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New bivalve species of *Tucetona*, *Pycnodonte* and *Ezocallista* from the Lower Miocene Kurosedani Formation at Fukushima, Yatsuo-machi in Toyama City, central Japan

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Abstract

Sixty-nine molluscan species have been recorded from the Lower Miocene Kurosedani Formation at the hitherto unknown locality, Fukushima, Yatsuo-machi in Toyama City. Most species are shallow-water dwellers living in tropical and subtropical areas. Based on their occurrence, they were transported from shallow water to the deep sea. The assemblage includes three new bivalve species: *Tucetona tsudai* n. sp., *Pycnodonte* (*Phygraea*) *matsubarai* n. sp. and *Ezocallista toyamaensis* n. sp. Four species of *Tucetona* including *T. tsudai* n. sp. have been described from the Lower Miocene to lowest Middle Miocene in Honshu. The last occurrence of *Pycnodonte* was also in the Early to earliest Middle Miocene in Honshu. They disappeared from Honshu by the Miocene Climatic Transition (MCT). *Ezocallista* might have first appeared in the tropical area during the Miocene Climatic Optimum (MCO) and adapted to colder water since MCT or the Late Miocene Cooling (LMC).

Key words: Tucetona, Pycnodonte, Ezocallista, Early Miocene, MCO

1. Introduction

In the Miocene warm period, Miocene Climatic Optimum (MCO; ca. 17 to 14.7 Ma; Methner et al., 2020; Sangiorgi et al., 2021), many warm-water species extended their distribution northwards in Honshu and southwestern Hokkaido (e.g. Chinzei, 1981, 1986a, b; Itoigawa and Shibata, 1986; Ozawa et al., 1995). The age of the Kurosedani Formation in Toyama Prefecture was assigned to the Early Miocene (about 17–16 Ma; Yanagisawa, 1999; Sato et al., 2010; Nakajima et al., 2019) and corresponds to the MCO. Since Oyama (1950) found the mangrove

swamp fauna from the Kurosedani Formation in Toyama Prefecture, it has been recorded also from the Lower Miocene Kadonosawa Formation as the northernmost distribution (Matsubara et al., 2004). From the Kurosedani Formation, many shallow-water molluscan species have been found and studied by many authors (Oyama, 1950; Tsuda, 1959, 1960; Fujii, 1961; Shimizu and Kaneko, 1992; Kaneko and Goto, 1992, 1997; Kaneko, 1994; Matsuura, 2009). Recently, some chemosynthetic species were found from the upper part of the formation by the present authors (Amano et al., 2019). Recently, three new bivalve species of *Tucetona*, *Pycnodonte* and

Ezocallista were found from the hitherto unknown locality in the upper part of the formation along with many other molluscan species. In this paper, we describe these new species and discuss the significance of these species.

2. Geological setting and molluscan fauna

Many molluscan fossils were recovered from the right bank of the Ida River, about 200 m downstream from the Jusangoku Bridge in Fukushima, Yatsuo-machi, Toyama City (36°35'7"N, 137°8'31"E) by the river channel improvement in 2006. At this locality, the Lower Miocene Kurosedani and the Upper Pliocene Mita formations crop out and are contacted by the fault. The Kurosedani Formation herein consists of mudstone intercalating some beds of muddy coarsegrained sandstone yielding granules and shells.

From the formation at this locality, 69 molluscan species consisting of 34 gastropod, 34 bivalve, and one scaphopod species were identified (Table 1). Among them, 22 gastropods, one scaphopods, and 26 bivalves have been identified to species level. Nineteen gastropod, one scaphopod, and 21 bivalve species have been already described and illustrated by Tsuda (1959), Kaneko and Goto (1992, 1997) and Matsuura (2009) (Table 1). Nipponocrassatella osawanoensis (Tsuda, 1959), Pseudoxyperas osawanoense (Tsuda, 1959) and their significance have already been described and discussed by the authors (Amano et al., in press). The following four species are newly recorded from the Kurosedani Formation in this study; Homalopoma hidensis Itoigawa, 1960, Eocylichna habei Itoigawa, 1958, Calyptraea tubura Otuka, 1934, Compsomyax iizukai (Yokoyama, 1925). Homalopoma hidensis and Eocylichna habei were known from the Lower Miocene Shukunohora Sandstone of the Akeyo Formation in Gifu Prefecture (Itoigawa et al., 1981, 1982). Calyptraea tubura and Compsomyax iizukai are recorded from many Lower Miocene and lower Middle Miocene deposits in northeastern Honshu to southwestern Honshu (Itoigawa et al., 1974; Amano et al., 2004; Matsubara et al., 2014). Moreover, as mentioned above, three new bivalve species of Tucetona, Pycnodonte, and Ezocallista were found.

Table 1. Molluscan fossils from the Kurosedani Formation at Fukushima, Yatsuo-machi.N*= Number of specimens, PR*= previously recorded by some authors (see text).

Species	N*	PR**
Homalopoma hidensis Itoigawa	1	
Ethalia sp.	1	
Calliotoma aff. simane Nomura and Hatai	1	
Turcica sp.	1	
Ginebis osawanoensis (Tsuda)	27	+
Turritella (Hataiella) yoshidai Kotaka Calyptraea tubura Otuka	28 2	+
Crepidula jimboana Yokoyama	5	+
Euspira meisensis (Makiyama)	28	+
Glossaulax coticazae (Makiyama)	19	+
Sinum ineptum (Yokoyama)	13	+
Cryptonatica sp.	22	
Naticidae gen. and sp. indet.	156	
Liracassis japonica (Yokoyama)	85	+
Gyrinium osawanoensis (Tsuda)	1	+
Ranellidae? gen. and sp. indet.	3	
Zeuxis sp.	1	
Ancisrtolepis ? sp.	1	
Siphonalia ikebei Tsuda	21	+
Babylonia kozaiensis kokozurana Nomura	4	+
Granulifusus sp.	6	
Chicoreus tiganouranus (Nomura)	2	+
Boreotrophon osawanoensis Tsuda	3	+
Strigatella notoensis Masuda	9	+
Olivella iwakiensis Nomura and Hatai	32	+
Conus (Asprella) tokunagai Otuka	3	+
Conus sp.	8	
Megasurcula yokoyamai (Otuka)	61	+
M. osawanoensis (Tsuda)	5	+
Splendrillia osawanoensis (Tsuda)	1	+
Fulgoraria sp.	11	
Cancellaria sp.	1	
Architectonica osawanoensis Tsuda	6	+
Eocylichna habei Itoigawa	2	
Fissidentalium yokoyamai (Makiyama) Leionucula sp.	59 1	+
Anadara ogawai (Makiyama)	12	+
Scapharca makiyamai (Hatai and Nisiyama)	9	+
Glycymeris (Glycymeris) rhynconelloides Nomura and Hatai	219	+
G. (Veletuceta) cisshuensis Makiyama	5	+
G. (V.) ikebei Itoigawa and Shibata	3	+
Tucetona tsudai n. sp.	18	
Limopsis osawanoensis (Tsuda)	63	+
Acesta sp.	2	
Pycnodonte (Phygraea) matsubarai n. sp.	93	
Saccostrea? sp.	1	
Ostrea sp.	2	
Chlamys itoigawae Masuda	69	+
Gloripallium cf. izurensis Masuda	4	
"Placopecten" osawanoensis (Tsuda)	13	+
Mizuhopecten kimurai (Yokoyama)	12	+
Nipponocrassatella osawanoensis (Tsuda)	69	+
Cyclocardia siogamensis (Nomura)	106	+
Lucinoma acutilineatum (Conrad)	4	+
Diplodonta ferruginata Makiyama	7	+
Clinocardium sp.	4	
Timoclea itoigawae (Tsuda)	1	+
Securella chitaniana (Yokoyama)	6	+
Pitar sp.	1	
Neogenella itoi (Makiyama)	1	+
Phacosoma nomurai (Otuka)	4	
P. akaisiana (Nomura)	13	+
Ezocallista toyamaensis n. sp.	26	
Compsomyax iizukai (Yokoyama)	3	
	1	+
	•	
Hiatula minoensis (Yokoyama) Spisula (Mactromeris) sp.	1	
Hiatula minoensis (Yokoyama) Spisula (Mactromeris) sp. Pseudoxyperas osawanoense (Tsuda)	1 16	+
Hiatula minoensis (Yokoyama)	1	+

All specimens treated here are stored at the Department of Paleontology and Anthropology, National Museum of Nature and Science, Tokyo (NMNS PM), Tsukuba, Ibaraki Prefecture.

3. Description of the new species

Class Bivalvia Linnaeus, 1758 Family Glycymerididae Dall, 1908

Genus Tucetona Iredale, 1931

Type species: Pectunculus flabellatus Tenison-Woods, 1878 (original designation). Recent, South Australia.

Diagnosis: "Shell subcircular to subtrigonal; beaks orthogyrate, small to moderate in size, narrow to broad; sculpture of about 18–46 rounded to rectangular radial ribs, bifurcate in some species, commarginal striae weak to strong; interspaces narrow to moderately wide, shallow to moderately deep; posterior and anterior adductor scars and pallial line well impressed; hinge plate moderately curved, narrow to moderately wide; teeth straight to moderately curved; hinge plate of about 18–20 taxodont teeth; ligament with 3–5 chevron grooves" (by Valentich-Scott and Garfinkle, 2011).

Tucetona tsudai Amano n. sp.

(Pl. 1)

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[New Japanese Name: Tsuda-uchiwa-gai]

Ethymology: The present new species is named after the late Dr. Karyu Tsuda, Emeritus Professor of Niigata University, who contributed to the geology and paleontology of Yatsuo-machi in Toyama City.

Type specimens: Holotype, NMNS PM 68976; Paratype 1, NMNS PM 68977; Paratype 2, NMNS PM 68978; Paratype 3, NMNS PM 68979.

Type Locality: Fukushima, Yatsuo-machi, Toyama City, Toyama Prefecture; Kurosedani Formation (36°35'7"N, 137°8'31"E).

Material: Eighteen specimens were collected from the type locality. Seventeen well-preserved specimens were measured.

Dimensions: see Table 2.

Diagnosis: Medium-sized *Tucetona*, sculptured by narrow, high and round-topped 24–30 radial ribs with broader interspaces than ribs themselves in some adult shells.

Description: Shell medium in size, attaining 41.5 mm in length, circular in shape (avg. H/L=0.99), moderately inflated (avg. T/L=0.24), equilateral. Antero-dorsal

Table 2. Measurements of *Tucetona tsudai* Amano n. sp. NR*= Number of radial ribs, AT**= Number of anterior teeth, MT***= Number of middle teeth, PT***= Number of posterior teeth.

Specimens (NMNS PM)	Type status	Length (mm)	Height (mm)	Γhickness (mm)	H/L	T/L	NR*	AT**	MT***	PT****	Valve
68976	Holotype	41.5	41.5	9.0	1.00	0.22	25	9	3	10	right
68977	Paratype 1	37.8+	-	8.8	-	-	25	7	6	8	right
68978	Paratype 2	30.9	31.4	7.3	1.02	0.24	30	8	5	7	right
68979	Paratype 3	29.5	28.3	7.1	0.96	0.24	25	7	-	7	right
68980-1		29.3	27.3	6.8	0.93	0.23	27	7	7	8	right
68980-2		25.3	25.3	5.9	1.00	0.23	28	8	-	9	right
68980-3		18.3+	17.3+	-	-	-	24	8	-	10	right
68980-4		16.7	17.2	4.2	1.03	0.25	27	6	6	6	left
68980-5		23.4+	-	-	-	-	26	7	-	-	right
68980-6		23.0+	-	-	-	-	30	9	-	8	left
68980-7		18.9+	-	-	-	-	25	-	-	-	right
68980-8		-	-	-	-	-	24	7	-	7	right
68980-9		17.0+	-	-	-	-	24	7	-	7	left
68980-10		16.1+	16.6	-	-	-	27	7	4	8	left
68980-11		18.1+	-	-	-	-	30	8	5	9	right
68980-12		13.6+	-	-	-	-	27	-	-	-	right
68980-13		14.4	-	-	-	-	27	5	5	5	right

margin nearly straight and gently sloping, gradually transitioning into rounded anterior margin; posterodorsal margin nearly strait and gradually transitioning into broadly rounded posterior margin; ventral margin arcuate. Umbo slightly produced above hinge line; beak slightly prosogyrate. Surface of main part of disc sculptured by 24 to 30 (avg. 26.2) narrow and roundtopped radial ribs with narrow interspaces in juvenile but becoming broader interspaces in adult shell, broader interspaces than ribs themselves in some shells (Pl. 1, fig. G), crossed by fine growth lines and some commarginal grooves. Surface of anterior and posterior sides of disc smooth except for fine growth lines and some commarginal grooves. Hinge plate rather wide, with five to nine (usually seven) horizontal small anterior teeth, three to seven vertical small middle teeth, five to ten inclined small posterior teeth and four to seven chevron-shaped ligamental grooves. Inner ventral margin strongly crenulate; 11 to 16 crenulations between anterior and posterior adductor muscle scars. Anterior adductor muscle scar ovate and posterior adductor scar subquadrate.

Remarks: Tucetona nozokiensis (Hatai and Nisiyama, 1951) was described from the lowest Middle Miocene Nozoki Formation in Yamagata Prefecture (Hatai and Nisiyama, 1951; Sato et al., 2016) and the lowest Middle Miocene Nataki Formation in Gifu Prefecture (Itoigawa et al., 1974; Itoigawa et al., 1981, 1982). Tucetona nozokiensis is different from T. tsudai n. sp. by having a more inflated shell (T/L=0.31 in the holotype, IGPS 72883), broader flat-topped radial ribs, and narrower interspaces.

Tucetona osawanoensis Tsuda, 1959 from the same Kurosedani Formation at Tsuzara and Ikeda, Toyama City can be distinguished from *T. tsudai* by having a smaller shell (about 20 mm in length), more numerous (35) and broader radial ribs than their interspaces, and fewer anterior teeth (four on the anterior side).

Tucetona tsudai n. sp. resembles T. pecten (Sowerby, 1840) from the Lower to Middle Miocene in western India by having a similar size (31.9 mm in length; Jain, 2014) and 26–30 radial ribs with broader interspaces than the ribs in large shells (Dey, 1961; Jain, 2014; Gopal et al., 2025). However, T. pecten can be discriminated from T. tsudai n. sp. by having more numerous teeth on each side (14–18; Dey, 1961).

Tucetona angsanana (Martin, 1922) was described from the Lower Miocene Nyalingdung Formation in Java, Indonesia. Tucetona angsanana differs from T. tsudai n. sp. by having a straight and horizontal dorsal margin, some weakly dichotomous radial ribs and no break between the anterior and posterior teeth.

Tucetona chichibuensis Hirayama, 1973 was proposed from the Lower Miocene Hiranita Formation in Chichibu basin, Saitama Prefecture, based on some ill-preserved specimens. However, it has a smaller shell (less than 16.0 mm in length) than *T. tsudai* n. sp. Moreover, its less numerous (20) and flat radial ribs enable us to separate it from the present new species.

Stratigraphic distribution: Early Miocene, Kurosedani Formation in Toyama Prefecture.

Family Gryphaeidae Vyalov, 1936 Subfamily Pycnodontinae Stenzel, 1959

Genus *Pycnodonte* Fischer de Waldheim, 1835 *Type species: Pycnodonte radiata* Fischer de Waldheim, 1835 (by original designation). Upper Cretaceous in Crimea.

Subgenus Phygraea Vyalov, 1936

Type species: Phygraea frauscheri Vyalov, 1936 (by original designation). Upper Paleocene in Australia.

Diagnosis: "LV umbo prominent, rising well above hinge line, no auricles, LV outline vertical-oval or prosocline oblique oval to horizontal oval, two last mentioned outlines inequilateral, with postero-dorsal margin concave and geniculate. Chomata shorter and less elaborate than in *Pycnodonte* (*Pycnodonte*). Commarginal puckers and welts feeble; radial ribs few or absent. Growth squamae mostly very closely appressed and surface of LV rather smooth" (by Stenzel, 1971).

Remarks: The subgenus Phygraea can be discriminated from Pycnodonte (s.s.) by having no auricle and no straight dorsal margin in the left valve. The subgenus Costeina Vyalov, 1965 is different from Phygraea by its numerous radial riblets only on the left valve. Neopycnodonte Stenzel, 1971 differs from Pycnodonte by having a usually small (up to 16 cm in Pycnodonte; less than 9 cm in Neopycnodonte; Stenzel, 1971), vertically elongated oval shell, thinner

shell wall and indistinct circumferential step separated from the commissural shelf.

Pycnodonte (Phygraea) matsubarai Amano n. sp. (Fig. 1, Pl. 2)

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[New Japanese Name: Matsubara-oobekkou-gaki] *Ostrea* cf. *denselamellosa* Lischke. Matsuura, 2009, pl. IV-7, fig. 23.

Ethymology: The present new species is named after the late Dr. Takashi Matsubara who first described and illustrated the Miocene *Pycnodonte* in Japan.

Type specimens: Holotype, NMNS PM 68983; Paratype 1, NMNS PM 68984; Paratype 2, NMNS PM 68985; Paratype 3, NMNS PM 68986; Paratype 4, NMNS PM 68987; Paratype 5, NMNS PM 68988; Paratype 6, NMNS PM 68989.

Type Locality: Fukushima, Yatsuo-machi, Toyama City, Toyama Prefecture; Kurosedani Formation (36°35'7"N, 137°8'31"E).

Material: Ninety-three specimens were collected from the type locality. Sixty-eight well-preserved specimens (26 left valves and 42 left valves) were measured.

Dimensions: see Tables 3, 4.

Diagnosis: Moderate-sized Phygraea with well inflated subcircular to oblique-oval right valve having no auricle, short vermiculate chomata, wide attachment area and sometimes brown bands on creamy colored valves; right valve smaller than left valve, mostly vertically elongate ovate and concaved shells with narrow commissural shelf, small auricle and short chomata.

Description: Shell medium-sized, attaining 75.0 mm in length of left valve; inequivalve, larger left valve than right valve.

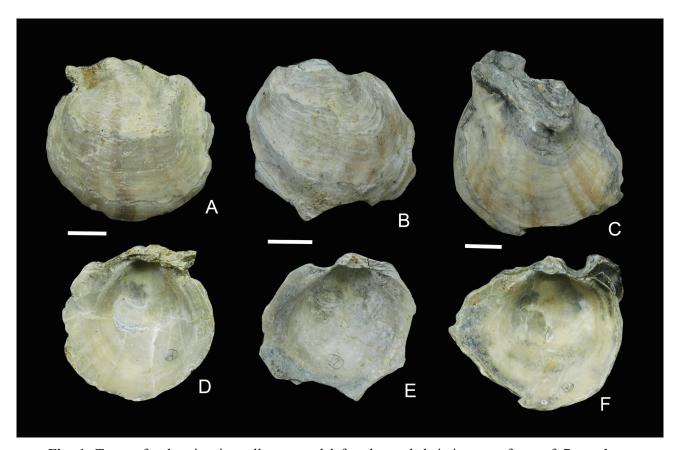


Fig. 1. Trace of coloration in well-preserved left vales and their inner surfaces of *Pycnodonte* (*Phygraea*) *matsubarai* Amano n. sp. A, D. Paratype 4. NMNS PM 68987. A, outer surface; D. inner surface. B, E. Paratype 5, NMNS PM 68988. B, outer surface; E. inner surface. C, F. Paratype 6, NMNS PM 68989. C, outer surface; F. inner surface.

Table 3. Measurements of left valve of <i>Pycnodonte (Phygraea) matsubarai</i> Amano n. sp. LPA*=
Length of posterior adductor muscle scar, LPAB**= Length between the top of the posterior adduc-
tor muscle scar and the beak.

Specimens (NMNS PM)	Type status	Length (mm)	Height (mm)	Thickness (mm)	LPA*(mm)	LPAB**(mm)	H/L	T/L	LPA/L	LPAB/H
68983	Holotype	75.0	70.3	27.3	17.1	29.0	0.94	0.36	0.23	0.41
68984	Paratype 1	68.0	63.9	31.5	-	26.6	0.94	0.46	-	0.42
68987	Paratype 4	42.5	42.1	14.4	8.0	12.6	0.99	0.34	0.19	0.30
68988	Paratype 5	36.5	35.9	10.6	6.8	12.3	0.98	0.29	0.19	0.34
68989	Paratype 6	49.3	43.8	16.1	11.8	15.0	0.89	0.33	0.24	0.34
68990-1		62.2	63.2	31.7	16,4	22.1	1.02	-	-	0.35
68990-2		58.5	55.2	27.7	12,6	16.0	0.94	0.47	-	0.29
68990-3		58.4	51.7	28.7	12.4	14.3	0.89	0.49	0.21	0.28
68990-4		49.4	48.3	-	-	-	0.98	-	-	-
68990-5		46.3	39.6	-	-	-	0.86	-	-	-
68990-6		52.7	46.5	16.9	11.6	-	0.88	0.32	0.22	-
68990-7		51.9	40.4	18.0	11.1	12.1	0.78	0.35	0.21	0.30
68990-8		41.3	47.3+	17.3	-	-	-	0.42	-	-
68990-9		41.8	44.8	19.7	9.3	11.7	1.07	0.47	0.22	0.26
68990-10		43.3	40.3	14.1	9.4	10.6	0.93	0.33	0.22	0.26
68990-11		38.4	37.2	14.6	9.3	10.6	0.97	0.38	0.24	0.28
68990-12		35.6	36.1	9.6	9.5	12.3	1.01	0.27	0.27	0.34
68990-13		19.1	24.1	7.8	4.4	7.4	1.26	0.41	0.23	0.31
68990-14		58.7	73.3	23.5	15.3	30.0	1.25	0.40	0.26	0.41
68990-15		64.5	68.8	14.3	16.1	25.2	1.07	0.22	0.25	0.37
68990-16		55.3	59.4	19.8	16.9	23.6	1.07	0.36	0.31	0.40
68990-17		41.6	47.9	11.3	-	-	1.15	0.27	-	-
68990-18		48.9	51.4	12.2	10.7	17.8	1.05	0.25	0.22	0.35
68990-19		36.0	30.7+	10.3	9.5	11.4	-	0.29	0.26	-
68990-20		36.4	39.1+	13.3	-	-	-	0.37	-	-
68990-21		27.6	29.4	8.7	6.1	7.0	1.07	0.32	0.22	0.24

Left valve relatively thin, well inflated (T/L= 0.27 to 0.49; avg. 0.38), subcircular to oblique-oval shape (H/L= 0.78 to 1.26; avg. 1.00) with wide attachment area and no auricle. Surface sculptured by irregular commarginal ridges; shell color generally gray but creamy with one to nine radial brown bands in three well-preserved valves (Fig. 1). Commissural shelf wide, delimited by circumferential step; chomata short and elaborated, vermiculate. Hinge area narrow with relatively small resilifer. Posterior adductor muscle scar elliptical, rather small (LPA/L= 0.19 to 0.27, avg. 0.23) and located at about one-third of height from beak (LPAB/H= 0.26 to 0.42, avg. 0.33).

Right valve smaller than left valve, up to 52.3 mm in length, moderately thick, mostly concave to flat (T/L= 0.09 to 0.21, avg. 0.15) and mostly vertically elongate ovate (H/L= 0.94 to 1.36, avg. 1.13) with small auricle. Shell color gray in adult, creamy in some young shells. Surface sculptured by many fine growth lines and some regular commarginal wrinkles.

Commissural shelf very narrow; chomata short in inner part of auricles. Hinge area narrow, but thick with relatively large resilifer. Dorsal margin nearly straight with centrally located umbo. Posterior adductor muscle scar subcircular, moderate in size (LPA/L= 0.32 to 0.48, avg. 0.39) and located at about two-fifth of height from beak (LPAB/H= 0.32 to 0.49, avg. 0.39).

Remarks: Matsuura (2009) illustrated one right valve from the Kurosedani Formation at Ikuridani in Toyama City as Ostrea denselamellosa Lischke. Unfortunately, its inner part was not illustrated, but its shape with the auricles and surface sculpture seems to be very similar to Pycnodonte (Phygraea) matsubarai n. sp.

Matsubara (2011) first described the Miocene *Pyc-nodonte* in Japan. He described and illustrated *Pyc-nodonte* (s.l.) sp. indet., based on the silicon rubber cast collected from the Toyo'oka Formation of the Hokutan Group in Hyogo Prefecture. The age of the formation was assigned to the late Early to earliest Middle Miocene by him. The right valve of his species has a vertically oval shell (higher than long) and

Table 4. Measurements of right valve of *Pycnodonte* (*Phygraea*) *matsubarai* Amano n. sp. LPA*= Length of posterior adductor muscle scar, LPAB**= Length between the top of the posterior adductor muscle scar and the beak.

Specimens (NMNS PM)	Type status	Length (mm)	Height (mm)	Thickness (mm)	LPA*(mm)	LPAB**(mm)	H/L	T/L	LPA/L	LPAB/H
68985	Paratype 2	52.3	60.0	8.8	15.4	24.7	1.15	0.15	0.41	0.41
68986	Paratype 3	44.7	59.3	6.4	15.6	24.6	1.33	0.14	0.41	0.41
68990-22		43.8	59.5	6.6	14.4	22.3	1.36	0.15	0.37	0.37
68990-23		40.8	52.1	6.2	14.2	22.4	1.28	0.15	0.43	0.43
68990-24		39.5	43.2	7.1	12.7	16.5	1.09	0.18	0.38	0.38
68990-25		33.6	44.4	4.7	9.8	17.3	1.32	0.14	0.39	0.39
68990-26		38.1	42.4	6.2	12.9	17.3	1.11	0.16	0.41	0.41
68990-27		37.2	37.9	3.8	9.8	14.2	1.02	0.10	0.37	0.37
68990-28		34.5	38.7	4.7	10.8	14.8	1.12	0.14	0.38	0.38
68990-29		32.9	44.0	5.0	10.9	21.6	1.34	0.15	0.49	0.49
68990-30		35.6	36.7	6.1	10.1	16.4	1.03	0.17	0.45	0.45
68990-31		29.8	35.4	3.3	7.5	11.8	1.19	0.11	0.33	0.33
68990-32		30.0	30.8	3.4	10.5	11.2	1.03	0.11	0.36	0.36
68990-33		29.4	31.9	6.7	8.7	12.6	1.09	0.23	0.39	0.39
68990-34		28.6	30.0	2.6	7.3	11.7	1.05	0.09	0.39	0.39
68990-35		30.8	32.0	5.1	10.2	13.2	1.04	0.17	0.41	0.41
68990-36		29.5	30.3	3.9	10.8	10.2	1.03	0.13	0.34	0.34
68990-37		25.8	33.4	3.8	-	-	1.29	0.15	-	-
68990-38		24.6	24.6	2.8	7.9	9.9	1.00	0.11	0.40	0.40
68990-39		27.7	27.8	3.9	-	-	1.00	0.14	-	-
68990-40		25.2	27.7	3.9	-	-	1.10	0.15	-	-
68990-41		17.2	21.5	3.4	5.9	6.8	1.25	0.20	0.32	0.32
68990-42		25.2	29.1	3.4	8.4	11.1	1.15	0.13	0.38	0.38
68990-43		43.5	46.3	5.6	11.4	17.9	1.06	0.13	0.39	0.39
68990-44		42.9	50.6	8.3	14.9	22.7	1.18	0.19	0.45	0.45
68990-45		42.8	45.7	7.6	13.4	21.9	1.07	0.18	0.48	0.48
68990-46		42.1	48.0	8.2	13.5	19.4	1.14	0.19	0.40	0.40
68990-47		38.8	42.8	5.0	12.1	14.3	1.10	0.13	0.33	0.33
68990-48		43.6	45.6	4.7	12.0	18.2	1.05	0.11	0.40	0.40
68990-49		35.4	39.8	4.0	11.8	13.2	1.12	0.11	0.33	0.33
68990-50		36.2	35.6	3.6	11.5	13.7	0.98	0.10	0.38	0.38
68990-51		27.8	34.2	5.8	9.1	13.0	1.23	0.21	0.38	0.38
68990-52		24.7	29.9	3.0	6.2	9.8	1.21	0.12	0.33	0.33
68990-53		24.8	27.0	3.3	-	-	1.09	0.13	-	-
68990-54		24.4	29.5	2.8	6.7	10.4	1.21	0.11	0.35	0.35
68990-55		24.1	25.6	3.2	3.3	9.2	1.06	0.13	0.36	0.36
68990-56		22.8	27.3	3.0	7.3	9.9	1.20	0.13	0.36	0.36
68990-57		20.8	25.1	3.6	3.5	9.4	1.21	0.17	0.37	0.37
68990-58		22.0	23.8	4.2	6.5	9.0	1.08	0.19	0.38	0.38
68990-59		22.7	23.7	2.3	7.4	11.7	1.04	0.10	0.49	0.49
68990-60		19.5	19.9	4.0	5.0	7.5	1.02	0.21	0.38	0.38
68990-61		15.6	14.7	3.0	-	-	0.94	0.19	-	-

seems to have a small posterior auricle. Moreover, the right valve has a wide commissural shelf with long chomata along its posterior step. These characteristics are not seen in *Pycnodonte* (*Phygraea*) *matsubarai*, n. sp.

Oyama et al. (1960) reidentified *Ostrea cassis* Nagao, 1928 from the Middle Eocene Okinoshima Formation as *Pycnodonta* [sic] cassis (Nagao) which was also erroneously referred to as *Ostrea crassis* [sic] by Hayami and Kase (1992). By examining the type specimens (IGPS no. 36031), there is no reason why

this smaller species (attaining 33.7 mm in length) was allocated to *Pycnodonte* because there are no chomata. Consequently, no Paleogene species of *Pycnodonte* have been described in Japan.

Vyalov (1948) described *Gryphaea* (*Phygraea*) tounali (Doncieux) var. circularis Vyalov, 1948 from the Eocene Suzak Stage deposits in Tajik Basin. The illustrated specimens are similar to *Pycnodonte* (*Phygraea*) matsubarai n. sp. in their size (up to about 77 mm in length of the left valve) and outline.

However, *P.* (*P.*) matsubarai can be distinguished from Vyalov's species by having a wider commissural shelf and shorter chomata in the left valve, and a straight dorsal margin as well as small auricles in the right valve.

Hayami and Kase (1992) described a Recent *Pyc-nodonte* (s.s.) taguchii as a new species from the submarine cave in Shimoji-shima of the Miyako Islands, Okinawa Prefecture. This Recent relict species is large (up to 123 mm in length) with auricles in both valves, a very wide commissural shelf and many radial gashes on the external surface which are not observed in *P.* (*Phygraea*) matsubarai n. sp.

Kurihara (2010) recorded *Pycnodonte* (*Phygraea*) sp. from the Middle Miocene Kobana Formation in Tochigi Prefecture. He noted that this species also occurred in the Lower Miocene Nenokami Sandstone in Saitama Prefecture and the Lower Miocene Kurosedani Formation in Toyama Prefecture. Although it is possible to identify his Kurosedani specimen with *P.* (*Phygraea*) *matsubarai* n. sp., the absence of a description and illustration of this species prevents us from exactly identifying.

The traces of coloration in this new species are in the form of radial brownish bands which were considered the result of deterioration of purplish bands (Stenzel, 1971). These bands have been frequently observed in the Exogyrinae (Stenzel, 1971). However, these bands were also recognized in two Cretaceous species of *Pycnodonte* in the U.S.A. (Stokes and Stifel, 1964; Bennington, 2001).

Stratigraphic distribution: Early Miocene, Kurosedani Formation in Toyama Prefecture.

Family Veneridae Rafinesque, 1815

Genus Ezocallista Kuroda in Kamada, 1962

Type species: Saxidomus brevisiphonata Carpenter, 1865 (by original designation). Recent, northern Pacific.

Diagnosis: "The hinge plate of "Ezo-wasure" is rather thin and weak; the anterior lateral tooth in the left valve is situated at the slightly lower margin-side on the hinge plate; the two hinge teeth in the left valve are nearly same in size, but the anterior tooth is elevated, and each of these teeth is independent (in

"Matsuyama-wasure-rui", the top of both teeth is a continuous reversed V-shape; its anterior wing (tooth) is elevated like a plate; the posterior wing (tooth) is thickened); the posterior plate (tooth) of the left valve is strong and elongated, whereas in "Matsuyama-wasure-rui", it is thin and plate-like; the posterior tooth (most posterior one among 3 teeth) is very large, and its crest is strongly grooved; the pallial sinus is rounded at the distal end, and is not truncated as in general "Matsuyamawasure-rui"; the pedal [retractor] muscle scar is very large, and is appeared just behind the anterior muscle scar; it is different from that in general "Matsuyama-wasure-rui", in which it is hidden in the inner side of the hinge plate and is not seen; the lunule is only surrounded by a fine groove. Periostracum is not glossy like a Japanese lacquer." (Kuroda, 1952; translated by Matsubara, 2013)

Remarks: This genus is closely related to Saxidomus Conrad, 1837 in its shape and hinge (Amano and Nemoto, 2020). However, it differs from Saxidomus by having a distinct lunule in the adult shell, no posterior gape, fewer commarginal ribs and a larger anterior lateral tooth.

Ezocallista toyamaensis Amano n. sp.

(P1.3)

urn:lsid:zoobank.org:act:78CB8E25-66EF-4BE5-B1C0-66C2153BB89B

[New Japanese Name: Toyama-wasure-gai] *Callista chinensis* (Holten). Kaneko and Goto, 1992, p. 15, pl. 7, figs. 8a, b; Kaneko and Goto, 1997, p. 13, figs. 4a, b.

Ethymology: The present new species is named after the prefecture name of type locality.

Type specimens: Holotype, NMNS PM 69007; Paratype 1, NMNS PM 69008; Paratype 2, NMNS PM 69009; Paratype 3, NMNS PM 69010; Paratype 4, NMNS PM 69011; Paratype 5, NMNS PM 69012.

Type Locality: Fukushima, Yatsuo-machi, Toyama City, Toyama Prefecture; Kurosedani Formation (36°35'7"N, 137°8'31"E).

Material: Twenty-six specimens were collected from the type locality. Six type specimens and one largest specimen were measured.

Dimensions: see Table 5.

Diagnosis: Moderate-sized *Ezocallista* with fine and low regular commarginal ribs, short anterior lateral teeth and rather thick and bifid posterior cardinal tooth in right valve, and no subumbonal pit on hinge plate.

Description: Shell equivalve, moderate-sized and thin for genus, attaining more than 59.7 mm in length, elongate ovate in shape (H/L= 0.69 to 0.78, avg. 0.73), moderately inflated (T/L= 0.23 to 0.25, avg. 0.24); antero-dorsal margin slightly concave, gradually transitioning into rounded anterior margin; postero-dorsal margin nearly straight, gently sloping into subtruncated posterior margin; ventral margin broadly arcuate. Umbo not protruding; inequilateral, beak situated at anterior one-third of shell length (AL/L= 0.27 to 0.38, avg. 0.32). Lunule long, lance-olate, shallowly depressed and demarcated by distinct groove; escutcheon long and flat. Surface sculptured by many low flat-topped commarginal ribs.

Hinge plate rather narrow. In right valve, lower anterior lateral tooth (AI) short and along with ventral side of hinge, upper anterior lateral tooth (AIII) very thin and parallel with dorsal margin; anterior cardinal tooth (3a) thin and inclined forward; middle cardinal tooth (1) also thin and vertical; posterior cardinal tooth (3b) thick and distinctly bifid, inclining posteriorly. In left valve, anterior lateral tooth (AII) inclined anteriorly; anterior cardinal tooth (2a) thin and vertical; middle cardinal tooth (2b) also thin and posetiorly inclined; posterior cardinal tooth (4b) very thin and long, parallel with postero-dorsal margin. Anterior adductor muscle

scar semi-circular; posterior one subquadrate, larger than anterior one; pallial sinus indistinct, moderately deep and round at its end. Inner ventral margin smooth.

Remarks: Kaneko and Goto (1992, 1997) described the Recent species, Callista chinensis (Holten, 1802) from the Kurosedani Formation at Tsuzara. However, C. chinensis can be easily separated by its narrowly rounded posterior end, shiny shell surface with very low commarginal ribs and parallel anterior (3a) and middle (1) cardinal teeth in the right valve which are invisible in their species. Judging from their illustration of shell shape and hinge, their "Callista chinensis" should be identified as Ezocallista toyamaensis n. sp.

The present new species is very similar to the Recent cold-water species, *Ezocallista brevisiphonata* (Carpenter, 1865) in having a similar shell outline and hinge. However, it is slightly different from the Recent species by having a smaller, thinner shell, deeper pallial sinus, strong and bifid posterior cardinal tooth (3b), short anterior lateral teeth (AI, AIII) in the right valve, strong anterior cardinal tooth (2a) and short anterior tooth (AII) like *Saxidomus*, and no subumbonal pit.

Hirayama (1954) proposed *Callista pseudobrevisiphonata* from the Middle Miocene Kobana Formation in Tochigi Prefecture. This species has a more highly ovate shell than *Ezocallista toyamaensis* n. sp. The absence of an illustration and description of hinge structure of *C. pseudobrevisiphonata* prevent us from exactly comparing both species.

Table 5. Measurements of	Ezocallista toyamaensis 1	Amano n. sp. AL*=	anterior length.

Specimens (NMNS PM)	Type status	Length (mm)	Height (mm)	Thickness (mm)	AL* (mm)	H/L	T/L	AL/L	Valve
69007	Holotype	39.6	30.7	9.7	12.8	0.78	0.24	0.32	left
69008	Paratype 1	50.9	34.2+	11.9	15.0	-	0.23	0.29	left
69009	Paratype 2	35.2	24.3	8.2	13.4	0.69	0.23	0.38	right
69010	Paratype 3	38.3+	29.6	10.2	-	-	-	-	right
69011	Paratype 4	50.3	35.9	12.8	13.8	0.71	0.25	0.27	right
69012	Paratype 5	37.9	27.7	9.3	12.3	0.73	0.25	0.32	right
69013		59.7+	-	-	-	-	-	-	left

Macrocallista kavranensis Ilyina, 1963 was described from the Middle Miocene Kakert Formation in western Kamchatka. Judging from shell shape, pallial sinus shape, hinge and surface sculpture, this species belongs to Ezocallista. However, M. kavranensis can be distinguished from Ezocallista toyamaensis n. sp. by having a non-bifid posterior cardinal tooth in the right valve and a more elongated anterior lateral tooth in the left valve.

Ezocallista kurodae Kamada, 1962 from the lower Oligocene Iwaki Formation in Fukushima Prefecture was allocated to Saxidomus by Amano and Nemoto (2020). Thus, the present new species is the oldest record of Ezocallista.

Stratigraphic distribution: Early Miocene, Kurosedani Formation in Toyama Prefecture.

4. Discussion

Sixty-nine molluscan species including three new species were identified from the hitherto unknown locality of the Lower Miocene Kurosedani Formation. Most species are characteristic species of the Kadonosawa fauna (Chinzei, 1978, 1981, 1986; Itoigawa, 1986; Itoigawa and Shibata, 1986; Tsuda et al., 1986) in the Miocene Climatic Optimum age. Except for Ginebis osawanoensis Tsuda, Fulgoraria sp., Leionucula sp. and Acesta sp., most Recent counterparts live in shallow water (Higo et al., 1999). Considering the lithofacies and occurrences of shells, it is likely that most shallow water dwellers were transported to deep waters by gravity flows. Most Recent counterparts live in subtropical or tropical waters. Amano et al. (in press) stressed the paleoclimatic significance of Pseudoxyperas osawanoense (Tsuda) as an indicator of the tropical or subtropical paleoclimate, which is concordant with the paleoclimate condition of the Kurosedani Formation as tropical (Ogasawara, 1994).

Three new bivalve species have been described herein; *Tucetona tsudai* n. sp., *Pycnodonte* (*Phygraea*) *matsubarai* n. sp. and *Ezocallista toyamaensis* n. sp. In total, four species of *Tucetona* were known from the Lower Miocene to the lowest Middle Miocene in central to northeast Honshu. In the living fauna, the genus has been recorded in the tropical and subtropical regions around southwestern

Japan and southwards (Habe, 1977; Higo et al., 1999; Matsukuma, 1984, 1986, 2000, 2017). No species of this genus has been reported from the Middle Miocene to the Late Miocene in Japan. This occurrence corresponds to the faunal succession by the cooling events since the Middle Miocene Climatic Transition (MMCT), recently discussed by Amano et al. (2025).

Other than the Recent species in the marine cave, *Pycnodonte* (s.s.) taniguchii Hayami and Kase, *Pycnodonte* is known from the late Early Cretaceous to Middle Miocene mainly in the Tethyan realm (Vyalov, 1948; Bobkova, 1961; Hayami and Kase, 1992; Kurihara, 2010). *P.* (*Phygraea*) matsubarai n. sp. corresponds to one of the youngest species of this subgenus. Hayami and Kase (1992) considered that *Pycnodonte* have been surviving in shallow warm seas. The occurrence of *P.* (*Phygraea*) matsubarai n. sp. from the Kurosedani Formation suggests that the genus could survive in the normal shallow water under the Miocene warmest climate (MCO). Most species of the genus might have suffered extinction by the MMCT.

As mentioned above, *Ezocallista toyamaensis* n. sp. is the oldest species of this genus. All Recent species of *Ezocallista*, *Boreotrophon*, and *Spisula* (*Mactromeris*) are known from cold waters (Higo et al., 1999). As it is difficult to imagine that such cold-water species could survive in warm water, they originally appeared also in the warm-water area and then adapted to the cold-water area since the MMCT or Late Miocene Cooling (LMC) as did *Saxidomus* (see Amano and Nemoto, 2020).

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6. References

- Amano, K., T. Hamuro, and M. Hamuro. 2004. Latest early-earliest middle Miocene deep-sea molluscs in the Japan Sea borderland. —the warm-water Higashibessho fauna in Toyama Prefecture, central Japan. Paleontological Research 8(1): 29–42.
- Amano, K., T. Hamuro, and M. Hamuro. in press. Crassatellid and Mactrid Bivalves from the Lower Miocene Kurosedani Formation in Toyama City, Toyama Prefecture, central Japan. Bulletin of the National Museum of Nature and Science, Series D 51.
- Amano, K., T. Haga, T. Sato, T. Hamuro, and M. Hamuro. 2025. Middle Miocene Climatic Transition in the Japan Sea borderland of Honshu. —Middle Miocene molluscan fauna from Unazukimachi-Oritate in Kurobe City, Toyama Prefecture, Japan—. Bulletin of the Mizunami Fossil Museum 52(1): 17–43.

DOI: 10.50897/bmfm.52.1 17

- Amano, K., Y. Miyajima, K. Nakagawa, T. Hamuro, and M. Hamuro. 2019. Cheomosymbiotic bivalves from the lower Miocene Kurosedani Formation in Toyama Prefecture, central Honshu, Japan. Paleontological Research 23(3): 208–219.
- Amano, K., and J. Nemoto, 2020. Evolution and coldwater adaptation of the genus *Saxidomus* (Bivalvia: Veneridae) in the Northwestern Pacific. Venus 78(3–4): 87–104.
- Bennington, J. B. 2001. Shell color and predation in the Cretaceous oyster *Pycnodonte convexa* from New Jersey. Long island Geologists' Abstracts 61. https://commons.library.stonybrook.edu/long-island-geologists-abstracts/61.
- Bobkova, N. N. 1961. Pozdnemelobye Ustpitsi Tadjikskoi Depressii [Late Creataceous oysters of the Tajik Basin]. Trudy VSEGEI [Transactions of VSEGEI], New Series 50: 1–141, pls. 1–32. (in Russia)

Carpenter, P. P. 1865. Diagnoses of new forms of Mollusca from the Vancouver District. Proceedings of the Zoological Society of London 1865: 201–204.

- Chinzei, K. 1978. Neogene molluscan faunas in the Japanese Islands: An ecologic and zoogeographic synthesis. Veliger 21(2): 155–170.
- Chinzei, K. 1981. The Kadonosawa Fauna. In Habe, T., and M. Omori, eds., Study of Molluscan Paleobiology, Professor Masae Omori Memorial Volume. Editorial committee of Study of Molluscan Paleobiology. Niigata University. Niigata. p. 207–212. (in Japanese with English abstract)
- Chinzei, K. 1986a. Faunal succession and geographic distribution of Neogene molluscan faunas in Japan. Palaeontological Society of Japan, Special Volume (29): 17–32.
- Chinzei, K. 1986b. Marine biogeography in Japan during early Middle Miocene as viewed from benthic molluscs. Palaeontological Society of Japan, Special Volume (29): 161–171.
- Conrad, T. A. 1837. Descriptions of new marine shells, from Upper California, collected by Thomas Nuttall, Esq. Journal of the Academy of Natural Sciences of Philadelphia 7: 227–268, pls. 17–20.
- Dall, W. H. 1908. The Mollusca and Brachiopoda. Bulletin of the Museum of Comparative Zoology at Harvard College 43: 204–487.
- Dey, A. K. 1961. The Miocene Mollusca from Quilon, Kerala, India. Memoirs of the Geological Survey of India, Palaeontologia Indica, New Series 36: 1–129.
- Fischer de Waldheim, G. 1835. Lettre a M. le Baron de Ferussac sur quelques genres de coquilles du Museum Demidoff et en particulier sur quelques fossiles de la Crimee. Societe Imperiale des Naturalistes Moscow Bulletin 8: 101–119.
- Fujii, S. 1961. On some Miocene arcid fossils from Japan. Part 1. *Trisidos yatsuoensis* and its allies. Venus 21(2): 217–222.
- Gopal, K. V., D. Chattopadhyay, and S. Dutta. 2025. Oligo-Miocene marine bivalves from the Kutch Basin (western India) and their biogeographic implications in the context of Tethyan closure. Historical Biology: 1–24.

DOI: 10.1080/08912963.2025.2463671

- Habe, T. 1977. Systematics of Mollusca in Japan: Bivalvia & Scaphopoda. Zukan-no-Hokuryukan. Tokyo. 372 p. (in Japanese)
- Hatai, K., and S. Nisiyama. 1951. A new Miocene *Glycymeris* from Japan. Saito Ho-On Kai Museum, Research Bulletin (21): 1–2.
- Hayami, I., and T. Kase. 1992. A new cryptic species of *Pycnodonte* from Ryukyu Islands: A living fossil oyster. Transactions and Proceedings of the Palaeontological Society of Japan, New Series (165): 1070–1089.
- Higo, S., P. Callomon, and Y. Goto. 1999. Catalogue and Bibliography of the Marine Shell-bearing Mollusca of Japan. Elle Scientific Publications. Yao. 749 p.
- Hirayama, K. 1954. A Miocene Mollusca from the Arakawa Group, Tochigi Prefecture, Japan (Part 1). Science Reports of the Tokyo Kyoiku Daigaku, Sec. C 3: 43–76, pls. 3–5.
- Hirayama, K. 1973. Molluscan fauna from the Miocene Hiranita Formation, Chichibu basin, Saitama Prefecture, Japan. Science Reports of the Tohoku University, 2nd Series, Special Volume (6): 163–177.
- Holten, H. S. 1802. Enumeratio systematica conchyliorum beat J. H. Chemnitzii quondam ecclesiae Zebaothi Havniae pastoris, plurim societum sodialis p. p. quae publica auctione venduntur die 7me Decembris ano pres. K. H. Scidelini. Copenhagen. 88 p.
- Ilyina, A. P. 1963. Mollyuski neogena Kamchatki [Molluscs from the Neogene of Kamchatka]. Trudy VNIGRI [Transaction of VNIGRI] 202: 1–242. (in Russian, title translated herein)
- Iredale, T. 1931. Australian molluscan notes. No. 1. Records of the Australian Museum 18 (4): 201–235.
- Itoigawa, J. 1958. On some cephalaspid Opisthobranchia from the Japanese Miocene. Transactions and Proceedings of the Palaeontological Society of Japan, New Series (29): 175–183, pl. 26.
- Itoigawa, J. 1960. Paleoecological strudies of the Miocene Mizunami Group, central Japan. Journal of Earth Sciences, Nagoya University 8(2): 246–300, pls. 1–6.
- Itoigawa, J. 1986. Temporal and spatial distributions of molluscan fauna in Late Cenozoic of Japan.

- Palaeontological Society of Japan, Special Volume (29): 47–54.
- Itoigawa, J., and H. Shibata. 1986. Molluscan fauna from the Setouchi Miocene Series, southwest Japan. Palaeontological Society of Japan, Special Volume (29): 149–159, pls. 16–17.
- Itoigawa, J., H. Shibata, and H. Nishimoto. 1974. Molluscan fossils of the Mizunami Group. Bulletin of the Mizunami Fossil Museum (1): 43–203. (in Japanese)
- Itoigawa, J., H. Shibata, H. Nishimoto, and Y. Okumura. 1981. Miocene fossils from the Mizunami group. 2. Molluscs. Monograph of the Mizunami Fossil Museum (3-A): 1–53. (in Japanese)
- Itoigawa, J., H. Shibata, H. Nishimoto, and Y. Okumura. 1982. Miocene fossils from the Mizunami group. 2. Molluscs (Continued). Monograph of the Mizunami Fossil Museum (3-B): 1–330. (in Japanese)
- Jain, R. L. 2014. Neogene fossils from Kathiawar, Gujarat, India with special emphasis on taxonomic description of molluses and corals. Palaeontologica Indica, New Series 55: 1–470.
- Kamada, Y. 1962. Tertiary marine Mollusca from the Joban coal-field, Japan. Palaeontological Society of Japan, Special Volume (8): 1–187, pls. 1–21.
- Kaneko, K. 1994. Molluscan fossils from the Tochizu Member of the Kurosedani Formation in Tateyamacho, Toyama Prefecture, Central Japan. Bulletin of the Tateyama Museum of Toyama (1): 3–11, pls. 1–2. (in Japanese with English abstract)
- Kaneko, K., and M. Goto. 1992. Miocene fossils from Ikuridani, Yatsuo Town, Toyama Prefecture. Special Publication from Toyama Science Museum (5): 1–86. (in Japanese)
- Kaneko, K., and M. Goto. 1997. Organisms of Ancient Toyama —Molluscan Fossils from the Kurosedani Formation. Tateyama Museum of Toyama.
 Tateyama. 79 p. (in Japanese; original title translated)
- Kurihara, Y. 2010. Middle and Late Miocene marine Bivalvia from the northern Kanto Region, central Japan. National Museum of Nature and Science Monographs 41: 1–87.
- Linnaeus, C. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species,

- cum characteribus, differentiis, synonymis, locis. Editio decima, reformata, Volume 1. Laurentius Salvius. Holmiae. 824 p.
- Martin, K. 1922. Die Mollusken der Njalindungschichten, Gasteropoda (Fortsetzung), Scaphopoda, Lamellibranchiata, Allgemeiner Theil. Sammlungen des geologischen Reichs-Museums in Leiden. Neue Folge 1(2–4): 471–496.
- Matsubara, T. 2010. Miocene shallow marine molluscs from the Hokutan Group in the Tajima area, Hyôgo Prefecture, southwest Japan. Bulletin of the Mizunami Fossil Museum (37): 51–113.
- Matsubara, T. 2013. The valid author of *Ezocallista* (Bivalvia: Veneridae) revisite. Venus 71(3–4): 227–231.
- Matsubara, T., K. Komori, and M. Oishi. 2004. Discovery of *Geolina* (Bivalvia: Corbiculidae) from the Miocene Kadonosawa Formation in the Ninohe area, Iwate Prefecture, northeastern Japan, and its paleobiogeographic significance. Journal of the Geological Society of Japan 110(12): 765–770. (in Japanese with English abstract)
- Matsubara, T., T. Sasaki, Y. Ito, and K. Amano. 2014. Illustrations of Cenozoic molluscan type specimens preserved in the University Museum, the University of Tokyo. Part16.The genus *Compsomyax* (Bivalvia: Veneridae). Chiribotan 45(2): 51 58. (in Japanese)
- Matsukuma, A. 1984. Glycymeridid bivalves from Japan and adjacent areas-VI. Descriptions of six new species and subspecies from lndo-Pacific Region. Venus 43(4): 269–299.
- Matsukuma, A. 1986. Cenozoic glycymeridid bivalves of Japan. Palaeontological Society of Japan, Special Volume (29): 77–94.
- Matsukuma, A. 2000. Family Glycymerididae. In: Okutani, T., ed., Marine Mollusks in Japan. Tokai University Press. Tokyo. pp. 859–861. (in Japanese and English)
- Matsukuma, A. 2017. Family Glycymerididae. In: Okutani, T., ed., Marine Mollusks in Japan, The Second Edition. Tokai University Press. Hiratsuka. pp. 513–515 (Atlas), 1169–1171 (Text). (in Japanese and English)
- Matsuura, N. 2009. Shinpan Ishikawa-no-Kaseki [Fossils of Ishikawa Prefecture (New Edition)].

Hokkoku Shimbun. Kanazawa. 273 p. (in Japanese, title translated herein)

Methner, K., M. Campani, J. Fiebig, N. Löffler, O. Kempf, and A. Mulch. 2020. Middle Miocene long-term continental temperature change in and out of pace with marine climate records. Scientific Reports.

DOI: 10.1038/s41598-020-64743-5.

- Nagao, T. 1928. Paleogene fossils of the Island of Kyushu, Japan, Part II. Science Reports of the Tohoku Imperial University, 2nd Series 12(1): 11–140, pls. 1–17.
- Nakajima, T., H. Iwano, T. Danhara, T. Yamashita, Y. Yanagisawa, Y. Tanimura, M. Watanabe, T. Sawaki, S. Nakanishi, H. Mitsuishi, O. Yamashina, and S. Imahori. 2019. Revised Cenozoic chronostratigraphy and tectonics in the Yatsuo Area, Toyama Prefecture, central Japan. Journal of the Geological Society of Japan 125(7): 483–516. (in Japanese with English abstract)
- Ogasawara, K. 1994. Neogene paleogeography and marine climate of the Japanese Islands based on shallow marine molluscs. Palaeogeography, Palaeoclimatology, Palaeoecology 108: 335–351.
- Otuka, Y. 1934. Tertiary structures of the northwestern end of the Kitakami Mountainland, Iwate Prefecture. Bulletin of the Earthquake Research Institute 12: 556–638, pls. 45–51.
- Oyama, K. 1950. Studies of fossil molluscan biocoenosis, No. 1. Biocoenological studies on the mangrove swamps, with description of new species from Yatsuo Group. Reports, Geological Survey of Japan (132): 1–15.
- Oyama, K., A. Mizuno, and T. Sakamoto. 1960. Illustrated handbook of Japanese Paleogene molluscs. Geological Survey of Japan. Kawasaki. 244 p., 71 pls.
- Ozawa, T., K. Inoue, S. Tomida, T. Tanaka, and T. Nobuhara. 1995. An outline of the Neogene warmwater molluscan faunas in Japan. Fossils (Palaeontological Society of Japan) (58): 20–27. (in Japanese with English abstract)
- Rafinesque, C. S. 1815. Analyse de la nature ou Tableau de l'univers et des corps organisés. Published by the author. Palermo. 224 p.
- Sangiorgi, F., W. Quaijtaal, T. H. Donders, S. Schouten, and S. Louwye. 2021. Middle Miocene

- temperature and productivity evolution at a Northeast Atlantic Shelf Site (IODP U1318, Porcupine Basin): global and regional changes. Paleoceanography and Paleoclimatology.
- DOI: 10.1029/2020PA004059.
- Sato, S., T. Chiba, T. Yamanaka, J. Nemoto, M. Shimamoto, and T. Matsubara. 2016. A catalogue of name-bearing type specimens of fossil Bivalvia (Mollusca) registered in the Tohoku University Museum. Bulletin of the Tohoku University Museum (15): 9–106.
- Sato, T., Y. Kanzaki, T. Okuyama, and S. Chiyonobu. 2010. Calcareous nannofossil biostratigraphy of the Miocene formations distributed in the Hokuriku to northern Japan. Scientific and Technical Reports of Graduate School of Engineering and Resource Science, Akita University (31): 37–45. (in Japanese with English abstract)
- Shimizu, M., and K. Kaneko. 1992. *Telescopium schencki* from the Miocene Kurosedani Formation at Do, Osawano-machi, Toyama Prefecture, Central Japan. Earth Science (Chikyu Kagaku) 46(6): 405–409. (in Japanese)
- Sowerby, G. B. 1825. A catalogue of the shells contained in the collection of the late Earl of Tankerville: arranged according to the Lamarckian conchological system: together with an appendix, containing descriptions of many new species. London. 92 p.
- Sowerby, G. B. 1840. Description of fossils from the Upper Secondary Formation of Cutch collected by C.W. Grant. Transactions of the Geological Society of London 2: 327–328.
- Stenzel, H. B. 1959. Cretaceous oysters of southwestern North America. International Geological Congress, 1956. El Sistema Cretacico v.1: 15–37.
- Stenzel, H. B. 1971. Treatise on invertebrate paleontology. Part N, Volume 3. Oysters. The University of Kansas. Lawrence. N954–N1224.

- Stokes, W. L., and P. B. Stifel. 1964. Color markings of fossil *Gryphaea* from the Cretaceous of Utah and new Jersey. Journal of Paleontology 38: 889–890.
- Tenison-Woods, J. E. 1878. On some new marine Mollusca. Transactions and Proceedings of the Royal Society of Victoria 14: 55–65.
- Tsuda, K. 1959. New Miocene molluscs from the Kurosedani Formation in Toyama Prefecture, Japan. Journal of the Faculty of Science, Niigata University, Series II 3(2): 67–110.
- Tsuda, K. 1960. Paleo-ecology of the Kurosedani fauna. Journal of the Faculty of Science, Niigata University, Series II 3(4): 171–203.
- Valentich-Scott, P., and E. R. Garfinkle. 2011. A new species of *Tucetona* (Bivalvia: Glycymerididae) from Mexico. Zootaxa 2769: 65–68.
- Vyalov, O. S. 1936. O klassifikatsii ustrits [On the classification of oysters]. Dokrady AN SSSR 4(1): 19–22. (in Russian, title translated herein)
- Vyalov, O. S. 1948. Paleogenobye Ustritsy Tadjik-skoy Depressii [Paleogene oysters of the Tajik Depression]. Trudy VNIGRI [Transaction of VNIGRI], Novaya Seriya [New Series] 38: 1–92, pls. 1–36. (in Russian, title translated herein)
- Vyalov, O. S. 1965. Nekotorye paleogenovye ustritsy [Some Paleogene oysters]. Lvov Geologicheskaya Obshchestvo, Paleontologicheskiy Sbornik [Lvov Geological Society, Paleontological Selection] 2(1): 5–13, pls. 1–4. (in Russian, title translated herein)
- Yanagisawa, Y. 1999. Diatom biostratigraphy of the lower to middle Miocene sequence in the Yatsuo area, Toyama Prefecture, central Japan. Bulletin of the Geological Survey of Japan 50(3): 139–165. (in Japanese)
- Yokoyama, M. 1925. Molluscan remains from the uppermost part of the Joban Coal-Field. Journal of the College of Science, Tokyo Imperial University 45(5): 1–34, pls. 1–6.

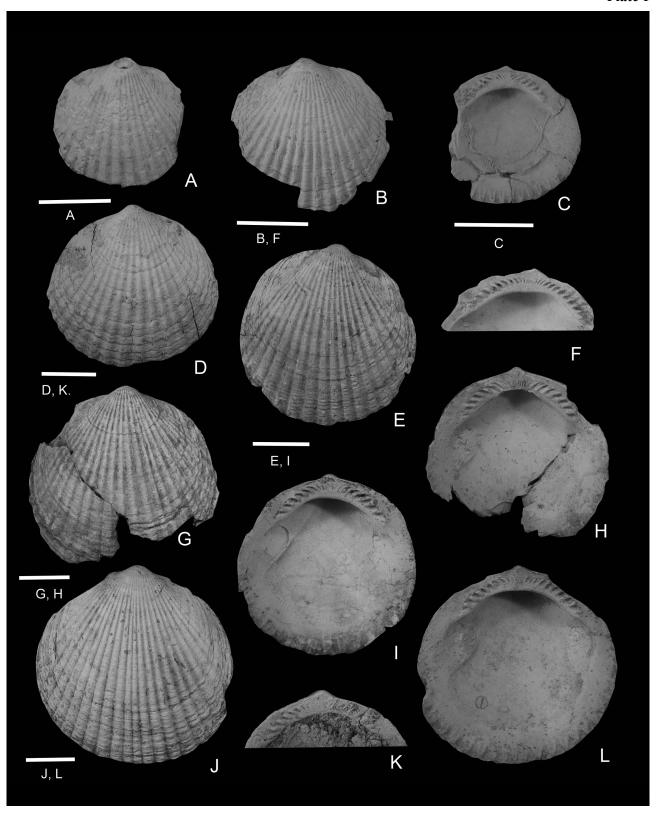
New bivalve species of *Tucetona*, *Pycnodonte* and *Ezocallista* from the Lower Miocene Kurosedani Formation at Fukushima, Yatsuo-machi in Toyama City, central Japan

Kazutaka Amano, Toshikazu Hamuro, and Masui Hamuro

Explanation of Plates 1–3

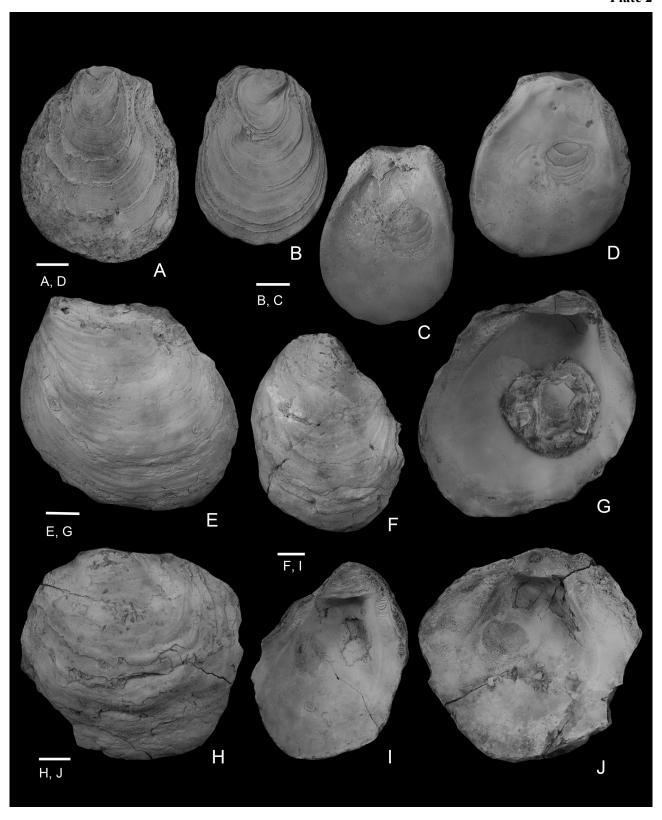
- Plate 1. Tucetona tsudai Amano n. sp. All scale bars= 10 mm.
- Fig. A. NMNS PM 68980-3, right valve.
- Figs. B, F. NMNS PM 68980-6, left valve; B, outer surface; F, hinge.
- Fig. C. NMNS PM 68980-10, left valve.
- **Figs. D, K.** Paratype 3, NMNS PM 68979, right valve; D, outer surface; K, hinge.
- **Figs. E, I.** Paratype 2, NMNS PM 68978, right valve; E, outer surface; I, inner surface.
- **Figs. G, H.** Paratype 1, NMNS PM 68977, right valve; G, outer surface; H, inner surface.
- **Figs. J, L.** Holotype, NMNS PM 68976, right valve; J, outer surface; L, inner surface.

Plate 1



- Plate 2. *Pycnodonte* (*Phygraea*) *matsubarai* Amano n. sp. All scale bars= 10 mm.
- **Figs. A, D.** Paratype 2, NMNS PM 68985, right valve; A, outer surface; D, inner surface.
- **Figs. B, C.** Paratype 3, NMNS PM 68986, right valve; B, outer surface; C, inner surface.
- **Figs. E, G.** Paratype 1, NMNS PM 68984, left valve; E, outer surface; G, inner surface.
- **Figs. F, I.** NMNS PM 68990-14, left valve; F, outer surface; I, inner surface.
- **Figs. H, J.** Holotype, NMNS PM 68983, left valve; H, outer surface; J, inner surface.

Plate 2



- Plate 3. *Ezocallista toyamaensis* Amano n. sp. AAM= Anterior adductor muscle scar, PAM= Posterior adductor muscle scar. White arrow shows the deepest point of pallial sinus. All scale bars= 10 mm.
- **Figs. A, K.** Paratype 1, NMNS PM 69008, left valve; A, hinge; K, outer surface.
- Fig. B. NMNS PM 69013, hinge of left valve.
- **Figs. C, F, N, O.** Paratype 4, NMNS PM 69011, right valve; C, enlargement of hinge; F, dorsal view; N, outer surface; O, inner surface.
- **Figs. D, J.** Paratype 3, NMNS PM 69010, right valve; D, hinge; J, outer surface.
- **Figs. E, L, M.** Paratype 5, NMNS PM 69012, right valve; E, dorsal view; L, outer surface; M, inner surface.
- Figs. G. Paratype 2, NMNS PM 69009, right valve, outer surface.
- **Figs. H, I.** Holotype, NMNS PM 69007, left valve; H, outer surface; I, inner surface.

Plate 3

