

Chapter 12

Ammonites as Inhabitants of Ancient Hydrocarbon Seeps



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12.1 Introduction

Ammonites are present in fossil methane seep deposits but are not ubiquitous. They occur in deposits that span the Devonian to Cretaceous. New evidence at several of these sites reveals that the ammonites probably lived at these seeps all their lives and did not float in after death. Because of their post-hatching planktonic phase, ammonites were able to disperse widely and were probably attracted to seeps because of the availability of food, becoming an integral part of the seep ecosystem. Thus, the study of the species composition and distribution of ammonites at seeps provides new insights into the mode of life of these animals.

The presence of ammonites at seep deposits also provides insights into the nature of the seeps as well. Like modern nautilus, ammonites were constrained by depth limitations (Westermann 1996). Thus, the depth of the methane seeps where

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ammonites lived could not have exceeded the depth limits of the ammonites themselves. In addition, the physical and chemical properties at the sites could not have exceeded the tolerance limits of ammonites with respect to temperature, salinity, and concentrations of hydrogen sulfide and oxygen.

12.2 Ammonite Paleobiology

Ammonites belong to the class Cephalopoda, one of the main classes of the Mollusca. They are closely related to squids, cuttlefish, and octopus. Studies of comparative morphology reveal that they are phylogenetically more closely related to the Coleoidea than to the Nautiloidea (Jacobs and Landman 1993). Nevertheless, because ammonites retain an external shell, many aspects of their growth and mode of life can be investigated in analogy with modern nautilus.

Ammonites were exclusively marine and lived in the water column. Depending on the species and ontogenetic stage, they may have lived near the bottom (demersal or nektobenthic) or higher up in the water column. Although the exact temperature and salinity requirements of ammonites are unknown, modern cephalopods cannot tolerate salinities below approximately 20 psu nor temperatures above 35 °C (Vidal et al. 2016). Most coleoids prefer fully oxygenated water, and this is consistent with facies and faunal associations for many ammonites. However, studies of modern nautilus indicate that it is tolerant of low-oxygen conditions (Wells and Wells 1985).

The external shell of both nautilus and ammonites is divided into two parts, the body chamber that contained the soft fleshy parts of the animal and the phragmocone, which is subdivided into a series of buoyancy chambers (Fig. 12.1a, b). The

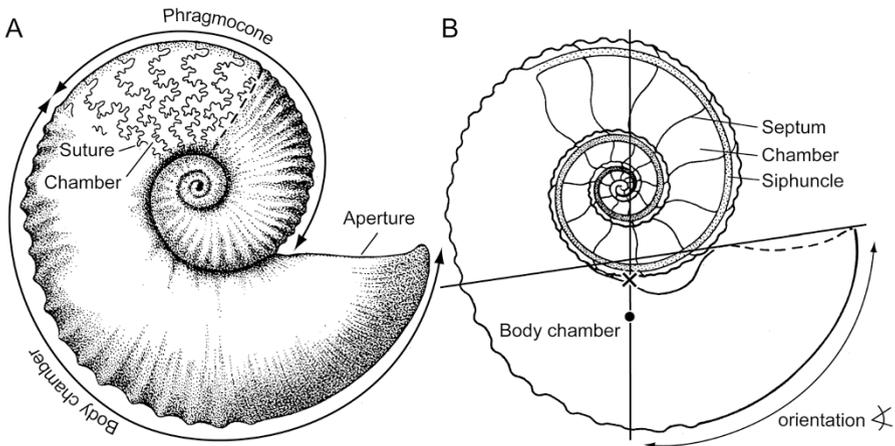


Fig. 12.1 Morphologic terms applied to ammonites, showing the external (a) and internal parts of the shell (b). The ammonite is oriented in its life position based on the centers of mass (•) and buoyancy (x)

chambers are separated by partitions called septa. The contact where the septum meets the inside surface of the outer shell wall is known as the suture.

During life, the shell functioned as a buoyancy apparatus that permitted the animal to maintain near neutral buoyancy as it grew. The mode of growth in nautilus has been well documented by Ward (1987). If we assume that ammonites followed the same mode of growth, a new chamber was secreted at the back of the body chamber as the animal grew at the aperture. The newly created chamber was initially filled with liquid, but as the animal grew larger, the liquid was removed through a thin tube called the siphuncle and replaced by a combination of gasses. The gasses in the newly formed chamber compensated for the additional weight of the soft tissue and shell as the animal grew. As a result, the animal would have maintained near neutral buoyancy in the water column, allowing it to swim and maneuver nearly weightlessly in the water column.

In nautilus, after the liquid is removed from the most recently formed chamber, the gas in the chamber attains a maximum pressure of 1 atm. Thus, the shell of nautilus, and by inference ammonites, is a pressure vessel that must withstand the compressive forces of the surrounding water. Nautilus is limited to a depth of 700 m, beyond which the shell implodes (Saunders and Ward 1987). Studies of the shape of the nautilus shell and septa, as well as the size and structure of the siphuncle, have yielded theoretical estimates in agreement with actual values (Hewitt and Westermann 1987). Similar studies on ammonites have also yielded depth estimates of the depth at which these animals probably lived (Hewitt 1996: Table 2), which are consistent with inferences based on the facies distributions and faunal associations of the ammonites. Thus, it is likely that ancyloceratids (e.g., *Baculites* and *Hoploscaphites*) lived at depths of less than 100 m whereas phylloceratids and lytoceratids (e.g., *Hypophylloceras* and *Anagaudryceras*, respectively) lived at depths of 200–300 m.

Ammonites, like other cephalopods, were probably capable of locomotion, although the exact propulsive mechanism is unknown (Cherns et al. 2021). In some ammonites, large muscle scars appear on the sides of the body chamber and have been interpreted as the scars of cephalic retractor muscles (Doguzhaeva and Mapes 2015). Many of these ammonites also exhibit a ventral sinus at the aperture, which may have accommodated the funnel or hyponome. Such ammonites could have used their retractor muscles to pull the body back into the shell while compressing the water in the mantle to produce a pulse-like jet, as described in nautilus by Chamberlain (1987). In ammonites with small dorsal and ventral muscle scars but no evidence of retractor muscle scars, two other propulsive mechanisms have been suggested. Some ammonites may have employed the same mechanism used by nautilus at low swimming speeds or at rest. The animal uses the mantle musculature to produce a respiratory stream that serves to aerate the gills, which generates a weak jet (Wells and Wells 1985). Jacobs and Landman (1993) have also suggested that some ammonites may have used a coleoid-like contractible mantle during swimming. Whatever the particular mechanism, it is unlikely that ammonites were capable of swimming as fast as squid or fish, simply because an external shell produces large drag forces. Nevertheless, some streamlined ammonites such as *Placenticer*

were better adapted to reduce drag and the acceleration forces that resist movement, especially at larger sizes and higher velocities (Jacobs and Chamberlain 1996; Naglik et al. 2015).

The orientation of the ammonite in the water column is a clue to the mode of life of the ammonite (Westermann 1996; Ritterbush and Bottjer 2012). For example, if the aperture faces downward, the animal can access food on the seafloor. The orientation of the aperture can be estimated by determining the centers of mass and buoyancy (Fig. 12.1b). This can be accomplished either experimentally or using computer models combined with CT scanning (Hoffmann et al. 2015). The results are expressed as the orientation angle of the aperture with respect to the vertical (Saunders and Shapiro 1986). In both ammonites and fossil nautilids, such methods involve a number of simplifying assumptions (Landman et al. 2010). For example, it is assumed that the phragmocone was entirely filled with air without any liquid present. If the last few chambers were filled with liquid, the angle of orientation increases (pointing upward). In addition, it is assumed that the soft body was uniformly distributed throughout the body chamber. If the soft body protruded beyond the aperture, the angle of orientation decreased (pointing downward). In adults of many heteromorph ammonites such as *Hoploscaphites* and *Didymoceras*, for example, the orientation of the aperture is 90 °, that is, the aperture faces upward (Landman et al. 2012a; Peterman et al. 2020). In contrast, in modern nautilus, the orientation of the aperture (at resting position) is approximately 30 °, that is, the aperture faces downward (Saunders and Shapiro 1986).

The diet of ammonites is difficult to reconstruct but is based on studies of the morphology of the buccal apparatus (Fig. 12.2) and gut contents in exceptionally well-preserved fossils. The buccal apparatus consists of a pair of upper and lower jaws and a tongue-like ribbon with tiny teeth (the radula) that lies between them. Tanabe et al. (2015) classified ammonite jaws into five morphotypes, each of which can be interpreted in terms of its function. For example, the rhynchaptychus-type jaw, which occurs in phylloceratids and lytoceratids, is equipped with calcareous tips on the apical end. Similar jaws are present in modern nautilus and may have been adapted to scavenging lobster carapaces on the seafloor. In contrast, the aptychus-type jaw, which occurs in ancyloceratids, features a lower jaw that ends in a blunt margin and may have been better adapted for passively feeding on small organisms in the water column, such as zooplankton (Kruta et al. 2011; Tanabe et al. 2015). This jaw is characteristic of the group of ammonites called the Aptychophora, which includes the Ancyloceratina and most of the Ammonitina (Engeser and Keupp 2002).

12.3 Methane Seep Deposits

The discussion below is organized geographically and alphabetically by country and only focuses on methane seep deposits that contain ammonites. Many of the descriptions in the literature only treat ammonites in passing. The list is not

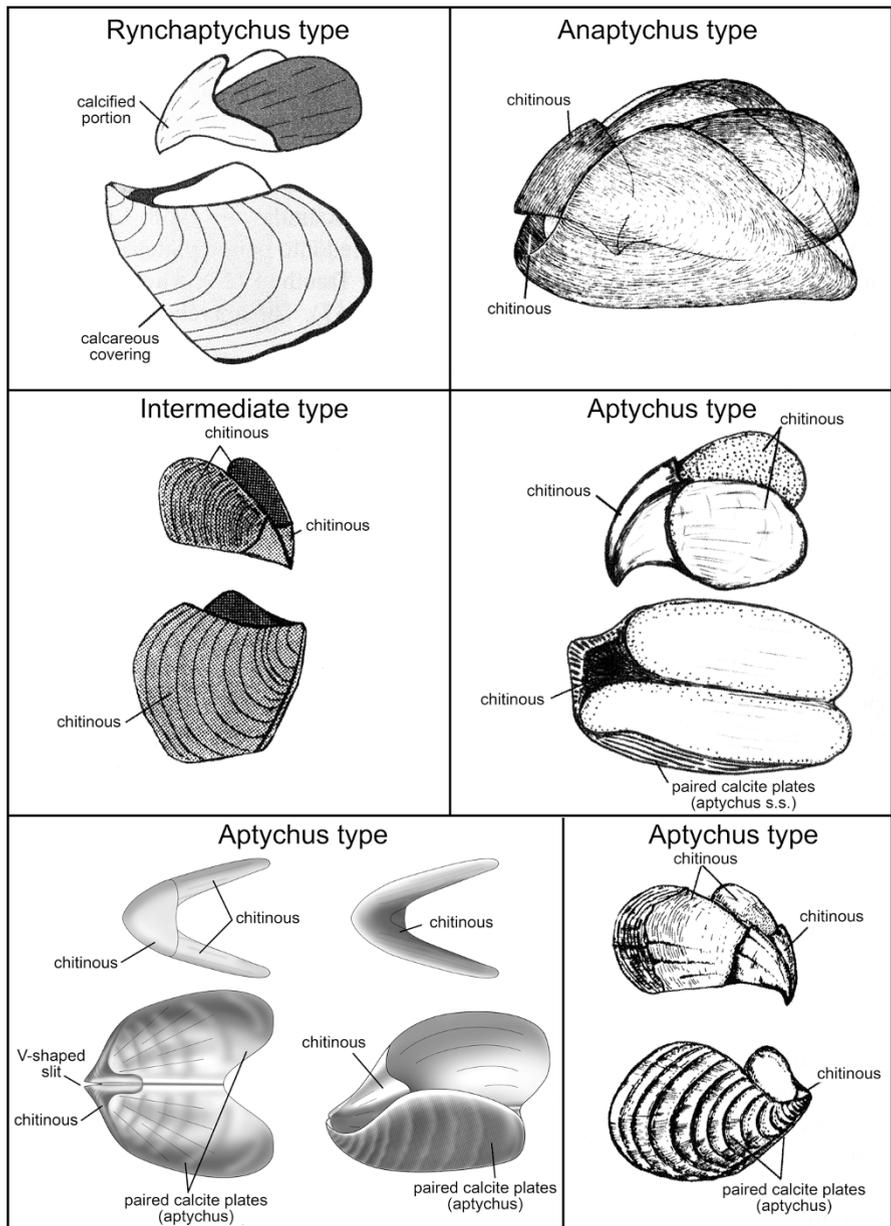


Fig. 12.2 Variety of jaws in Mesozoic ammonites. (Modified from Tanabe et al. 2015)

exhaustive but attempts to cover the best-known Paleozoic and Mesozoic seep deposits throughout the world. The list of ammonite species in seep deposits is presented in Appendix Table 12.1 with an estimated depth at which the ammonites

lived (<100 m, 100–200 m, and 200–300 m), mostly based on the conclusions in Hewitt (1996) and Westermann (1996).

12.3.1 *Antarctica*

Little et al. (2015) reported the presence of ammonites in methane seep deposits in Antarctica (Fig. 12.3f, g). These deposits occur in the lower Maastrichtian Snow Hill Formation on Snow Hill Island and in the lower-upper Maastrichtian Lopez de Bertodano Formation on Seymour Island (Witts and Little [this volume](#)). The fauna at the seeps is not very diverse and is dominated by an infaunal bivalve. In addition, the seep fauna is not restricted to the seeps (non-seep obligates) but also occurs in the surrounding shelf area.

In the Snow Hill Island Formation on Snow Hill Island, seep deposits consist of large cement-rich carbonate bodies filled with the bivalve *Thyasira townsendi*, many in life position, with a concentration of more than 120/m² forming a coquina. They are associated with numerous small ammonites and ammonite fragments, many of which appear to be juveniles (Fig. 12.3f, g). The ammonites belong to the genera *Gunnarites* and *Anagaudryceras*. Little et al. (2015) suggested that these ammonites “could have been current swept into the ‘*Thyasira*’ layers” and doubted that the ammonites lived at the site. While we agree that the ammonite deposit unquestionably represents a hydrodynamic accumulation (after all, ammonites lived in the water column, not in the sediment), the abundance of specimens, the presence of two species, and the fact that many of the specimens are juveniles suggest that the source of the ammonites was local, that is, from the seep. This conclusion is reinforced by the presence of additional ammonites including *Jacobites anderssoni* and *Gunnarites bhavaniformis* associated with *T. townsendi* in the interbeds between the cemented layers. Higher up in the section in the Lopez de Bertodano Formation on Seymour Island, similar carbonate bodies filled with *T. townsendi* are associated with several specimens of *Maorites seymouriensis*. Nearby sites at the same stratigraphic horizon have yielded additional ammonite species.

The seep deposits in the Lopez de Bertodano Formation on Seymour Island also contain concentrations of micrite-cemented carbonate burrow systems. The matrix of these concretions exhibits very low values of $\delta^{13}\text{C}$ ranging from -40% to -50% . Such values are indicative of C derived from methane, which is enriched in ^{12}C . Similar burrow-like systems have been observed in both ancient and modern seep deposits (Campbell 2006). Little et al. (2015) did not report any associated ammonites. However, Ivany and Artruc (2016) analyzed the carbon isotopic composition of the outer shell wall of a specimen of *Diplomoceras maximum* from this formation. They observed $\delta^{13}\text{C}$ values of as low as -30% and suggested that this ammonite was probably living in association with methane seeps. Furthermore, Tobin and Ward (2015) observed overall offsets of $\delta^{13}\text{C}$ between ammonites and

benthic mollusks in this formation. They suggested that this difference may reflect the incorporation of metabolic CO₂ in the secretion of the ammonite shells or possibly that the ammonites lived in close proximity to methane seeps.

The ammonites associated with the Antarctic seep deposits are mostly lycoceratids, phylloceratids, and desmoceratids. These groups prefer relatively deep water of 100–200 m. This depth is consistent with inferences about the environment of deposition by Little et al. (2015). *Diplomoceras maximum*, an ancyloceratid, is unrestricted in its depth preferences, ranging from relatively shallow to relatively deep.

12.3.2 Argentina

Kaim et al. (2016) reported a seep deposit (called “La Elina”) from the Neuquén-Mendoza Basin, Patagonia, west-central Argentina. The deposit occurs in the middle Toarcian (Lower Jurassic) Los Molles Formation and crops out over an area of approximately 2000 m². It is dominated by worm tubes and mollusks, most of which are gastropods and bivalves. Four species of ammonites are also present.

H. Parent (pers. comm. 2017) documented the abundance and size of the ammonites in the seep deposit and in the surrounding shale. *Calliphylloceras* sp. is abundant in the seep deposit and consists of juveniles (≈20 mm diameter) but is absent in the surrounding shale. *Phylloceras* sp. is rare in the seep deposit and also consists of juveniles (≈20 mm diameter); it is rare in the surrounding shale and occurs as fragmentary adults (≤400 mm diameter). *Hildaitoides retrocostatus* is abundant in the seep deposit and in the surrounding shale and consists of both juveniles and adults at both sites. *Phymatoceras* sp. is rare in the seep deposit and consists of fragments of adults; it is abundant in the surrounding shale where it also consists of fragments of adults. These ammonites indicate a relatively deep-water environment 100–200 m deep.

12.3.3 Canadian Arctic

Beauchamp and Savard (1992) and Willisicroft et al. (2017) described cold seep deposits in the Canadian Arctic that are associated with ammonites. The seep deposits occur on Prince Patrick and Ellef Ringnes Islands in the Lower Cretaceous (Aptian-Albian) Christopher Formation. This formation consists of shales and siltstones that were deposited in relatively deep water (<400 m) on the outer shelf to upper slope of the Sverdrup Basin and adjoining Eglinton Graben. The seep deposits appear as resistant carbonate mounds, beds, and crusts.

The fossil assemblage is dominated by bivalves followed by tube worms, gastropods, ammonites, scaphopods, and brachiopods. Fossils are scarce or absent in the surrounding shale. Two ammonite species were identified by Beauchamp and Savard (1992): *Arcthoplites* sp. and *Callizoniceras* (*Colvillia*) ex. aff. *crassicostata*. Williscroft et al. (2017) documented five additional ammonite species in their subsequent study of Ellef Ringnes Island: *Arcthoplites* (?) cf. *belli*, *Cleonicer* sp., *Beudanticeras* sp., *Puzosia* aff. *sigmoidalis*, and *Freboldiceras* aff. *irenense*.

12.3.4 England

A cold methane seep-ammonite association has been reported from the Sinemurian (Lower Jurassic) of England (Allison et al. 2008). The seep deposits occur in the rhythmically bedded limestone-marl-shale succession of the Blue Lias Formation. The deposits consist of conical mounds composed of micritic limestone as much 4 m in diameter and 1.5 m in height. One of the mounds contains foraminifera, crinoid ossicles, rare bivalves, and abundant ammonites. The ammonites, although not identified, are small (<1 cm in diameter), but complete.

12.3.5 France

One of the most ammonite-rich seep deposits occurs near Beauvoisin, Southeastern France (Rolin et al. 1990). The deposits occur at several horizons in lower-middle Oxfordian (Jurassic) black marls of the Terres Noires Formation. The deposits consist of massive micrite-cemented carbonate masses 1–15 m high and 1–20 m wide forming lenses or columns interbedded with calcareous shales. They are bordered by small concretions that rapidly disappear toward the margins. The carbonate masses and concretions are very fossiliferous compared to the much less fossiliferous black shales.

The carbonate masses are dominated by large infaunal lucinid bivalves, the largest of which is 18 cm long (bivalves comprise up to 30% of the rock). The bivalves are articulated, but not in life position. The deposits also contain a rich fauna of ammonites, most of which occur in the small irregular concretions on the margins of the masses (Fig. 12.3e, h, i). The ammonites include perispinctids and phylloceratids, including numerous *Sowerbyceras*, followed by opeliids, cardioceratids, and pachyceratids. In contrast, haploceratids, lytoceratids, and oecoptychiids are rare. Bourseau (1977) noted a difference in the preservation of ammonites based on their size, which he ascribed to a taphonomic bias. Small specimens and microconchs with peristomal modifications are well preserved whereas larger specimens and macroconchs are incomplete. He noted that the fauna includes a large number

of juveniles (approximately 30% of the individuals), a fact that was also noted by Landman et al. (2019). The deposits contain abundant aptychi (parts of the jaws of ammonites) and rhyncholites (parts of the jaws of nautilids). In addition, two genera of belemnites are present: *Hibolites* and *Duvalia*.

The fauna in the seeps is much richer than that in the surrounding shale. Rolin et al. (1990) did a comparative study of the fauna in the seeps and at nearby stratigraphically equivalent non-seep sites. Taking into account taphonomic differences (preservation in cemented carbonate concretions versus preservation in black shales), they noted that the fauna at the seeps is much more abundant with respect to bivalves, gastropods, ammonites, crustaceans, echinoderms, and fish. They concluded that all these animals were living at the seeps. Some of them such as the bivalves were restricted to the seeps, whereas the ammonites may have been “electifs” opting to remain at the seeps feasting on the abundant food source but equally at home elsewhere. Based on the abundance of ammonite juveniles, Bourseau (1977) also speculated that the ammonites may have preferentially laid their eggs at these sites.

Rolin et al. (1990) referred to the environment as bathyal or mesobathyal. The ammonites are dominated by phylloceratids and perispinctids (approximately 30% of the fauna). This assemblage suggests relatively deep water (80–150 m deep, according to one estimate cited in Bourseau (1977)). Evidently, these seeps occurred below the photic zone but served as a focus for ammonites and other fauna.

12.3.6 Greenland

Kelly et al. (2000) described limestone mounds (the Kuhnpasset Beds) in the Wollaston Foreland, Northeast Greenland, which contain ammonites. The mounds occur in upper Barremian (Lower Cretaceous) mudstones and are subcircular to subovoid in plan view and 1–3 m in diameter and up to 1.8 m in height. They are dominated by large lucinid and modiomorphid bivalves. In contrast, in the surrounding mudstone, bivalves are uncommon and consist of small nuculaceans and arcaceans, with larger inoceramids.

The mounds also contain several species of ammonites including lytoceratids, *Sanmartinoceras*, *Audouliceras*, and *Epicheloniceras*. In addition to the ammonites, the nautilid *Cymatoceras* is also present. Kelly et al. (2000) stated that “these cephalopods may represent active predators and scavengers, presumably attracted to the rich fauna of the mounds.”

12.3.7 Japan

Hikida et al. (2003) described a methane seep deposit from Omagari in the Nakagawa area, Hokkaido, Northern Japan, which contains ammonites. The deposit occurs in the Campanian (Upper Cretaceous) Omagari Formation and consists of an ellipsoidal calcareous mudstone 6 × 10 m in diameter and 5 m in thickness. It comprises two facies, a lower breccia facies and an upper worm tube boundstone facies. Jenkins et al. (2007) described additional deposits in the same area, which are better exposed. The environment of deposition is interpreted as “the interface between a continental-shelf margin and a continental slope” (Jenkins et al. 2007).

According to Hikida et al. (2003), the breccia facies contains abundant bivalves, gastropods, worm tubes, brachiopods, foraminifera, and a few ammonites (*Gaudryceras tenuiliratum*). All of the ammonite specimens are broken, and many of them are missing the body chamber. The same ammonite species was reported by Jenkins et al. (2007: Table 3) from their nearby site. In fact, this species is a common inhabitant in deeper-water environments (Westermann 1996).

12.3.8 Morocco

Many seep deposits associated with ammonites occur in Morocco. Some of the most spectacular are Devonian in age and are known as Kess Kess, which refers to the resemblance between the deposits and the dishes used to cook the famous Moroccan couscous (Belka 1998). The deposits appear as giant carbonate mud mounds that are conical to pinnacle in shape and up to 50 m in height, with circular to subcircular bases more than 100 m in diameter (Aitken et al. 2002; Cavalazzi et al. 2007; Berkowski and Klug 2011; Jakubowicz et al. [this volume](#)). The mounds are located on the Hamar Laghdad elevation 18 km east-southeast of Erfoud in the Anti-Atlas Mountains. Most of the mounds are Emsian (Early Devonian) in age, but the Hollard Mound in the eastern part of the elevation is Eifelian (Middle Devonian) in age (Peckmann et al. 1999, 2005).

The mounds have been interpreted as the sites of hydrocarbon seepage although the source of the methane is unclear and may have been thermogenic flowing along faults. The mounds formed on the continental shelf in relatively shallow water below wave base (Belka and Berkowski 2005; Cavalazzi et al. 2007). The mounds are composed of skeletal wackestones and mudstones. The fauna in the mounds is rich in invertebrates especially corals, arthropods, and crinoids and also includes ammonoids and orthoconic nautiloids. Klug (2002) noted *Agoniatites fecundus* in the uppermost layers of some of the mud mounds. However, the distribution and abundance of ammonoid species in the mud mounds and in the surrounding sediments have not yet been worked out in detail.

Smrzka et al. (2017) described a carbonate deposit in lower Turonian (Upper Cretaceous) black shales from the Amma Fatma Plage, southwest of Essaouira. The

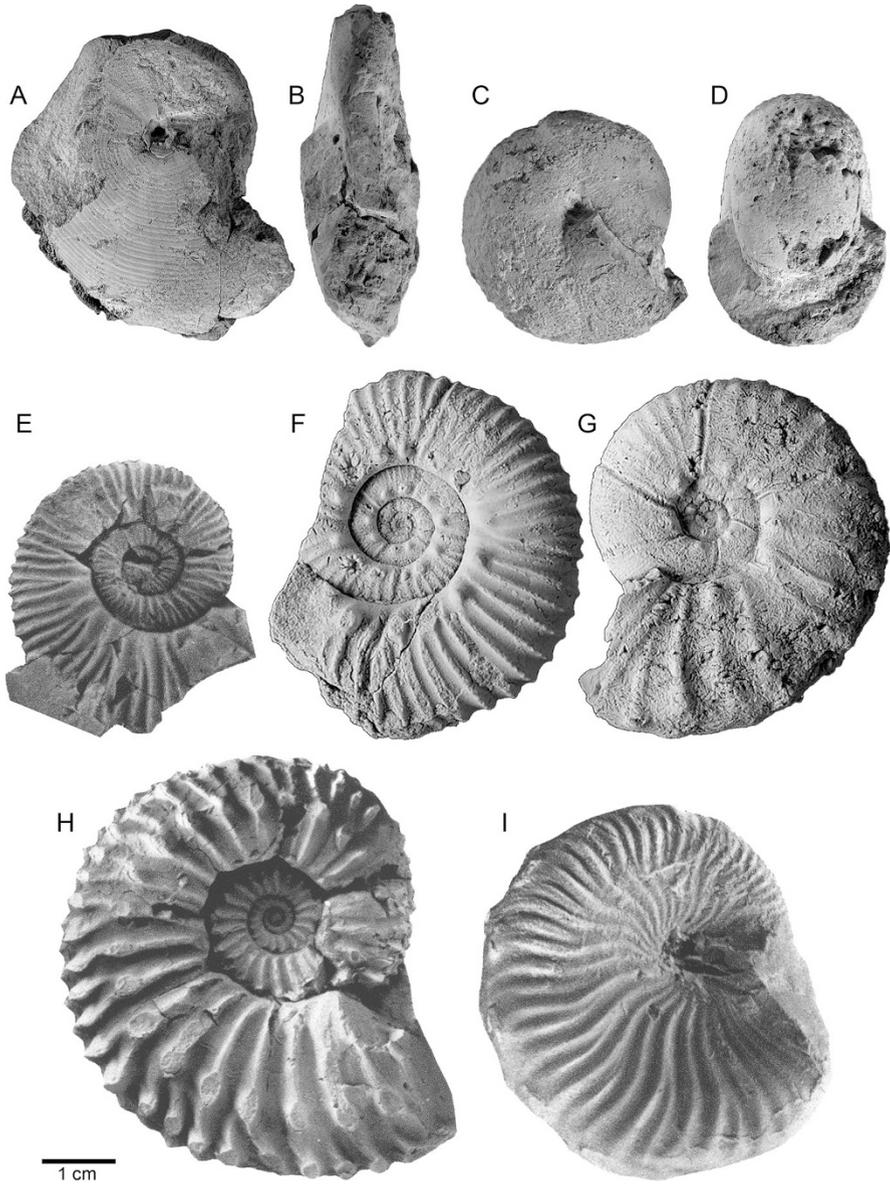


Fig. 12.3 Ammonites associated with methane seep deposits. (a, b) *Sagenites* sp., Norian (Upper Triassic), Oregon. (c, d) *Arcestes* sp., Norian (Upper Triassic), Oregon. (e) *Peltoceras* (*Parawedekindia*) sp. gr. *arduennense*, Oxfordian (Upper Jurassic), France (from Bourseau 1977). (f) *Gunnarites* sp., Maastrichtian (Upper Cretaceous), Antarctica (from Little et al. 2015). (g) *Jacobites anderssoni*, Maastrichtian (Upper Cretaceous), Antarctica (from Little et al. 2015). (h) *Cardioceras* (C.) sp. A, Oxfordian (Upper Jurassic), France (from Bourseau 1977). (i) *Taramelliceras* (*T.*) *obumbrans*, Oxfordian (Upper Jurassic), France (from Bourseau 1977). All figures are X 1

seep deposit formed in the Tarfaya Basin in relatively shallow water. It contains a low-diversity molluscan fauna consisting of bivalves, gastropods, and ammonites, but none of them represent seep-obligate species. The ammonites include juveniles and adults of *Benueites* sp. and *B. cf. benueensis*.

12.3.9 *New Zealand*

Kiel et al. (2012b) described methane seep deposits from New Zealand that contain ammonites. The deposits occur at Port Awanui on the Raukumara Peninsula, eastern North Island, New Zealand, and outcrop as reworked boulders along the shore. They are composed of calcareous mudstone and date from the late Albian-mid Cenomanian.

The fauna is dominated by lucinid and modiomorphid bivalves. Kiel et al. (2012b: Fig. 4) illustrated four ammonite specimens that occur in the deposits: *Scaphites equalis coverhamensis*, Kossmaticeratidae gen. et sp. indet., *Neograhamites cf. transitorius*, and a smooth, undescribed species. Based on the degree of endemism of the bivalves and gastropods, Kiel et al. (2012b) estimated that the environment of deposition was relatively deep on the outer shelf to upper slope. However, the presence of a species of *Scaphites* suggests a shallower depth of 100–200 m (Hewitt 1996).

12.3.10 *Novaya Zemlya*

Ammonites have been reported from seep deposits from the Arctic island of Novaya Zemlya (Hryniewicz et al. 2015). The deposits occur as isolated carbonate boulders that range from Late Jurassic to Early Cretaceous in age and are similar in age to the deposits in Svalbard (see below). The fauna is dominated by mollusks with fewer numbers of echinoderms, brachiopods, foraminifera, serpulids, and ostracods. In general, the fauna is not restricted to the seeps and resembles that of the surrounding non-seep shelf environments.

Ammonites occur in two kinds of boulders. They occur in calcareous sandstone boulders that contain 11 macro-invertebrate species, 9 of which are mollusks. The ammonites are mostly uncrushed with original shell structure including nacre. The most numerous specimens in these concretions are *Amoeboceras* sp., which occur as both mature and juvenile specimens. They are late Oxfordian to early Kimmeridgian in age. Because the venter is generally incomplete, they cannot be identified to species level. They are perisphinctids and according to Westermann (1996) probably lived at depths of 100–200 m.

Black limestone boulders contain 13 macro-invertebrate species that are well preserved. They include two specimens of *Craspedites okensis* of late Volgian (=

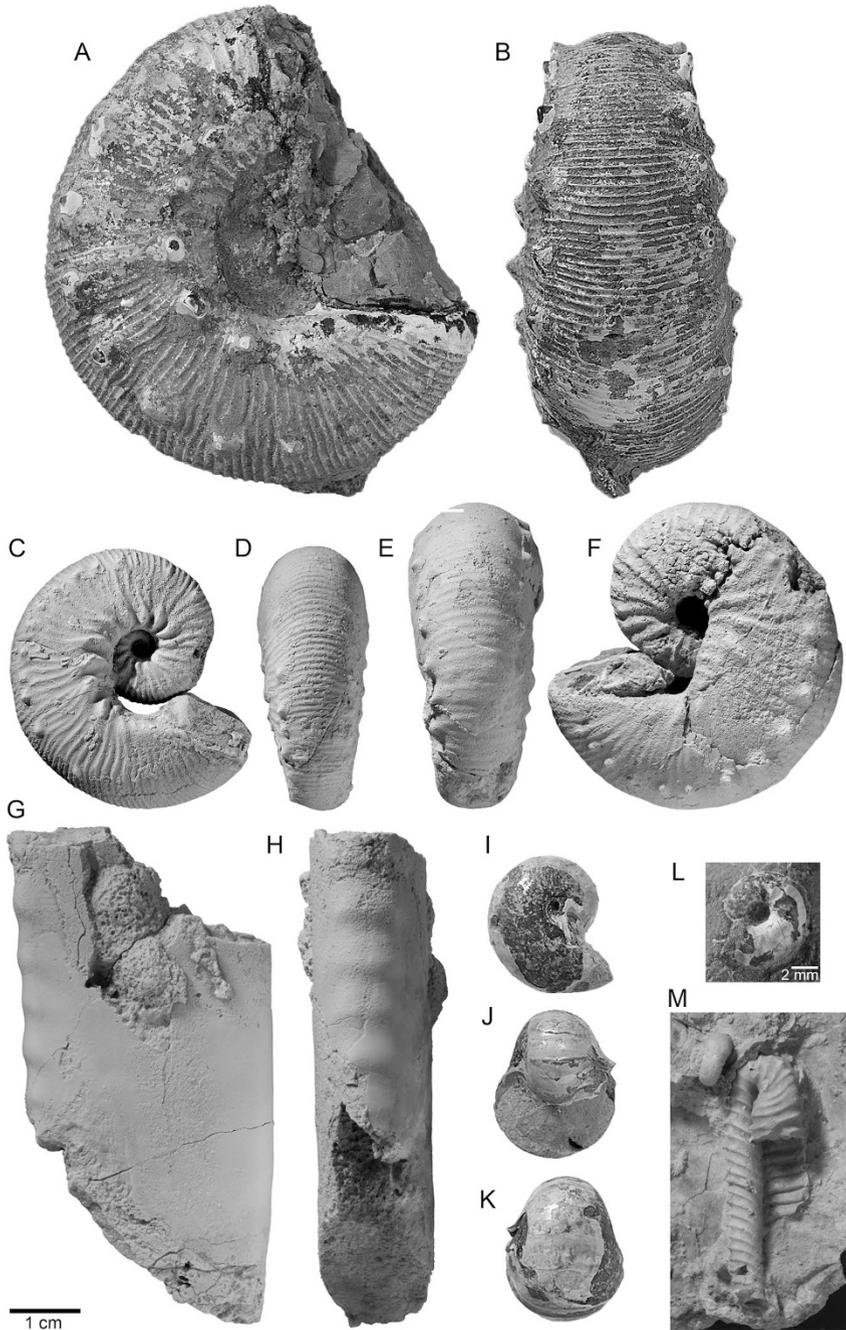


Fig. 12.4 Ammonites and nautilids associated with methane seep deposits, Upper Cretaceous (Campanian) Pierre Shale, South Dakota and Wyoming. (a) *Hoploscaphites nodosus*, microconch, AMNH 90781. (c, d) *Hoploscaphites gilberti*, microconch, USNM 547324. (e, f) *Hoploscaphites gilberti*, macroconch, USNM 83717. (g, h) *Baculites corrugatus*, AMNH 58544. (i-k) *Eutrephoceras dekayi*, AMNH 64529. (l) Juvenile of *Hoploscaphites*, AMNH 66244. (m) *Solenoceras bearpawense*, AMNH 108454. All figures are x 1 except (l). Abbreviations: AMNH American Museum of Natural History, USNM United States National Museum

late Tithonian) age. This is a stephanoceratid and, according to Hewitt (1996), would have lived at a depth of 100–200 m (Appendix Table 12.1).

12.3.11 Oregon, USA

Peckmann et al. (2011) described a seep deposit from the Norian (Upper Triassic) of Grant County, eastern Oregon. The deposit consists of two limestone bodies in the Rail Cabin Member of the Vesper Formation. The dominant fossil is the rhychonellide brachiopod *Halorella*. Other fossils are rare, but two ammonites have since been discovered at the site (A. Kaim, pers. comm., 2016) and are tentatively identified as *Sagenites* sp. and *Arcestes* sp. (Fig. 12.3a–d). It is likely that the same ammonites occur in other parts of the Rail Cabin Member, as documented in Taylor and Guex (2002).

12.3.12 Spitsbergen (Svalbard)

Ammonites have been reported from seep deposits (“carbonate bodies”) as much as 5 m in diameter in the uppermost Jurassic-lowermost Cretaceous of Spitsbergen (Hammer et al. 2011; Wierzbowski et al. 2011). The seep deposits occur in the Slottsmøya Member of the Agardhfjellet Formation in the Saaenfjordenniana area, which was deposited in a shallow epicontinental sea. The ammonites co-occur with abundant bivalves, gastropods, brachiopods, worm tubes, and a few belemnoids. None of these species is restricted to the seeps, that is, they are non-seep obligate but rather background fauna (Hryniewicz et al. 2014). The fact that obligate taxa are rare or absent appears to be a common feature of shallow-water vent and seep deposits (Dando, 2010).

A total of 153 ammonite specimens and 1 aptychus are present in 11 “carbonate bodies.” The ammonites consist of ten species belonging to six genera of the Ammonitina (*Craspedites*, *Kachpurites*, *Hectoroceras*, *Borealites*, *Surites*, and *Tollia*) and range in age from the late Volgian to latest Ryazanian. These are all perisphinctids and, according to Westermann (1996), would have probably lived at depths of approximately 100 m. All of the species are known from other regions outside of the seeps, although fragmentary specimens cannot be compared with other material.

12.3.13 Turkey

Kiel et al. (2017) reported methane seep deposits from the Upper Triassic (upper Carnian-lower Norian) of Turkey. The sites are located in the Kasımlar Basin in the Anamas Akseki autochthon in the Taurus Mountains. According to the authors,

“this basin is interpreted as a small ocean basin separating large carbonate platforms to the east and west, interspersed with several rifted continental fragments capped by Mesozoic carbonate platforms.” The seep deposits contain fragments of the ammonoid *Arcestes* sp.; it is unclear if they were living at the site.

12.3.14 Western Interior, USA

Ammonites are common in methane seep deposits in the US Western Interior (Colorado, Kansas, South Dakota, Montana, Wyoming, and Nebraska) (see Landman et al. [this volume](#)). Such deposits were first described by Gilbert and Gulliver (1895) along the Front Range of the Rocky Mountains in Colorado and were called “Tepee buttes.” These are geomorphic features that represent erosional remnants of the seep deposits. They appear as conical hills or mounds, usually in clusters, and are composed of limestone, up to 60 m in diameter and 10 m in height. They occur in the Upper Cretaceous Pierre Shale and Bearpaw Shale from central Montana to south-central Colorado and from the Front Range of the Rocky Mountains to western Kansas (Kauffman et al. 1996; Bishop and Williams 2000; Shapiro and Fricke 2002; Metz 2010; Larson et al. 2014; Ryan et al. 2020; Landman et al. [this volume](#)). They range in age from the middle Campanian to the early Maastrichtian. Kiel et al. (2012a) have also reported similar deposits from the upper Cenomanian Tropic Shale of Utah.

The seep deposits from the US Western Interior contain a diverse assemblage of organisms including ammonites, nautilids, bivalves, notably inoceramids, and aggregations of chemosymbiotic-harboring lucinids, gastropods, scaphopods, crinoids, asteroids, ophiuroids, crabs, echinoids, sponges, bryozoans, corals, tube worms, dinoflagellates, radiolaria, foraminifera, fish, and reptiles (Bishop and Williams 2000; Landman et al. 2012b; Larson et al. 2014; Meehan and Landman 2016; Hunter et al. 2016). A total of 30 molluscan species were reported at single sites from Campanian seep deposits in Colorado (Howe 1987). The diversity of organisms is higher at seeps with extensive carbonate deposits opposed to those without them, presumably because such deposits provided additional habitats for organisms that required hard substrates for attachment (Meehan and Landman 2016). In contrast, the shale surrounding the seep deposits is usually more depauperate and may have been characterized by more dysoxic water conditions.

Ammonites have been reported in the seep deposits of the Pierre Shale ranging from the top of the middle Campanian to the lower part of the lower Maastrichtian (Figs. 12.4 and 12.5). They span the *Baculites scotti/Didymoceras nebrascense* Zones, *D. stevensoni* Zone, *Exiteloceras jennyi* Zone, *D. cheyennense* Zone, *B. compressus/B. cuneatus* Zones, *B. reesidei* Zone, *B. jenseni* Zone, and *B. baculus* Zones (see Cobban et al. (2006) for a zonal chart of the area). Five to eight ammonite species occur in each of these zones and represent the genera *Baculites*, *Didymoceras*, *Exiteloceras*, *Hoploscaphites*, *Menuites*, *Nostoceras*, *Pachydiscus*, *Placentoceras*, *Solenoceras*, and *Spiroxybeloceras*. With one possible exception

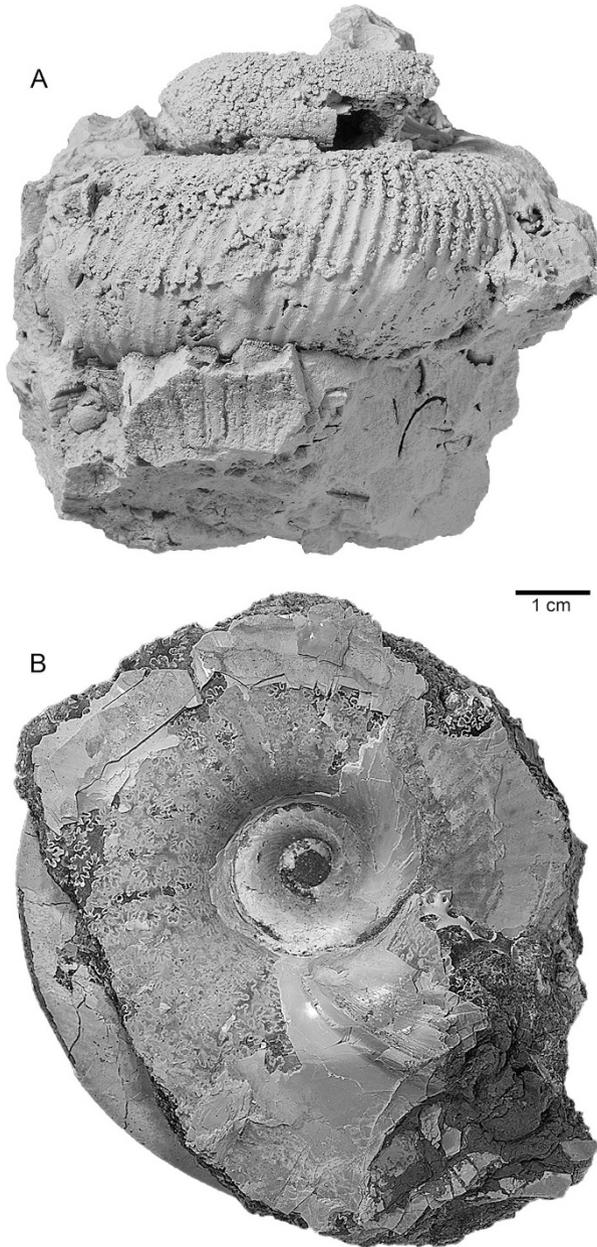


Fig. 12.5 Ammonites associated with methane seep deposits, Upper Cretaceous (Campanian) Pierre Shale, South Dakota and Nebraska. (a) *Didymoceras nebrascense*, AMNH 102288. (b) *Placentoceras intercalare*, AMNH 64499. All figures are x 1. Abbreviation: AMNH American Museum of Natural History

(*H. gilberti*), the species are not restricted to the seeps but also occur elsewhere in the basin (Landman et al. 2013).

The abundance of ammonites varies depending on the site. For example, in the same area with multiple seeps from the *Didymoceras nebrascense*/*Baculites scotti* Zones near Newell, Butte County, South Dakota, some seep deposits are more ammonite rich than others; still other seep deposits consist of nothing but carbonates and lucinids. In addition, the species composition varies depending on the seep deposit. For example, baculitid ammonites are generally more abundant than scaphitid ammonites, but the reverse is true in the *Baculites baculus* Zone in Niobrara County, Wyoming. Such variation may reflect differences in the abundance of food or concentration of oxygen, methane, or hydrogen sulfide.

Several lines of evidence have been marshalled to argue that ammonites lived at the seeps (Landman et al. 2012b, 2018):

1. Ammonites are much more abundant at the seep deposits than in the surrounding shale. Meehan and Landman (2016) reported a total of 17 specimens of *Hoploscaphites nodosus* from a seep deposit in the *Didymoceras cheyennense* Zone, Custer County, South Dakota. Landman et al. (2013) reported a total of 19 specimens of *H. gilberti* in a seep deposit from the *D. nebrascense* Zone, Weston County, Wyoming. In addition, one of us (N.L.L.), in association with S. Jorgensen, collected nearly 30 complete specimens of *H. gilberti* in a seep deposit from the *D. nebrascense* Zone, Fall River County, South Dakota. In contrast, the same ammonites are rare or absent in the surrounding shale.
2. In ammonites in which sexual dimorphs can be recognized, both dimorphs occur in the same seep deposit. For example, Landman et al. (2013) reported 12 macroconchs and 16 microconchs of *H. gilberti* in a seep deposit from the *D. nebrascense* Zone, Weston County, Wyoming.
3. Ammonite jaws and hooklike structures are present in seep deposits (Fig. 12.6). Because these structures are very delicate and easily lost after death, their presence suggests that the ammonites did not float into the sites after the animals died, but rather that they lived there.
4. Ammonites at seeps exhibit sublethal and lethal injuries (Fig. 12.7). Sublethal injuries are recognizable as scars on the shell and reflect attacks that occurred during the lifetime of the animal but did not result in death. Lethal injuries are indicated by missing pieces of shell, which tend to occur in the same position on the ammonite (Larson 2003; Takeda et al. 2016). Many of these injuries may have been inflicted at or near the seep sites, suggesting that the ammonites formed an integral part of an integrated community.
5. Many seep deposits contain both juveniles and adults of the same species (Rowe et al. 2020). For example, juveniles of *Hoploscaphites* and *Baculites* are common in seep deposits from the *Didymoceras cheyennense* Zone of southwestern South Dakota (Fig. 12.4).
6. In several of the seep deposits in South Dakota, the ammonites are well preserved and retain their original aragonitic shells. As a result, the isotope composition of the shells records, in principle, the original conditions in the water

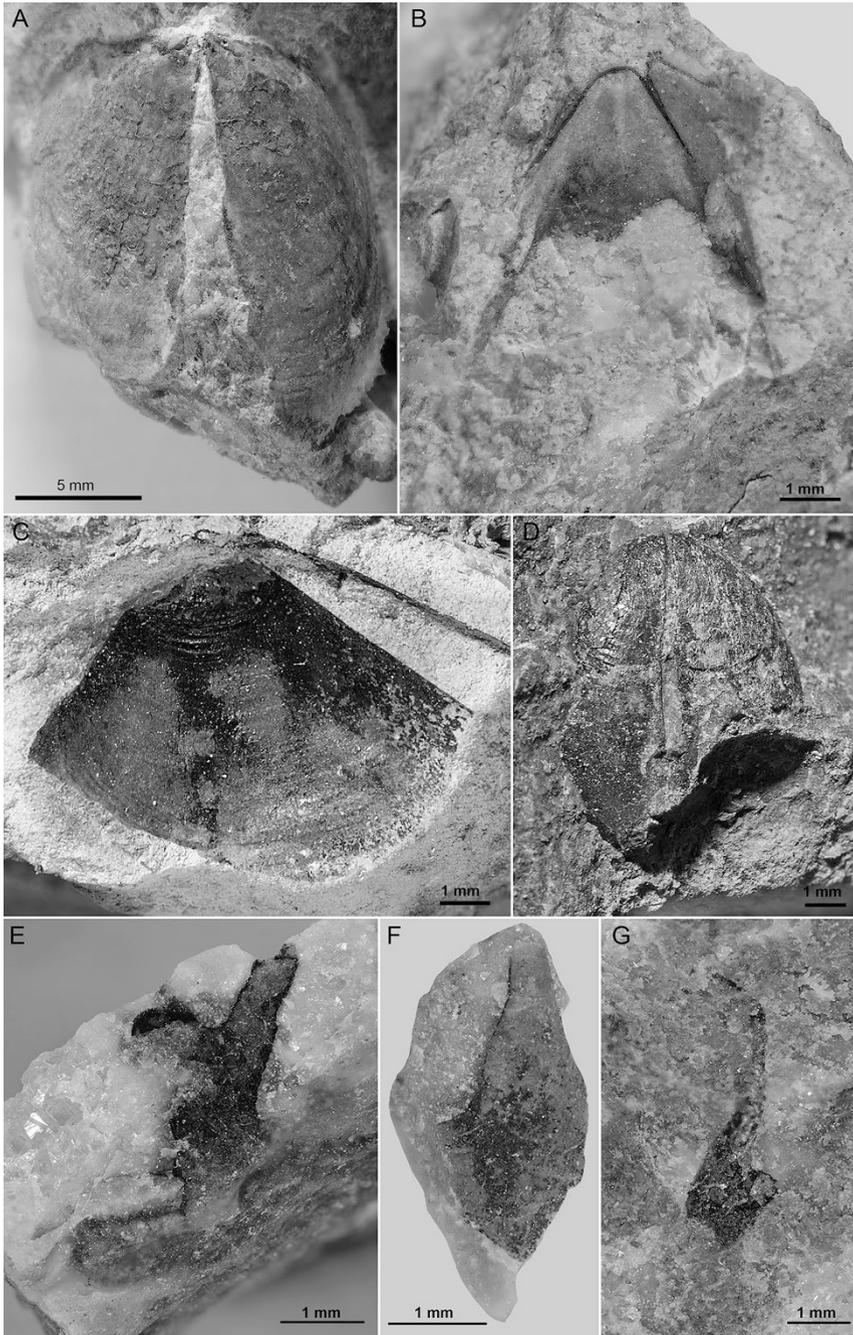


Fig. 12.6 Jaws and hooklike structures attributed to *Hoploscaphites* from seep deposits in the Upper Cretaceous (Campanian) Pierre Shale, South Dakota. (a) Lower jaw showing the midline slit, ventral view, apex on the top, AMNH 64532. (b) Upper jaw, apex on the top, AMNH 64547. (c) Impression of the left side of the lower jaw, midline slit on the right, AMNH 63423. (d) Lower jaw showing the midline slit, ventral view, apex on the top, AMNH 99198. (e) Hooklike structure showing one of the points projecting to the upper right, AMNH 63530. (f) Hooklike structure with the basal portion exposed on the bottom, AMNH 63531. (g) Hooklike structure with one point complete and one point broken, AMNH 64533. Abbreviation: AMNH American Museum of Natural History



Fig. 12.7 Healed injury on the outer flanks of *Placenticerus meeki*, AMNH 108168, methane seep deposit, Upper Cretaceous (Campanian) Pierre Shale, South Dakota. The injury was severe enough to affect the mantle. The adoral direction is toward the bottom of the photo. Figure is x 1. Abbreviation: *AMNH* American Museum of Natural History

column where the ammonites lived. A comparison of the carbon isotopic composition of the specimens at seeps with specimens of the same species from age-equivalent non-seep sites reveals a significant difference (Landman et al. 2012b; Cochran et al. 2015; Landman et al. 2018). The values of $\delta^{13}\text{C}$ are significantly lower in seep specimens than in age-equivalent non-seep specimens (Fig. 12.8). Anaerobic oxidation of ^{12}C -enriched methane at seeps produces a dissolved inorganic carbon reservoir with a low $\delta^{13}\text{C}$ signature that can be imprinted on seep carbonates as well as on the shells of mollusks living at the seeps. The low $\delta^{13}\text{C}$ of the well-preserved shells of ammonites from seeps compared with those of non-seep ammonites suggests that the seep ammonites were living in close proximity to the seep ecosystem.

In addition to methane seep deposits, ammonites have also been reported in association with reptile carcasses, which could represent relatively small, localized chemosynthetic communities. A mosasaur skeleton-ammonite association was discovered in the Campanian (Upper Cretaceous) Sharon Springs Member of the Pierre Shale, Niobrara County, Wyoming (D. Burnham, R. DePalma, pers. comm. 2016). It consists of a large, fairly complete, partially articulated skeleton of *Clidastes* associated with a 1-cm-thick ammonite layer that occurs just above and around the mosasaur

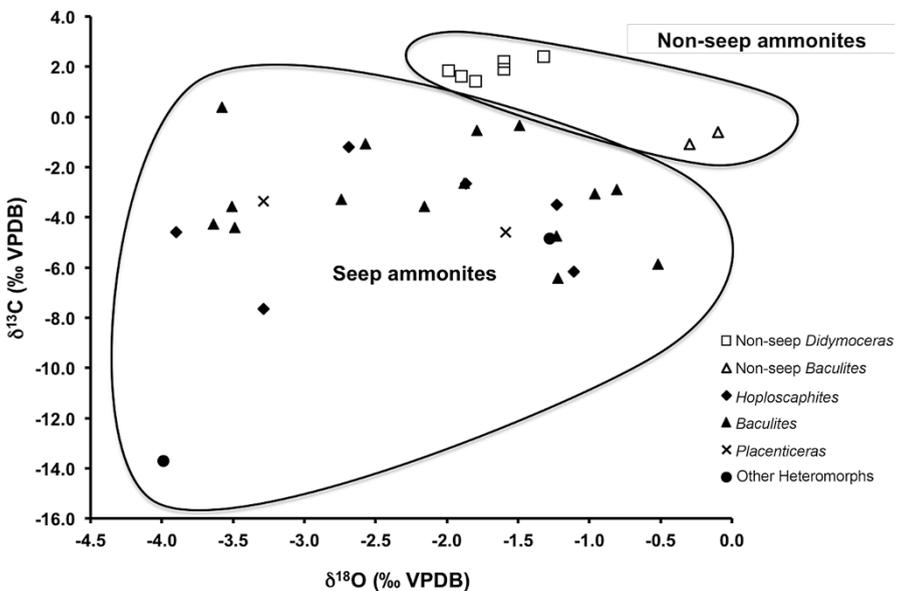


Fig. 12.8 Comparison of the carbon isotopic composition ($\delta^{13}\text{C}$ ‰VPDB) of well-preserved specimens of *Baculites compressus* collected at seep sites with specimens of the same species from age-equivalent non-seep sites. As a consequence of the impact of anaerobic methane oxidation on the $\delta^{13}\text{C}$ of the DIC reservoir from which the shells formed, the values of $\delta^{13}\text{C}$ are consistently lower in the specimens at the seeps, suggesting that they were living at the site. (Data from Landman et al. 2018)

(Fig. 12.9). The accumulation comprises thousands of small specimens of *Baculites haresi*, along with a few *Hoploscaphites*, all of which are juveniles with intact body chambers. The specimens of *B. haresi* are approximately 1–2 cm long and are oriented northwest-southeast with the apical ends pointing toward the southeast, implying a current from that direction (Fig. 12.10).

The Sharon Springs Member has been interpreted as having been deposited on an anoxic bottom (Gill and Cobban 1966; Byers 1979). The most common fossils are nektonic: mosasaurs, fish, squid (enchoteuthids), and ammonites (*Baculites haresi*). The only benthic organisms are large, flat-sided inoceramids, but these animals may have contained chemosymbiotic bacteria that helped them tolerate a low-oxygen environment (MacLeod and Hoppe 1992). Landman (1988) reported small juveniles of *Baculites* 5 mm in length sparsely preserved in small gray limestone

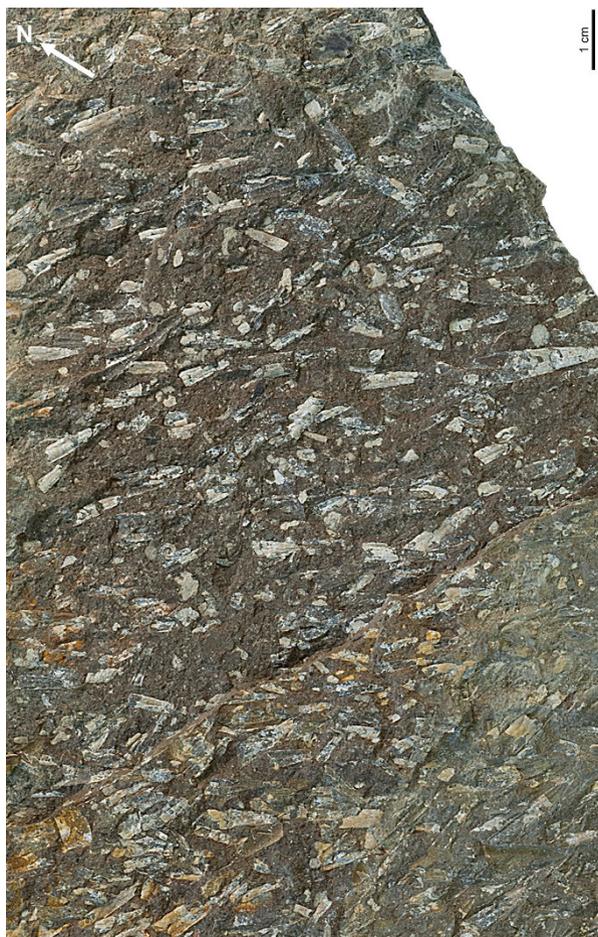


Fig. 12.9 Mass occurrence of juvenile specimens of *Baculites* and *Hoploscaphites*, PBMNH.10.115, associated with a mosasaur carcass in the Upper Cretaceous (Campanian) Sharon Springs Member of the Pierre Shale, Wyoming. North is toward the upper left. Figure is x 1. Abbreviation: *PBMNH* Palm Beach Museum of Natural History

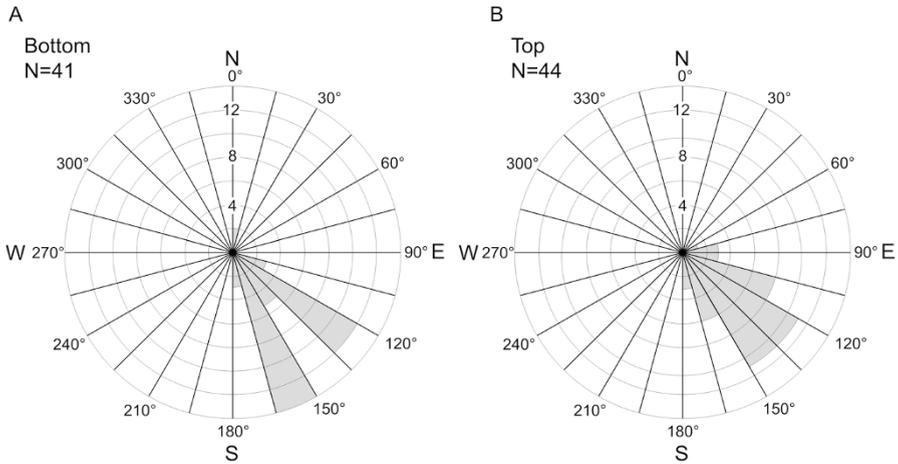


Fig. 12.10 Rose diagrams showing the orientation of the juvenile specimens of *Baculites* associated with the mosasaur carcass. The layer is 1 cm thick; the current direction is from the southeast

concretions in this stratigraphic interval. He interpreted the presence of such small juveniles as evidence that the ammonites lived well above the seafloor at this stage of their lives.

The mass occurrence of ammonite juveniles in association with the mosasaur skeleton is the first report of such an occurrence and could represent remains of a chemosynthetic-based community. Such systems have previously been reported in association with plesiosaurid skeletons in the Upper Cretaceous of Japan (Kaim et al. 2008). These communities depend on the anaerobic microbial decomposition of the organic compounds (lipids) in the bones of the reptile skeleton. In the Sharon Springs Member, more research is required to document the presence of other organisms living on and around the skeleton such as gastropods and bivalves as well as microborings in the bones. If this association represents the remains of a chemosynthetic-based community, the ammonites would have been attracted to the small organisms surrounding the rotting carcass as well as the rotting carcass itself.

The death and burial of the ammonites may have been due to rising anoxia. At the same time, a current must have resuspended fine sediment on the bottom and buried the ammonites. The southeast current parallels the shoreline to the west (Gill and Cobban 1966: Fig. 16, *Baculites obtusus* Zone) and would account for the preferred orientation of the ammonite specimens.

12.4 Conclusions

In many of the seep deposits described, ammonites are more abundant at the seeps than in the surrounding sedimentary rocks. The deposits in the US Western Interior and Southeastern France also contain ammonite jaws and hooklike structures, which are attributed to ammonites. Both kinds of structures are very delicate and could not have been transported into the sites after the ammonites died. In addition, the isotopic composition of well-preserved ammonites from the US Western Interior and Antarctica exhibits unusually low (light) values of $\delta^{13}\text{C}$ compared to those of ammonites from age-equivalent non-seep sites. All of this evidence suggests that the ammonites lived at these seeps.

However, ammonites were not restricted to seeps. Because they were able to disperse widely during the post-hatching phase, ammonites inhabited many other environments. Thus, they represent background taxa and are not seep obligate. Nevertheless, if an individual was lucky enough to stumble on a seep site, perhaps through olfactory cues, it may have stayed there for the rest of its life. The seep undoubtedly provided a nutrient-rich environment. Therefore, even though ammonites were mobile animals, they may have spent part or most of their lives at seeps. In addition, because many seeps occur in clusters (seep fields), ammonites may have drifted or migrated from one seep to another.

In seep deposits where the evidence suggests that ammonites lived at the seep, the ammonites can serve as a means of determining the paleodepth of the site (Appendix Table 12.1). In contrast, ammonites are rare or absent in deep-water hydrothermal vent deposits and probably did not live at these sites. For example, Kaim et al. (2021) reported a single gaudryceratid ammonite from a hydrothermal vent deposit in the Upper Cretaceous (upper Cenomanian-lower Turonian) Troodos Ophiolite in Cyprus. The depth at this site is estimated to have been 2500–5000 m, far exceeding the implosion depth of any ammonite.

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Appendix

Table 12.1 Ammonite species from methane seep deposits

Species	Source	Locality	Age	Water depth (m)
<i>Agoniatites fecundus</i>	Klug (2002)	Erfoud, Morocco	Emsian (Lower Devonian)	<100
<i>Sagenites</i> sp.	A. Kaim (pers. comm. 2016)	Oregon, USA	Norian (Upper Triassic)	100–200
<i>Arcestes</i> sp.	A. Kaim (pers. comm. 2016)	Oregon, USA	Norian (Upper Triassic)	100–200
<i>Arcestes</i> sp.	Kiel et al. (2016)	Turkey	Upper Carnian-lower Norian (Upper Triassic)	100–200
<i>Phylloceras</i> sp.	H. Parent (pers. comm. 2017)	Patagonia, Argentina	Toarcian (Lower Jurassic)	100–200
<i>Calliphylloceras</i> sp.	H. Parent (pers. comm. 2017)	Patagonia, Argentina	Toarcian (Lower Jurassic)	100–200
<i>Hildaitoides retrocostatus</i>	H. Parent (pers. comm. 2017)	Patagonia, Argentina	Toarcian (Lower Jurassic)	100–200
<i>Phymatoceras</i> sp.	H. Parent (pers. comm. 2017)	Patagonia, Argentina	Toarcian (Lower Jurassic)	100–200
<i>Perisphinctes (Otosphinctes) montfalconensis</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Perisphinctes (Otosphinctes) paturattensis</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Perisphinctes (Dichotomosphinctes) antecedens</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Perisphinctes rotöides</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Pseudogregoryceras iteni</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Euaspidoceras (E.) catena</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Euaspidoceras (E.) ovale</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Protophites christoli</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Subcardioceras excavatum</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Pachyceras (Tornquistes) kobyi</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Cardioceras (Subvertebriceras) densiplicatum</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200

(continued)

Table 12.1 (continued)

Species	Source	Locality	Age	Water depth (m)
<i>Campylites (C.) delmontanus delmontanus</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Campylites (Neoprionoceras) henrici henrici</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Taramelliceras (T.) obumbrans</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Taramelliceras (T.) dentostriatum</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Taramelliceras (T.) callicerum</i>	Bourseau (1977)	SE France	Oxfordian (Upper Jurassic)	100–200
<i>Amoeboceras</i> sp.	Hryniewicz et al. (2015)	Novaya Zemlya	Oxfordian-Kimmeridgian (Upper Jurassic)	100–200
<i>Craspedites (C.) okensis</i>	Hryniewicz et al. (2015)	Novaya Zemlya	Volgian (Upper Jurassic-Lower Cretaceous)	100–200
<i>Craspedites (C.) okensis</i>	Wierzbowski et al. (2011)	Spitsbergen	Volgian (Upper Jurassic-Lower Cretaceous)	<100
<i>Craspedites (Taimyroceras) originalis</i>	Wierzbowski et al. (2011)	Spitsbergen	Volgian (Upper Jurassic-Lower Cretaceous)	<100
<i>Kachpurites</i> sp.	Wierzbowski et al. (2011)	Spitsbergen	Volgian (Upper Jurassic-Lower Cretaceous)	<100
<i>Hectoroceras (?Shulginites)</i> sp.	Wierzbowski et al. (2011)	Spitsbergen	Volgian-Ryazanian (Upper Jurassic-Lower Cretaceous)	<100
<i>Borealites (Ronkinites) rossicus</i>	Wierzbowski et al. (2011)	Spitsbergen	Ryazanian (Lower Cretaceous)	<100
<i>Borealites (Pseudocraspedites)</i> sp.	Wierzbowski et al. (2011)	Spitsbergen	Ryazanian (Lower Cretaceous)	<100
<i>Surites (S.) spasskensis</i>	Wierzbowski et al. (2011)	Spitsbergen	Ryazanian (Lower Cretaceous)	<100
<i>Surites (S.) spasskenoides</i>	Wierzbowski et al. (2011)	Spitsbergen	Ryazanian (Lower Cretaceous)	<100
<i>Surites (Bojarkia) tzikwinianus</i>	Wierzbowski et al. (2011)	Spitsbergen	Ryazanian (Lower Cretaceous)	<100
<i>Tollia (T.) tolli</i>	Wierzbowski et al. (2011)	Spitsbergen	Ryazanian (Lower Cretaceous)	<100
<i>Sanmartinoceras</i> sp.	Kelly et al. (2000)	NE Greenland	Barremian (Lower Cretaceous)	100–200
<i>Audouliceras</i> sp.	Kelly et al. (2000)	NE Greenland	Barremian (Lower Cretaceous)	100–200
<i>Epicheloniceras</i> sp.	Kelly et al. (2000)	NE Greenland	Barremian (Lower Cretaceous)	100–200

Species	Source	Locality	Age	Water depth (m)
<i>Archthroplites</i> sp.	Beauchamp and Savard (1992)	Canadian Arctic	Aptian-Albian (Lower Cretaceous)	200–300
<i>Callizoniceras</i> (<i>Colvillia</i>) ex. aff. <i>crassicostata</i>	Beauchamp and Savard (1992)	Canadian Arctic	Aptian-Albian (Lower Cretaceous)	200–300
<i>Archthroplites</i> (?) cf. <i>belli</i>	Williscroft et al. (2017)	Canadian Arctic	Albian (Lower Cretaceous)	200–300
<i>Cleoniceras</i> sp.	Williscroft et al. (2017)	Canadian Arctic	Albian (Lower Cretaceous)	200–300
<i>Beudanticeras</i> sp.	Williscroft et al. (2017)	Canadian Arctic	Albian (Lower Cretaceous)	200–300
<i>Puzosia</i> aff. <i>sigmoidalis</i>	Williscroft et al. (2017)	Canadian Arctic	Albian (Lower Cretaceous)	200–300
<i>Freboldiceras</i> aff. <i>irenense</i>	Williscroft et al. (2017)	Canadian Arctic	Albian (Lower Cretaceous)	200–300
<i>Scaphites equalis coverhamensis</i>	Kiel et al. (2012b)	Raukumara Peninsula, New Zealand	Albian-Cenomanian (Middle Cretaceous)	100–200
Kossmaticeratidae gen. et sp. indet.	Kiel et al. (2012b)	Raukumara Peninsula, New Zealand	Albian-Cenomanian (Middle Cretaceous)	100–200
<i>Neograhamites</i> cf. <i>transitorius</i>	Kiel et al. (2012b)	Raukumara Peninsula, New Zealand	Albian-Cenomanian (Middle Cretaceous)	100–200
<i>Benueites</i> sp.	Smrzka et al. (2017)	Essaouira, Morocco	Turonian (Upper Cretaceous)	<100
<i>B.</i> cf. <i>benueensis</i>	Smrzka et al. (2017)	Essaouira, Morocco	Turonian (Upper Cretaceous)	<100
<i>Gaudryceras tenuiliratum</i>	Hikida et al. (2003) and Jenkins et al. (2007)	Hokkaido, Japan	Campanian (Upper Cretaceous)	200–300
<i>Baculites compressus</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Baculites corrugatus</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Baculites cuneatus</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Baculites eliasi</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Baculites pseudovatus</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Baculites scotti</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Baculites undatus</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100

Species	Source	Locality	Age	Water depth (m)
<i>Didymoceras cheyennense</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Didymoceras nebrascense</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Exiteloceras jenneyi</i>	This study	WI	Campanian (Upper Cretaceous)	<100
<i>Hoploscaphites brevis</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Hoploscaphites gilberti</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Hoploscaphites nodosus</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Hoploscaphites gilli</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Hoploscaphites plenus</i>	This study	WI	Maastrichtian (Upper Cretaceous)	<100
<i>Menuites oralensis</i>	This study	WI	Campanian (Upper Cretaceous)	<100
<i>Nostoceras monotuberculatum</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Pachydiscus</i> sp.	This study	WI	Campanian (Upper Cretaceous)	<100
<i>Placentoceras intercalare</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Placentoceras meeki</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Solenoceras bearpawense</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Spiroxybeloceras meekanum</i>	Larson et al. (2014)	WI	Campanian (Upper Cretaceous)	<100
<i>Hoploscaphites</i> sp.	This study	WI	Maastrichtian (Upper Cretaceous)	<100
<i>Diplomoceras maximum</i>	Ivany and Artruc (2016)	Seymour Island, Antarctica	Maastrichtian (Upper Cretaceous)	100–200
<i>Anagaudryceras</i> sp.	Little et al. (2015)	Snow Hills Island, Antarctica	Maastrichtian (Upper Cretaceous)	100–200
<i>Jacobites anderssoni</i>	Little et al. (2015)	Snow Hills Island, Antarctica	Maastrichtian (Upper Cretaceous)	100–200
<i>Gunnarites</i> sp.	Little et al. (2015)	Snow Hills Island, Antarctica	Maastrichtian (Upper Cretaceous)	100–200

Species	Source	Locality	Age	Water depth (m)
<i>Gunnarites bhavaniformis</i>	Little et al. (2015)	Snow Hills Island, Antarctica	Maastrichtian (Upper Cretaceous)	100–200
<i>Gunnarites antarcticus</i>	Little et al. (2015)	Snow Hills Island, Antarctica	Maastrichtian (Upper Cretaceous)	100–200
<i>Maorites seymouriensis</i>	Little et al. (2015)	Seymour Island, Antarctica	Maastrichtian (Upper Cretaceous)	100–200

The species are arranged in the table from geologically oldest on the top to geologically youngest at the bottom. The authors' names associated with each species are given in the "source" references. In Bourseau (1977), because of the large number of taxa, we did not include the species listed in open nomenclature. The "water depth (m)" refers to the maximum depth at which the ammonites lived based on the conclusions of Hewitt (1996) and Westermann (1996). Ryazanian, "Boreal" Berriasian; Volgian, "Boreal" Tithonian-Berriasian; WI, Kansas, Colorado, Wyoming, South Dakota, Montana, and Nebraska

References

- Aitken S, Collom CJ, Henderson CM et al (2002) Stratigraphy, paleoecology, and origin of Lower Devonian (Emsian) carbonate mud buildups, Hamar Laghdad, eastern Anti-Atlas, Morocco, Africa. *Bull Can Petrol Geol* 50:217–243
- Allison PA, Hesselbo SP, Brett CE (2008) Methane seeps on an early Jurassic dysoxic seafloor. *Palaeogeog Palaeoclimat Palaeoecol* 270:230–238
- Beauchamp B, Savard M (1992) Cretaceous chemosynthetic carbonate mounds in the Canadian Arctic. *PALAIOS* 7:434–450
- Belka Z (1998) Early Devonian Kess-Kess carbonate mud mound of the eastern Anti-Atlas (Morocco), and their relation to submarine hydrothermal venting. *J Sediment Res* 68:368–377
- Belka Z, Berkowski B (2005) Discovery of thermophyllic corals in an ancient hydrothermal vent community, Devonian. *Acta Geol Pol* 55:1–7
- Berkowski B, Klug C (2011) Lucky rugose corals on crinoid stems: unusual examples of subepidermal epizoans from the Devonian of Morocco. *Lethaia* 45:24–33
- Bishop GA, Williams AB (2000) Fossil crabs from tepee buttes, submarine seeps of the Late Cretaceous Pierre Shale, South Dakota and Colorado, USA. *J Crustac Biol* 20(2):286–300
- Bourseau J-P (1977) L'Oxfordien moyen à nodules des 'Terres Noires' de Beauvoisin (Drôme). *Nouv Arch Mus Hist Natl Lyon* 15:1–116
- Byers CW (1979) Biogenic structures of black shale paleoenvironments. *Postilla* 174:1–43
- Campbell KA (2006) Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: past development and future research directions. *Palaeogeog Palaeoclimat Palaeoecol* 232:362–407
- Cavalazzi B, Barbieri R, Ori GG (2007) Chemosynthetic microbialites in the Devonian carbonate mounds of Hamar Laghdad (Anti-Atlas, Morocco). *Sediment Geol* 200:73–88
- Chamberlain JA Jr (1987) Locomotion of *Nautilus*. In: Saunders WB, Landman NH (eds) *Nautilus: the biology and paleobiology of a living fossil*. Plenum Press, New York, pp 489–525

- Cherns L, Spencer ART, Rahman IA, Garwood RJ, Reedman C, Burca G, Turner MJ, Hollingworth NTJ, Hilton J (2021) Correlative tomography of an exceptionally preserved Jurassic ammonite implies hyponome-propelled swimming. *Geology*. <https://doi.org/10.1130/G49551.1>
- Cobban WA, Walaszczyk I, Obradovich JD et al (2006) A USGS zonal table for the Upper Cretaceous middle Cenomanian–Maastrichtian of the Western Interior of the United States based on ammonites, inoceramids, and radiometric ages. US Geological Survey Open-File Report 2006-1250, pp 1–46
- Cochran JK, Landman NH, Larson NL et al (2015) Geochemical evidence (C and Sr isotopes) for methane seeps as ammonite habitats in the Late Cretaceous (Campanian) Western Interior Seaway. *Swiss J Palaeontol* 134(2):153–165
- Dando PR (2010) Biological communities at marine shallow-water vent and seep sites. In: Kiel S (ed) *The vent and seep biota: aspects from microbes to ecosystems*, Topics in geobiology, vol. 33. Springer, Cham, pp 333–378
- Doguzhaeva L, Mapes RA (2015) The body chamber length variations and muscle and mantle attachments in ammonoids. In: Klug C, Korn D, DeBaets K et al (eds) *Ammonoid paleobiology*. Springer, Cham, pp 545–584
- Engeser T, Keupp H (2002) Phylogeny of aptychi-possessing *Neoammonoidea* (Aptychophora nov., Cephalopoda). *Lethaia* 24:79–96
- Gilbert GK, Gulliver FR (1895) Tepee Buttes. *Geol Soc Am Bull* 6:333–342
- Gill JR, Cobban WA (1966) The Red Bird section of the Upper Cretaceous Pierre Shale in Wyoming. *US Geol Surv Prof Pap* 393A:1–73
- Hammer Ø, Nakrem HA, Little CTS et al (2011) Hydrocarbon seeps from close to the Jurassic–Cretaceous boundary, Svalbard. *Palaeogeog Palaeoclimat Palaeoecol* 306:15–26
- Hewitt RA (1996) Architecture and strength of the ammonoid shell. In: Landman NH, Tanabe K, Davis RA (eds) *Ammonoid paleobiology*. Plenum, New York, pp 297–339
- Hewitt RA, Westermann GEG (1987) *Nautilus* shell architecture. In: Saunders WB, Landman NH (eds) *Nautilus: the biology and paleobiology of a living fossil*. Plenum, New York, pp 435–162
- Hikida Y, Suzuki S, Togo Y et al (2003) An exceptionally well-preserved fossil seep community from the Cretaceous Yezo Group in the Nakagawa area, Hokkaido, Japan. *Paleontolog Res* 7(4):329–342
- Hoffmann R, Lemanis R, Naglik C, Klug C (2015) Ammonoid buoyancy. In: Klug C, Korn D, De Baets K, Kruta I, Mapes RH (eds) *Ammonoid paleobiology: from anatomy to ecology*, Topics in geobiology, vol. 43. Springer, New York, pp 613–648
- Howe B (1987) Tepee buttes: a petrological, paleontological, and paleoenvironmental study of Cretaceous submarine spring deposits. Thesis, University of Colorado
- Hryniewicz K, Nakrem HA, Hammer Ø et al (2014) The palaeoecology of the latest Jurassic–earliest Cretaceous hydrocarbon seep carbonates from Spitsbergen, Svalbard. *Lethaia* 48:353–374
- Hryniewicz K, Hagström J, Hammer Ø et al (2015) Late Jurassic–Early Cretaceous hydrocarbon seep boulders from Novaya Zemlya and their faunas. *Palaeogeog Palaeoclimat Palaeoecol* 436:231–244
- Hunter A, Larson NL, Landman NH et al (2016) A new crinoid from cold methane seep deposits in the Upper Cretaceous Pierre Shale. *J Paleontol* 90(3):506–524
- Ivany LC, Artruc EG (2016) Isotope ecology of a giant heteromorph ammonite from Antarctica. In: Abstracts with programs. Geological Society of America, pp 145–144
- Jacobs DK, Chamberlain JA Jr (1996) Buoyancy and hydrodynamics in ammonoids. In: Landman NH, Tanabe K, Davis RA (eds) *Ammonoid paleobiology*. Plenum, New York, pp 169–224
- Jacobs DK, Landman NH (1993) Is nautilus a good model for the function and behavior of ammonoids? *Lethaia* 26:1–12
- Jakubowicz M, Berkowski B, Hryniewicz K, Belka Z (this volume) Middle Palaeozoic of Morocco: the earliest-known methane seep metazoan ecosystems. In: Kaim A, Cochran JK, Landman NH (eds) *Ancient hydrocarbon seeps*, Topics in geobiology. Springer, New York

- Jenkins RG, Kaim A, Hikida Y et al (2007) Methane-flux-dependent lateral faunal changes in a Late Cretaceous chemosymbiotic assemblage from Nakagawa area of Hokkaido, Japan. *Geobiology* 5:127–139
- Kaim A, Kobayashi Y, Echizenya H et al (2008) Chemosynthesis-based associations on Cretaceous plesiosaurid carcasses. *Acta Palaeontol Pol* 54(1):97–104
- Kaim A, Jenkins R, Hryniewicz K et al (2016) Early Mesozoic seeps and the advent of modern seep faunas. In: Abstracts, 1st international workshop on ancient hydrocarbon seep and cognate communities, Warsaw, Poland, June 2016
- Kaim A, Little CTS, Kennedy WJ et al (2021) Late Cretaceous hydrothermal vent communities from the Troodos Ophiolite, Cyprus: systematics and evolutionary significance. *Pap Palaeontol* 7(4):1927–1947
- Kauffman EG, Arthur MA, Howe B et al (1996) Widespread venting of methane-rich fluids in Late Cretaceous (Campanian) submarine seeps (Tepee Buttes), Western Interior Seaway, U.S.A. *Geology* 24:799–802
- Kelly SRA, Blanc E, Price SP et al (2000) Early cretaceous giant bivalves from seep-related limestone mounds, Wollaston Forland, Northeast Greenland. In: Harper EM, Taylor JD, Crame JA (eds) *The evolutionary biology of the Bivalvia*, Geological society special publication, no. 177. Geological Society of London, London, pp 227–246
- Kiel S, Weiser F, Titus AL (2012a) Shallow-water methane-seep faunas in the Cenomanian Western Interior Seaway: no evidence for onshore-offshore adaptations to deep-sea vents. *Geology* 40(9):839–842
- Kiel S, Birgel D, Campbell KA, Crampton JS, Schiøler P, Peckmann J (2012b) Cretaceous methane-seep deposits from New Zealand and their fauna. *Palaeogeog Palaeoclimat Palaeoecol* 390:17–34
- Kiel S, Krystyn L, Demirtas F et al (2017) Late Triassic mollusk-dominated hydrocarbon-seep deposits from Turkey. *Geology* 45(8):751–754
- Klug C (2002) Quantitative stratigraphy and taxonomy of late Emsian and Eifelian ammonoids of the eastern Anti-Atlas (Morocco). *Cour Forschunginst Senckenb* 238:1–109
- Kruta I, Landman NH, Rouget I et al (2011) The role of ammonites in the Mesozoic marine food web revealed by jaw preservation. *Science* 331:70–72
- Landman NH (1988) Early ontogeny of Mesozoic ammonites and nautilids. In: Wiedmann J, Kullmann J (eds) *Cephalopods present and past*. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp 215–228
- Landman NH, Kennedy WJ, Cobban WA et al (2010) Scaphites of the 'nodosus group' from the Upper Cretaceous (Campanian) of the Western Interior of North America. *Am Mus Natl Hist Bull* 342:1–242
- Landman NH, Cobban WA, Larson NL (2012a) Mode of life and habitat of scaphitid ammonites. In: Neige P, Rouget I (eds) *Cephalopods present and past*, 8th international symposium, Dijon, 30 August 30–2 September 2010, vol 45. *Geobios*, pp 87–98
- Landman NH, Cochran JK, Larson NL et al (2012b) Methane seeps as ammonite habitats in the U.S. Western Interior Seaway revealed by isotopic analyses of well-preserved shell material. *Geology* 40:507–510
- Landman NH, Kennedy WJ, Cobban WA et al (2013) A new species of *Hoploscaphites* (Ammonoidea: Ancyloceratina) from cold methane seeps in the Upper Cretaceous of the U.S. Western Interior. *Am Mus Novit* 3781:1–39
- Landman NH, Cochran JK, Slovacek M et al (2018) Isotope sclerochronology of ammonites (*Baculites compressus*) from methane seep and non-seep sites in the Late Cretaceous Western Interior Seaway, USA: implications for ammonite habitat and mode of life. *Am J Sci* 318:603–639
- Landman NH, Witts JD, Garb MP et al (2019) Ammonites as an integral part of cold methane seep faunas: comparison of sites from the Upper Jurassic of France and the Upper Cretaceous of North America. In: Abstracts with programs. Geological Society of America, pp 197–195

- Landman NH, Cochran JK, Brezina J et al (this volume) Methane seeps in the Late Cretaceous Western Interior Seaway, USA. In: Kaim A, Cochran JK, Landman NH (eds) Ancient hydrocarbon seeps, Topics in geobiology. Springer, New York
- Larson NL (2003) Predation and pathologies in the Late Cretaceous ammonite family Scaphitidae. *Mid-Am Paleontol Soc (MAPS) Digest* 26(3):1–30
- Larson NL, Brezina J, Landman NH et al (2014) Hydrocarbon seeps: unique habitats that preserved the diversity of fauna in the Late Cretaceous Western Interior Seaway. https://www.academia.edu/4641897/Hydrocarbon_seeps_unique_habitats. Accessed 4 Nov 2021
- Little CTS, Birgel D, Boyce AJ et al (2015) Late Cretaceous (Maastrichtian) shallow water hydrocarbon seeps from Snow Hill and Seymour Islands, James Ross Basin, Antarctica. *Palaeogeog Palaeoclimat Palaeoecol* 418:213–228
- MacLeod KG, Hoppe KA (1992) Evidence that inoceramid bivalves were benthic and harbored chemosynthetic symbionts. *Geology* 20:117–120. [https://doi.org/10.1130/0091-7613\(1992\)020<0117:ETIBWB>2.3.CO;2](https://doi.org/10.1130/0091-7613(1992)020<0117:ETIBWB>2.3.CO;2)
- Meehan K, Landman NH (2016) Faunal associations in cold-methane seep deposits from the Upper Cretaceous Pierre Shale, South Dakota. *PALAIOS* 31(6):291–301
- Metz CL (2010) Tectonic controls on the genesis distribution of Late Cretaceous, Western Interior Basin hydrocarbon seep mounds (Tepee Buttes) of North America. *J Geol* 118:201–221
- Naglik C, Tajika A, Chamberlain J, Klug C (2015) Ammonoid locomotion. In: Klug C, Korn D, De Baets K, Kruta I, Mapes RH (eds) Ammonoid paleobiology: from anatomy to ecology, Topics in geobiology, vol. 43. Springer, New York, pp 649–688
- Peckmann J, Walliser OH, Riegel W et al (1999) Signatures of hydrocarbon venting in a Middle Devonian carbonate mound (Hollard Mound) at the Hamar Laghdad (AntiAtlas, Morocco). *Facies* 40:281–296
- Peckmann J, Little CTS, Gill F et al (2005) Worm tube fossils from the Hollard Mound hydrocarbon-seep deposit, Middle Devonian, Morocco: Paleozoic seep-related vestimentiferans? *Palaeogeog Palaeoclimat Palaeoecol* 227:242–257
- Peckmann J, Kiel S, Sandy MR et al (2011) Mass occurrences of the brachiopod *Halorella* in Late Triassic methane-seep deposits, eastern Oregon. *J Geol* 119:207–220
- Peterman DJ, Yacobucci MM, Larson NL, Ciampaglio C, Linn T (2020) A method to the madness: ontogenetic changes in the hydrostatic properties of *Didymoceras* (Nostoceratidae: Ammonoidea). *Paleobiology* 46(2):237–258
- Ritterbush KA, Bottjer DJ (2012) Westermann Morphospace displays ammonoid shell shape and hypothetical paleoecology. *Paleobiology* 38(3):424–446
- Rolin Y, Gaillard C, Roux M (1990) Ecologie des pseudobiohermes des Terres Noires jurassiques liés à des paléo-sources sous-marine: le site Oxfordien de Beauvoisin (Drôme, Bassin du Sud-Est, France). *Palaeogeog Palaeoclimat Palaeoecol* 80:79–105
- Rowe A, Landman NH, Witts J et al (2020) Late Cretaceous methane seeps as habitats for newly hatched ammonites. *PALAIOS* 35:1–13
- Ryan D, Witts JD, Landman NH (2020) Paleocological analysis of a methane seep in the Late Cretaceous (Maastrichtian) Western Interior, USA. *Lethaia* 54:185–203
- Saunders WB, Shapiro EA (1986) Calculation and simulation of ammonoid hydrostatics. *Paleobiology* 12:64–79
- Saunders WB, Ward PD (1987) Ecology, distribution, and population characteristics of *Nautilus*. In: Saunders WB, Landman NH (eds) *Nautilus: the biology and paleobiology of a living fossil*. Plenum, New York, pp 137–162
- Shapiro RS, Fricke H (2002) Tepee buttes: fossilized methane-seep ecosystems. In: Leonard EM et al (eds) High Plains to Rio Grande rift: Late Cenozoic evolution of Central Colorado, vol 3. Geological Society of America Field Guide, pp 94–101
- Smrzka D, Zwicker J, Kolonic S et al (2017) Methane seepage in a Cretaceous greenhouse world recorded by an unusual carbonate deposit from the Tarfaya Basin, Morocco. *Depositional Rec* 3(1):4–37

- Takeda Y, Tanabe K, Sasaki T et al (2016) Durophagous predation on scaphitid ammonoids in the Late Cretaceous Western Interior Seaway of North America. *Lethaia* 49(1):28–42
- Tanabe K, Kruta I, Landman NH (2015) Ammonoid buccal mass and jaw apparatus. In: Klug C, Korn D, DeBaets K et al (eds) *Ammonoid paleobiology*. Springer, Cham, pp 429–484
- Taylor DG, Guex J (2002) The Triassic/Jurassic system boundary in the John Day Inlier, east-central Oregon. *Geology* 64:3–28
- Tobin TS, Ward PD (2015) Carbon isotope ($\delta^{13}\text{C}$) differences between Late Cretaceous ammonites and benthic mollusks from Antarctica. *Palaeogeog Palaeoclimat Palaeoecol* 428:50–57
- Vidal EAG et al (2016) Cephalopod culture: current status of main biological models and research priorities. In: Vidal EAG (ed) *Advances in cephalopod science: biology, ecology, cultivation and fisheries*, *Advances in marine biology*. Elsevier, New York, pp 1–98
- Ward PD (1987) *The natural history of nautilus*. Allen and Unwin, Boston
- Wells MJ, Wells J (1985) Ventilation and oxygen uptake by *Nautilus*. *J Exp Biol* 118:297–312
- Westermann GEG (1996) Ammonoid life and habitat. In: Landman NH, Tanabe K, Davis RA (eds) *Ammonoid paleobiology*. Plenum, New York, pp 607–707
- Wierzbowski A, Hryniewicz K, Hammer Ø et al (2011) Ammonites from hydrocarbon seep carbonate bodies from the uppermost Jurassic-lowermost Cretaceous of Spitsbergen and their biostratigraphical importance. *Neues Jahrb Geol Palaontol Abh* 262(3):267–288
- Williscroft K, Grasby SE, Beauchamp B et al (2017) Extensive Early Cretaceous (Albian) methane seepage on Elleff Ringnes Island, Canadian High Arctic. *Geol Soc Am Bull* 129(7/8):788–805
- Witts JD, Little CTS (this volume) Fossil methane-seep deposits and communities from the Mesozoic of Antarctica. In: Kaim A, Cochran JK, Landman NH (eds) *Ancient hydrocarbon seeps*, *Topics in geobiology*. Springer, New York