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Inquilinism of a baculite by a dynomenid crab from the Upper Cretaceous of South Dakota

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ABSTRACT

We describe a small crab inside the phragmocone of a heteromorph cephalopod *Baculites* sp. smooth from the Gammon Ferruginous Member (lower Campanian) of the Pierre Shale in Butte County, South Dakota. The crab *Ferricorda kimberlyae* (Bishop, 1987) is well preserved with its carapace and pereiopods parallel to and between two septa of the phragmocone. Because of its superb preservation, the specimen is unlikely to have been washed into the phragmocone. The crab probably retreated into the phragmocone chamber to avoid predation or to molt and was subsequently buried by an influx of rapid sedimentation. This is the first instance of inquilinism by a crab in a heteromorph ammonite. Despite the rarity of such fossils, the occurrence of crabs inside ammonite shells was probably not uncommon on sea floors during the Mesozoic. Morphological details of the specimen reveal that *Ferricorda* is a dynomenid crab.

INTRODUCTION

Documenting biologic interactions and behavior in the geologic past is challenging. But in rare instances, the behavior is preserved in the fossil record. Today, regardless of where crabs live, they are prey for many organisms including octopuses, fish, birds, mammals, and even

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other crabs (Warner, 1977). To avoid predation, crabs have evolved an array of adaptations including a tough exoskeleton and camouflage and burrowing and sheltering behaviors. The type of shelter a crab makes or seeks is largely dependent on the environment in which it lives (see numerous examples cited within "Remarks" section in Schäfer, 1951; Williams, 1984). Crabs along rocky coasts build permanent homes between the rocks (Gilbey et al., 2008). In contrast, on a soft substrate, crabs can burrow into the sediment to build shelters (Waterman, 1960; Warner, 1977). Once the burrow is constructed, the crab continues to excavate and maintain it. In environments in which a permanent shelter is not an option, a crab can duck into anything available. Some crabs will conceal themselves under sea grasses (Hay et al., 1989) whereas others (*Inarchus*) live under the tentacles of sea anemones (Hartnoll, 1970). Stone crabs have been observed to seek shelter under large mollusc shells (Beck, 1995).

We document the presence of a crab inside the phragmocone of a baculitid ammonite (hereafter called a baculite) from the Pierre Shale of South Dakota. This occurrence represents an example of inquilinism, a term used by biologists to describe an association in which one animal lives inside the other, but does not harm the host (Fraaye and Jäger, 1995a, 1995b). In this instance, the crab occupied an empty ammonite shell, using it as a temporary, but ultimately fatal shelter. The Late Cretaceous Western Interior Seaway, as represented by the Pierre Shale, was characterized by a muddy, occasionally, anoxic bottom. If enough shell debris accumulated in a single place, a hard substratum could develop (Landman and Klofak, 2012), but most of the sea floor was soft, with nowhere to hide. In such circumstances, empty mollusc shells may have been the best option for shelter. The abundance of baculites and crabs at the study site suggests that a crab-baculite association was probably fairly common.

GEOLOGIC SETTING

One of the most fossiliferous sites in the Upper Cretaceous of the Western Interior of North America occurs in the upper part of the Gammon Ferruginous Member of the Pierre Shale on the north flank of the Black Hills Uplift at the Heart Tail Ranch, Butte County, South Dakota (figs. 1, 2). The locality was described by Gill and Cobban (1966), Robinson et al. (1964), and Bishop (1985a). The fossiliferous interval is bounded by the Groat Sandstone below and Bentonite "H" of Knechtel and Patterson (1956) above. The interval is approximately 20 m thick and consists of bentonitic silty shale containing large grayish-red to blackish-red sideritic concretions and small grayish-orange apatite concretions (fig. 3). It occupies the lower Campanian *Baculites* sp. smooth Zone and crops out over an area of more than 8 km^2.

Baculites are extremely abundant in a 4 m thick interval representing tens of thousands of specimens, forming what Bishop (1985a) called a "baculite epibole." Nearly all the specimens are large and presumably mature; they consist of both macroconchs and microconchs. They occur loose in the shale and in sideritic concretions. The baculites are steinkerns, commonly with pieces of aragonitic outer shell still attached. They bear traces of muscle scars and encrustation by epizoans (Klinger and Kennedy, 2001; Henderson et al., 2002; Larson, 2012).

Decapod crustaceans are also very abundant, particularly in a 7 m thick interval just above the peak abundance of *Baculites* sp. smooth, called the "crab epibole" by Bishop (1985a). The crustacean fauna is dominated by *Protocallianassa*, *Necrocarcinus*, and *Hoploparia* and is slightly older than the *Dakoticancer* Assemblage, which first appears in the upper Campanian *Exiteloceras jennyi* Zone (Bishop, 1985a). Most of the crabs are preserved in apatite concretions (Bishop, 2007). Other faunal elements in the Gammon Ferruginous Member at this site are much less abundant than the baculites and decapod crustaceans. They include the ammonites *Placenticeras*, *Platyscaphites*, and *Pachydiscus* (a handful of specimens), bivalves, gastropods, scaphopods, bony fish, sharks, and mosasaurs.

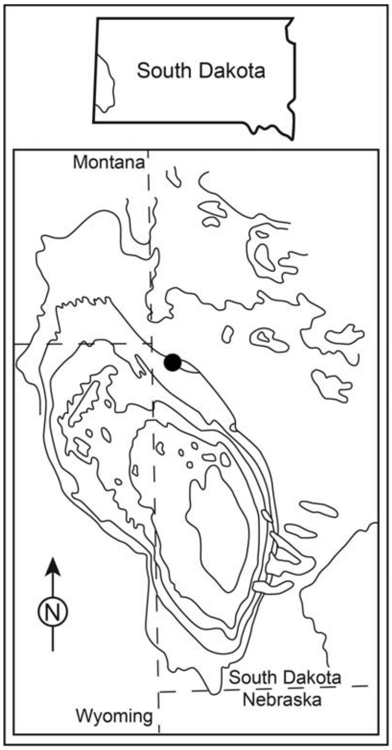

FIGURE 1. Map of AMNH loc. 3296 (dot), *Baculites* sp. smooth Zone, Gammon Ferruginous Member of the Pierre Shale, N1/2 sec. 27 T. 11 N., R. 2 E., north of Belle Fourche, Antelope Butte quadrangle, Butte County, South Dakota (modified after Bishop, 1985a).

DESCRIPTION OF CRAB-BACULITE ASSOCIATION

AMNH 47103 consists of a crab inside a piece of a baculite phragmocone (fig. 4). The phragmocone is composed of a single chamber 37.8 mm high, with a septum on each end, known as a "buffalo stone" by the Plains Indians (Landman, 1983; Larson, 2012). The crab is squeezed against one of the septa, which is partly broken. The carapace faces the anterior end of the baculite and rests with its horizontal plane at a nearly perpendicular angle to the long axis of the phragmocone. When first collected, only the carapace was visible where the septum of the phragmocone was partly broken. Careful preparation completely revealed the specimen, including all of the attached pereiopods. The phragmocone does not contain any fecal pellets or shell debris.

The crab is approximately 15 mm wide and 14 mm long. The carapace is separated into three transverse regions by the deep cervical and branchial grooves. It is nearly circular and strongly arched longitudinally and transversely. The rostrum is triangular and downturned. The anterolateral margin is keeled but not tuberculate. The transverse grooves are strong, but the medial groove becomes obsolete posteriorly in the intestinal region. A well-developed postcervical groove bisects the inflated epibranchial region transversely.

The remains of all five pereiopods are preserved. The cheliped is compact and subrounded and the propodus is coarsely reticulate. The fingers are not preserved. The carpus is narrow and sculptured and the merus is robust and triangular. Pereiopods 2, 3, and 4 (ambulatory legs) are smooth and tubiform, and are two to three times longer than broad. The dactyli are indented on the anterior end by a pronounced longitudinal furrow. The propodi are also tubular and

FIGURE 2. AMNH loc. 3296, South Dakota. **A.** Overview of the outcrop with students for scale. **B.** Close-up of a baculite body chamber with pieces of the outer shell wall still attached. Length of baculite ≈ 20 cm. **C.** Broken fragments of baculites. Length of the fragment in the foreground ≈ 5 cm. **D.** Nearly complete baculite with body chamber extending to the upper left and phragmocone to the lower right. Length of baculite ≈ 30 cm.

smooth, approximately two times longer than broad, with some irregular pits, and with a similar longitudinal furrow anteriorly. The carpi are smooth and triangular. The meri are not exposed, but a CT scan of one of the left pereiopods reveals that the merus is tubular and approximately five times longer than broad (fig. 5).

The crab is identified as *Ferricorda kimberleyae* (Bishop, 1987). This species was originally assigned to *Dromiopsis* based on two specimens from this locality (Bishop, 1987). The carapace of the holotype is 19.8 mm wide and 19.1 mm long. Three more specimens were described by Schweitzer and Feldmann (2010: 426) who reassigned this species to *Ferricorda* based on morphological details of the carapace. It is one of nine species of early Campanian decapod crustaceans from the Heart Tail Ranch locality (Bishop 1985a, 1987).

Schweitzer and Feldmann (2010) placed *Ferricorda* in the family Sphaerodromiidae within the Dromioidea. However, the presence of a reduced pereiopod 5 and a nonreduced pereiopod 4 in *Ferricorda* suggests that this species is better assigned to the Dynomenidae (Van Bakel and Guinot, in press). In the Dynomenidae, pereiopod 5 is reduced and carried subdorsally while the fully developed pereiopod 4 functions as a walking leg. In the Dromiidae, in contrast, pereiopods 4 and 5 are reduced and carried (sub)dorsally (e.g., Guinot et al., 2013). Based on carapace morphology, *Ferricorda* appears closely related to the Eocene dynomenid genus *Eotrachynotocarcinus* (see Beschin et al., 2007: pls. 2, 3).

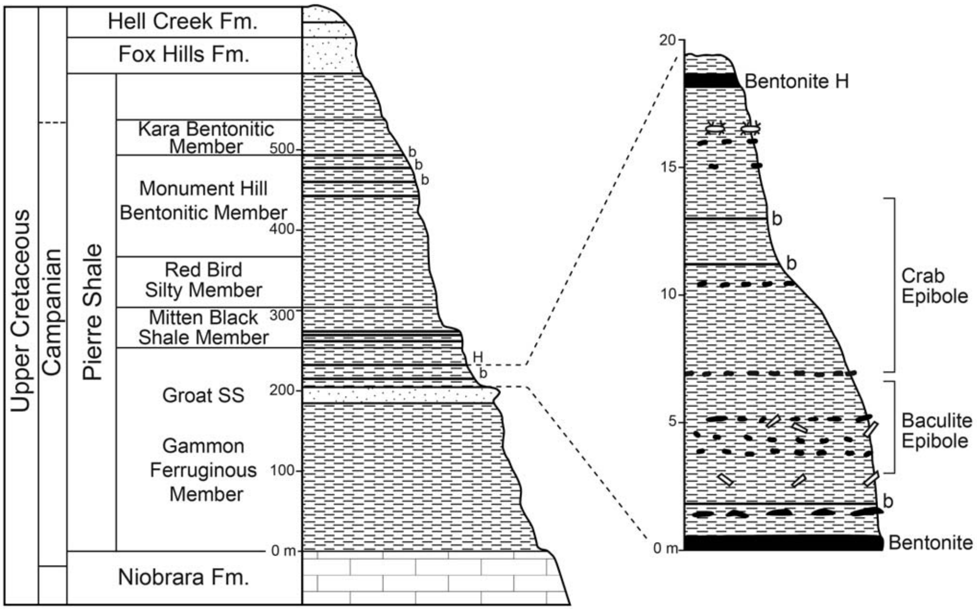

FIGURE 3.Stratigraphic section of the Pierre Shale at AMNH loc. 3296 showing the baculite and crab epiboles (modified after Bishop, 1985a). Abbreviation: **b,** bentonite.

ENVIRONMENT OF DEPOSITION

During the time of deposition of the Gammon Ferruginous Member, the exact position of the shoreline relative to the Heart Tail Ranch is unknown. However, during the time of deposition of the slightly younger *Baculites obtusus* Zone, the shoreline was approximately 400 km to the west (Cobban et al., 1994). The sea was probably approximately 100 m deep with normal or slightly brackish salinity (Gill and Cobban, 1966). Based on oxygen isotopic analyses of ammonite shells and jaws, Kruta et al. (2014) estimated that the temperature of the water averaged 28°C. During this time, the seaway was periodically covered with volcanic ash, forming bentonitic muds.

Bishop (1987) hypothesized that the periodic ash falls may have changed the chemistry, temperature, and turbidity of the water causing the death of the plankton. According to him, the nutrient flux to the bottom would have resulted in a rapid increase in the population of infaunal deposit feeders, mostly polychaete worms. This would have, in turn, caused an explosion of the crab population, which fed on the worms. After exhausting the supply of worms, the population of crabs would have itself crashed, thus providing a new source of food for the worms. The presence of giant sulfur-mediating bacteria, such as *Thiomargaritta* (Schulz et al., 1999), in the anoxic mud of the Late Cretaceous sea bottom is thought to have resulted in the phosphatization of the decapod assemblages (Bishop and Williams, 2005). This sequence of events can explain the periodic appearance and disappearance of fossiliferous assemblages of crabs and infaunal deposit feeders at the Heart Tail Ranch and elsewhere in the Pierre Shale of the U.S. Western Interior.

The ash falls may also have contributed to the periodic death of the nekton, including the baculites. Kruta et al. (2011) examined the morphology of the buccal apparatus in these ammonites. It consists of a large shovellike lower jaw and a radula with thin delicate teeth.

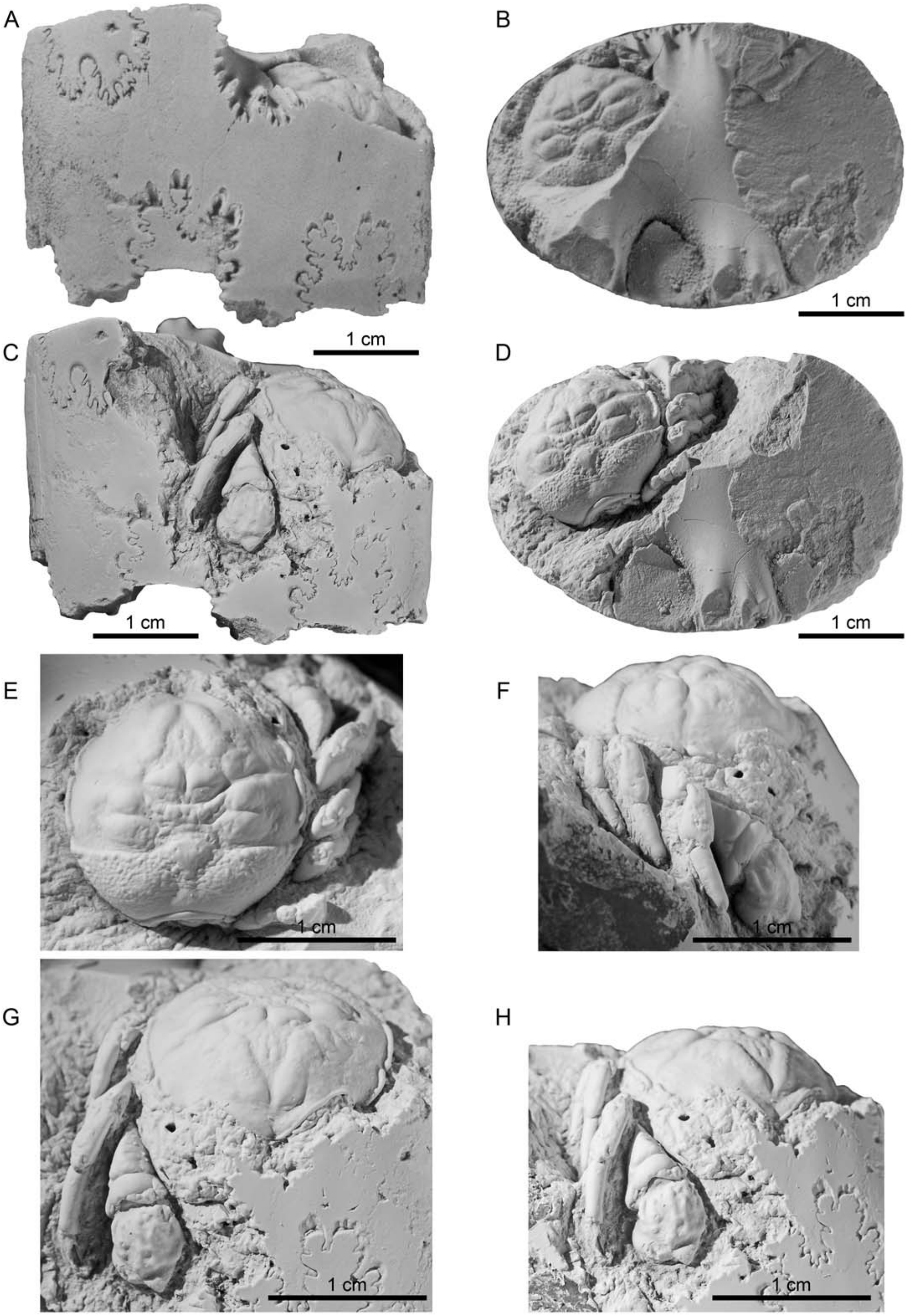
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FIGURE 4. **A.** Right side of AMNH 47103 before preparation of the crab. The carapace is visible on top right. **B.** Adoral side of the baculite before preparation of the crab. The specimen is rotated 180° from A, so that the crab is better exposed. **C.** Right side of the baculite after preparation. Legs 1–3 and the cheliped of the crab are visible. **D.** Adoral side of the baculite after preparation. The specimen is rotated 180° from C, so that the crab is better exposed. **E.** Close-up of the crab showing the carapace, anterior of the abdomen, legs 1–4, and cheliped. **F.** Lateral view of the right side of the crab showing legs 1–4 and the cheliped. The merus, carpus, and propodus are visible on the legs. **G.** Anterior view of the crab showing the anterior portion of the carapace, cheliped, and legs 1 and 2. **H.** Right anterior view of the crab showing the first three legs and the cheliped. The carpus and propodus are visible and perhaps the dactylus on the first leg.

Kruta et al. (2011) argued that this buccal apparatus was designed to filter plankton. The volcanic ash would have increased the turbidity of the water, making the filtering process more difficult or even impossible. In addition, if the plankton were killed, the baculites would have simply starved to death. Nearly all of the baculites at the site are mature and consist of both dimorphs, suggesting that they may have migrated into the area to mate and spawn (Larson et al, 2010). However, no ammonite embryonic shells have yet been discovered in the sediment to support this hypothesis.

The rates of sedimentation at the study site must have varied over time, alternating between short events of rapid sedimentation followed by longer periods of nondeposition. The presence of jaws preserved inside the body chambers of several baculites from this locality (Landman et al., 2007) testifies to the fact that these specimens were buried rapidly. Using CT scanning, Kruta et al. (2011) identified even delicate radular teeth nestled between the upper and lower jaws in some specimens. Evidently, these baculites must have been buried before the soft parts decomposed. Similarly, the crab inside the broken phragmocone that we describe must have been buried rapidly enough to preserve the pereiopods. Such episodes of rapid burial may have been due to occasional currents associated with storms or enhanced river discharge.

However, for most of the time, the rate of sedimentation must have been relatively slow. One piece of evidence in support of this hypothesis is the presence of encrusting organisms on the inside surfaces of baculite shells, indicating that the shells must have rested on the sea floor for some time before burial. For example, internal molds of baculites are commonly covered with ctenostome bryozoans called *Pierrella larsoni* Wilson and Taylor, 2013, which are preserved as pits on the inside surface of the shell wall (fig. 6A). The attachment bases of the bryozoan zooecia are oval to teardrop shaped. The zooecia are arranged in lines with narrow tubular connections. As soon as the bryozoan attached to the shell, it effectively protected the part of the shell immediately below it from dissolution on the sea floor (Palmer et al., 1993). Gill and Cobban (1966: A40) reported this same phenomenon in baculites from the Pierre Shale at Red Bird, Wyoming, and stated “the depth of each pit (as much as 0.1 mm) represents the amount of shell dissolved between the time that the zooecium was formed and the time that it was covered by sediment. The floor of the pits on internal molds of some of the ammonites is lined with nacreous shell, which also shows that the shell was once thicker.”

Other epizoans that encrusted the inside surface of baculite shells are limpets probably belonging to *Anisomyon* (fig. 5B). For example, in AMNH 64711, the left side of the internal mold of the body chamber is covered with five limpets. The bases of the limpets face toward

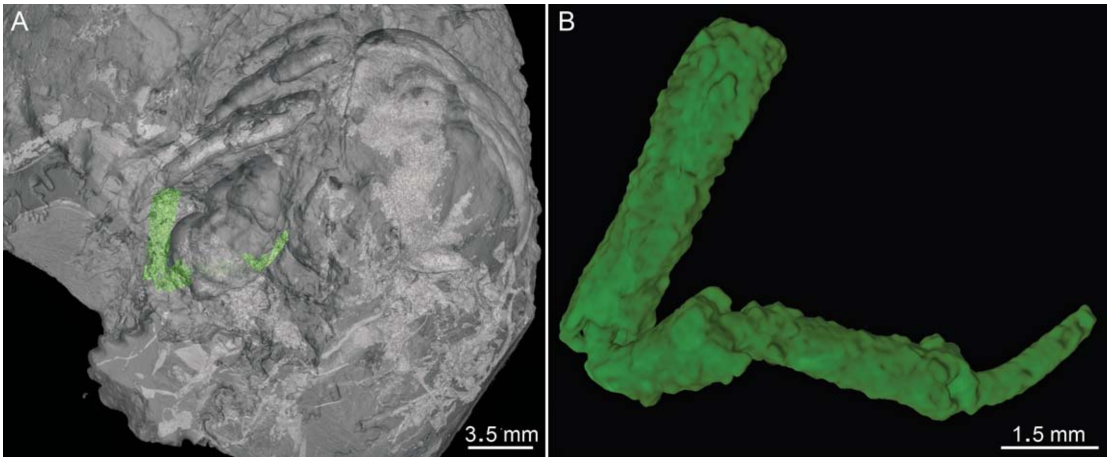

FIGURE 5. CT scan of AMNH 47103. **A.** Surface rendering of the crab (view most similar to that in 4G). The green shading shows the pereiopod embedded in the matrix. **B.** 3-D reconstruction of the pereiopod (generated with the Phoenix V|tomex CT scanner at the AMNH; 240 kv; voxel size = 25 μm; segmentation = VG Studio Max Volume Graphics).

the outside of the internal mold, indicating that the animals were encrusted on the inside surface of the shell. The limpets are oval, approximately 2.0 mm long and 1.5 mm wide. Although Gill and Cobban (1966: A27, pl. 11, figs. 1, 2) did not report any limpets on baculites from Red Bird, Wyoming, they noted the presence of minute scratchlike marks, each consisting of from four to six parallel bars. They argued that these scratches were caused by the rasping action of an organism, presumably a limpet, on the inside surface of the empty body chamber (for a further discussion about these scratches, see Akpan et al., 1982).

Many baculite internal molds are covered with small pits (fig. 6C–E). The pits occur on the body chamber, not the phragmocone, and are more common near the adoral end. The pits are circular to elliptical, 0.3 to 0.8 mm in diameter, and 0.2 mm in depth. Traces of shell material are sometimes preserved on the bottom of the pits. The pits correspond to pedestals on the inside surface of the shell. Gill and Cobban (1966: A27) noted such pits on the internal molds of baculites from Red Bird, Wyoming, and stated that they "represent the attachment area of some small organisms that lived near the open end of empty baculite shells. Each of these very small attachment areas on the baculite shells was shielded from dissolution by sea water. Inasmuch as the surface of the shell not covered by these organisms was dissolved to some extent, the attachment areas now appear as pits on the internal molds of living chambers." An alternative explanation has also been suggested, namely, that the pits mark the attachment sites of egg capsules laid down inside the empty body chamber, possibly by baculites themselves (Larson et al., 2010; Larson, 2012). According to this interpretation, the baculites of one generation laid their eggs in the empty shells of a previous generation (for a recent discussion about ammonite eggs, see Etches et al., 2008).

In both of these interpretations, the pits would have formed in the empty baculite shells after the death of the ammonites. In contrast, Klinger and Kennedy (2001: 102, figs. 81, 82) proposed that the structures were caused by an infestation of parasites during the lifetime of the baculites. They noted that some of the pillars on the inside surface of the shell wall corresponding to the pits are hollow rather than solid. This could have resulted only from the decay of an organic body. According to this hypothesis, the pillars are blister pearls formed by the baculites during their lifetime. Indeed, blister pearls are a common phenomenon in molluscs, especially bivalves (Landman et al., 2001), and have also been reported from Devonian ammonoids (DeBaets et al., 2011).

Another indication that empty baculite shells rested on the sea floor for some time is the ubiquitous presence of fecal pellets (fig. 6F–H). Fecal pellets have been widely reported in the living chambers of ammonites from the Pierre Shale of the U.S. Western Interior (Gill and Cobban, 1966; Bishop, 1981). The pellets are sometimes concentrated in burrows, but more commonly are scattered throughout the shell. They vary in shape from ovoid to spherical and in size from 0.25 to 3.0 mm. Most of them are solid in cross section, but some of the larger pellets show a more complex morphology. The majority of fecal pellets were undoubtedly produced by infaunal deposit feeders, for example, polychaete worms. However, the larger pellets with a more complex internal structure could represent crustacean microcoprolites (fig. 6G) (for a description of crustacean microcoprolites preserved in ammonite shells, see Kietzmann and Palma, 2014). Such microcoprolites would have been produced by crabs living inside the baculite shells.

EXPLANATION OF CRAB-BACULITE ASSOCIATION

With the abundance of crabs and empty shells of baculites on the sea floor, we argue that the crab inside the phragmocone in our study (AMNH 47103) is an example of inquilinism by a crab in a heteromorph ammonite. Because of its superb preservation with all five pereiopods, the crab is unlikely to have been washed into the phragmocone. If hydraulic processes were responsible, the crab would have been more disarticulated, and possibly associated with stray pieces of shell debris. The excellent preservation also suggests that the crab is a corpse and not a molt. The crab probably retreated into the phragmocone chamber through a breach in the outer shell or septum and was subsequently buried by an influx of rapid sedimentation. The fact that the carapace is squeezed against one of the septa and lies at a right angle to the horizontal indicates that it was transported forward and rotated 180° perhaps due to the compaction and pressure of the viscous mud.

The cooccurrence of tens of thousands of baculite shells (Landman et al., 2007) and hundreds of decapod crustaceans (Bishop, 1985a) at the same locality suggests that an inquiline preservation of decapods in baculite shells must have been very common at this site, although this is the only specimen known to date. This crab was exposed thanks to a fortuitous break in the baculite shell, but surely other such specimens are present and await discovery.

The crab probably entered the baculite shell to avoid predation. Examples of predation on crabs are very rare in the fossil record, but Bishop (1972) reported an injured specimen from the lower Maastrichtian *Baculites grandis* Zone of the Pierre Shale in South Dakota, which was bitten by a small fish. Jäger and Fraaye (1997) also documented the remains of small decapod crustaceans in the stomach contents of large ammonite shells from the lower Toarcian Posidoni-

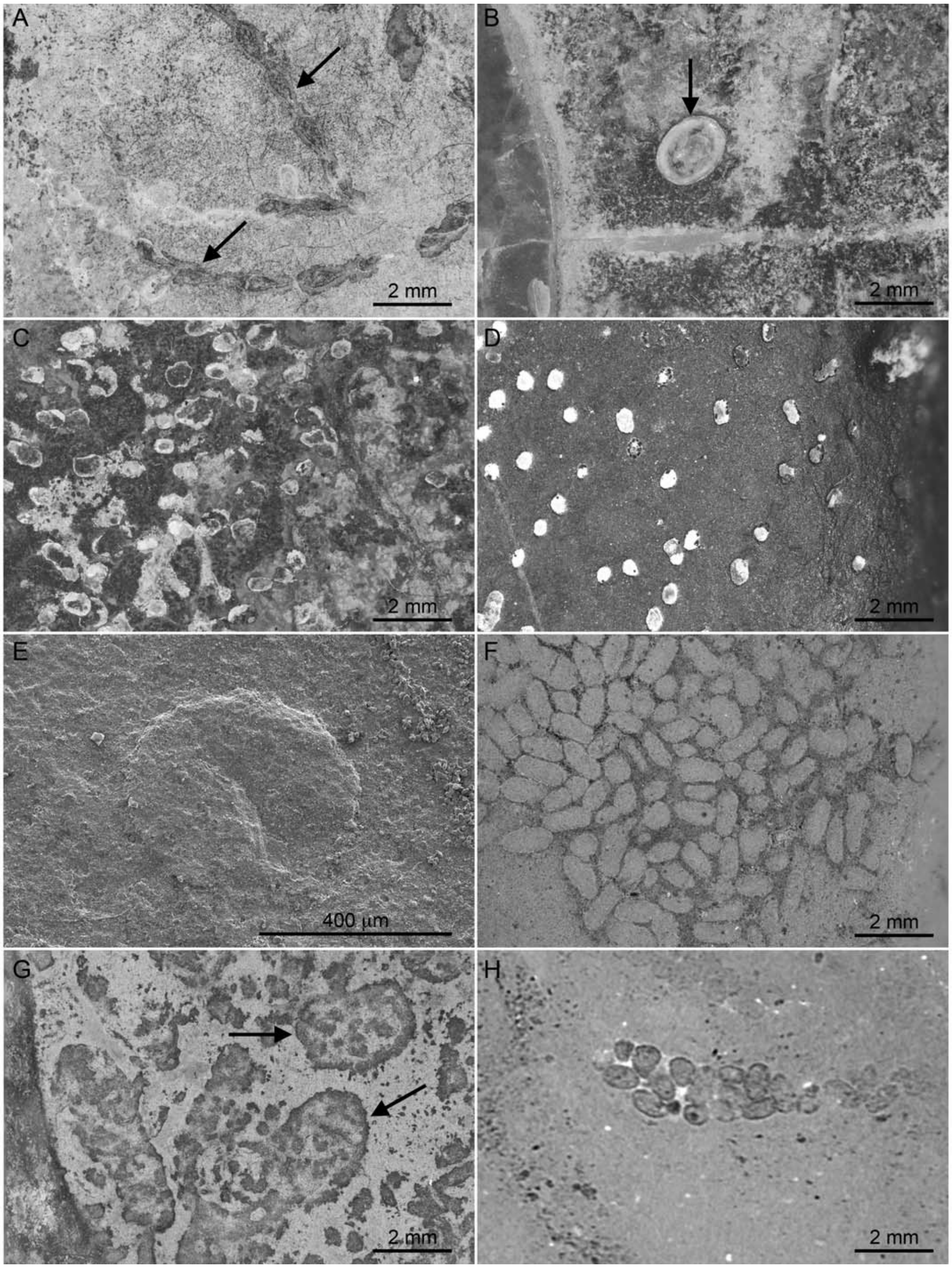

FIGURE 6. Evidence of postmortem encrustation of baculite shells on the sea floor during deposition of the Gammon Ferruginous Member of the Pierre Shale, Butte County, South Dakota (AMNH loc. 3296 and nearby sites on the Heart Tail Ranch). **A.** Ctenostome bryozoan *Pierrela larsoni* Wilson and Taylor, 2012 (arrow) on the internal mold of a baculite, AMNH 51795. **B.** Close-up of a limpet (arrow) on the internal mold of a baculite, AMNH 64711. The base of the limpet faces toward the outside of the internal mold. **C.** Pits on the surface

enschiefer in southern Germany. Indeed, in the face of danger, ammonite shells must have provided some of the few places for a crab to hide on the fine-grained sea bottom of Mesozoic seas (Fraaye and Jäger, 1995a).

Inquilinism in the Fossil Record of Cephalopods

Fossil evidence for the sheltering behavior of crabs is scarce. However, crabs have been reported in association with burrows (Glaessner, 1969; Sellwood, 1971; Richards, 1975; Stillwell et al., 1997; Bishop, 1986b, fig. 3; 1988; Bishop et al., 1998: 248; Bishop and Williams, 2005), crevices in reefs and bioherms (Müller et al., 2000; Garassino and Krobicki, 2002; Fraaije, 2003), eel grass beds (Fraaije, 2003), mangroves (Schweitzer et al. 2003), and molluscan shells (Glaessner, 1969; Bishop, 1985b, 1986a, 1986c).

Most examples of decapod crustaceans preserved within cephalopod shells come from the Jurassic of Europe. Klompmaker and Fraaije (2012: table 2) reported three lobsters inside an ammonite body chamber from the lower Toarcian Posidonienschiefer. The lobsters form a tight cluster with their tails oriented toward each other. The lobsters must have entered the shell while it was still lying on the seafloor, possibly to avoid predation. Alternatively, they may have been attracted to the decomposing body of the ammonite as a source of food. Fraaye and Jäger (1995a) reported another example of a single lobster (*Palaeastacus*?) inside the body chamber of an ammonite from the same locality. The lobster is surrounded by masses of elliptical to subspherical pellets 1.5–2.0 mm in diameter, which are interpreted as crustacean microcoprolites. This association suggests that the lobster was a long-term resident of the ammonite shell.

A few examples of inquilinism by crustaceans in ammonite shells have also been reported from the Cretaceous of Europe. Wright and Collins (1972: pl. 10, figs. 1a, b) described a more or less complete specimen of a brachyuran crab *Diaulax* inside the body chamber of a Cenomanian ammonite from Somerset, England. Kennedy (2013: 466, text-fig. 12) described a small specimen of the lobster *Palaeastacus* inside the body chamber of *Schloenbachia* from the lower Cenomanian of Western Kazakhstan. The specimen consists of the carapace and associated thoracic segments pressed against the curved surface of the venter. The anterior of the lobster faces the aperture of the body chamber. Ernst (1967: 219) documented a long chela (3 cm in length) of a brachyuran crab inside the body chamber of *Pachydiscus* from the Campanian of Germany.

Crabs also inhabited the empty shells of nautilids, either for temporary refuge or more permanent residence. Fraaije and Pennings (2006) reported brachyuran crabs inside shells of *Eutrephoceras* from the upper Paleocene of Spain. Two of the crab specimens (*Glyphithyreus* and *Palaeocarpilius*) occur inside a body chamber and the third specimen (*Eocarpilius*) occurs inside a broken phragmocone.

of the internal mold of a baculite, AMNH 64692. **D.** Pits on the surface of the internal mold of a baculite, AMNH 64712. **E.** Close-up of a pedestal on the inside surface of the outer shell wall, which corresponds to a pit on the internal mold of the baculite, AMNH 63586B. **F.** Cluster of fecal pellets in a burrow in the internal mold of a baculite, AMNH 52365. **G.** Large fecal pellets with a complex internal structure (arrows) in the internal mold of a baculite, AMNH 64963. The pellets could represent crustacean microcoprolites. **H.** Cluster of fecal pellets in the internal mold of a baculite, revealed by CT scanning, AMNH 66253.

Interestingly, an inquiline mode of preservation has even been reported for Paleozoic trilobites inside the shells of orthoconic nautiloids, indicating a long-term association between arthropods and cephalopod shells. Davis et al. (2001) reported trilobites inside nautiloid shells from the Ordovician of North America and the Silurian of Wales and the Czech Republic. Based on the preservation and mode of occurrence of these fossils, the authors argued that the trilobites entered the empty nautiloid shells to seek refuge. Ladd (1928: 387) also noted the association between nautiloids and trilobites and stated, "Evidently the dead shells of the large cephalopods served as retreats or molting places for *Vogdesia* [a genus of trilobites] because rolled specimens of the trilobite can frequently be obtained by breaking the body chambers of the cephalopods. Indeed the surest way to obtain perfect specimens is to…crack open all the water-worn cephalopods encountered."

CONCLUSIONS

The specimen of *Ferricorda* in a piece of a baculite phragmocone described here is an example of inquilinism by a crab in a heteromorph ammonite. The crab probably retreated into the broken phragmocone chamber and was subsequently buried by an influx of rapid sedimentation. Although this phenomenon is not well documented in the fossil record, the use of empty ammonite shells by decapod crustaceans must have been fairly common on the fine-grained sea floors of Mesozoic seas where rock ledges and other crevices were unavailable for shelter. However, few scientists dare to split the body chamber of a well preserved ammonite in the hopes of finding sheltering organisms inside. The best approach to enrich our knowledge of the inquiline use of cephalopod shells is CT scanning.

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