



Wood-fall associations from Late Cretaceous deep-water sediments of Hokkaido, Japan

STEFFEN KIEL, KAZUTAKA AMANO, YOSHINORI HIKIDA AND ROBERT G. JENKINS

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Sunken wood (wood-fall) in the deep sea today is colonized and consumed by diverse invertebrate communities that show phylogenetic relationships to the chemotrophic fauna on whale carcasses, hydrothermal vents and hydrocarbon seeps. Here we document Late Cretaceous examples of wood-fall communities from deep-water sediments of the Yezo Group on Hokkaido, Japan, consisting of provannid, skeneiform, and patelliform gastropods, and thyasirid and nuculanid bivalves. These species are similar or identical to those found on plesiosaur bones and at hydrocarbon seeps in the same sediments, showing that many members of the modern chemotrophic deep-sea fauna colonized this range of habitats at least since Late Cretaceous time. We also document for the first time faecal chimneys in boreholes in these wood fragments, which were presumably built by xylophagain bivalves. □ *Chemosynthetic communities, deep sea, ecology, evolution, shipworms, wood-fall.*

Steffen Kiel [steffen.kiel@gmx.de], Institut für Geowissenschaften, Christian-Albrechts-Universität Kiel, Ludewig-Meyn-Str. 10, 24118 Kiel, Germany, and Department of Paleobiology, Smithsonian Natural History Museum, Box 37012, Washington DC 20013-7012, USA; Kazutaka Amano [amano@juen.ac.jp], Department of Geoscience, Joetsu University of Education, Joetsu 943-8512, Japan; Yoshinori Hikida [inmhikida@coral.ocn.ne.jp], Nakagawa Museum of Natural History, Hokkaido 098-2626, Japan; Robert G. Jenkins [robert@eps.s.u-tokyo.ac.jp], University Museum and Department of Earth and Planetary Science, University of Tokyo, Tokyo 113-0033, Japan; manuscript received on 21/10/07; manuscript accepted on 28/01/08.

Invertebrate communities living on sunken wood (wood-fall) in the deep sea are known since the 1970s (Turner 1978; Wolff 1979). These communities are complex ecosystems consisting mainly of molluscs, polychaetes and crustaceans. Among these are species that seek shelter, graze on xylophagous microbes, predator, scavenger and even chemotrophic species that utilize sulphides resulting from the decay of the wood, of the metabolic by-products of wood-boring bivalves, or because the wood blocks the sediment's access to oxygen in the overlying water, making the sediment anoxic (Turner 1978; Wolff 1979; Dell 1987; Marshall 1988; Steineck *et al.* 1990; Hasegawa 1997; Sirenko 2004; Kiel & Goedert 2006b; Pailleret *et al.* 2007). Deep-sea wood-boring bivalves of the pholadid subfamily Xylophaginae are considered keystone species in this environment, because they transform the energy stored in the wood into nutrients that are digestible for other animals, either in form of faecal pellets for detritus-feeder or as flesh or carrion for predator and scavenger (Turner 1978).

Especially the microbe-grazing and the chemosymbiotic taxa include several clades that also occur in other reducing environments in the deep sea, including sunken whale carcasses, hydrocarbon seeps and hydrothermal vents (Van Dover 2000; Warén & Bouchet

2001; Smith & Baco 2003). The small mytilids *Idas* and *Adipicola* received particular attention because these wood- and bone-inhabitants are genetically the most basal members of the mytilid clade that also includes the iconic vent-inhabitant *Bathymodiolus* (Distel *et al.* 2000). It was concluded that mytilids used sunken wood as an adaptational 'stepping stone' to hydrothermal vents (Distel *et al.* 2000; Jones *et al.* 2006; Samadi *et al.* 2007). Potentially, also other of the many clades that are shared between wood, bones, seeps, and vents could have had a similar adaptational history.

The fossil record of wood-fall communities is still sparse. Around 30 individual sites are known from late Eocene to early Miocene deep-water sediments in western Washington State, USA, which have a fauna that consists mostly of modern genera (Kiel & Goedert 2006a, b). Two potential middle Jurassic wood-fall communities in Poland are dominated by an entirely different set of molluscs (Kaim 2006, 2008). The aim of the present paper is to document a species-rich wood-fall community and xylophagain faecal chimneys from Late Cretaceous deep-water sediments of the Yezo Group in northern Hokkaido, Japan, and to discuss the evolutionary implications of our findings.

Geological setting

The Yezo Group has recently been redefined by integrating of the Lower, Middle and Upper Yezo Groups and the Hakobuchi Group into the Yezo Group (Takashima *et al.* 2004). This group represents an elongate belt of fluvial to deep-marine sediments that stretches in a north to south direction through the entire island of Hokkaido, Japan, with deepening facies from west to east. These sediments were deposited in the Yezo fore-arc basin along the circum North Pacific margin during the Cretaceous (Okada 1983; Takashima *et al.* 2004). They rest on an ancient island arc consisting of the Horokanai ophiolite and of the calc-alkaline and alkaline volcano-sedimentary sequences of the Sorachi Group, and are unconformably overlain by late Eocene, non-marine and shallow-marine sediments of the Ishikari and Poronai groups, or by younger Neogene deposits (Takashima *et al.* 2002, 2004).

In our study area, the Nakagawa area in northern Hokkaido (Fig. 1A), the upper part of the Yezo Group (formerly Upper Yezo and Hakobuchi Groups)

crocks out and is divided, in ascending order, into the Nishichirashinai, Omagari, Osoushinai and Hakobuchi Formations (Takahashi *et al.* 2003; Takashima *et al.* 2004). The Nishichirashinai and Omagari Formations consist of intercalations of sandstone, siltstone, and mudstone beds with numerous slump structures. The Osoushinai Formation is represented mainly by grey to dark grey siltstone with some intercalations of muddy sandstone, and the Hakobuchi Formation contains sandstones that sometimes show hummocky cross-stratification, and conglomerates beds. Thus, the upper part of the Yezo Group in the Nakagawa area generally shows an upward-shallowing facies trend from continental slope to offshore depositional settings.

Material and methods

The material was collected by the authors in September 2006, and consists of two calcareous concretions found as float on the banks of the Akita Creek and the Wakkawenbetsu River (Fig. 1B, C). The Akita Creek sample was found to the west of Otomi Village,

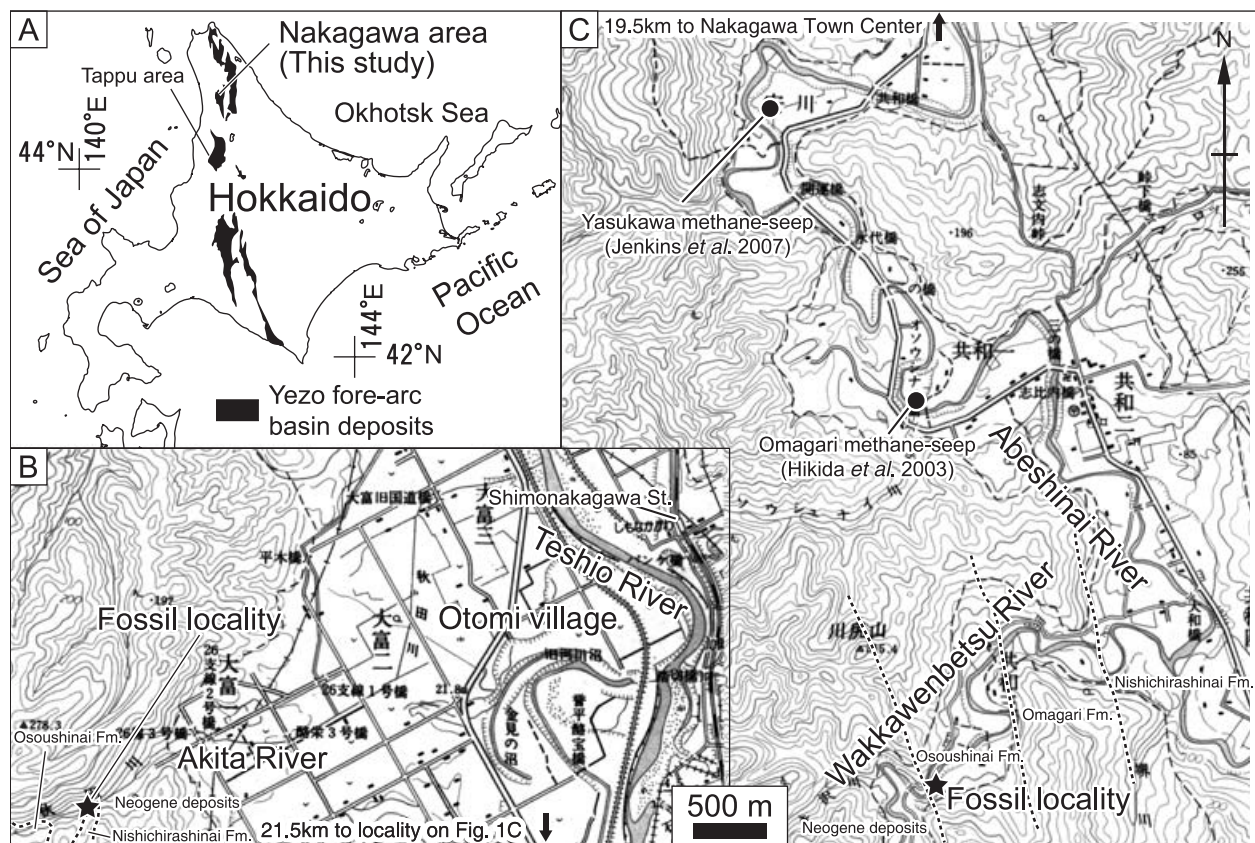


Fig. 1. Locality maps for the wood-falls described herein. □A. Overview of Hokkaido, Japan, with indication of Cretaceous Yezo forearc basin deposits. □B. Locality of the Akita Creek sample near Otomi Village. □C. Locality of the Wakkawenbetsu River sample. Dotted lines show geological divisions as indicated by Hashimoto *et al.* (1967) and Takahashi *et al.* (2007).

a few hundred meters upstream in the bed of the Akita Creek, a tributary of the Teshio River (Fig. 1B). In the sampling area the Late Cretaceous Nishichirashinai and Osoushinai formations of the Yezo Group crop out, as well as Neogene deposits (Fig. 1B). The Nishichirashinai Formation is composed mainly of grey siltstones or sandy siltstones, which are either well bioturbated (mixed silt grains and very fine sand grains) or preserve laminations, and contains ammonoids and inoceramids indicative of a Coniacian age (Takahashi *et al.* 2003, 2007). The sedimentary features of the Akita wood-fall concretion show that it is derived from the Nishichirashinai Formation. The Wakkawebetsu River sample was collected as float on the river bank about 2 km upstream from the confluence of the Wakkawebetsu and Abeshinai Rivers (Fig. 1C). The locality is situated 2.5 km south of the Late Cretaceous 'Omagari methane-seep', which is well known for its excellently preserved seep fauna (Hikida *et al.* 2003; Jenkins *et al.* 2007a). Both the Omagari and the Osoushinai formations crop out along the Wakkawebetsu River. Although our sample was collected as float, the lithology of the concretion, its sampling point, and the presence of the inoceramid *Sphenoceras* sp. indicate that it is derived from the upper part of the Osoushinai Formation, which represents Campanian outer shelf deposits.

Specimens were extracted from the concretions in the laboratory using a rock saw, a hammer, and an air scribe. Samples for scanning electron microscope photography were cleaned using an ultrasound bath, mounted on stubs, coated with gold and photographed using a CamScan Series 4 operating at 20 KV. Some specimens were photographed using a JVC KY-F75U digital camera attached to an optical microscope. Pieces of the wood-bearing concretions were used to make petrographic thin sections (30 μ m thickness). They were viewed with an Olympus BH-2 microscope and photographed using a Leica DFC320 digital camera. All figured specimens are catalogued in the University Museum of the University of Tokyo (UMUT MM 29512-29520).

Akita creek wood-fall

Description

The wood in this concretion is fragmentary and shows several boreholes with diameters of up to 8 mm. The concretion had a size of ca. 20 \times 20 \times 20 cm. The wood is permineralized and partially replaced by pyrite. Cluster or large networks of dendroidal pyrite grow adjacent to the wood but also several centimetres away from the wood fragments. The sediment around

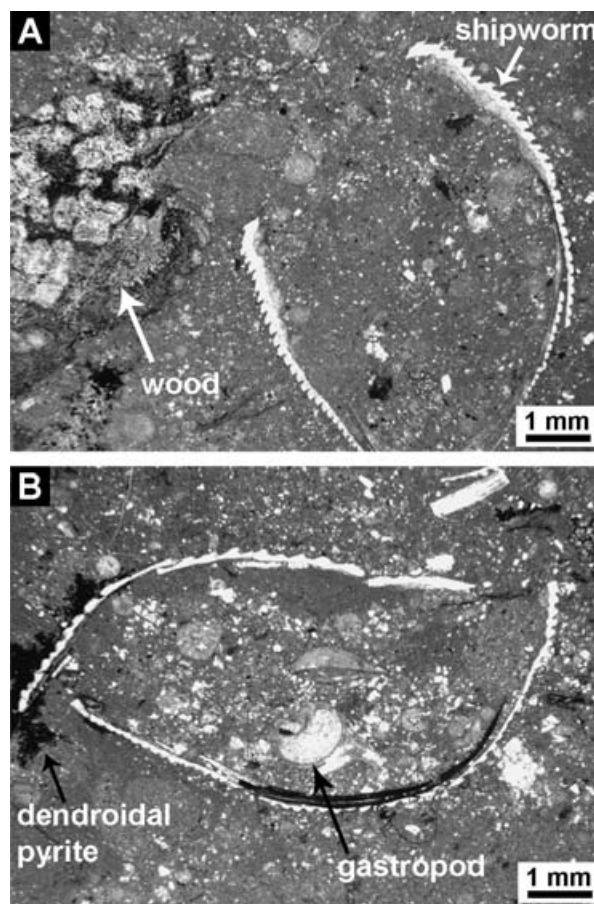


Fig. 2. Mode of occurrence and wood-boring bivalves of the Akita Creek wood-fall site. □A. Overview showing a permineralized and pyritized wood fragment on the left and a terebratulid or xylophagid shell with strong teeth on the right, surrounded by bioturbated detrital sediment. □B. Another terebratulid or xylophagid shell, with globular skeneiform gastropod and other detritus inside, dendroidal pyrite growing on the left side of the shell. To the right of the shell is an inoceramid fragment.

the wood contains abundant calcareous microfossils, and shows signs of moderate bioturbation. Well-preserved and abundant molluscs occur attached to, or less than 10 mm away from, the wood fragments (Fig. 2). Among these, gastropods include two possible provannids, two skeneimorphs, and a limpet. The bivalves include the xylophagid or terebratulid (Fig. 2), a thyasirid and a nuculanid, and there is also an echinoid spine. The limpet, of which we have 16 specimens, has a posterior apex, an oval outline, and shows concentric sculpture only (Fig. 3A–C). The anterior slope is convex; the posterior slope is concave in juveniles, convex in adults, and the species probably reached 10 mm in length. The shell wall in adults is relatively thick (~0.2 mm), and although it is mostly recrystallized, it shows at least two layers of different colour. This indicates patellogastropod affinities, because (i) cocculiniform limpets have very thin

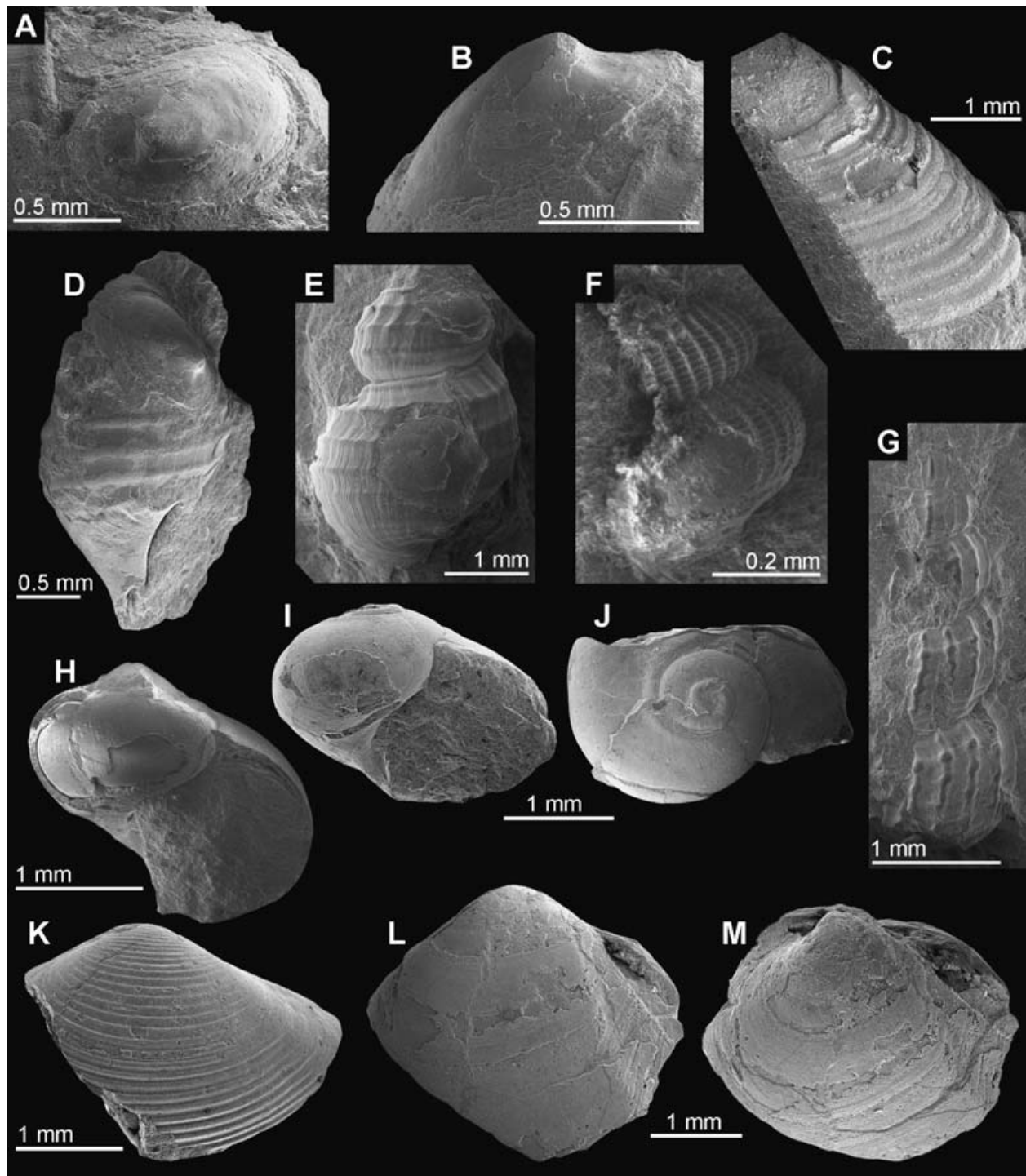


Fig. 3. Fauna of the Akita Creek wood-fall community. □A–C, Limpet. □A, B, Juvenile specimen in apical and ventral view; the specimen is attached to the provannid gastropod on fig. D (UMUT MM 29512). □C, Fragment of an adult specimen showing the commarginal ornamentation (UMUT MM 29513). □D, Provannid gastropod with strongly developed spiral sculpture, limpet of figs. A and B attached to its apical side. □E, Provannid with mainly spiral sculpture (UMUT MM 29514). □F, Isolated provannid larval shell (UMUT MM 29515). □G, Slender provannid with mainly axial sculpture (UMUT MM 29516). □H, Globular skeneiform gastropod (UMUT MM 29517). □I, J, Low-spired skeneiform gastropod; the apical view shows the subsutural ridge characteristic for this species (UMUT MM 29518). □K, Nuculanid bivalve having a smooth surface around the posterior end (UMUT MM 29519). □L, M, Two views on the thyasirid bivalve (UMUT MM 29520).

shells (Kiel 2004, 2006a), and (ii) a very similar style of preservation with distinct coloration can be seen in the patellogastropod *Pectinodonta palaeoxyloidea* from Eocene–Oligocene wood-falls in Washington (Lindberg & Hedegaard 1996; SK, own observation). A species very similar in size, shape and ornamentation has been described as '*Patella* sp.' by Kase & Shigeta (1996, p. 765, figs 2.8, 2.9, 2.12) from the lower Santonian of the upper part of the Yezo Group in the Sakasazawa valley (ca. 70 km south of the Akita Creek site) and might be the same species as the one documented here. The two high-spined gastropods, of which we have four specimens each, are considered here to belong to the provannids or a closely related group because we found a provannid-type larval shell with them (Fig. 3F) and because of their similarities to other provannid gastropods. One of our two species has a high whorl profile, strong opisthocyrt to opisthocline ribs that are nodular where they are crossed by fine spiral ribs (Fig. 3G); the largest specimen is 3.3 mm high. This species is very similar if not identical to a provannid-like gastropod from the Obira (Cenomanian) and Yasukawa (lower Campanian) seep sites on Hokkaido (Jenkins *et al.* 2007b, fig. 5.3; Kaim *et al.* in press, fig. 3K–Q), and from two Late Cretaceous plesiosaur falls on Hokkaido (Kaim *et al.* 2008). The other possible provannid has a lower whorl profile, a subsutural collar and dominantly spiral sculpture (Fig. 3D, E); the largest specimen is 3.3 mm high. It is distinct from the other provannid and provannid-like gastropods described from the Cretaceous seep of Hokkaido (cf. Kaim *et al.* in press), but is quite similar to the Eocene–Oligocene *Provanna antiqua* Squires, 1995 from seeps and wood-falls in Washington (Goedert & Campbell 1995; Squires 1995; Kiel 2006b; Kiel & Goedert 2006b).

Among the about 30 often fragmentary skeneimorph specimens, two species can be distinguished. These include a very low-spined species with thin shell (Fig. 3I, J) and a globular species with a more elevated spire and slightly thicker shell (Fig. 3H). The latter species shows remnants of intersected crossed platy microstructure, which is a common microstructure among small and thin-shelled skeneimorph gastropods (Hedegaard 1997; Kiel 2004). Protoconch morphologies of these two species are unknown, which hampers a more precise taxonomic identification. The low-spined form appears to be more common. Two specimens of a small thyasirid were found. The species seems to have one straight or slightly concave posterior fold at an angle slightly less than 90° to the anterior margin. The posterior fold is narrow, accompanied by a broad posterior sulcus (Fig. 3L, M), and the incomplete specimens are up to 4 mm long. A similarly small thyasirid was illustrated by Tashiro (2004) from the

upper Albian to lower Cenomanian of the middle part of the Yezo Group in Horokanai, northern Hokkaido, but it differs from our species in lacking a submarginal sulcus. In addition, there are four specimens of an oval and weakly rostrate nuculanid (Fig. 3K) that is sculptured by commarginal ribbles, reaches up to 5 mm in length, and has some low concentric ribs that obliquely cut the ventral margin, similar to *Mesosaccella insignis* from the Albian Miyako Group in north-eastern Honshu (Nagao 1934). Moreover, the smooth surface of the posterior end of these specimens is also recognized in '*Nuculana*' *posterolaevia* from Eocene to Oligocene seeps, whale and wood-falls in Washington (Kiel & Goedert 2007).

Palaeoecological interpretation

The close proximity of the wood-dependent gastropods to the wood fragments indicates that the Akita Creek wood-fall assemblage represents a wood-fall community that was preserved *in situ*. In its faunal composition it is surprisingly similar to its modern and Cenozoic counterparts, at least in respect to fossilizable, shell-bearing taxa. Five of the species, the limpet, the two provannids and the two skeneiform gastropods most likely grazed on xylophagous microbes, like their modern analogues (Marshall 1985, 1988; Warén & Bouchet 2001). In total abundance, these five species comprise ca. 90% of the entire fauna. In addition, the thyasirid might have utilized sulphides resulting from the presence of the wood, either by the decaying wood itself, by the decaying metabolic by-products of wood-boring bivalves or because the wood blocks the sediment's access to oxygen in the overlying water, making the sediment anoxic. These mechanisms were assumed as sulphide-source of thyasirids at Eocene and Oligocene wood-falls (Kiel & Goedert 2006a, b). Certain extant thyasirids having the size of those reported here are asymbiotic (Dufour 2005). However, our species also occurs at several Cretaceous seep sites on Hokkaido (unpublished data), thus we consider it unlikely that the Akita wood-fall thyasirid was asymbiotic. The nuculanid probably was a general deep-sea dweller and bears no ecological implications for the Akita Creek wood-fall community.

Wakkawenbetsu river faecal chimneys

Description

This wood piece is extensively bored and surrounded by abundant inoceramid shells (Fig. 4A), including

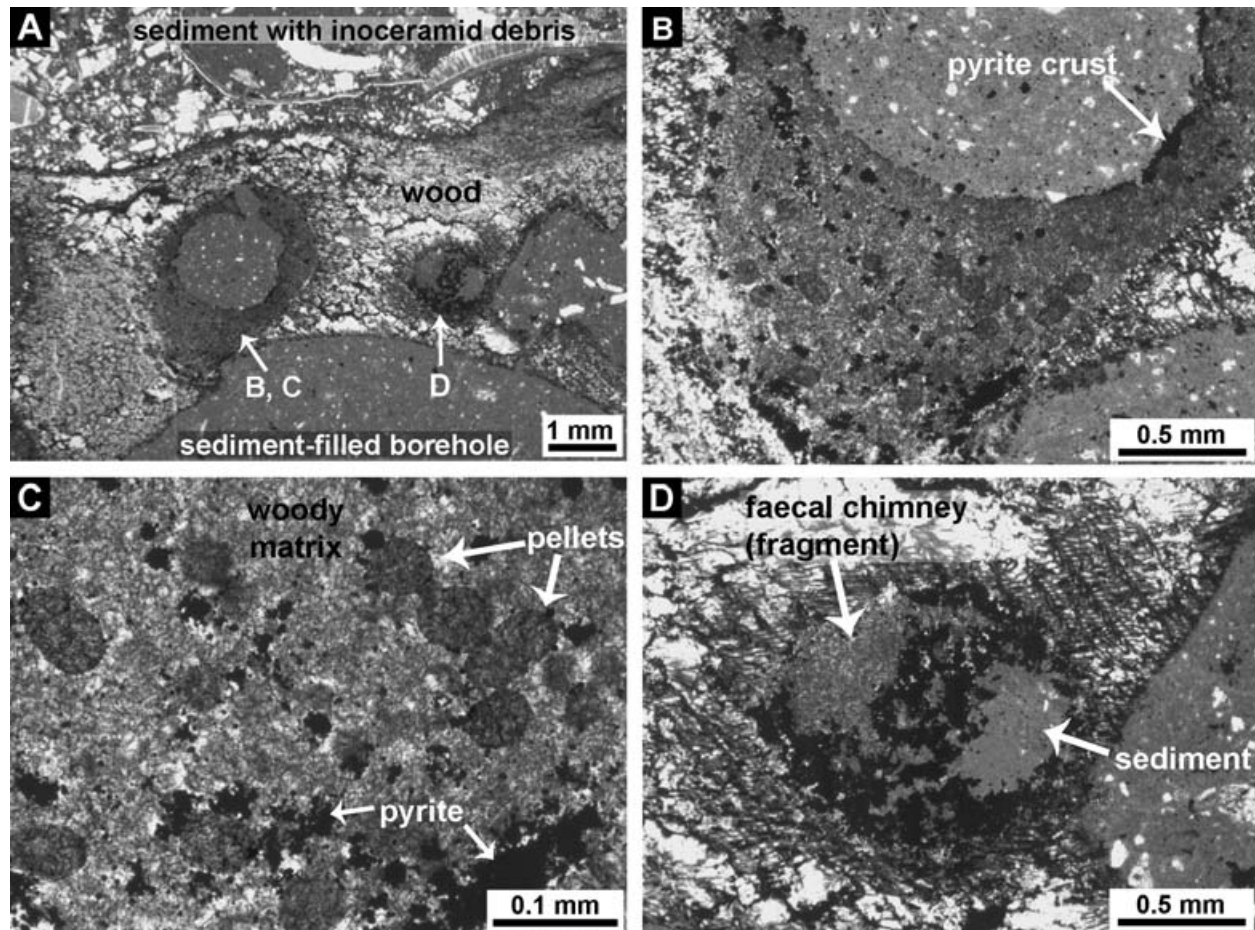


Fig. 4. Late Cretaceous wood from the Wakkawenbetsu River with faecal chimneys in xylophagous boreholes. □A. Overview showing an extensively bored wood section; two boreholes with faecal chimneys in the centre of the image; surrounding matrix in the upper part of the image shows abundant inoceramid fragments. □B. Close up on the left borehole in fig. A, with faecal chimney showing mushy wood and woody faecal pellets composing the faecal chimney, and the very thin layer of wood between the borehole with faecal chimney and the large borehole below. □C. Close up showing the elongate-spherical shape of the faecal pellets, and the pyrite clusters. □D. Close up on the right borehole, here the fragment of the faecal chimney shows no distinct faecal pellets.

intact specimens of *Sphenoceramus* sp. In addition, there is a well-preserved thyasirid, and a large fragment of an arcoid with *Parallelodon*-like hinge dentition. The concretion had a size of ca. $20 \times 20 \times 10$ cm. The matrix of the concretion contains few small pyrite clumps but lacks the large dendroidal pyrite clusters or networks seen in the Akita Creek wood-fall. Only a few boreholes show dendroidal pyrite clusters (Fig. 4D); most boreholes have a diameter of around 8 mm and are filled by detrital sediment only. Two small (< 3 mm) boreholes show linings resembling xylophagous faecal chimneys seen in cross-section (Purchon 1941). The larger of the two boreholes is 2.8 mm wide and 2 mm high, and is almost completely encrusted by a faecal chimney. The sediment-filled interior of this chimney is almost circular with a diameter of 1.5 mm (Fig. 4A). The wall of the faecal chimney consists of a matrix of light brown mushy wood and randomly distributed

oval pellets (Fig. 4B). These pellets have a maximum dimension of 0.8×0.5 mm, a very sharply delimited outer margin, and consist of mushy wood but have a darker colour than the surrounding matrix, suggesting that they have a higher density (Fig. 4C). The inner margin of the faecal chimney is partially lined with a thin crust of pyrite, and clusters of pyrite framboids occur within the matrix of the faecal chimney. The smaller borehole is almost circular, has a diameter of 1.1 mm and shows a pellet-free fragment of a faecal chimney (Fig. 4A, D). Most of the borehole is filled with pyrite clusters with irregular margins (Fig. 4D). No shells of wood-boring bivalves were seen in either of these two boreholes.

Palaeoecological interpretation

The abundant and randomly oriented inoceramid fragments in the matrix of the Wakkawenbetsu

concretion suggest that the wood and the shells were transported along the seafloor to their final place of deposition and that this assemblage does not represent an *in situ* wood-fall site like the Akita Creek community. Inoceramid fragments are the most common fossil in these sediments and most likely were washed together with the wood fragments during transport.

Faecal chimneys like those described here are today build exclusively by certain members of the pholadid subfamily *Xylophaginae* (Purchon 1941; Turner 1955; Voight 2007). In contrast to the teredinids, which attack wood that is floating on the ocean's surface, xylophagains attack wood only once it is deposited on the seafloor, largely in deep water (Turner 1955, 1966, 1973). Applying uniformitarianism, the faecal chimneys documented here show that this piece of wood was colonized by xylophagains on the seafloor.

The other boreholes in the Wakkawebetsu wood that lack faecal chimneys and calcitic linings are less conclusive. They could lack faecal chimneys because (i) they were bored by xylophagains that do not build such chimneys, like certain modern species of *Xylophaga* or *Xylopholas* (cf. Voight 2007), or the Late Cretaceous *Xylophagella* (cf. Turner 1969, p. 722); (ii) they were bored by a *Xyloredo*-like xylophagain which starts to build calcitic linings very late during its ontogeny (cf. Turner 1972) and had not yet reached the lining-building age, although this possibility is unlikely because even the boreholes with the largest diameters (and thus presumably with mature specimens) lack linings; or (iii) the linings or chimneys in these boreholes were lost when the wood was transported along the seafloor. Thus, the organism that bored the boreholes that lack faecal chimneys and calcitic linings remains elusive.

Discussion

Origin of the modern wood-fall fauna

Wood evolved in the Palaeozoic and must have been washed into the sea and sunken to the seafloor ever since. But when animals started to take advantage of this source of food remains elusive. Many of the molluscan genera that inhabit wood falls today can be traced back into the fossil record only into Late Eocene time (Kiel & Goedert 2006b). Based on the notion that many of the modern members of wood-fall communities, including limpets, provannid and skeneiform gastropods, and neogastropods were already present in the Late Cretaceous, Kiel & Goedert (2006b) predicted that the modern wood-fall ecosystem evolved during this time. This prediction seems to be

supported by the Akita Creek wood-fall community, which includes several of these taxa. Turner (1978) considered *Xylophaga* as the key taxon in many modern wood-falls, because these animals transform the energy stored in the wood into nutrients that are digestible for other animals, either in form of faecal pellets for detritus-feeder or as flesh or carrion for predator and scavenger. The faecal chimneys reported here were most probably produced by species of *Xylophaga*, hence the presence of this keystone taxon further supports a Late Cretaceous origin of the modern wood-fall ecosystem. In contrast, the two Middle Jurassic (Bathonian) wood-fall communities reported from southern Poland (see Kaim 2006, in press) are dominated by triphoroidean, maturifusid, and calliotropid gastropods, which are unknown from modern wood-falls.

Relation to the chemotrophic deep-sea fauna

Ongoing work on modern examples of vent, seep and whale-fall faunas and the discoveries of new types of reducing habitats over the last 30 years have shown that many taxa that were initially considered endemic to one particular reducing environment in fact colonize many of them. For example, neomphalid gastropods were considered endemic to hydrothermal vents until *Retiskenea* was found at cold seeps and the wood-inhabiting *Leptogyra* was identified as neomphalid (Warén & Bouchet 2001; Kiel & Goedert 2006b); the bathymodiolin mussel *Idas* was long known from wood and bones in the deep sea (Dell 1987) and has recently been found at cold seeps in the Mediterranean (Olu *et al.* 2004); and the cocculiniform limpet *Pyropelta* was initially described from hydrothermal vents (McLean & Haszprunar 1987) and most species of this genus are today known to colonize vents, seeps, whale and wood-falls (Warén & Bouchet 2001). A similar overlap in faunal composition of wood, whale bone and seep communities has been documented for the fossil-rich and well-studied Eocene to Oligocene deep-water sediments in western Washington State, USA (Goedert & Squires 1990; Goedert & Campbell 1995; Goedert *et al.* 1995; Kiel & Goedert 2006a, b; and references therein), as well as for the Miocene deep-water deposits in Hokkaido and Honshu (Amano & Little 2005; Majima *et al.* 2005; Amano *et al.* 2007). The deep-water sediments of the Yezo Group on Hokkaido, northern Japan, provide insights into a similar variety of habitats of Late Cretaceous age. The Akita Creek wood-fall community shows a considerable overlap in its faunal composition with other reducing environments in the Yezo Group: provannid and skeneiform gastropods similar, if not identical, to those described here occur

at two Turonian and Coniacian plesiosaur skeletons (Kaim *et al.* 2008), and these taxa have also been reported from Cenomanian to Campanian methane seeps nearby (Hikida *et al.* 2003; Jenkins *et al.* 2007b). At the same seep sites thyasirid bivalves identical to those from the Akita Creek and Wakkawebetsu River sites occur (own unpublished data). In addition, the slender provannid reported here is quite similar to the 'cerithioid gastropods A and B' described by Little *et al.* (1999) from a vent community in the Late Cretaceous (Turonian) Troodos ophiolite on Cyprus.

In sum, comparing the Akita wood-fall community to fossil and Recent examples of wood, bone, seep and vent communities shows that many members of the modern chemotrophic deep-sea fauna colonize this range of habitats at least since Late Cretaceous time. Richness estimates on the diverse whale- and wood-fall communities in Washington State have shown that around 20 sites are necessary to get a reliable picture of the regional pool of species that is able to colonize these environments (Kiel & Goedert 2006a). Thus, we expect that continued sampling in the Yezo Group will substantially increase the range of taxa that colonized Late Cretaceous wood-falls, and will further increase the similarities between these communities and other sulphide- and microbe-rich habitats.

Kase & Shigeta (1996) reported large numbers of patellogastropod limpets from calcareous concretions in Late Cretaceous deep-water sediments of the Yezo Group. As patellogastropod limpets usually live on hard substrates, their presence in muddy deep-water sediments needed explanation. Based on the presence of limpet home scars on ammonite shells found in these sediments, Kase *et al.* (1994) and Kase & Shigeta (1996) suggested that the limpets were once attached to drifting ammonite shells and fell to the seafloor when their host shells became waterlogged. Although Kase & Shigeta (1996) did not report that wood was associated with the limpets in these concretions, they neither reported ammonite shells with them, and we find it plausible that also these limpets lived on woody substrates, like the limpet reported here.

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