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Boreal species of *Macoma* (Bivalvia: Tellinidae) from the Middle to Upper Pleistocene deposits in the southwestern part of the Japan Sea

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Abstract

From the Middle to Upper Pleistocene deposits on the seabed at upper bathyal depth in the southwestern part of Japan Sea, five species of *Macoma* (*Macoma*) were recovered with some cold-water species; *Macoma* (*Macoma*) *lipara* Dall, 1916a, *M.* (*M.*) *scarlatoi* Kafanov and Lutaenko, 1997, *M.* (*M.*) *golikovi* Scarlato and Kafanov, 1988, *M.* (*M.*) *lama meridionalis* Scarlato, 1981 and *M.* (*M.*) *moesta* (Deshayes, 1855). All species are living in Primorye, Hokkaido and northwards. It has been elucidated that one of the characteristic species of the Omma-Manganji fauna, *M. praetexta oinomikadoi* Otuka, 1939 is a junior synonym of *M.* (*M.*) *lipara* Dall, 1919 living in Primorye *via* Bering Sea to California. This *Macoma*-dominated assemblage was deposited in the glacial stage, MIS 6 (~185–135 ka) and similar to that of the Lower Pleistocene Hamada Formation in Aomori Prefecture.

Key words: *Macoma*, Bivalvia, cold-water, Middel to Late Pleistocene, Japan Sea

1. Introduction

From the Pliocene to Pleistocene deposits off Yamaguchi Prefecture, southwestern part of the Japan Sea, some molluscan fossils have been recovered (Okamoto, 1978; Okamoto and Honza, 1978; Okamoto and Ibaraki, 1988; Amano et al., 2021). These fossils include some characteristic species of the Omma-Manganji fauna (Otuka, 1939) in which the cold-water species are predominant. From the off-Mishima Island, Yamaguchi Prefecture, Okamoto and Honza (1978) and Okamoto and Ibaraki (1988) listed up the following characteristic species and the related species of the Omma-Manganji fauna; *Anadara amicula* (Yokoyama, 1925), *Mizuhopecten tokyoensis hokurikuensis* (Akiyama, 1962) and *M.* cf. *yokoyamae* (Masuda, 1962). Ito (1990) illustrated *Mizuhopecten tokyoensis* (Tokunaga, 1906) from the lower sublittoral depth (87–125 m) of Wakasa Bay. Although he reported it as a living species, Matsubara et al. (2022) considered this species from the seabed as an extinct one. Amano et al. (2021) described *Neptunea* (*Neptunea*) *sakurai* (Ozaki, 1958) from the Middle to Upper Pleistocene deposits in the upper bathyal depth of southwestern part of the Japan Sea.

One of the authors, Akira Inada, acquired plenty fossil specimens of the tellinid *Macoma* Leach, 1819 species from upper bathyal depth off San-in, southwestern part of the Japan Sea through commercially operated

bottom trawls. In this paper, we describe the species of *Macoma* and significance of its occurrence.

2. Materials and Methods

Plenty fossil specimens of *Macoma* species were recovered from the seabed of the southwestern part of the Japan Sea (35°43'32" N, 130°59'08" E, 419 m depth; Fig. 1). Among them, 361 specimens of *Macoma* are well-preserved and available for the present study.

From the siltstone rock attached to the *Macoma* species, few specimens of coccolithophore were picked up and identified by one of the authors, Tokiyuki Sato. Among them, very few specimens of *Emiliania huxleyi* (Lohmann) Hay and Mohler in Hay et al., 1967 have been found, comparing with those of *Gephyrocapsa* spp. (small). Such occurrence has been recognized from the Middle to Late Pleistocene (265 ka to 90 ka) (Thierstein et al., 1977; Sato et al., 2009).

Measurements of shells are followed mainly by Kamenev and Nadtochy (1999, fig. 1). The shell length (L), shell height (H), thickness (T), anterior end length (AL), maximal distance from posterior end to top of pallial sinus (L1) and minimal distance from top of pallial sinus to anterior adductor muscle scar (L2) were measured.

Institutional Abbreviations: NMNS, Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Japan; NSMT, Department of Zoology, National Museum of Nature and Science, Tsukuba, Japan; UMUT, University Museum of the University of Tokyo, Japan; USNM, United States National Museum, Washingotn, USA.

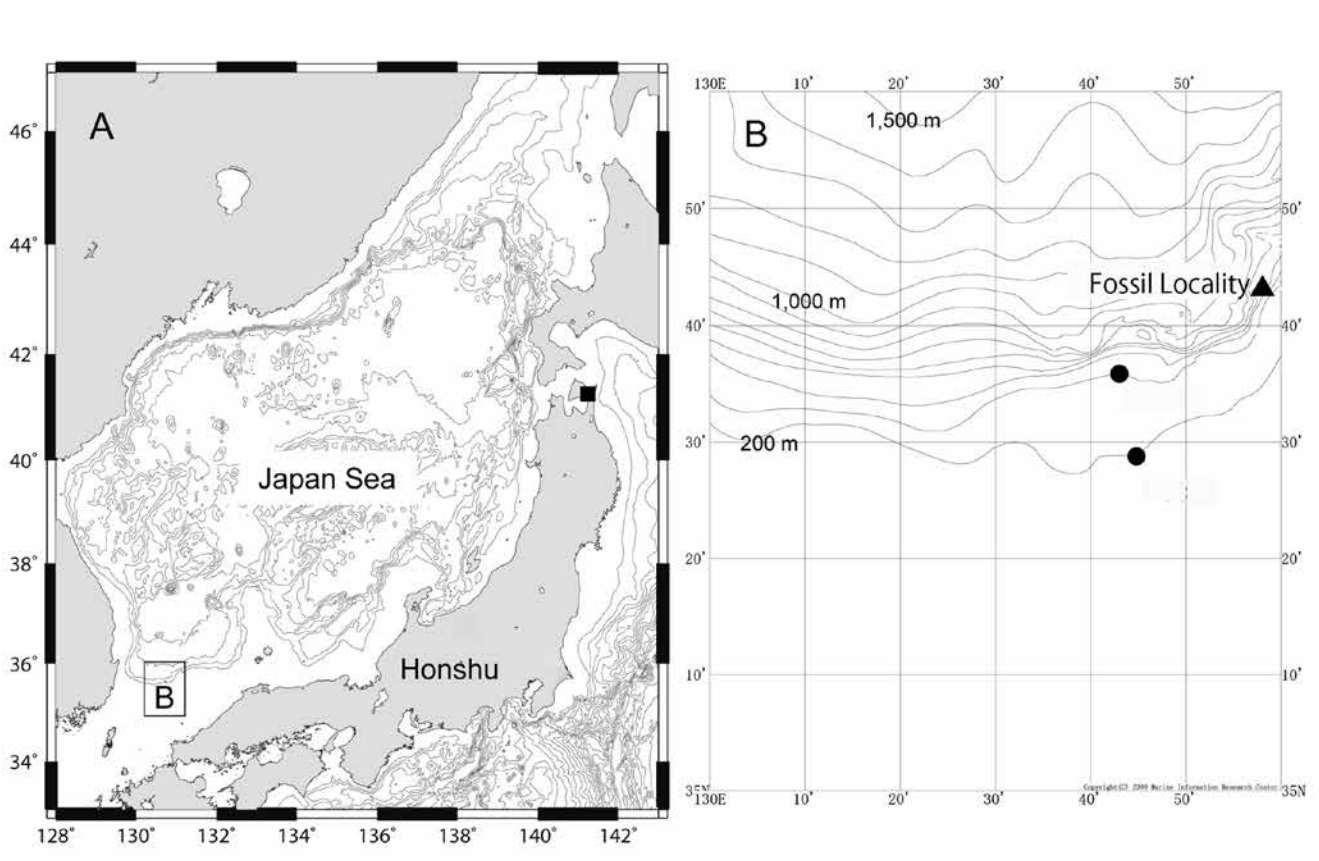

Fig. 1. Locality of the fossils. A squire area "B" shown in the map "A" (left) is enlarged in the right. A black triangle shows the fossil locality herein studied. A black circle shows the localities of *Neptunea sakurai* Ozaki by Amano et al. (2021). A black square in A shows the locality of the Hamada Formation. This figure is modified from the Figure 1 by Amano et al. (2021) published in the Nautilus, vol. 135, p. 54.

3. Molluscan fossils

As a result of examination, the following five species of *Macoma* have be identified: *Macoma* (*Macoma*) *lipara* Dall, 1916a, *M.* (*M.*) *scarlatoi* Kafanov and Lutaenko, 1997, *M.* (*M.*) *golikovi* Scarlato and Kafanov, 1988, *M.* (*M.*) *lama meridionalis* Scarlato, 1981 and *M.* (*M.*) *moesta* (Deshayes, 1855). These *Macoma* species are now living in the boreal regions in Hokkaido and northwards and correspond to the widely distributed boreal or circumboreal species by Lutaenko and Noseworthy (2014) which are unfamiliar to the most Japanese malacologists and paleontologists.

They are also associated with the following cold-water infaunal bivalves; *Scapharca akitaensis* (Noda, 1966), *Pandorella wardiana* (A. Adams, 1859), *Clinocardium* (*Ciliatocardium*) *ciliatum tchukuchense* Kafanov, 1981 and *Serripes groenlandicus* (Bruguière, 1789). Other than the last species, the preservations of the associated bivalves are poor. Based on the ecological data by Higo et al. (1999) and Kafanov (2001) of the associated species except for the ill-preserved *S. akitaensis,* the siltstone was deposited from 40 to 260 m in depth.

4. Systematics

Family Tellinidae Blainville, 1814
Genus *Macoma* Leach, 1819

Subgenus *Macoma* Leach, 1819

Type species: *Macoma tenera* Leach, 1819 by monotype [=*Tellina calcarea* Gmelin, 1791].

Macoma (Macoma) lipara Dall, 1916a

(Plate 1, figs. 1–4)

Macoma brota lipara Dall, 1916a, p. 36; Dall, 1916b, p. 414; Oldroyd, 1924a, p. 53, p. 209, pl. 10, fig. 1; Oldroyd, 1924b, p. 171, pl. 42, fig. 6; Dunnill and Ellis, 1969, p. 9, 24, 26, 27, 33, figs. 3-1a–d, fig. 9b.

Macoma praetexta oinomikadoi Otuka, 1939, p. 28, pl. 2, figs. 15–18.

Macoma (*Macoma*) *oinomikadoi* Otuka, 1939. Iwai, 1959, p. 60, pl. 2, fig. 18; Iwai, 1965, p. 44, pl. 19, figs. 2, 3; Shimaguchi and Nara, 2015, pl. 8, figs. 5, 6.

Macoma oinomikadoi Otuka, 1939. Hatai et al., 1961, pl. 2, figs. 12a, b; Sakagami et al., 1966, pl. 7, fig. 6; Masuda, 1982, p. 306, pl. 153, figs. 1434a, b; Ogasawara and Naito, 1983, pl. 7, figs. 1, 11a, b.

Macoma (s.s.) *praetexta oinomikadoi* Otuka, 1939. Shikama, 1964, pl. 48, figs. 11a, b.

Macoma calcarea (Gmelin, 1791). Sakagami et al., 1966, pl. 8, figs. 3a, b. [*non Tellina calcarea* Gmelin, 1791]

Macoma (*Macoma*) *lipara* Dall, 1916a. Coan, 1971, p. 24, pl. 6, fig. 29; Coan et al., 2000, p. 410, pl. 85; Moore, 2003, G21, pl. 5, fig. 2; Huber et al., 2015, p. 294.

Macoma brota Dall, 1916a. Petrov, 1982, p. 109, pl. 20, figs. 14a, b. [*non Macoma brota* Dall, 1916a]

Macoma (*Macoma*) sp. Lutaenko and Noseworthy, 2012, p. 73, pl. 49, figs. A, B, text-fig. 28.

Type Locality: Off Fort Rupert, Queen Charlotte Strait, Vancouver Island, British Columbia.

Type Material: Holotype, USNM 223032.

Material examined: 177 specimens of right valve and 144 specimens of left valve.

Measurements of illustrated specimens (mm): NMNS PM 68783-1, L= 87.2, H= 64.9, T= 19.5, AL= 43.8, L1= 51.7, L2= 21.2; NMNS PM 68783-47, L= 66.7, H= 47.7, T= 8.5, AL= 37.5, L1= 40.7, L2= 15.7; NMNS PM 68783-178, L=80.3, H= 58.9, T= 14.0, AL= 47.1, L1= 53.4, L2= 9.5; NMNS PM 68783-235, L=58.8, H= 42.4, T= 10.2, AL= 34.1, L1= 39.2, L2= 8.7.

Remarks: The specimens from the southwestern part of the Japan Sea are characterized by the large and heavy shell (max. length= 87.2 mm, *see* Table 1), high ovate in shape (H/L= 0.66 to 0.78, avg. 0.73), a wide hinge plate, a thick pallial line with many fine radial striations, a high and short pallial sinus (L1/L = 0.54 to 0.71, avg. 0.60) in the right valve, a deep pallial sinus (L1/L= 0.65 to 0.76, avg. 0.69) in the left valve, double-crested pedal retractor scar and three cruciform muscle scars. Although the posterior margin is more acutely rounded than *Macoma* (*Macoma*) *lipara* Dall, 1916a illustrated by Oldroyd (1924a, b) and Coan et al. (2000), the holotype specimen (USNM 223032) and the British Columbia specimen by Dunnil and Ellis (1969) has rather acutely rounded posterior margin like the Japan Sea fossil specimens.

Judging from the characters of fossil specimens, it is possible to identify the Japan Sea fossils with *M.* (*M.*) *lipara* now living from Alaska to California.

Otuka (1939) proposed *M. praetexta oinomikadoi* as a new subspecies from the Lower Pleistocene Hamada Formation in Aomori Prefecture, northernmost Honshu, Japan. After that, most paleontologists ranked it up to the species and described it from the Lower Pleistocene deposits in central Hokkaido and the Japan Seaside of Northeast Honshu. Moreover, this "extinct" species has been considered as a member of Omma-Manganji fauna (Otuka, 1939) which was flourished mainly in the Japan Sea borderland during the Pliocene to Early Pleistocene. Since Otuka (1939) first described it, nobody compared this species with *M.* (*M.*) *lipara*. As a result of examination of type specimens of *M. praetexta oinomikadoi* (UMUT CM 13154, 13155, 13156, 12835a), it has become clear that shell outline and thickness of this species is very much alike the Recent species, *M.* (*M.*) *lipara*. Moreover, the Otuka's species has a wide hinge plate, a high pallial sinus in the right valve, double-crested pedal retractor scar, three cruciform scars, a thick pallial line with many radial striations just like as *M.* (*M.*) *lipara*. *Macoma praetexta oinomikadoi* (max. L=60.2 mm) has smaller shell than *M. (M.) lipara*. However, except for the maximum size, there is no distinct difference between *M. praetexta oinomikadoi* and *M.* (*M.*) *lipara.* Thus, *M. praetexta oinomikadoi* can be judged as a junior synonym of *M.* (*M.*) *lipara*.

Oyama (1961) considered *M. praetexta oinomikadoi* as a junior synonym of the Recent species, *M.* (*M.*) *calcarea* because of a wide variation of the latter. Although he pointed out that *M. praetexta oinomikadoi* has a heavier and more rounded shell than *M.* (*M.*) *calcarea*, he did not notice the differences of the wide hinge plate and thick pallial line with radial striation. Also, he did not compare *M. praetexta oinomikadoi* with *M.* (*M.*) *lipara*. Thus, his treatment of the synonymy cannot be accepted.

When Sakagami et al. (1966) illustrated *M. oinomikadoi* [= *M.* (*M.*) *lipara*] from the Lower Pleistocene Tomikawa Formation, they also illustrated one right valve of *M. calcarea* (pl. 8, figs. 3a, b). However, their *M. calcarea* has a wide hinge plate and a high pallial sinus which are not observed in *M. calcarea*, but in *M.* (*M.*) *lipara*.

Petrov (1982) described *Macoma brota* Dall, 1916a from the Upper Pleistocene Attarman Formation in Kamchatka Peninsula. His species has a heavy and rather large shell (max. length, 60 mm), somewhat rounded posterior margin, a wide hinge plate, a thick pallial line with radial striations, and a deep pallial sinus in the left valve. These characteristics are observed in *M.* (*M.*) *lipara*.

When Lutaenko and Norseworthy (2012) described *Macoma* (*Macoma*) sp. from the Peter the Great Bay. This species has 61 mm in length, a thick shell, a wide hinge plate and the pallial line with many radial striations. Moreover, its posterior margin is not truncated like as *M.* (*M.*) *brota* Dall, 1916a. This feature is match those of *M.* (*M.*) *lipara*.

Comparison: The Recent species, *M. brota* is the most similar species to *M.* (*M.*) *lipara* in its size, thickness, and shell shape. However, *M.* (*M.*) *brota* has a truncated posterior margin and a relatively large pedal retractor scar.

Macoma astori Dall, 1909 was described from the Upper Miocene Empire Formation in Oregon has a similar shell outline with *M.* (*M.*) *lipara*. Grant and Gale (1931) suggested that *Macoma brota* var. *lipara* Dall, 1916a is a junior synonym of this species. When Talmadge (1972) compared the Recent specimens with the fossil specimens from the Pliocene Wildcat Group in California and Empire Formation in Oregon, he stated that it is impossible to discriminate both specimens. However, Addicott (1976) denied their opinions because *M. astori* has a straight posterior margin and strongly flexed posterior part in the right valve. Based on the illustration of the holotype by Moore (1963), Addicott's claim on the shell shape difference between *M. astori* and *M. lipara* is acceptable.

The Recent species, *Macoma* (*Macoma*) *calcarea* (Gmelin, 1791) is close to *M.* (*M.*) *lipara*. However, *M.* (*M.*) *calcarea* from the Bering Sea stored at NSMT is different from the latter by its lower shell (H/L= 0.64 to 0.81; avg. 0.70), narrower hinge plate even in large shells, thinner pallial line without radial striations, lower pallial sinus in the right valve, and indistinct pedal retractor scar.

Distribution: Pliocene to Holocene in California (Addicott, 1976). Pliocene, Alekhin Formation in Kunashir Island (Zhidkova et al., 1972). Early Pleistocene, Tomikawa Formation in Hokkaido (Sakagami et al., 1966), Higashimeya, Daishaka and Hamada Formations in Aomori Prefecture (Otuka, 1939; Iwai, 1959, 1965; Hatai et al., 1961; Masuda, 1982; Shimaguchi and Nara, 2015), Jozenji Formation in Yamagata Prefecture (Ogasawara and Naito, 1983). Middle to Late Pleistocene, siltstone in the southwestern part of the Japan Sea (this study). Late Pleistocene, Attarman Formation in eastern Kamchatka (Petrov, 1982). Recent, Primorye (Peter the Great Bay) (Lutaenko and Noseworthy, 2012), Bering Sea to California, sand or silt, 20 to 260 m in depth (Coan et al., 2000).

Macoma (Macoma) scarlatoi Kafanov and Lutaenko, 1997

(Plate 2, figs. 1–4)

Macoma calcarea (Gmelin, 1791). Habe, 1955, p. 18, pl. 1, figs.14, 15; Yamamoto and Habe, 1959, p. 105, pl. 9, figs. 17, 19; Habe, 1961, p. 138, pl. 62, fig. 13; Habe, 1964, p. 202, pl. 62, fig. 13; Habe and Ito, 1965, p. 145, pl. 49, fig. 6, pl. 50, fig. 11; Sakagami et al., 1966, pl. 6, figs. 3a, b; Noda et al., 1984, pl. 5, fig. 12; Akamatsu, 1984, pl. 5, fig. 3; Akamatsu and Suzuki, 1990, pl. 3, fig. 6; Akamatsu and Suzuki, 1992, pl. 5, fig. 4. [*non Tellina calcarea* Gmelin, 1791]

Macoma orientalis Scarlato in Golikov and Scarlato, 1967, p. 122, fig. 105; Scarlato, 1976, p.104, fig. 246; Zhidkova et al., 1972, pl. 8, fig. 13, pl. 9, figs. 2, 5, pl. 41, fig. 6; Volova and Scarlato, 1980, p. 75, fig. 72; Scarlato, 1981, p. 363, fig. 363; Evseev, 1981, p. 134, pl. 4, fig. 13, pl. 8, fig. 5; Gladenkov et al., 1992, pl. 7, fig. 3; Lutaenko and Volvenko, 2009, p. 25, pl. 5, figs. A–D.

Macoma (*Macoma*) *calcarea* (Gmelin, 1791). Habe, 1977, pl. 46, figs. 2, 3; Masuda et al., 1981, pl. 5, fig. 16, pl. 6, fig. 5. [*non Tellina calcarea* Gmelin, 1791]

Macoma calcarea calcarea (Gmelin, 1791). Baba, 1990, pl. 34, figs. 13a, b. [*non Tellina calcarea* Gmelin, 1791]

Macoma (*Macoma*) *scarlatoi* Kafanov and Lutaenko, 1997, p. 51, text-figs. 1–3, 5, 7, 9–11, pl. 19, fig. 1; Lutaenko, 1999, pl. 2, fig. 8; Lutaenko, 2005, p. 74, pl. 7, fig. T, pl. 9, fig. L; Lutaenko and Noseworthy, 2012, p. 70, pl. 47, figs. A–D, text-fig. 25; Huber et al., 2015, p. 295, 296; Lutaenko and Volvenko, 2017, pl. 28; Lutaenko and Volvenko, 2023, p. 140.

Type Locality: Possjet Bay, Russia

Type Material: Holotype, N9732 in the Zoological Institute of RAN; Paratypes, N11459/Bv-1443 in the Zoological Museum of Far East University.

Material examined: 14 specimens of right valve and 12 specimens of left valve.

Measurements of illustrated specimens (mm): NMNS PM 68784-2, L= 52.2, H= 38.3, T=8.8, AL= 27.8, L1= 27.6, L2=16.5; NMNS PM 68784-4, L= 49.3, H= 35.6, T= 7.7, AL= 29.6, L1= 29.0, L2= 12.2; NMNS PM 68784-15, L=57.8, H= 43.9, T= 9.9, AL= 31.7, L1= 40.2, L2= 8.3; NMNS PM 68784-20, L=49.6, H= 37.6, T= 8.6, AL= 26.7, L1= 35.4, L2= 5.8.

Remarks: The specimens treated here are characterized by the moderate size (max. length= 57.8 mm, *see* Table 1), high ovate in shape (H/L= 0.71 to 0.79, avg. 0.75), thin shell, more inflated left valve than the right (avg. T/L=0.18 in left valve, 0.16 in right valve), a narrow hinge plate, a straight antero-dorsal margin just before the beak and forming an obtuse angle to the posterior part of postero-dorsal margin, rather low pallial sinus in the left valve and two blunt ridges from the beak to the postero-ventral corner and to the middle part of posterior margin with a very shallow dent in the right valve. These characteristics are shared with *M.* (*M.*) *scarlatoi*.

Kafanov and Lutaenko (1997) proposed a new name, *Macoma* (*Macoma*) *scarlatoi* for *M. orientalis* Scarlato in Golikov and Scarlato, 1967 because *M. orientalis* became to be a junior primary homonym of *Macoma* (*Cymatoica*) *orientalis* (Dall, 1890) (*see* ICZN 57.2 and 57.4).

Comparison: Habe (1977) noted this species is synonymous with the Recent species *M. calcarea* without any reasons. However, *M.* (*M.*) *scarlatoi* is easily discriminated from *M.* (*M.*) *calcarea* by having a subtruncated posterior margin, a well inflated shell with a strait dorsal margin before umbo making a protruding antero-dorsal part.

Macoma calcarea yokohamaensis Aoki, 1960 described from the Middle Pleistocene Nakazato

Formation in Kanagawa Prefecture is another similar subspecies to *M.* (*M.*) *scarlatoi* in having a straight dorsal margin before umbo. This subspecies can be separated from *M.* (*M.*) *scarlatoi* by having a smaller shell (max. length= 34.5 mm), lower shell (H/L= 0.66 to 0.70) and higher pallial sinus in the right valve.

Distribution: Pliocene, Limintevayam Formation in Karaginskyi Island (Gladenkov et al., 1992), Upper part of the Alekhin Formation in Kunashir Island and Parusnaya Formation in Itrup Island (Zhidkova et al., 1972). Early Pleistocene, Yuchi, Zaimokuzawa and Tomikawa Formation in Hokkaido (Sakagami et al., 1966; Masuda et al., 1981; Noda et al., 1984; Akamatsu, 1984; Akamatsu and Suzuki, 1990), Hamada Formation in Aomori Prefecture (this study; NMNS PM 5881). Middle to Late Pleistocene, siltstone in the southwestern part of the Japan Sea (this study). Late Pleistocene Miyata Formation in Kanagawa Prefecture (Baba, 1990). Recent, Mutsu Bay (Yamamoto and Habe, 1959), Primorye, Hokkaido, Aniva and Terpenia Bays in South Sakhalin and Avachin Inlet in Kamchatka, Arctic Sea of Canada, 10 to 130 m in depth (Scarlato, 1981).

Macoma (*Macoma*) *moesta* (Deshayes, 1855)

(Plate 3, figs. 1, 2)

Tellina moesta Deshayes, 1855, p. 361; Sowerby, 1868, pl. 52, sp. 306.

Macoma krausi Dall, 1900, p. 307, 322, pl. 4, fig. 8.

Macoma alaskana Dall, 1900, p. 309, 323–325, pl. 3, fig. 5; Oldroyd, 1924a, p. 55, pl. 4, fig. 5; Oldroyd, 1924b, p. 177, pl. 13, fig. 14; Dunnill and Ellis, 1969, p. 6, figs. 2-2a–2d.

Tellina (Macoma) moesta Deshayes, 1855. Jensen, 1905a, p. 38, pl. 1, figs. 4a–4c; Jensen, 1905b, p. 345, text-fig. 4.

Macoma oneilli Dall, 1919, p. 20, pl. 2, fig.1; Oldroyd, 1924a, p. 173, pl. 40, fig. 7.

Macoma moesta (Deshayes, 1855). Oldroyd, 1924b, p. 173; Grant and Gale, 1931, p. 370, pl. 20, fig. 3; Ockelmann, 1958, p. 120, pl. 2, fig. 13; MacGinitie, 1959, p. 182, pl. 21, figs. 1–3, pl. 23, fig. 10, pl. 24, figs.1–3; Kotaka, 1962, p. 153, pl. 35, figs. 20, 21; Lubinsky, 1980, p. 42, pl. 9, figs. 3, 6, 9, 12; Scarlato, 1981, p. 361, fig. 360; Kiel, 2000, p. 61, text-figs. 66, 67; Huber et al., 2015, p. 295; Lutaenko and Volvenko, 2017, pl. 30.

Macoma moesta moesta (Deshayes, 1855). Coan, 1971, p. 28, pl. 7, figs. 35–37, text-fig. 16.

Macoma (*Macoma*) *moesta alaskana* Dall, 1900. Coan, 1971, p. 29, pl. 7, fig. 38, text-fig.17.

Macoma (*Macoma*) *moesta* (Deshayes, 1855). Coan et al., 2000, p. 411, pl. 85.

non Macoma moesta (Deshayes, 1855). Habe and Ito, 1965, p. 144, pl. 50, figs. 5, 6; Tsuchida and Kurozumi, 1995, p. 27, pl. 5, fig. 6. [= *Macoma* (*Macoma*) *coani* Kafanov and Lutaenko, 1999]

non Macoma moesta (Deshayes, 1855). Okutani et al., 2009, p. 210, fig. 4N; Matsukuma, 2017, p. 1257, pl. 552, fig. 3 [= *Tellina* (*Macoma*) *loveni* Jensen, 1905a]

Type Locality: "Northern Ocean"(Cumming Collection)

Type Material: BM(NH), without regulation number.

Material examined: Four specimens of right valve and three specimens of left valve.

Measurements of illustrated specimens (mm): NMNS PM 68787-4, L= 24.9, H= 17.1, T=3.2, AL= 15.1, L1= 12.5, L2= 6.2; NMNS PM 68787-7, L= 33.3, H= 22.8, T= 4.9, AL= 18.3, L1= 20.2, L2= 5.2.

Remarks: The specimens from the southwestern part of the Japan Sea have very thin, shiny, small sized shell (max. length= 39.0 mm, *see* Table 1), elongate in shape (H/L= 0.63 to 0.70, avg. o.68), rather posteriorly located umbo (AL/L= 0.55 to 0.66, avg. 0.59), rather straight postero-dorsal margin and subtruncated posterior margin, a narrow hinge plate, a shallow pallial sinus (L1/L =0.48 and 0.50) in the right valve, a moderately deep pallial sinus (L1/L= 0.61 to 0.64; L2/L= 0.13 to 0.15) in the left valve. From these characteristics, the fossil specimens can be identified with *Macoma* (*Macoma*) *moesta* (Deshayes, 1855).

As already pointed out by Coan (1971), *M. krausi* Dall, 1900, *M. alaskana* Dall, 1900 and *M. oneili* Dall, 1919 are synonyms of *M.* (*M.*) *moesta*. Moreover, *M. moesta* described by Habe and Ito (1965) and Tuchida and Kurozumi (1995), living in the shallow sandy bottom is synonymous with *Macoma* (*Macoma*) *coani* Lutaenko, 1999.

Comparison: *Macoma* (*Macoma*) *coani* has a thin and similar sized and outline of shell like as *M.* (*M.*) *moesta*. However, *M.* (*M.*) *coani* is different from *M.* (*M.*) *moesta* by having a translucent shell, a narrow hinge plate and one white line from beak to the posterior margin in the inner side. Moreover, *M.* (*M.*) *coani* prefer the upper subtidal zone (5–15 m) and the fine muddy sand bottom (Kafanov and Lutaenko, 1999) while *M.* (*M.*) *moesta* lives in the silty bottom of the deeper water (2–270 m).

Macoma (*Macoma*) *praetexta* (v. Martens, 1865) looks like the rather elongate specimens of *M.* (*M.*) *moesta*. However, *M.* (*M.*) *praetexta* can be easily distinguished from the latter by having more deeper pallial sinus (*see* Amano, 1996).

Distribution: Late Miocene to Pliocene Etchegoin Formation in California (Grant and Gale, 1931). Middle to Late Pleistocene, siltstone in the southwestern part of the Japan Sea (this study). Recent, Peter the Great Bay to western Sakhalin in the Japan Sea, northern Hokkaido, Aniva, and Terpeniya Bays in South Sakhalin, western Kamchatka in the Okhotsk Sea, Barents Sea to Chukotsk Sea, Bofort Sea, Baffin Sea, east Greenland and Spitsbergen Island, 2–270 m (Scarlato, 1981).

***Macoma (Macoma) lama meridionalis* Scarlato, 1981**

(Plate 3, figs. 3, 4)

Macoma calcarea (Gmelin, 1791). Kaseno and Matsuura, 1965, pl. 17, figs. 4, 5. [*non Tellina calcarea* Gmelin, 1791]

Macoma praetexta (v. Martens, 1865). Ogasawara, 1977, pl. 14, figs. 13a, b, pl. 15, fig. 2, 7; Goto and Kaneko, 1993, p. 14, pl. 8, figs. 3a, b, c [*non Tellina praetexta* v. Martens, 1865]

Macoma lama meridionalis Scarlato, 1981, p. 360, fig. 356–358; Amano, 1996, p. 290, pl. 1, figs. 2, 3, 6, 7, 10.

Macoma (*Macoma*) *nasuta* (Conrad, 1837). Matsuura, 1992, pl. V-20 (7), fig. 7; Matsuura, 2009, pl. IV-22 (7), fig. 3. [non *Tellina nasuta* Conrad, 1837]

Macoma lama Bartsch, 1929. Lutaenko, 2005, p. 74, pl. 9, fig. K; Lutaenko and Volvenko, 2017, pl.27.

Type Locality: Mordvinova Bay, north of Tunaicha Lake, eastern coast of South Sakhalin (20 m in depth).

*Type Materia*l: Holotype, N9700 in the Zoological Institute of RAN.

Material examined: Two specimens of right valve and two specimens of left valve.

Measurements of illustrated specimens (mm): NMNS PM 68786-2, L= 32.9, H= 24.0, T=5.4, AL= 16.8, L1= 19.1, L2= 8.6; NMNS PM 68786-3, L= 33.8, H= 24.2, T= 4.8, AL= 14.4, L1= 26.6, L2= 1.3.

Remarks: The specimens from the southwestern part of the Japan Sea have a thin medium sized and shiny shell (max. length= 38.2 mm, see Table 1), elongate ovate shape (H/L= 0.70 to 0.73, avg. 0. 71), anteriorly located umbo (AL/L= 0.42 to 0.51, avg. 0.45), a pointed posterior end, a narrow hinge plate, a moderate pallial sinus (L1/L = 0.58) in the right valve, a very deep pallial sinus, attaining near the anterior adductor muscle scar (L1/L= 0.78 and 0.79; L2/L= 0.04 and 0.05) in the left valve. From these characteristics, the fossil specimens are identified with *Macoma* (*Macoma*) *lama meridionalis* Scarlato, 1981.

As Amano (1996) discussed in detail, this subspecies is misidentified for the specimens from the Lower Pleistocene Omma Formation as *Macoma calcarea* (Gmelin) by Kaseno and Matsuura (1965), *M. praetexta* (v. Martens) by Ogasawara (1977) and Goto and Kaneko (1993) and *M.* (*M.*) *nasuta* (Conrad) by Matsuura (1992, 2009). This subspecies first appeared after the climate cooling event at Datum A (2.75 Ma) in Honshu and seems to be flourished in the Japan Sea.

Comparison: Although Coan et al. (2000) did not recognize *meridionalis* as an independent subspecies, *Macoma* (*Macoma*) *lama lama* Bartsch, 1929 from the west coast of Kamchatka can be separated from *M.* (*M.*) *lama meridionalis* by having a higher shell (H/L of the type= 0.79), a straight postero-dorsal margin, a shallower pallial sinus in the left valve which does not touch or very near the anterior adductor muscle scar (*see* Higo et al., 2001).

Distribution: Early Pleistocene, Sasaoka Formation in Akita Prefecture (Amano et al., 2011), Mita Formation (upper part) in Toyama Prefecture (Amano et al., 2008), Omma Formation in Ishikawa Prefecture (Kaseno and Matsuura, 1965; Ogasawara, 1977; Matsuura, 1992, 2009; Goto and Kaneko, 1993; Amano, 1996). Middle Pleistocene, Shibikawa Formation in Akita Prefecture (Amano, 1996). Middle to

Late Pleistocene, siltstone in the southwestern part of the Japan Sea (this study). Recent, Possjet Bay to South Sakhalin in the Japan Sea, Aniva, Mordvinova and Terpeniya Bays in South Sakhalin, South Kurile Islands, 15–60 m (Scarlato, 1981).

Macoma (*Macoma*) *golikovi* Scarlato and Kafanov, 1988

(Plate 3, figs. 5–7)

?*Macoma calcarea* (Gmelin, 1791). Kaseno and Matsuura, 1965, pl. 17, fig. 7. [*non Tellina calcarea* Gmelin, 1791]

?*Macoma anser* Oyama, 1950. Kaseno and Matsuura, 1965, pl. 18, fig. 2. [*non Macoma* (*Macoma*) *anser* Oyama, 1950 =*Tellina contabulata* Deshayes, 1855]

Macoma oribiculata Scarlato, 1981, p. 361, fig. 360; Gladenkov and Sinelnikova, 1984, p. 219, pl. 53, figs. 9, 14, 16; Lutaenko and Volvenko, 2009, p. 25, pl. 5, figs. E, F. [*non Macoma orbiculata* Kanno, 1958]

Macoma arnheimi Dall, 1916a. Evseev, 1981, p. 135, pl. 1, figs. 1, 4.

Macoma golikovi Scarlato and Kafanov, 1988, p. 959; Kafanov, 1999, p. 78, text-figs. 2A–F; Lutaenko, 1999, p. 269, pl. 2, fig. 1; Coan et al., 2000, p. 413, pl. 85.

Macoma lukini Kamenev, 1990, p. 129–131, figs. 2, 3; Kamenev, 1995, figs. 7–10.

Type Locality: Japan Sea side of South Sakhalin.

Type Material: Holotype, N9730 in the Zoological Institute of RAN; Paratypes, 1446/Bv-1430 in the Zoological Museum of Far East University.

Material examined: Three specimens of right valve and two specimens of left valve.

Measurements of illustrated specimens (mm): NMNS PM 68785-1, L= 45.4, H= 38.3, T=8.8, AL= 23.4, L1= 25.4, L2= 10.9; NMNS PM 68785-3, L= 48.0, H= 40.9, T= 9.2, AL= 24.7, L1= 30.0, L2= 11.3; NMNS PM 68785-5, L= 39.4, H= 35.3, T= 8.4, AL= 19.8, L1= 30.2, L2= 2.6.

Remarks: The specimens from the southwestern part of the Japan Sea have a thin medium sized shell (max. length= 49.8 mm, *see* Table 1), subcircular shape (H/L= 0.80 to 0.90, avg. 0. 85), a narrow hinge plate, a moderate pallial sinus (L1/L = 0.56 and 0.63) in the right valve, a deep pallial sinus (L1/L= 0.74 and 0.77) in the left valve and two cruciform muscle scars. From these characteristics, the fossil specimens can be safely identified with *Macoma* (*Macoma*) *golikovi* Scarlato and Kafanov, 1988.

Scarlato (1981) described a new species, *Macoma orbiculata* from the Japan Sea side of South Sakhalin. When Scarlato and Kafanov (1988) noticed that the species name was preoccupied by the Japanese fossil, *Macoma orbiculata* Kanno, 1958 from the Lower Miocene Nenokami Formation in Saitama Prefecture, they proposed *M. golikovi* for the Sakhalin species as a new replacement name.

Macoma lukini was described as a new species by Kamenev (1990) from the Yankich Island of central Kurile Islands. However, it is elucidated that *M. lukini* is a junior synonym of *M.* (*M.*) *golikovi* by Kafanov (1999).

Kaseno and Matsuura (1965) just illustrated "*Macoma calcarea* (Gmelin)" and "*M. anser* Oyama" from the Lower Pleistocene Omma Formation. However, their two specimens of "*M. calcarea*" (pl. 7, figs. 4, 5) was reidentified as *Macoma* (*Macoma*) *lama meridionalis* Scarlato, 1981 by Amano (1996). Another one specimen of "*M.* (*M.*) *calcarea*" (pl. 7, fig. 7) and "*M. anser* Oyama" (pl. 8, fig. 2) have a subcircular shell like as *M.* (*M.*) *golikovi.*

Evseev (1981) described this species as *Macoma arnheimi* Dall, 1916a (p. 134, pl. I, figs. 1, 4) from the Holocene deposits of Cape Povorotny, eastern part of Peter the Great Bay. Lutaenko (1999) considered it as the same species of *M.* (*M.*) *golikovi.*

According to Kamenev et al. (2004), this species is mainly a suspension-feeder in Kraternaya Bight of Yankich Island while *M.* (*M.*) *calcarea* is a deposit feeder.

Comparison: The well-known fossil species in Japan, *Macoma optiva* (Yokoyama, 1923) resembles *M.* (*M.*) *golikovi* in its subcircular outline. However, As pointed by Matsubara (2011), the Miocene species has a larger shell, attaining 90 mm in length and a shorter and more angular pallial sinus. Moreover, *M.* (*M.*) *optiva* has heavier shell than *M.* (*M.*) *golikovi.*

Distribution: Middle Miocene, Etolon Formation in Kamchatka (Gladenkov and Sinelnikova, 1984). ? Early Pleistocene, Omma Formation in

Ishikawa Prefecture (Kaseno and Matsuura, 1965). Middle to Late Pleistocene, siltstone in the southwestern part of the Japan Sea (this study). Holocene, deposits off Cape Povorotny, eastern part of Peter the Great Bay (Evseev, 1981). Recent, Tatar Strait to Kievka Bay of southern Primorye in the Japan Sea, Terpeniya Bay in South Sakhalin, Shimushir and Yankich Islands of Kurile Islands, Avacha Inlet of Kamchatka, Commander Island in Bering Sea, Alaska to Puget Sound in Washington, intertidal to ca. 200 m in depth (Kafanov, 1999; Coan et al., 2000).

5. Discussion

Judging from the distribution of the five *Macoma* species, they belong to boreal, widely distributed boreal and boreal-arctic species (Lutaenko and Norseworthy, 2014). Except for the subtropical-lowboreal species, *Pandorella wardiana* (A. Adams), *Clinocardium* (*Ciliatocardium*) *ciliatum tchukuchense* Kafanov and *Serripes groenlandicus* (Bruguière) are widely distributed boreal and boreal-arctic species respectively.

The distribution of these species shows that the climate was similar to that of the Primorye and northwards. Especially, as described above, there has been no distinct fossil record of *M.* (*M.*) *moesta* and few doubtful records of *M.* (*M.*) *golikovi* in Japan. These data suggests that the siltstone yielding five species of *Macoma* in the southwestern part of the Japan Sea was deposited during the glacial stage in the Middle to Late Pleistocene (265 to 90 ka). The glacial age in this time span corresponded to MIS 6 (~185–135 ka; Ehlers et al., 2011). In this stage, global sea-level reconstructions indicate a sea-level drop of more than 100 m toward the end of MIS 6. Sea surface temperature was 5°C lower than present (Elderfield et al., 2012; Margari et al., 2014).

Amano et al. (2021) described *Neptunea* (*Neptunea*) *sakurai* (Ozaki) from the Middle to Upper Pleistocene deposits in the southwestern part of the Japan Sea. This species was considered as a representative extinct species of the Pliocene to Early Pleistocene Omma-Manganji fauna in the Japan Sea borderland. Moreover, this species has been recorded from the Lower Pleistocene Hamada Formation in Aomori Prefecture (Hatai et al., 1961; Amano, 1997; Shimaguchi and Nara, 2015). Moreover, the *Macoma*-dominant fossils herein studied are also shared with some bivalve species from the Hamada Formation. They include *Macoma* (*Macoma*) *lipara* Dall (=*M. praetexta oinomikadoi* Otuka), *M.* (*M.*) *scarlatoi* Kafanov and Lutaenko, *Pandorella wardiana* (A. Adams). *Clinocardium* (*Ciliatocardium*) *ciliatum chikagawaense* Kotaka, 1950 from the Hamada Formation is very similar to *C.* (*C.*) *ciliatum tchukuchense* herein obtained. From these, in the glacial stage MIS 6, many species of the Lower Pleistocene deposits in Northeast Honshu migrated southward to the southwestern part of the Japan Sea.

Table 1. Measurements of five species of *Macoma*. * Number of individuals..

Species	N*	Max. L	H/L(Avg.)	T/L (Avg.)	AL/L (Avg.)	L1/L (Avg.)	L2/L (Avg.)
Macoma (*Macoma*) *lipara* Dall (RV)	177	87.2	0.73	0.15	0.57	0.60	0.23
Macoma (*Macoma*) *lipara* Dall (LV)	144	80.3	0.73	0.15	0.56	0.69	0.14
Macoma (*Macoma*) *scarlatoi* Kafanof and Lutaenko (RV)	14	52.2	0.74	0.16	0.58	0.57	0.26
Macoma (*Macoma*) *scarlatoi* Kafanof and Lutaenko (LV)	12	57.8	0.75	0.18	0.53	0.69	0.13
Macoma (*Macoma*) *golikovi* Scarlato and Kafanov (RV)	3	48.0	0.83	0.19	0.52	0.59	0.24
Macoma (*Macoma*) *golikovi* Scarlato and Kafanov (LV)	2	49.8	0.90	0.21	0.43	0.75	0.05
Macoma (*Macoma*) *lama meridionalis* Scarlato (RV)	2	32.9	0.73	0.17	0.46	0.58	0.27
Macoma (*Macoma*) *lama meridionalis* Scarlato (LV)	2	38.2	0.71	0.15	0.44	0.78	0.04
Macoma (*Macoma*) *moesta* (Deshayes) (RV)	4	28.4	0.69	0.13	0.62	0.49	0.24
Macoma (*Macoma*) *moesta* (Deshayes) (LV)	3	39.0	0.66	0.15	0.56	0.64	0.14

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Boreal species of *Macoma* (Bivalvia: Tellinidae) from the Middle to Upper Pleistocene deposits in the southwestern part of the Japan Sea

Kazutaka Amano, Akira Inada, and Tokiyuki Sato

Explanation of Plates 1–3

Plate 1

***Macoma* (*Macoma*) *lipara* Dall.**

Figs. 1a, b. NMNS PM 68783-235, left valve.

Figs. 2a, b. NMNS PM 68783-47, right valve.

Figs. 3a, b. NMNS PM 68783-178, left valve.

Figs. 4a, b. NMNS PM 68783-1, right valve.

All scale bars show 10 mm.

Plate 1

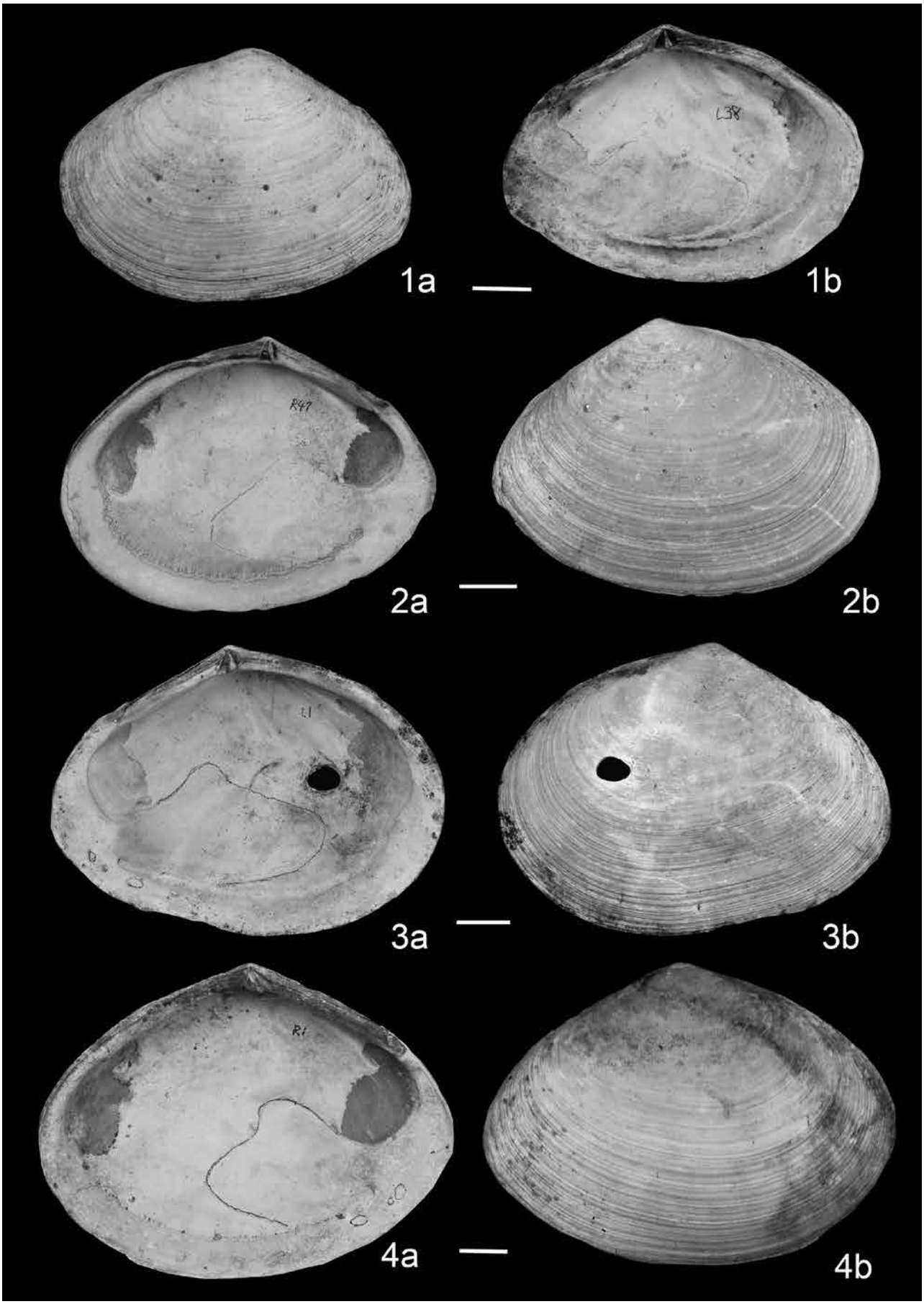

Plate 2

***Macoma* (*Macoma*) *scarlatoi* Kafanov and Lutaenko.**

Figs. 1a, b. NMNS PM 68784-20, left valve.

Figs. 2a, b. NMNS PM 68784-4, right valve.

Figs. 3a, b. NMNS PM 68784-2, right valve.

Figs. 4a, b. NMNS PM 68784-15, left valve.

All scale bars show 10 mm.

Plate 2

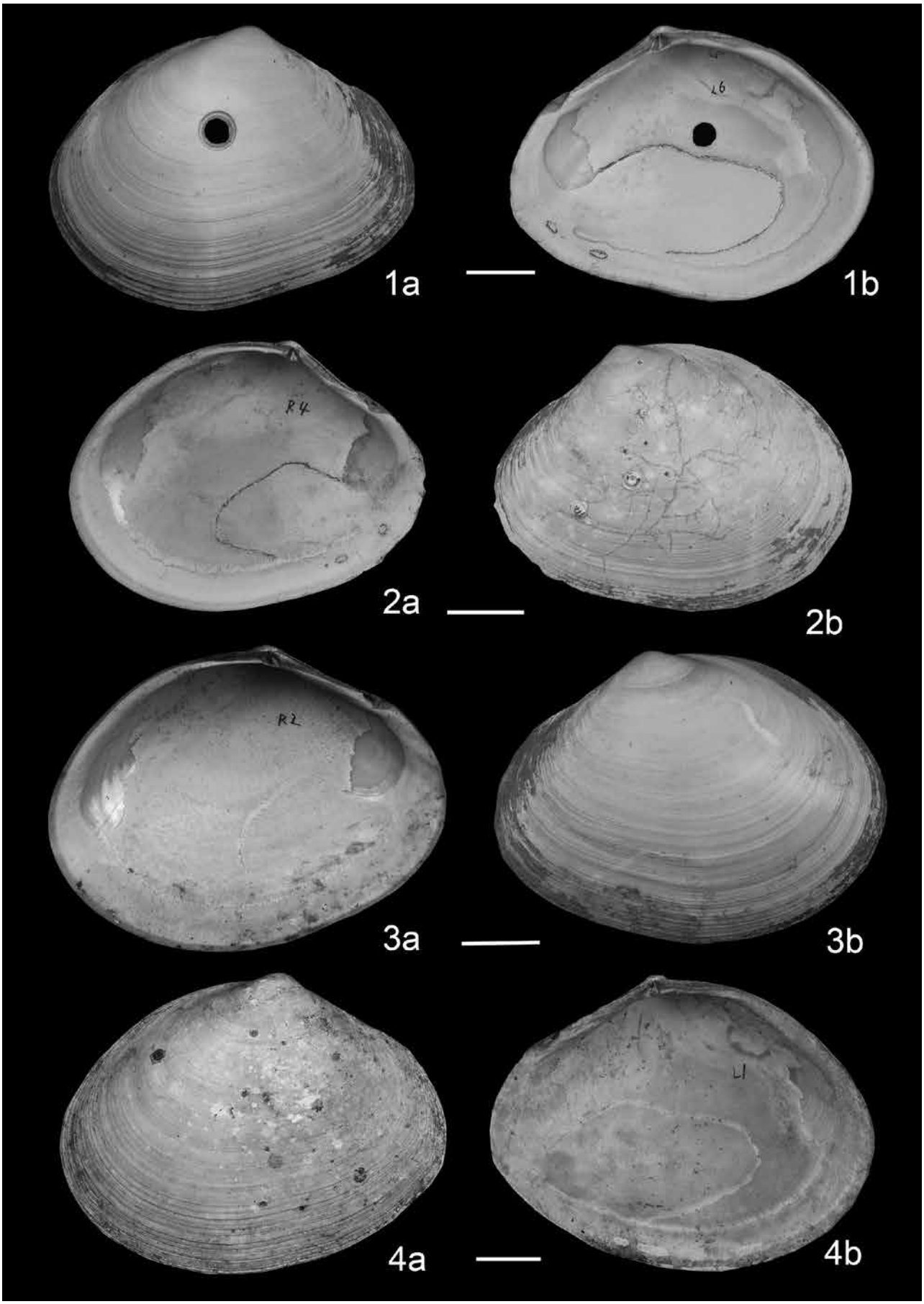

Plate 3

Figs. 1, 2. *Macoma* (*Macoma*) *moesta* (Dehsayes).
1a, b, NMNS PM 68787-7, left valve; 2a, b, NMNS PM 68787-4, right valve.

Figs. 3, 4. *Macoma* (*Macoma*) *lama meridionalis* Scarlato
3a, b, NMNS PM 68786-3, left valve; 4a, b, NMNS PM 68786-2, right valve.

Figs. 5–7. *Macoma* (*Macoma*) *golikovi* Scarlato and Kafanov
5a, b, NMNS PM 68785-5, left valve; 6a, b, NMNS PM 68785-1, right valve; 7, NMNS PM 68785-3, right valve.

All scale bars show 10 mm.

Plate 3