo Kondo (Kochi University) for his useful information on the fossil records of some species of *Scapharca*, Ken-ichi Nakao (Tokushima Prefectural Museum) for his help in examining the fossils from the Tsunozu Formation in Shimane Prefecure and Norimasa Suzuki (Daisen City) for his help to collect the fossil specimens from the Tentokuji Formation. We also thank Takami Nobuhara (Shizuoka University) and two anonymous reviewers for their critical review and useful comments.

References

Akamatsu, M. 1980. Warm-water fauna from the Nopporo Hill, Hokkaido. *Annual Report of the Historical Museum of Hokkaido* (8): 1–35. (in Japanese, title translated)

Akamatsu, M. 1984. On the so-called Shishinai fauna from the Ishikari Hills, Hokkaido. *Annual Report of the Historical Museum of Hokkaido* (12): 1–33. (in Japanese)

Akamatsu, M. 1987. Stratigraphic position and faunal characteristics of middle Pleistocene warm-water extralimital molluscan fossils from the hills around the Ishikari Lowland, Hokkaido. *Journal of the Geological Society of Japan* 93: 809–821. (in Japanese with English abstract)

Akamatsu, M. 1992. Molluscan shells collected from the Busse Lake, southern Sakhalin, and its characteristics. *Memoirs of the Historical Museum of Hokkaido* (31): 25–40. (in Japanese with English abstract)

Akamatsu, M. & Suzuki, A. 1990. Pleistocene molluscan faunas in central and Southwestern Hokkaido. *Journal of the Faculty of Science, Hokkaido University, Series IV* 22: 529–552.

Akamatsu, M. & Suzuki, A. 1992. Stratigraphy and paleoenvironment of the lower Pleistocene on the hills around the Ishikari Lowland, Hokkaido. *Annual Report of the Historical Museum of Hokkaido* (20): 1–30. (in Japanese with English abstract)

Amano, K. 1994. Pliocene molluscan fauna and its paleoenvironment in Matsunoyama-machi, Niigata Prefecture. *Journal of Geography* 103: 653–673. (in Japanese with English abstract)

Amano, K. 2001. Pliocene molluscan fauna of Japan Sea borderland and the paleoceanographic conditions. *Biological Science* (*Tokyo*) 53: 178–184. (in Japanese)

Amano, K. 2005. 6 Migration and adaptation of late Cenozoic cold-water molluscs in the North Pacific. *In*: Elewa, A. M. (ed.), *Migration of Organisms. Climate·Geography·Ecology*, pp. 127–150. Springer-Verlag, Berlin, Heiderberg.

Amano, K. 2007. The Omma-Manganji fauna and its temporal change. *Fossils* (*Palaeontological Society of Japan*) (82): 6–12. (in Japanese with English abstract)

Amano, K. 2019a. Two new gastropods from the late Pliocene Omma-Manganji fauna in the Japan Sea borderland of Honshu, Japan. *Paleontological Research* 23: 85–94.

Amano, K. 2019b. Two warm-water species of Trochoidea (Gastropoda) from Pliocene deposits on the Japan Sea side of Honshu, Japan, with remarks on the influence of the onset of Northern hemisphere glaciation. *The Nautilus* 133: 57–66.
Amano, K. 2020. Molluscan fossils from the Kitakanegasawa Formation in Aomori Prefecture, Japan, with remarks on the northern limit of the Tsushima Warm Current during the late Pliocene. *Bulletin of the National Museum of Nature and Science, Series C* (*Geology & Paleontology*) (46): 87–98.
Amano, K. & Nemoto, J. 2020. Evolution and cold-water adaptation of the genus *Saxidomus* (Bivalvia: Veneridae) in the Northwestern Pacific. *Venus* (*Journal of the Malacological Society of Japan*) 78: 87–104.
Amano, K., Hamuro, M. & Sato, T. 2008. Influx of warm-water current to Japan Sea during the Pliocene-based on analyses of molluscan fauna from the Mita Formation in Yatsuo-machi of Toyama City. *Journal of the Geological Society of Japan* 114: 516–531. (in Japanese with English abstract)
Amano, K., Ichikawa, A. & Koganezawa, S. 1988. Molluscan fauna from the Nadachi Formation around Osuga Bridge in Nadachi Town, Nishikubiki-gun —Studies on the molluscan fossi1s from the westem part of Joetsu district, Niigata Prefecture (Part 3)—. *Bulletin of the Joetsu University of Education* 7: 63–71. (in Japanese with English abstract)
Amano, K., Suzuki, M. & Sato, T. 2000. Warm-water influx into Japan Sea in the middle Pliocene — Molluscan fauna from the Tentokuji Formation around Mt. Taihei in Akita Prefecture. *Journal of the Geological Society of Japan* 106: 299–306. (in Japanese with English abstract)
Ando, Y. 1971. Pleistocene molluscan fossils from Oji in Tokyo Pref. (Tokyo formation) 1, Q-11. *Atlas of the Japanese Fossils* 14 (82): 2 maps + 1 fig. + 1 plate + explanation. (in Japanese)
Baba, K. 1990. *Molluscan Fossil Assemblages of the Kazusa Group, South Kwanto, Central Japan.* 445 pp. Keio-Yochisha, Tokyo. (in Japanese with English description of new taxa)
Cho, E. S., Jung, C. G., Sohn, S. G., Kim, C. W. & Han, S. J. 2007. Population genetic structure of the ark shell *Scapharca broughtonii* Schrenck from Korea, China, and Russia based on COI gene sequences. *Marine Biotechnology* 9: 203–216.
Evseev, G. A. 1981. *Bivalve molluscan assemblage in the post-Glacial beds of the shelf of Japan Sea*. 160 pp. Hauka, Moscow. (in Russian, title translated)
Feng, Y., Li, Q. & Kong, L. 2015. Molecular phylogeny of Arcoidea with emphasis on Arcidae species (Bivalvia: Pteriomorphia) along the coast of China: Challenges to current classification of arcoids. *Molecular Phylogenetics and Evolution* 85: 189–196.
Fujie, T. 1958. Fossil molluscs from the Pleistocene Shishinai Formation. 1. Fossil Pelecypoda. *Cenozoic Research* 28: 663–679. (in Japanese)
Fujiyama, I. 1982. Shells from the Quaternary. *In*: Fujiyama, I, Hamada, T. & Yamagiwa, N. (eds), *Illustrated encyclopedia of the Japanese fossils for students*, pp. 338–362. Hokuryukan, Tokyo. (in Japanese, title translated)
Gallagher, S. J., Kitamura, A., Iryu, Y., Itaki, T., Koizumi, I. & Hoiles, P. W. 2015. The Pliocene to recent history of the Kuroshio and Tsushima Currents: a multi-proxy approach. *Progress in Earth and Planetary Science* 2: 17. https://doi.org/10.1186/s40645-015-0045-6
Goto, T., Nasuno, S., Irizuki, T., Ohira, H. & Hayashi, H. 2014. Fission track age for MT1 tuff bed and paleoenvironment in the Upper Pliocene Mita Formation, Toyama Prefecture, Central Japan. *Journal of the Geological Society of Japan* 120: 71–76. (in Japanese with English abstract)
Habe, T. 1965. The arcid subfamily Anadarinae in Japan and its adjacent areas (Mollusca). *Bulletin of the National Science Museum, Tokyo* 8: 71–85.
Habe, T. 1977. *Systematics of Mollusca in Japan: Bivalvia and Scaphopoda*. 372 pp. Zukan-no-Hokuryukan, Tokyo. (in Japanese)
Habe, T. & Ito, K. 1965. *Shells of the World in Colour. Vol. 1.* 176 pp., 56 pls. Hoikusha, Osaka. (in Japanese)
Habe, T. & Kosuge, S. 1967. *Common Shells of Japan in Color. Vol. 3*. 223 pp., 64 pls. Hoikusha, Osaka. (in Japanese)
Hayasaka, S. 1961. The geology and paleontology of the Atsumi Peninsula, Aichi Prefecture, Japan. *Science Reports of the Tohoku University, Second Series* (*Geology*) 33: 1–103, pls 1–12.
Higo, S., Callomon, P. & Goto, Y. 1999. *Catalogue and Bibliography of the Marine Shell-bearing Mollusca of Japan.* 749 pp. Elle Scientific Publication, Yao.
Huber, M. 2010. *Compendium of Bivalves. A Full-Color Guide to the World's Marine Bivalves. A Status on Bivalvia after 250 Years of Research.* 901 pp. Conchbooks, Hackenheim.
Ishii, H. 1987. Late Pleistocene and Holocene bivalve mollusks of Osaka City and adjacent area. *Special Publications from the Osaka Museum of Natural History* 19: 1–36, pls 1–20. (in Japanese with English preface)

Itaki, T. 2016. Transitional changes in microfossil assemblages in the Japan Sea from the Late Pliocene to Early Pleistocene related to global climatic and local tectonic events. *Earth and Planetary Science* 3:11. https://doi.org/10.1186/s40645-0087-4
Jimbo, Y., Majima, R., Ichimura, T., Kusu, C., Nozaki, A. & Utsunomiya, M. 2017. An extinct naticid species *Glossaulax hyugensis* (Shuto) (Mollusca: Gastropoda) from the Lower Pleistocene Imaizumi Sandstone and Conglomerate Member in the Nojima Formation (Kazusa Group, central Japan): Discovery and implications. *Fossils* (*Palaeontological Society of Japan*) (102): 63–71. (in Japanese with English abstract)
Kanno, S., Masuda, F., Amano, K. & Ito, M. 1978. Molluscan assemblage from Hanamurogawa River in the Tsukuba Science City. *Tsukuba Environmental Studies* (3): 169–180. (in Japanses, title translated)
Kano, K., Takarada, S., Makimoto, H., Tsuchiya, N. & Bunno, M. 2001. *Geology of the Yunotsu and Gotsu Districts. With Geological Sheet Map at 1: 50,000.* Geological Survey of Japan, 129 pp. (in Japanese with English abstract)
Kawase, M., Ichihara, T. & Kawai, H. 2015. Pleistocene marine molluscs from the Atsumi Group, central Japan. *Bulletin of the Mizunami Fossil Museum* (41): 51–131. (in Japanese with English abstract)
Kinoshita, T. & Isahaya, T. 1934. Catalogue of the shell bearing molluscs from Hokkaido, no. 1. *Scientific Reports of the Fisheries Survey, Hokkaido Fisheries Experimental Station* 33: 1–19, pls 1–15. (in Japanese)
Kira, T. 1959. *Coloured Illustrations of the Shells of Japan. Enlarged and Revised Edition*. 239 pp. Hoikusha, Osaka. (in Japanese)
Kira, T. 1962. *Shells of Western Pacific in Color, vol. I.* 224 pp., 72 pls, Hoikusha, Osaka.
Kitamura, A. & Kimoto, K. 2006. History of the inflow of the warm Tsushima Current into the Sea of Japan between 3.5 and 0.8 Ma. *Palaeogeography, Palaeoclimatology, Palaeoecology* 236: 355–366.
Kitamura, A. & Kondo, Y. 1990. Cyclic changes of sediments and molluscan associations caused by glacio-eustatic sea level changes during the early Pleistocene —a case study of the middle part of the Omma Formation at the type locality—. *Journal of the Geological Society of Japan* 96: 19–36. (in Japanese with English abstract)
Kobayashi, I. 1976. Internal structure of the outer shell layer of *Anadara broughtonii* (Schrenck). *Venus* (*The Japanese journal of Malacology*) 35: 63–72. (in Japanese with English abstract)
Kobelt, W. 1891. Die Gattung Arca L. In Abbildungen nach der Natur mit Beschreibungen. *Systematisches Conchylien-Cabinet von Martini und Chemnitz* 8: 1–238.
Kuroda, T. 1930. An illustrated catalogue of the Japanese shells (4). *Venus* 2: app. 27–34. (in Japanese)
Kuroda, T., Habe, T. & Oyama, K. 1971. *The Sea Shells of Sagami Bay*. 741 pp. (in Japanese) + 489 pp. (in English), 121 pls. Maruzen, Tokyo.
Li, F. 2004. Order Arcoida. *In*: Qi, Z. (ed.), *Seashells of China*, pp. 213–224. China Ocean Press, Beijing.
Liang, C., Yang, A., Liu, Z., Zhou, L. & Wu, B. 2011. Morphological variations and discriminant analysis of different geographical populations of *Scapharca broughtonii* Schrenck. *Marine Sciences* 35: 108–113. (in Chinese with English abstract)
Lutaenko, K. A. 1993. Subfamily Anadarinae (Bivalvia: Arcidae) of the Russian Far East coast. *Korean Journal of Malacology* 9: 27–32.
Lutaenko, K. A. & Noseworthy, R. G. 2012. *Catalogue of the Living Bivalvia of the Continental Coast of the Sea of Japan* (*East Sea*). 247 pp. Dalnauka, Vladivostok.
Lutaenko, K. A. & Noseworthy, R. G. 2019. Contribution to the knowledge of the marine bivalve mollusk fauna of Gangwon Province, Korea. *Journal of Asia-Pacific Biodiversity* 12: 14–44.
Lutaenko, K. A., Noseworthy, R. G. & Choi, K-S. 2019. Marine bivalve mollusks of Jeju Island (Korea). Part 1. *Korean Journal of Malacology* 35: 149–238.
Masuda, K., Hayasaka, S. & Noda, H. 1983. Shell bearing molluscs in Sendai Bay, northeast Honshu, Japan. *Saito Ho-on Kai Museum of Natural History, Research Bulletin* 51: 1–29, pls 1–5.
Matsukuma, A. & Okutani, T. 2000. Family Arcidae. *In*: Okutani, T. (ed.), *Marine Mollusks in Japan*, pp. 845–855. Tokai University Press, Tokyo. (in Japanese and English)
Matsukuma, A. & Okutani, T. 2017. Family Arcidae. *In*: Okutani, T. (ed.), *Marine Mollusks in Japan, The Second Edition*, pp. 509–512 (Atlas), pp. 1165–1168 (Text). Tokai University Press, Hiratsuka. (in Japanese and English)
Matsumoto, M. & Hayami, I. 2001. Molecular phylogenetics and taxonomic characters of the Anadarinae (Bivalvia). *Fossils* (*Palaeontological Society of Japan*) (69): 25–34. (in Japanese with English abstract)
Matsuura, N. 1977. Molluscan fossils from the Late Pleistocene marine terrace deposits of Hokuriku Region, Japan Sea side of Central Japan. *Science Reports of Kanazawa University* 22: 117–162, pls 1–20.
Matsuura, N. 1985. Successive change of the marine molluscan faunas from Pliocene to Holocene in Hokuriku

Region, Central Japan. *Bulletin of the Mizunami Fossil Museum* (12): 71–158. (in Japanese with English abstract)
Min, D. 2004. *Mollusks in Korea*. 566 pp. Min Molluscan Research Institute, Seoul. (in Korean)
Nagamori, H. 1998. Molluscan fossil assemblages and paleo-environment of the Pliocene strata in the Hokushin District, Nagano Prefecture, Central Japan. *Earth Science (Chikyu Kagaku)* 52: 5–25. (in Japanese with English abstract)
Nakagawa, T., Fukuoka, O., Fujii, S., Chiji, M. & Nakamura, T. 1993. Fossil shell assemblages in the Holocene Takahama shell bed discovered at Takahama-cho, western part of Fukui Prefecture, Central Japan. *Monograph of the Fukui City Museum of Natural History* (1): 1–113. (in Japanese with English abstract)
Nemoto, N. & Akimoto, Y. 1990. Marine molluscan fauna of Joban coast, Fukushima Prefecture, Pacific coast of northeastern Honshu. *Research Report of Taira Geological Society* (18): 3–50. (in Japanese with English abstract)
Nishimura, S. 1981. *Sea and Life of the Earth: An Introduction to Marine Biogeography*. 284 pp. Kaimei-sha, Tokyo. (in Japanese)
Nobuhara, T. 2003. Molluscan fossils from the middle Pleistocene Hamamatsu Formation at the locality in Sahama-cho, Hamamatsu City, Shizuoka Prefecture, where *Palaeoloxodon naumanni* was recovered. *Shizuoka Chigaku* (87): 41–51. (in Japanese, title translated)
Noda, H. 1966. Cenozoic Arcidae of Japan. *Science Reports of the Tohoku University, Second Series* (*Geology*) 38: 1–161, pls 1–14.
Nyst, P. H., 1848. Tableau Synoptique et Synonimique des Espèces vivantes et fossils de la Familie des Arcacées, Part 1. Genre *Arca*. *Mémoires de l'Académie royale des sciences, des lettres et des beaux-arts de Belgique* 22: 1–79.
Ogasawara, K. 1981. Paleogeographic significance of the Omma-Manganzian fauna of the Japan Sea Borderland. *Saito Ho-on Kai Museum Research Bulletin* (49): 1–17, pl. 1.
Ogasawara, K. 1986. Notes on origin and migration of the Omma-Manganzian fauna, Japan. *Palaeontological Society of Japan, Special Papers* (29): 227–244.
Ogasawara, K. 1994. Neogene paleogeography and marine climate of the Japanese Islands based on shallow-marine molluscs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108: 335–351.
Ogasawara, K., Masuda, K. & Matoba, Y. 1986. *Neogene and Quaternary Molluscs from the Akita Oil-field, Japan.* 310 pp. Commemorative Association of Professor Taisuke Takayasu's Retirement and Supporters' Foundation of Mineral Industry Museum, Mining College, Akita University, Akita. (in Japanese)
Ohara, S. 1968. *Geological Atlas of the Chiba Prefecture. No. 5, Bivalvia.* 91 pp. Chiba-Ken Chigaku Kyôiku Kenkyu-Kai [Research Group of Earth Science of Chiba Prefecture], Chiba. (in Japanese)
Oka, T. 1992. Upper Cenozoic formations in the Ishikari Hills, Hokkaido. *Report of the Geological Survey of Hokkaido* (63): 109–135. (in Japanese with English abstract)
Okumura, K. 1994. *Fossils from the Pleistocene Ninomiya Formation Distributed in Oiso Town.* 68 pp. 15 pls. Oiso Town. (in Japanese, title translated)
Okutani, T., Tagawa, M. & Horikawa, H. 1989. *Bivalves from Continental Shelf and Slope around Japan. The Intensive Research of Unexploited Fishery Resources on Continental Slopes.* 190 pp. Japan Fisheries Resource Conservation Association, Tokyo. (in Japanese and English)
Omori, M. 1971. Pleistocene molluscan fossils from northern district of Chiba Pref. (Narita formation) 5 (Tako-machi district), Q-15. *Atlas of the Japanese Fossils* 16 (92): 2 maps + 1 fig. + 1 plate + explanation. (in Japanese)
Otuka, Y. 1936. Pliocene Mollusca from Manganzi in Kotomo-mura, Akita Pref. Japan. *Journal of the Geological Society of Japan* 43: 726–736, pls 41–42.
Otuka, Y. 1939a. Mollusca from the Cainozoic System of eastern Aomori Prefecture, Japan. *Journal of the Geological Society of Japan* 44: 23–31, pl. 2.
Otuka, Y. 1939b. Tertiary crustal deformation in Japan, with short remarks on Tertiary palaeogeography. *Jubilee Publication in the Commemoration of Prof H. Yabe's 60th Birthday* 2: 481–619.
Oyama, K. 1973. Revision of Matajiro Yokoyama's type Mollusca from the Tertiary and Quaternary of the Kanto Area. *Palaeontological Society of Japan, Special Papers* (17): 1–148, pls 1–57.
Ozaki, H. 1958. Stratigraphical and paleontological studies on the Neogene and Pleistocene formations of the Tyoshi district. *Bulletin of the National Science Museum, New Series* 4: 1–182, pls 1–24.
Ozaki, H., Fukuda, O. & Ando, Y. 1957. List of fossil mollusks from the Tokumaru Shell Bed of the Pleistocene Tokyo Formation. *Bulletin of the National Science Museum, New Series*, 3: 162–175, pls 25–33.
Ozaki, M. & Komatsubara, T. 2014. *1:200,000 Land geological map in the Ishikari Depression and its*

surrounding area with explanatory note. 28 pp. S-4. Seamless Geoinformation of Coastal Zone "Southern Coastal Zone of the Ishikari Depression", Geological Survey of Japan. (in Japanese with English abstract)

Ozawa, T., Tanaka, T. & Tomida, S. 1998. Pliocene to early Pleistocene warm water molluscan fauna from the Kakegawa Group, Central Japan. *Nagoya University Furusawa Museum, Special Report* (7): 1–205.

Qi, Z., Ma, X, Wang, Z., Lin, G., Xu, F., Dong, Z., Li, F. & Lu, R. 1989. *Mollusca of Huanghai and Bohai.* 309 pp., 13 pls. Agricultural Publishing House, Beijing. (in Chinese)

Reeve, L. A. 1843–44. Monograph of the genus *Arca*. *Conchologia Iconica* 2: *Arca* pls 3–17.

Reinhart, P. W. 1943. Mesozoic and Cenozoic Arcidae from the Pacific slope of North America. *Geological Society of America, Special Papers* (47): 1–117.

Sato, T., Sato, N., Yamasaki, M., Ogawa, Y. & Kaneko, M. 2012. Late Neogene to Quaternary paleoenvironmental changes in the Akita area, Northeast Japan. *Journal of the Geological Society of Japan* 118: 62–73. (in Japanese with English abstract)

Scarlato, O. A. 1981. Bivalve molluscs from the middle latitude of the western part of the Pacific Ocean. *Taxonomic Monograph of Fauna USSR* 126: 1–479. (in Russian)

Schrenck, L. v. 1867. Mollusken des Amur-landes und Nordjapanischen Meeres. *Reisen und Forschungen im Amur-Lande in den Jahren 1854-1856* Bd. 2 pt. 3: 259–974, pls 12–30.

Takao, A. 1996. Quaternary Tsunozu Formation and plant fossils. *Geoscience Report of the Shimane University* (15): 79–92. (in Japanese)

Taki, I. & Oyama, K. 1954. Matajiro Yokoyama's the Pliocene and later faunas from the Kwanto region in Japan. *Palaeontological Society of Japan*, *Special Papers* (2): 1–68, pls 1–49.

Tamura, T. 1960. *Proliferation of Shallow-sea Life* (*Senkai Zoshokugaku*). *Collected Works of Fisheries Science* (*Suisangaku Zenshu*) *2*. 368 pp. Kouseisha-Kouseikaku, Tokyo. (in Japanese, title translated)

Tanaka, T. & Aranishi, F. 2016. Comparative genetic characterization of ark shell *Scapharca broughtonii* in Northeast Asia. *Journal of Shellfish Research* 35: 421–427.

Toba, C. 2009. *The Sea Shells of Iwate Prefecture*. 135 pp. Daiichi Insatsu, Rikuzen-Takata. (in Japanese)

Tokunaga, S. 1906. Fossils from the environs of Tokyo. *Journal of the College of Science, Imperial University, Tokyo, Japan* 21: 1–96, pls 1–6.

Tsuchida, E. & Kurozumi, T. 1993. Fauna of marine mollusks of the sea around Otsuchi Bay, Iwate Prefecture (6) Bivalvia-3. *Otsuchi Marine Research Center Report* (21): 1–31. (in Japanese)

Tsunozu Research Group 1983. The Tsunozu Group and the Oe-Takayama Volcanoes in the central part of Shimane Prefecture. *Monograph of the Association for the Geological Collaboration in Japan* (25): 151–160. (in Japanese with English abstract)

Xu, F. & Zhang, S. 2008. *An illustrated Bivalvia Mollusca Fauna of China Seas*. 336 pp. Science Publishing House, Beijing. (in Chinese)

Yamakawa, G. 1911. Some species of Arca from environs of Tokyo. *Journal of the Geological Society of Tokyo* 18: 6–29, pls 3–7. (in Japanese and English)

Yanagisawa, Y. & Amano, K. 2003. Diatom biostratigraphy and paleoceanography of the Pliocene sequence in the western part of Joetsu City, Niigata Prefecture, central Japan. *Bulletin of the Geological Survey of Japan* 54: 63–93. (in Japanese with English abstract)

Yano, S. 1986. Stratigraphy, depositional environments and geologic ages of the southern part of the Oiso Hills, Kanagawa Prefecture. *Geoscience Reports of the Shizuoka University* (12): 191–208. (in Japanese with English abstract)

Yokogawa, K. 1997. Morphological and genetic differences between Japanese and Chinese red ark shell *Scapharca broughtonii*. *Fisheries Science* 63: 332–337.

Yokoyama, M. 1920. Fossils from Miura Peninsula and its immediate north. *Journal of the College of Science, Imperial University of Tokyo* 39: 1–193, pls 1–20.

Yokoyama, M. 1922. Fossils from upper Musashino of Kazusa and Shimosa. *Journal of the College of Science, Imperial University of Tokyo* 44: 1–200, pls 1–17.

Zhang, S., Zhang, J., Chen, Z. & Xu, F. 2016. *Mollusks of the Yellow Sea and Bohai Sea.* 421 pp. Science Publishing House, Beijing. (in Chinese)

Zhao, R., Cheng, J. & Zhao, D. 1982. *Marine Molluscs of Dalian.* 167 pp., 22 pls. China Ocean Publishing House, Beijing. (in Chinese, title translated herein)

(Received September 14, 2020 / Accepted January 1, 2021)

アカガイ（二枚貝綱：フネガイ科）とその近縁種の起源と生物地理学的変遷

天野和孝・小森加成江

要　約

アカガイ *Scapharca broughtonii* とその近縁種が本州日本海側の上部鮮新統から発見された。これはアカガイとその近縁種の最古の記録である。サトウガイ *Scapharca satowi* も秋田県の上部鮮新統天徳寺層のアカガイと同じ産地から報告されている。これらの化石記録は，遺伝的に近縁なアカガイとサトウガイが後期鮮新世までに半閉鎖的な日本海に流入した暖流の北限付近で種分化したことを示唆している。本種の冷温帯水域からの最古の記録は北海道中部の中部更新統の伊達山層からの化石である。このことは，アカガイは中期更新世に冷水域に適応進化したことを示唆している。