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Discovery of chemosynthesis-based association on the Cretaceous basal leatherback sea turtle from Japan

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We report a Late Cretaceous chemosynthetic community fueled by decomposing basal leatherback sea turtle on the ocean floor in the western Pacific. The fossil association representing this community has been recovered from the matrix of a concretion containing a single carapace of *Mesodermochelys* sp. from Late Cretaceous outer shelf to upper slope deposit of northern Hokkaido, Japan. The carapace displays boreholes most likely performed by boring bivalves, and is associated with molluscan shells, mainly *Provanna* cf. *nakagawensis* and *Thyasira tanabei*. Since this association is similar to fauna already known from Late Cretaceous hydrocarbon seeps, sunken wood, and plesiosaur-falls in Hokkaido, it is suggested that all types of chemosynthesis-based communities in the Late Cretaceous of western Pacific may have belonged to the same regional pool of animals and were not yet fully differentiated into three independent types of communities as it is known today. This finding also indicates that the sulfophilic stage of the vertebrate-fall communities was supported not only by plesiosaur carcasses, which were previously reported, but also by sea turtle carcasses. It highlights the possibility of surviving vertebrate-fall communities through the end-Cretaceous mass extinction event on carcasses of sea turtles which are the only large marine vertebrates surviving this event.

Key words: Dermochelyoidea, Provannidae, Thyasiridae, vertebrate-fall, chemosynthesis-based ecosystem, Cretaceous, Japan.

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Introduction

Vertebrate-falls (e.g., whale-falls) on the sea floor support unique macrofaunal communities during its decaying and burial processes (Smith et al. 1989, 2015). Smith et al. (2002) and Smith and Baco (2003) proposed four ecologic stages in the development of modern whale-fall communities, i.e., mobile-scavenger, enrichment-opportunistic, sulfophilic, and reef stages. Vertebrate-fall communities attracted the attention of marine biologists after

their discovery in 1989 partially because close relatives of organisms associated with enrichment-opportunistic and sulfophilic stages have also been found at deep-sea hydrothermal vents and/or hydrocarbon seeps. Hence, it is hypothesized that the vertebrate-fall habitats may have an important role in progressive adaption of organisms inhabiting hydrothermal vent and hydrocarbon seep environments, i.e., they serve as evolutionary stepping stones (Distel et al. 2000; Miyazaki et al. 2010; Lorion et al. 2013; Smith et al. 2015), although Kiel (2016) argues that biogeo-

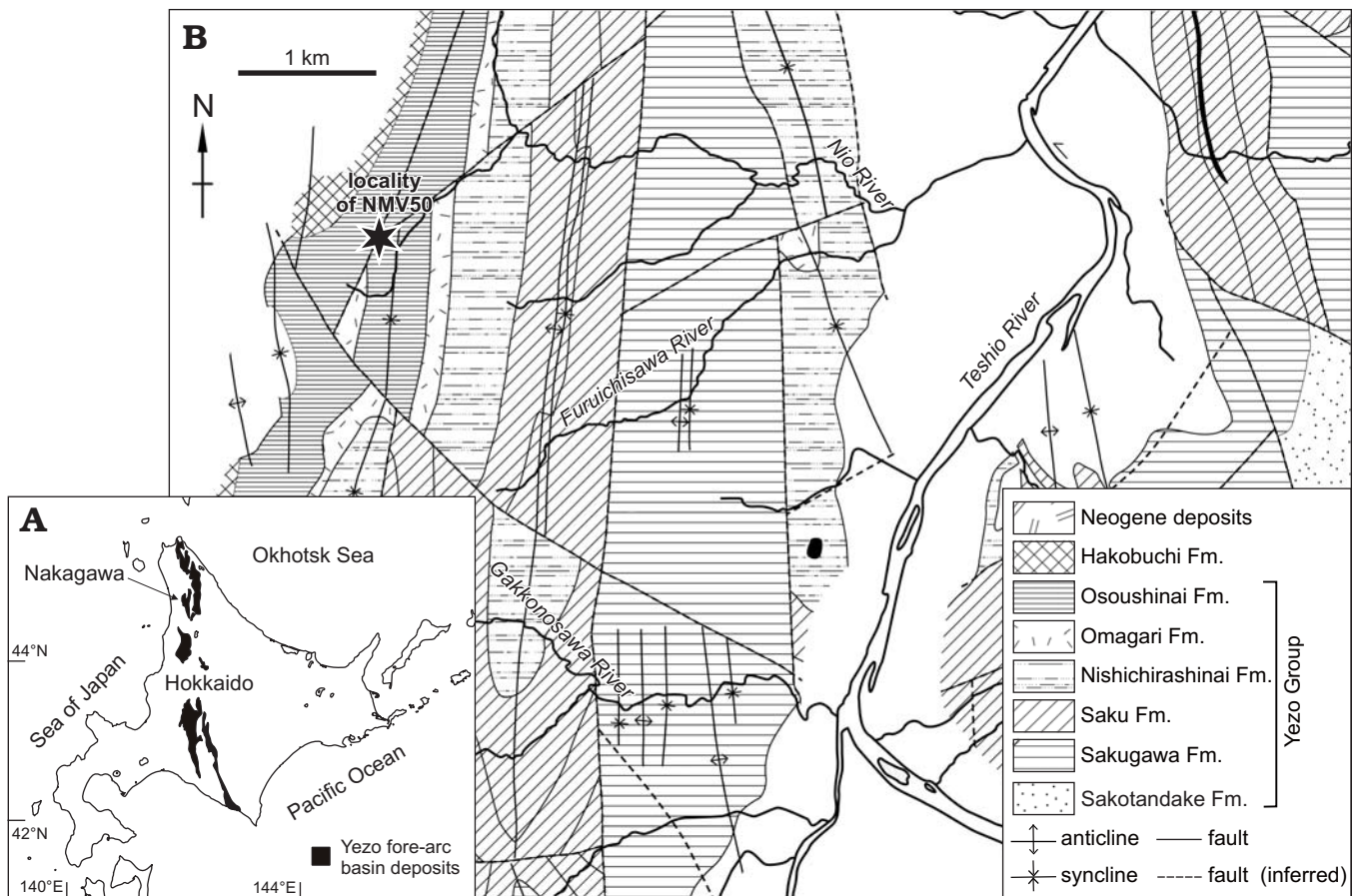


Fig. 1. Geology of the locality where the nodule containing *Mesodermochelys* sp. (NMV50) and associated invertebrate fossils were found. **A.** Map of Hokkaido with distribution of Yezo Group, Cretaceous fore-arc basin deposits. **B.** Detailed geological map of the Nakagawa Area, after Hashimoto et al. (1967).

graphic connectivity among chemosynthetic communities does not support dispersal stepping stone hypothesis. Fossil record of vertebrate-fall communities is essential in addressing this debate, regrettably it is still rather sparse, especially in the Mesozoic times when whales had not yet evolved. During that time only marine reptiles would have been important sources of large organic-falls on the deep-sea floor. According to Kaim et al. (2008b), who discovered chemosynthetic communities associated with two plesiosaurian carcasses from Upper Cretaceous Yezo Group, northern Japan, marine reptile carcasses can also support chemosynthetic life in a similar way to modern and ancient whale carcasses. However, majority of the large marine reptiles (plesiosaurs and mosasaurs) became extinct at or even before the K/Pg boundary (Motani 2009). Since whales first appeared in Eocene (Thewissen et al. 1994), there is ca. 15 Myr gap between plesiosaur extinction and whale appearance. Sea turtles are one of a few groups of large marine organisms which survived the Cretaceous/Paleogene extinction event (Motani 2009). Other groups, suggested to sustain chemosynthesis-based associations during that period, are large fishes (Dell 1987; Kiel 2008) and large sea-birds (Kiel et al. 2011). Lorion et al. (2009) deployed several possible substrates, including sea turtle

bones, to check their suitability for development of vertebrate-fall communities. They found that bathymodiolins, which have chemosynthetic bacteria in their gills, had successfully colonized deployed turtle bones. In addition, Marshall (1994) reported a single specimen of the limpet *Osteopelta* cf. *mirabilis* from a middle Eocene leatherback turtle *Dermodochelys* sp. from New Zealand which strongly resembles *O. mirabilis* from modern whale-falls. Recently, Danise and Higgs (2015) reported traces of bone-eating *Osedax* worm, considered to be heterotrophic (Tresguerres et al. 2013), from mid-Cretaceous plesiosaur and sea turtle bones. Thus, although it has been known since some time that sea turtle-falls could sustain vertebrate-fall communities in the geological past, details of chemosynthetic invertebrate associations with sea turtle-falls in the Mesozoic Era are still largely unknown. Here we present an example of chemosynthesis-based community on Cretaceous sea turtle *Mesodermochelys* sp. from Late Cretaceous Yezo Group in Hokkaido, Japan.

Institutional abbreviations.—ESKU, Earth Science Course, Kanazawa University, Kanazawa City, Ishikawa Prefecture, Japan; NMV, Nakagawa Museum of Natural History Vertebrate collections, Nakagawa Town, Hokkaido, Japan.

Material and methods

The Cretaceous sea turtle *Mesodermochelys* sp. (NMV 50; Dermochelyidae; Chelonioidea; Sato et al. 2012) and associated fauna were found in a large carbonate nodule (ca. 600 mm in diameter) by an amateur fossil collector, Fujiyuki Endo in the year 2001 at the tributary of Nio River in Nakagawa Town, northern Hokkaido, Japan where only the Osoushinai Formation of Yezo Group is cropping out (Fig. 1; Hashimoto 1967; Takahashi et al. 2003, 2007). The turtle fossil was extracted from the nodule with assistance from Nakagawa Museum of Natural History volunteers using chemical (formic acid) and mechanical preparations. To prevent dissolution by formic acid, the bones were frequently coated by paraloid (plastic) dissolved in acetic acid solvent. Along with most of the concretion matrix, it is likely that several molluscan fossils were also dissolved during the chemical procedure. However, the mechanical procedures that were carried out simultaneously with the chemical procedures, enabled recovery of some molluscan fossils from the subdivided concretions. The samples were first observed by naked-eyes and then the extracted molluscan fossils were studied with the aid of binocular and scanning electron microscopes (JSM-6010LV, JEOL) at the ESKU.

Geological setting

The Yezo Group consists of Cretaceous marine clastic sediments (Takashima et al. 2004) formed in the Yezo fore-arc basin along the western margin of a subduction zone in the northwestern Pacific. The deposits of Yezo Group are distributed along a meridional belt in Hokkaido, Japan. The upper part of the Yezo Group and the Hakobuchi Formation, which unconformably overlie the Yezo Group, are distributed along the Nio River where the sea turtle was discovered. The upper part of the Yezo Group in this area is subdivided into the Sakugawa, Saku, Nishichirashinai, Omagari, and Osoushinai formations, in order of descending age. Among them, only the Osoushinai Formation crops out along the turtle-yielding tributary of Nio River. The Osoushinai Formation is composed of grey to dark grey siltstone with intercalations of sandstone. The underlying Omagari Formation is composed of mudstone with frequent intercalations of turbidite sandstone beds with many slump structures which were deposited on the landward slope of the trench. The overlying Hakobuchi Formation is mainly composed of sandy shallow water deposits with distinct hummocky cross-stratification. The Osoushinai Formation is located between these two types of deposits and thus most likely formed in the outer shelf to the upper continental slope setting (Jenkins et al. 2007; Takahashi et al. 2007; Kaim et al. 2009; Kiel et al. 2009). The age of Osoushinai Formation is assigned to Campanian, Late Cretaceous (Takahashi et al. 2003, 2007).

Results

Preservation of sea turtle carapace.—Nearly half of the large carapace of *Mesodermochelys* sp. (at least ca. 445 mm wide and ca. 435 mm long; Sato et al. 2012) was preserved in the investigated nodule (Fig. 2). Estimated total carapace length is ca. 700 mm. The carapace bears several bore holes, each hole is one to few centimeters in diameter, and the holes are distributed both on the external and internal

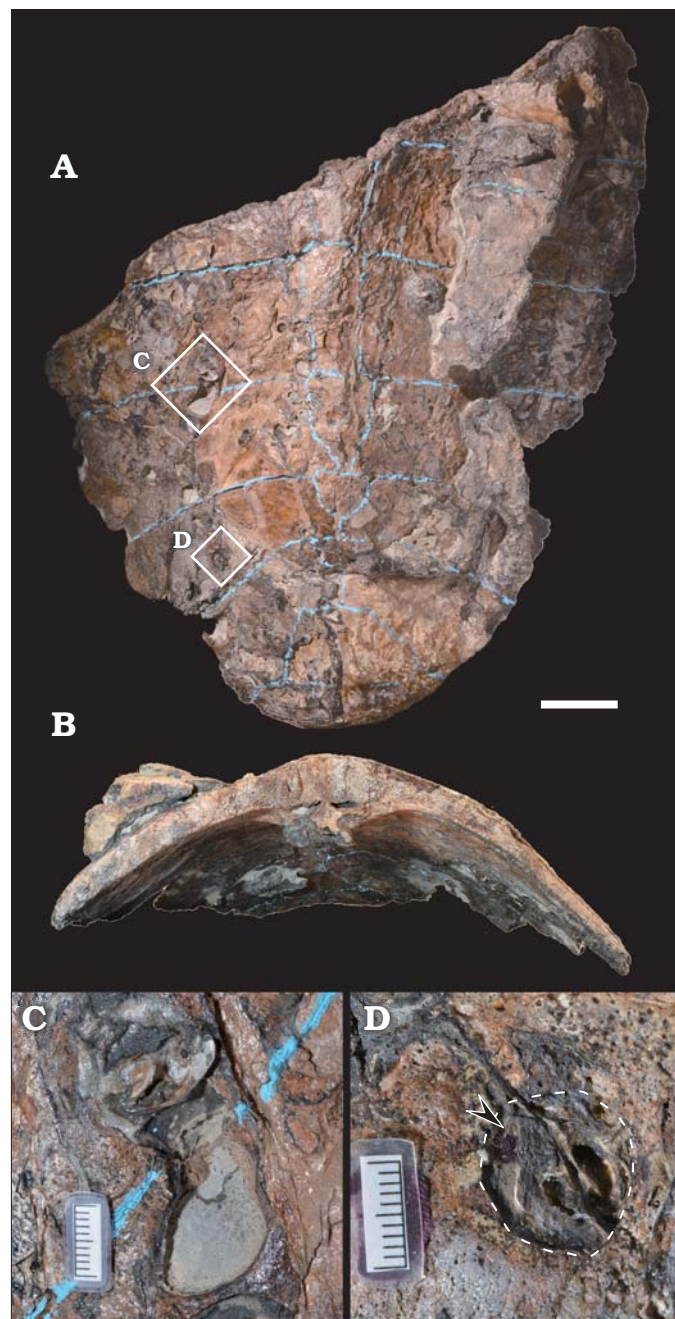


Fig. 2. Basal leatherback sea turtle *Mesodermochelys* sp. (NMV50) from Nio Creek, Nakagawa, Japan, Campanian, Upper Cretaceous. Carapace with drill holes on its surface, in dorsal (A) and anterior (B) views. Examples of drill holes (C, D), showing probable bivalve (arrow) in the hole (dashed line). Scale bars A, B, 50 mm; C, D, 10 mm.

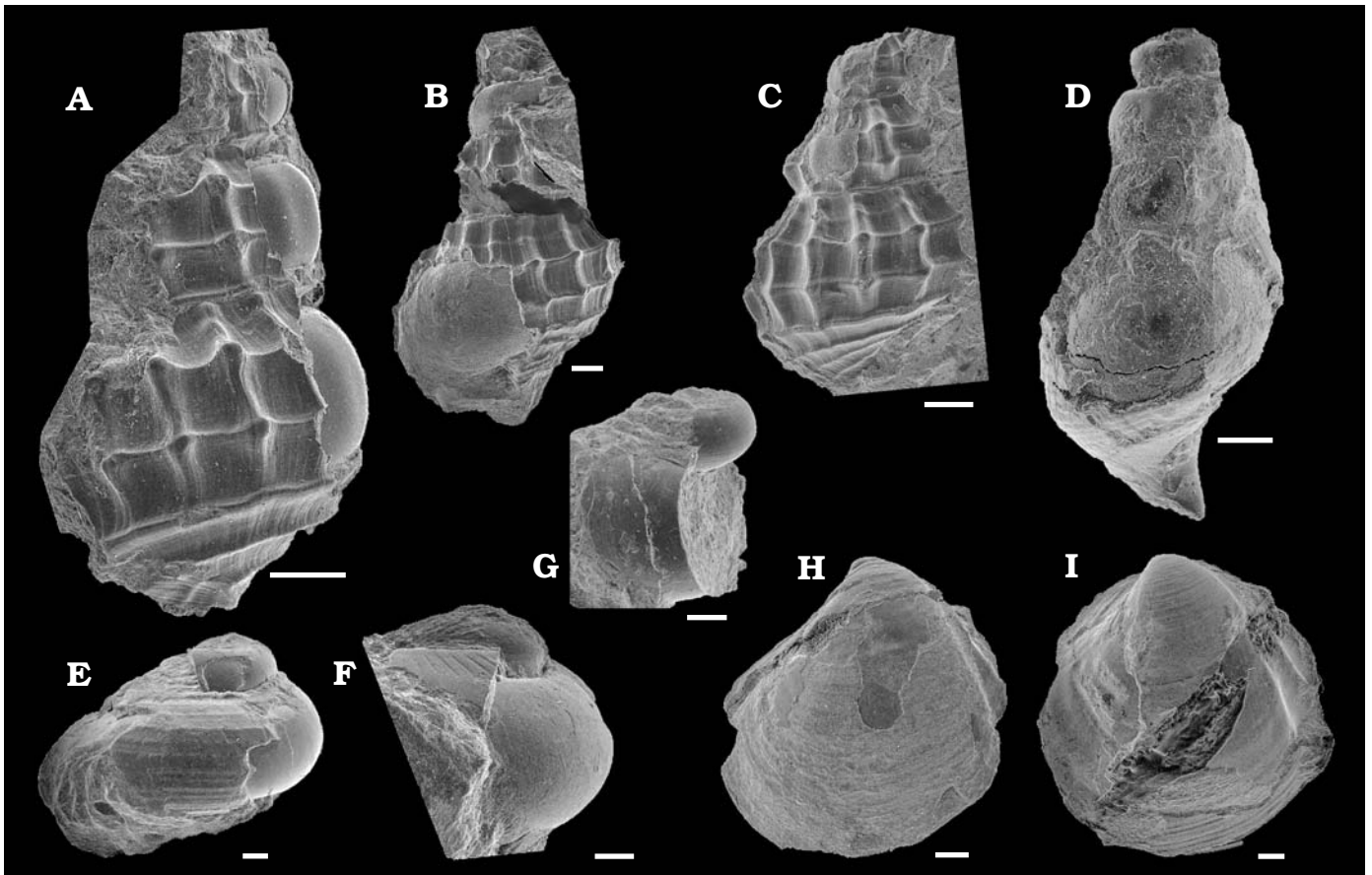


Fig. 3. SEM images of invertebrate fossils associated with the basal leatherback sea turtle *Mesodermochelys* sp. from Nio Creek, Nakagawa, Japan, Campanian, Upper Cretaceous. **A–C.** Abyssochrysoid gastropod *Provanna* cf. *nakagawensis* Kaim, Jenkins, and Warén, 2008a (A, NMV50-M01; B, NMV50-M04; C, NMV50-M09). **D.** ?Abyssochrysoid gastropod (NMV50-M11). **E.** Trochoid gastropod *Hikidea* cf. *yasukawensis* (Kaim, Jenkins, and Hikida, 2009) (NMV50-M03). **F.** ?Campaniloid gastropod ?*Gyrodes* sp. (NMV50-M10). **G.** ?Cephalaspid gastropod (NMV50-M06). **H, I.** Thyasirid bivalve *Thyasira tanabei* Kiel, Amano, and Jenkins, 2008 (H, NMV50-M02; I, NMV50-M12). Scale bars 500 μ m.

surfaces. Several holes contain invertebrate shells, probably boring bivalves. However, due to the fragile nature of the carapace, it would have been difficult to extract these shells without damaging it. Hence, we refrained from extracting these invertebrate shells. The cancellous bones, which are below the external cortex layer of the carapace, were partially exposed. Some of the exposed areas were due to the action of boring mollusks. Other parts of the carapace were exposed by the action of formic acid at the time of sample preparation. In addition, selected sections of the carapace exhibited cancellous bones covered in a layer of sediments without a cortex layer; the cortex layer has apparently been removed prior to burial.

Mollusks associated with sea turtle fall.—In total 12 molluscan fossils were found in the matrix surrounding *Mesodermochelys* sp. (NMV50; Fig. 3). The exact positions of the pieces of matrix containing the mollusc fossils within the nodule are not known. However, considering the size of the nodule, these fossils were distributed within a 150 mm radius of the sea turtle carapace. Most of the molluscan fossils were preserved with the original shell mineralogy and have not been subjected to significant diagenesis. The

shell substance preservation state is much better than fossils from Late Cretaceous hydrocarbon seeps in Hokkaido (e.g., Jenkins et al. 2007; Kaim et al. 2008a, 2009) and appears to be pristine aragonite. Among the fossils associated with the turtle, abyssochrysoid gastropod *Provanna* cf. *nakagawensis* (Fig. 3A–C) is the most common species (three specimens), while *Thyasira tanabei* (Fig. 3H, I) is the second common species (two articulated specimens). The remaining taxa are represented by single specimens and have been identified preliminarily as *Hikidea* cf. *yasukawensis* (Fig. 3E), ?*Gyrodes* sp. (Fig. 3F), ?cephalaspid gastropod (Fig. 3G), ?abyssochrysoid gastropod (Fig. 3D). Additionally, we noticed one unidentified bivalve and two other shell fragments. *P.* cf. *nakagawensis* and *H.* cf. *yasukawensis* found in this study are very similar to *Provanna nakagawensis* and *H. yasukawensis* from Late Cretaceous Omagari and Yasukawa seeps in the Nakagawa, respectively (Kaim et al. 2008a, 2009). *P. nakagawensis* from the Omagari and Yasukawa seeps are characterized by spiral ornament consisting of two median prominent ribs and blunt nodes present at the intersections of spiral and axial ribs (Kaim et al. 2009). Strength of spiral ribs and nodes

are variable among the specimens from seeps (Kaim et al. 2009), and *P. cf. nakagawensis* (Fig. 3A–C) reported in this paper shows stronger ribs and nodes than the *P. nakagawensis* from the Omagari and Yasukawa seeps. *Hikidea yasukawensis* displays variable strengths of spiral ornaments; the *H. cf. yasukawensis* reported in this paper has strong spiral ornament with faint ribs similar to *H. yasukawensis* from the Yasukawa seep (Kaim et al. 2009: fig. 5B, C). Identification of other gastropods is still not clear at this moment and pending further study in the future. *Thyasira tanabei* is commonly found in the Cretaceous seeps in Japan (Kiel et al. 2008; Hryniewicz et al. 2017).

Discussion

The combination of *Provanna*, *Hikidea*, and *Thyasira* associated with the Late Cretaceous sea turtle *Mesodermochelys* sp. from the Nakagawa area indicates that sea turtle deadfalls supported chemosynthetic life in the Late Cretaceous. All three taxa are known to be members of other chemosynthesis-based ecosystems. Species of abyssochryoid *Provanna* constitute one of the most common groups of gastropods in seeps, vertebrate-falls and sunken woods, at least since the Late Cretaceous (Johnson et al. 2010; Kaim et al. 2008a, b; Kiel et al. 2009). Some extant large-sized taxa of abyssochryoids (*Alviniconcha* and *Ifremeria*), classified so far jointly with *Provanna*, host endosymbiotic sulfur-oxidizing and/or methanotrophic bacteria in their bodies. However, according to both molecular and fossil data, it seems that large-sized abyssochryoids most likely diverged from small-sized ones already in Jurassic/Early Cretaceous (compare Johnson et al. 2010; Kaim et al. 2014; Chen et al. 2016). The small-sized abyssochryoids are unknown to host symbiotic bacteria; they are rather grazers on microbial mats (Warén and Bouchet 1986; Desbruyères et al. 2006). The species found in the studied turtle-fall are tiny and possess tall shells reminiscent of modern, grazing abyssochryoids. This type of abyssochryoids is known also from ancient vertebrate-falls, e.g., Cenozoic whale-falls and Cretaceous plesiosaur-falls (Kiel and Goedert 2006; Kaim et al. 2008b). Kaim et al. (2008b) illustrated plesiosaur bones corroded by dense aggregations of microborings and impregnated by pyrite crystals, and concluded that the abyssochryoid gastropods fed on the microbial mats composed of sulfur-oxidizing bacteria covering the bones. Since we refrained from sectioning the single carapace at our disposal we do not have at this point any evidence of microbial activity on the carapace of *Mesodermochelys* sp. reported herein. Nevertheless, judging from the exclusive occurrences of *Provanna* in chemosynthetic environments (Kaim et al. 2012), where it grazes on microbial mats, we expect that *Provanna cf. nakagawensis* reported in this paper most likely also grazed on microbial mats developed on bones of *Mesodermochelys* sp. In addition, *Provanna* sp. was also found in a Late Cretaceous wood-fall (Kiel et al. 2009). Thus, this finding reinforces

the idea that several taxa of abyssochryoid gastropods were already adapted to seep, vertebrate-fall and sunken-wood environments in the Cretaceous (Johnson et al. 2010). Due to the limited numbers and incomplete specimens found so far, it is difficult to make a species level comparison between these communities, however we hope that the increasing number of records of Cretaceous chemosynthesis-based communities in Hokkaido, and especially in Nakagawa region, will allow us to compare them at species level in the near future. *Hikidea* is a genus recently established by Kaim et al. (2014) for small-sized taxa similar to the Recent *Cantrainea* which also occurs at seeps. *Hikidea* now consists of four nominal species and all are restricted to hydrocarbon seeps (Kaim et al. 2014, 2017). Recently Kiel et al. (2017) reported a *Hikidea*-like gastropod from Late Triassic seep in Turkey, however, it needs further investigations to confirm this identity because of its poor preservation (Kaim et al. 2017). In Nakagawa area, *H. yasukawensis* and *H. omagariensis* abundantly occur in Yasukawa and Omagari seeps, respectively (Jenkins et al. 2007; Jenkins and Hikida 2011; Kaim et al. 2009). In addition, *Hikidea* sp. and *Hikidea*-like species occurred in Late Cretaceous hydrocarbon seeps in Nakagawa and California (Kaim et al. 2009, 2014), a plesiosaur fall (Kaim et al. 2008b), and a sunken wood (Kiel et al. 2009) jointly with the abyssochryoid gastropods, and has not yet been reported from non-chemosynthesis-based ecosystems. Thyasirids are a well-known infaunal bivalve group that lives in chemosynthetic environments. Although the detailed taxonomy of thyasirids is still poorly understood, the species described herein clearly belongs to *Thyasira tanabei* known from Cretaceous seeps and a sunken wood in Japan (Kiel et al. 2008, 2009; Hryniewicz et al. 2017). Dufour (2005) pointed out that many Recent large-sized species of thyasirids host chemosymbiotic bacteria. The shell length of *T. tanabei* is moderate, around 10 mm (Kiel et al. 2008), thus, it is difficult to judge whether *T. tanabei* hosted chemosynthetic bacteria. In total, at least half of the species found next to the investigated turtle carapace are known to be members of Late Cretaceous chemosynthetic communities. The remaining specimens are pending further taxonomic work, which may prove to be difficult due to their incomplete preservation. However the *Provanna–Hikidea–Thyasira* association alone points out to the development of chemosynthesis-based community on the Late Cretaceous sea turtle *Mesodermochelys* sp.

Since chemosynthesis-based associations were reported from the Late Cretaceous plesiosaur carcasses (Kaim et al. 2008b), it was hypothesized that other marine reptiles could also have supported vertebrate-fall communities (Vrijenhoek et al. 2009). Among marine reptiles, sea turtles are one of the rare groups to survive K/Pg boundary, and thus it is important to confirm their ability to support vertebrate deadfall communities. It is also worth to note that modern leatherback sea turtles have high oily subcutaneous insulation (Zug and Parham 1996) and decomposing of these fats may generate additional amounts of hydrogen

sulfides by sulfate-reducing bacteria. This may make carcasses of these turtles particularly attractive to chemosynthesis-based communities in spite of their smaller sizes (in comparison to plesiosaurs and whales). Danise and Higgs (2015) reported traces of the bone-eating *Osedax*, which consumes lipids within the bones, in the Cretaceous sea turtles highlighting the susceptibility of turtle carcasses to develop the enrichment opportunistic stage. The finding in this paper confirms that the sea turtle-fall could also support the sulfophilic stage in the development of vertebrate-fall community as early as in the Cretaceous in a similar way to plesiosaur-falls (Kaim et al. 2008b; Danise and Higgs 2015). As suggested in several papers (e.g., Danise and Higgs 2015; Smith et al. 2015) the lipid content in the bone is crucial to develop the sulfophilic stage. Majority of marine reptiles had (and still have) cancellous bones—which are an adaptation to aquatic environment—with the lipids filling its marrow space (Houssaye 2013; Nakajima et al. 2014; Danise and Higgs 2015). Therefore, the other Mesozoic marine reptiles could potentially have had capability to develop such vertebrate-fall communities. In the case of ichthyosaur from the Late Jurassic of the UK, Danise et al. (2014) found the mobile scavenger, enrichment opportunistic and reef stages of a vertebrate-fall community, but no sulfophilic stage. Danise et al. (2014) argued that the absence of sulfophilic stage in their ichthyosaur-fall is due to its small size (ca. 3 m long) or too shallow depositional environment. Estimated carapace length of the *Mesodermochelys* reported herein is ca. 700 mm, therefore, its total length would be around 1 m. Although the amount of lipids within these bones and the total body weight are unknown, the size of the *Mesodermochelys* sp. is definitely smaller than the ichthyosaur from the UK. Thus, we think that the size alone would not be a reason for the absence of sulfophilic stage in the Late Jurassic ichthyosaur. The more plausible explanation stems from the shallow water setting of its deposition, where animals of photosynthetic communities may outcompete animals typical of sulfophilic stage (Danise et al. 2014), or perhaps inverse correlation between abundance of *Osedax* and chemosynthetic microbial mats with epifaunal assemblages suggested by Alfaro-Lucas et al. (2017). Dick (2015) also reported ichthyosaur-fall from *Posidonia* shale which did not sustain chemosynthetic community, but instead displayed increased biodiversity and biomass of background taxa around the carcass.

Another plausible explanation may come from the absence of macro bone eaters and/or drilling organisms on the ichthyosaur-falls described by Danise et al. (2014) and Dick (2015). In the modern oceans, activity of sulfate-reducing bacteria and resulting amount of released hydrogen sulfide is increased when the hard surface compact cortical layer of bone is mechanically torn off or drilled through, e.g., by *Osedax* worms, allowing sufficient amount of sulfate containing sea water to penetrate lipid rich cancellous bones (Deming et al. 1997; Treude et al. 2009), although excessive degradation of bones and organic matter within the bones

by *Osedax* may also decrease the production of hydrogen sulfide due to higher oxygen content hampering the activity of sulfate reducing bacteria (Alfaro-Lucas et al. 2017). Vrijenhoek (2009) estimated splitting age of *Osedax* from other siboglinids during the Eocene or Cretaceous based on different molecular clock calibrations. Fossil evidence of the *Osedax* traces found from mid Cretaceous sea turtle and plesiosaur bones (Danise and Higgs 2015) supports the slower clock calibration for estimation of splitting age of *Osedax* from other siboglinid worms. Thus, the bone degradation has been accelerated since the mid Cretaceous and the sulfophilic stage of the vertebrate-fall community might have occurred more frequently since then.

In the case of Late Cretaceous *Mesodermochelys* carcass, there are many drill holes in the carapace which could have been made by boring bivalves (Fig. 2C, D). This kind of borings performed by bivalves on whale bones is known also from mammal and fish bones (Belaústegui et al. 2012). We do not know exact ecological impact on the formation of chemosynthetic community by these borings at this moment, however, they could facilitate the exposure of the cancellous layer of the bone before burial, and therefore, seawater could penetrate into the bones accelerating bacterial degradation of lipids within the bones. Subsequently, the hydrogen sulfide could have been released and the chemosynthesis-based organisms could flourish on the Late Cretaceous sea turtle-fall.

In addition, Kiel (2015) pointed out that the lowering sulfate concentrations in the Late Cretaceous sea water resulted in fewer emission of sulfides at seeps. The same phenomenon could result in a limited reaction of microbial sulfate-reduction in bones of vertebrate-falls in the Late Cretaceous (Kiel 2015). This hypothesis can explain why there are only few records of chemosynthetic communities on Cretaceous vertebrate-falls and no large-scaled (ca. < 100 mm length) chemosynthetic fauna in them.

Conclusions

One-meter sized Late Cretaceous basal leatherback sea turtle *Mesodermochelys* sp. and associated molluscan fauna were recovered from the Late Cretaceous outer shelf to slope deposits in northern Hokkaido, Japan. The molluscan fossils are represented mainly by abyssochrysoid gastropod *Provanna* and thyasirid bivalves. Similar composition was revealed in the Late Cretaceous plesiosaur-fall associations in Hokkaido and Cretaceous seeps worldwide. Modern relatives of these mollusks are also well known members of chemosynthetic communities. Thus, the molluscan fossils associated to the Late Cretaceous *Mesodermochelys* sp. can be interpreted as the chemosynthetic community developed on decaying Late Cretaceous sea turtle. This is the first certain record of chemosynthesis-based community associated with a sea turtle in geologic time, and it shows that sea turtle falls had the capability to sustain chemosynthesis-based communities during the Late Cretaceous equally well as plesiosaur falls.

It is worth to stress that sea turtles are one of the very few groups of marine reptiles that survived the K/Pg mass extinction event. Thus, sea turtle falls could form a link in the evolutionary history of vertebrate falls between Cretaceous plesiosaur falls and Eocene-to-Recent whale-falls.

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