

# The Prolific Afterlife

On the deep seafloor, the carcasses of the largest mammals give



## KEY CONCEPTS

- A single dead whale can nourish a specialized ecosystem that lasts for decades.
- Some signs suggest that whale-fall ecosystems have exchanges with other deep-seafloor communities, such as hydrothermal vents.
- Species similar to those at whale falls may have depended on dead marine reptiles for hundreds of millions of years.

—The Editors

On a routine expedition in 1987, oceanographers in the submersible *Alvin* were mapping the typically barren, nutrient-poor seafloor in the Santa Catalina Basin, off the shore of southern California. On the final dive of the trip, the scanning sonar detected a large object on the seafloor. Piercing through the abyssal darkness down at 1,240 meters, *Alvin*'s headlights revealed a 20-meter-long whale skeleton partly buried in sediment. On reviewing the dive videotapes, expedition leader Craig Smith and his team saw that the skeleton was probably either a blue or a fin whale. The creature appeared to have been dead for years, but the bones and their surroundings teemed with life—wriggling worms, centimeter-size clams, little snails and limpets, and patches of white microbial mats. The skeleton was a thriving oasis in a vast, desertlike expanse.

Almost a year later Smith, an oceanographer at the University of Hawaii at Manoa, returned for a proper study of the skeleton site. His team described several species previously unknown to science, plus some that had been observed only in unusual environments, such as at deep-sea hydrothermal vents.

Since then, investigators have documented dozens of communities that are supported by sunken whale carcasses and have described more than 400 species that are living in and around them, of which at least 30 have not been seen anywhere else. The research has begun to sketch out a picture of how these surprising whale-fall

communities work and how they have evolved.

The first hint that dead whales could host specialized animal communities came as early as 1854, when a zoologist described a new species of centimeter-size mussel extracted from burrows in floating whale blubber collected off the Cape of Good Hope in South Africa. When industrial deep-sea trawling began in the 20th century, researchers learned that such dependence on dead whales was not a freak occurrence. From the 1960s onward an increasing number of whale skulls and other bones with attached specimens of new mollusk species were recovered from nets around Scotland, Ireland, Iceland and particularly the Chatham Rise to the east of New Zealand. One bone specimen trawled off the South African coast in 1964 was covered with the same small mussel first seen in 1854 in roughly the same area.

Mussels were not the only new animals found in recovered whale bones: a tiny, previously unknown species of limpet—limpets are snail-like mollusks with conical rather than spiral shells—was described in 1985, soon followed by others. The limpets were named *Osteopelta* because of their association with bones.

But not until Smith's fortuitous discovery in 1987 did the full extent of the ecological novelty of sunken dead whales become clear. The mollusk species his team found were especially interesting. The clams and mussels belonged to groups known to harbor chemosynthetic bacteria. Such bacteria can draw energy from inorganic chemi-

DOUG ALVES



# of Whales

life to unique ecosystems • By Crispin T. S. Little

cal, and they sometimes form the basis of entire ecosystems. (The earliest organisms, before life “invented” photosynthesis and introduced oxygen into the biosphere, were chemosynthetic, although they had a different metabolism from that of modern chemosynthetic organisms.) Most of the mollusks were known only from other chemosynthesis-based sites: the mussels from sunken wood and hydrothermal vents; vesicomid clams from vents and cold seeps, where fluids rich in methane and other hydrocarbons leak onto the seafloor; lucinid clams from seeps and anoxic sediments (seafloor sediments lacking oxygen); and a snail from anoxic sediments.

The similarities led Smith and his co-workers to suggest in 1989 that whale skeletons might act as “stepping-stones” for deep-sea animals to spread from one chemosynthetic community to another. Whether creatures can move between communities from one generation to the next or whether species spread on much longer timescales is a question that is still open to this day.

## The Making of an Ecosystem

To understand the workings and duration of whale-fall communities, Smith and his colleagues set up a logistically tricky—and somewhat smelly—project in 1992.



They began to take whales that had washed up on the Californian coast and tow them out sea and then sink them in deep waters with up to 2,700 kilograms of steel ballast to counteract the buoyancy of decomposition gases. (Most whales are negatively buoyant when they die and thus sink rather than get beached.) Next they visited the sunken carcasses at regular intervals using *Alvin* or remotely operated vehicles (ROVs). The researchers sank three gray whales over a period of six years and visited these regularly up until 2000. They also revisited the original skeleton found in 1987 and another discovered in 1995.

Whale falls, they observed, go through three partially overlapping ecological stages. The first, which they called the mobile scavenger stage, starts when the whale carcass arrives on the seafloor. Hordes of hagfish tunnel through the meat, while a few sleeper sharks take larger bites. These scavengers strip away the bulk of the whale soft tissue—blubber, muscle and internal organs—and together consume 40 to 60 kilograms

**[THE AUTHOR]**



**Crispin T. S. Little** is a senior lecturer in paleontology at the University of Leeds in England. He has been working for the past 14 years on the macroevolutionary history of animal communities found at hydrothermal vents, hydrocarbon seeps and whale falls. On a recent oceanographic cruise he achieved a long-standing personal goal of diving in the *Alvin* submersible to active vents 2.5 kilometers deep on the Pacific seafloor.

a day (the weight of a small person). Even so, the feast can last up to two years, depending on the size of the whale.

The second stage, called the enrichment opportunist stage, lasts up to two years. During this period high-density, though low-diversity, communities of animals colonize the sediments surrounding the whale carcasses and the newly exposed bones. The animals feed directly on the large amounts of blubber and other scraps of nutritious soft tissue left over by the scavengers. This stage is dominated by polychaetes (bristle worms) and crustaceans.

Finally, once the soft tissue is gone, the whale falls enter the third, and longest, phase, known as the sulfophilic stage. Specialized bacteria anaerobically break down lipids contained in the bones. Unlike aerobic bacteria, which would use the molecular oxygen (O<sub>2</sub>) dissolved in seawater to digest nutrients, these microorganisms use dissolved sulfate (SO<sub>4</sub>) as their source of oxygen and release hydrogen sulfide (H<sub>2</sub>S) as waste. Animals cannot use this gas directly as a source of

COURTESY OF CRISPIN T. S. LITTLE (Little); JEN CHRISTIANSEN (whale-fall illustration); CATHERINE WILSON (species inset illustrations)

**[STAGES OF A WHALE-FALL COMMUNITY]**

# A GIFT THAT KEEPS ON GIVING

A dead whale that sinks to the seafloor brings a sudden bonanza of food to the dark, desertlike expanse. The community of organisms that springs up undergoes three ecological stages. Each stage is characterized by different species and different food webs—although at many such sites, the stages can overlap.

## SCAVENGER STAGE

Hagfish—primordial relatives of vertebrates that are virtually blind and live on the muddy seafloor—eat much of the blubber and muscle tissue, helped by other scavengers, including sleeper sharks and some crabs.

DURATION: UP TO 2 YEARS

## OPPORTUNIST STAGE

Animals feed on leftover scraps of meat and blubber and on whale oil that has soaked the surrounding sediment. This second wave of scavengers includes snails, bristle worms and hooded shrimp. Meanwhile “zombie worms” [see illustration on page 84] begin to spread their roots into the bones and feed on their lipid content.

DURATION: UP TO 2 YEARS



energy, and in fact the gas is typically poisonous to them. But certain chemosynthetic bacteria can. They take  $O_2$  from the seawater to oxidize the sulfide, generating energy for growth. Animals can then either exploit such bacteria symbiotically (as do mussels and vesicomid and lucinid clams) or feed on them by grazing bacterial mats (as do limpets and snails). For reasons that are not yet well understood, whale bones are extremely rich in lipids—a 40-ton whale carcass may contain 2,000 to 3,000 kilograms—and their decomposition is a slow process. As a consequence, for a large whale the sulfophilic stage can last up to 50 years, even perhaps a century.

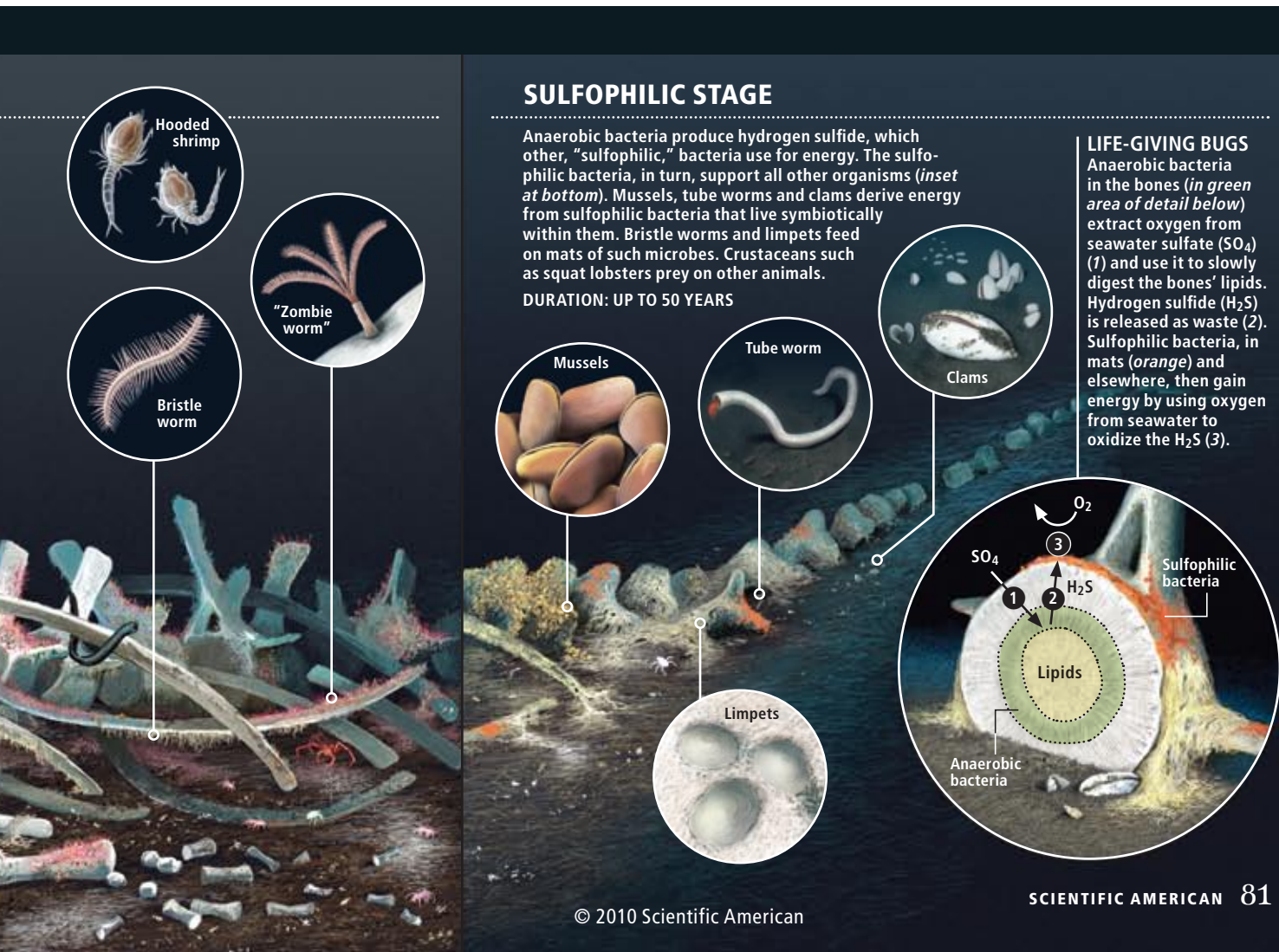
Using these data—together with their estimate that around 69,000 great whales die every year—Smith and his co-workers guessed that there might be 690,000 skeletons of the nine largest whale species rotting in the world's oceans at any one time. (Of course, before industrial whaling caused a dramatic crash in large-whale populations during the past two centuries, considerably more whale falls would have been ac-

tive, perhaps as many as six times more.) The average distance from one whale to the next would then be just 12 kilometers; along the migration route of gray whales, the average distance may be as short as five kilometers. Such spacing may be close enough for larvae to disperse from one site to another, which the team saw as further support for their stepping-stone model for the dispersal of chemosynthetic organisms between whale falls, hydrothermal vents and cold seeps.

### Night Creatures Calling

Ever since Smith and his colleagues set up their whale-fall experiment, sinking large dead whales has proved quite popular; three other groups, based in Sweden, Japan and Monterey, Calif., have been conducting similar experiments. Other whale skeletons have been found by chance in various deep-water sites, for example, at the Torishima Seamount south of Japan and in Monterey Bay. The newer studies have confirmed that a consistent group of organisms depends on whale falls throughout the world's oceans. But the stag-

**There may be 690,000 skeletons of the nine largest whale species rotting in the world's oceans at any one time.**



### SULFOPHILIC STAGE

Anaerobic bacteria produce hydrogen sulfide, which other, "sulfophilic," bacteria use for energy. The sulfophilic bacteria, in turn, support all other organisms (*inset at bottom*). Mussels, tube worms and clams derive energy from sulfophilic bacteria that live symbiotically within them. Bristle worms and limpets feed on mats of such microbes. Crustaceans such as squat lobsters prey on other animals.

DURATION: UP TO 50 YEARS

### LIFE-GIVING BUGS

Anaerobic bacteria in the bones (*in green area of detail below*) extract oxygen from seawater sulfate ( $SO_4$ ) (1) and use it to slowly digest the bones' lipids. Hydrogen sulfide ( $H_2S$ ) is released as waste (2). Sulfophilic bacteria, in mats (*orange*) and elsewhere, then gain energy by using oxygen from seawater to oxidize the  $H_2S$  (3).

## FOSSIL RELATIVES

Various fossil whales show signs of having sustained communities similar to those of modern whale falls—including many of the invertebrates that depend on symbiotic sulfide-oxidizing bacteria. One specimen from Middle Miocene (about 12 million years ago) rocks on Hokkaido Island, Japan, was surrounded by several shells of mollusks, including snails of the genus *Provanna* (spiral shells below, both about half a centimeter tall), a vesicomyid clam (*Adulomya chitanii*, 4 cm) and a mussel (*Adipicola*, 2 cm). These fossils help researchers understand the origin of whale-fall communities.



es seen in the Santa Catalina skeletons are not as apparent elsewhere.

One reason for the discrepancy may be that the experimental sites selected by the Smith team are relatively oxygen-poor, leading to reduced decomposition rates. Another reason might be the activities of the extraordinary worm *Osedax* (Latin for “bone devourer”), also known as the zombie worm. This small animal—one centimeter or less in length—was first described in 2004 from a Monterey Bay whale and later found at the experimental sites in Sweden and Japan. Still later, researchers found the worm at the southern Californian whale falls as well—where at first it had been overlooked—but in smaller numbers.

*Osedax* has little appendages that stick out into the water column for gas exchange but can be retracted into a mucous tube if disturbed. The animal then looks like a blob of mucus adhering to the bone surface. Just like certain intestinal parasites, *Osedax* has no digestive tract at all as an adult—no mouth, stomach or anus. But uniquely, it uses green, fleshy “roots” to tunnel into exposed whale bones, presumably to obtain lipids or proteins, or both, for symbiotic bacteria contained within its roots. (The worm’s reproductive strategy is also unusual. All adults are female, but each carries in its body dozens of tiny males that never pass the larval stage—and whose only role, it seems, is to produce sperm.)

*Osedax* is closely related to the giant tube worms that live at many vent and seep communities. Genetic evidence suggests that it is around 40 million years old, about the same age as vesicomyid clams and whales.

The tunneling activity of *Osedax* rapidly destroys the exposed whale bones, which likely speeds up the sulfophilic stage for an infested

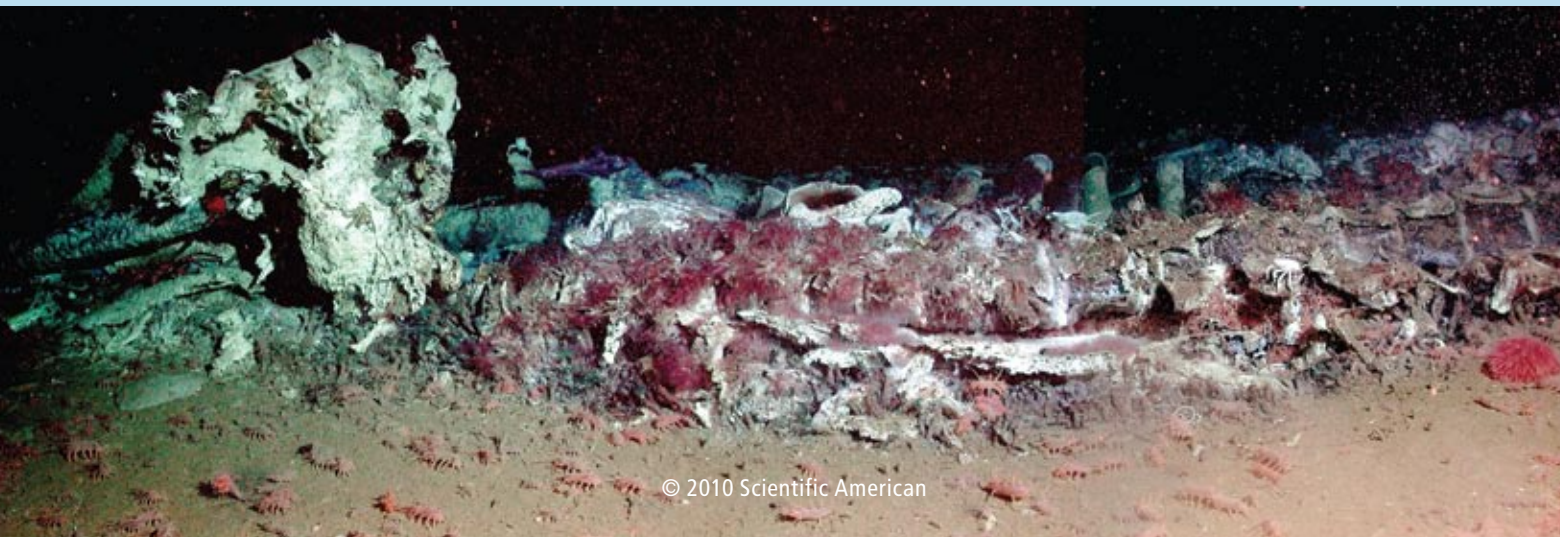
skeleton, thus affecting its entire habitat. The finding could mean that many whale falls are active on the seafloor for less time than was originally thought. This time reduction poses a challenge to the stepping-stone hypothesis, because fewer active whale falls should make it more difficult for animals (or their larvae) to get from one chemosynthetic site to another.

## Bones of Contention

Whereas vents and cold seeps have been around since the early earth—and vents in particular may be where life got started in the first place—the appearance of whales is, of course, relatively recent. A natural question is when and how have ecosystems evolved that seem to depend on whale carcasses for their existence, which in turn should help clarify their connection to other deep-sea communities. The obvious place to look is in the fossil record.

Although many fossil whales have been found over the past 150 years, it was only in 1992 that the first ancient whale-fall communities were recognized, in Washington State rocks from the Oligocene (34 million to 23 million years ago). Intense interest in these bizarre communities has since turned up more examples. Among them are some fossils from the Miocene (23 million to five million years ago) found in California and in three sites in Japan—including two that I have worked on with my colleague Kazutaka Amano of the Joetsu University of Education. All these ancient whale-fall communities are recognized as such by the presence of mollusk fossils belonging to groups that host chemosynthetic bacteria or graze on microbial mats at chemosynthetic sites. As might be expected, the fossil record of whale-fall assemblages contains no remains of

LYING 2,891 METERS DEEP in Monterey Bay, Calif., this 10-meter-long gray whale provides nourishment for a thriving community, including scavenging sea cucumbers (*Scotoplanes globosa*, crawling on foreground) and bone-eating worms (*Osedax rubiplumus*, on bones). The three shots that make up this montage were taken in 2002; some of the bones seen here have since completely decomposed.



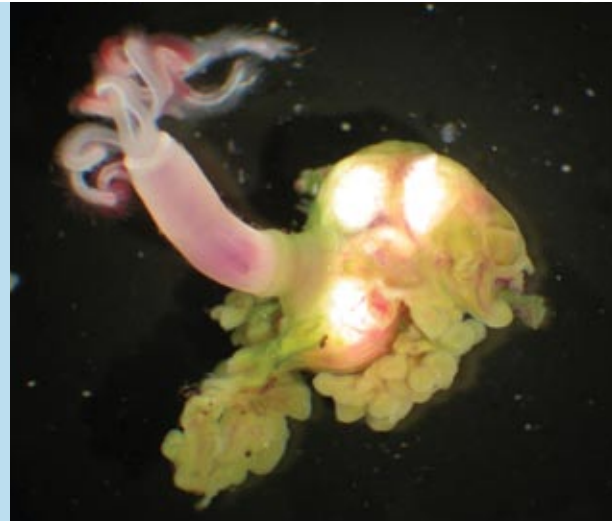
soft-bodied animals such as worms, because soft body parts decay readily. So no one knows yet whether worms such as *Osedax* lived there.

In 2006 Steffen Kiel, then at the University of Leeds in England, and Jim Goedert of Seattle's Burke Museum of Natural History and Culture pointed out that the earliest whale-fall communities from the late Eocene and the Oligocene were dominated by clams that also occur in nonchemosynthetic habitats; the chemosynthetic mollusks that characterize modern whale falls in the sulfophilic stage do not show up until the Miocene fossils. The researchers concluded that the early whales were not yet large enough to host sulfophilic communities. Recently, however, a small Miocene whale skeleton was found in cliffs on a Californian island that had associated vesicomid clams. This discovery suggests that it is not so much a whale's size that matters to the chemosynthetic mollusks. Instead the relative lipid content in whale bones probably increased over the past 20 million years or so, perhaps because it enhanced survival as whales moved into open-ocean environments.

In fact, ever since the discovery of whale-fall communities, researchers have suspected that similar communities may have existed even earlier than the first whales, in the sunken carcasses of ancient marine reptiles, among them plesiosaurs, ichthyosaurs and mosasaurs. These reptiles were among the dominant predators of the Mesozoic oceans. (The Mesozoic, the geologic era that stretches from 251 million to 65 million years ago, comprises the Triassic, the Jurassic and the Cretaceous and thus the entire time when the dinosaurs ruled on land.) This idea received a strong boost in 1994 with the description of a single fossil specimen of the limpet *Osteopelta* from a turtle bone in Eocene sediments from New Zealand. Although the Eocene is more recent than the Mesozoic, the discovery demonstrated that whale-fall limpets were also able to live on reptile bones and thus perhaps on the extinct Mesozoic marine reptiles as well.

Then, in 2008, a research group from Japan and Poland reported the discovery of bones of two plesiosaur skeletons originally around 10 meters long with associated provannid snail specimens from upper Cretaceous rocks in Japan. Because provannids are only known from chemosynthetic sites, the scientists suggested that the sunken plesiosaurs were able to support a community comparable to the sulfophilic stage of modern whale falls. But these reptiles went extinct 65 million years ago along with the di-

**ZOMBIE WORMS, also known as *Osedax* (Latin for "bone devourer"), grow "roots" in dead whale bones, which they slowly consume. The worms seem to live exclusively at whale falls. This *Osedax frankpressi* has been removed from a whale bone to show its root system (green) and ovaries (white); typically only the one-centimeter-long body (pink) and its plumes would be visible. At least five different species of *Osedax* have been discovered so far.**



nosaurus. That is more than 20 million years before whales evolved, suggesting that there may have been a repeated evolution of specialized communities of animals dependent on large vertebrate carcasses sinking to the seafloor.

The Japanese and Polish group showed convincingly that the plesiosaur bones looked internally very like modern whale bones, with lots of marrow space that would have contained lipids in life. Whether the bones were in fact rich in lipids will not be easy to determine, however. On the other hand, it seems that many groups of animals present in whale-fall sulfophilic communities were already present in seep, wood-fall and probably vent communities and that they avidly exploited the newly evolved chemosynthetic habitat when whales evolved.

The fossil record of whale falls remains rather scant, with data coming almost exclusively from Japan and the Western coast of the U.S. Fossil evidence of *Osedax* could be especially helpful, given the organism's unique ability to shape the modern communities. Although the lack of a skeleton makes it unlikely that direct evidence of the worm will be found, the borings it makes in whale bones may be recorded in fossils, and many investigative groups are actively searching for them.

The global distribution of modern whale-fall communities is also still poorly characterized. So far only a few whale carcasses have been found, and we know nothing about several areas that have large whale populations, such as Antarctica and the Southern Ocean. More finds, both active and fossil, will be necessary to reveal whether the ecology and evolutionary history of whale falls are truly linked to those of reptile falls and how both types of ecosystems relate to the other deep-sea chemosynthetic communities. ■

## **MORE TO EXPLORE**

**The Mammals That Conquered the Seas.** Kate Wong in *Scientific American*, Vol. 286, No. 5, pages 70–79; May 2002.

**Ecology of Whale Falls at the Deep-Sea Floor.** Craig R. Smith and Amy R. Baco in *Oceanography and Marine Biology: An Annual Review*, Vol. 41, pages 311–354; 2003.

**Expanding the Limits of Life.** Alexander S. Bradley in *Scientific American*, Vol. 301, No. 6, pages 62–67; December 2009.