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

ANDRZEJ KAIM, ROBERT G. JENKINS, and YOSHINORI HIKIDA


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 hikidae*). 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. 2007a, b), while first taxonomic description of gastropods from Creta-
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, 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; UMET, 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 (Cenomanian) 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 muddy sediments, 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 al. 2008b) as provannids and hokkaidoconchids. Ataphrus tesioensis was later identified as a provannid by Bassermann (1913) and also as a provannid by Hikida et al. (2003) and presented as a provand by Kaim et al. (2008a).
Table 1. Late Cretaceous gastropods described by Nagao (1932, 1939) from the Nakagawa area. Original spelling retained.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nagao 1932</strong></td>
<td></td>
</tr>
<tr>
<td><em>Tessarolax japonicus</em> Yabe and Nagao, 1928</td>
<td>Sakaizawa, a tributary of Abeshinai river</td>
</tr>
<tr>
<td><em>Tessarolax acutimarginatus</em> Nagao, 1932</td>
<td>Nigorikawa, a small tributary of the Abeshinai river</td>
</tr>
<tr>
<td><em>Rostellaria japonica</em> Nagao, 1932</td>
<td>Omoshiroshibets, a tributary of the Abeshinai</td>
</tr>
<tr>
<td><em>Avellana problematica</em> Nagao, 1932</td>
<td>Left bank of the Abeshinai, south of Shibunnai</td>
</tr>
<tr>
<td><strong>Nagao 1939</strong></td>
<td></td>
</tr>
<tr>
<td><em>Ataphrus tesioensis</em> Nagao, 1939</td>
<td>A small tributary of the Abesinai river, near the postal service station</td>
</tr>
<tr>
<td><em>Margaretia sachaliniensis</em> Nagao, 1939</td>
<td>Omosirusibetu, Ososinaizawa, tributaries of the Abesinai river</td>
</tr>
<tr>
<td><em>Natica (Lunatia) ainuana</em> Nagao, 1939</td>
<td>Ososinaizawa, a tributary of the Abesinai river</td>
</tr>
<tr>
<td><em>Natica (Lunatia) denselineata</em> Nagao, 1940</td>
<td>Sibunnaiizawa, a tributary of the Abesinai river and a point along the latter river, 300 m upstream from the mouth of its tributary, the Wakkawen</td>
</tr>
<tr>
<td><em>Dicroloma (Perissoptera) sp. indet</em></td>
<td>Abesinai river</td>
</tr>
<tr>
<td><em>Pyropsis sp. indet.</em></td>
<td>Middle course of the Abesinai river</td>
</tr>
<tr>
<td><em>Semifissus (Trochofusus) tuberculatus</em> Nagao, 1939</td>
<td>Abesinai river, about 100 m upstream from the junction with Sakaizawa</td>
</tr>
<tr>
<td><em>Surculites fusoides</em> Nagao, 1939</td>
<td>Omosirusibetu, a small tributary of the Abesinai river</td>
</tr>
<tr>
<td><em>Fusus volutodermoides</em> Nagao, 1939</td>
<td>The Ososinaizawa, a tributary of the Abesinai river</td>
</tr>
<tr>
<td><em>Avellana problematica</em> Nagao, 1932</td>
<td>Abesinai-gawa</td>
</tr>
</tbody>
</table>

Table 2. Gastropods from the Omagari and Yasukawa seep sites and their Recent counterparts. In bold are species constituting 93% of each association respectively.

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

* known only from the Caribbean
** known only from the Lau Basin
? relation to species from the Omagari and Yasukawa sites uncertain
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 solenomyid, 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 nagakawensis 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) mactreformis 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 nagakawensis 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 Linneé, 1758
Class Gastropoda Cuvier, 1798
Order Patello gastropoda Lindberg, 1986
Superfamily Lottioidea Gray, 1840
Family Acmaeidae Forbes, 1850
Subfamily Pectinodontinae Pilsbry, 1891
Genus Bathya cmaea Okutani, Tsuchida, and Fujikura, 1992
Type species: Bathycmaea 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 Bathycmaea 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.

Bathy cmaea cf. subnipp oica Sasaki, Okutani, and Fujikura, 2003
Fig. 2.
2007 Bathy cmaea cf. subnipp oica Sasaki, Okutani, and Fujikura, 2003; Jenkins et al. 2007a: 371, fig. 2B, C.

Material.—Eight specimens from the Omagari site: six specimens at U MUT 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 U MUT 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. 2D3).

Discussion.—The shells under consideration are most similar to the Recent B. subnipp oica 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 acmaeid 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.
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
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.


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.

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-
sed shell and uneven aperture with neither concentric nor radial ornamentation on any portion of the shell. S. vestimenti−fericola 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 diageneis 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. 3D3, D4).

**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. vestimenti−fericola 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, 1814]). 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 watsoni (Dickerson, 1916), has been reported by Kiel (2008) from Eocene wood−fall association in Washington State, USA. Abundant occurrences of Homalopoma domicenonci Moroni, 1966 are reported by Moroni (1966) from the Miocene “Calcarea a Lucine” in Italy which have been later identified to be seep carbonates (Taviani 1994; Peckmann et al. 1999). H. abeshinaeiensis described below represents the oldest record of Homalopoma reported so far from chemosynthesis−based communities.

**Homalopoma abeshinaeiensis** sp. nov.

**Fig. 4.**

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

**Holotype:** UMIT 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 UMIT 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 collateral threads. Intersections of spiral and axial ornamentation nodose. Nodes elongated according to the di-
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
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 (B₁) and another view (B₂) showing inclination of the aperture. C. UMUT MM30155 in lateral view (C₁) and another view (C₂) showing inclination of the aperture. D. UMUT MM30156 in lateral view (D₁) and another view (D₂) showing inclination of the aperture. E. UMUT MM30157 in lateral view. F. Holotype (UMUT MM30158) in apertural (F₁) and lateral (F₂) views. G. UMUT MM30159 in lateral view. H. UMUT MM30160 in lateral view. I. UMUT MM30161 in lateral view (I₁) and details of ornamentation (I₂). J. UMUT MM30162, aggregation of three specimens and an operculum; J₁, general view; J₂, the operculum. K. UMUT MM30163 in lateral view (K₁), shell microstructure (K₂) including the inner nacreous (n) and fibrous prismatic (fp) layers, and details of shell ornamentation (K₃).
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 collonins. 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 pannemense (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

Fig. 6. The turbinid gastropod Cantrainea yasukawensis sp. nov. from the Campanian (Upper Cretaceous) Yasukawa seep site in Hokkaido, Japan. A. UMIT MM30164 in lateral (A₁), apertural (A₂), and umbilical (A₃) view; A₄, details of inner lip. B. UMIT MM30154 in apical view. C. UMIT MM30156 in apical view. D. UMIT MM30159 in apical view. E. UMIT MM30157 in apical view. F. UMIT MM30155 in latero-apical view. G. UMIT MM30160 in apical view. H. Holotype (UMIT MM30158) in umbilical view. I. UMIT MM30153 in umbilical view.
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 collonids 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. yasukawensis* 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). 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. 5I).

*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 paskentensis* (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.
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 proscoline. *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-
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. yasakawensis*. 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 gross morphology strongly recollects *Margarites 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 venti gastropod recovered so far from the Omagari 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.

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

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 (A1) lateral (A2, A3), umbilical (A4), and apical (A5) views. **B.** UMUT MM30172 in apical (B1) and lateral (B2) views; B3, cross section through outer layer. **C.** Juvenile UMUT MM30173 in apical (C1), and lateral (C2–C4) views. **D.** Holotype (UMUT MM30174) in apical (D1) and lateral (D2–D4); note change in ornamentation in D4. **E.** NMM 229 in apical (E1), apertural (E2), and umbilical (E3) views.
Distribution.—Cataegis includes deep water species known from the Caribbean (McLean and Quinn 1987; Hickman and McLean 1990; Wärén 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 (Wärén and Bouchet 1993; García 2002; Gill et al. 2005). *Cataegis* sp. has also been found in seeps off Costa Rica (Anders Wärén, 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-
ally classified as *Cataegis* because they lack an umbilicus and possess 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.

DOI: 10.4202/app.2009.0042
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 Provanina. *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 “Gakkonošawa provannid” from Cretaceous Gakkonošawa 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. 11B3), a shell layer organization known from Provannidae (Kiel 2004).
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 opisthocyt 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, 1840
Genus Sulcoactaeon Coissmann, 1895

Type species: Acteonina 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 2.14 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 whors with incised suture. Aperture is circular and tangential. No apertural 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...
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.

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 (A1), lateral (A2), and apical (A3) views; A4, close up of the aperture. B. Gastropoda indet. 1 (UMUT MM30186) in apertural (B1), lateral (B2), and apical (B3) views. C. Gastropoda indet. 2 (UMUT MM30187) in apertural (C1), lateral (C2), and apical (C3) views; C4, fibrous prismatic shell outer layer, C5, cross lamellar inner layer. D. Neogastropoda indet. (UMUT MM30188) in lateral (D1) and apical (D2) 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 DOI: 10.4202/app.2009.0042
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 4.4 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 anti or most 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.
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
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); however, it never occurs in such a density. Only Moroni (1966), who described *Homalopoma domeniconis*, Moroni, 1966 from the Miocene “Calcarea 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 *Retiskelea*. 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 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 abe-shinaiensis* 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 domeniconis*, Moroni, 1966 from the Miocene “Calcarea 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 *Retiskelea*. This assumption, however, cannot be validated based on the available material.

**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

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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 Bathypupurinopsis,* which together constitute latest known occurrence of the group.

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**Table 1.** 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 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 abe-shinaiensis* 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 domeniconis*, Moroni, 1966 from the Miocene “Calcarea 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 *Retiskelea*. This assumption, however, cannot be validated based on the available material.
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 provannid (Kaim et al. 2008a; AK and RGJ unpublished data). Kaim et al. (2008b) described two chemosynthesis-based associations from Turoanian 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 provannid/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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