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Chemosynthesis-based associations on Cretaceous plesiosaurid carcasses

ANDRZEJ KAIM, YOSHITSUGU KOBAYASHI, HIROKI ECHIZENYA, ROBERT G. JENKINS, and KAZUSHIGE TANABE



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The objective of this report is to document first Mesozoic occurrences of chemosynthesis-based communities developed on large marine reptile carcasses. Micro-grazing provannid gastropods (typical of chemosynthetic communities) are associated with plesiosaurid skeletons in the Upper Cretaceous deposits of Hokkaido, northern Japan. The cancellous bones of the examined plesiosaurid bones contain a ubiquity of iron sulfides within the bone trabeculae, which provides evidence of anaerobic sulfate reduction of the bone lipids. We also report numerous microborings in the bone trabeculae, which might result from the activity of sulfur-oxidizing bacteria. This finding addresses the hotly debated problem of the emergence and radiation of whale bone faunas. We postulate that vertebrate bone environments in the Northwest Pacific region were settled repeatedly by animals from a regional pool of chemosynthesis-based communities that flourished in the methane seeps and/or hot vents that were present during the Late Cretaceous–Miocene.

Key words: Plesiosauridae, Provannidae, vertebrate-bone community, chemosynthetic community, Cretaceous, Japan.

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Introduction

The discoveries of hot vent (Lonsdale 1977), cold seep (Paull et al. 1984), and whale bone (Smith et al. 1989) communities on the bottom of the Recent deep seas has attracted the public eye by their distinctiveness, high levels of endemicity, and unusual behavioral traits of their animals. The biology, ecology, and evolution of such communities became a hotly debated topic in the scientific world (Smith et al. 1989; Tunnicliffe and Juniper 1990; Allison et al. 1991; Martill et al. 1991, 1995; Squires et al. 1991; Hogler 1994; Smith and Baco 2003; Amano and Little 2005; Kiel and Goedert 2006; Amano et al. 2007). While discussing their emergence and evolution it was hypothesized that large marine reptile carcasses could play a role—as so-called evolutionary stepping stones—in the progressive evolution from normal faunas to hot vent/cold seep communities (Smith et al. 1989; Martill et al. 1991; Distel et al. 2000). Although the existence of such associations was hypothesized in a number of publications (Martill et al. 1991, 1995; Hogler 1994), supporting fossil evidence remained unknown (Hogler 1994; Kiel and Goedert 2006). Herein we present such a highly anticipated discovery of a chemosynthesis-based association on marine reptile carcasses.

Institutional abbreviations.—EPUT, Department of Earth and Planetary Science, University of Tokyo, Japan; UHR, Hokkaido University Museum, Sapporo, Japan; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Material and methods

We analyzed herein two plesiosaur partial skeletons called thereafter Turonian skeleton and Coniacian skeleton. The bones of the Turonian skeleton were mostly extracted from the rock matrix by means of mechanical preparation before beginning this study. However, the portion remaining in the rock matrix yielded some gastropod specimens. The skeleton is identified as a pliosaurid plesiosaur based on a partially preserved skull and numerous teeth. The skull length is approximately 1.5 m, close to the size of a skull of Late Cretaceous pliosaur *Brachauchenius lucasi* estimated to reach up to 11 m in length (Carpenter 1996).The Coniacian skeleton is still in preparation, though several mollusk specimens have been already recovered. This partial skeleton lacks its skull and is identified as a plesiosaur due to the presence of nutritive foramina for blood vessels on the ventral surface of the

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vertebrae (Storrs 1991). The specimen preserves six dorsal vertebrae, ribs, gastralia, and the left ilium. The neurocentral sutures are fused in all preserved vertebrae, indicating that this individual was an adult. The width of the centrum is approximately 140 mm, close to the size of vertebrae from some Late Cretaceous plesiosaurs ranging 8–12 m in length (Welles 1952). A single tooth of a cow shark was found associated with the Coniacian plesiosaur specimen.

Several gastropod specimens have been left attached to the Coniacian skeleton. Some others have been extracted from the plesiosaur, coated with platinum, and examined on Philips XL20 scanning electron microscope at ZPAL. Four chips of bones detached from Coniacian specimen have been cut and thin-sectioned at ZPAL laboratory for microscopic examination. The thin sections were observed and photographed on transmitted light microscopes Olympus BX50 at ZPAL and Nikon Eclipse E600POL with CCD camera Zeiss Axio Cam MRc5 at EPUT.

Geological setting

Two plesiosaur partial skeletons have been found in Late Cretaceous (Turonian and Coniacian) continental slope deposits of Yezo Group (Okada 1983; Takashima et al. 2004) of the Haboro area, northwest Hokkaido (Fig. 1). Yezo Group is interpreted as deposits of Cretaceous fore-arc basin located on the western part of North Pacific margin (Okada 1983; Takashima et al. 2004). The individual of Turonian age (UHR 33108) was found in six boulders dispersed at the left tributary of the Shirochiunezawa Creek and apparently derived from the Shirochi Formation (Toshimitsu 1985; Okamoto et al. 2003). The Shirochi Formation is represented by intercalations of mudstone and sandstone beds. The sandstone beds are mostly turbidites and debris flow deposits (Toshimitsu 1985) therefore the formation is interpreted as deposited on a continental slope.

The Coniacian specimen (UHR 33109) was recovered from a small outcrop at the right bank of the Shirochiunezawa Creek about 250 m down of the Turonian specimen. The locality crops out siltstones of Lower Haborogawa Formation. The formation is represented mainly by gray to dark gray massive siltstone (Okamoto et al. 2003) and displays upward-coarsening of the sediment (Okamoto et al. 2003). This feature is interpreted as a regressive trend leading to a change from continental slope to outer shelf setting. According to Okamoto et al. (2003), Haborogawa Formation (lower and upper parts) corresponds to Nishichirashinai, Omagari, and Osoushinai Formations in Nakagawa area of the northern Hokkaido. The Santonian–Campanian Omagari Formation is known to yield several methane-seep associations (Hikida et al. 2003; Jenkins et al. 2007a, b).

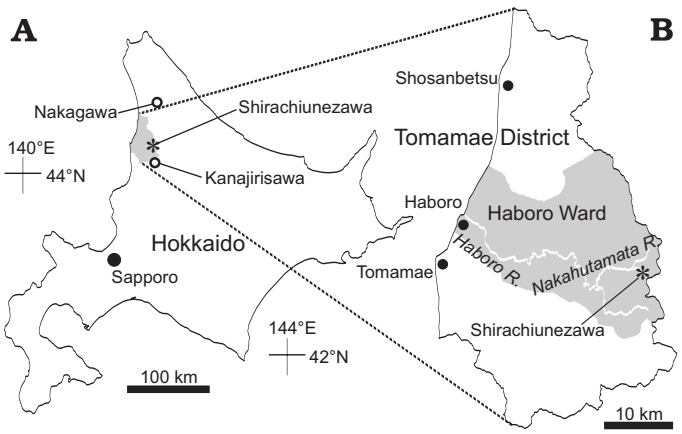


Fig. 1. Sketch maps of Hokkaido, northern Japan (**A**) and Tomamae District (**B**) with discussed localities indicated.

Mollusks associated to plesiosaur skeletons

The rock matrix remaining in the Turonian skeleton yielded eight specimens of melanoid-shaped gastropods with strong axial and spiral sculpture. The Coniacian skeleton provided 36 specimens of similar gastropods, two specimens of vetigastropods, and eight bivalve fragments. The fossil invertebrates were found adjacent to the bone (Fig. 2J) or in its immediate proximity (usually less than 50 mm). Most of the gastropod specimens in the Coniacian plesiosaur are concentrated in the cavity of the posterior part of the dorsal vertebrae (Fig. 2A). Some other specimens were found in the crevices between the centra (Fig. 2H–K). These specimens are preserved with original shell microstructure and apparently were not significantly affected by diagenesis, though their juvenile whorls are missing.

The melanoid-shaped gastropods are represented by at least two species (Fig. 3A, E, F, J, K). One of the species (Fig. 3A) is very similar to a new species of *Desbruyeresia* (Fig. 3B, C) described by Kaim et al. (in press), from the Cenomanian methane seep deposits in the Kanajirisawa Creek, Tappu area, about 30 km south of the Haboro plesiosaur localities (Fig. 1A). The provannids at the Kanajirisawa appear in mass occurrences and some of the specimens preserve decollate protoconchs (Fig. 3C), which are typical of these gastropods (Warén and Bouchet 1993). Another gastropod species (Fig. 3D) from the Turonian skeleton is very similar to a Campanian provannid (Fig. 3I) reported by Kaim et al. (in press) from the Nakagawa area (Fig. 1), northern Hokkaido (50 km NE from the plesiosaur localities). The species from locality Gakkonosawa exhibits the same type of macro- and microornamentation. The differences between specimens from plesiosaur bones and from methane seeps of adjacent areas seem to be of only specific importance. The only similar gastropods which could by misidentified as provannids are cerithiids. However, cerithiids have a very different protoconch. Such gastropods have never been found in the methane seeps of Japan. Moreover, in modern seep/vent faunas worldwide there is only a single published record of cerithiid gastropods: *Lirobittium* is

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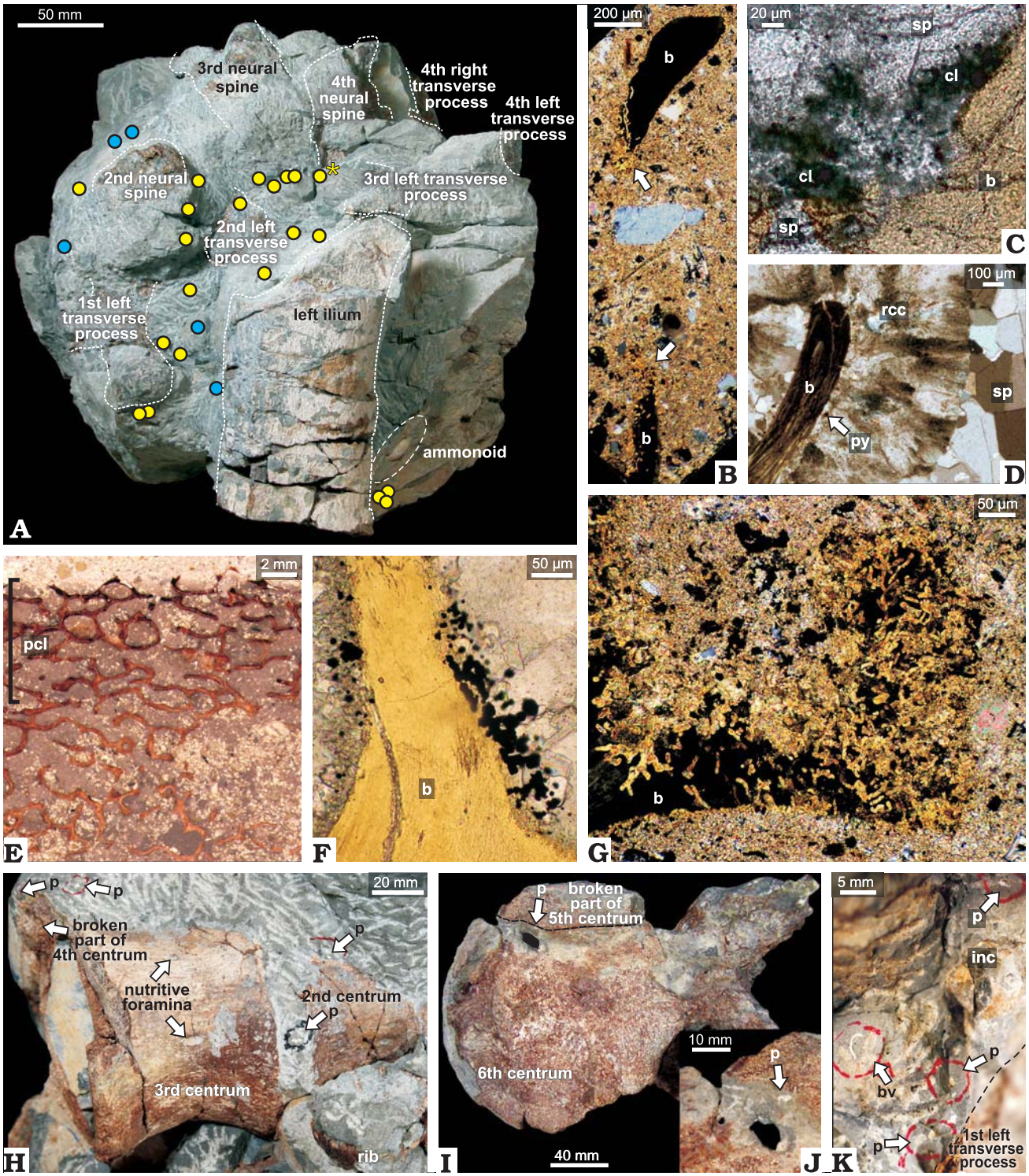


Fig. 2. Plesiosaur bones from the Coniacian slope deposits of Shirochiunezawa Creek, Haboro area of Hokkaido, Japan. **A**. Whole specimen UHR 33109 in dorsolateral view preserving four dorsal vertebrae and left ilium with gastropods (yellow circles) and bivalves (blue circles) embedded in the rock matrix in the bone cavities. Asterisked specimen is from Fig. 3A. **B**. Thin section of the bone (b; black in crossed polars); the bone is embedded in a carbonate matrix (mottled) containing some siliciclastic grains. Note a part of the bone in between the arrows that was totally disintegrated by possible bacterial activity. **C**. Clotted fabric (cl for cloths) in micritic matrix surrounded by sparry calcite (sp), b for bone. **D**. A section through cancellous bone showing thin layer of cement containing framboidal pyrite (py and arrow) and overgrown by radiaxial calcite cement (rcc); sp is for sparite. **E**. A section through cancellous bone showing trabecular structure; pcl (pyrite concentration layer) indicates the 7 mm-thick layer within the bone periphery that is enhanced by iron sulfide. **F**. Thin section through a bone trabecula (b; yellow) with framboidal crystals of iron sulfide (opaque); the bone is embedded in sparry calcitic cement (grey). **G**. Trabecula (b) with heavily bored tip by possible bacterial activity. **H**. Ventral view of centra (anterior to the right) with provannid gastropods indicated by p. **I**. Anterior view of 6th and a part of 5th centra detached from the specimen on A and H. **J** Magnified fragment from I showing position of the provannid gastropod. **K**. Magnification of a cavity from A showing position of provannids (p), unidentified bivalve (bv), and inoceramid *Inoceramus uwajimensis* (inc).

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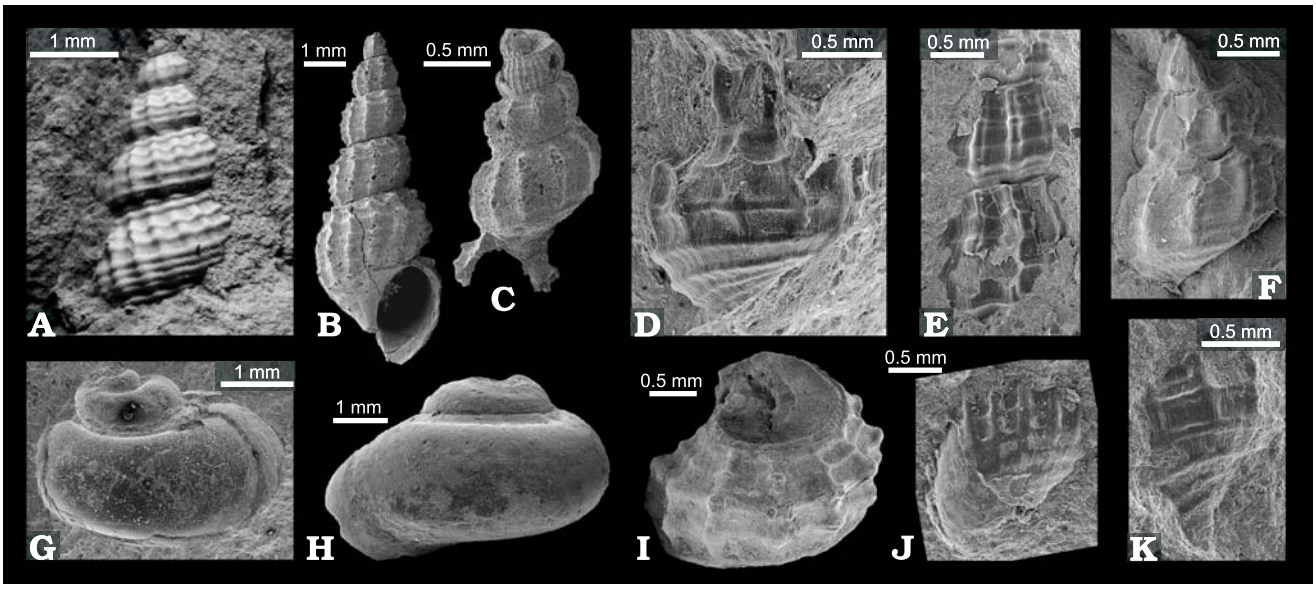


Fig. 3. Gastropods from the Late Cretaceous plesiosaur bones and seeps of Hokkaido, Japan. **A**, **E**, **J**. Provannidae gen. et sp. indet. 1 (UHR 33109m1, UHR 33109m2, and UHR 33109m3 respectively) from the Coniacian plesiosaurid bone association at Shirochiunezawa Creek (Haboro area), very similar to a new species of *Desbruyeresia* (**B**, **C**) from the Cenomanian methane seep deposits of Kanajirisawa Creek (Tappu area), UMUT MM29355 and UMUT MM29357 respectively (described in detail by Kaim et al. in press). **C**. Specimen UMUT MM29357 possesses a decollate protoconch typical of Provannidae. **D**. Provannidae gen. et sp. indet. 3 (UHR 33110m1) from the Turonian plesiosaurid bone association at Shirochiunezawa Creek, very similar to an undescribed provannid (**I**) from the Campanian methane seep deposits at Gakkonosawa Creek (Nakagawa area), UMUT MM29364; similar or the same species (**K**) is also found in the Coniacian plesiosaurid bone association at Shirochiunezawa Creek (Haboro area), UHR 33109m4. **F**. Provannidae gen. et sp. indet. 2 from Coniacian plesiosaurid bone association at Shirochiunezawa Creek (Haboro area), UHR 33109m5. **G**. Outer mould of vetigastropod gen. et sp. indet (UHR 33109m6) from Coniacian plesiosaurid bone association at Shirochiunezawa Creek (Haboro area), very similar to an ataphrid gastropod (**H**) from the Campanian methane seep deposits at Omagari (Nakagawa area), UMUT unregistered specimen.

recorded from seeps off California by Levin et al. (2000). There are no undoubted cerithiids from fossil hot vents and cold seeps. It seems that cerithiids are just now on their way to chemosynthesis-based communities. Cerithiids are also unknown from the continental slope deposits in the Cretaceous of Japan. They are known only from shallow-water sediments (Nagao 1932, 1939; Nagao and Ôtatume 1938; Hayami and Kase 1977; Kase 1984). Therefore, taking into account all above we interpret the melanoid-shaped gastropods as species of *Provanna* and *Desbruyeresia* (both Provannidae) though diagnostic protoconchs have not been preserved in specimens from plesiosaurs.

The vetigastropod (Fig. 3G; nacreous layer is present) associated with the plesiosaur bones morphologically resembles ataphrid-like gastropods (Fig. 3H), which are common in the methane seep deposits of the Nakagawa area (Jenkins et al. 2007a, b). The remnants of the bivalves found at the bones are poorly preserved and we could identify only a single specimen of an inoceramid *Inoceramus uwajimensis* Yehara, 1924 (Fig. 2K).

Petrographic and microstructural features of the plesiosaur specimens

The plesiosaur bones under consideration display trabecular structure (Fig. 2E) similar to those known from the whale bones. This structure is considered an adaptation to a fully aquatic mode of life (Ricqlès and Buffrénil 2001). The marrow spaces between the trabeculae are filled with sparry calcitic cement (Fig. 2F) or carbonate matrix (Fig. 2B, G) containing some unidentified clay minerals. Some parts of the matrix display clotted fabric (Fig. 2C), which is primarily a microbial feature (e.g., Riding 2000; Peckmann and Thiel 2004). Moreover, some bone trabeculae are covered by a layer of banded botryoidal-like radiaxial calcitic cements (Fig. 2D). This might be a Cretaceous counterpart of aragonitic botryoidal cements which are believed to be linked to microbial activity (Teichert et al. 2005; Peckmann et al. 2007). These petrographic features are commonly found in ancient and Recent methane seep deposits (e.g., Greinert et al. 2002; Campbell et al. 2002; Peckmann and Thiel 2004). The 7 mm thick layer (pcl in Fig. 2E) within the bone periphery is enhanced in iron sulfide coating trabeculae surfaces in a similar manner to the Recent whale bones (Allison et al. 1991). Thin sections made from a bone chip from the Coniacian specimen at Shirochiunezawa revealed numerous occurrences of framboidal pyrite crystals (up to 25 μm in diameter) on the surface of the bone with some of the trabeculae covered by pyrite layers of variable thickness (Fig. 2F). The outer bone surfaces are extensively bored, exhibited by cylindrical holes (Fig. 2B, G) with an average diameter of 5 μm and a length of up to 100 μm. At some places the bone is totally disintegrated by the borings (Fig. 2B). Similar struc-

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tures and degree of disintegration have been reported from Miocene whale falls (Amano and Little 2005; Amano et al. 2007). Amano and Little (2005: 352) stated that microborings "fall into the size range of microborings made by algae, bacteria and fungi" but simultaneously they interpret these borings as "possibly microbial" (Amano and Little 2005: 345) and furthermore they compare them to the borings reported from the modern whale bones by Deming et al. (1997). Amano et al. (2007: 240) subsequently infer "putative bacterial mats (for which we have no direct evidence) on the bones and surrounding sediment surface. These mats may have been grazed by *Provanna*? sp.". Regrettably, the microborings are poorly documented from Recent whale carcasses being restricted to the figure 5c in Allison et al. (1991). It seems, however, sufficient to compare the microborings reported from Oligocene (conference abstract of Spangler and Shapiro 2007 that needs confirmation in a peer reviewed journal) and Miocene (Amano and Little 2005; Amano et al. 2007) whale falls, and Cretaceous plesiosaur falls (this paper) with the "small tubes" described by Allison et al. (1991: 80) from Recent whale falls. Allison et al. (1991) did not provide any evidence as for the origin of these microborings, however, Deming et al. (1997) reported a high concentration of bone penetrating bacteria—with predominance of submicron-sized cocci and less frequent rod-shaped forms—in the peripheral region of the Recent whale bone. Moreover, the density of the bacteria is negatively correlated with lipid content of the bone (Deming et al. 1997) which suggests that the bacterial community is fuelled by the lipids. Simultaneously, Deming et al. (1997) reported also a dense community of microbial mats composed mainly of filamentous bacteria with minor component of rods and cocci. Deming et al. (1997) did not suggest any connection between microtubes reported by Allison et al. (1991) and examined bacteria but no other organisms viable to perform such borings were reported neither by Allison et al. (1991) nor Deming et al. (1997). It seems therefore to be sound to argue that the microborings and bacteria in Recent whale bones are related each other.

Although we have no direct evidence of the bacterial origin of the borings in plesiosaur bones as they fall into size range of boring made not only by bacteria but also algae and fungi (compare e.g., Underwood et al. 1999; Vogel and Marincovich 2004; Wisshak et al. 2005), nevertheless they are analogous to the structures reported from both Recent whale falls (Allison et al. 1991) and we conclude that it is most parsimonious to interpret them as traces of bacterial activity until another origin of Recent borings in whale falls is reported. Further work on the morphology and identity of the borings from fossil both whale and plesiosaur bones is pending as similar structures are known also from fish teeth (Underwood et al. 1999) and sirenian bones (Astibia et al. 2005).

The presence of pyrite layers within the bone periphery and the trabeculae suggests anaerobic microbial decomposition of the bone organic compounds (lipids), resulting in sulfate reduction and the release of the sulfides into the local environment (Allison et al 1991; Deming et al. 1997; Amano and Little 2005; Amano et al. 2007). It remains unclear if tiny provannids from the plesiosaur bones had bacterial symbionts, as the latter are reported so far only from the large provannids (Warén and Bouchet 1993; Desbruyères et al. 2006) and small species have yet to be examined in this respect (Anders Warén, personal communication 2007). Nevertheless our provannids were probably grazing upon putative bacterial mats as do their Recent counterparts (Warén and Bouchet 1993; Desbruyères et al. 2006). The presence of a bacterial mat and its grazers on plesiosaur carcasses may correspond to the sulfophilic stage in the ecological succession of whale fall communities (Bennett et al. 1994; Smith and Baco 2003; Kiel and Goedert 2006; Smith 2007). This suggests that plesiosaur carcasses, similar to their whale counterparts, may have passed through similar ecological successional stages (i.e., a mobile scavenger stage, an enrichment opportunistic stage, and a sulfophilic stage). Such a scenario has been predicted theoretically (Martill et al. 1991, 1995; Hogler 1994) for large marine reptiles but never addressed by reliable fossil evidence (Hogler 1994; Kiel and Goedert 2006).

Discussion

The fossil record of whale fall communities is extremely scarce and limited to Japan and US Pacific Coast (Goedert et al. 1995; Amano and Little 2005; Kiel and Goedert 2006; Amano et al. 2007). Kiel and Godert (2006) argue that the oldest-known whale falls (Eocene–Oligocene) from the US Pacific Coast lacked the sulfophilic stage, preserving rather a "chemosymbiotic opportunistic stage". The latter stage "…is characterized by species from wood-falls and from the background fauna which are adapted to reducing environments and most likely took advantage of elevated sulfide levels in the sediments underneath and around the whale carcass, rather than from anaerobic breakdown of bone lipids" (Kiel and Goedert 2007: 2629). After examination of faunal composition in these associations Kiel and Goedert (2006) concluded that the bones of primitive, small-bodied Oligocene–Eocene whales provided too small amount of oil to sustain organisms typical of the sulfophilic stage. This supposition, however, has been weakened recently by Pyeson and Haasl (2007), who have discovered a small whale fossil from Miocene rocks from California that is closely associated with vesicomyid bivalves. Moreover, Spangler and Shapiro (2007) argue in a conference abstract that whale bones from the Oligocene locality at the Sekiu River (Kiel and Goedert 2006) provided several features indicating bacterial degradation of the bones. If confirmed in a peer reviewed journal it might indicate that also Oligocene–Eocene whale falls could sustain communities at sulfophilic stage although impoverished in the taxonomic composition. Undoubted whale bone communities that preserve the faunal association typical of sulfophilic stage are those known from the Miocene of Japan

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(Amano and Little 2005; Amano et al. 2007). These associations consists of fauna typical of whale bone communities including *Adipicola*, *Calyptogena*, and *Provanna* (Amano and Little 2005; Amano et al. 2007).

Our plesiosaur skeleton did not provide any of the large mytilid and/or vesicomyid bivalves which rely fully or partly on sulphide-oxidizing endosymbionts and characterize the 'sulfophilic stage' in the whale bone community. However, recent investigations (Amano and Kiel 2007) have not confirmed any of the large vesicomyids from the Cretaceous methane seeps in Japan. The bivalves reported by Kanie and various co-workers (Kanie et al. 1993, 1996, 2000; Kanie and Kuramochi 1996; Kanie and Nishida 2000) and Hikida et al. (2003) appear to be rather lucinids (Amano and Kiel 2007). Moreover, even these bivalves are rather uncommon in the Cretaceous methane seeps. For example, there is only a single large bivalve specimen from large methane seep carbonate at Omagari (Hikida et al. 2003; own investigations). Therefore, it is no wonder that they were not discovered at plesiosaur carcasses. We found a few shells of small bivalves and all but one inoceramid are non-identifiable because of the preservation state. We believe that further investigations will reveal also plesiosaur fall associations with bivalves typical at chemosynthesis-based communities.

The relatively large number of provannids associated with ataphrid-like vetigastropods from plesiosaur bone associations corresponds well to the similar but better diversified Late Cretaceous methane seep associations known from adjacent areas (Jenkins et al. 2007a, b; see also Hikida et al. 2003). Miocene whale fall associations from Japan display similar patterns of taxonomic composition to the contemporary methane seeps (Amano et al. 2007). The impoverished taxonomic composition of plesiosaur fall communities and their similarity to much more diversified coeval methane seep communities may suggest that the vertebrate fall communities have been established several times by immigrants from other chemosynthesis-based communities when appropriately sized vertebrate carcasses appeared at deep sea floor. Such a conclusion is supported by our findings of plesiosaur bone associations exclusively in the vicinity of other chemosynthesis-based communities.

The finding of chemosynthesis-based communities on plesiosaur falls addresses also the idea of vertebrate bones acting as evolutionary and dispersal stepping stones (Smith et al. 1989; Martill et al. 1991; Distel et al. 2000). Taking into account similarity of plesiosaur communities to synchronous seep communities we may suppose that the former could act as stepping stones between some methane seeps. The impoverished taxonomic composition of plesiosaur bone associations may suggest that their evolutionary importance in development of chemosynthesis-based communities (at least methane seeps) might be limited. However, with the material at hand it is difficult to argue if our findings document 'incipient' or opportunistic colonization of a sulphide-rich substrate from adjacent cold seeps that was not repeated geographically or temporally until the evolution of whales in the Eocene or it is just the negligence of vertebrate paleontologists who do not pay attention for tiny mollusks associated with large skeletons. Another factor which has to be taken into consideration is a diagenetic alteration of the calcareous (especially aragonitic) shell material in localities where bones are well preserved. Nevertheless we feel confident that careful studies on skeletons from rock formations yielding also cold seep associations will provide additional reptile bone associations.

Conclusions

Two dozen-meter large plesiosaurid skeletons (one pliosaur and one plesiosaur) from Upper Cretaceous deep water deposits of Japan are associated with chemosynthesis-based associations of invertebrates. The composition of the associations strongly recollects coeval methane seep associations from the same area, though the former being impoverished in the taxonomic composition. Several petrographic features obtained from bone thin sections, e.g., clotted fabric, banded botryoidal-like radiaxial calcitic cements, framboidal pyrite crystals arranged in layers covering bone trabeculae, and peripheral bone layer enhanced in sulfide coatings, strongly suggest bacterial activity analogous to the one reported from modern examples of whale bone communities. The cylindrical holes extensively penetrating the outer bone surfaces may be interpreted as bacterial in origin although fungal affiliation is also possible. Further investigations on this matter are still pending.

Our findings indicate that vertebrate fall communities could develop several times in the geological past not only on whale falls but also on marine Mesozoic reptiles. The similarity of the plesiosaur bone and coeval methane seep associations strongly supports the idea that vertebrate bones could act as dispersal stepping stones for chemosynthesis-based communities, at least in the Late Cretaceous. There is still no enough data to argue about the role of reptile fall communities in the evolution of chemosynthesis-based communities. We expect a number of further discoveries of reptile bone associations from the regions yielding fossils of other types (especially methane seeps) of chemosythesis-based associations.

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