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Trophonopsis Bucquoy, Dautzenberg and Dollfus, 1882 (Gastropoda, Muricidae) from the Plio-Pleistocene deposits in Japan

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Abstract. **The Plio-Pleistocene *Trophonopsis* in northern Japan consists of seven species: *T. kamchatkana* (Dall), *T. uyemurai* (Yokoyama), *T. sasae* Sawada, *T. vermeiji* Amano, sp. nov., *T.* aff. *densicostata* Golikov in Golikov and Scarlato, *T.* aff. *undocostata* Golikov and Sirenko and *T.* sp.. *Trophon toyamai* Hatai and Nisiyama and *T. kagaensis* Hatai and Nisiyama are synonymous with *Trophonopsis uyemurai*. By the end of the early Pleistocene, *T. uyemurai*, *T. sasae* and *T. vermeiji* became extinct and *T.* aff. *undocostata* and *T.* sp. might have become extinct, owing to decrease of salinity in shallow water during the low stands of the glacial Pleistocene.**

Key words: ***Trophonopsis*, Muricidae, Pliocene, Pleistocene, Japan**

Introduction

Trophonopsis Bucquoy, Dautzenberg and Dollfus, 1882 is a genus of common trophonine gastropods and now flourishes in the northwestern Pacific (Kuroda, 1953; Tiba and Kosuge, 1985a; Egorov, 1993). Five species of this genus have been described from Plio-Pleistocene deposits in Japan as of the genera *Fusus* Helbling, 1779, *Trophon* Montfort, 1810, and *Trophonopsis* Bucquoy, Dautzenberg and Dollfus, 1882: *Fusus uyemurai* Yokoyama, 1926a, *Trophon toyamai* Hatai and Nisiyama, 1938, *Trophon kagaensis* Hatai and Nisiyama, 1939, *Trophonopsis* (*Boreotrophon*) *sasae* Sawada, 1962 and *Trophonopsis* sp. described by Baba (1990). These species have not been revised since their description. I collected many specimens of *Trophonopsis* including hitherto undescribed species from the Plio-Pleistocene deposits mainly in the Japan Sea borderland.

Previously, I used the distribution history and paleoceanography of buccinid and muricid gastropods to study the Plio-Pleistocene condition of the Japan Sea (Amano, 2004). Deep-water species of *Buccinum* Linnaeus, 1758, *Neptunea* Röding, 1798 and Ancistrolepidinae Habe and Sato, 1972 diversified in the semienclosed Japan Sea from the Pliocene to early Pleistocene and then became extinct during the middle to late Pleistocene glacial low stands. By contrast, shallow-water genera such as *Nucella* Röding, 1798, *Ceratostoma* Herrmansen, 1846, *Ocinebrellus* Jousseaume, 1880 and *Lirabuccinum* Vermeij, 1991 have broader distributions and lower diversities than the deep-water forms. Only a few species of them became extinct during the glacial Pleistocene in the Japan Sea and on the Pacific coast of Japan.

Although species of *Trophonopsis* have a non-planktotrophic larval stage as do the buccinids mentioned above, they live in shallower depths than the deep-water buccinids (Egorov, 1993; Higo *et al.*, 1999). Knowledge of the ecology of *Trophonopsis* can therefore elucidate the effects of environmental change on species at moderate depths in the Japan Sea.

In this paper, I describe the Plio-Pleistocene species of this genus in Japan and discuss the questions of diversity, extinction and biological response to environmental change.

Material and methods

New specimens were collected by hand from fourteen localities (Figure 1; see also Appendix). All material is housed at the Joetsu University of Education (JUE). I also reexamined the fossil and Recent specimens including some type material stored at University Museum of the University of Tokyo (UMUT), To-

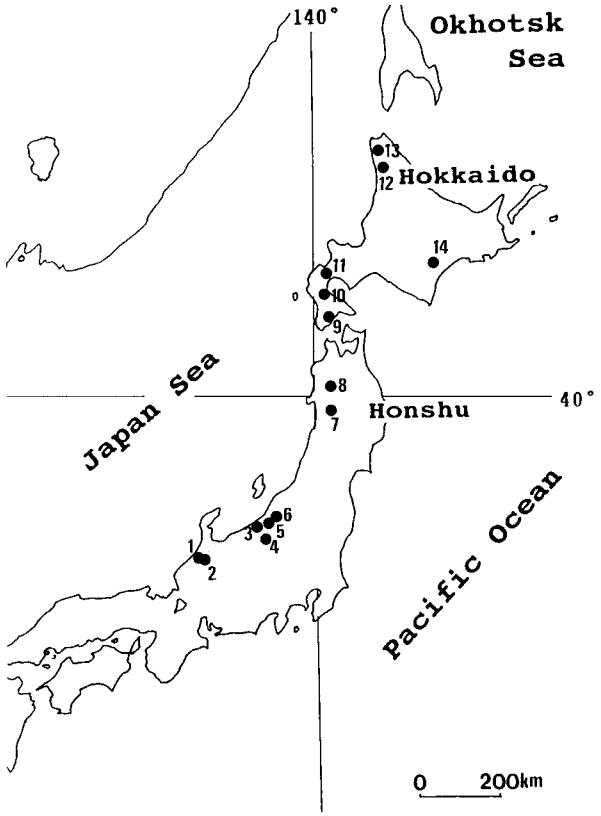

Figure 1. Fossil locality of the Plio-Pleistocene *Trophonopsis* in Japan.

hoku University (IGPS), National Science Museum (NSMT), Zoological Institute of Russian Academy of Science (ZISPb) and Dr. K. Baba's (Keio Gijuku Yochisha) private collection.

I have measured or evaluated the following characters: shell height, diameter, spire height, length of siphonal canal, number and shape of axial ribs on the penultimate and body whorls, number of spiral cords on the penultimate and body whorls and angulation of shoulder.

Systematic descriptions

Family Muricidae Rafinesque, 1815
Subfamily Trophoninae Cossmann, 1903
Genus ***Trophonopsis*** Bucquoy, Dautzenberg and Dollfus, 1882

Type species.—*Murex muricatus* Montagu, 1803.

Remarks.—There is much confusion about the classification of Trophoninae. Based on Radwin and D'Attilio (1976), Egorov (1993) and Houart (2001), *Trophonopsis* is characterized by narrow or broad axial ribs, narrow spiral cords, smooth or rarely denticulated inner surface of outer lip, long and broadly open siphonal canal. This genus is distinguished from *Boreotrophon* Fischer, 1884 by usually having distinct spiral cords. *Nipponotrophon* Kuroda and Habe in Kuroda *et al*., 1971 differs from *Trophonopsis* in its axial ribs with spines at the intersections with spiral cords as well as at the shoulder. *Abyssotrophon* Egorov, 1993 has a thin fragile shell, a keel or some distinct spiral cords and many thin axial riblets.

McLean (1996) proposed a new genus *Scabrotrophon* for the eastern Pacific trophonines which had been described as *Trophonopsis* or *Nipponotrophon* by Radwin and D'Attilio (1976) and others. Houart (2001) used this genus name for *Trophon fabricii* from the northern Atlantic region. According to McLean (1996), *Trophonopsis* differs from his new genus by having more dominant axial than spiral sculpture in early whorls, prominent ribs overriden by spiral sculpture and labial denticles. Despite his restricted usage of *Scabrotrophon* to the eastern Pacific species, all northwestern *Trophonopsis* must be included in his concept of *Scabrotrophon*. However, as described below, the northwestern Pacific species include forms with strong axial ribs such as *T. uyemurai* Yokoyama, 1926a. The type species of *Trophonopsis* in the Mediterranean Sea has small denticles at the inner side of the outer lip. By contrast, few species with such denticles live in the north Atlantic region. As shown in Amano and Vermeij (2003), presence of the denticles in muricids depends on climate and predation. Additionally, *Trophonopsis* aff. *densicostata* Golikov in Golikov and Scarlato, 1985 as described later has weak crenulations at the outer lip. A definitive taxonomic solution will require detailed examination of European and north Pacific fossils and molecular data. In this paper, I use the genus name *Trophonopsis* for the northwestern Pacific species.

Trophonopsis okutanii Noda, 1991 described from the Pliocene Yonabaru Formation in Okinawa Island shares with *Abyssotrophon soyoae* (Okutani, 1959) one keel on each whorl, two spiral cords on the last whorl and many thin axial plates. Some other fossil and Recent species also have rather strong spiral cords and many thin axial riblets. They include *Trophon acharya* Yokoyama, 1926 from the lower Pleistocene Sawane Formation of Sado Island, *Trophonopsis delicata* Kuroda, 1953 from southeast of Ishinomaki (143 m in depth), and *Trophonopsis crystallina* Kuroda, 1953 from off Miyako (177 m in depth). *Trophonopsis crystallina* has already been treated as a species of *Abyssotrophon* by Tsuchiya (2000). I agree

with Tsuchiya's opinion and tentatively classify all the species above in *Abyssotrophon*, not *Trophonopsis*.

There is uncertainty about the generic position of *Trophon* (*Boreotrophon*) *scitulus* Dall, 1891 (including *Trophonopsis scitula emphatica* Habe and Ito, 1965) and *Trophon* (*Boreotrophon*) *elegantulus* Dall, 1907. Egorov (1993) treated *Trophonopsis emphatica* as a separate species under the genus *Trophonopsis* and classified *Trophon scitulus* and *T. elegantulus* as *Nipponotrophon* and *Boreotrophon* respectively. Tiba and Kosuge (1985b) included *Trophonopsis scitula emphatica* in *Nipponotrophon scitulus* and treated *T. elegantulus* as a species of *Nipponotrophon*. Fossils of these two species were also described by Baba (1990) from the Pleistocene deposits of Japan. They should be included in *Nipponotrophon* because they have spines at all intersections of axial ribs and spiral cords; Tiba and Kosuge (1985b) and Tsuchiya (2000) reached the same conclusion.

Trophon suborpheus was proposed by Yokoyama (1926b), based on a specimen from the lower Pleistocene Sawane Formation of Sado Island. Hatai and Nisiyama (1952) included this species in *Trophonopsis*. However, judging from the type specimen (UMUT CM no. 23114), this species must be included in Ocinebrinae Cossmann, 1903 because of its partly sealed siphonal canal.

Houart (1994) allocated *Trophonopsis densicostata* discussed below to the genus *Nipponotrophon* without giving any reasons. The specimen illustrated by him as *N. densicostata* differs from the type specimen of *T. densicostata*, especially in its sculpture. From the outline and the sculpture of the holotype specimen, *T. densicostata* should be assigned to the genus *Trophonopsis*.

Consequently, Plio-Pleistocene *Trophonopsis* in Japan consists of seven species: *T. kamchatkana* (Dall, 1902), *T. uyemurai* (Yokoyama, 1926a), *T. sasae* Sawada, 1962, *T. vermeiji* Amano, sp. nov., *T.* aff. *densicostata* Golikov in Golikov and Scarlato, 1985, *T.* aff. *undocostata* Golikov and Sirenko, 1992 and *T.* sp.

Trophonopsis kamchatkana (Dall, 1902)

Figures 2.1a–b

Boreotrophon (*Trophonopsis*) *kamchatkanus* Dall, 1902, p. 541–542.
Neptunea (*Trophonopsis*) *kamchatkanus* Dall. Dall, 1921, p. 111, pl. 10, fig. 7.
Trophon kamchatkanus Dall. Oldroyd, 1927, p. 41, pl. 30, fig. 10.
Trophonopsis kamchatkanus (Dall). Kuroda, 1953, p. 189, 199; Habe and Ito, 1965, p. 37, text-fig. 13; Golikov and Scarlato, 1971, p. 194–195, text-fig. 6; Golikov and Gulbin, 1977, p. 225–226; Abbott, 1974, p. 191, text-fig. 2002; Golikov and Scarlato, 1985, p. 423; Tiba and Kosuge, 1985a, p. 15-29–15-30.
Boreotrophon kamchatkanus Dall. Kosuge, 1972, pl. 8, fig. 6.
Trophonopsis sp. Baba, 1990, p. 155–156, pl. 9, fig. 14.
Trophonopsis kamchatkana (Dall, 1902). Tsuchiya , 2000, p. 401, pl. 199, fig. 190; Higo *et al*., 2001, p. 62, fig. G2223.

Diagnosis.—Medium-sized *Trophonopsis* having an angulated shoulder with a keel, 17–23 low axial ribs, 3–8 spiral cords, many granulations at the intersections of axial ribs and spiral cords.

Holotype.—Height 25 mm, diameter 12 mm, USNM no. 109178.

Type Locality.—Southeast coast of Kamchatka (96 fathoms).

Material examined.—One specimen described by Baba (1990) as *Trophonopsis* sp. (Dr. Baba's collection no. 50176; Height = 10.7 mm, diameter = 5.4 mm) from the middle Pleistocene Sanuki Formation in Chiba Prefecture was reexamined.

Description.—Shell small for the species, consisting of four teleoconch whorls and 1.5 smooth protoconch whorls. Body whorl large, occupying half of shell height. Shoulder more or less angulated with keel; area above shoulder gently sloping without spiral cords. Spiral cords narrow but distinct, three on penultimate whorl and six on body whorl. Axial ribs thin, strong, 15 on penultimate whorl and 17 on body whorl including keel. Weak granulations formed at intersections of spiral cords and axial ribs, pointed at shoulder. Basal part of body whorl ornamented with only weak growth lines. Aperture pyriform; outer lip thin and smooth; inner lip with thin callus. Siphonal canal long, occupying about one-third of shell height, somewhat turned to left.

Remarks.—*Trophonopsis* sp. described by Baba (1990) can be assigned with *T. kamchatkana* because of its shell sculpture and form of the siphonal canal despite its pointed shoulder. Generally, trophonine gastropods vary in the expression of spines on the shoulder. One imperfect juvenile specimen consisting of three teleoconch whorls and two whorls of protoconch (JUE no. 15815; Height = 6.5 mm +, diameter = 3.3 mm) was also collected from the lower Pleistocene Setana Formation. The specimen is covered by granulations on its surface, four spiral cords and 15 axial ribs on the body whorl. The number of cords and ribs is less than in adult specimens, due to its small size. These are the first fossil records of *T. kamchatkana*.

When he described the Recent fauna around Otsuchi Bay, Iwate Prefecture, Tsuchida (1991) identified trophonine specimens as *Trophonopsis* (*Trophonopsis*) *delicatus* Kuroda. However, his specimens have strong axial ribs and granulations at the intersections of axial ribs and spiral cords as in *T. kamchatkana*.


1a
1b
2a
3a
3b
4
5a
6
2b
5b
7
8
10
9
11a
12
13
11b

Table 1. Measurement of *Trophonopsis uyemurai*.

Loc.	Formation	Number of specimens	H (mm)[1)]	D (mm)[2)]	NSP[3)]	NSB[4)]	NAP[5)]	NAB[6)]
1	Omma F.	JUE no. 15801-1	42.1	—	5	17	—	17
1	Omma F.	JUE no. 15801-2	38.5	—	6	25	14	16
2	Omma F.	JUE no. 15802	44.0	22.3	6	25	14	17
3	Nadachi F.	JUE no. 15235	30.6	18.2	5	22	18	21
4	Seguchi F.	JUE no. 15803	19.0	11.6	—	12+	—	17
5	Ikenosawagawa F.	JUE no. 15804	41.3	19.8	5	22	—	20
6	Shiroiwa F.	JUE no. 15805	—	—	5	—	17	16
7	Tentokuji F.	JUE no. 15806-1	22.8	14.1	4	18	18	19
7	Tentokuji F.	JUE no. 15806-2	22.0	15.3	4	—	15	19
7	Tentokuji F.	JUE no. 15806-3	20.2	13.7	—	17	16	22
8	Sasaoka F.	JUE no. 15807	28.7	17.9	5	—	—	22
12	Yuchi F.	JUE no. 15808-1	35.1	20.4	5	17	—	23
12	Yuchi F.	JUE no. 15808-2	42.9	22.7	5	17	—	19
12	Yuchi F.	JUE no. 15808-3	34.4	22.5	5	17	17	24
13	Sarabetsu F.	JUE no. 15809	20.4	11.5	5	15	17	18
14	Osarushinai F.	JUE no. 15810-1	26.3	13.1	4	19	15	—
14	Osarushinai F.	JUE no. 15810-2	35.6	20.5	—	17	—	17

[1)] Height, [2)] Diameter, [3)] Number of spiral cords on penultimate whorl, [4)] Number of spiral cords on body whorl, [5)] Number of axial ribs on penultimate whorl, [6)] Number of axial ribs on body whorl.

His illustrated specimen slightly differs from *T. kamchatkana* by having many more axial ribs (27–28) and a high spire. It may be considered that the specimen is an extreme form of *T. kamchatkana*.

Trophonopsis barvicensis (Johnston, 1825) from northern Europe, the Azores and Morocco resembles *T. kamachatkana* in having a similar shell outline and number of spiral cords (6–7 on the last whorl), but *T. barvicensis* has fewer axial ribs (12–15 on the last whorl) than *T. kamchatkana*.

Stratigraphic and geographic distribution.—Early Pleistocene Setana Formation in Hokkaido. Middle Pleistocene Sanuki Formation in Chiba Prefecture. Recent; western part of Bering Sea, Kurile Islands, Hokkaido, Kashima-nada and northern Japan Sea (95–1530 m in depth) (Egorov, 1993; Tiba and Kosuge, 1985a; Higo *et al*., 1999; Tsuchiya, 2000).

Trophonopsis uyemurai (Yokoyama, 1926)

Figures 2.2a–b, 2.4–2.13

Fusus uyemurai Yokoyama, 1926a, p. 238–239, pl. 30, fig. 4.
Trophon toyamai Hatai and Nisiyama, 1938, p. 256–257, figs. 3, 4.
Trophon kagaensis Hatai and Nisiyama, 1939, p. 153, pl. 9, figs. 8, 9, 13, 14; Ogasawara, 1977, pl. 21, figs. 5a–b; Matsuura, 1992, pl. 5–14 (1).
Trophonopsis kagaensis Hatai and Nisiyama. Kaseno and Matsuura, 1965, pl. 3, fig. 3.
Boreotrophon uyemurai (Yokoyama). Kanno *et al*., 1980, p. 15–16, pl. 4, figs. 4a–b; Noda *et al*., 1984, pl. 5, figs. 1a–b, 2a–b.
Trophonopsis kagaensis (Hatai and Nisiyama). Matsui, 1985, p. 174, pl. 22, fig. 13; Amano *et al*., 1988, p. 68, pl. 2, figs. 16a–b; Nemoto and O'Hara, 2005, pl. 2, figs. 11a, b.
Boreotrophon kagana (Hatai and Nisiyama). Goto *et al*., 1993, p. 17, pl. 11, figs. 10a–b.

Diagnosis.—Large *Trophonopsis* with slightly depressed area above shoulder, 16–25 stout axial ribs and 15–25 strong spiral cords.

Holotype.—Height 33 mm, diameter 16.2 mm, UMUT CM no. 23016.

Type Locality.—Riverside cliff about 11.5 km upstream on the Uttsu River, Embetsu Town, Hokkaido.

Material examined.—Twenty-two specimens from 11 localities collected by hand were examined. Among them, seventeen rather well preserved shells were measured (Table 1). Additionally, the type specimens

Figure 2. Plio-Pleistocene *Trophonopsis* and its compared species (1). **1a–b.** *Trophonopsis kamchatkana* (Dall), height = 10.7 mm, Dr. Baba's no. 50176, illustrated as *T.* sp. by Baba (1990). **2a–b, 4–13.** *Trophonopsis uyemurai* (Yokoyama); 2a–b, Holotype of *Trophon kagaensis* Hatai and Nisiyama, height = 26.8 mm, IGPS no. 62422; 4, 10, Specimens collected from the Yuchi Formation from which *Fusus uyemurai* Yokoyama was originally described, 4, height = 42.9 mm, JUE no. 15810-2, 10, height = 34.4 + mm, JUE no, 15810-3, Loc. 12; 5a–b, 6, Type specimens of *Trophon toyamai* Hatai and Nisiyama, 5a–b, Holotype, height = 42.8 mm, IGPS no. 7844, 6, Topotype, height = 43.5 mm, IGPS no. 7372; 7, 8, First specimens collected from eastern Hokkaido, 7, height = 35.6 mm, JUE no. 15810-2, 8, height = 26.3 mm, JUE no. 15810-1, Loc. 14; 9, height = 20.4 mm, JUE no. 15809, Loc. 13; 11a, b, height = 44.0 mm, JUE no. 15802, Loc. 2; 12, Slightly deformed specimen, height = 41.3 mm, JUE no. 15804, Loc. 5; 13, height = 33.9 + mm, JUE no. 15807-4, Loc. 7. **3a–b.** *Trophonopsis nodulosa* Golikov, Holotype, height = 24.4 mm, ZISPb no. 33810/1, off Vzmorie village, South Sakhalin.

Table 2. Measurements of the type specimens of *Fusus uyemurai*, *Trophon toyamai*, and *T. kagaensis*.

"Species name"	Formation	Number of specimens	Type	H (mm)[1)]	D (mm)[2)]	NSP[3)]	NSB[4)]	NAP[5)]	NAB[6)]
Fusus uyemurai	Yuchi F.	UMUT CM no. 23016	Holotype	33.0	16.2	3	ca. 15	17	20
Trophon toyamai	Tentokuji F.?	IGPS no. 7844	Holotype	42.8	27.0	4	17	17	25
	Tentokuji F.?	IGPS no. 7372	Topotype	43.5	24.3	4	17	17	25
	Tentokuji F.?	IGPS no. 7372	Topotype	28.9	16.6	4	17	18	22
Trophon kagaensis	Omma F.	IGPS no. 62422	Holotype	26.8	17.9	6	18	17	17
	Omma F.	IGPS no. 62422	Paratype	19.3	11.5	4	18	12	14

[1)] Height, [2)] Diameter, [3)] Number of spiral cords on penultimate whorl, [4)] Number of spiral cords on body whorl, [5)] Number of axial ribs on penultimate whorl, [6)] Number of axial ribs on body whorl.

of *Trophon toyamai* Hatai and Nisiyama, 1938 (IGPS no. 7844, 7372) and *Trophon kagaensis* Hatai and Nisiyama, 1939 (IGPS no. 62422) were also reexamined (Table 2).

Description.—Shell large for the genus, attaining 44.0 mm in height, thick, ovate-fusiform, with six teleoconch whorls and 1.5 smooth protoconch whorls. Body whorl large, occupying about three-fifths of total shell height. Shoulder more or less angulated; area above shoulder flat or slightly depressed with only axial sculpture. Spiral cords distinct, rounded at top, 3–6 (commonly 5) on penultimate whorl 15–25 (commonly 17) on body whorl and with nearly equal interspaces. Axial ribs rude and stout, sometimes sharp at top, 12–19 (commonly 17) on penultimate whorl, 15–25 on body whorl with wider interspaces. Basal part of body whorl ornamented with spiral cords. Aperture ovate; inner side of outer lip smooth; inner lip with thin callus. Siphonal canal long, occupying about one-third of shell height, somewhat turned to left.

Remarks.—*Trophon toyamai* was established by Hatai and Nisiyama (1938), based on specimens from the Wakimoto (= Tentokuji?) Formation in Akita Prefecture. They distinguished *T. toyamai* from *Fusus uyemurai* in that *T. toyamai* has many more spiral cords and axial ribs (Table 2). *T. kagaensis* Hatai and Nisiyama, 1939 from the Omma Formation in Ishikawa Prefecture was distinguished from *F. uyemurai* by having a more angulated shoulder, more elevated axial ribs and more numerous and stronger cords. Unfortunately, the type specimen of *F. uyemurai* is now missing. However, a specimen from the Yuchi Formation from which the type of *F. uyemurai* was obtained has a similar number of spiral cords and axial ribs to *T. toyamai* (Tables 1, 2). Generally speaking, it is difficult to separate any trophonine gastropod species by the elevation of axial ribs because of their wide range of variation. *T. kagaensis* has a similar number of spiral cords to the Yuchi specimen (Tables 1, 2). For these mentioned reasons, both *T. toyamai* and *T. kagaensis* are synonyms of *F. uyemurai* (= *Trophonopsis uyemurai*).

Trophonopsis nodulosa Golikov in Golikov and Scarlato, 1985 (Figures 2.3a–b) now living in the Okhotsk Sea and Tatar Strait (57–103 m in depth) is similar to *T. uyemurai* in having 16 stout axial ribs on the body whorl and long siphonal canal. However, the holotype of *T. nodulosa* (ZISPb no. 33810/1) is smaller (24.4 mm in height, 13.4 mm in diameter) and has fewer spiral cords (13 on the body whorl) than *T. uyemurai*. Moreover, *T. nodulosa* lacks a depressed area above the shoulder and spiral cords on the lower part of the base. Despite these differences, *T. nodulosa* may be a descendant of *T. uyemurai* because of its stout axial ribs which are not observed in any other Recent trophonine species.

Stratigraphic and geographic distribution.—Pliocene: Nadachi, Seguchi, Ikenosawagawa, and Shiroiwa Formations in Niigata Prefecture, Tentokuji and Sasaoka Formations in Akita Prefecture, Yuchi and Sarabetsu Formations in Hokkaido, Tomioka Formation in Fukushima Prefecture. Early Pleistocene: Omma Formation in Ishikawa Prefecture and Osarushinai Formation in Hokkaido.

Trophonopsis sasae Sawada, 1962

Trophonopsis (*Boreotrophon*) *sasae* Sawada, 1962, p. 50–51, pl. 2, fig. 12–13.

Diagnosis.—Medium-sized *Trophonopsis* with 10 axial ribs and 10–11 very weak spiral cords on body whorl, and short siphonal canal.

Holotype.—Height 23.0 mm, diameter 10.5 mm, MEMIT no. 60001.

Paratype.—Height 23.5 mm, diameter 12.0 mm, MEMIT no. 60002.

Type Locality.—Roadside cliff, 1,200 m NNW of Kitatoyotsu railway station, Oshamanbe Town, Hokkaido (Loc. 39 of Sawada, 1962).

Original description.—"Shell medium in size, elongate ovate-fusi-form, with rather long curved anal canal. Protoconch with a globose nucleus and two and a

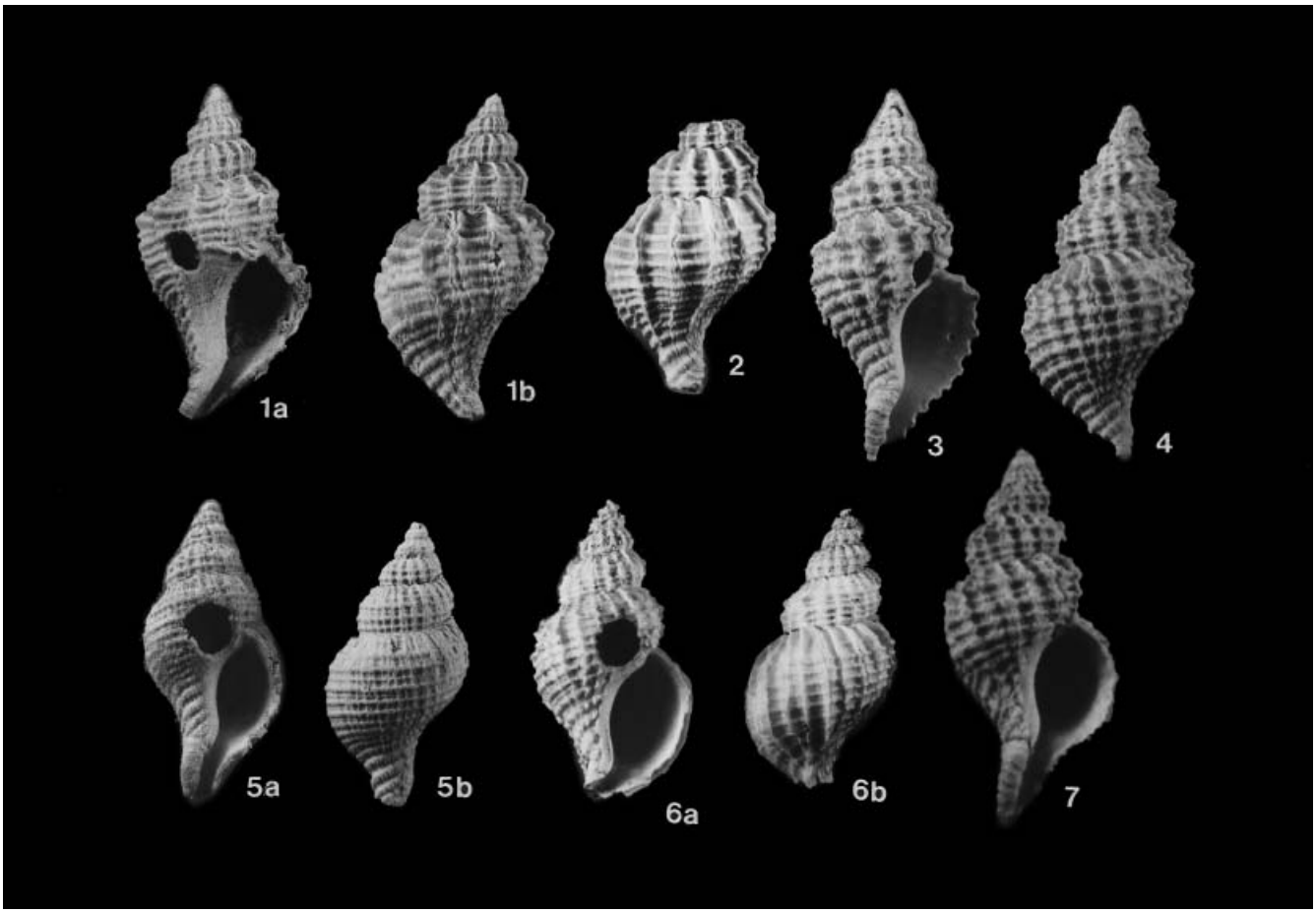

Figure 3. Plio-Pleistocene *Trophonopsis* and its compared species (2). **1a–b, 2.** *Trophonopsis vermeiji* Amano, sp. nov.; 1a–b, Holotype, height = 17.2 mm, JUE no. 15811; 2, Paratype, height = 19.7 + mm, JUE no. 15812-1; Loc. 9. **3, 4, 7.** *Trophonopsis* aff. *densicostata* Golikov; 3, height = 14.9 mm, JUE no. 15816-2; 4, height = 14.2 mm, JUE no. 15816-3; 7, height = 14.9 mm, JUE no. 15816-5; Loc. 11. **5a–b.** *Trophonopsis* aff. *undocostata* Golikov and Sirenko, height = 15.9 mm, JUE no. 15818, Loc. 10. **6a–b.** *Trophonopsis* sp., height = 20.0 mm, JUE no. 15817-1, Loc. 10.

half volutions which are smooth on younger but sculpture in adult with sharp, rounded varices with no angle at shoulder, ten varices on the body whorl, sharp separated widely from one another; penultimate whorl with well defined longitudinals and fine spiral interstitial striations; four weak spirals on body whorl among which abapical one weakest and appearing rather later, base with six to seven spirals. Aperture elongately oval in form, canal rather long and curved, height of aperture and canal subequal with that of spire.''

Remarks.—The type material and type locality may be lost or destroyed. A few trophonine specimens were collected from Loc. 10 near the type locality of this species, described as *Trophonopsis* sp. in this paper. However, no specimens resembling *T. sasae* can be found among them.

Trophonopsis sasae resembles *T. fabricii* (Beck in Möller, 1842) living in Iceland, Greenland to New England in having similar number (9–10 in *T. fabricii*) of lamellate axial ribs. However, *T. fabricii* has fewer spiral cords (6–8) and a longer siphonal canal than *T. sasae*.

Stratigraphic and geographic distribution.—Early Pleistocene Chinkope (= Setana) Formation (only from the type locality).

Trophonopsis vermeiji Amano, sp. nov.

Figures 3.1a–b, 3.2

Diagnosis.—Medium *Trophonopsis* with surface cancellated by 11–15 round-topped spiral cords and 12–14 low platy axial ribs, slightly angulated shoulder

Table 3. Measurements of *Trophonopsis vermeiji* Amano, sp. nov.

Loc.	Formation	Number of specimens	Type	H (mm)[1)]	D (mm)[2)]	NSP[3)]	NSB[4)]	NAP[5)]	NAB[6)]
9	Tomikawa F.	JUE no. 15811	Holotype	17.2	9.2	6	13	14	12
9	Tomikawa F.	JUE no. 15812-1	Paratype	19.7+	11.5	4	14	12	12
9	Tomikawa F.	JUE no. 15812-2	Paratype	8.6	4.8	2	11	14	14
9	Tomikawa F.	JUE no. 15813		16.7+	9.8	4	15	—	12
11	Setana F.	JUE no. 15814		10.5	5.4	4	13	11	13
T[7)]	Daishaka F.	IGPS no. 15804		16.6	6.7	5	14	11	12

[1)]Height, [2)]Diameter, [3)]Number of spiral cords on penultimate whorl, [4)]Number of spiral cords on body whorl, [5)]Number of axial ribs on penultimate whorl, [6)]Number of axial ribs on body whorl, [7)]Tsurugasaka, Aomori City, Aomori Prefecture.

and short siphonal canal turned to left.

Holotype.—JUE no. 15811 (*see* also Table 3).

Paratype.—JUE nos. 15812-1, JUE no. 15812-2 (*see* also Table 3).

Type Locality.—Riverside cliff about 400 m upstream on the Tomikawa River, Kamiiso Town, Hokkaido.

Material examined.—Other than the type material, four specimens from three formations were examined. All dimensions are shown in Table 3.

Description.—Shell medium for the genus, attaining 19.7 mm in height, thick, ovate-fusiform, with five teleoconch whorls and two smooth protoconch whorls. Body whorl large occupying about three-fourth of shell height. Shoulder slightly angulated with a keel; area above shoulder wide and gently sloping with one round-topped spiral cord and axial ribs. Spiral cords distinct, rounded at top, 2–6 (usually 4) on penultimate whorl, 11–15 on body whorl including a keel as well as one cord above shoulder. Interspaces of cords wider than cords themselves above shoulder but narrow below it. Axial ribs low but platy, 11–14 on penultimate whorl, 12–14 on body whorl with wider interspaces. Basal part of body whorl ornamented with spiral cords and weak axial ribs. Aperture ovate; outer lip smooth; inner lip with thin callus. Siphonal canal short, turned to left.

Remarks.—*Trophonopsis vermeiji* sp. nov. can be distinguished from *T. sasae* by its much lower spire and more numerous axial ribs and spiral cords. The spiral cords are distinct and form a cancellated surface in this new species.

Tsuchiya (2000) also illustrated a cancellated specimen as *Trophonopsis concinnus* A. Adams, 1863. His species can be easily distinguished from *T. vermeiji* by its less numerous spiral cords (two on the penultimate and seven on the body whorl) and a straight siphonal canal. The Recent *Trophonopsis* sp. living off Etorofu and Habomai Islands (60–400 m) also resembles this new species in size (max. height = 25.4 mm), number of axial ribs on the body whorl (13–18) and cancellated surface. However, the Recent species differs from *T. vermeiji* by its slightly more slender shell, lack of angulation at shoulder and less numerous spiral cords on the penultimate whorl (3). Judging from the outline of the shell and ornamentation in Tsuchiya's *T. concinna* and the *T.* sp. from Etorofu and Habomai Islands, these Recent specimens may represent descendants of the new species.

Trophonopsis vermeiji differs from *T. fabricii* by having more numerous lamellate axial ribs (9–10 in *T. fabricii*) and left-turned siphonal canal.

Stratigraphic and geographic distribution.—Early Pleistocene: Tomikawa and Setana Formations in Hokkaido, and Daishaka Formation in Aomori Prefecture.

Etymology.—This new species is named after Professor Geerat J. Vermeij, University of California at Davis who has contributed to the taxonomy of Muricidae as well as the theory of evolution.

Trophonopsis aff. ***densicostata*** Golikov in Golikov and Scarlato, 1985

Figures 3.3, 3.4, 3.7

Trophonopsis sp. Tsuchida, 1991, p. 3, pl. 1, fig. 4.

Material examined.—Eight specimens from Loc. 11 were examined and measured (Table 4).

Description.—Shell small (maximum height, 14.9 mm), slender, consisting of six teleoconch whorls and 1.5 to 2 smooth protoconch whorls. Spire high, occupying about half of shell height. Shoulder more or less angulated with keel; area above shoulder gently sloping with one spiral cord and axial ribs. Surface cancellated by spiral cords and axial ribs. Spiral cords distinct, round-topped, three to six on penultimate whorl and 13–15 on body whorl, with nearly equal or narrower interspaces. Axial ribs semitransparent, low

Table 4. Measurements of *Trophonopsis* aff. *densicostata*.

Number of specimens	H (mm)[1)]	D (mm)[2)]	NSP[3)]	NSB[4)]	NAP[5)]	NAB[6)]
JUE no. 15816-1	13.8	6.1	6	14	15	18
JUE no. 15816-2	14.9	6.8	5	13	14	17
JUE no. 15816-3	14.2	6.4	5	14	16	18
JUE no. 15816-4	13.5	6.0	6	15	14	17
JUE no. 15816-5	14.9	6.8	5	13	14	17
JUE no. 15816-6	11.9	5.0	5	14	14	16
JUE no. 15816-7	11.5+	5.5	4	14	13	18
JUE no. 15816-8	10.5	4.8	3	13	11	10

[1)] Height, [2)] Diameter, [3)] Number of spiral cords on penultimate whorl, [4)] Number of spiral cords on body whorl, [5)] Number of axial ribs on penultimate whorl, [6)] Number of axial ribs on body whorl.

and platy, 11–15 on penultimate whorl and 10–18 on body whorl including keel. Basal part of body whorl sculptured by strong spiral cords and weak axial ribs. Aperture ovate; outer lip rather thick and its inner side weakly crenulated; inner lip with thin callus. Siphonal canal moderate, turned to left.

Remarks.—Most characteristics of this species are shared with *Trophonopsis densicostata* Golikov in Golikov and Scarlato (1985) known from the Okhotsk Sea (75 m depth). *T. densicostata* is characterized by a slender outline, a high spire, angulated whorls with a keel, 8–10 spiral cords and 10–14 semitransparent axial ribs. The number of spiral cords in this fossil species is slightly more than in *T. densicostata*. Because there are so few fossil specimens, the number of spiral cords may inreality have varied enough to match the number in Recent shells. Thus, the fossil species is slightly different from *T. densicostata* in having a smaller shell (height of the type specimen of *T. densicostata* = 50 mm) and a shorter siphonal canal. However, such slight differences do not make a convincing case for separating these few fossil specimens from *T. densicostata* as a new species.

Tsuchida (1991) described *Trophonopsis* sp. from the coarse-grained or gravelly bottom at 80–120 m depth in Otsuchi Bay, Iwate Prefecture. His species is small (height = about 16 mm), slender, angulated, with six whorls without protoconch, a high spire and short siphonal canal turned to left. The surface is cancellated with 9–10 spiral cords on the body whorl and thin axial ribs. Judging from the above features, the Otsuchi specimens are identical to the fossil species.

The outline of *Trophonopsis* aff. *densicostata* is also similar to *T. maltzani* (Kobelt and Küster, 1878) from the eastern Pacific. The latter species is up to 30–45 mm in height and has fewer axial ribs (10–12) than *T.* aff. *densicostata*. Moreover, *T.* aff. *densicostata* has a siphonal canal turned to the left while *T. maltzani* has a straight canal.

Stratigraphic and geographic distribution.—Early Pleistocene Setana Formation in Hokkaido. Recent, mouth of Otsuchi Bay (80–120 m in depth).

Trophonopsis aff. ***undocostata*** Golikov and Sirenko, 1992

Figures 3.5a–b

Material examined.—One specimen from Loc. 10. Height 15.9 mm, diameter 7.5 mm, JUE no. 15818.

Description.—Shell small, slender, consisting of four teleoconch whorls and two smooth protoconch whorls. Body whorl somewhat large, occupying two-thirds of shell height. Shoulder well rounded. Surface cancellated by spiral cords and axial ribs. Spiral cords distinct, round-topped, four on penultimate whorl and 14 on body whorl, with nearly equal or wider interspaces. Axial ribs very low but distinct, 23 on penultimate whorl and 34 on body whorl. Basal part of body whorl sculptured by strong spiral cords and growth lines. Aperture ovate; outer lip rather thick; inner lip with thin callus. Siphonal canal moderate and straight.

Remarks.—This species resembles *Trophonopsis undocostata* Golikov and Sirenko, 1992 from off the Kurile Islands (140 m depth) in its similar number of axial ribs and spiral cords (13 spiral cords and 36–54 axial ribs on body whorl) and a large body whorl. According to the original description, the maximum size of *T. undocostata* is 23 mm in height but the holotype is only 7.8 mm in height. Thus, the size of this fossil species is included in the range of *T. undocostata*. However, the fossil species differs slightly from the Recent one by its weak spiral cords and straight as well as narrow siphonal canal. Having only one specimen from one locality prevents me from establishing a new species.

Stratigraphic and geographic distribution.—Early Pleistocene Setana Formation in Hokkaido.

Table 5. Species characteristics of the Plio-Pleistocene *Trophonopsis* in Japan.

Species	H (mm)[1)]	D (mm)[2)]	AS[3)]	NSB[4)]	NAB[5)]	Depth (m)[6)]	Geologic range
T. uyemurai	44.0	22.3	++	15–25	15–25	–	Plio.-E. Pleist.
T. sasae	23.0	10.5	–	10–11	10	–	E. Pleist.
T. vermeiji	19.7	11.5	+	11–15	12–14	–	E. Pleist.
T. sp.	20.0	10.8	–	12–15	16–17	–	E. Pleist.
T. aff. *undocostata*	15.9	7.5	–	14	34	–	E. Pleist.
T. kamchatkana	10.7	5.4	+	3–8	17–23	95–1,530	E. Pleist.-Rec.
T. aff. *densicostata*	14.9	6.8	+	13–15	10–18	80–120	E. Pleist.-Rec.

[1)] Height, [2)] Diameter, [3)] Angulated shoulder, [4)] Number of spiral cords on body whorl, [5)] Number of axial ribs on body whorl, [6)] after Egorov (1993), Tiba and Kosuge (1985a), Higo *et al.* (1999), Tsuchiya (2000) and Tsuchida (1991).

Trophonopsis sp.

Figures 3.6a–b

Material examined.—Two specimens from Loc. 10. Height 20.0 mm, diameter 10.8 mm, JUE no. 15817-1; Height 16.3 mm, diameter 9.1 mm, JUE no. 15817-2.

Description.—Shell medium for the genus, attaining 20.0 mm in height, thick, ovate-fusiform, with six teleoconch whorls. Body whorl large, occupying about two-thirds of shell height. Shoulder well rounded. Spiral cords distinct but low, rounded at top, 6 on penultimate whorl, 12–15 on body whorl. Interspaces of cords wider than cords themselves. Axial ribs semitransparent and platy, 16–17 on penultimate whorl, 14–21 on body whorl with wider interspaces. Aperture ovate; outer lip smooth; inner lip with thin callus. Siphonal canal short, partly broken, distinctly turned to left.

Remarks.—This species is similar to *Trophonopsis sasae* in having a rounded shoulder, platy axial ribs and a short siphonal canal. However, this species can be distinguished from *T. sasae* by having strong and more numerous spiral cords (10–11 in *T. sasae*) and more numerous axial ribs (10 in *T. sasae*).

Trophonopsis vermeiji resembles this species in its similar number of spiral cords. The slightly angulated whorl and low, less numerous axial ribs of *T. vermeiji* further distinguish it from *T.* sp.

Having only two specimens from one locality precludes me from naming a new species.

Stratigraphic and geographic distribution.—Early Pleistocene Setana Formation in Hokkaido.

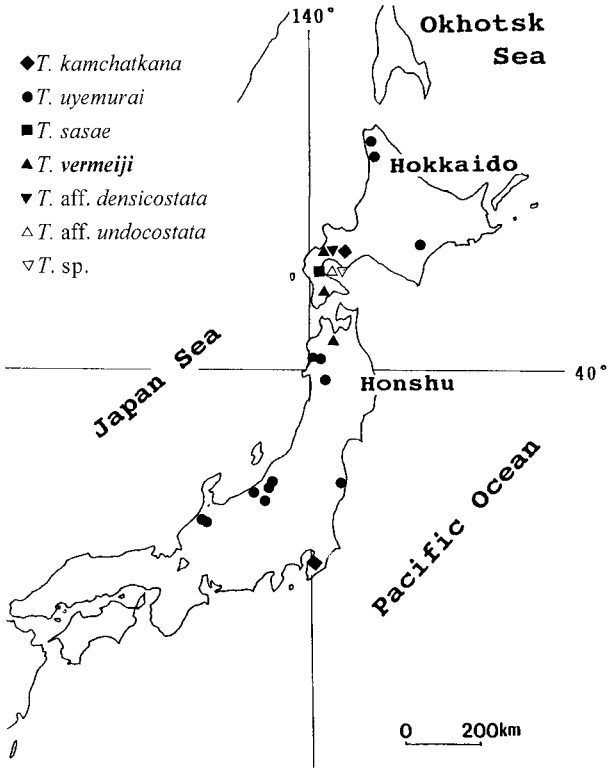

Figure 4. Distribution of the Plio-Pleistocene *Trophonopsis* in Japan.

Discussion

Summing up the stratigraphic range, the Japanese *Trophonopsis* diversified in the Early Pleistocene (Table 5). In the Pliocene, only one species, *T. uyemurai* flourished in the Japan Sea borderland (Figure 4). In the late Pliocene, this species expanded its distribution to the Pacific side. *T. uyemurai* became extinct at the end of the early Pleistocene. From this distribution pattern, *T. uyemurai* is a characteristic species of the Pliocene to early Pleistocene Omma-Manganji fauna (Otuka, 1939) in the Japan Sea borderland. This species has been collected from fine- to coarse-grained sandstone which was deposited in the upper sublittoral zone judging from the associated fauna from the same locality or formation (Chinzei, 1973; Noda *et al.*, 1982, 1984; Kitamura and Kondo, 1990; Amano, 1994).

In the early Pleistocene, two endemic species appeared around the Tsugaru Strait, which is a marginal area of the Japan Sea. *Trophonopsis sasae* and *T. vermeiji* are known only from southwestern Hokkaido and northernmost Honshu (Figure 4). Recent species from the northwest Pacific and Okhotsk Sea (or their ancestors) also appeared at this time; *T. kamchatkana*, *T.* aff. *densicostata* and *T.* aff. *undocostata* occurred only from the Setana Formation in southwestern Hokkaido. In the Setana stage, many boreal elements expanded their distribution southward into Hokkaido in conjunction with the reopening of the Bering Strait (Suzuki and Akamatsu, 1994). Such cooling caused the speciation at the marginal part of the Japan Sea and the appearance of the above-mentioned boreal-type species. *T. uyemurai* was still living at this time in the main part of the Japan Sea.

By the end of the early Pleistocene, *T. uyemurai*, *T. sasae* and *T. vermeiji* became extinct and *T.* aff. *undocostata* and *T.* sp. might have become extinct. As already pointed by Amano (2004), the upper and lower sublittoral species became extinct because of decreased salinity in the mostly enclosed Japan Sea. According to Egorov (1993), most trophonine species are stenohaline molluscs, living at salinity of 28–34‰. Climatologically, *T. uyemurai* lived in the mild- to cool-temperate zone (Ogasawara, 1994). The eastern Hokkaido population of *T. uyemurai* might have become extinct as a result of cooling at about 0.7 Ma (Suzuki and Akamatsu, 1994).

From the middle Pleistocene Sanuki Formation in Kanto Region, Pacific side of central Japan, only the species *Trophonopsis kamchatkana* has been collected. The scarcity of *Trophonopsis* of this age is due to the rarity of lower sublittoral deposits in Japan.

Consequently, the genus *Trophonopsis* diversified in the early Pleistocene in northern Japan, owing to the cooling event. This genus includes three extinct species (*T. uyemurai*, *T. sasae* and *T. vermeiji*) and two species not exactly identified (*T.* aff. *undocostata* and *T.* sp.). *T. kamchatkana* first appeared in the Japan Sea borderland and now lives in the western part of the Bering Sea, northern Pacific and northern Japan Sea. *T.* aff. *densicostata* also originated in the Japan Sea borderland and lives on the Pacific side of northeast Honshu. The pattern of these two species corresponds to the type B of Amano (2004). The distribution of *Trophonopsis* thus resembles that of the deep-water buccinids mentioned in the introduction.

It is noteworthy that the descendant species (*T. nodulosa*, "*T. concinna*" and *T. undocostata*) of the extinct species and the two surviving species (*T. kamchatkana* and *T.* aff. *densicostata*) are still living in and around the northern Japan Sea and the Okhotsk Sea. Recently, the lower sublittoral bivalve, *Limopsis oliveri* was described as a new species from the Okhotsk Sea by Amano and Lutaenko (2004). This species is a descendant of the Plio-Pleistocene *L. adamsiana* Yokoyama, 1920. Thus the Okhotsk Sea acts as a refuge for the descendants of many Plio-Pleistocene species that lived in the lower sublittoral zone of northern Japan.

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Appendix

List of localities

I collected some specimens of *Trophonopsis* fossils by hand from the following localities.

Loc. 1 River bank at about 1.1 km upstream of Sai-kawa River, Kanazawa City, Ishikawa Prefecture. 36°31′40″N, 136°41′11″E. Lower Pleistocene Omma Formation.

Loc. 2 Kami-Nakamachi, Kanazawa City, Ishikawa Prefecture. 36°30′56″N, 136°42′25″E. Lower Pleistocene Omma Formation.

Loc. 3 Cliff near Osuga Bridge, Joetsu City, Niigata Prefecture. (= Fossil locality of Amano *et al*., 1988) 37°8′34″N, 138°6′37″E. Pliocene Nadachi Formation.

Loc. 4 River bank at about 1.2 km to the east of Higashi-Yamadera, Joetsu City, Niigata Prefecture. 37°0′9″N, 138°21′26″E. Pliocene Seguchi Formation.

Loc. 5 River bank of Shibumi River near Tazawa-Ohashi Bridge, Tokamachi City, Niigata Prefecture. 37°8′11″N, 138°38′35″E. Pliocene Ikenosawagawa Formation.

Loc. 6 Shiroiwa, Ojiya City, Niigata Prefecture. 37°19′51″N, 138°49′54″E. Pliocene Shiroiwa Formation.

Loc. 7 Cliff along Yodogawa River, Awasegai, Daisen City, Akita Prefecture. 39°37′4″N, 140°18′54″E. PlioceneTentokuji Formation.

Loc. 8 Large cliff at 1 km upstream of Usui-zawa, Fujisato Town, Akita Prefecture. 40°15′34″N, 140°15′2″E. Pliocene Sasaoka Formation.

Loc. 9 River bank 400 m upstream on the Tomikawa River, Hokuto City, Hokkaido. 41°47′57″N, 140°37′18″E. Lower Pleistocene Tomikawa Formation.

Loc. 10 50 m upstream a small stream at Okawa, Yakumo Town, Hokkaido. (= Loc. 2 of Amano and Lutaenko, 2004) 42°20′18″N, 140°17′00″E. Lower Pleistocene Setana Formation.

Loc. 11 River bank 2.5 km upstream on the Soebetsu River, Kuromatsunai Town, Hokkaido. 42°41′2″N, 140°16′55″E. Lower Pleistocene Setana Formation.

Loc. 12 River bank 100 m downstream from Toyama Bridge on the Nijusangogawa River, Teshio Town, Hokkaido. 44°50′18″N, 141°53′55″E. Pliocene Yuchi Formation.

Loc. 13 Cliff at the back of Bakkai Shrine, Wakkanai City, Hokkaido. 45°18′23″N, 141°37′26″E. Pliocene Sarabetsu Formation.

Loc. 14 Large cliff near Inashibetsu Shrine, Makubetsu Town, Hokkaido. 42°54′6″N, 143°17′47″E. Lower Pleistocene Osarushinai Formation.