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Chemosymbiotic bivalves from the lower Miocene Kurosedani Formation in Toyama Prefecture, central Honshu, Japan

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Abstract. Many molluscan fossils have been found from the turbidite deposits of the lower Miocene Kurosedani Formation at Kakuma in Toyama City. They include six chemosymbiotic bivalves, namely Solemyidae gen. et sp. indet., *Nucinella* sp., *Luinoma* cf. *acutilineatum* (Conrad), *Conchocele yatsuoensis* sp. nov., *Pliocardia kawadai* (Aoki) and *Adulomya chitanii* Kanehara. This is the oldest record of chemosymbiotic species in the Japan Sea region. *Nucinella* has been unknown from the Cenozoic deposits in the Japan Sea borderland and from the Recent Japan Sea. Moreover, the vesicomyids *P. kawadai* and *A. chitanii* are shared with those from the lower Miocene Honya Formation in Fukushima Prefecture and from the middle Miocene Nupinai Formation in eastern Hokkaido. This supports our hypothesis that the invasion of chemosymbiotic species from the Pacific side to the Japan Sea took place soon after the formation of a deep-sea basin in the Japan Sea.

Key words: Chemosymbiotic bivalves, *Conchocele*, Kurosedani Formation, Miocene, *Nucinella*

Introduction

Chemosynthetic communities inhabit deep-sea hydrothermal vents, hydrocarbon seeps and organic falls by relying on chemoautotrophic bacteria for nutrition (Van Dover, 2000). These communities have been recorded from the Cretaceous to Recent in Japan (Majima *et al.*, 2005). Among them, four whale-fall communities and two wood-fall communities have been also recognized (Amano and Little, 2005; Amano *et al.*, 2007b; Kiel *et al.*, 2008; Jenkins *et al.*, 2018; Amano *et al.*, 2018). Other than these communities, most faunas are hydrocarbon seep faunas in Japan. Moreover, no Cretaceous and Paleogene seep communities have been recorded on the Japan Sea side in contrast with several Cretaceous and Paleogene records in Hokkaido and on the Pacific side (Majima *et al.*, 2005; Amano and Jenkins, 2011; Amano *et al.*, 2013).

As the Japan Sea was formed as a marginal sea at least by *ca.* 18 Ma (Ninomiya *et al.*, 2014), only two hydrocarbon seep communities are recorded from the lower Miocene Taishu Group in Tsushima Island, westernmost part of the sea (Ninomiya, 2011, 2012) and from the uppermost lower to lowermost middle Miocene Higashibessho Formation in Toyama, central Honshu (Amano *et al.*, 2001, 2004). Four chemosymbiotic species occurred from the Higashibessho Formation at Shimo-sasahara; the lucinid *Lucinoma acutilineatum* (Conrad), the thyasirid *Thyasira tokunagai* Kuroda and Habe, the vesicomyids *Pliocardia kawadai* (Aoki) and *Adulomya hamuroi* Amano and Kiel (Amano *et al.*, 2001, 2004; Amano and Kiel, 2011).

We newly found molluscan fossils including chemosymbiotic bivalves from the lower Miocene Kurosedanai Formation 600 m southeast of Kakuma nearby Shimo-sasahara in Toyama City. This fauna includes six chemosymbiotic species such as a large *Nucinella* and a new species of *Conchocele* and corresponds to the oldest record of chemosymbiotic bivalves from the main part of the Japan Sea region. Hence, we shall describe the fauna and discuss its biogeographic significance.

Material and methods

Many molluscan fossils occurred from a large outcrop located 600 m southeast of Kakuma in Toyama

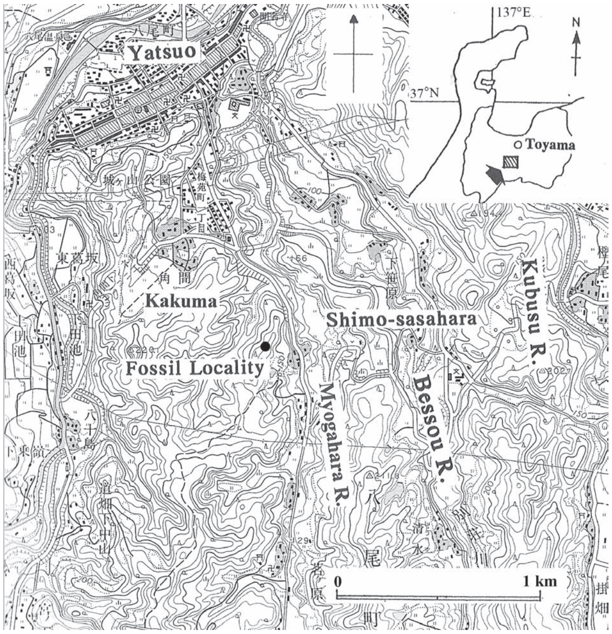

Figure 1. Locality of the fossils (using the topographical map of "Yatsuo", scale 1:25,000, published by the Geospatial Information Authority of Japan).

City, Toyama Prefecture (Figure 1). Turbidite deposits are exposed at this locality and consist of alternating medium-grained sandstones (about 20 cm in thickness) and dark gray mudstones (about 5 cm in thickness). Both rocks yield many small plant fragments. This horizon is stratigraphically about 75 m below the locality of the Higashibessho Formation at Shimo-sasahara and is included in the Monmyoji Alternation Member which is the uppermost part of the lower Miocene Kurosedani Formation (Sakamoto and Nozawa, 1960; Yanagisawa, 1999).

Twenty-two species of bivalves, six species of gastropods and one species of scaphopod have been identified from both mudstone and sandstone at this locality (Table 1). Among them, six chemosymbiotic bivalves are included, namely the nucinellid *Nucinella* sp., Solemyidae gen. et sp. indet., the lucinid *Lucinoma* cf. *acutilineatum* (Conrad), the thyasirid *Conchocele yatsuoensis* sp. nov., and the vesicomyids *Pliocardia kawadai* (Aoki) and *Adulomya chitanii* Kanehara. Other than one specimen of *Lucinoma* found in a small calcareous concretion, other specimens of chemosynthetic species were collected from sandstone or mudstone.

Most species from the mudstone are deep-water dwellers such as *Lamellinucula hokoensis* (Kanehara), *Acila* (*Acila*) *submirabilis* Makiyama, *Bathymalletia inermis* (Yokoyama), *Portlandia* (*Portlandella*) *lischkei* (Smith), *Delectopecten* sp., *Periploma yokoyamai* Makiyama, *Poromya osawanoensis* Tsuda and *Ginebis osawanoensis* (Tsuda). On the other hand, some shallow-sea species such as *Anadara* sp., *Mactra* sp., *Donacilla* sp., *Cardilia toyamaensis* Tsuda, *Veremolpa minoensis* Itoigawa and

Table 1. List of molluscan fossils from the Kurosedani Formation at the fossil locality near Kakuma. Numbers mean number of individuals (number in parenthesis = articulated specimens). *, chemosymbiotic bivalve; °, shallow-water species; M, mudstone; S, sandstone.

Species	M	S
Solemyidae gen. et sp. indet.*	1	
Nucinella sp.*		1
Lamellinucula hokoensis (Kanehara)	3 (1)	
Acila (*Acila*) *submirabilis* Makiyama	2 (2)	
Bathymalletia inermis (Yokoyama)	4	3
Neilonella tsukigawaensis Kurihara	2	
Portlandia (*Portlandella*) *lischkei* (Smith)	1	
Anadara sp.°		1
Limopsis sp.		1
Delectopecten sp.	7	
Propeamussium sp.		1
Lucinoma cf. *acutilineatum* (Conrad)*		3
Conchocele yatsuoensis sp. nov.*		13 (2)
Merisca sp.	1	
Mactra sp.°		1
Donacilla sp.°		1
Cardilia toyamaensis Tsuda°		1
Pliocardia kawadai (Aoki)*	8 (2)	26 (3)
Adulomya chitanii Kanehara*		48 (48)
Veremolpa minoensis Itoigawa°		17
Periploma yokoyamai Makiyama	2	1
Poromya osawanoensis Tsuda	1	
Ginebis osawanoensis (Tsuda)	1	
Protorotella depressa Makiyama°		5
Cryptonatica sp.	1	3
Eocylichna sp.	3	
Eoscaphander corpulenta (Yokoyama)	8	
Bowdenatheca sp.	18	
Laevidentalium sp.		1

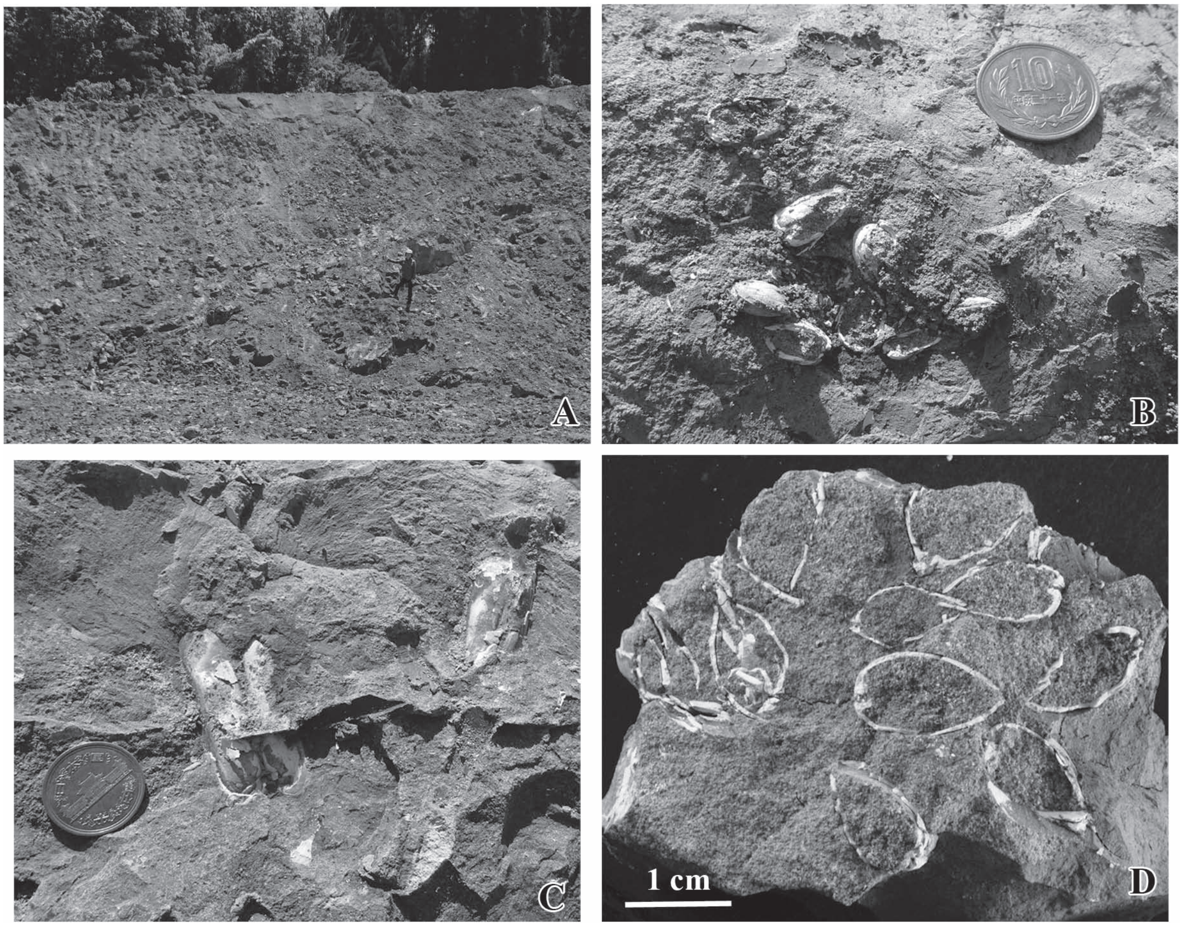

Figure 2. Occurrence of the chemosymbiotic bivalves. **A,** outcrop of the fossil locality; **B,** occurrence of *Pliocardia kawadai* (Aoki) showing local aggregation in sandstone; **C, D,** occurrence of *Adulomya chitanii* Kanehara from sandstone; C, occurrence in the deposits; D, cross section of aggregation of *Adulomya chitanii* from sandstone.

Protorotella depressa Makiyama co-occurred with deep-water shells such as *Bathymalletia inermis* (Yokoyama), *Propeamussium* sp. and some chemosymbiotic species in the sandstone (Table 1). These shallow-water species can be interpreted as having been transported from shallow water to the deep sea by turbidity currents. On the other hand, although *Adulomya chitanii* occurred as aggregations of articulated valves from the sandstone (Figure 2D), this species might have lived near the deep-sea depositional site because of its deep-sea paleoecology and occurrence. *Pliocardia kawadai* occurred from both mudstone and sandstone. In both cases, this species includes some articulated valves. Several articulated specimens of this species were locally crowded together even in the sandstone (Figure 2B). From this occurrence, this species also might have lived in the deep-sea depositional site.

We measured the following dimensional characters of the fossils: shell length, height, and anterior length. Moreover, for *Conchocele* species, we also measured the apical angle. All illustrated and measured specimens are stored at the National Museum of Nature and Science, Tsukuba (NMNS). Other institutional abbreviations are as follows: TKD, Department of Geology and Mineralogy, Faculty of Science, Tokyo Kyoiku Daigaku, Tokyo (now University of Tsukuba); IGPS, Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Sendai.

Systematic description

Family Nucinellidae Vokes, 1956
Genus ***Nucinella*** Wood, 1851

Type species.—*Pleurodon ovalis* Wood, 1840; Recent North Atlantic.

Nucinella sp.

Figure 3A, B, D, E

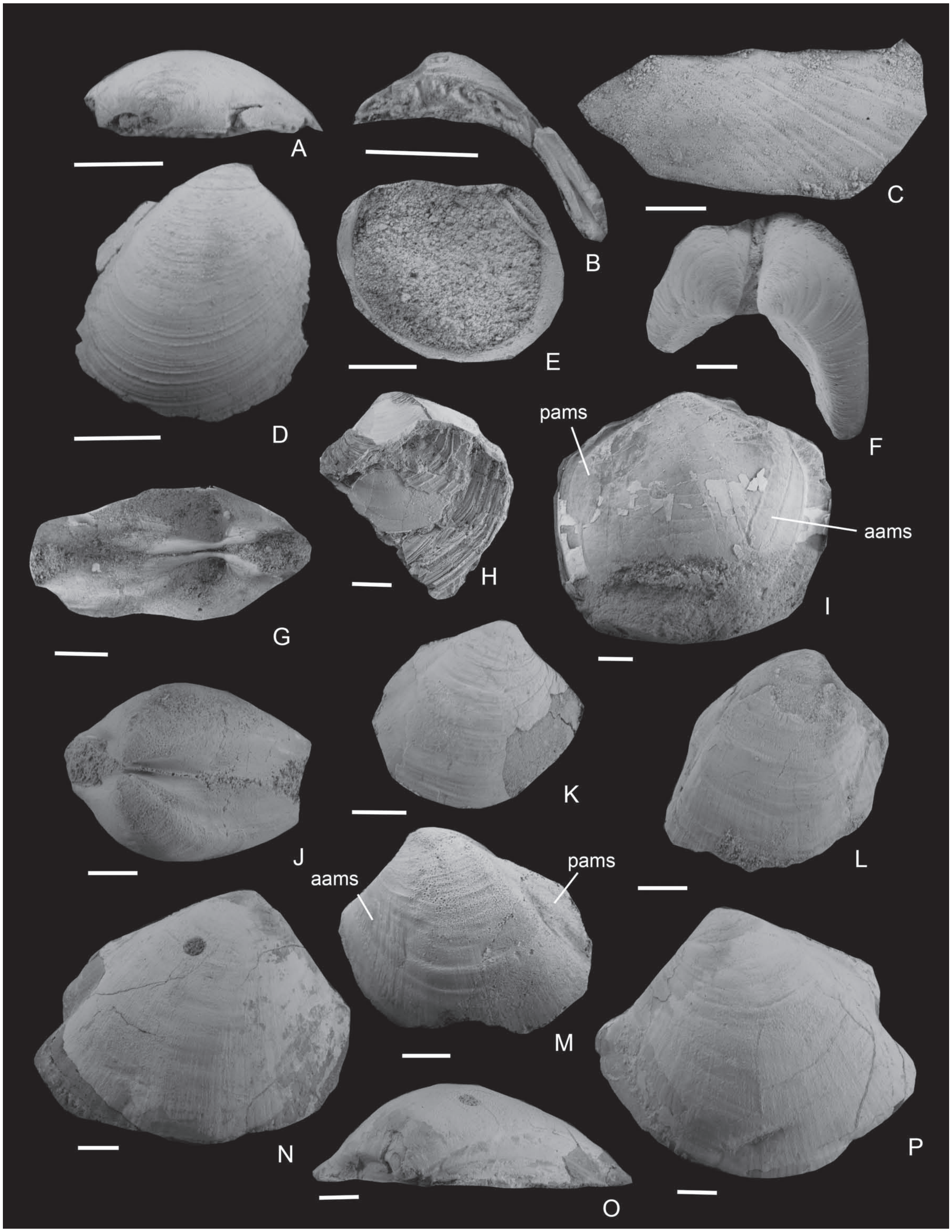

Figure 3. Chemosymbiotic bivalves except for the vesicomyids from the Kurosedani Formation at Kakuma. **A, B, D, E,** *Nucinella* sp., NMNS PM 27995; A, dorsal view; B, hinge area of left valve; D, frontal view of left valve; E, silicone rubber cast of inner mold after extracting shells; **C,** Solemyidae gen. et sp. indet., NMNS PM 27996, outer cast of right valve (silicone rubber); **F, G, J–P,** *Conchocele yatsuoensis* sp. nov.; F, N–P, holotype, NMNS PM 27999; F, dorsal view (silicone rubber); N, right valve; O, dorsal view; P, left valve; G, J, M, paratype, NMNS PM 28000; G, silicone rubber cast of inner mold, showing edentulous hinge; J, dorsal view of inner mold; M, inner mold of left valve; K, paratype, NMNS PM 28001, right valve; L, paratype, NMNS PM 28002, right valve showing many fine radial riblets; **H, I,** *Lucinoma* cf. *acutilineatum* (Conrad); H, NMNS PM 27998, left compressed valve; I, NMNS PM 27997, left valve. Abbreviations: aams, anterior adductor muscle scar; pams, posterior adductor muscle scar. All scale bars show 5 mm.

Material examined.—One left valve, NMNS PM 27995 was examined.

Dimension.—Length, 13.6 mm+; height, 13.2 mm.

Description.—Shell large for genus, thin-walled, moderately inflated, nuculiform, inequilateral. Umbo produced above hinge line; beak opisthogyrate and located at anterior two-thirds of shell length. Anterodorsal margin short, nearly straight and anterior margin broadly arcuated; ventral margin well rounded; posterior margin nearly straight. Hinge plate rather wide and narrow triangular flat area existing below beak; anterior four cardinal teeth straight, long and slightly oblique anteriorly; two middle teeth short, nearly perpendicular to base of hinge plate; posterior four teeth long and oblique posteriorly; anterior lateral tooth long. Surface smooth except for regular growth lines and very weak fine radial striations. Inner surface of ventral margin smooth. Anterior muscle scar and pallial line unknown.

Remarks.—The present species is closely similar to the Recent species *Nucinella maxima* (Thiel and Jackel, 1931) from the Zanzibar Channel, off Tanzania in having a large nuculiform shell (12.5 mm in height) with a produced umbo above the hinge line. However, the Kurosedani species differs from *N. maxima* by its numerous cardinal teeth (seven in *N. maxima*) and smaller middle cardinal teeth.

Nucinella viridis Matsukuma, Okutani and Tsuchi, 1982 living off Nojimazaki, Boso Peninsula, central Honshu also has a similar shape and size (up to 10.4 mm) to the Kurosedani species. However, *Nucinella viridis* can be easily distinguished from the Kurosedani species in having less numerous teeth (three anterior and two posterior teeth).

Nucinella gigantea Amano, Jenkins and Hikida, 2007 from the Campanian Omagari Formation can be separated from the Kurosedani species in having a larger shell (up to 18.4 mm in length) and fewer cardinal teeth (six in *N. gigantea*).

Some species of *Nucinella* over 10 mm have been recorded from the seep carbonates from uppermost Jurassic to lowermost Cretaceous deposits on Spitsbergen Island (Hryniewicz *et al.*, 2014), mid-Cretaceous deposits at Awanui II on the North Island of New Zealand (Kiel *et al.*, 2013), Campanian Omagari Formation in Hokkaido (Amano *et al.*, 2007a), and the upper Eocene to lower Oligocene Tanamigawa Formation in Honshu (Amano *et al.*, 2013). The Kurosedani species is the first record of the Miocene *Nucinella* found with some chemosymbiotic bivalves.

Stratigraphic and geographic distribution.—Early Miocene: Kurosedani Formation in Toyama Prefecture.

Family Thyasiridae Dall, 1900

Genus ***Conchocele*** Gabb, 1866

Type species.—*Thyasira bisecta* Conrad, 1849; Miocene, Astoria Formation, Oregon, USA.

Conchocele yatsuoensis sp. nov.

Figure 3F, G, J–P

Etymology.—The present new species is named for the old town name around the type locality.

Type specimens.—Holotype, NMNS PM 27999; paratypes, NMNS PM 28000–28002.

Type locality.—Outcrop located 600 m southeast of Kakuma in Toyama City, Toyama Prefecture; Kurosedani Formation.

Material.—All of the nine specimens treated here were collected from the type locality.

Dimensions.—See Table 2.

Diagnosis.—Small-sized and thin-shelled *Conchocele* with deep posterior sulcus, deeply excavated lunule demarcated by distinct groove, weakly developed medial flat area, posterior adductor scar confined to inside of posterior fold, and edentulous hinge.

Description.—Shell small for genus, up to 39.8 mm, thin, subtriangular in shape (height/length = 0.75–1.19), equivalve and inequilateral; apical angle ranging from 91° in small specimen to 111° in adult. Anterodorsal margin slightly concave, making right angle with rounded ventral margin; posterodorsal margin long and nearly straight. Umbo situated at anterior one-fourth to two-fifths of shell length. Posterior sulcus wide and deep; posterior fold wide and medially swelled. Lunule very deep, long and broad. Medial flat area from beak to ventral margin distinct in larger specimens. Hinge plate very narrow and edentulous. Anterior adductor muscle scar moderately elongate, slightly detaching with pallial line; posterior adductor scar ovate, confined to inner part of posterior sulcus and fold, not extending to main disc. Shell surface sculptured by irregular commarginal undulations; weathered surface sometimes sculptured by many very weak radial striations.

Remarks.—*Conchocele yatsuoensis* sp. nov. is most closely similar to *C. excavata* (Dall, 1901) living in the deep sea (800–2520 m) from off Juan de Fuca to Baja California (Coan *et al.*, 2000) and shallow sea (9–120 m) from Guaymas to Costa Rica (Coan and Valentich-Scott, 2012) in its thin and small shell, medial flat area, excavated lunule and medially swelled posterior sulcus. However, the new species can be distinguished by having a lower shell and a less swelled posterior fold.

Conchocele compacta minor Omori, 1954 described from the middle Miocene Kobana Formation in Tochigi Prefecture has also a rather small shell (up to 20.8 mm in

Table 2. Measurements of *Conchocele yatsuoensis* sp. nov. *H/L* = height/length; *AL/L* = anterior length/length.

Specimens	Type	Length (mm)	Height (mm)	*AL* (mm)	Apical angle (°)	*H/L*	*AL/L*	Valve
NMNS PM 27999	holotype	39.8	31.9	10.0	106	0.80	0.25	right
NMNS PM 28000	paratype	25.9	19.5	5.2	106	0.75	0.20	left
NMNS PM 28001	paratype	16.3	15.6	4.2	101	0.96	0.26	right
NMNS PM 28002	paratype	19.3	22.9	5.2	109	1.19	0.27	right
NMNS PM 28003		25.9	22.4	9.9	111	0.86	0.38	left
NMNS PM 28004		31.0	27.2	10.3	107	0.88	0.33	left
NMNS PM 28005		20.6	18.9	8.8	103	0.92	0.43	left
NMNS PM 28006		16.3	15.6	4.7	103	0.96	0.29	right
NMNS PM 28007		8.9	8.1	2.4	91	0.91	0.27	left

length) and an excavated lunule. However, *C. compacta minor* has 27 to 30 distinct radial ribs on the surface which are not observed in the new species. When Kamada (1962) described *C. compacta minor* from the lower Miocene Kokozura Formation in northern Ibaraki Prefecture, he pointed out the similarity between this subspecies and *Thyasira subexcavata* Yabe and Nomura, 1925 probably from the same formation. As a matter of fact, the latter species shares small size, medial flat area and excavated lunule with *Conchocele yatsuoensis* sp. nov. and *C. compacta minor*. However, based on our observations, the holotype of *T. subexcavata* (IGPS 6973) has a short auricle above the posterior fold which is a characteristic feature of the genus *Thyasira* Lamarck, 1818.

Conchocele yatsuoensis sp. nov. can be easily distinguished from *C. bisecta* (Conrad, 1849), the type species of *Conchocele*, by having a smaller and subtriangular shell. The new species is also different from *Conchocele taylori* Hickman, 2015 reexamined and recorded from Paleogene deposits on both sides of the northern Pacific by Hryniewicz *et al.* (2017) by having a subtriangular shell despite sharing small shell size.

Stratigraphic and geographic distribution.—Early Miocene: Kurosedani Formation in Toyama Prefecture.

Family Vesicomyidae Dall and Simpson, 1901
Subfamily Pliocardiinae Woodring, 1925
Genus ***Pliocardia*** Woodring, 1925

Type species.—*Anomalocardia bowdeniana* Dall, 1903; Pliocene, Bowden Formation in Jamaica.

Pliocardia kawadai (Aoki, 1954)

Figure 4C, E, J–O

Lamelliconcha kawadai Aoki, 1954, p. 36, pl. 2, figs. 1, 10, 12–15, 22.
Vesicomya kawadai (Aoki). Kamada, 1962, p. 88, pl.8, fig. 2a, b; Amano *et al.*, 2001, p. 192, figs. 3–5, 8–11; Amano *et al.*, 2007b, fig. 3D, E, G, J.
Pliocardia kawadai (Aoki). Amano and Kiel, 2012, p. 80, figs. 2–4, 6, 7, 9–12.

Type specimen.—Holotype, TKD 5909.

Type Locality.—Donosaku, Kamikatayose (= Taira-Kamikatayose-Donosaku), Iwaki City, Fukushima Prefecture; lower Miocene Kabeya (= Honya) Formation.

Material examined.—Eight specimens were examined. All dimensions are shown in Table 3.

Remarks.—The hinge structure of Kurosedani specimens is consistent with the type specimens of this species. These specimens are characterized by their medium-sized (up to 43.1 mm), veneriform shell with shallow lunular incision. Although Amano and Kiel (2012) described the pallial sinus as shallow and V-shaped, the depth of the sinus varies from specimen to specimen. The sinus of the Kurosedani specimen is very shallow just before the posterior muscle scar (Figure 4N).

Pliocardia? *tanakai* Miyajima, Nobuhara and Koike, 2017 from the middle Miocene Bessho Formation in Nagano Prefecture is distinguished from *P. kawadai* by having a lower shell and by lacking a pallial sinus.

Stratigraphic and geographic distribution.—Early Miocene: Honya Formation in Fukushima Prefecture and Kurosedani Formation in Toyama Prefecture. Latest early Miocene to earliest middle Miocene: Higashibessho Formation in Toyama Prefecture. Middle Miocene: Nupinai Formation in Hokkaido.

Genus ***Adulomya*** Kuroda, 1931

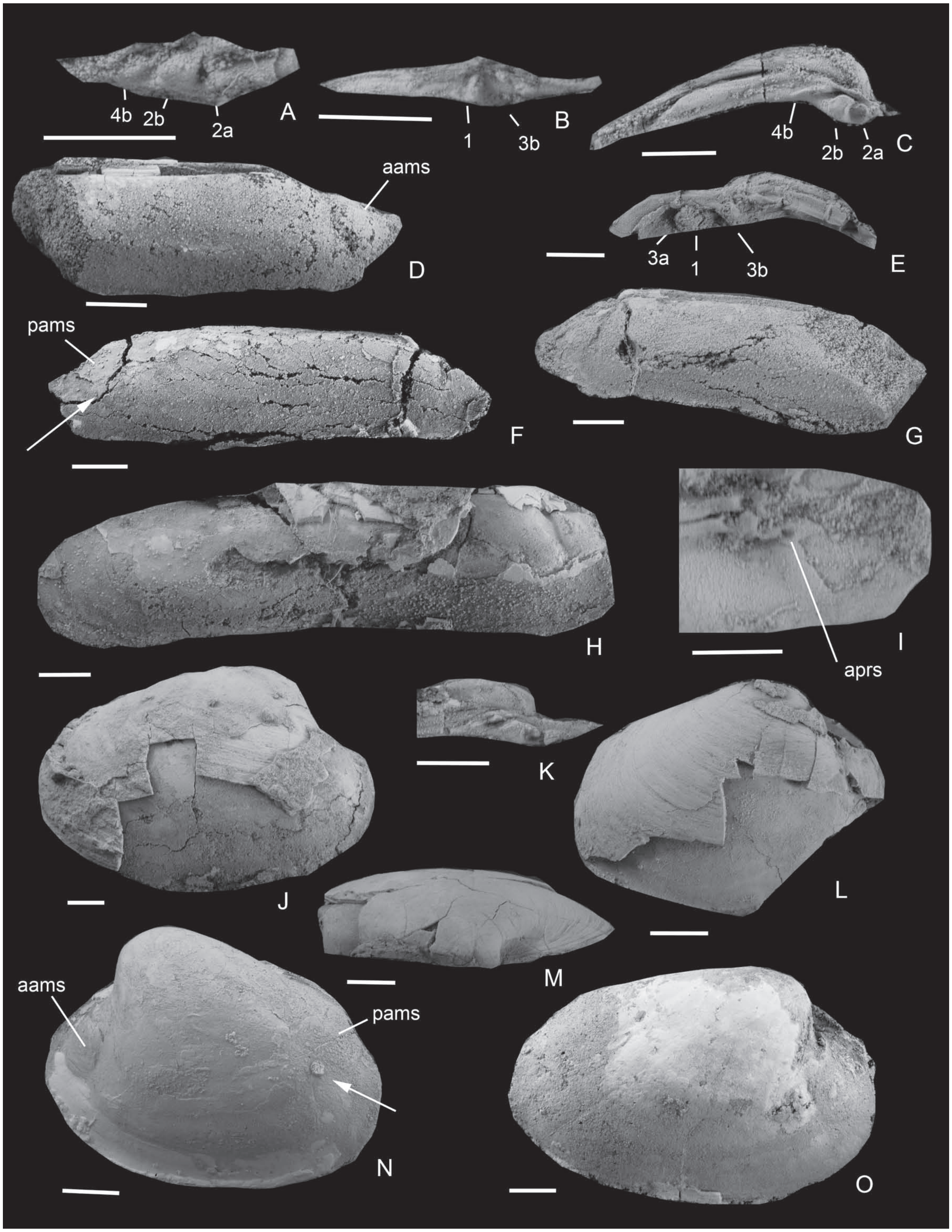

Figure 4. Vesicomyid bivalves from the Kurosedani Formation at Kakuma. **A, B, D, F–I,** *Adulomya chitanii* Kanehara; A, B, NMNS PM 28019, hinge of left (A) and right (B) valve; D, NMNS PM 28016, right valve; F, G, NMNS PM 28017; F, right valve showing a V-shaped pallial sinus (white arrow); H, NMNS PM 28020, right valve; I, NMNS PM 28018, hinge area of both valves (silicone rubber); **C, E, J–O,** *Pliocardia kawadai* (Aoki); C, NMNS PM 28013, hinge plate of left valve; E, NMNS PM 28015, hinge plate of right valve (silicone rubber); J, NMNS PM 28011, right valve; K, M, NMNS PM 28014, hinge plate of left valve (K) and dorsal view (M) showing demarcated lunule by the groove; L, NMNS PM 28012, right valve; N, NMNS PM 28008, inner surface of left valve, having a shallow V-shaped pallial sinus; O, NMNS PM 28010, inner surface of right valve. Abbreviations: aams, anterior adductor muscle scar; apms, anterior pedal muscle scar; pams, posterior adductor muscle scar. All scale bars show 5 mm.

Table 3. Measurements of *Pliocardia kawadai* (Aoki). *H/L* = height/length; *AL/L* = anterior length/length.

Specimens	Length (mm)	Height (mm)	*AL* (mm)	*H/L*	*AL/L*	Valve
NMNS PM 28008	31.8	23.4	7.9	0.74	0.25	left
NMNS PM 28009	33.3	24.7	7.8	0.74	0.23	left
NMNS PM 28010	39.3	24.3	7.8	0.62	0.20	right
NMNS PM 28011	43.1	28.6	13.2	0.66	0.31	right
NMNS PM 28012	24.2+	18.3	–	–	–	right

Type species.—*Adulomya uchimuraensis* Kuroda, 1931; Middle Miocene Bessho Formation, Nagano Prefecture, central Honshu.

Adulomya chitanii Kanehara, 1937

Figure 4A, B, D, F–I

Adulomya chitanii Kanehara, 1937, p. 19, pl. 5, figs. 1, 6–9; Kamada, 1962, p. 39, pl. 1, figs. 4–7; Amano and Kiel, 2011, p. 80, figs. 3–12.
"*Adulomya*" *chitanii* Kanehara. Aoki, 1954, p. 31, pl. 1, figs. 9–11.
Calyptogena chitanii (Kanehara). Kanno and Akatsu, 1972, pl. 8, figs. 13, 14; Amano and Little, 2005, fig. 6B–D; Amano and Jenkins, 2007, fig. 2C; Amano *et al.*, 2007, fig. 3C, F, H.
Calyptogena sp., Yamaoka, 1993, pl. 4, figs. 1, 6, 7.
? *Calyptogena chitanii* (Kanehara). Shikama and Kase, 1976, pl. 2, fig. 6; Hirayama, 1973, p. 175, pl. 15, figs. 12, 13; Yamaoka, 1993, pl.4, figs. 2, 3.
? *Akebiconcha chitanii* (Kanehara). Hayashi and Miura, 1973, pl. 1, fig. 26; Hayashi, 1973, pl. 5, fig. 6.
non *Akebiconcha chitanii* (Kanehara). Kanno and Ogawa, 1964, pl. 1, figs. 17, 18; Kanno and Arai, 1964, pl. 1, figs. 19–22; Kanno, 1967, p. 401, pl. 1, figs. 9–11, 15.

Type specimen.—IGPS 87339 as neotype designated by Amano and Kiel (2011).

Type locality.—Tangozawa, Iwaki City, Fukushima Prefecture; Miocene, Honya Formation.

Material examined.—Although 48 specimens were obtained, most specimens are fragments. Only seven imperfect specimens were examined.

Remarks.—The Kurosedani specimens have a rather small size for the genus, up to 55.5 mm in length, elongate-quadrate shape (height/length = 0.29). Two cardinal teeth (1, 3b) in the right valve and three ones (2a, 2b, 4b) in the left valve can be observed. Also a small and deep pedal retractor scar was observed just above the anterior adductor muscle scar. Very small and V-shaped pallial sinus can be recognized just before the posterior adductor muscle scar. Based on these characters, the Kurosedani specimens are safely identified with *Adulomya chitanii* Kanehara, 1937.

Adulomya hamuroi Amano and Kiel, 2011 from the uppermost lower to lowermost middle Miocene Higashibessho Formation at Shimo-sasahara is similar to *A. chitanii*. However, *A. hamuroi* is different from *A. chitanii* by having a higher shell (height/length = 0.38–0.47), no pallial sinus, thick anterior cardinal tooth (1) and slightly bifid posterior cardinal tooth (3b) in the right valve.

Stratigraphic and geographic distribution.—Early Miocene: Honya, Mizunoya and Kamenoo formations in Fukushima Prefecture, the Toyohama Formation of Morozaki Group in Aichi Prefecture and the Kurosedani Formation in Toyama Prefecture. Middle Miocene: Nupinai Formation in Hokkaido.

Discussion

From the Kurosedani Formation, many molluscan fossils have been described by Tsuda (1959, 1960). Based on the occurrence of molluscs, Tsuda (1960) estimated that the upper part of the Kashio Member (Tsuda, 1953) which mostly overlaps with the Monmyoji Member (Sakamoto and Nozawa, 1960) was deposited in deep water with some transported species from shallow water. As mentioned above, the assemblage from Kakuma also shows the same pattern of occurrence. Six chemosymbiotic bivalves have been first recognized from the turbidite deposits of the lower Miocene Kurosedani Formation, namely, *Nucinella* sp., Solemyidae gen. et sp. indet., *Lucinoma* cf. *aculilineatum*, *Conchocele yatsuoensis* sp. nov., *Pliocardia kawadai* and *Adulomya chitanii*. They correspond to the earliest records of chemosymbiotic bivalves in the Japan Sea region. From the lower Miocene Middle Formation (*ca.* 16 Ma) of the middle part of the Taishu Group on Tsushima Island, westernmost part of the Japan Sea, some ill-preserved chemosynthetic species such as the solemyid *Acharax* spp., the bathymodiolines *Bathymodiolus* sp. and *Adipicola* sp., the vesicomyid *Calyptogena* spp. [= *Adulomya*? spp.] were described and illustrated (Ninomiya, 2011; Table 4). However, the identifications of these taxa are somewhat problematic even at the genus level because that author did not make them based on the hinge and inner structure. According to Yanagisawa (1999), the *Crucidenticula kanayae* zone (16.3–16.9 Ma; Yanagisawa and Akiba, 1998) was recognized in the lower part of the Higashibessho Formation conformably overlying the Kurosedani Formation. From these data, the chemosymbiotic species from the Kurosedani Formation at Kakuma are probably the oldest record in the Japan Sea region.

As discussed by Amano *et al.* (2004), both shallow- and deep-water assemblages of the Higashibessho Formation conformably overlying the Kurosedani Formation

Table 4. Comparison of the chemosymbiotic bivalves from the Kurosedani Formation with the other Japanese early to middle Miocene hydrocarbon-seep bivalves.

Species	Japan Sea side				Pacific Ocean side			
Areas	Japan Sea side				Pacific Ocean side			
Prefectures	Toyama	Toyama	Nagano	Nagasaki	Hokkaido	Fukushima	Ibaraki	Wakayama
Formations	Kurosedani	Higashibessho	Bessho	Taishu Group (middle part)	Nupinai	Honya	Kokozura	Shikiya
Acharax johnsoni (Dall)					x			
A. yokosukensis Kanie and Kuramochi							x	cf.
Acharax spp.				x				
Solemyidae gen. et sp. indet.	x							
Nucinella sp.	x							
Bathymodiolus akanudaensis (Kuroda)			x					
Bathymodiolus sp.				x				
Adipicola sp.				x				
Lucinoma acutilineatum (Conrad)	cf.	x					x	
Lucinoma? sp.								x
Conchocele bisecta (Conrad)					x	x	x	
C. minor Omori							x	
C. yatsuoensis sp. nov.	x							
Pliocardia kawadai (Aoki)	x	x			x	x		
Pliocardia? *tanakai* Miyajima, Nobuhara and Koike			x					
Adulomya chitanii Kanehara	x				x	x		
A. hamuroi Amano and Kiel		x						
A. uchimuraensis (Kuroda)			x					x
A. akanudaensis (Tanaka)			x					
Calyptogena spp. [=*Adulomya*? spp.]				x				
Archivesica sakoi Amano, Jenkins, Ohara and Kiel								x
References	This study	Amano *et al.* (2001, 2004)	Miyajima *et al.* (2017)	Ninomiya (2011)	Amano and Kiel (2011, 2012)	Amano and Kiel (2011, 2012)	Amano and Ando (2011)	Amano *et al.* (2014)

are similar to those of Setouchi Province, which is connected to the the Pacific Ocean. During the latest early to earliest middle Miocene, the Japan Sea was connected to the Pacific Ocean by deep-sea pathways. The age of the Kurosedani fauna from Kakuma corresponds to the timing of the formation of a deep-sea basin in the Japan Sea, and is just after the invasion of warm shallow-water fauna into the Japan Sea (Chinzei, 1991; Sato *et al*., 2010).

The early to middle Miocene hydrocarbon seep faunas in Japan have few common species with each other

Table 5. Species of the genus *Nucinella* found from fossil hydrocarbon-seep sites.

Species name	Locality	Age	Max. length (mm)	Reference
Nucinella svalbadensis Hryniewicz, Little and Nakrem	Spitsbergen Is.	latest Jurassic to earliest Cretaceous	32.0	Hryniewicz *et al.* (2014)
N. gigantea Amano, Jenkins and Hikida	Hokkaido	Cenomanian to Campanian	18.4	Amano *et al.* (2007a), Kiel *et al.* (2008)
Nucinella sp.	North Is. of NZ	mid-Cretaceous	*ca.* 5?	Kiel *et al.* (2013)
Nucinella sp.	Honshu	late Eocene to early Oligocene	22.5	Amano *et al.* (2013)

(Table 4). The Kurosedani fauna from Kakuma shares the vesicomyid *Pliocardia kawadai* with the Higashibessho fauna at Shimo-sasahara but is more similar to the early to middle Miocene faunas from the Pacific side of northern Japan. Occurrences of the vesicomyids *Pliocardia kawadai* and *Adulomya chitanii* from the Kurosedani Formation are common to the lower Miocene Honya Formation, Fukushima Prefecture, northeastern Honshu and the middle Miocene Nupinai Formation in eastern Hokkaido (Table 4). These data support our hypothesis that the invasion of chemosymbiotic species to the Japan Sea took place soon after its formation (*ca.* 18 Ma) along a migration route from northern Japan through central Honshu, in contrast with the Higashibessho normal deep-sea fauna. In the late early Miocene, the Pacific Ocean and the Japan Sea were connected through central Honshu (see Iijima and Tada, 1990; Kano *et al*., 1991).

The occurrence of *Nucinella* sp. from the Kurosedani Formation is the first record from the Cenozoic deposits in the Japan Sea region as well as the Recent Japan Sea. The Cenozoic occurrence of this genus was previously confined to the Pacific side of southern Honshu and Kyushu (Matsukuma *et al*., 1982; Amano *et al*., 2013). Moreover, there is no record of this genus from the Recent Japan Sea (Higo *et al*., 1999). According to Higo *et al.* (1999), *Nucinella ovalis* (Jeffreys, 1879) is distributed in the Korea Strait (= Tsushima Strait, westernmost part of the Japan Sea). However, Habe (1977) had already suggested that this species might be a synonym of *Huxleyia sulcata* A. Adams, 1860. Recently, it is becoming clear that two small nucinellids living off Oman possess chemosymbiotic bacteria in their gills (Oliver and Taylor, 2012). This finding confirms the speculation on the symbiosis of some *Nucinella* species with sulphide-oxidizing bacteria based on their gutless condition (Reid, 1990) and fossil occurrences (Amano *et al*., 2007a). Except for one doubtful record from the Late Triassic (Peckmann *et al.*, 2011), four large-sized species of *Nucinella* have been recorded from the latest Jurassic to the early Oligocene seep sites (Table 5). It is plausible that the Kurosedani species (13.6 mm in length) is the youngest fossil record of this genus from a hydrocarbon seep site, judging from its shell size and associated fauna.

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Author contributions

Kazutaka Amano initiated the study and was primarily responsible for the taxonomic aspects. Yusuke Miyajima extracted fossils from rocks and found *Nucinella* sp. in this process. Kenyu Nakagawa first found this fauna including a new species of *Conchocele* and informed this occurrence to K. A. Masui Hamuro and Toshikazu Hamuro collected plenty of fossils and sent to K. A. and Y. M. All authors contributed to the writing of the paper.