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Methane-flux-dependent lateral faunal changes in a Late Cretaceous chemosymbiotic assemblage from the Nakagawa area of Hokkaido, Japan

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ABSTRACT

A Late Cretaceous carbonate body (2 m in maximum diameter) surrounded by clastic rocks, recently discovered in the Nakagawa area (Hokkaido, Japan), is interpreted as a methane-seep deposit, on the basis of negative carbon isotopic composition (as low as –43.5‰), variable sulphide sulphur isotopic composition, high carbonate content, and *in situ* fractures. It most likely formed owing to methane-bearing pore-water diffusion. We estimate that the concentration of methane decreased toward the margin of the carbonate body, and that only small carbonate concretions were precipitated at a certain distance from the methane-seep centre. These spatial characteristics coincide well with the observed pattern of faunal distribution. The gastropod-dominated association (indeterminate abyssochrysids and ataphrids and the acmaeid limpet *Serradonta* sp. are most common) co-occurs with lucinid and thyasirid bivalves (*Thyasira* sp., *Myrtea* sp., and *Miltha* sp.), and was found within and just above the methane-derived carbonate body. *Acharax* and *Nucinella* (solemyoid bivalves) are more typical of the peripheral part of the methane-influenced sediments. We suggest that this pattern of faunal distribution reflects the decreasing concentration of methane and apparently also hydrogen sulphide when moving from the centre of discharge toward the periphery of the methane seep.

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INTRODUCTION

The unexpected discovery of hydrothermal-vent and cold-seep communities dependent on chemosynthetic bacteria for their major energy sources (Lonsdale, 1977; Corliss *et al.*, 1979; Suess *et al.*, 1985) stimulated large-scale investigation in all the world's oceans. Since the 1970s, such highly specialized animals have been found at various sites where bottom water is enriched with sulphide and methane supplied from hydrothermal vents, cold-seeps, ground-water seeps, whale skeletal remains, sunken driftwood, and even from rotting cargo of a sunken ship (Marshall, 1988; Smith *et al.*, 1989; Dando *et al.*, 1992; Tunnicliffe, 1992; Hasegawa, 1997; Sibuet & Olu, 1998; Van Dover, 2000).

The methane discharging from a methane seep usually originates from the activity of methanogens and through carbonate reduction or acetate fermentation under anoxic conditions. It can also be formed by the thermal decomposition of organic matter (Whiticar, 1999; Kotelnikova, 2002). The methane migrating from its place of origin up to the sea-floor undergoes both aerobic and anaerobic oxidation. The oxidation of organic matter generally takes place owing to several oxidants in the marine water column, which penetrate methane-containing sediment (Aller, 2004). Sulphates are utilized in the last phase of this process (Aller, 2004). For this reason, methane oxidization from sulphates takes place first in the base of the sulphate-reducing zone (Valentine, 2002). Recently, it has been shown that the anaerobic oxidation of methane (AOM) is mediated by consortia of anaerobic methane-oxidizing archaea (ANME) and sulphate-reducing bacteria (SRB; Orphan *et al.*, 2002). When the methane discharges into a well-oxidized environment, the aerobic oxidation of the methane may also be mediated by methanotrophic bacteria (Aharon, 2000).

The AOM reaction leads to an increase in alkalinity, which is favourable for the precipitation of carbonate minerals

(Michaelis *et al.*, 2002; Peckmann & Thiel, 2004). Such methane-derived carbonates are relatively easily recognizable in the geological record, because they have a highly ^{13}C-depleted carbon isotopic signal and contain biomarkers that originated due to the activity of methane-related micro-organisms (Peckmann & Thiel, 2004; Birgel *et al.*, 2006a,b).

The macro-organisms in communities having diffusive or effusive activity (i.e., hot vents and cold/methane seeps) are faced with the serious problem of how to survive in an environment with a high content of toxic hydrogen sulphide (usually from a few to 25 mM in Recent methane seeps; Stakes *et al.*, 1999; Sahling *et al.*, 2002; Levin, 2005), and how to supply this compound to their intracellular symbionts (Childress *et al.*, 1991). The differences in the ability of particular organisms to cope with these problems influence the pattern of faunal distribution. Sahling *et al.* (2002) reported for Hydrade Ridge, in the Cascadia margin off Oregon, that sulphur-oxidizing bacteria (*Beggiatoa*), vesicomyid bivalves (*Calyptogena*), and solemyid bivalves (*Acharax*) are distributed according to a gradient in hydrogen sulphide concentration. *Beggiatoa* occurs in the proximity of methane discharges with the highest sulphide concentration, whereas *Calyptogena* surrounds the bacterial mat, and *Acharax* occupies the periphery of the seep (fig. 2 in Sahling *et al.*, 2002). A similar pattern has also been reported for other modern methane seeps (MacDonald *et al.*, 1989; Barry *et al.*, 1997; Olu *et al.*, 1997; Rathburn *et al.*, 2003; Levin *et al.*, 2003; Orphan *et al.*, 2004). Although faunal distribution in modern chemosynthesis-based communities evidently is mainly controlled by hydrogen sulphide concentrations (Barry *et al.*, 1997; Sahling *et al.*, 2002; Knittel *et al.*, 2005; Levin, 2005), other factors, including depth and organism-generated microhabitats, may also be relevant (Sahling *et al.*, 2003; Bergquist *et al.*, 2003; Levin, 2005).

Several researchers have described the distribution pattern of fossils within and/or around ancient methane-seep deposits (Gaillard *et al.*, 1992; Beauchamp & Savard, 1992; Kauffman *et al.*, 1996; Kelly *et al.*, 2000; Campbell *et al.*, 2002; Peckmann *et al.*, 2002; Campbell, 2006). However, few workers have analysed both lithological and geochemical data to decipher the relationship between the lateral distribution of fossils and the spatial zonation of ancient methane-bearing pore fluids.

The fossil record of chemosynthesis-based communities suggests that they experienced a major faunal turnover during the Mesozoic, particularly in the Late Jurassic to Late Cretaceous (Campbell & Bottjer, 1995; Little & Vrijenhoek, 2003; Kiel & Little, 2006). Many modern benthic invertebrate groups entered vent/seep habitats in this time interval. Recent molecular analyses of dominant vent and seep taxa suggest that they likely diversified during the past 100 Myr, in the Cretaceous and early Cainozoic (Black *et al.*, 1997; Van Dover *et al.*, 2002; Little & Vrijenhoek, 2003). Thus, the Cretaceous was a crucial period in the origin and evolution of modern vent and seep taxa. A precondition for clarifying the evolution of chemosynthesis-based communities is deciphering the spatial-distribution pattern of taxa at Cretaceous methane-seep sites.

A great number of fossil and modern chemosynthetic communities occur in the Japanese islands (Majima *et al.*, 2005). One of the best-preserved Late Cretaceous chemosynthetic communities is in the Omagari Formation, Upper Yezo Group at the Omagari site, in the Nakagawa area of northern Hokkaido (Hikida *et al.*, 2003). Hikida *et al.* (2003) inferred the presence of a fossil chemosynthetic community associated with a methane seep at this site, based on carbon isotopic composition, petrographical features, and a fauna of tube worms, lucinid bivalves, tiny gastropods and brachiopods. Regrettably, the carbonate body with this association is located on an isolated islet in the Abeshinai River. At present, it is not possible to examine the entire sequence with its lateral variations, or the boundary between the carbonate body and surrounding siliciclastic sediments. During our field studies in the Nakagawa area, we discovered additional carbonate bodies in the Omagari Formation. We inferred that these bodies formed due to methane-seep activity but, in contrast to the Omagari site, their relationship to the host sediments is exposed well.

In this study we focus on a newly discovered locality at Yasukawa and analyse the mode of occurrence, synsedimentary structures, and carbon and oxygen isotope ratios of methane-derived carbonates, along with the sulphur isotopic composition of pyrite. Our objective is to trace spatial physico-chemical changes in the Cretaceous methane seep and to learn their importance for the distribution of the chemosynthesis-dependent assemblage.

GEOLOGICAL SETTING

A thick marine-clastic sequence was deposited in the Yezo fore-arc basin along the western margin of a subduction zone in the circum-northwestern Pacific during the Cretaceous (post-Aptian; Takashima *et al.*, 2004). This sequence is widely distributed along more than 1000 km from northern Sakhalin to southern Hokkaido (Matsumoto, 1942; Shigeta & Maeda, 2005). Takahashi *et al.* (2003) divided post-Aptian Cretaceous deposits in the Nakagawa area into the Lower Yezo, Middle Yezo, Upper Yezo, and Hakobuchi Groups, in ascending order (Fig. 2). The Upper Yezo Group in this area is subdivided into the Nishichirashinai, Omagari, and Osoushinai Formations, in ascending order (Fig. 2; Takahashi *et al.*, 2003). The methane-influenced carbonate bodies discussed in this study developed during sedimentation of the Omagari Formation (Fig. 2). The largest known methane-seep-related carbonate body in the Nakagawa area, reported by Hikida *et al.* (2003) at the Omagari site, crops out near the junction between the Abeshinai River and the Osoushinai Creek (Fig. 1A). The carbonate bodies at the Yasukawa site are located about 3 km downstream from the Omagari site (1 km downstream from the juncture with Tannosawa Creek; Fig. 1A). Carbonate bodies at this site are

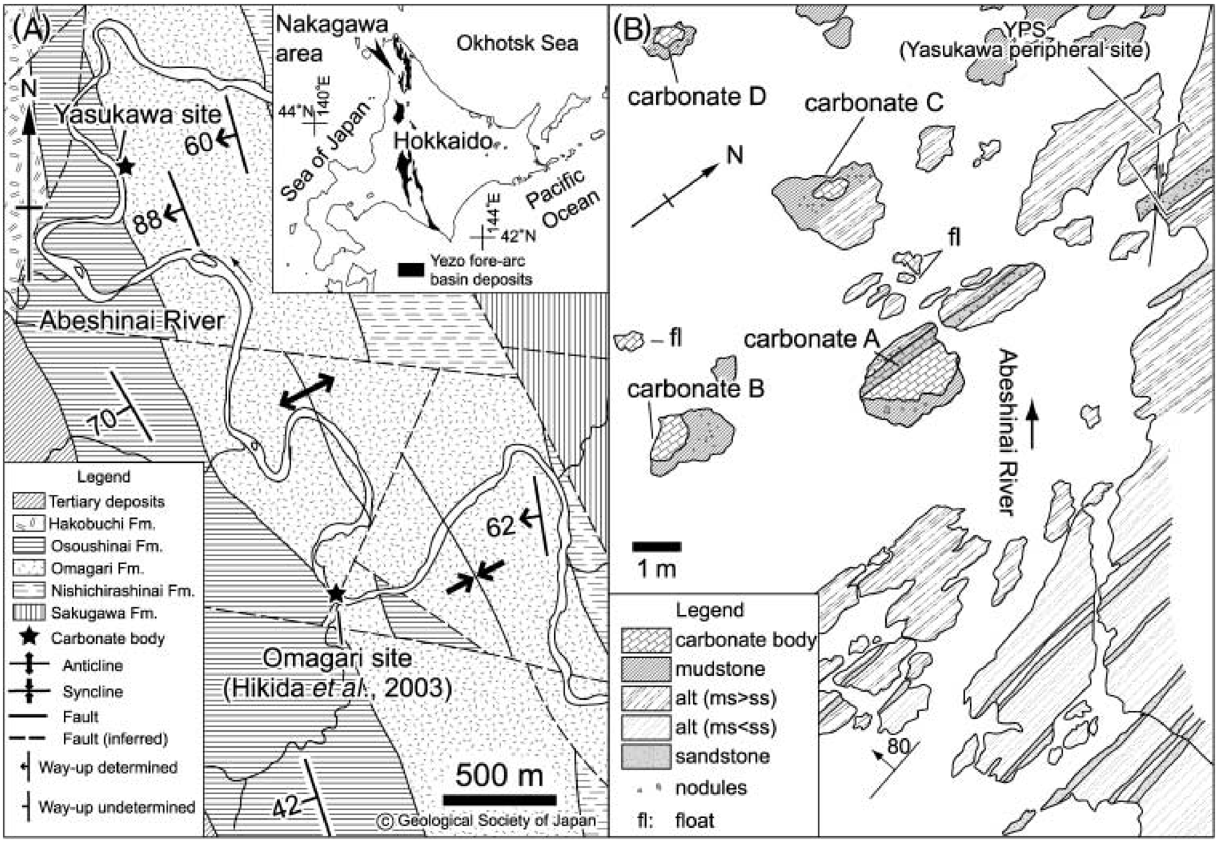

Fig. 1 Sketch maps of Hokkaido and the Nakagawa area showing Yasukawa (44°40′37″N, 142°1′27″E) and Omagari (44°39′26″N, 144°2′25″E). (A) Geological map of the middle reach of the Abeshinai River. Modified after Takahashi *et al*. (2003, fig. 1). (B) Geological sketch of the Yasukawa site (plan view). Four *in situ* carbonate bodies, A–D, are exposed in the top sequence of the Omagari Formation; alt, alternating beds of sandstone and mudstone; ss, sandstone; ms, mudstone.

emplaced within sediments in the upper part of the Omagari Formation, and have been dated as Lower Campanian based on the first occurrence of *Inoceramus* (*Platyceramus*) *japonicus* (Takahashi *et al*., 2003). The Omagari Formation is characterized by alternating greenish sandstone and sandy siltstone, with common intercalations of pebble- to boulder-size gravel beds. These sandstone beds include rip-up clasts in places, and exhibit incomplete Bouma sequences interpreted as turbidites. Based on their poorly sorted texture and matrix-supported structure, the gravel beds are interpreted as debris-flows. The intercalated mudstone is poorly sorted, and typically contains very coarse sand grains and granules. In addition, there are syndepositional and early post-depositional structures consisting of slumping folds. These lithological features and sedimentary structures suggest that the Omagari Formation was deposited at the interface between a continental-shelf margin and a continental slope.

MATERIAL AND METHODS

Detailed observations were made of the mode of occurrence, and the lithological and palaeontological properties, of the largest carbonate body at the Yasukawa site [carbonate body A (CBA), Fig. 1B], as well as the distribution patterns of small concretions around it. We also examined the sedimentological features of surrounding clastics at a locality 5 m northeast from CBA [Yasukawa peripheral site (YPS), Fig. 1B]. Representative rock samples and macrofossils were collected from various portions of the carbonate body and its enclosing strata. Taxonomic identification was made whenever possible. Small (<10 mm) fossils were coated with platinum-palladium using an ion coater, and studied using Hitachi S-2400S and Philips XL20 scanning electron microscopes at the Department of Earth and Planetary Science, the University of Tokyo (EPUT), and the Institute of Paleobiology, Polish Academy of Sciences (ZPAL), respectively. The carbonate rock and concretion samples were cut normal to the bedding plane and polished by a graded series of carborundum powders, and finally by 0.25 μm diamond powder. Thin-sections were prepared, upon which standard observations were performed by plane- and cross-polarized and reflected light microscopy. X-ray diffraction analysis (XRD) was carried out on un-oriented slurries using a diffractometer with Cu Kα radiation to identify the mineralogy of the carbonate samples (Tucker & Wright, 1990).

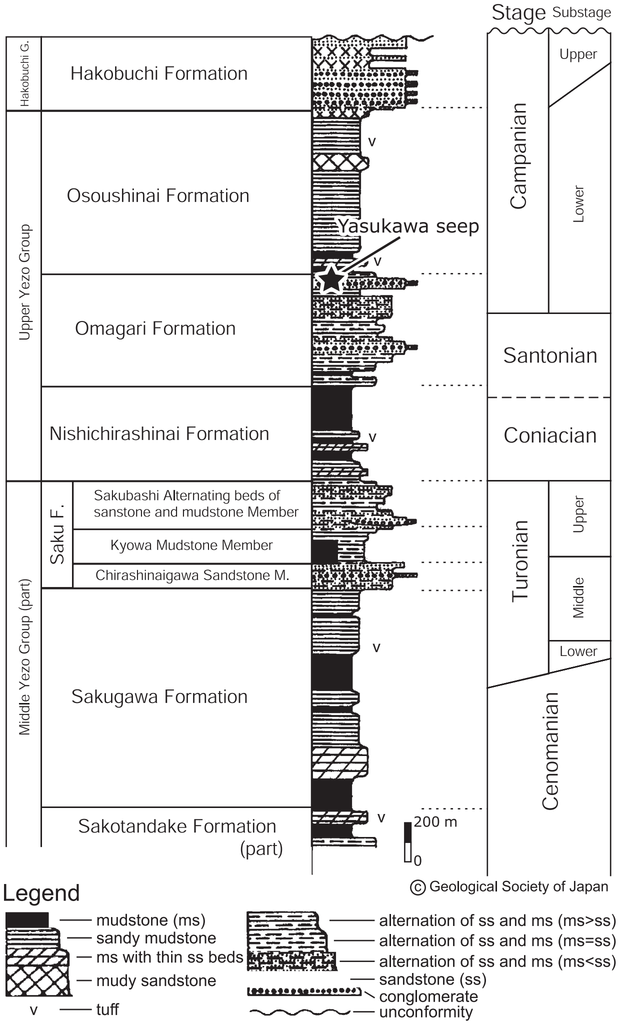

Fig. 2 Schematic geological columnar section of the Nakagawa area. Modified from Takahashi *et al*. (2003; Fig. 5).

The relative carbonate content of each sample was analysed, as follows. Powdered samples were heated at 90 °C for 24 h to dehydrate them, then weighed in quantities of approximately 1 g, and put into centrifuge tubes. One normal hydrochloric acid was then added to the tubes, which were gently rotated so as to mix the samples and the acid, in order to dissolve all the carbonate. This reaction was carried out over 12 h, after which Milli-Q (Millipore, Billerica, MA, USA) water was poured into the tubes, which were then centrifuged at 400 *g* for 50 min. The resulting supernatants were washed, and Milli-Q was again added to the tubes. The centrifuge process was repeated at least three times. The tubes with residues were then dried at 90 °C for more than 12 h. The dried samples were weighed to calculate their carbonate content.

Powdered samples (about 2 to 10 mg each) obtained by microdrilling of the small pieces of rock and shell carbonate were used for carbon and oxygen isotopic analyses. Carbon dioxide was produced from each sample by reaction with 100% phosphoric acid *in vacuo* (25 °C), and analysed with a Finnigan MAT252 (Thermo Fisher Scientific Inc., Wattham, MA, USA) mass spectrometer at EPUT. Carbon and oxygen isotopic values are expressed relative to the PDB standard. For both carbon and oxygen isotopes, the external precision of the standard was less than 0.03‰, with the standards being run at the beginning and the end of the sample series. Sulphur isotopic analyses were made from powdered samples obtained from 1 cm^3 carbonate cubes. The powdered samples were washed with dilute hydrochloric acid to remove carbonate and sulphate minerals, and then oxidized from sulphide to sulphate by reaction with concentrated nitric acid and bromine. Sulphate ions were precipitated as barite by adding a $BaCl_2$ solution. Sulphur dioxide gas for sulphur isotope analysis was prepared by the V_2O_5 and SiO_2-heating methods described by Yanagisawa & Sakai (1983). Sulphur isotopic composition of the evolved sulphur dioxide gas was measured with a Finnigan Delta Plus mass spectrometer. Values of $\delta^{34}S$ are reported relative to the CDT scale. The external precision of the standard for sulphur isotopes was less than 0.05‰, with the standards run every twelve samples.

RESULTS

Lithology

The geology of the study site is shown in Fig. 1B and consists of mudstone with thin, intercalated sandstone beds. The sandstone beds are mostly a few centimetre thick (but range up to 40 cm) and are not cemented, except in the proximity of carbonate bodies. Four such bodies larger than 50 cm in diameter, here named A to D (Fig. 1B), are present at this site. The largest, and thus the best for tracing lateral changes in lithology and learning its palaeontological content, is CBA (Fig. 3). The lithological and geochemical features of this carbonate body and surrounding clastic rocks at YPS are given in Table 1.

The lithology of CBA can be divided into upper and lower parts (Fig. 3 A-1). The lower part is composed mainly of fractured dark grey to greyish black, micritic limestone (Fig. 3), in association with several layers of fractured sandstone and tuffaceous siltstone. Both brittle and ductile deformation was exhibited in the fractures. Some peloids, including coated grains and networked brown to white calcite rim cement layers, are evident (Fig. 3F). Micritic limestone in the lower part has a clotted fabric. Fractured sandstone and tuffaceous siltstone are cemented by microspar and sparry calcite, or in some cases by siderite. Some of the peloids are coated grains with nuclei that are enveloped by micritic cement (Fig. 3F). The nuclei of the coated grains are fractured grey siltstone and fractured tuffaceous siltstone (Fig. 3F). Almost all of the peloids are covered by radiaxial calcite cement (Fig. 3F). Mostly medium- to coarse-grained sand-size grains are cemented in the upper part of CBA, but granule-size grains are sometimes

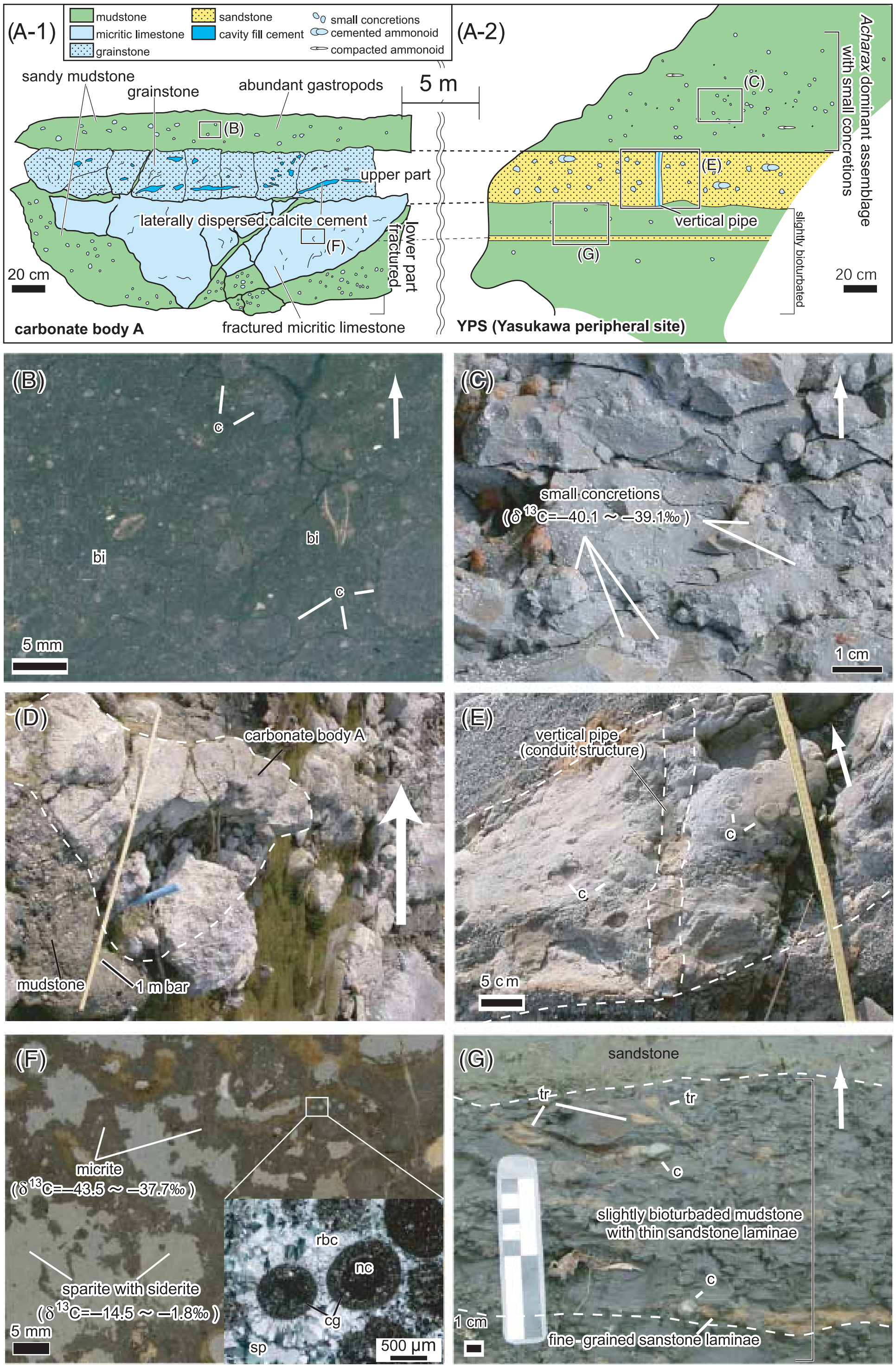

Fig. 3 Outcrop sketch drawing (A) and photographs (B–G) of carbonate body A (CBA) and its lateral extension (YPS). The distance between CBA (A-1) and YPS (A-2) is 5 m, as indicated by the scale at the top. (B) Photograph of a slab sample from sandy mudstone just above CBA. (C) Outcrop photograph of mudstone with numerous small concretions at YPS. (D) Outcrop photograph of CBA. (E) Outcrop photograph of the 40 cm-thick sandstone bed at YPS. Vertical pipe (conduit pipe) cuts through the 40 cm-thick sandstone bed. (F) Fractured fabric in the lower part of CBA and a cross-polarized thin-section photograph of coated grains. (G) Slightly bioturbated mudstone underlying the 40 cm-thick sandstone bed at YPS. Carbon isotope ratios are shown in (C) and (F). The ratios were standardized to PDB. Abbreviations: c, concretion; bi, bivalve fossil; nc, nuclei; cg, coated grain; rbc, radiaxial bladed calcite cement; sp, sparry calcite; tr, trace fossil. The arrows point toward the stratigraphically younger strata.

Table 1 Meso- and microscopic structures and isotopic characteristics of the carbonate body A (CBA) and its interpreted origin at Yasukawa peripheral site (YPS) and carbonate body A (CBA) at the Yasukawa site. The isotope ratios are standardized to PDB. AOM: anaerobic oxidation of methane

		Mesoscopic view	Microscopic view	Chemical features	Interpretation
YPS		Small concretions	Micrite, clotted fabric	High magnesian calcite $\delta^{13}C$: –40.1 to –39.1‰ $\delta^{18}O$: –2.7 to –2.2‰	Precipitated by AOM
CBA	Lower part	Fractured greyish black limestone	Micrite, peloids, coated grains, radiaxial calcite cement, clotted fabric	Low and high magnesian calcite $\delta^{13}C$: –43.5 to –39.8‰ $\delta^{18}O$: –2.7 to –0.4‰	Precipitated by AOM
		Fractured sandstone and taffaceous siltstone	Blocky spar, sparry calcite, siderite	Low magnesian calcite $\delta^{13}C$: –14.5 to –1.8‰ $\delta^{18}O$: –11.3 to –6.2‰	Precipitated in late diagenetic stage
	Upper part	Cemented sandstone	Micrite, radiaxial calcite cement	High magnesian calcite $\delta^{13}C$: –42.0 to –37.7‰ $\delta^{18}O$: –3.1 to –1.9‰	Precipitated by AOM
		Rim of laterally dispersed calcite cement layer	Radiaxial calcite cement	High magnesian calcite $\delta^{13}C$: –42.0‰ $\delta^{18}O$: –2.5‰	Precipitated by AOM
		Centre of the laterally dispersed calcite cement layer	Sparry calcite	Low magnesian calcite $\delta^{13}C$: –7.0 to –1.9‰ $\delta^{18}O$: –11.3 to –10.1‰	Precipitated in late diagenetic stage

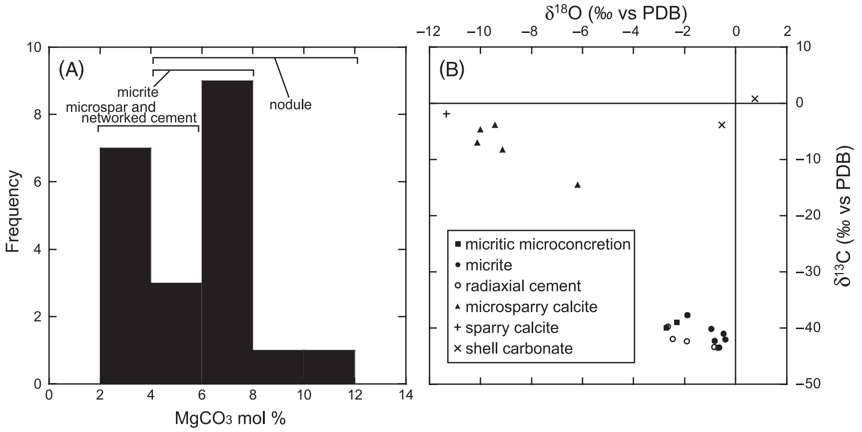

Fig. 4 (A) Magnesium content of carbonate body A and surrounding microconcretions at the Yasukawa site. (B) Carbon and oxygen isotopic composition of carbonate body A (CBA) and micro-concretions just above CBA and at YPS.

present. The upper part of the deposit is characterized by laterally dispersed layers of calcite cement and networked brown to white calcite cement. The laterally dispersed calcite rim-cement is composed of radiaxial-bladed calcite. Sparry calcite is dominant in the centre of the laterally dispersed calcite rim-cement layer. No peloids were observed in the upper part. The mudstone just above CBA includes abundant fossils and centimetre-scale micritic concretions (Fig. 3B). The carbonate content of the lower part of CBA, consisting of micritic limestone, is 84%, and of the upper part, consisting of cemented sandstone, is 66%.

The layer of carbonate-cemented sandstone at CBA grades laterally to non-carbonate cemented sandstone at YPS, where it bears numerous concretions measuring up to 10 cm in diameter. A vertical conduit-pipe structure cuts through the sandstone bed (Fig. 3E). A considerable number of centimetre-size concretions (few mm to 2 cm in diameter) are present in the overlying mudstone, with some bioturbation but no fracturing evident (Fig. 3C).

Stable isotopic analyses

The data on $MgCO_3$ mole% of $CaCO_3$ solid solution in CBA, as determined by X-ray diffraction patterns, show a range from 2 to 12% (Fig. 4A). The carbon and oxygen isotopic compositions of CBA and small concretions from the YPS are shown in Fig. 4B. In this report, they are expressed as isotope ratios versus the PDB standard. The isotopic composition of micritic limestone, radiaxial calcite rim-cement and small concretions ranges from –43.5 to –37.7‰ for $\delta^{13}C$ and from –2.7 to –0.4‰ for $\delta^{18}O$. The values for microspar and sparry calcite cement range from –14.5 to –1.8‰ for $\delta^{13}C$ and from –11.3 to –6.2‰ for $\delta^{18}O$. Aragonitic shells of the bivalve molluscs, *Acharax cretacea* and *Nanonavis* sp., have isotopic

Table 2 Sulphide sulphur isotopic composition at carbonate body A (CBA) and surrounding clastic rocks at Yasukawa peripheral site (YPS). The sulphur isotopic composition is expressed relative to the CDT standard in ‰

	Sample no.	δ^{34}S (‰)
CBA	1	−10.5
	2	9.6
	3	11.0
	4	8.8
	5	−0.5
	6	2.3
YPS	1	−7.0
	2	−6.7
	3	−8.5
	4	−5.1
	5	−7.7
	6	−8.2

values of −3.9 to 0.8‰ for δ^{13}C and −0.5 to 0.8‰ for δ^{18}O. The sulphur isotopic composition of sulphide from both CBA and YPS is shown in Table 2. Pyrite extracted from CBA has a wide range of δ^{34}S values ranging from −10.5 to 11.0‰ vs. CDT, whereas pyrite from YPS has a narrow range of −8.5 to −5.1‰ vs. CDT.

Palaeontology

A list of the most common macrofaunal remains extracted from carbonate body A (including an overlying 15 cm-thick horizon of sandy siltstone) and YPS is given in Table 3 and Fig. 5. CBA and the overlying 15-cm-thick horizon yielded over 50 specimens of tiny gastropods. Almost all the fossils are obtained from the non-cemented sediment or micritic limestone. The most common fossils are unidentified abyssochrysids whose juveniles (Fig. 5.3) are similar to the Recent provannid *Desbruyeresia melanioides*, Ataphridae gen. et sp. indet. (Fig. 5.2) similar to some species of Recent turbinid *Cantrainea*, and the acmaeid limpet *Serradonta* sp. (Fig. 5.1). We also found numerous small thyasirid and lucinid bivalves (*Thyasira* sp., *Myrtea* sp., and *Miltha* sp.). Worm tubes (probably vestimentiferans) are rare. There were no molluscs at YPS, except for ammonoids in the sandstone layer, which is the lateral equivalent of the cemented sandstone at CBA. However, gastropods and bivalves are abundant in the overlying mudstone, although less common than at CBA. We also found the solemyoid bivalves *A. cretacea* and *Nucinella* sp., which are rare at CBA. A detailed taxonomic description of the molluscs found at the Yasukawa site is in progress.

DISCUSSION

Identification of an ancient methane seep

The negative δ^{13}C values of the micrite, and networked radiaxial calcite rim-cement indicate that the carbon was derived from biogenic or thermogenic methane (Whiticar, 1999; Peckmann & Thiel, 2004). It is likely that carbonate precipitation occurred as a result of increasing alkalinity caused by AOM (Michaelis *et al.*, 2002; Lein, 2004; Peckmann &

Table 3 List of fossils extracted from within and just above carbonate body A (CBA) and surrounding clastic rocks at Yasukawa peripheral site (YPS) at the Yasukawa site, giving individual numbers and ratios. Note the rarity of *Acharax cretacea* and *Nucinella* sp. in the proximity of the methane seep (i.e., CBA). *n*: number of individuals. Each disarticulated bivalve valve is shown in brackets and was counted as half an individual

		CBA		YPS	
Class	Species	*n*	%	*n*	%
Vestimentifera	?vestimentiferan tube	2	2.1	0	0.0
Gastropoda	Abyssochrysidae gen. et sp. indet.	19	20.2	9	14.4
	Serradonta sp.	2	2.1	0	0.0
	Ataphridae gen. et sp. indet.	17	18.1	5	8.0
	other gastropods	5	5.3	3	4.8
Bivalvia	*Acharax cretacea* Kanie and Nishida	1	1.1	9	14.4
	Nucinella sp.	2	2.1	6 (1)	10.4
	Leionucula formosa (Nagao)	0	0.0	0 (1)	0.8
	Acila (*Truncacila*) *hokkaidoensis* (Nagao)	7 (7)	11.2	10 (2)	17.6
	Nuculana (*Ezonuculana*) *mactraeformis* Nagao	9 (10)	14.9	0	0.0
	Propeamussium yubarense (Yabe and Nagao) var.	0	0.0	0 (1)	0.8
	Myrtea ezoensis (Nagao)	0	0.0	0 (1)	0.8
	Myrtea sp.	0	0.0	1	1.6
	Miltha sp.	2	2.1	1	1.6
	Thyasira sp.	7 (11)	13.3	5 (5)	12.0
Cephalopoda	*Gaudryceras tenuiliratum Yabe*	1	1.1	1	1.6
	unidentified ammonoids	1	1.1	1	1.6
Scaphopoda	*Fissidentalium* cf. *otatumei* (Nagao)	0	0.0	3	4.8
Crustacea	unidentified decapods	5	5.3	3	4.8
	Total	94	###	63	100

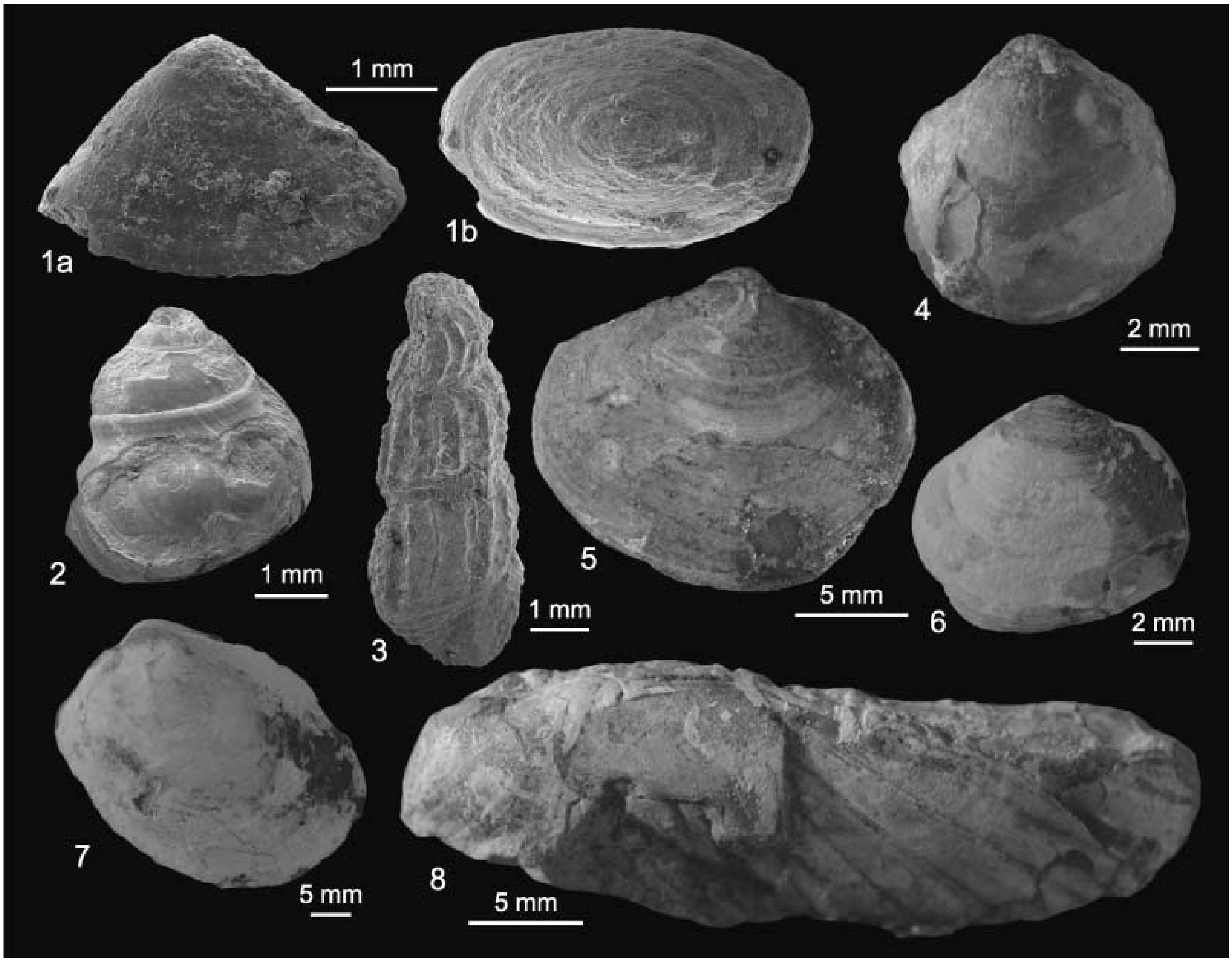

Fig. 5 Mollusc fossils from the Yasukawa site. 1a, b. *Serradonta* sp. lateral (A) and apical (B) views. 2. Ataphridae gen. et sp. indet. 3. Abyssochrysidae gen. et sp. indet. 4. *Thyasira* sp. 5. *Miltha* sp. 6. *Myrtea ezoensis*. 7. *Nucinella* sp. 8. *Acharax cretacea*.

Thiel, 2004). These interpretations are also supported by the presence of biomarkers typical of the anaerobic methane-oxidizing archaea (e.g., PMI and crocetane with a highly negative carbon isotope ratio as low as −122‰ vs. PDB) in the carbonate body (Jenkins, 2006). On the other hand, the ^{13}C-enriched isotope ratios in the other carbonate textures (microsparry and sparry calcite cement) at CBA indicate that all of them were precipitated in the absence of, or with only inconspicuous amounts of, AOM. Petrographic observations show that the microsparry and sparry calcite grew during a much later phase than the micrite and networked radiaxial calcite rim-cement. In other words, the AOM influence might have weakened over time during formation of the carbonate body.

The petrographic and geochemical characteristics of the Yasukawa carbonate body A are: (1) a high carbonate content that is comparable in volume to the initial porosity volume of unconsolidated clastic sediments (Matsumoto, 1978; Ritger *et al.*, 1987); (2) a high magnesium content (Fig. 4A) similar to those of carbonates formed under the influence of seawater (Matsumoto, 1978; Ritger *et al.*, 1987); (3) very local *in situ* fracturing (Fig. 3), indicating the presence of vigorous fluid flow and its discharge to the seafloor (Aiello, 2005); (4) a negative sulphur isotopic composition for sulphides, indicating the influence of bacterial sulphate reduction (Kohn *et al.*, 1998; Peckmann *et al.*, 2001); and (5) similar oxygen isotope values for early-diagenetic carbonates and molluscan shell carbonates, suggesting that both precipitated from isotopically similar water and at almost the same temperatures. These oxygen isotope values closely resemble the values from Campanian shells of benthic animals examined from outer-shelf to upper-slope settings in the northwestern Pacific (Moriya *et al.*, 2003). These characteristics strongly suggest that the early-diagenetic carbonates precipitated just below the sediment/seawater interface in the zone of bacterial sulphate reduction.

Table 4 Summarized lithological and geochemical features of carbonate body A (CBA, the inferred centre of the methane seep) and surrounding clastic rocks at Yasukawa peripheral site (YPS) (inferred peripheral zone of the methane seep) and their characteristic taxa

		CBA	YPS
Lithology	Texture	*In situ* fractures	No fractures but weakly bioturbated
	Size of carbonate	2 m in width and 1 m in height	Up to 10 cm in diameter concretions
$\delta^{34}S$ of sulphide		–10.5 to 11.0‰	–8.5 to –5.1‰
Typical taxa		Vestimentiferans and *Serradonta*	*Acharax* and *Nucinella*
Interpretation		Centre of methane seep	Peripheral zone of methane seep

Fossil assemblages from Yasukawa differ from 'typical' marine fossil assemblages in clastic facies of the Omagari Formation in both faunal composition and mode of occurrence. We identified lucinid, thyasirid, and solemyoid bivalves and the acmaeid gastropod *Serradonta*, which are typical members of modern and fossil chemosynthesis-based communities (Reid, 1990; Krueger *et al.*, 1996; Taylor & Glover, 2000; Warén *et al.*, 2003; Sasaki *et al.*, 2003; Little & Vrijenhoek, 2003; Gill *et al.*, 2005; Kiel & Campbell, 2005; Kiel, 2006). Molluscs typical of normal-marine (i.e., non-seep) conditions in the Omagari Formation include the trigoniid *Yaadia*, oysters, inoceramids, and ammonoids, all of which occur allochthonously in sandstone and gravel beds transported by debris flows or turbidity currents (Takahashi *et al.*, 2003). In rare cases, nuculoid bivalves such as *Acila*, *Nanonavis*, and *Nuculana* (*Ezonuculana*), and some inoceramids, were found *in situ* in the mudstone (Takahashi *et al.*, 2003; A. Takahashi, pers. com. 2006). Only nuculoid bivalves are common to both environments.

Centre of the methane seep at Yasukawa

There are several distinctly contrasting lithological and geochemical features between CBA and YPS (see Table 4). First, the greater amounts of methane-derived calcium carbonate at CBA strongly suggest that AOM activity was higher at the precipitation site of the carbonate body than in the surrounding lithology. Second, *in situ* fractures occur only at CBA, implying that vigorous fluid flow and/or high hydrostatic pressure typified CBA formation. Third, a variable range of sulphur isotopic compositions at CBA suggests an exhaustion of sulphate due to bacterial sulphate reduction. This interpretation follows Peckmann *et al.* (2001), who attributed varying sulphur isotopic compositions to a limited incursion of seawater sulphate in pore water, followed by its almost complete consumption due to bacterial sulphate reduction in a closed system.

Our observations strongly suggest that the concentration of methane decreased from CBA toward YPS. Furthermore, it is also probable that the concentration of hydrogen sulphide, probably produced by sulphate-reducing bacteria coupled with anaerobic methane-oxidizing archaea (Orphan *et al.*, 2002), decreased from CBA toward YPS. Elvert *et al.* (2005) recently reported that increasing hydrogen sulphide concentration indicates an intensive reaction of AOM.

Pattern of fossil distribution at the Yasukawa methane seep

The Yasukawa site yields moderately rich and relatively well-preserved fossil assemblages dominated by bivalves and gastropods, compared to other ancient methane-seep localities. Worm tubes (probably vestimentiferan) are uncommon and found only in or close to carbonate bodies. In contrast, at the coeval Omagari site, such tubes are found as mass occurrences (Hikida *et al.*, 2003). This difference apparently reflects the longevity of the methane seep and/or the strength of its discharge. The carbonate body containing worm tubes at the Omagari methane-seep reaches 5 m in height, whereas the largest carbonate body at the Yasukawa site (CBA) is only 1 m high.

The uncommon occurrence of worm tubes at the Yasukawa site positively correlates with the rarity of *Serradonta* (Jenkins *et al.*, in press). This gastropod is a strongly laterally compressed acmaeid limpet known also from Recent methane seeps around Japan. Its shape is an adaptation for utilizing vestimentiferan tubes as a substrate (Okutani *et al.*, 1992; Sasaki *et al.*, 2003). This gastropod is not found in siliciclastic rocks around the Yasukawa carbonate body A (YPS), but is very common in the Omagari vestimentiferan rich fossil methane-seep carbonate. This distribution strongly suggests that *Serradonta* had already evolved to live on vestimentiferan tubes by the Cretaceous (Jenkins *et al.*, in press).

The most common gastropods at the Yasukawa site, both at CBA and at YPS, are unidentified abyssochrysids and ataphrids. None of the Recent abyssochrysids is known to be a member of chemosynthetic ecosystems (Bouchet, 1991; Killeen & Oliver, 2000) and, as pointed out by McArthur & Tunnicliffe (1998), they are more likely to be 'normal' deep-water gastropods. On the other hand, most pre-Neogene fossil abyssochrysids have been found in chemoautotrophy-based associations. Eocene abyssochrysids are known from Barbados (Kugler *et al.*, 1984; Gill *et al.*, 2005) and the US Pacific Coast (Squires, 1995; Goedert & Kaler, 1996); in both cases they were found in ancient methane seeps. Several Mesozoic (Late Jurassic to Early Cretaceous) methane-seep gastropods from the US Pacific Coast (Stanton, 1895; Campbell & Bottjer, 1993; Campbell *et al.*, 1993) are likely to be abyssochrysids, although they are described under a variety of names, and a revision is pending. These gastropods are notably absent from the coeval Omagari site. The reason for such a distribution remains unclear, but it seems that abyssochrysids preferred lower concentrations of hydrogen sulphide, since they are common not only in close proximity to CBA but also to the more distant YPS. Taking into account the close relationship of abyssochrysids and provannids, the latter being typical of chemoautotrophy-based communities, the occurrence of abyssochrysids in ancient methane seeps needs a re-evaluation.

Ataphridae, a diverse group of Mesozoic smooth-shelled vetigastropods, have not been reported previously from ancient methane seeps. The exact taxonomic position of this family among Vetigastropoda is still uncertain. Warén (in Bouchet *et al.*, 2005) has suggested that ataphrids may represent ancestors of Recent Trochaclididae. Our ataphrids, however, are more similar to some turbinids and especially to some species of *Cantrainea*. Two species of *Cantrainea* from modern seeps around Japan were recently described (Okutani & Fujikura, 1990; Okutani, 2001; Sasaki *et al.*, 2005), but their ecology and exact habitat are unknown. The other gastropods at Yasukawa are rare and their taxonomic description is now in progress.

The most striking feature of the bivalve assemblage at the Yasukawa site is the absence of large lucinids, which are reported from the Omagari site (Hikida *et al.*, 2003). Smaller lucinids are represented by rare *Myrtea* and *Miltha*. Living *Myrtea* reportedly contains chemoautotrophic bacteria in their gills (Dando *et al.*, 1985; Taylor & Glover, 2000), but Recent species are more characteristic of relatively shallow-water settings rather than methane seeps. *Miltha* is known from several fossil methane seeps in Japan and New Zealand (see summary in Campbell, 2006) but is unknown in analogous modern offshore settings. Thyasirid bivalves are much more common. *Thyasira* is abundant both at CBA and at YPS. Several species of this genus are reported to contain chemoautotrophic bacteria in their gills (Southward, 1986; Reid, 1990). The distribution of *Thyasira* sp. at Yasukawa implies that this species also was chemosymbiotic.

The other bivalves yielding chemoautotrophic bacteria are solemyoids. At the Yasukawa site, *Achatax cretacea* (Solemyidae) and *Nucinella* sp. (Nucinellidae) were found in both CBA and the surrounding clastic rocks at YPS (see Table 3; Amano *et al.*, in press). *Acharax* is a well-known bivalve that typically colonizes peripheral zones of modern methane seeps and hot vents (Sahling *et al.*, 2002; Knittel *et al.*, 2003; Treude *et al.*, 2003), or ancient seeps with diffuse hydrocarbon-rich fluid flow (Nesbitt & Campbell, 2004). *Nucinella* is a deep-water bivalve with a wide but scattered distribution both in Recent seas and in the fossil record (La Perna, 2005). Judging from the absence of a gut in *Nucinella* (Kuznetsov & Schileyko, 1984), at least some species may rely on chemoautotrophic bacteria in their life strategy (Reid, 1990). *Nucinella* is occasionally found in the vicinity of methane-seep communities (Sasaki *et al.*, 2005). The distribution of solemyoid bivalves is surprisingly consistent at Yasukawa, where they are rare in the vicinity of CBA and common in the peripheral clastic rocks (YPS).

Other bivalves relatively common at the Yasukawa site include nuculids and nuculanids (Table 3). Recent species of these groups are non-chemosymbiotic (Reid, 1990), and possibly they represent deep-sea generalists in methane-seep settings. We also regard occurrences of dentalid scaphopods at YPS as opportunistic, while the presence of ammonoids and a single shell of a propeamussid bivalve is most probably fortuitous. Finally, remnants of decapods are relatively common in CBA and YPS, suggesting that these animals could also be seep related.

The faunal distribution pattern we describe above (abyssochrysids and ataphrids at the methane-seep centre and solemyoids, *Acharax* and *Nucinella* in the peripheral zone) closely resembles the pattern reported from Hydrate Ridge in the Cascadia Margin off Oregon by Sahling *et al.* (2002) and Knittel *et al.* (2005). Such a pattern was related by these workers to the gradient of hydrogen sulphide concentrations around a methane seep. A significant difference between Hydrate Ridge seeps and the Yasukawa seep is the absence of the bivalve *Calyptogena* at the latter. Instead, we encountered an association of gastropods at the centre of the Yasukawa methane seep. Possible reasons for this difference are: (1) The methane discharge at Yasukawa was probably much weaker than the one at Hydrate Ridge; the size of CBA is just 2 m in diameter. (2) *Calyptogena* has been known from dense accumulations in methane seeps since the Palaeogene, but only a single specimen of alleged *Calyptogena* has been reported from the Omagari methane seep (Hikida *et al.*, 2003). Most probably, *Calyptogena* first formed dense populations in the Eocene (Peckmann *et al.*, 2002). The abyssochrysid- and ataphrid-dominated association from the centre of the Yasukawa methane seep is surprising and requires further studies on other Cretaceous seep associations of Japan.

CONCLUSIONS

The Campanian (Late Cretaceous) carbonate body observed in the Omagari Formation at the Yasukawa site, Nakagawa area, northern Hokkaido, Japan, is interpreted here as an ancient methane-seep deposit on the basis of extremely negative carbon isotope ratios. Methane-bearing pore water rose to near the seafloor when the methane-derived carbonates were formed. This interpretation is strengthened by petrographic observations, showing high carbonate content, the existence of high-magnesium calcite, *in situ* fractures, and conduit structures. The coincidence of sedimentological and petrographic data and the faunal distribution in this chemosynthetic association also support the hypothesis that the carbonate bodies were centres of methane discharge, while YPS represents its peripheral zone. The distribution pattern of the fossils at Yasukawa roughly corresponds to that observed at modern methane seeps.

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REFERENCES

Aharon P (2000) Microbial processes and products fueled by hydrocarbons at submarine seeps. In *Microbial Sediments* (eds Riding RE, Awramik SM). Springer, Berlin, pp. 270–281.

Aiello IW (2005) Fossil seep structures of the Monterey Bay region and tectonic/structural controls on fluid flow in an active transform margin. *Palaeogeography, Palaeoclimatology, Palaeoecology* **227**, 124–142.

Aller RC (2004) Conceptual models of early diagenetic processes: the muddy seafloor as an unsteady, batch reactor. *Journal of Marine Research* **62**, 815–835.

Amano K, Jenkins RG, Hikida Y (in press) A new gigantic Nucinella (Bivalvia: Solemyoida) from the Cretaceous cold-seep deposit in Hokkaido, northern Japan. *The Veliger*.

Barry JP, Kochevar RE, Baxter CH (1997) The influence of pore-water chemistry and physiology on the distribution of vesicomyid clams at cold seeps in Monterey Bay: implications for patterns of chemosynthetic community organization. *Limnology and Oceanography* **42**, 318–328.

Beauchamp B, Savard M (1992) Cretaceous chemosynthetic carbonate mounds in the Canadian Arctic. *PALAIOS* **7**, 434–450.

Bergquist DC, Ward T, Cordes EE, McNelis T, Howlett S, Kosoff R, Hourdez S, Carney R, Fisher CR (2003) Community structure of vestimentiferan-generated habitat islands from Gulf of Mexico cold seeps. *Journal of Experimental Marine Biology and Ecology* **289**, 197–222.

Birgel D, Peckmann J, Klautzsch S, Thiel V, Reitner J (2006a) Anaerobic and aerobic oxidation of methane at Late Cretaceous seeps in the Western Interior Seaway, USA. *Geomicrobiology Journal* **23**, 565–577.

Birgel D, Thiel V, Hinrichs KU, Elvert M, Campbell KA, Reitner J, Farmer JD, Peckmann J (2006b) Lipid biomarker patterns of methane-seep microbialites from the Mesozoic convergent margin of California. *Organic Geochemistry* **37**, 1289–1302.

Black MB, Halanych KM, Maas PAY, Hoeh WR, Hashimoto J, Desbruyeres D, Lutz RA, Vrijenhoek RC (1997) Molecular systematics of vestimentiferan tubeworms from hydrothermal vents and cold-water seeps. *Marine Biology* **130**, 141–149.

Bouchet P (1991) New records and new species of *Abyssochrysos* (Mollusca, Caenogastropoda). *Journal of Natural History* **25**, 305–313.

Bouchet P, Rocroi JP, Frýda J, Hausdorf B, Ponder WF, Valdés Á, Warén A (2005) Classification and nomenclator of gastropod families. *Malacologia* **47**, 1–368.

Campbell KA (2006) Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: past developments and future research directions. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* **232**, 362–407.

Campbell KA, Bottjer DJ (1993) Fossil cold seeps. *National Geographic Research & Exploration* **9**, 326–343.

Campbell KA, Bottjer DJ (1995) Brachiopods and chemosymbiotic bivalves in Phanerozoic hydrothermal vent and cold seep environments. *Geology* **23**, 321–324.

Campbell KA, Carlson C, Bottjer DJ (1993) Fossil cold seep limestone and associated chemosynthetic macroinvertebrate faunas, Jurassic-Cretaceous Great Valley Group, California. In *Advances in the Sedimentary Geology of the Great Valley Group*, *Sacramento Valley*, *California* (eds Graham SA, Lowe DR). Society of Economic Paleontologists and Mineralogists, Pacific Section, Tulsa, Oklahoma, pp. 37–50.

Campbell KA, Farmer JD, Des Marais D (2002) Ancient hydrocarbon seeps from the Mesozoic convergent margin of California: carbonate geochemistry, fluids and palaeoenvironments. *Geofluids* **2**, 63–94.

Childress JJ, Fisher CR, Favuzzi JA, Sanders NK (1991) Sulfide and carbon dioxide uptake by the hydrothermal vent clam, *Calyptogena magnifica*, and its chemoautotrophic symbionts. *Physiological Zoology* **64**, 1444–1470.

Corliss J, Dymond J, Gordon L, Edmond J, Herzen R, Ballard R, Green K, Williams D, Bainbridge A, Crane K, Vanandel T (1979) Submarine thermal springs in the Galapagos Rift. *Science* **203**, 1073–1083.

Dando PR, Southward AJ, Southward EC, Terwilliger NB, Terwilliger RC (1985) Sulfur-oxidizing bacteria and hemoglobin in gills of the bivalve mollusk *Myrtea spinifera*. *Marine Ecology Progress Series* **23**, 85–98.

Dando PR, Southward AJ, Southward EC, Dixon DR, Crawford A, Crawford M (1992) Shipwrecked tube worms. *Nature* **356**, 667.

Elvert M, Hopmans EC, Treude T, Boetius A, Suess E (2005) Spatial variations of methanotrophic consortia at cold methane seeps: implications from a high-resolution molecular and isotopic approach. *Geobiology* **3**, 195–209.

Gaillard C, Rio M, Rolin Y, Roux M (1992) Fossil chemosynthetic communities related to vent or seeps in sedimentary basins: the pseudobioherms of southeastern France compared to other World examples. *PALAIOS* **7**, 451–465.

Gill FL, Harding IC, Little CTS, Todd JA (2005) Palaeogene and Neogene cold seep communities in Barbados, Trinidad and Venezuela: an overview. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* **227**, 191–209.

Goedert JL, Kaler KL (1996) A new species of *Abyssochrysos* (Gastropoda: Loxonematoidea) from a Middle Eocene cold-seep carbonate in the Humptulips Formation, western Washington. *The Veliger* **39**, 65–70.

Hasegawa K (1997) Sunken wood-associated gastropods collected from Suruga Bay, Pacific side of central Honshu, Japan, with description of 12 new species. *National Science Museum Monographs* **12**, 59–123.

Hikida Y, Suzuki S, Togo Y, Ijiri A (2003) An exceptionally well-preserved fossil seep community from the Cretaceous Yezo Group in the Nakagawa area, Hokkaido. *Paleontological Research* 7, 329–342.

Jenkins RG (2006) Late Cretaceous marine chemosynthetic paleoecosystem in Northern Hokkaido, Japan, reconstructed from paleontological, stable isotopic and organic geochemical analyses. Unpublished PhD Thesis, Department of Earth and Planetary Science, The University of Tokyo, Tokyo, Japan.

Jenkins RG, Kaim A, Hikida Y (in press) Antiquity of the substrate choice among acmaeid limpets from Late Cretaceous chemosynthesis-based communities. *Acta Palaeontologica Polonica* **52**(2), in press.

Kauffman EG, Arthur MA, Howe B, Scholle PA (1996) Widespread venting of methane-rich fluids in Late Cretaceous (Campanian) submarine springs (Tepee Buttes), Western Interior. *Geology* **24**, 799–802.

Kelly SRA, Blanc E, Price SP, Whitham AG (2000) Early Cretaceous giant bivalves from seep-related limestone mounds, Wollaston Forland, Northeast Greenland. In *The Evolutionary Biology of the Bivalvia* (eds Harper EM, Taylor JD, Crame JA). Geological Society, London, pp. 227–246.

Kiel S (2006) New records and species of molluscs from Tertiary cold-seep carbonates in Washington State, USA. *Journal of Paleontology* **80**, 121–137.

Kiel S, Campbell KA (2005) *Lithomphalus enderlini* gen. et sp. nov. from cold-seep carbonates in California–a Cretaceous neomphalid gastropod? *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* **227**, 232–241.

Kiel S, Little CTS (2006) Cold-seep mollusks are older than the general marine mollusk fauna. *Science* **313**, 1429–1431.

Killeen IJ, Oliver PG (2000) A new species of *Abyssochrysos* (Gastropoda: Loxonematoidea) from the Oman margin. *Journal of Molluscan Studies* **66**, 95–98.

Knittel K, Boetius A, Lemke A, Eilers H, Lochte K, Pfannkuche O, Linke P, Amann R (2003) Activity, distribution, and diversity of sulfate reducers and other bacteria in sediments above gas hydrate (Cascadia margin, Oregon). *Geomicrobiology Journal* **20**, 269–294.

Knittel K, Losekann T, Boetius A, Kort R, Amann R (2005) Diversity and distribution of methanotrophic archaea at cold seeps. *Applied and Environmental Microbiology* **71**, 467–479.

Kohn MJ, Riciputi LR, Stakes D, Orange DL (1998) Sulfur isotope variability in biogenic pyrite: reflections of heterogeneous bacterial colonization? *American Mineralogist* **83**, 1454–1468.

Kotelnikova S (2002) Microbial production and oxidation of methane in deep subsurface. *Earth-Science Reviews* **58**, 367–395.

Krueger D, Gustafson R, Cavanaugh C (1996) Vertical transmission of chemoautotrophic symbionts in the bivalve *Solemya velum* (Bivalvia: Protobranchia). *Biological Bulletin* **190**, 195–202.

Kugler HG, Jung P, Saunders JB (1984) The Joes River Formation of Barbados and its fauna. *Eclogae Geologicae Helvetiae* **77**, 675–705.

Kuznetsov AP, Schileyko AA (1984) On the gutless Protobranchia (Bivalvia). *Biologicheskie nauki* **2**, 39–49 (in Russian).

La Perna R (2005) A gigantic deep-sea Nucinellidae from the tropical West Pacific (Bivalvia: Protobranchia). *Zootaxa* **881**, 1–10.

Lein AY (2004) Authigenic carbonate formation in the ocean. *Lithology and Mineral Resources* **39**, 1–30.

Levin LA (2005) Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes. *Oceanography and Marine Biology – An Annual Review* **43**, 1–46.

Levin LA, Ziebis W, Mendoza GF, Growney VA, Tryon MD, Brown KM, Mahn C, Gieskes JM, Rathburn AE (2003) Spatial heterogeneity of macrofauna at northern California methane seeps: influence of sulfide concentration and fluid flow. *Marine Ecology-Progress Series* **265**, 123–139.

Little CTS, Vrijenhoek RC (2003) Are hydrothermal vent animals living fossils? *Trends in Ecology & Evolution* **18**, 582–588.

Lonsdale P (1977) Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep-Sea Research* **24**, 857–863.

MacDonald IR, Boland GS, Baker JS, Brooks JM, Kennicutt MC, Bidigare RR (1989) Gulf of Mexico hydrocarbon seep communities.2. Spatial-distribution of seep organisms and hydrocarbons at Bush Hill. *Marine Biology* **101**, 235–247.

Majima R, Nobuhara T, Kitazaki T (2005) Review of fossil chemosynthetic assemblages in Japan. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* **227**, 86–123.

Marshall BA (1988) Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. *Journal of Natural History* **22**, 949–1004.

Matsumoto R (1978) Stage of formation and origin of authigenic carbonates and carbonate rocks in the coalfield regions. *Geological Society of Japan*, *Memoir* **15**, 35–52.

Matsumoto T (1942) Fundamentals in the Cretaceous stratigraphy of Japan. Part I. *Memoirs of the Faculty of Science*, *Kyushu Imperial University-Series D*, *Geology* **1**, 129–280.

McArthur AG, Tunnicliffe V (1998) Relics and antiquity revisited in the modern vent fauna. In *Modern Ocean Floor Processes and the Geological Record* (eds Mills RA, Harrison K). The Geological Society, London, pp. 271–291.

Michaelis W, Seifert R, Nauhaus K, Treude T, Thiel V, Blumenberg M, Knittel K, Gieseke A, Peterknecht K, Pape T, Boetius A, Amann R, Jorgensen BB, Widdel F, Peckmann J, Pimenov NV, Gulin MB (2002) Microbial reefs in the Black Sea fueled by anaerobic oxidation of methane. *Science* **297**, 1013–1015.

Moriya K, Nishi H, Kawahata H, Tanabe K, Takayanagi Y (2003) Demersal habitat of Late Cretaceous ammonoids: evidence from oxygen isotopes for the Campanian (Late Cretaceous) northwestern Pacific thermal structure. *Geology* **31**, 167–170.

Nesbitt EA, Campbell KA (2004) Spatial and stratigraphic distribution of fossils from diffuse seeps in a Pilocene shelf setting, Cascadia Convergent Margin. *Geological Society of America Abstract with Programs* **36**, 314.

Okutani T (2001) Six new bathyal and shelf trochoidean species in Japan. *Venus*, *Journal of the Malacological Society of Japan* **60**, 121–127.

Okutani T, Fujikura K (1990) A new turbinid gastropod collected from the warm seep site in the Minami-Ensei Knoll, west of Amami-Oshima Island, Japan. *Venus*, *The Japanese Journal of Malacology* **49**, 83–91.

Okutani T, Tsuchida E, Fujikura K (1992) Five bathyal gastropods living within or near the *Calyptogena*-community of the Hatsuchima Islet, Sagami Bay. *Venus*, *The Japanese Journal of Malacology* **51**, 137–148.

Olu K, Lance S, Sibuet M, Henry P, Fiala-Médioni A, Dinet A (1997) Cold seep communities as indicators of fluid expulsion patterns through mud volcanoes seaward of the Barbados accretionary prism. *Deep-Sea Research Part I – Oceanographic Research Papers* **44**, 811–841.

Orphan V, House C, Hinrichs K, McKeegan K, DeLong E (2002) Multiple archaeal groups mediate methane oxidation in anoxic cold seep sediments. *Proceedings of the National Academy of Sciences of the USA* **99**, 7663–7668.

Orphan VJ, Ussler W, Naehr TH, House CH, Hinrichs KU, Paull CK (2004) Geological, geochemical, and microbiological heterogeneity of the seafloor around methane vents in the Eel River Basin, offshore California. *Chemical Geology* **205**, 265–289.

Peckmann J, Thiel V (2004) Carbon cycling at ancient methane-seeps. *Chemical Geology*, **205**, 443–467.

Peckmann J, Reimer A, Luth U, Luth C, Hansen BT, Heinicke C, Hoefs J, Reitner J (2001) Methane-derived carbonates and authigenic pyrite from the northwestern Black Sea. *Marine Geology* **177**, 129–150.

Peckmann J, Goedert JL, Thiel V, Michaelis W, Reitner J (2002) A comprehensive approach to the study of methane-seep deposits from the Lincoln Creek Formation, western Washington State, USA. *Sedimentology* **49**, 855–873.

Rathburn AE, Perez ME, Martin JB, Day SA, Mahn C, Gieskes J, Ziebis W, Williams D, Bahls A (2003) Relationships between the distribution and stable isotopic composition of living benthic foraminifera and cold methane seep biogeochemistry in Monterey Bay, California. *Geochemistry Geophysics Geosystems* **4**, 1–28, doi: 10.1029/2003GC000595.

Reid RGB (1990) Evolutionary implications of sulphide-oxidizing symbioses in bivalves. In *The Bivalvia – Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986* (ed. Morton B). Hong Kong University Press, Hong Kong, pp. 127–140.

Ritger S, Carson B, Suess E (1987) Methane-derived authigenic carbonates formed by sudcution-induced pore-water expulsion along the Oregon / Washington margin. *Geological Society of America Bulletin* **98**, 147–156.

Sahling H, Rickert D, Lee RW, Linke P, Suess E (2002) Macrofaunal community structure and sulfide flux at gas hydrate deposits from the Cascadia convergent margin, NE Pacific. *Marine Ecology Progress Series* **231**, 121–138.

Sahling H, Galkin SV, Salyuk A, Greinert J, Foerstel H, Piepenburg D, Suess E (2003) Depth-related structure and ecological significance of cold-seep communities-a case study from the Sea of Okhotsk. *Deep-Sea Research Part 1* **50**, 1391–1409.

Sasaki T, Okutani T, Fujikura K (2003) New taxa and new records of patelliform gastropods associated with chemoautosynthesis-based communities in Japanese waters. *The Veliger* **46**, 189–210.

Sasaki T, Okutani T, Fujikura K (2005) Molluscs from hydrothermal vents and cold seeps in Japan: a review of taxa recorded in twenty recent years (1984–2004). *Venus, Journal of the Malacological Society of Japan* **64**, 87–133.

Shigeta Y, Maeda H (2005) Yezo Group research in Sakhalin-A historical review. *National Science Museum Monographs* **31**, 1–24.

Sibuet M, Olu K (1998) Biogeography, biodiversity and fluid dependence of deep-sea cold seep communities at active and passive margin. *Deep-Sea Research Part 2* **45**, 517–567.

Smith CR, HK, Wheatcroft RA, Jumars PA, Deming JW (1989) Vent fauna on whale remains. *Nature* **341**, 27–28.

Southward EC (1986) Gill symbionts in thyasirids and other bivalve molluscs. *Journal of the Marine Biological Association of the United Kingdom* **66**, 889–914.

Squires RL (1995) First fossil species of the chemosynthetic-community gastropod *Provanna*: localized cold-seep limestone in upper Eocene and Oligocene rocks, Washington. *The Veliger* **38**, 30–36.

Stakes DS, Orange D, Paduan JB, Salamy KA, Maher N (1999) Cold-seeps and authigenic carbonate formation in Monterey Bay, California. *Marine Geology* **159**, 93–109.

Stanton TW (1895) Contributions to the Cretaceous paleontology of the Pacific coast: the fauna of the Knoxville beds. *Bulletin of the United States Geological Survey* **133**, 1–132.

Suess E, Carson B, Ritger S, Moore JC, Jones ML, Kulm LD, Cochrane GR (1985) Biological communities at vent sites along the subduction zone off Oregon. *Bulletin of the Biological Society of Washington* **6**, 475–484.

Takahashi A, Hirano H, Sato T (2003) Stratigraphy and fossil assemblage of the Upper Cretaceous in the Teshionakagawa area, Hokkaido, northern Japan. *Journal of the Geological Society of Japan* **109**, 77–95.

Takashima R, Kawabe F, Nishi H, Moriya K, Wani R, Ando H (2004) Geology and stratigraphy of forearc basin sediments in Hokkaido, Japan: cretaceous environmental events on the north-west Pacific margin. *Cretaceous Research* **25**, 365–390.

Taylor JD, Glover EA (2000) Functional anatomy, chemosynbiosis and evolution of the Lucinidae. In: *Evolutionary Biology of the Bivalvia* (eds Harper EM, Taylor JD, Crame JA). Geological Society, London, pp. 207–225.

Treude T, Boetius A, Knittel K, Wallmann K, Jorgensen BB (2003) Anaerobic oxidation of methane above gas hydrates at Hydrate Ridge, NE Pacific Ocean. *Marine Ecology Progress Series* **264**, 1–14.

Tucker ME, Wright VP (1990) *Carbonate Sedimentology*. Blackwell Science, Oxford.

Tunnicliffe V (1992) The nature and origin of the modern hydrothermal vent fauna. *PALAIOS* 7, 338–350.

Valentine DL (2002) Biogeochemistry and microbial ecology of methane oxidation in anoxic environments: a review. *Antonie Van Leeuwenhoek International Journal of General and Molecular Microbiology* **81**, 271–282.

Van Dover CL (2000) *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton University Press, Princeton, New Jersey.

Van Dover CL, German CR, Speer KG, Parson LM, Vrijenhoek RC (2002) Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* **295**, 1253–1257.

Warén A, Bengtson S, Goffredi SK, Van Dover CL (2003) A hot-vent gastropod with iron sulfide dermal sclerites. *Science* **302**, 1007.

Whiticar M (1999) Carbon and hydrogen isotope systematics of bacterial formation and oxidation of methane. *Chemical Geology* **161**, 291–314.

Yanagisawa F, Sakai H (1983) Thermal-decomposition of barium-sulfate vanadium pentaoxide silica glass mixtures for preparation of sulfur-dioxide in sulfur isotope ratio measurements. *Analytical Chemistry* **55**, 985–987.