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Gastropods from Late Cretaceous Omagari and Yasukawa hydrocarbon seep deposits in the Nakagawa area, Hokkaido, Japan

ANDRZEJ KAIM, ROBERT G. JENKINS, and YOSHINORI HIKIDA



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Sixteen gastropod species from two Campanian (Upper Cretaceous) hydrocarbon seep localities in Hokkaido, Japan are described. Seven species are new: the acmaeid limpet *Serradonta omagariensis*; three turbinids: *Homalopoma abeshinaiensis*, *Cantrainea yasukawensis*, and *C. omagariensis*; the trochid *Margarites sasakii*; the seguenzioid *Cataegis nakagawensis*; and the provannid *Provanna nakagawensis*. The most common species in the investigated localities are acmaeid limpets (*S. omagariensis*), tiny turbinids (*H. abeshinaiensis*, *C. yasukawensis*, *C. omagariensis*), and provannids/hokkaidoconchids (*P. nakagawensis* and *Hokkaidoconcha hikidai*). The Upper Cretaceous associations described here do not resemble Lower Cretaceous associations known from other regions but are composed of species similar to gastropods from Recent hydrocarbon seeps and hydrothermal vents in the Northwestern Pacific. This strongly suggest that this region possesses a regional pool of gastropods in chemosynthesis-based communities at least since Late Cretaceous time. The only group of gastropods described here which has no Recent counterpart is the Hokkaidoconchidae. A comparison to gastropods from plesiosaur falls and sunken wood of the same age and region strongly suggest that these invertebrate communities do not differ significantly from the coeval hydrocarbon seep communities described herein.

Key words: Gastropoda, hydrocarbon seeps, Cretaceous, Hokkaido, Japan.

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Introduction

The discovery of chemosynthesis-based communities was probably one of the biggest surprises in the marine biology of 20th century (Desbruyères et al. 2006). The basic source of nourishment in such communities comes largely from microbial chemosynthetic processes due to sulfur and/or methane oxidation (Van Dover 2000). There are three basic types of substrates where these communities develop: hydrothermal vents, cold seeps, and vertebrate falls. Sunken wood communities are also partially chemosynthetically fuelled (Kiel and Goedert 2006a, b). Cold seeps develop in places where pore waters rich in methane, ammonia, and sulfide reach the sea bottom. Most typically the seep communities appear in brine seeps at the continental margins, subduction zones along convergent margins, and also over the salt diapirs (Van Dover 2000). Although Recent vent and seep communities have been explored to a relatively large extent—including those from Japanese waters (Kojima 2002; Sasaki et al. 2005)—but their fossil record remains poorly known and therefore the historical development of chemosynthesis-based communities is still of debate (Little and Vrijenhoek 2003; Campbell 2006; Kiel and Little 2006). Fossil chemosynthesis-based associations are relatively well researched in Japan (Majima et al. 2005) but it mostly concerned their post-Cretaceous record. Recent investigations on Upper Cretaceous hydrocarbon seep carbonates from Hokkaido, Japan (Kaim and Jenkins 2008) revealed well preserved and diverse fossil material of chemosynthesis-based associations from this time interval. Although exotic carbonates in the Cretaceous of Hokkaido were long-known to Japanese geologists (Hashimoto et al. 1967; Tanabe et al. 1977), their hydrocarbon seep origin had not been realized until the 1990s. Seep carbonates were first identified in the Mikasa region (Kanie et al. 1993), then in the Tappu area (Kanie et al. 1996, Kanie 2000), and finally in the Nakagawa region (Hikida et al. 2003). Previous taxonomic treatments of the fauna from hydrocarbon seep carbonates in Hokkaido concerned mainly bivalves (Kanie et al. 1993, 1996, 2000; Amano et al. 2007; Kiel et al. 2008a), while gastropods remained poorly known. Some preliminary identifications were provided by Hikida et al. (2003) and Jenkins et al. (2007a, b) while first taxonomic description of gastropods from Creta-

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ceous hydrocarbon seep carbonates in Hokkaido came from Kaim et al. (2008a). However, that paper described exclusively provannids and hokkaidoconchids and the remaining gastropods were not covered. This paper provides description of gastropods from two hydrocarbon seep localities in the Nakagawa region: Omagari and Yasukawa. It also discusses the importance of this fauna for deciphering the evolution of chemosynthesis-based associations.

Institutional abbreviations.—DEPUT, Department of Earth and Planetary Sciences, Faculty of Science, University of Tokyo, Japan; NMM, Nakagawa Museum of Natural History, Nakagawa, Japan; NSMT, National Museum of Nature and Science, Tokyo, Japan (formerly National Science Museum); ORI, Ocean Research Institute, University of Tokyo, Japan; UMUT, University Museum, University of Tokyo, Tokyo, Japan. ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland.

Other abbreviation.—σ, standard deviation.

Material and methods

The gastropods described in this paper are from the Omagari and Yasukawa seep sites located along Abeshinai river, Nakagawa area, Hokkaido, Japan (Fig. 1), collected during several field seasons and were also obtained from wet-sieving of weakly consolidated muddy sediments (mesh size 0.5 mm). Specimens were cleaned, mounted on stubs, coated with platinum, and examined on Hitachi S-2400S and Philips XL20 scanning electron microscopes at DEPUT and ZPAL respectively. A single specimen of *Bathyacmaea* cf. *subnipponica* (Fig. 2A) was photographed without coating on the SEM at NSMT, courtesy of Takenori Sasaki, with help by Hiroshi Saito. The microstructure of *Gigantocapulus* sp. has been investigated with a Hitachi S-4500 at ORI. Some specimens were light-photographed in the photo-lab of ZPAL. The photographs of *Cantrainea nuda* have been kindly provided by Takenori Sasaki (UMUT).

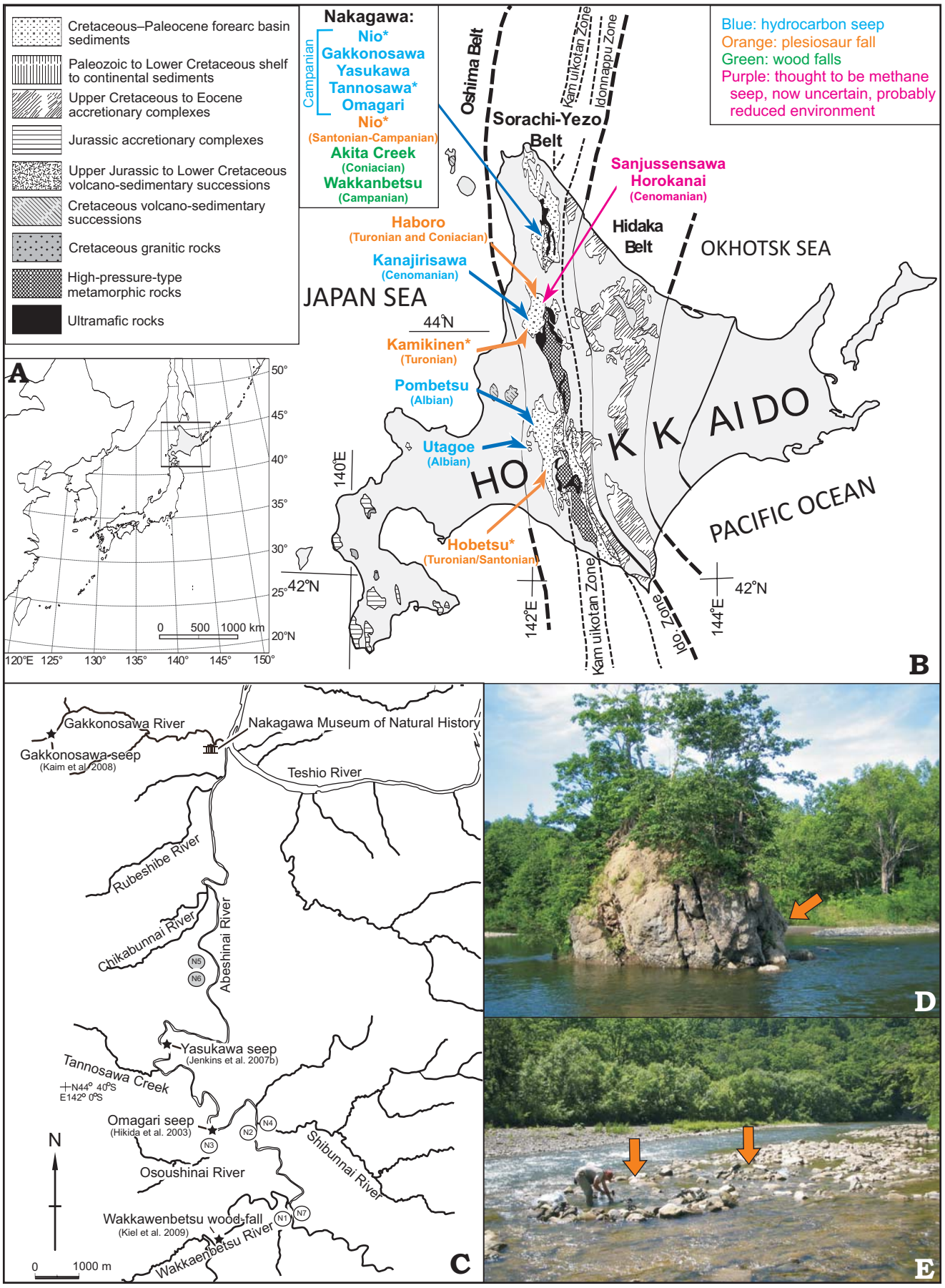
Geological setting

Fossil hydrocarbon seep deposits are distributed in Hokkaido along a meridional belt of outcrops of the Yezo Group. This sequence is composed of marine-clastic deposits sedimented in the Yezo fore-arc basin along the western margin of a subduction zone in the circum-northwestern Pacific during the Cretaceous (Takashima et al. 2004). It is noteworthy that the oldest (Albian) seep carbonates are located in the southern part of the belt (Utagoe and Pombetsu), a Cenomanian seep site in the Tappu area (Kanajirisawa) is located in the middle part of the belt, and the youngest examples (Campanian) are located in the northern part of the belt in the Nakagawa area. There are three published localities from the latter region: Omagari, Yasukawa, and Gakkonosawa. The Gakkonosawa seep carbonate (Kaim et al. 2008a) differs from the remaining two in the type of fossil preservation: the fossils from Gakkonosawa are silicified while the fossils from Omagari and Yasukawa retain original mineralogy or are re-crystallized into calcite. The samples from Gakkonosawa are still being processed and the gastropods from this locality will be published elsewhere. Both the Omagari and Yasukawa carbonate bodies occur within upper part of the Omagari Formation and are dated as Campanian (Takahashi et al. 2007). The Omagari Formation is characterized by alternations of sandstone and sandy siltstone with some intercalated gravel beds, and is interpreted as deposited at the interface of a continental-shelf margin and a continental slope (Jenkins et al. 2007b). Gastropods from the Omagari Formation in the reaches of the Abeshinai river were previously studied by Nagao (1932, 1939). However, it seems that the majority of his material (Table 1) came from "normal" sediments, although there could be two possible exceptions. It seems likely that *Ataphrus tesioensis* Nagao, 1939 and *Margarites sachalinensis* Nagao, 1939 could belong to chemosynthesis-based associations as similar gastropods are described here. Unfortunately, Nagao's (1932, 1939) localities are only very briefly described and it is difficult to state if the gastropods were from seep carbonates. Preliminary identifications of gastropods from the Omagari site were provided by Hikida et al. (2003) while Kaim et al. (2008a) reported provannids and hokkaidoconchids from Omagari, Yasukawa, and Gakkonosawa.

Omagari.—The 10-meter-wide seep carbonate body forms a small islet in the Abeshinai river near the mouth of its tributary, the Osoushinai river (Fig. 1D). The seep deposit yielded large numbers of probable vestimentiferan worm tubes, abundant small gastropods and many small- to medium-sized bivalves. The seep carbonate in Omagari was first mentioned by Hashimoto et al. (1967) who reported dense assemblage of tube-like trace fossils, which were later identified (Hikida et

Fig. 1. **A**. Geological map of Hokkaido, Japan, showing the distribution of Cretaceous chemosynthesis-based associations. Localities asterisked are authors' unpublished data. **B**. Location of Hokkaido on the Northwestern Pacific Coast (after Takashima et al. 2004). **C**. Gastropod-bearing fossil localities in the Nakagawa area. Localities in circles are those of Nagao (1932, 1939), see also Table 1: N1, Sakaizawa; N2, left bank of the Abeshinai, south of Shibunnai; N3, Ososinaizawa, a tributary of the Abesinai river; N4, Sibunnaizawa, a tributary of the Abesinai river an a point along the latter river, 300 m upstream; N5, Abesinai river; N6, Middle course of the Abesinai river; N7, Abesinai river, about 100 m upstream from the junction with Sakaizawa. N5 and N6 (shaded) are uncertain, the Nigorikawa locality is out of map range (south from the map), and two localities ("Omoshiroshibets, a tributary of the Abeshinai" and "a small tributary of the Abesinai river, near the postal service station") have not been recognized. Investigation of YH revealed that "Omoshiroshibets" is apparently a locality in Enbetsu area and not along the Abeshinai River. **D**. The Omagari site with the gastropod-rich area indicated by an arrow. **E**. The Yasukawa site with the gastropod-rich areas indicated by arrows. →

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Table 1. Late Cretaceous gastropods described by Nagao (1932, 1939) from the Nakagawa area. Original spelling retained.

Taxa	Locality
Nagao 1932	
Tessarolax japonicus Yabe and Nagao, 1928	Sakaizawa, a tributary of Abeshinai river
*Tessarolax acutimarginatu*s Nagao, 1932	Nigorikawa, a small tributary of the Abeshinai river
Rostellaria japonica Nagao, 1932	Omoshiroshibets, a tributary of the Abeshinai
Avellana problematica Nagao, 1932	Left bank of the Abeshinai, south of Shibunnai
Nagao 1939	
Ataphrus tesioensis Nagao, 1939	A small tributary of the Abesinai river, near the postal service station
Margarites sachalinensis Nagao, 1939	Omosirusibetu, Ososinaizawa, tributaries of the Abesinai river
Natica (*Lunatia*) *ainuana* Nagao, 1939	Ososinaizawa, a tributary of the Abesinai river
Natica (*Lunatia*) *denselineata* Nagao, 1940	Sibunnaizawa, a tributary of the Abesinai river and a point along the latter river, 300 m upstream from the mouth of its tributary, the Wakkawen
Dicroloma (*Perissoptera*) sp. indet	Abesinai river
Pyropsis sp. indet.	Middle course of the Abesinai river
Semifusus (*Trochofusus*) *tuberculatus* Nagao, 1939	Abesinai river, about 100 m upstream from the junction with Sakaizawa
Surculites fusoides Nagao, 1939	Omosirusibetu, a small tributary of the Abesinai river
Fusus volutodermoides Nagao, 1939	The Ososinaizawa, a tributary of the Abesinai river
Avellana problematica Nagao, 1932	Abesinai-gawa

Table2. Gastropods from the Omagari and Yasukawa seep sites and their Recent counterparts. In bold are species constituting 93% of each association respectively.

Species in Omagari and Yasukawa	Omagari number of specimens	Omagari %	Yasukawa number of specimens	Yasukawa %	Related species from Recent chemosynthesis-based communities off Japan (but see * and **)
Bathyacmaea cf. *subnipponica* Sasaki, Okutani, and Fujikura, 2003	8	0.7	1	0.4	*Bathyacmaea subnipponica* Sasaki, Okutani, and Fujikura, 2003
Serradonta omagariensis sp. nov.	**431**	**36**	7	2.9	*Serradonta vestimentifericola* Okutani, Tsuchida, and Fujikura, 1992
Homalopoma abeshinaiensis sp. nov.	**269**	**22**	–	–	*Homalopoma laevigatum* (Sowerby, 1914)
Cantrainea yasukawensis sp. nov.	–	–	**134**	**55**	*Cantrainea nuda* Okutani, 2001
Cantrainea omagariensis sp. nov.	**310**	**26**	–	–	*Cantrainea nuda* Okutani, 2001
Margarites sasakii sp. nov.	37	3.1	–	–	*Margarites ryukyuensis* Okutani, Sasaki, and Tsuchida, 2000
Cataegis nakagawensis sp. nov.	4	0.3	–	–	*Cataegis meroglypta* McLean and Quinn, 1987*
Provanna nakagawensis sp. nov.	**74**	**6.2**	3	1.2	*Provanna shinkaiae* Okutani and Fujikura, 2002
Hokkaidoconcha hikidai Kaim, Jenkins, and Warén, 2008	–	–	**96**	**39**	–
Neogastropoda indet.	–	–	1	0.4	?*Oenopota ogasawarana* Okutani, Fujikura and Sasaki, 1993
?*Sulcoactaeon* sp.	–	–	1	0.4	
Naticiform gastropod	24	2	–	–	?*Retiskenea diploura* Warén and Bouchet, 2001
Skeneiform gastropod	**44**	**3.7**	–	–	?*Helicrenion reticulatum* Warén and Bouchet, 1993**
Gastropoda indet. 1	1	0.1	–	–	–
Gastropoda indet. 2	–	0	1	0.4	–
Gigantocapulus sp.	–	0	1	0.4	–
TOTAL	1202	100	245	100	

* known only from the Caribbean

** known only from the Lau Basin

? relation to species from the Omagari and Yasukawa sites uncertain

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al. 2003) as possible vestimentiferan worm tubes. The most comprehensive treatment of the Omagari seep has been provided by Hikida et al. (2003) who preliminarily identified fossils from this locality. Kiel et al. (2008a) have recently reviewed bivalves from the Omagari site noting the occurrences of an unidentified solemyid, *Acila* (*Truncacila*) *hokkaidoensis* (Nagao, 1932), *Nuculana* sp., *Nipponothracia* cf. *ponbetsensis* Kanie and Sakai, 1997, *Thyasira* sp., and a poorly preserved lucinids. Kaim et al. (2008a) reported an unidentified provannid gastropod which is described as *Provanna nakagawensis* sp. nov. herein. For a full list of gastropods from this locality see Table 2.

Yasukawa.—The Yasukawa site consist of several methane-influenced carbonate bodies distributed on a bank of the Abeshinai river (Fig. 1E) about 3 km downstream from the Omagari site (Jenkins et al. 2007b). Jenkins et al. (2007b) described the locality in detail and also studied the distribution of fossils in the locality. Later, Jenkins et al. (2008) identified biomarkers typical for anaerobic oxidation of methane from this site. Jenkins et al. (2007a, b) preliminarily identified several fossils occurring at Yasukawa site. Amano et al. (2007) described *Nucinella gigantea* Amano, Jenkins, and Hikida, 2007 from this locality while Kiel et al. (2008a) reviewed the remaining bivalves including *Acharax cretacea* Kanie and Nishida, 2000, *Leionucula formosa* (Nagao, 1930), *Acila* (*Truncacila*) *hokkaidoensis* (Nagao, 1932), *Nuculana* (*Ezonuculana*) *mactraeformis* Nagao, 1932, *Propeamussium yubarense* (Yabe and Nagao, 1928), *Thyasira tanabei* Kiel, Amano, and Jenkins, 2008, and several poorly preserved lucinids. Kaim et al. (2008a) reported an unidentified provannid (*Provanna nakagawensis* sp. nov. herein) and *Hokkaidoconcha hikidai* Kaim, Jenkins, and Warén, 2008. For a full list of gastropods from this locality see Table 2.

Systematic paleontology

Phylum Mollusca Linné, 1758

Class Gastropoda Cuvier, 1798

Order Patellogastropoda Lindberg, 1986

Superfamily Lottioidea Gray, 1840

Family Acmaeidae Forbes, 1850

Subfamily Pectinodontinae Pilsbry, 1891

Genus *Bathyacmaea* Okutani, Tsuchida, and Fujikura, 1992

Type species: *Bathyacmaea nipponica* Okutani, Tsuchida, and Fujikura, 1992, by monotypy; Recent, Sagami Bay, Japan.

Discussion.—The genus concept is based mainly on radula characters (Sasaki et al. 2003). The shells of *Bathyacmaea* are rather similar to shells of *Pectinodonta* Dall, 1882 and the only, although rather tenuous difference lies in the central position of the apex in *Serradonta* while in *Pectinodonta* it is rather subcentral anteriorly. Therefore, without knowledge of the radula the delimitation is difficult. Both genera have species with robust cancellate ornamentation but Sasaki et al. (2003) also described *B. tertia* Sasaki, Okutani, and Fujikura, 2003 with a smooth shell.

Stratigraphic and geographic range.—Recent hydrothermal vents and hydrocarbon seeps in the Western Pacific. Upper Cretaceous hydrocarbon seep deposits in Japan.

Bathyacmaea cf. *subnipponica* Sasaki, Okutani, and Fujikura, 2003

Fig. 2.

2003 *Bathyacmaea* cf. *nipponica* Okutani, Tsuchida, and Fujikura, 1992; Hikida et al. 2003: 338, fig. 10: 3.

2007 *Bathyacmaea* cf. *subnipponica* Sasaki, Okutani, and Fujikura, 2003; Jenkins et al. 2007a: 371, fig. 2B, C.

Material.—Eight specimens from the Omagari site: six specimens at UMUT and two at NMM including specimen NMM-228 illustrated in Hikida et al. (2003). One specimen from Yasukawa (UMUT MM29353) was already illustrated by Jenkins et al. (2007a: fig. 2C). The specimen illustrated by Jenkins et al. (2007a) on fig. 2B was mislabeled as collected at the Yasukawa site, actually the specimen UMUT MM29352 came from the Omagari site (Fig. 2B herein).

Dimensions.—The largest specimen (NMM-228) is 5.9 mm long, 4.5 mm high, and 2.8 mm high.

Description.—The shell is patelliform, oval in outline. The shell width is about 76% and height is about 50% of its length respectively. The shell surface is ornamented by regularly spaced concentric annulations and irregular radial riblets. The apex is relatively high, corroded, and situated slightly anteriorly of the center at 47% of the shell length. The microstructure is obliterated by diagenesis in the examined specimens, however, shell seems to be composed of at least three layers (Fig. $2D_3$).

Discussion.—The shells under consideration are most similar to the Recent *B. subnipponica* from the Nankai Trough, off Japan (Sasaki et al. 2003) in having a relatively high shell, oval outline, irregular radial riblets, and sturdy concentric ornamentation. Taking into account the large temporal distance and the imperfect preservation of the Cretaceous specimens we leave the latter in open nomenclature.

Genus *Serradonta* Okutani, Tsuchida, and Fujikura, 1992

Type species: *Serradonta vestimentifericola* Okutani, Tsuchida, and Fujikura, 1992, by monotypy; Recent, Sagami Bay, Japan.

Discussion.—The most striking shell character of *Serradonta* delimiting this genus from other acmaeids is the strongly elongated and compressed shell that is an adaptation for life on vestimentiferan tubes (Okutani et al. 1992; Sasaki et al. 2003). The uneven aperture is caused by this way of attachment to the narrow and rounded substrate.

Similar adaptations are known from other limpets both from hydrothermal vents as well as normal environments. Some lepetodrilid limpets have somewhat compressed shells

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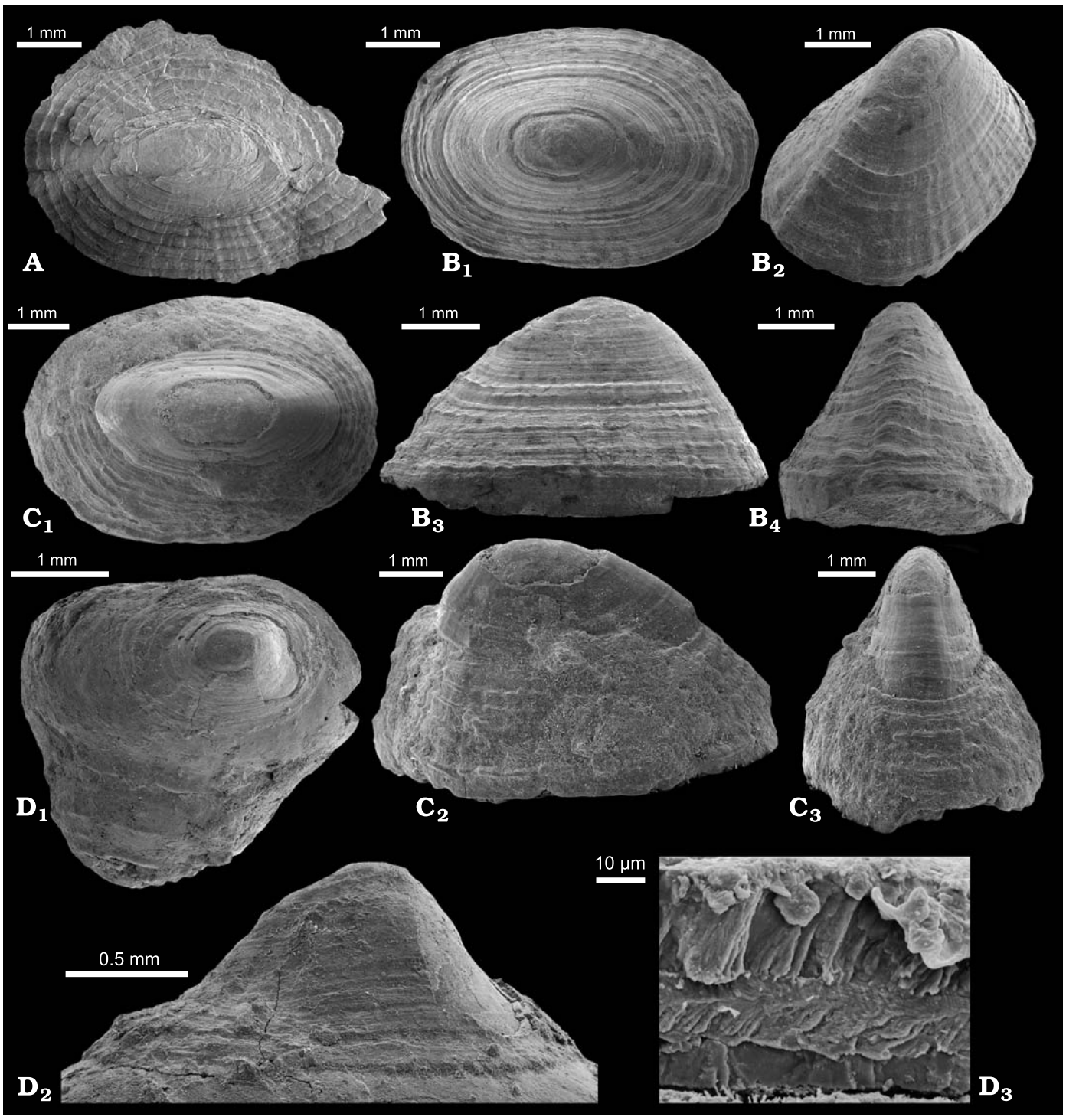


Fig. 2. The acmaeid gastropod *Bathyacmaea* cf. *subnipponica* Sasaki, Okutani, and Fujikura, 2003 from the Campanian (Upper Cretaceous) Omagari (**A**–**C**) and Yasukawa (**D**) seep sites in Hokkaido, Japan. **A**. NMM-228 in apical view. **B**. UMUT MM30143 in apical (B_1), postero-lateral (B_2), lateral (B_3), and posterior views. **C**. UMUT MM30144 in apical (C_1), lateral (C_2), and anterior (C_3) views. **D**. UMUT MM29353 attached to *Cantrainea yasukawensis* sp. nov. in apical (D_1) and lateral (D_2) view; D_3 is a cross section through the shell showing three layers obliterated by diagenesis.

when they live attached to tubeworms at hydrothermal vents (Desbruyères et al. 2006). Some lepetellids living on empty polychaete tubes secrete shells of similar shape (Verrill 1880) while some neolepetopsids are reported to change their shell shape after changing substrate from mussel shells to worm tubes (Warén and Bouchet 2009). The lottiid limpet *Flexitectura* from the Ukrainian Miocene (Anistratenko and Anistratenko 2007) has a very similar shell shape to *Serradonta*, apparently as an adaptation for life on bryozoan branches (compare Anistratenko and Anistratenko 2007). Undoubtedly, limpets acquired such an adaptation several times. *Serradonta* is confined to the region of Japanese Islands and this narrow

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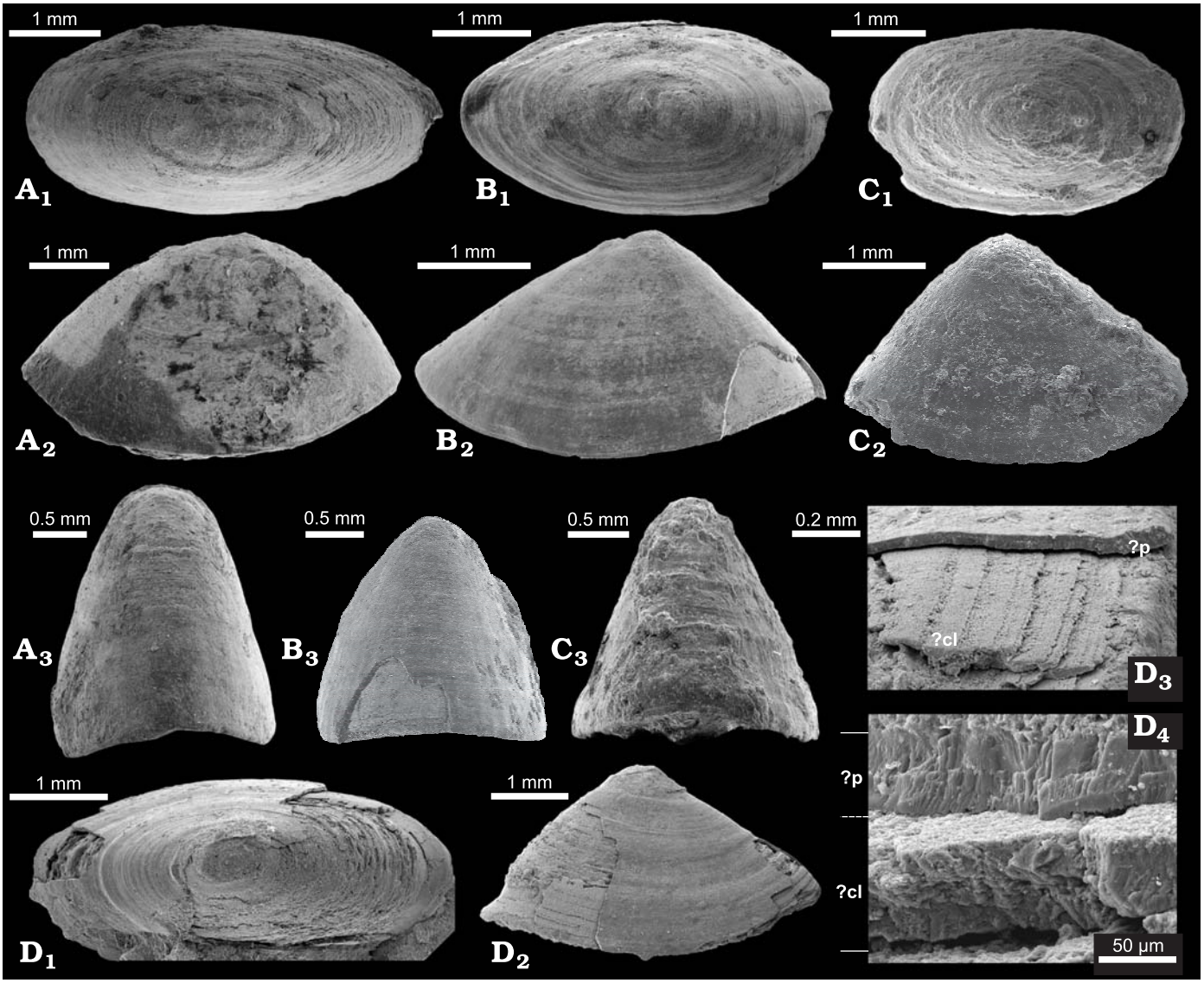


Fig. 3. The acmaeid gastropod *Serradonta omagariensis* sp. nov. from the Campanian (Upper Cretaceous) Omagari (A, B, D) and Yasukawa (C) seep sites in Hokkaido, Japan. **A**. Holotype (UMUT MM29351) in apical (A_1), lateral (A_2), and anterior (A_3) views. **B**. UMUT MM30145 in apical (B_1), lateral (B_2), and anterior views. **C**. UMUT MM30146 in apical (C_1), lateral (C_2), and posterior (C_3) views. **D**. UMUT MM30147 in apical (D_1) and lateral (D_2) views; D_3, illustrates layering of the shell while D_4 is a cross section through shell showing two layers obliterated by diagenesis. Abbreviations: p, prismatic; cl, cross lamellar.

geographic distribution and ecological occurrence suggest that the Recent and fossil species belong to the same genus.

Stratigraphic and geographic range.—Recent hydrocarbon seeps off Japan. Upper Cretaceous hydrocarbon seep deposits in Japan.

Serradonta omagariensis sp. nov.

Fig. 3.

2003 *Serradonta* cf. *vestimentifericola* Okutani, Tsuchida, and Fujikura, 1992; Hikida et al. 2003: 338, fig. 10: 4, 5.

2007 *Serradonta* cf. *vestimentifericola* Okutani, Tsuchida, and Fujikura, 1992; Jenkins et al. 2007a: 371, fig. 2A.

2007 *Serradonta* sp.; Jenkins et al. 2007b: 134, fig. 5.1.

Etymology: After the type locality.

Holotype: UMUT MM29351 (Fig. 3A), almost complete shell lacking protoconch.

Type locality: Omagari site, Nakagawa area, Northern Hokkaido, Japan. Coordinates 44°39’ 26’’ N, 144°2’ 25’’ E.

Type horizon: Fossil hydrocarbon seep deposits of Omagari Formation, Campanian, Upper Cretaceous.

Material.— 431 moderately to well preserved specimens from Omagari. 371 specimens at UMUT and 60 at NMM. Seven specimens from Yasukawa (all housed at UMUT). The specimen illustrated by Jenkins et al. (2007a) on fig. 2A was mislabeled as collected from Yasukawa; actually the specimen UMUT MM29351 (designated here as holotype) came from Omagari (Fig. 3A herein).

Dimensions.—The average shell length is 4.0 mm ± σ 0.63, shell width 1.8 mm ± σ 0.25, and shell height 2.3 mm ± σ 0.50 in the material of 41 specimens measured from Omagari site.

Diagnosis.—*Serradonta*-type shells with strongly compres-

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sed shell and uneven aperture with neither concentric nor radial ornamentation on any portion of the shell. *S. vestimentifericola* Okutani, Tsuchida, and Fujikura, 1992 is ornamented throughout the ontogeny and *S. kanesunosensis* Sasaki, Okutani, and Fujikura, 2003 is ornamented only on the juvenile shell. *Serradonta omagariensis* is usually higher than wide while the Recent species are wider than high.

Description.—The shell is patelliform with elliptical aperture. The shell width ranges 34–64% (average 46 ± σ 5.7, n = 41) of shell length. The apex is situated slightly subcentral anteriorly (at 36–50% of shell length, average 44 ± σ 4.5). There is no ornamentation apart from concentric growth lines. The protoconch and inner surface of teleoconch are unknown. The microstructure is obliterated by diagenesis in the examined specimens but it seems to be composed of at least one inner (possibly cross lamellar) layer and two (possibly prismatic) outer layers (Fig. $3D_3$, D_4).

Discussion.—The shell shape of *Serradonta* is heavily influenced by its way of life on the worm tubes. It seems that the shell shape variation depends on the shape and size of the tubes. A preliminary survey of 41 specimens from the Omagari site shows a rather wide range of shell dimensions. In spite of that the shells of *S. omagariensis* differs from other species of the genus in being higher than wide. Moreover, all specimens are of small size similarly to *S. kanesunosensis* (that is, however, slightly wider than *S. omagariensis*) while *S. vestimentifericola* achieves a much larger size (Okutani et al. 1992). The size, however, may be determined by the smaller size of the worm tubes for *S. omagariensis* and *S. kanesunosensis*. An independent character differentiating the species is the timing of the appearance of ornamentation during the ontogeny (see diagnosis). *S. omagariensis* is the sole species of *Serradonta* known from the fossil record. The species is relatively common at the Omagari hydrocarbon seep where great abundances of worm tubes are reported, whereas it is relatively rare at the Yasukawa hydrocarbon seep where worm tubes are uncommon (Jenkins et al. 2007a, b; see also Table 2).

Stratigraphic and geographic range.—Omagari and Yasukawa hydrocarbon seeps in Nakagawa area of northern Hokkaido, Japan. Campanian, Upper Cretaceous.

Order Vetigastropoda Salvini-Plawen, 1980

Superfamily Trochoidea Rafinesque, 1815

Family Turbinidae Rafinesque, 1815

Subfamily Ataphrinae Cossmann, 1915

Tribe Colloniini Cossmann, 1917

Remark.—Recently Gründel (2008) included Colloniini Cossmann, 1917 as a tribe of Ataphrinae Cossmann, 1915. Indeed some of the colloniins described below are quite similar to some Jurassic and Cretaceous ataphrins and they were preliminary identified by Jenkins et al. (2007a, b) and Kaim et al. (2008a) as such. The molecular evidence suggests (Williams et al. 2008) that colloniins should be considered as a distinct superfamily of vetigastropods.

Genus *Homalopoma* Carpenter, 1864

Type species: *Turbo sanguinaeus* Linné, 1758, original designation; Recent, Mediterranean.

Discussion.—The concept of *Homalopoma* unites species having small turbiniform anomphalous shells. The type species has a shell with well developed spiral ornament but some species have only weak spiral ribs (e.g., *H. baculum* [Carpenter, 1864]) or even smooth shells (e.g., *H. laevigatum* [Sowerby, 1914]). Similar but consistently much larger are shells of the seemingly closely related *Cantrainea* Jeffreys, 1883 (see discussion below). Here we include only a strongly ornamented species in *Homalopoma* while two other, weakly ornamented species are assigned to *Cantrainea*.

Distribution.—*Homalopoma* is a species-rich genus with a worldwide distribution. It occurs from shallow water to bathyal depths. Some species of *Homalopoma* (e.g., *H. laevigatum*) are reported from sunken wood off Japan (Okutani 2000). An undescribed species occurs also at hot vent in Mariana Arch (Anders Warén, personal communication 2008). An unnamed fossil species of *Homalopoma* was reported by Gill et al. (2005) from Eocene–Miocene aged hydrocarbon seep deposits on Barbados and two other unnamed species are reported from two Eocene hydrocarbon seeps of Washington State, USA by Goedert and Squires (1990). Another species, *Homalopoma wattsi* (Dickerson, 1916), has been reported by Kiel (2008) from Eocene wood-fall association in Washington State, USA. Abundant occurrences of *Homalopoma domeniconii* Moroni, 1966 are reported by Moroni (1966) from the Miocene "Calcare a Lucine" in Italy which have been later identified to be seep carbonates (Taviani 1994; Peckmann et al. 1999). *H. abeshinaiensis* described below represents the oldest record of *Homalopoma* reported so far from chemosynthesis-based communities.

Homalopoma abeshinaiensis sp. nov.

Fig. 4.

Etymology: After the Abeshinai River in which the Omagari seep carbonate is located.

Holotype: UMUT MM30150, Fig. 4C, moderately preserved shell with no protoconch.

Type locality: Omagari site, Nakagawa area, Northern Hokkaido, Japan. Coordinates 44°39'26'' N, 144°2'25'' E.

Type horizon: Fossil hydrocarbon seep deposits of the Omagari Formation, Campanian, Upper Cretaceous.

Material.—269 moderately preserved specimens: 252 shells at UMUT and 17 shells at NMM.

Dimensions.—The holotype is 5.26 mm high and 4.57 mm wide.

Diagnosis.—Shell low turbiniform, whorls moderately inflated, ornamented by numerous spiral ribs and strongly prosocline collabral threads. Intersections of spiral and axial ornamentation nodose. Nodes elongated according to the di-

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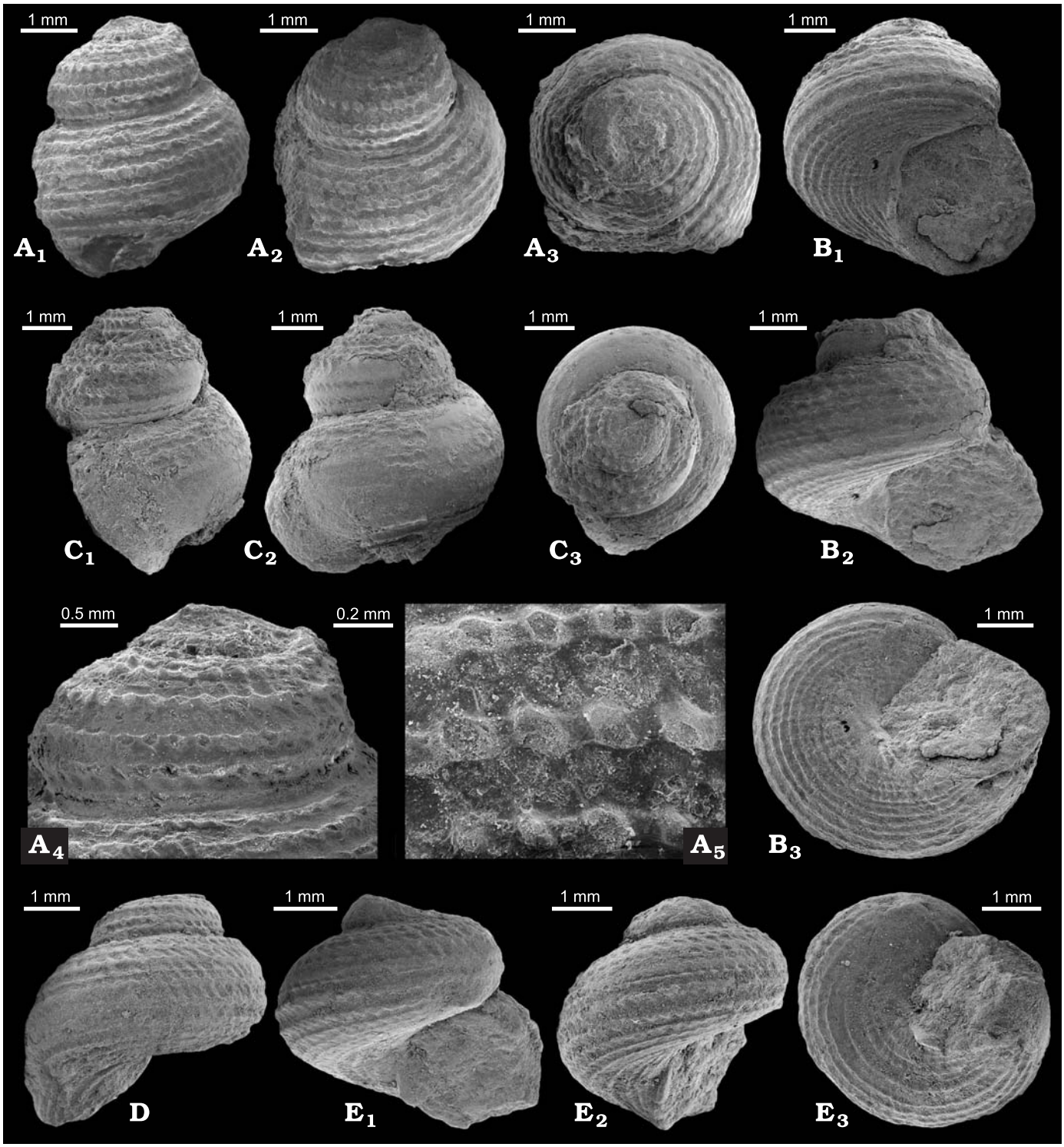


Fig. 4. The turbinid gastropod *Homalopoma abeshinaiensis* sp. nov. from the Campanian (Upper Cretaceous) Omagari seep site in Hokkaido, Japan. **A**. UMUT MM30148 in lateral (A_1), latero-apical (A_2), and apical (A_3) views; A_4, juvenile whorl; A_5, details of shell ornamentation. **B**. UMUT MM30149 in apertural (B_1), lateral (B_2), and umbilical (B_3) views. **C**. Holotype (UMUT MM30150) in lateral (C_1, C_2) and apical (C_3) views. **D**. UMUT MM30151 in lateral view. **E**. UMUT MM30152 in apertural (E_1), lateral (E_2), and umbilical (E_3) views.

rection of collabral threads. No clear demarcation between lateral flank and base of the shell. Base ornamented by numerous spiral ribs. *H. abeshinaiensis* differs from other species of *Homalopoma* in its clearly nodose intersections between spiral ribs and axial threads.

Description.—The protoconch is unknown. The shell is turbiniform with numerous spiral ribs. The earliest preserved whorls are ornamented by four spiral ribs but their number increases to eight on the later flank and eight on the base. The ribs are of similar strength although some secondaries are

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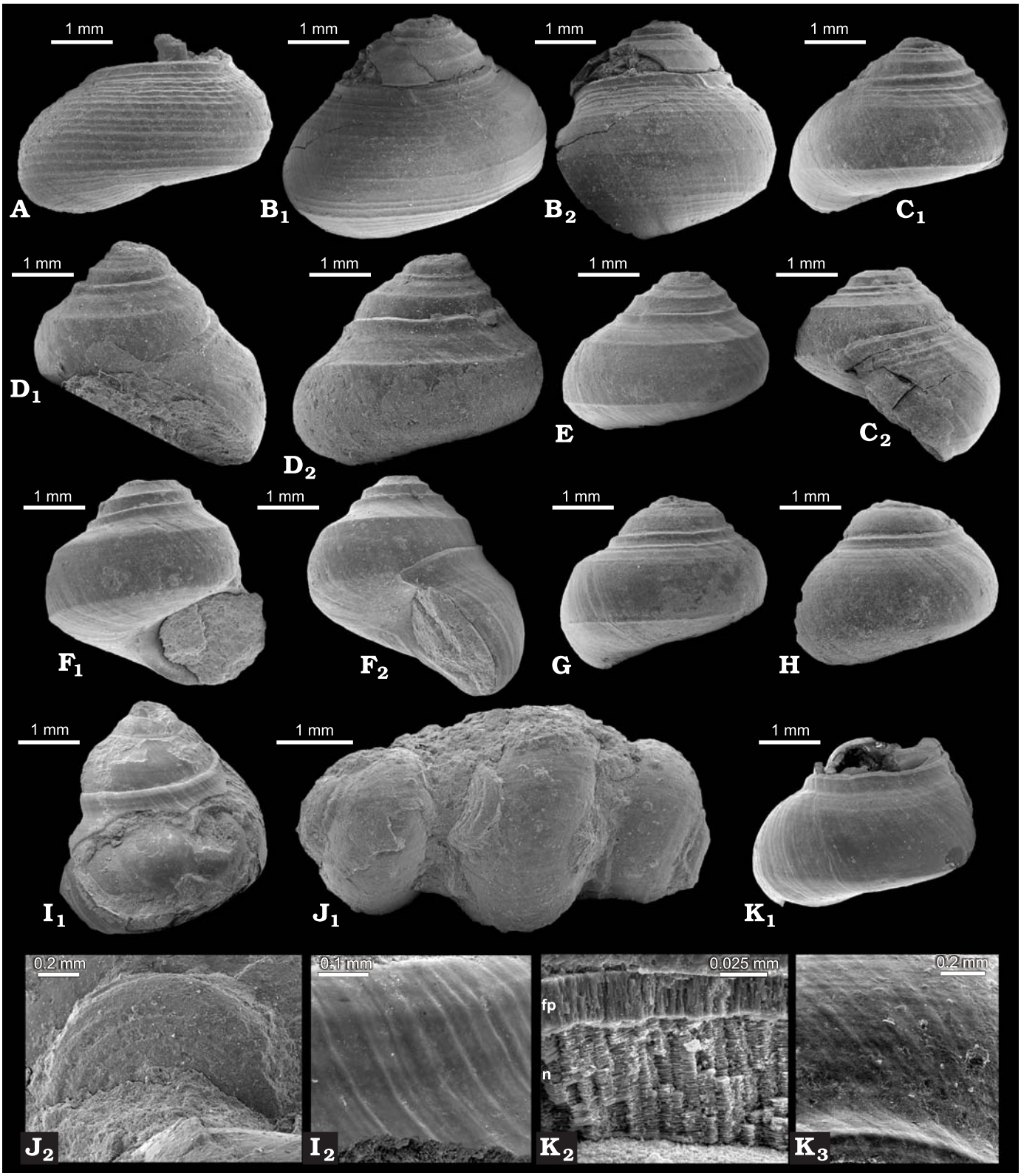


Fig. 5. The turbinid gastropod *Cantrainea yasukawensis* sp. nov. from the Campanian (Upper Cretaceous) Yasukawa seep site in Hokkaido, Japan. **A**. UMUT MM30153 in lateral view. **B**. UMUT MM30154 in lateral view (B_1) and another view (B_2) showing inclination of the aperture. **C**. UMUT MM30155 in lateral view (C_1) and another view (C_2) showing inclination of the aperture. **D**. UMUT MM30156 in lateral view (D_2) and another view (D_1) showing inclination of the aperture. **E**. UMUT MM30157 in lateral view. **F**. Holotype (UMUT MM30158) in apertural (F_1) and lateral (F_2) views. **G**. UMUT MM30159 in lateral view. **H**. UMUT MM30160 in lateral view. **I**. UMUT MM30161 in lateral view (I_1) and details of ornamentation (I_2). **J**. UMUT MM30162, aggregation of three specimens and an operculum; J_1, general view; J_2, the operculum. **K**. UMUT MM30163 in lateral view (K_1), shell microstructure (K_2) including the inner nacreous (n) and fibrous prismatic (fp) layers, and details of shell ornamentation (K_3).

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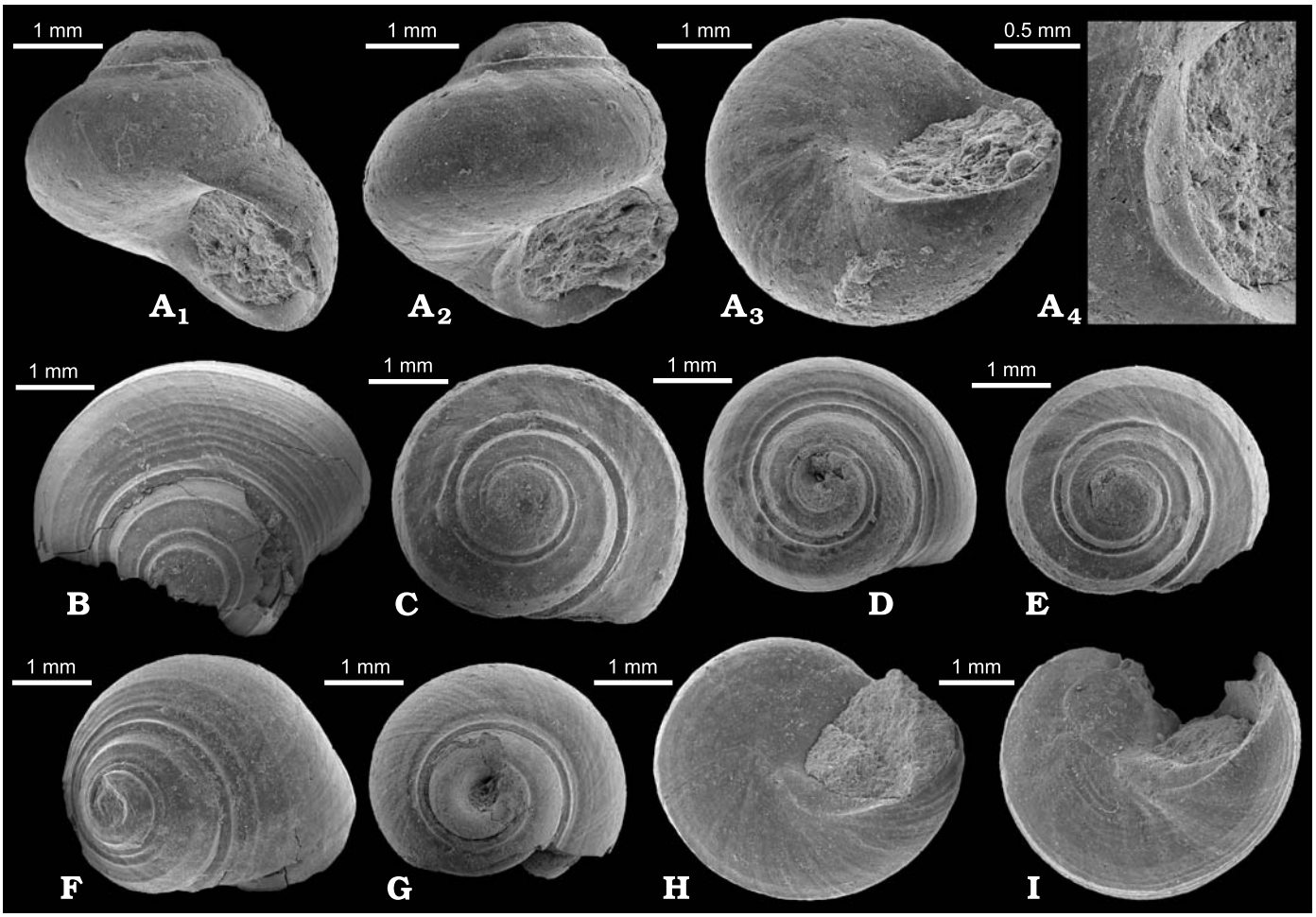


Fig. 6. The turbinid gastropod *Cantrainea yasukawensis* sp. nov. from the Campanian (Upper Cretaceous) Yasukawa seep site in Hokkaido, Japan. **A**. UMUT MM30164 in lateral (A_1), apertural (A_2), and umbilical (A_3) view; A_4, details of inner lip. **B**. UMUT MM30154 in apical view. **C**. UMUT MM30156 in apical view. **D**. UMUT MM30159 in apical view. **E**. UMUT MM30157 in apical view. **F**. UMUT MM30155 in latero-apical view. **G**. UMUT MM30160 in apical view. **H**. Holotype (UMUT MM30158) in umbilical view. **I**. UMUT MM30153 in umbilical view.

weaker. The ultimate whorl is characterized by a slightly dipping suture line. The generating curve is circular, aperture tangential, and peristome uninterrupted. The outer lip is smooth. The inner lip is usually with a narrow callus and there is no umbilicus but a shallow crescent-shaped depression between the inner lip and first spiral rib on the base.

Discussion.—*Homalopoma abeshinaiensis* recalls numerous Recent shallow-water *Homalopoma*-like collonins. However, the strongly ornamented species have usually no nodes on the spiral ribs [e.g., *H. nocturnum* (Gould, 1861)] or the nodes occur only on primary ribs and are absent on the secondaries [e.g., *H. amussitatum* (Gould, 1861)]. *H. abeshinaiensis* is very common at the Omagari seep but unknown so far from Yasukawa. *H. abeshinaiensis* is rather small as for this genus.

Stratigraphic and geographic range.—Omagari hydrocarbon seep in Nakagawa area of northern Hokkaido, Japan. Campanian, Upper Cretaceous.

Genus *Cantrainea* Jeffreys, 1883

Type species: *Turbo peloritanus* Cantraine, 1835, original designation; originally described as fossil from Plio-Pleistocene of Sicily, later found also living in Mediterranean Sea and Bay of Biscay.

Discussion.—The concept of *Cantrainea* unites large *Homalopoma*-like colloniids. Some authors consider *Cantrainea* to be a subgenus of *Homalopoma* (e.g., Knight et al. 1960: 270). Recent authors, however, follow Marshall (1979) and accept the full generic status of *Cantrainea*. Nevertheless, Marshall (1979: 551) stated that the whole group of *Homalopoma*-like gastropods should be assessed more critically. A potentially good character for distinguishing *Cantrainea* and *Homalopoma* in the fossil record is the presence of a concave subsutural ramp in the former genus. The type species of *Cantrainea* and also some other species: *Cantrainea panamense* (Dall, 1908), *C. inexpectata* Marshall, 1979, *C. jamsteci* (Okutani and Fujikura, 1990), *C. macleani* Warén and Bouchet, 1993, and *C. yoyottei* Vilvens, 2001 have a wide ramp whereas *C. nuda* Okutani, 2001 is totally smooth apart from a finely pleated subsutural cord (Fig. 7G herein). The latter species is known from a single specimen (Fig. 7G) and its diagnosis is based solely on the shell characters. As already mentioned by Okutani (2001) the generic assignment

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of this species is tentative pending examination of the soft body. The lack of concave subsutural ramp might have resulted from general simplification of the sculpture in this species.

Distribution.—*Cantrainea* includes about a dozen large species of colloniids from deep waters of different regions of all world oceans. At least three species are known from chemosynthesis-based communities. *C. jamsteci* has been described from hydrothermal vent at the Minami Ensei Knoll (Ryukyu Islands, Japan) by Okutani and Fujikura (1990) and *C. panamense* has been recently reported from Concepción hydrocarbon seep off Chile (Sellanes et al. 2008). *C. macleani* has been described from a hydrocarbon seep on Louisiana Slope but it has also been reported from a station that "is not situated in the vicinity of any known hydrocarbon seep" (Warén and Bouchet 1993: 10) and therefore not an obligate chemosynthetic community member. Although Okutani (2001) did not report any connection of *C. nuda* to chemosynthesis-based community, such community was described indeed from "Depression B" of Minami Ensei Knoll by Hashimoto et al. (1995). Therefore, it seems to be most likely that *C. nuda* is a member of such community. A single occurrence of *Cantrainea* from ancient chemosynthetic-based associations has been reported from the Miocene Freeman's Bay Limestone on Trinidad (Gill et al. 2005).

Cantrainea yasukawensis sp. nov.

Figs. 5, 6.

2007 Ataphridae gen. et sp. indet.; Jenkins et al. 2007a: 8, fig. 5: 2.
2007 ataphrid gastropod; Jenkins et al. 2007b: 371, fig. 2c.

Etymology: After the type locality.

Holotype: UMUT MM30158, Figs. 5F and 6H, well preserved shell without protoconch.

Type locality: Yasukawa site, Nakagawa area, Northern Hokkaido, Japan. Coordinates 44°40'37'' N, 142°1'27'' E.

Type horizon: Ancient hydrocarbon seep deposits of Omagari Formation, Campanian, Upper Cretaceous.

Material.—134 moderately to well preserved specimens without protoconchs.

Dimensions.—The holotype is 3.59 mm high and 3.9 mm wide.

Diagnosis.—Shell turbiniform with flat-topped or slightly concave ramp at the suture. The upper part of the lateral flank slightly concave. Growth lines strongly prosocline. Spiral ornamentation variable. *C. yaskukawensis* is much smaller than any living species of *Cantrainea* and also smaller that *C. omagariensis* described below. Moreover, it has a higher ultimate whorl in comparison to its width than *C. omagariensis*. *C. yasukawensis* is also much smaller than the similarly smooth-shelled Recent *C. nuda* Okutani, 2001; it differs also in having a subsutural ramp rather than a pleated cord and no knob on the inner lip of the aperture that is characteristic for *C. nuda* (Fig. 7G).

Description.—The protoconch is unknown. The shell is turbiniform with variable spiral ornamentation. The most typical example (see holotype, Figs. 5F and 6H) has a wide concave subsutural ramp and the base demarcated by a weak and rather rounded angulation. Some other specimens have a pattern of delicate faint ribs (Fig. 5B, C) and the base demarcated by clear angulation at some specimens accompanied by a spiral rib (Fig. 5E, H). Some shells of *C. yasukawensis* lack any ornament apart from a narrow subsutural ramp (Figs. 5K, 6A). However, even on these smooth specimens there are some spiral undulations visible under higher magnification (Fig. $5K_3$). The shell wall is relatively thick and bi-layered. Inner nacreous layer is three times thicker than the outer prismatic layer. The ultimate whorl is characterized by slightly dipping suture line. The generating curve is circular, aperture tangential, and peristome uninterrupted. The outer lip is smooth. The inner lip has usually a narrow callus and there is no umbilicus. In some specimens, especially these smooth-shelled, there is a callosity extended over the umbilical area (Fig. 5F). Apertural elaborations are absent. The operculum is calcareous and concentric in the visible part (Fig. 5J).

Discussion.—*C. yasukawensis* is a species with highly variable shell ornamentation. Such plasticity in shell morphology is also observed in other gastropods inhabiting chemosynthesis-based communities and the most conspicuous examples are those of provannid gastropods: *Provanna variabilis* Warén and Bouchet, 1986 from Recent hydrothermal vents on East Pacific Rise and *Provanna antiqua* Squires, 1995 from Paleogene hydrocarbon seeps in Washington State (Squires 1995). *Paskentana paskentaensis* (Stanton, 1895) from Early Cretaceous seep associations is another example of highly variable species (Kiel et al. 2008). *C. yasukawensis* is common in the proximity of methane influenced carbonate bodies and is also present in the peripheral areas of the hydrocarbon seep (Jenkins et al. 2007a). This gastropod was preliminarily identified by Jenkins et al. (2007a, b) as an ataphrid and after a detailed examination it seems that *Cantrainea* is the best place for it although the latter genus includes mostly much larger collonins. *C. yasukawensis* is strikingly similar to the Recent *C. nuda*. The latter species differs from *C. yasukawensis* especially in having a distinctive knob on the inner lip (Okutani 2001). The other possible place for *C. yasukawensis* is *Homalopoma* which includes small- and medium sized collonins. The species of *Homalopoma*, however, have usually evenly convex shells with no concave subsutural ramp.

Stratigraphic and geographic range.—Yasukawa hydrocarbon seep in Nakagawa area of northern Hokkaido, Japan. Campanian, Upper Cretaceous.

Cantrainea omagariensis sp. nov.

Fig. 7A–F.

2008 ataphrid gastropod; Kaim et al. 2008b: 100, fig. 3h.

Etymology: After the type locality.

Holotype: UMUT MM30166, Fig. 7B, moderately preserved shell with no protoconch.

Type locality: Omagari site, Nakagawa area, Northern Hokkaido, Japan. Coordinates 44°39'26'' N, 144°2'25'' E.

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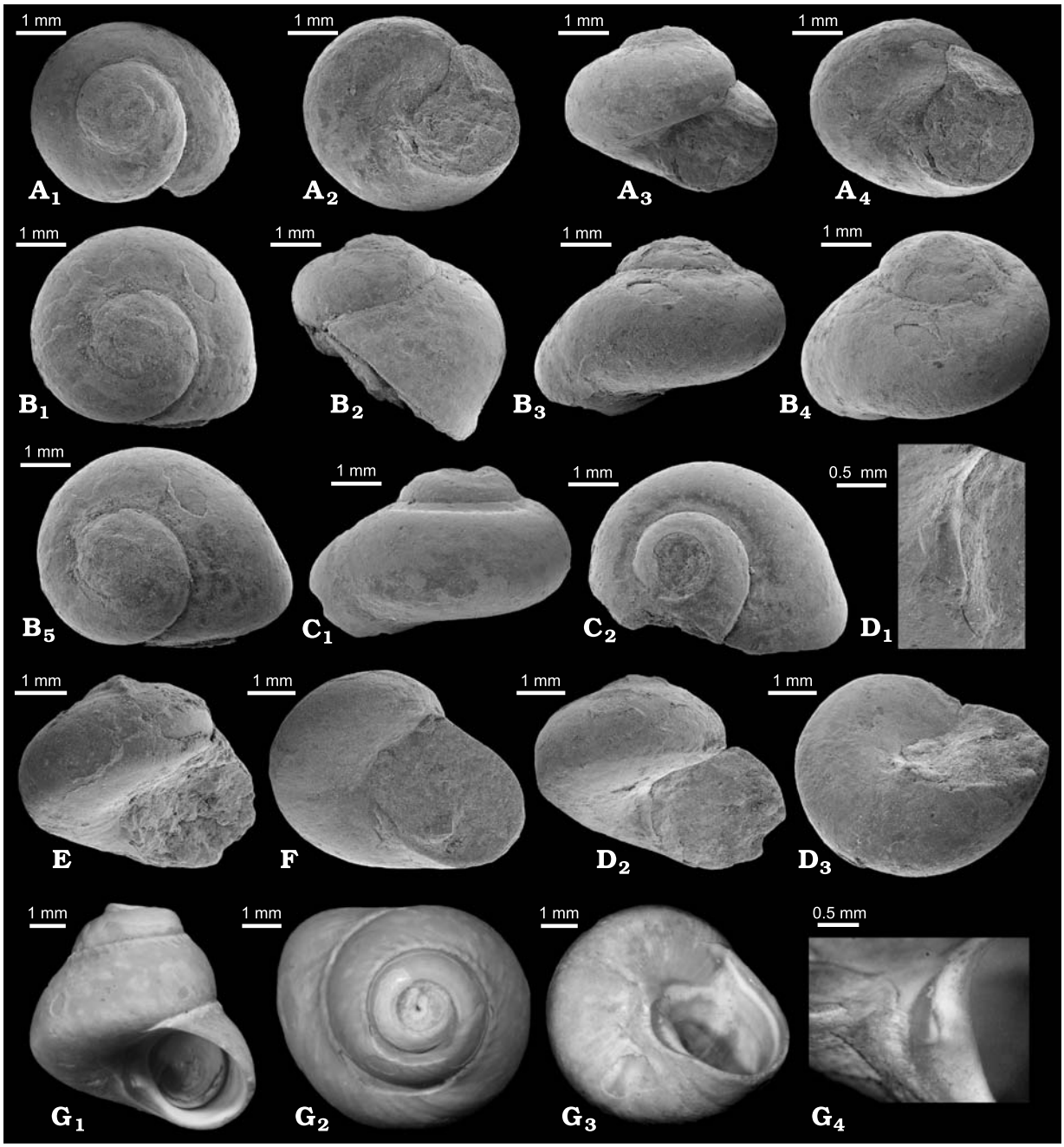


Fig. 7. Turbinid gastropods of the genus *Cantrainea* from chemosynthesis-based communities. **A–F**. *Cantrainea omagariensis* sp. nov. from Campanian (Upper Cretaceous) Omagari seep site in Hokkaido, Japan. **A**. UMUT MM30165 in apical (A_1), umbilical (A_2), lateral (A_3), and apertural views (A_4). **B**. Holotype (UMUT MM30166) in apical (B_1, B_5), lateral (B2, B3), and latero-apical (B_4) views. **C**. UMUT MM30167 in lateral (C_1) and apical (C_2) views. **D**. UMUT MM30168; details of inner lip (D_1), apertural (D_2) and umbilical (D_3) views. **E**. UMUT MM30169 in lateral view. **F**. UMUT MM30170 in apical view. **G**. Recent *Cantrainea nuda* Okutani, 2001 from "depression B" of the Minami Ensei Knoll, Okinawa Trough, Japan (NSMT-Mo 73040) in lateral (G_1), apical (G_2), and umbilical (G_3) views; G_4, details of inner lip.

Type horizon: Fossil hydrocarbon seep deposits of Omagari Formation, Campanian, Upper Cretaceous.

Material.—310 moderately preserved specimens without protoconchs: 225 at UMUT and 85 at NMM, all from the Omagari site.

Dimensions.—The holotype is 4 mm high and 4.66 mm wide.

Diagnosis.—Shell low turbiniform, moderately inflated. Surface smooth apart from narrow subsutural ramp. Growth lines strongly prosocline. *C. omagariensis* is slightly larger than *C. yasukawensis* but smaller than any other species of *Cantrainea*. *C. omagariensis* differs also from *C. yasukawensis* in having a lower ultimate whorl in comparison to its width. *C. omagariensis* is smaller than *C. nuda* Okutani, 2001 and differs also in having a subsutural ramp rather than a pleated cord and no knob on the inner lip.

Description.—The protoconch is unknown. The shell is tur-

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biniform, smooth apart from a narrow subsutural ramp. The transition between lateral flank and the base is rounded with no demarcation. The shell wall is relatively thick and bi-layered; the inner layer is nacreous and the outer layer is prismatic. The ultimate whorl is characterized by a slightly dipping suture line. The generating curve is circular, aperture tangential, and peristome uninterrupted. The outer lip is smooth. The inner lip is poorly preserved in all available specimens but it seems to be narrow. The umbilicus is absent although in some specimens a poorly developed umbilical chink is visible. The latter feature may have resulted, however, from erosion of the inner lip.

Discussion.—*C. omagariensis* is very similar to *C. yasukawensis*. The latter species, however, is smaller and much more variable morphologically, especially in respect to its spiral ornamentation. *C. omagariensis* has a much more stable morphology and is represented only by smooth shells. A similar species is known from a single specimen found at "a small tributary of the Abesinai-gawa" (Abeshinai River) in the Nakagawa area from rocks of Senonian age (Nagao 1939: 215); *Ataphrus tesioensis* Nagao, 1939 differs from *C. omagariensis* in lacking subsutural ramp and in having "...prominent bundles of lines of growth near the suture, with numerous longitudinal impressed lines..." (Nagao 1939: 214), a feature not observed on our specimens. Further studies are needed to substantiate relation between these two species. *C. omagariensis* is very common at the Omagari seep site. A similar although poorly preserved shell has been reported from a plesiosaur fall association by Kaim et al. (2008b). Another similar shell has been reported by Kiel et al. (2009) as "low-spired skeneiform gastropod" from the Upper Cretaceous Akita Creek wood-fall association (Kiel et al. 2009: 77).

Stratigraphic and geographic range.—Omagari hydrocarbon seep in Nakagawa area of northern Hokkaido, Japan. Campanian, Upper Cretaceous.

Family Trochidae Rafinesque, 1815

Genus *Margarites* Gray, 1847

Type species: *Trochus helicinus* Fabricius 1780 (? = *Turbo helicinus* Phipps, 1774) by original designation pro *Margarita* Leach, 1819 (preoccupied); Recent, Arctic Sea.

Margarites sasakii sp. nov.

Fig. 8.

2003 *Margarites* sp.; Hikida et al. 2003: 338, fig. 10: 1, 2.

Etymology: In honour of Dr. Takenori Sasaki.

Holotype: UMUT MM30174, Fig. 8D, moderately preserved shell without protoconch.

Type locality: Omagari site, Nakagawa area, Northern Hokkaido, Japan. Coordinates 44°39'26'' N, 144°2'25'' E.

Type horizon: Fossil hydrocarbon seep deposits of Omagari Formation, Campanian, Upper Cretaceous.

Material.—37 moderately to poorly preserved specimens from the Omagari site; 35 at UMUT and two at NMM already illustrated by Hikida et al. (2003).

Dimensions.—The holotype is 9.42 mm high and 12.86 mm wide; NMM 229 is 10.85 mm high and 12.7 mm wide. Note that both shells are incomplete.

Diagnosis.—Shell turbiniform, whorls inflated. Juvenile and adolescent whorls ornamented by spiral cords present both on the lateral flank and the base. Umbilicus absent. *M. sasakii* differs from other species of the genus by the absence of an umbilicus.

Description.—The protoconch is not preserved. The shell is turbiniform with a dark-brown amorphous outermost layer (Fig. $8B_3$). This might be a re-crystallized calcitic outer layer (Kiel and Goedert 2007) or even fossilized periostracum. Juvenile whorls are ornamented by spiral cords. There are four ribs at the lateral flank, one on the demarcation with the base and at least four on the base. The ribs fade away at the terminus being only weak undulations crossed by strongly enhanced prosocline growth lines. Some of these structures are apparently growth interruptions. The generating curve is circular, aperture tangential, and peristome uninterrupted. Apertural elaborations are absent.

Discussion.—The shells under consideration are difficult to classify as they could be included in many different vetigastropod genera. We preliminarily classify them as *Margarites* pending better preserved material. *M. sasakii* differs from other species of *Margarites* by lacking an umbilicus and possessing spiral cords also on the base. However, the remaining gross morphology strongly recollects *M. ryukyuensis* Okutani, Sasaki, and Tsuchida, 2000 from a Recent chemosynthesis-based community in the Okinawa Trough (Okutani et al. 2000). The other similar genus is the seguenzioid *Cataegis* McLean and Quinn, 1987 that lacks an umbilicus but usually possesses much stronger ornamentation (see e.g., McLean and Quinn 1987; Hickman and McLean 1990; Warén and Bouchet 1993; Fu and Sun 2006). Another similar genus is the trochid *Pseudotalopia* Habe, 1961, which again possesses an umbilicus and much more delicate ornamentation (Okutani 2000). *M. sasakii* is the largest vetigastropod recovered so far from the Omagarii seep site. It is usually poorly preserved but easily identifiable due to its dark brown outer layer.

Stratigraphic and geographic range.—Omagari hydrocarbon seep in Nakagawa area of northern Hokkaido, Japan. Campanian, Upper Cretaceous.

Superfamily Seguenzioidea Verrill, 1884

Family Chilodontidae Wenz, 1938

Subfamily Cataeginae McLean and Quinn, 1987

Genus *Cataegis* McLean and Quinn, 1987

Type species: *Homalopoma finkli* Petuch, 1987 as senior synonym of *Cataegis toreuta* McLean and Quinn, 1987; original designation. Recent, Caribbean.

Discussion.—*Cataegis* was primarily described as a trochid of uncertain familial affinity (McLean and Quinn 1987; Hickman and McLean 1990). Bouchet et al. (2005) included Cataeginae as a subfamily of Chilodontidae Wenz, 1938 in

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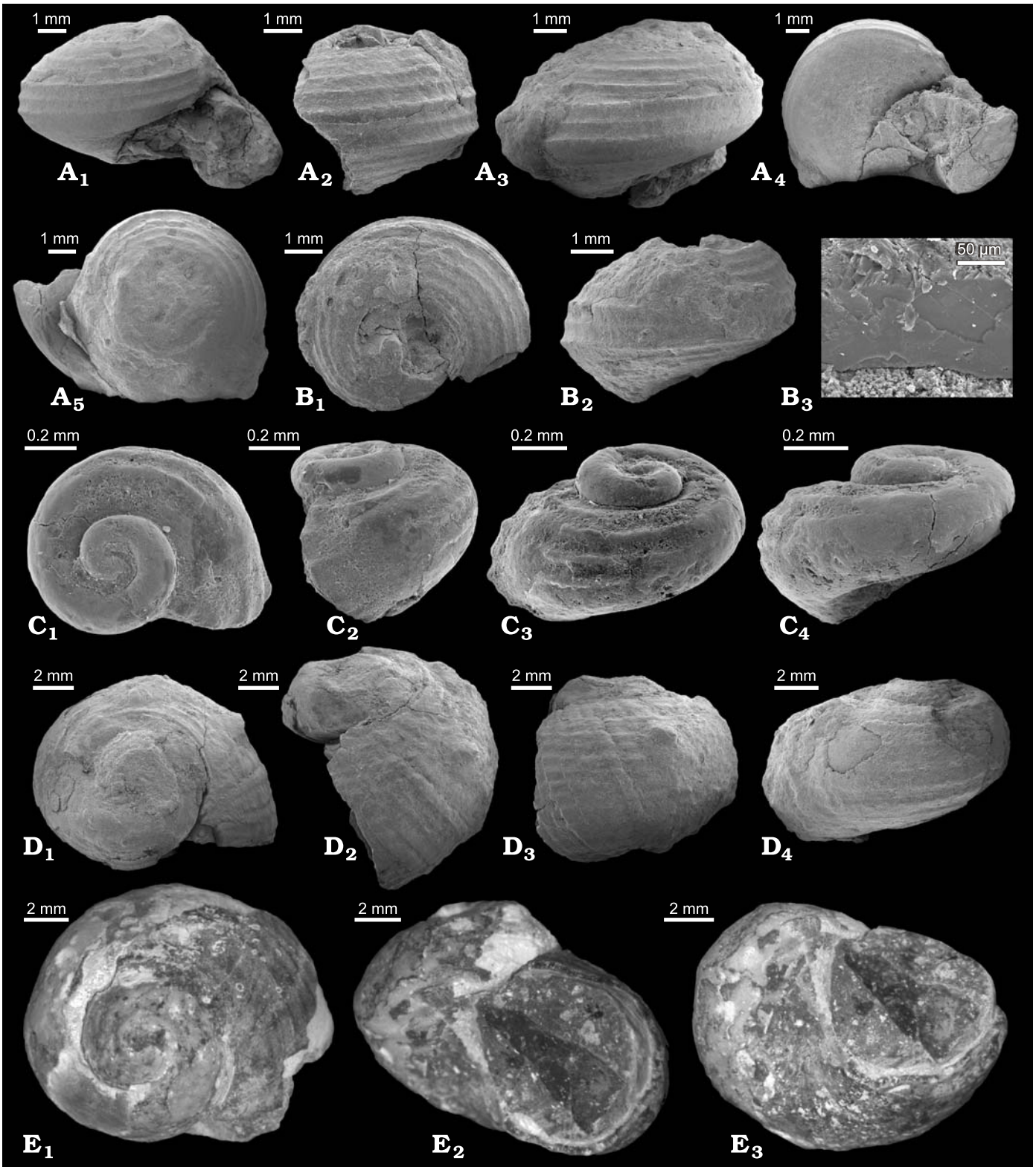


Fig. 8. The trochid gastropod *Margarites sasakii* sp. nov. from the Campanian (Upper Cretaceous) Omagari seep site in Hokkaido, Japan. **A**. UMUT MM30171 in apertural (A_1) lateral (A_2, A_3), umbilical (A_4), and apical (A_5) views. **B**. UMUT MM30172 in apical (B_1) and lateral (B_2) views; B_3, cross section through outer layer. **C**. Juvenile UMUT MM30173 in apical (C_1), and lateral (C_2–C_4) views. **D**. Holotype (UMUT MM30174) in apical (D_1) and lateral (D_2–D_4); note change in ornamentation in D_4. **E**. NMM 229 in apical (E_1), apertural (E_2), and umbilical (E_3) views.

Seguenzioidea. Recent molecular investigations by Kano (2008) revealed that *Cataegis* indeed goes to Seguenzioidea; the remaining family Chilodontidae appears to be a polyphyletic taxon and needs further investigations.

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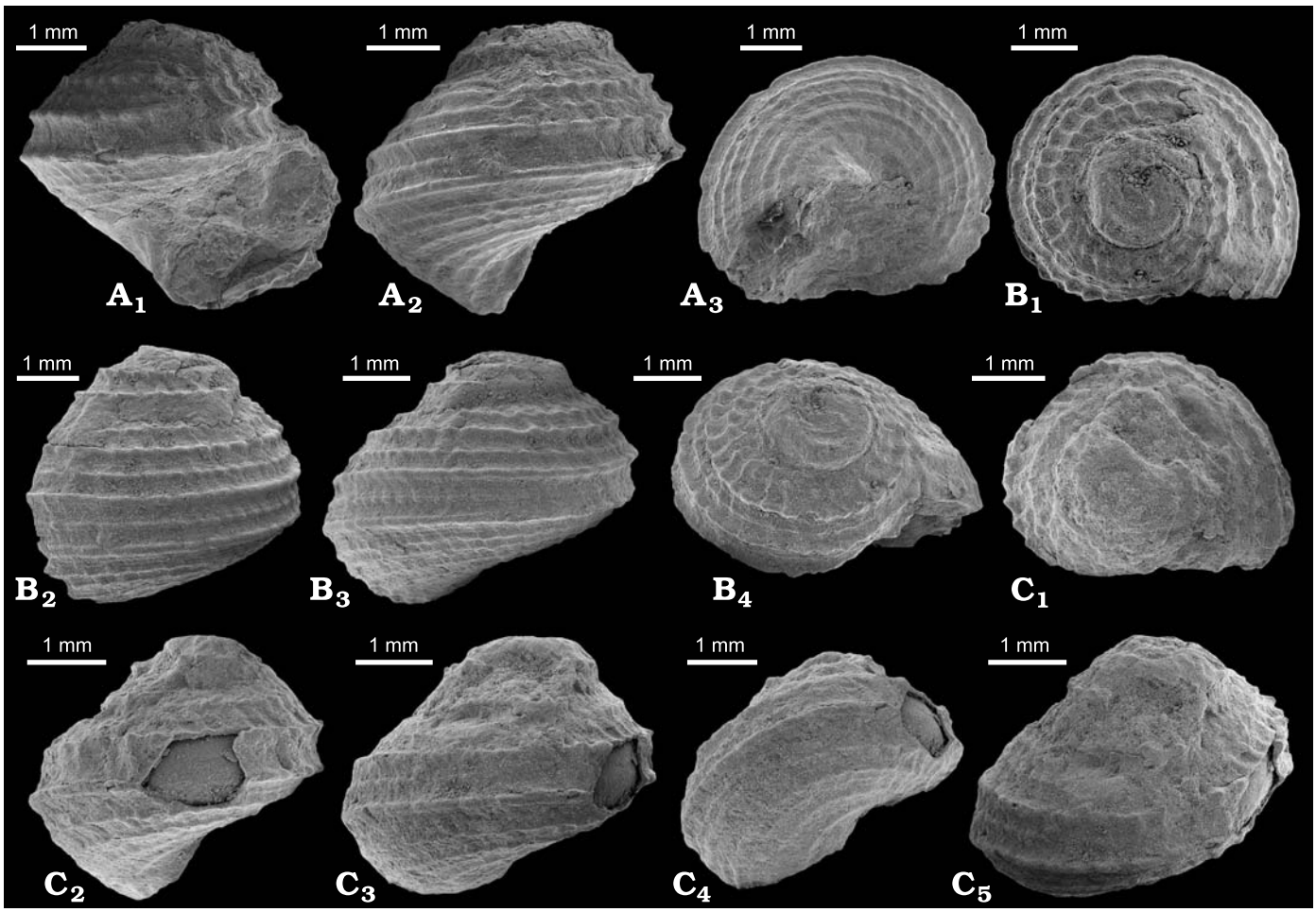


Fig. 9. The seguenzioid gastropod *Cataegis nakagawensis* sp. nov. from the Campanian (Upper Cretaceous) Omagari seep site in Hokkaido, Japan. **A**. Holotype (UMUT MM30175) in apertural (A_1), lateral (A_2), and umbilical (A_3) views. **B**. UMUT MM30176 in apical (B_1), lateral (B_2, B_3), and latero-apical (B_4) views. **C**. UMUT MM30177 in apical (C_1), lateral (C_2, C_3), latero-umbilical (C_4), and latero-apical (C_5) views.

Distribution.—*Cataegis* includes deep water species known from the Caribbean (McLean and Quinn 1987; Hickman and McLean 1990; Warén and Bouchet 1993) and from the Pacific (McLean and Quinn 1990; Fu and Sun 2006). At least one species, *C. meroglypta* McLean and Quinn, 1987 is known from hydrocarbon seep on the Louisiana Slope (Warén and Bouchet 1993; García 2002; Gill et al. 2005). *Cataegis* sp. has also been found in seeps off Costa Rica (Anders Warén, personal communication 2009). Gill et al. (2005) reported occurrences of *C. meroglypta* from Cenozoic Caribbean seep carbonates. The species has been identified in the Oligocene or Early Miocene Sub-Oceanic Fault Zone seeps of Barbados and also the Miocene Freeman's Bay Limestone seep fauna (Gill et al. 2005). Moroni (1966) reported *Phasianema taurocrassum* Sacco, 1895 from the Miocene "Calcare a Lucine" (seep carbonates according to Taviani 1994 and Peckmann et al. 1999) which is quite similar to *Cataegis*.

Cataegis nakagawensis sp. nov.

Fig. 9.

Etymology: After Nakagawa town, located close to the type locality.

Holotype: UMUT MM30175, Fig. 9A, moderately preserved shell with no protoconch.

Type locality: Omagari site, Nakagawa area, Northern Hokkaido, Japan. Coordinates 44°39'26'' N, 144°2'25'' E.

Type horizon: Fossil hydrocarbon seep deposits of Omagari Formation, Campanian, Upper Cretaceous.

Material.—Four moderately preserved specimens without protoconchs.

Dimensions.—The holotype is 4.1 mm high and 4.91 mm wide.

Diagnosis.—Shell turbiniform, whorls ornamented with beaded spiral cords. Two of the cords form spiral keels on the lower part of the flank. *C. nakagawensis* differs from other species of the genus by having two distinctly keeled cords.

Description.—The protoconch is not preserved. The shell is turbiniform with whorls ornamented by six spiral cords. Two of them are stronger transforming into two keels. The lower keel is located at the angulation demarcating the flank from the base, while the other one is located slightly below the mid part of the flank. There are three cords above the upper keel and one cord between the keels. The base is ornamented by five beaded spiral cords. There is no umbilicus and the aperture is poorly preserved.

Discussion.—The shells under consideration are provision-

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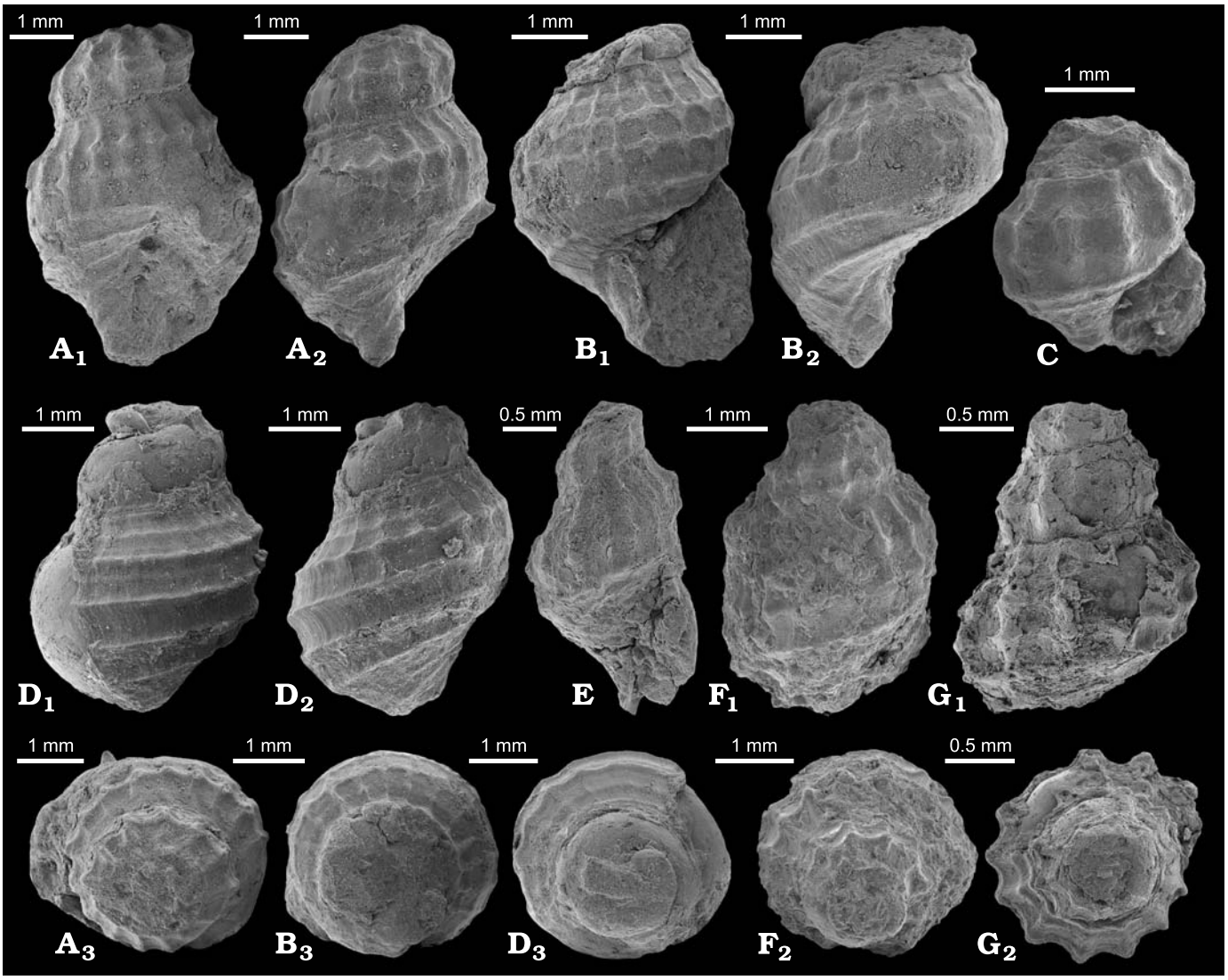


Fig. 10. The provannid gastropod *Provanna nakagawensis* sp. nov. from the Campanian (Upper Cretaceous) Omagari (**A**–**D**) and Yasukawa (**E**–**G**) seep sites in Hokkaido, Japan. **A**. Holotype (UMUT MM30178) in apertural (A_1), lateral (A_2), and apical (A3) views. **B**. UMUT MM30179 in apertural (B_1), lateral (B_2), and (B_3) views. **C**. UMUT MM29362 in apertural view. **D**. UMUT MM30180 in lateral (D_1, D_2) and apical (D_3) views. **E**. UMUT MM30181 in apertural view. **F**. UMUTMM30182in lateral (F_1) and apical (F_2) views. **G**. UMUT MM19363 in lateral (G_1) and apical (G2) views.

ally classified as *Cataegis* because they lack an umbilicus and posses strong spiral cords on the flank and also on the base. *Cataegis* has not been noted so far from Japan. The nearest extant occurrences are *C. leucogranulata* from Taiwan (Fu and Sun 2006) and *C. celebesensis* from Indonesia (McLean and Quinn 1987).

Stratigraphic and geographic range.—Omagari hydrocarbon seep in Nakagawa area of northern Hokkaido, Japan. Campanian, Upper Cretaceous.

Order Caenogastropoda Cox, 1959

Superfamily Abyssochrysoidea Tomlin, 1927

Family Provannidae Warén and Ponder, 1991

Genus *Provanna* Dall, 1918

Type species: *Trichotropis* (*Provanna*) *lomana* Dall, 1918. Recent; US Pacific Coast; by monotypy.

Provanna nakagawensis sp. nov.

Fig. 10.

2008 Yasukawa provannid; Kaim et al. 2008a: 427, fig. 3D, E, I.
2008 Omagari provannid; Kaim et al. 2008a: 427, fig. 3F, J.

Etymology: After Nakagawa town, located close to the type locality.

Holotype: UMUT MM30178, Fig. 10A, moderately preserved shell with no protoconch.

Type locality: Omagari site, Nakagawa area, northern Hokkaido, Japan. Coordinates 44°39’26’’N, 144°2’25’’E.

Type horizon: Fossil hydrocarbon seep deposits of the Omagari Formation, Campanian, Upper Cretaceous.

Material.—76 moderately to poorly preserved specimens without protoconchs from the Omagari site and three poorly preserved specimens from the Yasukawa site.

Dimensions.—The holotype is 5.36 mm high and 3.35 mm wide.

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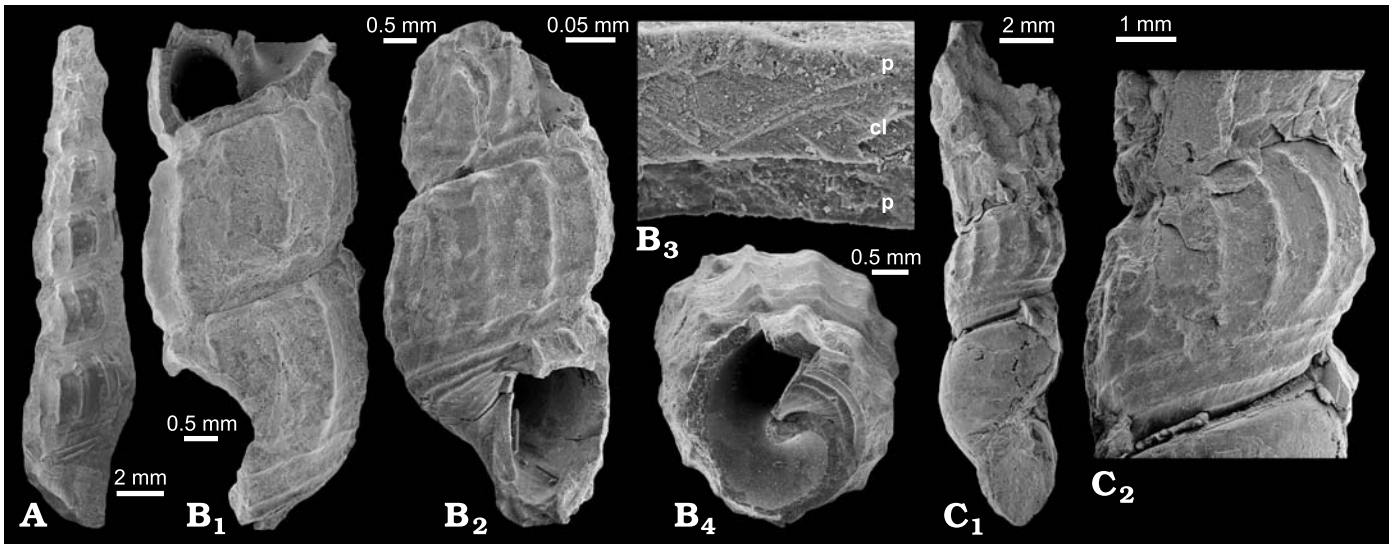


Fig. 11. The hokkaidoconchid gastropod *Hokkaidoconcha hikidai* Kaim, Jenkins, and Warén, 2008 from the Campanian (Upper Cretaceous) Yasukawa seep site in Hokkaido, Japan. **A**. Holotype (UMUT MM29391) in lateral view. **B**. UMUT MM30183 in lateral (B_1), apertural (B_2), and apical (B_4) views; B_3, cross section through the shell displaying inner and outer prismatic (p) layers and middle cross-lamellar (cl) layer. **C**. UMUT MM30184 in apertural view (C_1) and details of ornamentation (C_2).

Diagnosis.—Shell of small size, rather high, moderately inflated. Spiral ornament consists of two median prominent ribs and additional weaker rib adapically to the primary ribs. Spiral ribs intersected by orthocline axial ribs, which may fade away later in ontogeny. Blunt nodes present at intersections of spiral and axial ribs.

Description.—The shell is of small size, thin, melanoid to rissoid in shape with strong spiral and axial sculpture. In some specimens the axial sculpture is weak or absent. The protoconch is unknown. Spiral ribs are strong on juvenile whorls, two prominent ones and one weaker, which occur adapically of the other two. There might be an additional rib appearing abapically of the prominent ribs on some larger shells. The base is demarcated from the lateral flank by an additional strong spiral rib. The base is usually ornamented by 2–3 spiral ribs. Axial ribs orthocline, equally strong as spirals on the juvenile whorls and fading out on the adolescent whorls in some specimens. Aperture poorly preserved on the available specimens.

Discussion.—This thin-shelled species, although fairly common at the Omagari site, is usually poorly preserved. In this respect it is similar to many Recent species of *Provanna*. *P. nakagawensis* is most similar to Recent *P. shinkaiae* Okutani and Fujikura, 2002 from the Japan Trench. The latter species is also thin-shelled and ornamented by two prominent ribs but lacks the weaker adapical rib (Okutani and Fujikura 2002). Moreover, *P. shinkaiae* has beaded or spiny intersections of spiral and axial ribs, while in *P. nakagawensis* blunt nodes appear there. Other similar species include *P. pacifica* (Dall, 1908) and *P. goniata* Warén and Bouchet, 1986 known from the eastern Pacific; both, however, are much larger than *P. nakagawensis* (Warén and Bouchet 1986). It is likely that one of the provannid shells (UMUT MM 29514) reported by Kiel et al. (2009: fig. 3E) from the Upper Cretaceous Akita Creek wood-fall association from Hokkaido belongs to *P. nakagawensis*. Also the provannid specimens reported by Kaim et al. (2008a) as "Gakkonosawa provannid" from Cretaceous Gakkonosawa seep carbonate may belong to *P. nakagawensis*.

Stratigraphic and geographic range.—Omagari and Yasukawa hydrocarbon seeps in Nakagawa area of northern Hokkaido, Japan. Campanian, Upper Cretaceous.

Family Hokkaidoconchidae Kaim, Jenkins, and Warén, 2008

Genus *Hokkaidoconcha* Kaim, Jenkins, and Warén, 2008

Type species: *Hokkaidoconcha tanabei* Kaim, Jenkins, and Warén, 2008; Kanajirisawa Creek, Tappu area, Hokkaido, Japan; Middle Cenomanian (Late Cretaceous); original designation.

Hokkaidoconcha hikidai Kaim, Jenkins, and Warén, 2008

Fig. 11.

Remarks.—*Hokkaidoconcha hikidai* has been recently described by Kaim et al. (2008a). Since preparation of the latter paper we have found additional specimens of this species. Regrettably none of these has the protoconch preserved. Nevertheless we found some specimens in the seep periphery (see zonation of the Yasukawa seep in Jenkins et al. 2007b) with original shell microstructure preserved. The shell consists of a thin prismatic outer layer, a thick cross-lamellar middle layer, and a moderately thick prismatic inner layer (Fig. $11B_3$), a shell layer organization known from Provannidae (Kiel 2004).

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Suborder Neogastropoda Thiele, 1929

Neogastropoda indet.

Fig. 12D.

Material.—Single incomplete shell (UMUT MM30188) from Yasukawa partially embedded in the rock matrix.

Dimensions.—The visible part of the shell UMUT MM30188 is 4.44 mm high and 3.77 mm wide.

Description.—Only lateral flank of half-whorl is preserved. The shell possesses a wide ramp at the suture. There are seven sturdy orthocline axial ribs and approximately twelve much weaker spiral ribs on the visible part of the shell. The ramp is demarcated from the flank by an additional spiral rib ornamented with blunt nodes appearing at the intersections with axial ribs. There is an additional spiral rib on the ramp surface. The shell is elongated abapically suggesting the presence of a siphonal notch or channel.

Discussion.—The shell under consideration is too incompletely preserved to be assigned to any genus or species. There are similar neogastropods known from Recent seep/vent communities off Japan. Especially similar are some species of *Oenopota* described by Okutani and Fujikura (1992) and Okutani et al. (1993). A similar species from an Oligocene seep carbonate in Washington State has been classified by Kiel (2006) as *Benthomangelia*? sp. The species under consideration differs both from the Recent Japanese and Oligocene American species in having orthocline rather than opisthocyrt axial ribs. It should be stated here, however, that there is also a number of shallow water neogastropods in the Cretaceous to which the Yasukawa specimen can be related.

Subclass Heterobranchia Gray, 1840

Order Heterostropha Fischer, 1885

Superfamily Acteonelloidea Gill, 1871

Family Bullinidae Gray, 1850

Genus *Sulcoactaeon* Cossmann, 1895

Type species: *Actaeonina striato-sulcata* Zittel and Goubert, 1861; Glos, Normandy, France; ?Oxfordian (Late Jurassic); original designation.

?*Sulcoactaeon* sp.

Fig. 12A.

Material.—Single incomplete shell (UMUT MM30185) from Yasukawa.

Dimensions.—The shell UMUT MM30185 is 2.96 mm high and 1.41 mm wide.

Description.—The shell is broadly spindle-like, 1.41 times as high as broad. Early whorls are poorly preserved. Teleoconch whorls are ornamented by numerous spiral furrows. The last whorl possesses a narrow subsutural ramp and two furrows just below the ramp. All other furrows (approx. 12) are present in the abapical part of the whorl. The density of the furrows increases abapically. The aperture is D-shaped. The inner lip is narrow. A narrow umbilical chink is present. Neither teeth nor other apertural elaborations are visible.

Discussion.—*Sulcoactaeon* is a genus known so far from Bajocian to Valanginian times (Kaim 2004) although it is considered by some authors (Bandel et al. 2000) as a subgenus of the Recent *Bullina* (family Bullinidae). The most important shell character of Bullinidae is the absence of teeth or columellar plications on the inner lip. Such features are not observed at the specimen under consideration. Nevertheless, due to generally poor preservation, there is a possibility that these features are not preserved in our specimen and that is why we classified it as *Sulcoactaeon* with some hesitation. Sohl (1964) described some species of *Acteon* and *Troostella* from Upper Cretaceous shallow water sediments of the US Gulf Coast which have an oblique low fold on the columella with which later merges—and is not expressed on the inner lip. Our specimen may also be related to this group. The understanding of relations between fossil groups of acteonelloids is still rather limited and out of scope of this paper. Kiel (2006) described similar species from Oligocene cold seep carbonates of Washington State as *Acteon* sp. He reported a presence of "...weak plication at base" (Kiel 2006: 129) in his specimen.

Naticiform gastropod

Fig. 13.

Material.—24 specimens from Omagari site: 23 specimens at UMUT and one at NMM.

Dimensions.—The best preserved shell UMUT MM30190 (Fig. 13B) is 1.96 mm high and 2.04 mm wide.

Description.—The shell is small, globose, smooth apart from prosocline growth lines. Early whorls are poorly preserved but the protoconch is apparently orthostrophic. Teleoconch consists of 3–3.5 inflated whorls with incised suture. Aperture is circular and tangential. No aperture elaborations are visible. Umbilicus is absent.

Discussion.—The shells under consideration are difficult to classify due to their poor preservation. The small size and tangentially located circular aperture may suggest that the shells belong to neomphalid *Retiskenea*. The specimens from the Omagari site are similar in gross morphology to the Recent *Retiskenea diploura* Warén and Bouchet, 2001 living in the Japan Trench (Okutani and Fujikura 2002). The latter species, however, possesses slit-like umbilicus, a character not observed in our specimens. Similar is also *Retiskenea statura* (Goedert and Benham, 1999) from Eocene and Oligocene cold seep carbonates of Western Washington (Goedert and Benham 1999, Kiel 2006, Campbell et al. 2008). The state of the umbilicus in *R. statura* is not reported by any of the abovementioned authors and the published illustrations are not conclusive on that matter. It seems, however, that there is no umbilicus in the holotype of Goedert and Benham (1999: fig. 2A) and the specimen described by

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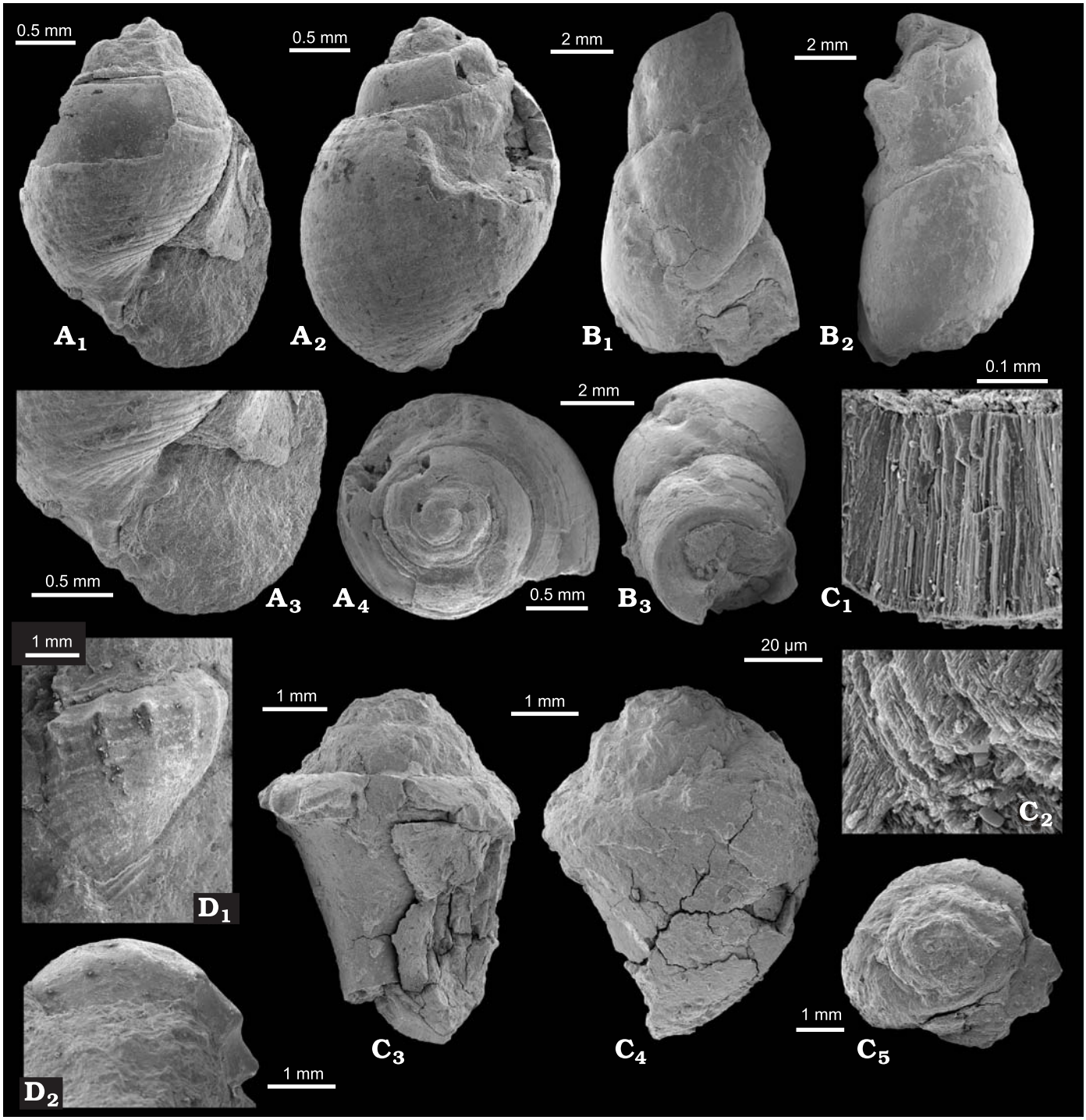


Fig. 12. Gastropods from the Campanian (Upper Cretaceous) Omagari (**B**) and Yasukawa (**A**, **C**, **D**) seep sites in Hokkaido, Japan. **A**. ?*Sulcoactaeon* sp. (UMUT MM30185) in apertural (A_1), lateral (A_2), and apical (A_4) views; A_3, close up of the aperture. **B**. Gastropoda indet. 1 (UMUT MM30186) in apertural (B_1), lateral (B2), and apical (B3) views. **C**. Gastropoda indet. 2 (UMUT MM30187) in apertural (C_3), lateral (C_4), and apical (C_5) views; C_1, fibrous prismatic shell outer layer, C_2, cross lamellar inner layer. **D**. Neogastropoda indet. (UMUT MM30188) in lateral (D_1) and apical (D_2) views.

Kiel (2006) (Steffen Kiel, personal communication 2009). Campbell et al. (2008) reported a species *Retiskenea*? *kieli* Campbell, Peterson, and Alfaro, 2008 from Lower Cretaceous seep carbonates of California. The shells from the Omagari site are higher spired than the latter species. The most important shell character of *Retiskenea* is a protoconch with reticulate pattern (Warén and Bouchet 2001). Unfortunately the protoconch ornamentation is not preserved in any of our specimens; therefore, we decided to leave this gastropod unnamed—potentially it may represent an entirely different group of gastropods—pending collection of better preserved specimens.

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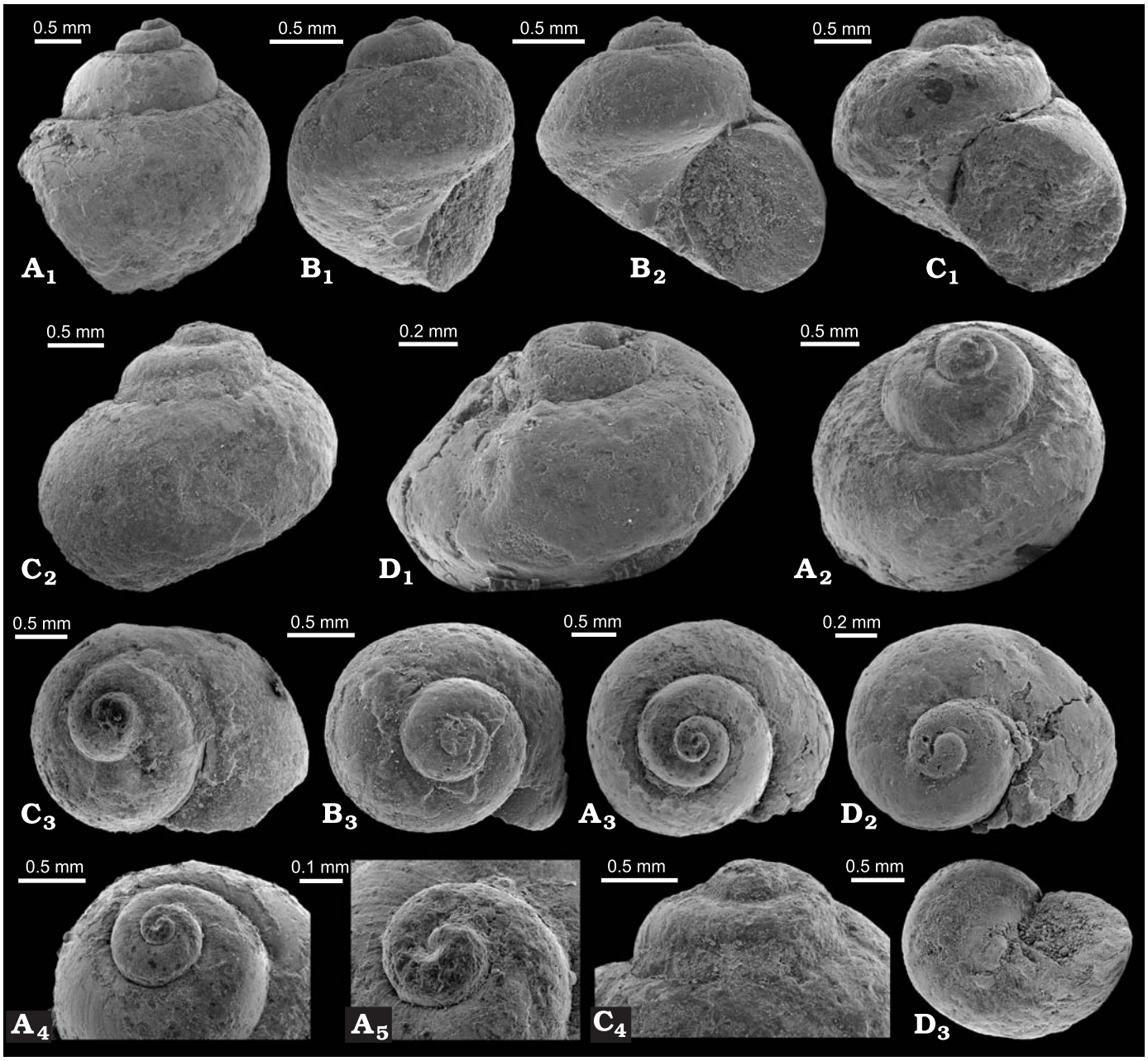


Fig. 13. Naticiform gastropod from the Campanian (Upper Cretaceous) Omagari seep site in Hokkaido, Japan. **A**. UMUT MM30189 in lateral (A_1), latero-apical (A_2), and apical (A_3) views; A_4, close up of the juvenile whorls, A_5, close up of the initial whorl. **B**. UMUT MM30190 in lateral (B_1), apertural (B_2), and apical (B_3) views. **C**. UMUT MM30191 in apertural (C_1), lateral (C_2), and apical (C_3) views; C_4, close up of the juvenile whorls in lateral view. **D**. UMUT MM30192 in lateral (D_1), apical (D_2), and umbilical (D_3) views.

Skeneiform gastropod

Fig. 14.

Material.—44 poorly preserved shells from the Omagari site, all deposited at UMUT.

Dimensions.—The best preserved shell UMUT MM30193 (Fig. 14A) is 2.2 mm high and 1.14 mm wide.

Description.—The shell is small and skeneiform with 3–3.5 inflated whorls and the suture deeply incised. Initial whorl poorly preserved at all accessible specimens but apparently orthostrophic. The teleoconch is smooth. The umbilicus is wide open with no sculpture on the basal area. The aperture is drawn out peripherally and is cemented to the preceding whorl in the parietal part.

Discussion.—The shells under consideration are of very simple morphology observed in a number of gastropod groups including small trochids, skeneids, neomphalids, and heterobranchs. It seems that the initial whorl is orthostrophic and therefore affinities to the heterobranchs are less likely though some heterobranchs have the heterostrophy obscured. Among vent and seep taxa a small trochid *Helicrenion reticulatum* Warén and Bouchet, 1993 possesses very similar shell (Warén

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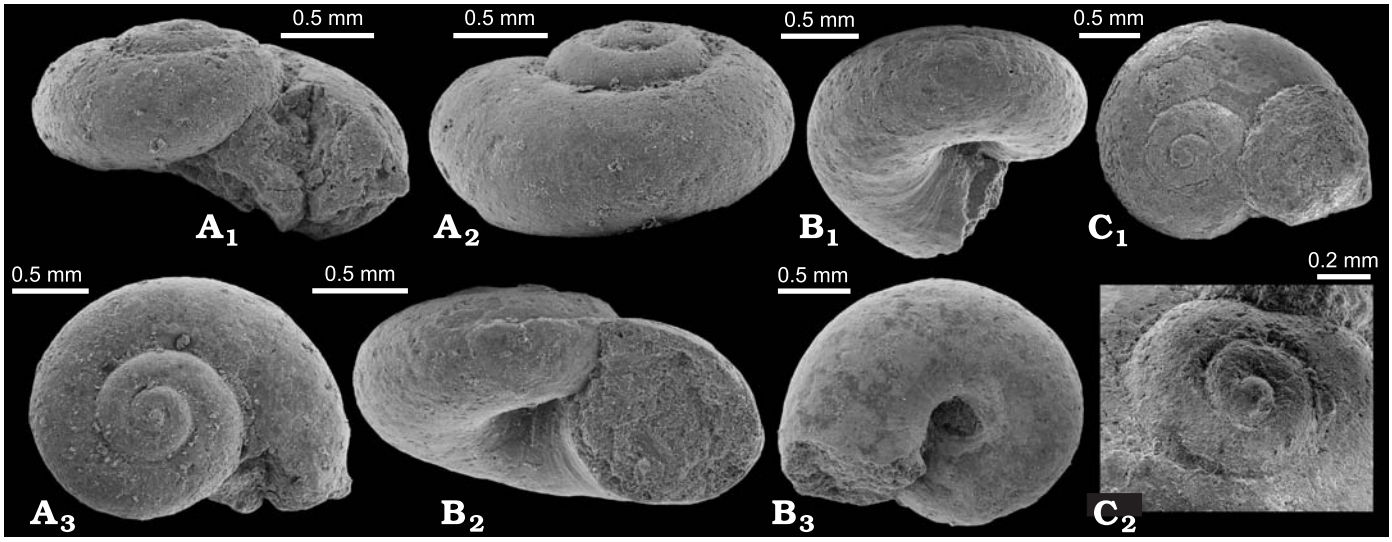


Fig. 14. Skeneimorph gastropod from the Campanian (Upper Cretaceous) Omagari seep site in Hokkaido, Japan. **A**. UMUT MM30193 in apertural (A_1), lateral (A_2), and apical (A_3) views. **B**. UMUT MM30194 in lateral (B_1), apertural (B_2), and umbilical (B_3) views. **C**. UMUT MM30195 in apical view (C_1) and close up of initial whorls (C_2).

and Bouchet 1993; Desbruyères et al. 2006). The latter species is characterized by large net-like pattern on its protoconch. This character unfortunately is not preserved on our specimens and that is why we decided to leave the species unnamed. Similar shells from Oligocene cold-seep carbonates of Washington State have been classified by Kiel (2006) as the peltospirid *Depressigyra*? sp. This identification, however, remains uncertain as the protoconch ornament could not be observed.

Gastropoda indet. 1

Fig. 12B.

Material.—A single incomplete shell from Omagari.

Dimensions.—The shell UMUT MM30186 (Fig. 12B) is 10.9 mm high and 5.82 mm wide.

Description.—The shell is elongated with 2.5 whorls preserved. The whorls are weakly inflated and their surface is smooth. The suture is weakly incised. It remains unsure if this lack of ornamentation is original character or resulted from peeling off the outermost layer. The protoconch and aperture characters are unknown.

Discussion.—The only strongly elongated gastropod in the seep localities under consideration is *Hokkaidoconcha hikidai*. However, the latter species occurs exclusively in Yasukawa and its shell expansion is much weaker. The shell under consideration may belong to a weakly preserved neogastropod. Better preserved material is necessary to confirm this supposition.

Gastropoda indet. 2

Fig. 12C.

Material.—A single incomplete shell from Yasukawa.

Dimensions.—The shell UMUT MM30187 (Fig. 12C) is 5.45 mm high and 4.62 mm wide (note that the shell is laterally compressed).

Description.—The shell is globose, low spired and it possesses an enveloping last whorl. The shell surface is smooth. The shell consists of two layers. Inner layer is cross-lamellar while outer layer is fibrous prismatic.

Discussion.—The taxonomic position of this cassid-like shell remains unresolved pending additional better preserved material.

Class incertae sedis

Family Gigantocapulidae Beu, 2007

Genus *Gigantocapulus* Hayami and Kanie, 1980

Type species: *Helcion giganteus* Schmidt, 1873; North Pacific region; Campanian (Late Cretaceous); original designation.

Gigantocapulus sp.

Fig. 15.

Material.—Single juvenile shell from Yasukawa.

Dimensions.—The shell UMUT MM30196 (Fig. 15) is 4.4 mm high, 5.9 mm long, and 4 mm wide.

Description.—The small shell is limpet-shaped with high elevated apex. The apex is located anteriorly (or posteriorly depending on interpretation of the animal). The majority of the shell is ornamented by thick concentric undulations. The shell becomes irregular in its anteriormost part displaying irregular shell growth expressed by meandering undulations. Aperture elliptical. Shell composed of three layers: outermost layer very thin and most probably fibrous prismatic. Medial layer also thin and crossed foliate recollecting irregular crossed foliate microstructure of Fuchigami and Sasaki (2005). The microstructure of the thick inner layer remains unrecognized.

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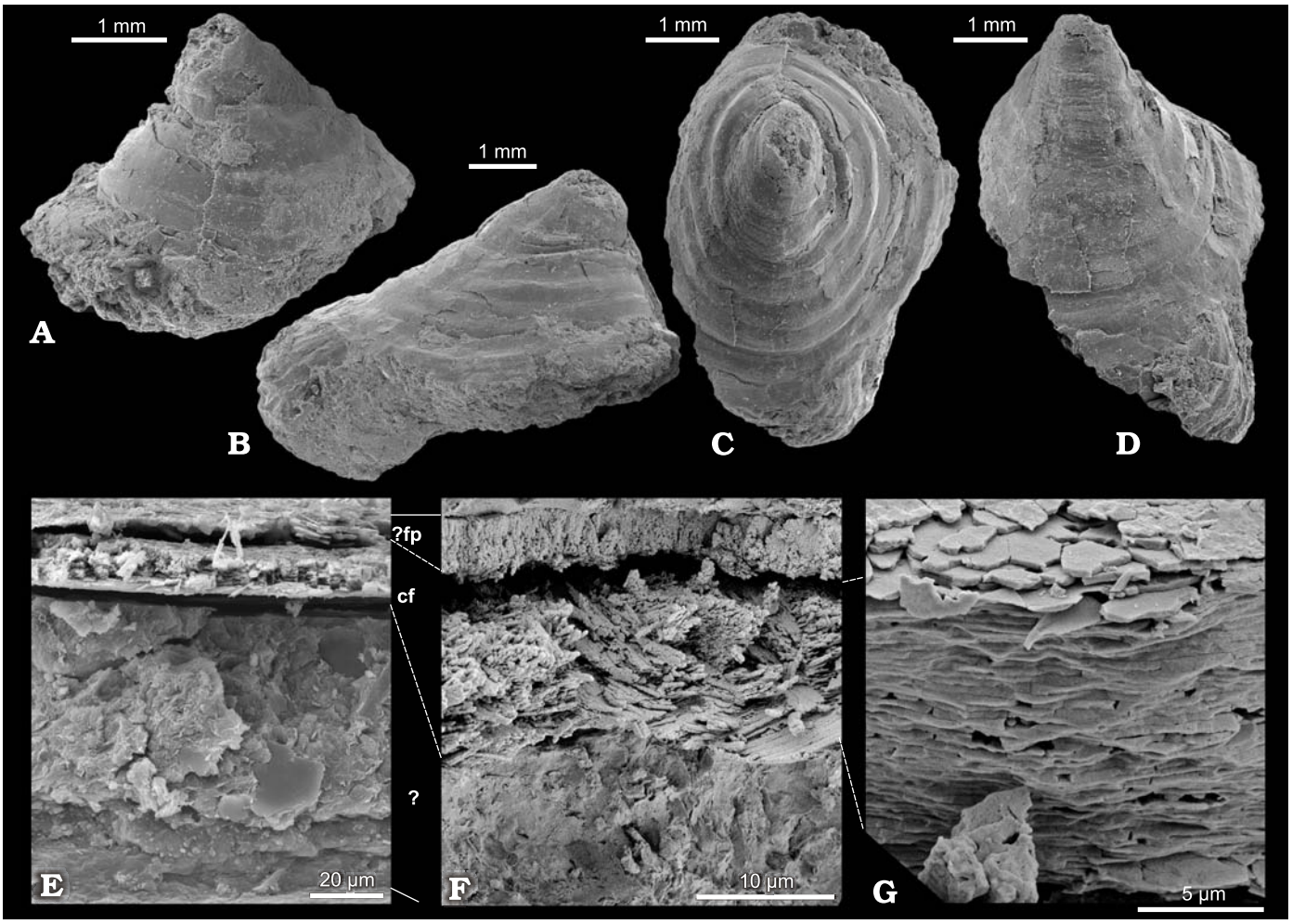


Fig. 15. A juvenile specimen (UMUT MM30196) of *Gigantocapulus* sp., a mollusk of uncertain taxonomic affinity in lateral (**A**, **B**), apical (**C**), and posterior (**D**) views. **E**. Cross section through the shell displaying three layers: an outer, possibly fibrous prismatic (fp), a middle cross foliate (cf), and an inner layer of uncertain microstructure. **F**. Another section showing the same layers. **G**. Close up of the foliated structure, uppermost part of the layer consist of polygonal plates resembling broken semifoliated structure or detached tablets of nacreous structure.

Discussion.—The taxonomic position of *Gigantocapulus* has been recently reviewed by Beu (2007), who stated that this genus may represent a tergomyan monoplacophoran, a vanicoroid gastropod, or a separate, extinct gastropod group. It is beyond the scope of this paper to argue on high level classification of this mollusk, however, the presence of crossed foliated layer may suggest patellogastropod affinity.

Discussion

Historical background.—The Late Cretaceous record of gastropods from chemosynthesis-based associations is surprisingly poor in comparison to the Early Cretaceous and Cenozoic record. It is basically limited to two cold seep localities in California and hydrothermal vent deposits Troodos ophiolite, Cyprus. The Romero Creek (Upper Campanian) and Moreno Gulch (Santonian) seep deposits in California yielded only two species of *Hokkaidoconcha*, a single species in each locality (Kiel et al. 2008b). The Cypriot vent deposits also revealed only hokkaidoconchid/provannid gastropods (Little et al. 1999; Kaim et al. 2008a). This is in contrast to Late Jurassic/Early Cretaceous seep localities which have abundant and diverse gastropod associations, for example in some sites in California (Campbell et al. 2008; Kiel et al. 2008b), the Crimea (Kiel and Peckman 2008), the Carpathians (Ascher 1906), France (Macsotay 1980), and Antarctica (Kaim and Kelly 2009). There is also relatively good Cenozoic record of gastropods from chemosynthesis-based associations (Moroni 1966; Marshall 1985, 1994; Goedert and Squires 1990; Taviani 1994; Squires 1995; Goedert and Kaler 1996; Amano and Little 2005, Gill et al. 2005; Kiel 2006; Kiel and Goedert 2006a, b, 2007; Amano et al. 2007; Kiel and Peckmann 2007). Therefore, the localities in Hokkaido (especially Omagari and Yasukawa) yielding rich and relatively well preserved Late Cretaceous hydrocarbon seep gastropod associations fill the gap between Early Cretaceous and Eocene (Fig. 16). Surprisingly, the only taxa which occur both in the Early and Late Cretaceous associations are hokkaidoconchids. They are common in numerous

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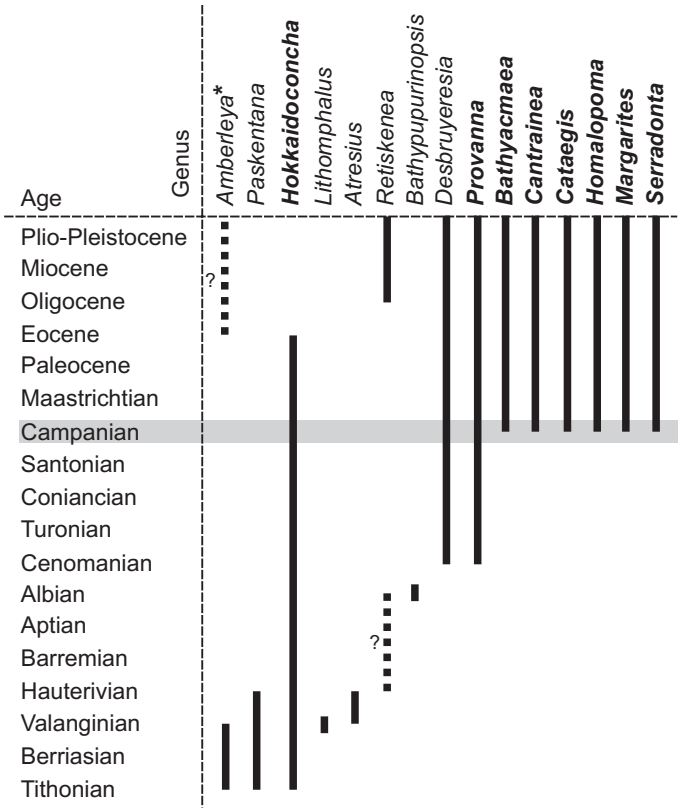


Fig. 16. List of gastropod genera and their stratigraphical ranges in Cretaceous chemosynthesis-based associations. The genera in bold occur in the Campanian (Late Cretaceous) hydrocarbon seep sites in Nakagawa area. Note discrepancy in the composition of Lower and Upper Cretaceous gastropod associations. *Similar to *Amberleya* is *Bathybembix* that is known from chemosynthesis-based associations since Eocene and noted also in their Recent counterparts (Kiel and Goedert 2006b; Kiel et al. 2008b).

localities in the Early Cretaceous (Kaim et al. 2008a; Kiel et al. 2008b) and also are present in two Late Cretaceous localities in California (Kiel et al. 2008b). In Hokkaido they co-occur with provannids, which are allegedly their derivatives (Kaim et al. 2008a). Hokkaidoconchids may occur also in the Eocene–Miocene of Barbados (Gill et al. 2005; Kaim et al. 2008a) and the Eocene of Washington State (Goedert and Kaler 1996; Kaim et al. 2008a). These Cenozoic localities constitute latest known occurrence of the group.

Faunal composition of the associations.—The seep sites at Omagari and Yasukawa provided abundant and relatively diverse gastropod associations. In sum we examined 1202 specimens from Omagari and 245 specimens from Yasukawa representing 16 species (Table 2). The Omagari site is the oldest-known hydrocarbon seep site with an ubiquity of gastropod limpets, which are very common in Recent seep and vent communities. *Serradonta omagariensis* constitutes 36% of the gastropod association in Omagari. It is a rather peculiar gastropod adapted for living on worm tubes which occur in great numbers in this locality (Jenkins et al. 2007a). *Serradonta* is an acmaeid gastropod restricted nowadays to seeps around Japan (Sasaki et al. 2005). The important component of both and Omagari and Yasukawa seeps are turbinids. In Omagari they are represented by *Homalopoma abeshinaiensis* and *Cantrainea omagariensis* which together constitute 48% of the association. In Yasukawa turbinids are represented only by *Cantrainea yasukawensis*, which constitutes more than half (55%) of the association. Such an abundance of turbinids is rather surprising as such a composition is unknown from ancient and Recent chemosynthesis-based communities. *Homalopoma* has been reported from Recent sunken wood (Okutani 2000) and occurs at a hot vent in Mariana Arch (Anders Warén, personal communication 2008) and has been identified in the Eocene hydrocarbon seep deposits from Washington State (Goedert and Squires 1990) and Barbados (Gill et al. 2005); however, it never occurs in such a density. Only Moroni (1966), who described *Homalopoma domeniconii* Moroni, 1966 from the Miocene "Calcare a Lucine", noted that in some localities this species is very common. *Cantrainea* is also a rather uncommon taxon in Recent chemosynthesis-based associations. There are three species of this genus living in Recent cold seep on the Louisiana Slope (Warén and Bouchet 1993), in Chile (Sellanes et al. 2008), and at hydrothermal vent off Japan (Okutani and Fujikura 1990) respectively, but again they are rather uncommon at these sites. Of special interest is a species described by Okutani (2001) seemingly from a hydrothermal vent in the Okinawa Trough as *Cantrainea nuda* as it closely resembles the species of *Cantrainea* from Omagari and Yasukawa. *C. nuda* is based on a single shell and the species has not been collected alive since its first discovery, suggesting that it is a rather uncommon species. Gill et al. (2005) reported presence of *Cantrainea* sp. in seep carbonate of the Miocene Freeman's Bay Limestone, Trinidad. The trochid *Margarites sasakii* reaches moderately high number of specimens contributing 3% to the entire association at the Omagari site. A similar species is known from vents in the Okinawa Trough (Sasaki et al. 2005). The hokkaidoconchid *Hokkaidoconcha* is present only in the much lower flux Yasukawa site where it occurs abundantly constituting 39% of the association, while it is absent in the much higher flux Omagari seepage, where it possibly is replaced by *Provanna* (6.2% of the gastropod association). Neomphalids have not been found at the Omagari and Yasukawa sites although the naticiform gastropod might represent a species of *Retiskenea*. This assumption, however, cannot be validated based on the available material.

Comparison of Omagari and Yasukawa associations.—The two localities under consideration are geographically very close each other and apparently also stratigraphically. The most conspicuous difference between the two sites is in size of the seep carbonates. The carbonate body at the Omagari site reaches 5 m in height, whereas the Yasukawa site consists of a series of smaller carbonate bodies, the largest of which is only 1 m high. Jenkins (2007b) argued that this difference apparently reflects the longevity of the hydrocarbon

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seep and/or the flux. This difference most probably influenced the associations' composition. Jenkins et al. (2007a) described a positive relationship between the presence of worm tubes and *Serradonta* limpets in Omagari and Yasukawa. At the Omagari site, where plenty of worm tubes are present, *Serradonta* limpets are very common. At the Yasukawa site worm tubes are rather uncommon, coincident with low number of *Serradonta* specimens. Interesting is that *Provanna nakagawensis* occurs at both sites (although much more commonly at the Omagari site), while *Hokkaidoconcha hikidai* occurs exclusively at the Yasukawa site. It might be hypothesized that *H. hikidai* could not tolerate higher concentrations of methane and/or sulfide in Omagari. Also the absence of *Homalopoma* from the Yasukawa site is difficult to explain, especially because *Cantrainea* (another turbinid) is abundant at both localities even though there are two different species of *Cantrainea* present in each of the sites. Noteworthy is also the absence of the naticiform gastropod and the skeneiform gastropod from the Yasukawa site. Their abundance at the Omagari site suggests that they were typical animals at hydrocarbon seep communities (unless Omagari seep carbonate recorded unusual community). The number of species at the Omagari and Yasukawa sites is almost equal (10 and 9 respectively) but it is noteworthy that five species make 93% of all gastropods at Omagari, while only two species constitute 93% of all gastropod specimens at Yasukawa (Table 2).

Other Cretaceous chemosynthesis-based associations in Hokkaido.—Gastropods from other hydrocarbon seep carbonates in Japan are poorly known. Gastropods are relatively common in the Cenomanian seep carbonate at Kanajirisawa (Kaim et al. 2008a) and the Albian seep carbonate at Utagoe (AK and RGJ unpublished data), and in both cases they are dominated by hokkaidoconchids and provannid-like species. The Albian Pombetsu seep has not revealed any good gastropod material. The Gakkonosawa seep provided only a few gastropod specimens, mostly provannids (Kaim et al. 2008a; AK and RGJ unpublished data). Kaim et al. (2008b) described two chemosynthesis-based associations from Turonian and Coniacian plesiosaur falls reporting numerous specimens of provannids and a vetigastropod very similar to *Cantrainea omagariensis*. Kiel et al. (2008) described two Campanian sunken wood associations from the Nakagawa area. One of these, the Akita Creek wood fall, contained also some gastropods including two possible provannids, two skeneimorphs, and a limpet. At least one of the provannids (Kiel et al. 2009: fig. 3E) is similar to *Provanna nakagawensis* from the Omagari and Yasukawa seep sites while the skeneimorphs recall *Cantrainea omagariensis*. Only the Akita wood fall limpet seems to have no seep counterparts in the Cretaceous of Hokkaido. Moreover, a single specimen of that limpet has recently been found associated with a piece of wood from the Yasukawa River (Steffen Kiel, personal communication 2009). The new finding may suggest that this limpet might be an important and distinct member of the local wood-fall fauna. Otherwise it seems that the gastropod composition of the chemosynthesis-based associations was relatively uniform in hydrocarbon seeps, plesiosaur falls, and sunken wood. The most important gastropod groups in such communities were provannids/hokkaidoconchids, turbinids (especially species of *Cantrainea*), and, at least in hydrocarbon seeps, acmaeid limpets. This suggests that these communities might not yet differentiated into three different types as it has been observed for their Recent counterparts. This pattern seems to be neutral to the hypothesis of evolutionary and dispersal stepping stones between particular types of chemosynthesis-based associations (Smith et al. 1989; Martill et al. 1991; Distel et al. 2000) as apparently the species could migrate from every type of the community to another type in the Cretaceous of Hokkaido. The impoverished taxonomic composition of plesiosaur bone- and wood-fall associations may suggest that they document "incipient" or opportunistic colonization of a sulfide-rich substrate from adjacent hydrocarbon seeps (Kaim 2008a; Kiel et al. 2009).

Conclusions

The Omagari and Yasukawa seep sites revealed the most plentiful and most diversified gastropod associations from Late Cretaceous chemosynthesis-based communities. They fill the gap between the recently documented (Campbell et al. 2008; Kiel et al. 2008) gastropod associations from the Early Cretaceous and their much better investigated post-Cretaceous counterparts. The gastropods from the Omagari and Yasukawa seep sites are much more similar to post-Cretaceous seep faunas than to their Early Cretaceous counterparts. The only group that connects Late Jurassic/Early Cretaceous and Late Cretaceous associations are the hokkaidoconchids (Kaim et al. 2008a, b; Kaim and Kelly 2009). The remaining groups display a remarkable similarity to their Recent counterparts from the vicinity of the Japanese islands and the Western Pacific in general. This suggests that there was a regional pool of animals that flourished in chemosynthesis-based communities since the Late Cretaceous until today. The similarities among gastropod associations (but also bivalve associations, see Kiel et al. 2008a, b; also AK and RGJ unpublished data) in Late Cretaceous hydrocarbon seeps, vertebrate falls, and wood falls strongly suggests that these faunas were not yet differentiated into three distinctive types of communities.

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