

Encrustation of inarticulate brachiopods on scaphitid ammonites and inoceramid bivalves from the Upper Cretaceous U. S. Western Interior

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ABSTRACT:

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The inarticulate brachiopod *Discinisca* is a rare faunal element in the Upper Cretaceous of the U.S. Western Interior. We report two occurrences of encrustation of *Discinisca* on a scaphitid ammonite (scaphite) and several inoceramids from the lower Maastrichtian *Baculites baculus/Endocostea typica* Biozones of the Pierre Shale at two localities. Six specimens of *Discinisca* are present on a single specimen of *Hoploscaphites crassus* from east-central Montana. They occur along the furrow at the mature apertural margin. Because the brachiopods are restricted to the margin and do not occur on the rest of the shell, it is likely that they encrusted the ammonite during its lifetime. If so, this implies that the soft body of the scaphite did not cover the outside surface of the aperture, leaving this area vulnerable to epizoan attachment. A total of 13 specimens of *Discinisca* are also present on four specimens of *Cataceramus? barabini* from east-central Wyoming. The brachiopods occur in crevices on the outside of the shells and may have encrusted the inoceramids after their death as the shells began to break down and delaminate, resulting from the decomposition of the organic matrix holding them together. Based on the faunal assemblages at both localities, the presence of *Discinisca* may indicate environments with either low oxygen levels and/or few predators or competitors.

Key words: Inarticulate brachiopods; Pierre Shale; Maastrichtian; Inoceramids; Ammonites; Encrustation.

INTRODUCTION

The presence of epizoans can reveal critical clues about the paleoenvironments they inhabited and the paleobiology and taphonomy of the animals they encrusted. One of the epizoans that has received wide attention is the inarticulate brachiopod *Discinisca* (e.g.,

Seilacher 1960; Watson 1982; Harries 1993; Bitner *et al.* 2010). However, in spite of these studies, this brachiopod is rare in the fossil record because it tends to occur in cryptic habitats and its organophosphatic shell readily degrades during early diagenesis (Emig 1983, 1990, 1997). In addition, it is not well cemented to the substratum but is attached instead by an organic thread, i.e.,

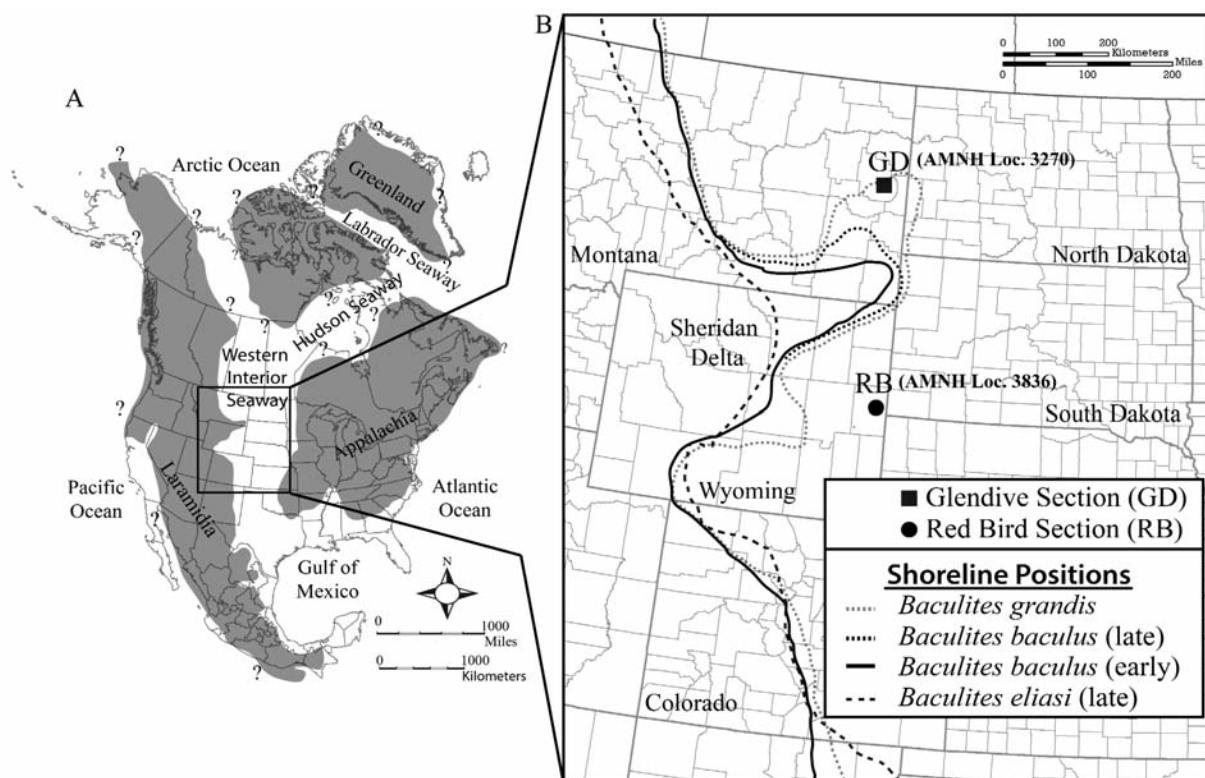
the pedicle, which decays after death (Taylor and Todd 1990; Wilson and Taylor 2001). Its rarity is also probably due to its small size and a collecting bias towards larger and more conspicuous taxa.

Although the Upper Cretaceous U.S. Western Interior contains one of the best known faunas in the world, the record of brachiopods in this area is very poor compared to coeval sequences elsewhere, such as in Europe (e.g., Bitner and Pisera 1979; Owen 2002). The rarity of brachiopods, most notably articulate forms, in this region is thought to be the result of relatively inhospitable environmental conditions including low-oxygen concentrations and brackish water (Kauffman and Caldwell 1993). Most reported occurrences of brachiopods in the U.S. Western Interior have been restricted to the inarticulate brachiopod *Lingula*, as documented in published and unpublished faunal lists in paleontological reports and dissertations (e.g., Davidson 1966; Gill and Cobban 1966). However, only a small number of these papers include detailed descriptions of the brachiopods (e.g., Warren 1937; Kirkland 1996; Sava 2007). *Discinisca* has previously been reported from the Cenomanian–Turonian boundary interval of Arizona, Utah, Colorado, Kansas, Nebraska, South Dakota, and Montana (Elder 1987; Harries 1993a, 1993b; Kirkland 1996) as well as the upper Campanian of Colorado (Sava 2007).

Here we document the occurrence of *Discinisca* in the lower Maastrichtian Pierre Shale of Montana and Wyoming. It is present on a scaphitid ammonite (hereafter called a scaphite) and several inoceramid bivalves in the same biostratigraphic interval. The presence of this inarticulate brachiopod reveals clues about the paleoenvironment of the Western Interior Seaway (WIS) and the paleobiology of the scaphite and the inoceramids, both of which are extinct organisms.

GEOLOGICAL AND GEOGRAPHICAL SETTING

During the Late Cretaceous, the WIS extended from Mexico to the western Canadian Arctic flooding the actively subsiding Western Interior Foreland Basin (Text-fig. 1). This basin was delineated by the active Cordilleran Orogenic Belt to the west and the low-lying stable platform of the conterminous United States and



Text-fig. 1. Location of the study areas within the context of the reconstructed paleogeography of the Late Cretaceous Western Interior Seaway. A – Generalized map of North America showing land distribution during the deposition of the lower Maastrichtian *Baculites baculus* Biozone (shoreline based on Gill and Cobban 1973; Slattery *et al.* 2015). B – Map showing the location of Glendive, Dawson County, Montana, and Red Bird, Niobrara County, Wyoming, and the position of the western shoreline of the Western Interior Seaway, as reconstructed by Cobban (unpublished maps), Reiskind (1975), and Slattery (in review) for the upper Campanian *Baculites eliasi* Biozone to lower Maastrichtian *Baculites grandis* Biozone (modified from Slattery *et al.*, in revision)

Canada to the east. During the early Maastrichtian (the age of the specimens examined here), the western shoreline of the Seaway prograded basinward due to a fall in eustatic sea level as well as the influence of the regional uplift associated with the onset of the Laramide Orogeny. These combined effects culminated in the final retreat of the WIS from North America during the Paleocene (for a more detailed review, see Slattery *et al.* [2015] and references therein).

The specimens used in this study were collected from the offshore-marine Pierre Shale, which was deposited during the Campanian to Maastrichtian. This unit consists of shales and silty shales intercalated with concretionary horizons, which likely represent flooding surfaces (or parasequence boundaries). The Pierre Shale covers parts of Montana, North Dakota, South Dakota, Colorado, Nebraska, New Mexico, Kansas, and Wyoming (Cobban and Reeside 1952; Landman *et al.* 2010). The specimens used in this study consist of one scaphite and four inoceramids, all of which are encrusted by the epibiont *Discinisca*. This species of *Discinisca* has not yet been described and we simply refer to it as *Discinisca* rather than *Discinisca* sp. All specimens are deposited at the American Museum of Natural History, New York, New York (AMNH).

LOCALITIES

The *Discinisca*-encrusted scaphite is from the Pierre Shale at AMNH locality 3270 along the Cedar Creek Anticline south of Glendive, Dawson County, Montana (Text-fig. 1). This area was described previously by Bishop (1967, 1973), Grier and Grier (1992, 1998, 2007), and Walaszczyk *et al.* (2001). The specimen is from the layer designated as “scaphite concretions” by Bishop (1973), which occurs approximately 1 m below a distinctive 7.5-cm-thick bentonite. According to Bishop (1973), the base of this layer coincides with the base of the lower Maastrichtian *Baculites baculus* Biozone (Text-fig. 2A).

The *Discinisca*-encrusted inoceramids are from AMNH locality 3836 at the informal Pierre Shale reference section exposed along the Old Woman Creek Anticline near Red Bird, Niobrara County, Wyoming (Text-fig. 1), previously described by Gill and Cobban (1966) and Hicks *et al.* (1999). The specimens were collected from a limestone concretionary horizon 44 m above the base of the upper unnamed shale member in the lower Maastrichtian *Baculites baculus/Endocostea typica* Biozones. This biostratigraphic assignment is supported by the presence of abundant specimens of *E. typica* and rare specimens of juvenile *B. baculus* in concretions 10 m be-

low this horizon (Text-fig. 2B). Additional, but isolated, *Discinisca* specimens were also identified at 31 and 77 m above the base of the upper unnamed shale member in the *Baculites baculus* Biozone (Text-fig. 2B).

ASSOCIATED FAUNA

The faunal assemblage in the scaphite concretionary layer at Glendive, Montana, has previously been described by Bishop (1967) and Landman *et al.* (2015). As the name implies, this layer is dominated by scaphites, mainly *Hoploscaphites crassus* and *H. plenus*. In addition to five cephalopod species, this layer also contains 38 invertebrate species including bivalves, gastropods, scaphopods, corals, echinoids, and bryozoans, as well as fish bits, trace fossils, and plant remains (see Appendix, Table 1 for a complete species list including the author and date of each species, as given in the references). The benthos is dominated by infaunal (e.g., *Nucula*) and semi-infaunal (e.g., *Dentalium*) taxa (Appendix, Table 1). Only 30% of the bivalve species are epifaunal. Most of the fauna (approximately 70% of the specimens) are either deposit feeders or carnivores (Appendix, Table 1).

The faunal assemblage at Red Bird, Wyoming, has been documented by Slattery *et al.* (in revision). In contrast to the assemblage in the scaphite concretionary layer, the assemblage at Red Bird is much less diverse (Appendix, table 2). It is dominated by epifaunal, suspension-feeding inoceramid bivalves, which is characteristic of most of the *Baculites baculus/Endocostea typica* Biozones at Red Bird, Wyoming (Gill and Cobban 1966; Slattery *et al.*, in revision). The only other taxon that is abundant at this horizon is *Discinisca*.

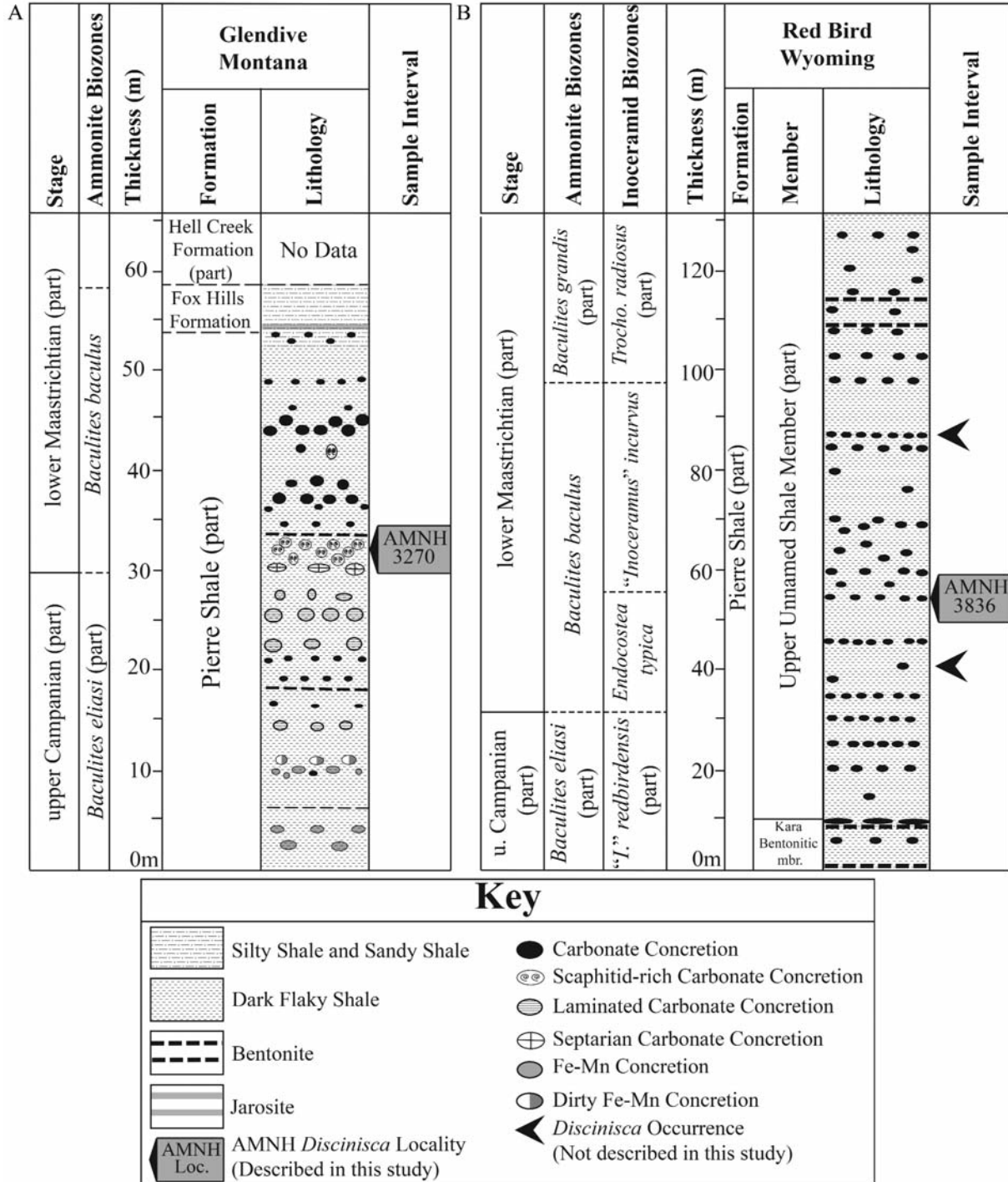
DESCRIPTION OF SPECIMENS

Scaphite: The specimens of *Discinisca* occur at the aperture of a mature specimen of *Hoploscaphites crassus*. It is a macroconch, which is interpreted as a female following conventional wisdom (e.g., Landman *et al.* 2010). As in other scaphites, the morphology of the aperture in mature shells differs from that in juvenile shells. At maturity, the shell wall bends sharply inward at nearly a right angle and then deflects outward terminating in a thin flared lip (Text-fig. 3). As a result, a narrow constriction or furrow develops on the outside of the shell. This furrow is very prominent on the venter and flanks, but disappears on the dorsum. It is usually filled with a thin layer of sediment after burial of the shell.

The six specimens of *Discinisca* (numbered I to VI in Text-fig. 4) occur near or in the furrow on the ventral

side of the scaphite shell. Five of them (II-VI) form a row along the outer edge of the furrow on its adapical side, and one of them (I) appears to be perched just below the flared lip. They are nearly oval in outline with a smooth subconical brachial (dorsal) valve with a max-

imum height of 0.7 mm. The shells are relatively small; the maximum diameters of the brachiopods are 2.2, 2.8, 2.9, 0.9, 2.0, and 2.0 mm, as measured from I through VI, respectively. It is difficult to determine the orientation of these specimens on the scaphite shell, but



Text-fig. 2. Stratigraphic sections for the upper Campanian to lower Maastrichtian strata at Glendive, Dawson County, Montana, and Red Bird, Niobrara County, Wyoming. Shaded boxes with AMNH locality numbers correspond to stratigraphic horizons containing the epizoan *Discinisca* encrusting *Hoploscaphites* and *Cataceramus*? Arrows indicate additional horizons where *Discinisca* specimens were discovered, but not described in this paper (modified from Bishop 1967; Slattery *et al.*, in revision

in V, the acute margin of the oval outline points towards the right side of the scaphite.

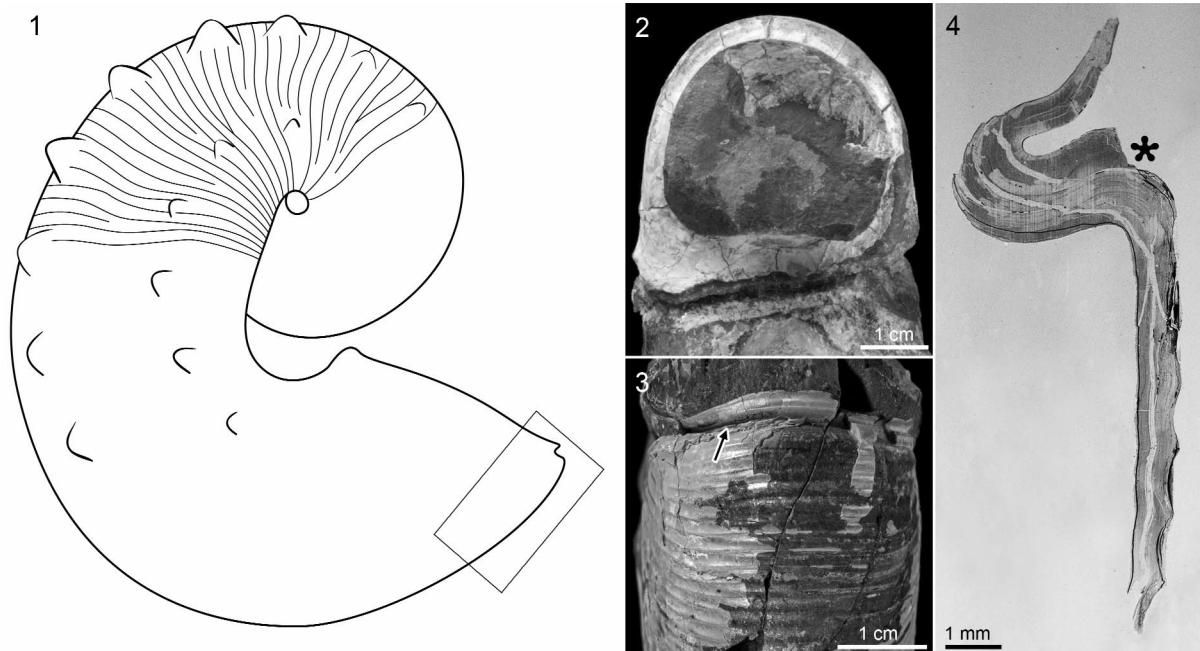
Three of the *Discinisca* retain their original outer shell layer. During preparation, a fragment of the outer shell wall popped off, permitting an examination of the inside surface of the brachial valve (Text-fig. 5). Scars of the two elongate anterior adductor muscles are present, forming a horse-shoe-like shape and confirm the identification of these specimens as *Discinisca*. At high magnification, the scars show a granular surface. It is possible that the scar of a posterior adductor muscle is also present, but it is unclear.

Inoceramid: A total of 13 specimens of *Discinisca* (lettered A to M in Text-figs 6, 7) occur on two right valves (AMNH 102488 and 102489), one broken left valve (AMNH 102490), and one shell fragment (AMNH 102491) of *Cataceramus? barabini*. All four inoceramids occur in the same shell cluster within a single concretion. The surfaces of the inoceramids are highly fractured due to a combination of freeze-thaw action during weathering as well as sample preparation. The brachiopods were serendipitously revealed when the nacreous layer of the inoceramid shells accidentally flaked off the steinkerns during the preparation process. Under high magnification, several specimens of *Discinisca* appear to be partially covered by a thin layer of nacreous

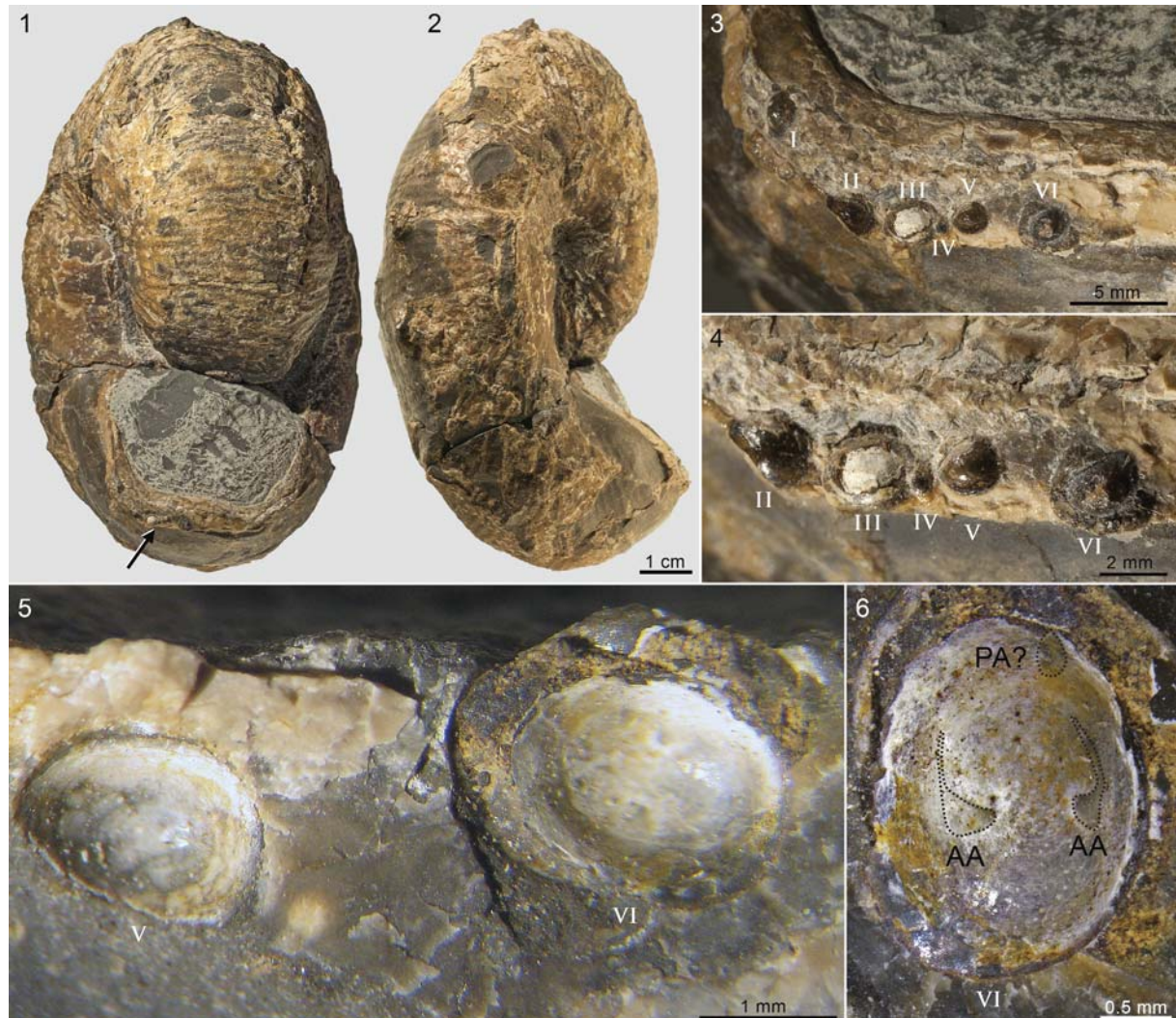
inoceramid shell and others appear to be resting on top of a thin nacreous shell layer (compare Text-fig. 7.2, which appears to be partially covered by nacre with Text-fig. 7.3, which appears to be resting on nacre).

The inoceramids vary in their degree of encrustation by *Discinisca*. In AMNH 102488, a right valve, one large *Discinisca* encrusts the disc of the shell along the upper part of the anterior face (Text-fig. 6.1, 6.2A). It is partially covered by a small fragment of nacreous shell. This specimen also exhibits a unique feature that may either be a scar or shell deformity. Two smaller, partially overlapping, specimens are located slightly more centrally (Text-fig. 6.1, 6.2B, C). In AMNH 102489, a right valve, two relatively large *Discinisca* occur on the disc close to the posterior margin (Text-fig. 6.3, 6.4D, I) and four smaller specimens occur along a prominent ruga (Text-fig. 6.3, 6.4E-H). In AMNH 102490, a partial left valve with neither the umbo nor the early growth stages preserved, only a single small *Discinisca* is present (Text-fig. 6.5, 6.6J). In AMNH 102491, an inoceramid fragment, three small specimens of *Discinisca* are present and rest directly on the steinkern (Text-fig. 6.7, 6.8K-M).

All of the *Discinisca* on the inoceramids are oval in outline with a smooth conical brachial (dorsal) valve approximately 0.4 mm in height. The lack of distinguishing features makes it impossible to determine the ori-



Text-fig. 3. Morphology of the apertural margin at maturity in scaphites, as illustrated by photos of mature macroconchs of *Hoploscaphites plenus* (Meek, 1876), *H. brevis* (Meek, 1876), and *H. nodosus* (Owen, 1852), as documented by Landman *et al.* (2010). 1 – Schematic drawing of the right side of a scaphite, showing the furrow at the apertural margin (rectangle). 2 – Head-on view of the contracted aperture at maturity. 3 – Ventral view showing the furrow (arrow) near the aperture. 4 – Cross-section of the shell wall at the apertural margin. The anterior direction is toward the top. As the shell approaches the apertural margin, it bends sharply inward and then reflects outward. The asterisk marks the location of the *Discinisca* on the study specimen, which is a mature macroconch of *H. crassus* (Coryell and Salmon, 1934)



Text-fig. 4. 1, 2 – Apertural and right lateral views of *Hoploscaphites crassus* (Coryell and Salmon, 1934), AMNH 63597, AMNH loc. 3270, *Baculites baculus* Biozone, Pierre Shale, Cedar Creek Anticline, Dawson County, Montana. Arrow points to the apertural lip. 3, 4 – Close-ups of the apertural lip showing the six specimens of *Discinisca* (numbered I to VI). 5 – Chunk of matrix that broke off from the scaphite, rotated 180° from 4, showing the interiors of the brachial valves in two specimens of *Discinisca* (V and VI). 6 – View of the interior of one of the specimens of *Discinisca* (VI), rotated approximately 90° clockwise from 5, showing the anterior adductor muscles (AA) and possible posterior adductor muscle (PA?)

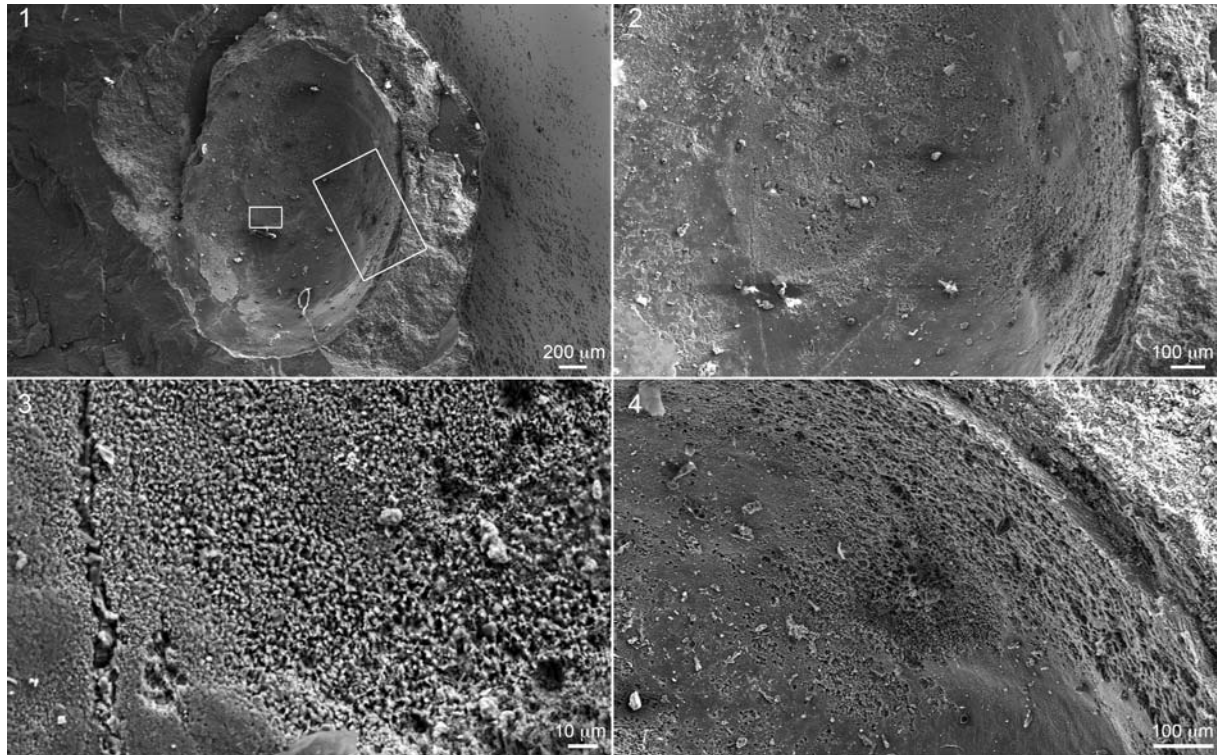
entation of the brachiopods on the inoceramid shells. The specimens of *Discinisca* are all small with maximum diameters of 4.1 (A), 2.7 (B), and 2.2 mm (C) in AMNH 102488; 3.2 (D), 1.8 (E), 1.9 (F), 2.2 (G), 1.5 (H), and 3.8 mm (I) in AMNH 102489; 2.2 mm (J) in AMNH 102490; and 2.5 (K), 1.6 (L), and 1.5 mm (M) in AMNH 102491.

DISCUSSION

Paleoenvironment: In the latest Campanian, the WIS underwent a transgression followed by a regression in

the early Maastrichtian (i.e., T-R cycle 9 of Kauffman 1977; also see Krystinik and DeJarnett 1996). This transgressive-regressive cycle, known as the Bearpaw Cyclothem, produced distinct lithological and paleontological patterns reflecting variation in water depth and proximity to the shoreline (Slattery *et al.*, in revision). The variation resulted from a complex interplay involving eustasy, sea-floor topography, and tectonics (Kauffman 1997; Krystinik and DeJarnett 1996; Slattery *et al.* 2015).

During the early Maastrichtian, the western shoreline of the Seaway in the study area was controlled by the position and extent of the Sheridan Delta, which was



Text-fig. 5. SEMs of the interior brachial valve of one of the specimens of *Discinisca* (VI). 1 – Overview of the shell. 2 – Close-up of the anterior adductor muscle scars. 3 – The surface of the anterior adductor muscle scar is granular. 4 – Close-up of the right anterior adductor muscle scar

prograding eastward. During the deposition of the lower Maastrichtian *Baculites baculus*/*Endocostea typica* Zones, the Glendive and Red Bird localities were at least 150 and 175 km, respectively, from the shoreline (Text-fig. 1; Gill and Cobban 1966; Slattery *et al.*, in revision). The exact depth of the WIS at the time is unknown but it was probably less than 70 m at both localities (Gill and Cobban 1966).

A comparison between the global record of eustatic sea level change and the local record of sea level change during the early Maastrichtian reveals a difference between northern Wyoming and Montana (Text-fig. 8). In Montana, the fall in sea level was relatively rapid due mainly to local tectonic events and, to a lesser degree, eustasy. In contrast, in northern Wyoming, the drop in sea level was initially slow, but subsequently was more rapid, due mainly to eustatic changes.

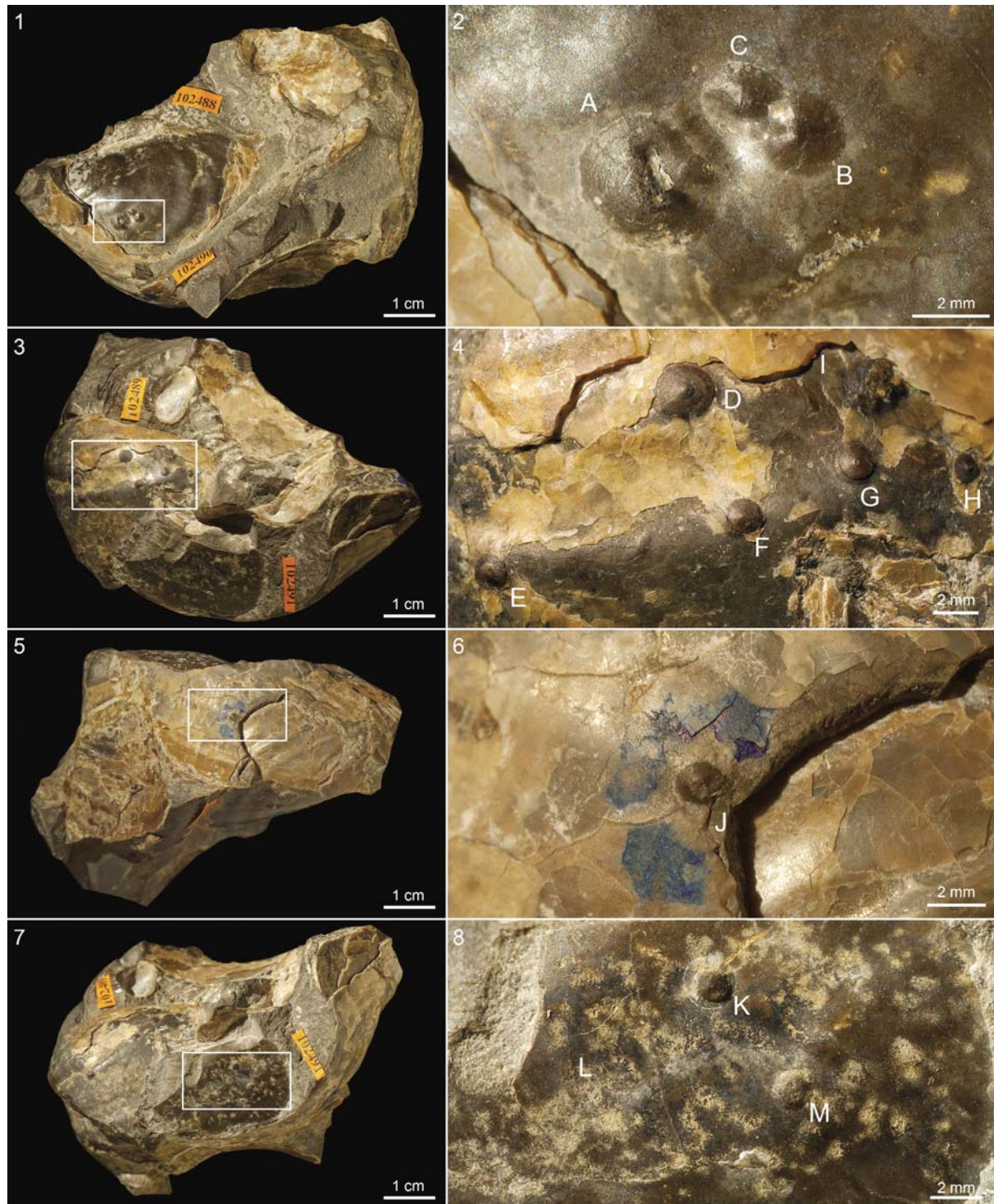
The scaphite concretionary layer at Glendive is characterized by a relatively diverse benthic fauna that reflects an offshore marine community inhabiting a soft substrate in a fairly well-oxygenated water column (Table 1). The dominant control on the composition of the benthos appears to have been substrate conditions, as indicated by the abundance of mobile infaunal deposit-feeding taxa (e.g., *Dentalium*, *Nucula*; Table 1)

that favor soft substrates in a well-oxygenated water column (see Rhoads and Young 1970; Wignall 1993; Kaim and Sztajner 2012). In contrast, the epifaunal taxa are less abundant (Table 1) and, because of the lack of a firm substrate, are attached to other shells, which they use as “shell islands” (*sensu* Kauffman 1977). The scaphite concretionary horizon is underlain by the “barren zone” (*sensu* Bishop 1973), which is characterized by bedded concretions and rare fossils of demersal scaphites and epifaunal inoceramids. Above the scaphite concretionary layer, the abundance and diversity of the benthos increases (Bishop 1967).

Utilizing the paleoenvironmental criteria outlined in Slattery *et al.* (in revision), the faunal assemblage at Glendive suggests that the water was relatively deep and that the oxygen levels were relatively low during the deposition of the upper Campanian *Baculites eliasi* Biozone corresponding to the “barren zone.” A drop in sea level during the deposition of the *B. baculus* Biozone resulted in increased oxygenation of the bottom, promoting a diverse benthic community. In an eperic sea, such as the WIS, a drop in sea level would have improved oxygenation on the bottom due to increased water-column mixing, which was dependent on a combination of water depth and storm frequency (Slattery *et al.*, in revision).

This paleoenvironmental interpretation is supported by the stratigraphic profile for central Montana as well as the eustatic sea-level curve for this interval (Text-figs 2, 8). Thus, we suggest that the scaphite concretionary layer that

contains the *Discinisca* specimens probably formed during an ephemeral oxygenation event in a relatively deep-water setting, allowing the development of a diverse faunal assemblage. The specimen of *Hoploscapites crassus*



Text-fig. 6. *Cataceramus? barabini* (Morton, 1834), AMNH loc. 3836, *Baculites baculus/Endocostea typica* Biozones, Pierre Shale, near Red Bird, Niobrara County, Wyoming, with close-ups of the encrusting epizoan *Discinisca*. 1, 2. AMNH 102488. 3, 4. AMNH 102489. 5, 6. AMNH 102490. 7, 8. AMNH 102491



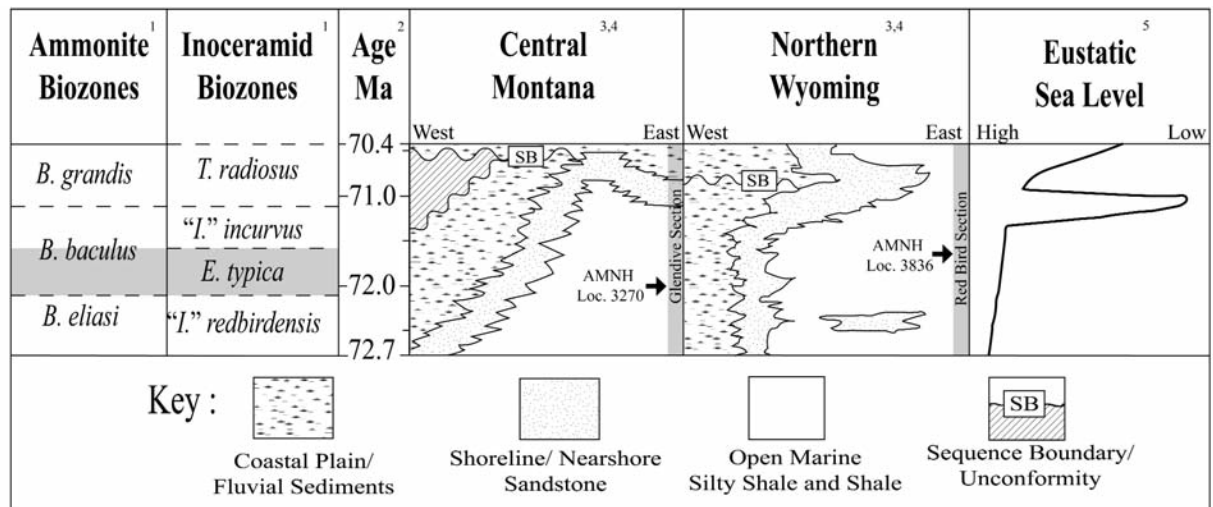
Text-fig. 7. Close-ups of four specimens of *Discinisca* on AMNH 102489, *Cateceramus? barabini* (Morton, 1834), lettered accordingly, AMNH loc. 3836, *Baculites baculus/Endocostea typica* Biozones, Pierre Shale, near Red Bird, Niobrara County, Wyoming. In figs 1, 2, the brachiopods appear to be partially covered by a nacreous layer whereas in figs 3, 4, the brachiopods appear to rest on top of a nacreous layer

provided an attachment site for the *Discinisca* and served as a cryptic habitat, discouraging potential competitors and predators. In addition, if the encrustation of *Discinisca* occurred during the lifetime of the scaphite (see the reasons for this argument below), the mobile mode of life of the scaphite would have further protected the brachiopod from predation.

A single concretion from the scaphite concretionary layer was recently analyzed by Landman *et al.* (2015). They documented 90 scaphites, representing three species of *Hoploscaphites*, most of which are adults. They further speculated that the abundance of adults in this concretion reflected an ecological event, such as an ephemeral plankton bloom, in the area. Such a bloom may have attracted adult scaphites into the region to feed on the plankton or on organisms higher up in the food web. Because most of the scaphite shells exhibit lethal injuries, Landman *et al.* (2015) argued that they accumulated on the bottom as a result of predation, perhaps from a mosasaur or shark. The ammonites may not have been killed all at once, but possibly over a protracted period of days or weeks. The accumulation of dead ammonites on the sea bottom acted in turn as a sed-

iment trap, entraining additional shell debris. This accumulation also promoted the development of a local community including numerous scavenging gastropods that were attracted to the area to feed on the high concentration of scaphite carcasses (Landman *et al.* 2015).

In contrast to east-central Montana, the *Baculites baculus/Endocostea typica* Biozones at Red Bird, Wyoming, are characterized by a low to moderate faunal diversity (Table 2) that typifies an offshore marine setting on a firm muddy sea bottom with low oxygen levels in the overlying water column (Table 2; Slattery *et al.*, in revision). This interpretation is based upon the presence of abundant inoceramid bivalves that are thought to have been eurytopic opportunists that exploited oxygen-deficient environments with reduced predation intensities (Kauffman 1982; Sageman 1989; Harries and Crampton 1998; Kauffman *et al.* 2007). This interpretation is also consistent with the paucity of other epifaunal, semi-infaunal, and shallow-infaunal species (Table 2), indicating the long-term presence of dysoxic conditions near the sediment-water interface. As suggested by Sageman (1989), the oxic-dysoxic boundary in the WIS may have periodically fluctuated up or



Text-fig. 8. Upper Campanian to lower Maastrichtian biostratigraphic, chronostratigraphic, and lithostratigraphic patterns across central Montana and northern Wyoming (modified from Slattery *et al.*, in revision¹; Cobban *et al.* 2006; ²Ogg *et al.* 2012; ³Gill and Cobban 1973; ⁴Krystinik and DeJarnett 1995; ⁵Miller *et al.* 2005). Gray highlighting indicates age and geographic location of study

down over short intervals of time as a result of water column mixing and the rate of bacterial decay, affecting the oxygen levels near the sea bottom. When the oxygen levels fell, benthic diversity decreased, whereas when they rose, benthic diversity increased.

Today, disciniscids are present in low-predation, low-competition settings, such as cryptic habitats (e.g., beneath rocks; Paine 1962; Brunton and Hiller 1990; Kato 1996). As also documented for closely related lingulid brachiopods, disciniscids are probably tolerant of low oxygen levels, at least for short intervals of time. Such conditions prevailed in shallow-marine habitats during the Early Paleozoic when brachiopods were dominant (Emig 1997). Indeed, disciniscids have been reported today from intertidal zones in close proximity, i.e., within several centimeters, to environments with low oxygen levels (Kato 1996). Harries (1993) considered *Discinisca* as a disaster taxon because of its appearance directly above the last major extinction pulse associated with the Cenomanian–Turonian (C–T) mass extinction, an event linked with Oceanic Anoxia Event 2. He argued that the abundance of *Discinisca* increased at the boundary as a result of a reduction in predators and competitors due to low-oxygen conditions.

The reconstruction of the paleoenvironment at Red Bird, Wyoming, during the deposition of the *Baculites baculus/Endocostea typica* Biozones is thus consistent with the presence of *Discinisca*. The setting was characterized by relatively low oxygen levels and low faunal diversity. The low diversity would have resulted in reduced competition and predation on *Discinisca*. At the

same time, the abundance of inoceramid shells littering the muddy sea floor would have provided ample hard ground for attachment.

Encrustation of the scaphite: The encrustation of *Discinisca* on *Hoploscaphites crassus* is one of the few documented examples of epizoans on scaphites. Landman *et al.* (2012, p. 95) speculated that this paucity may indicate that the surface of the scaphite shell was covered with a thin periostracum or mucus-like slime that prevented attachment of epizoans. The only other report of epizoans encrusting scaphites is by Hattin (1982, p. 75) who described juvenile cirripeds on the phragmocones and body chambers of a species of *Clioscapites* from the Smoky Hill Chalk Member of the Niobrara Chalk in western Kansas. Hattin (1982) did not illustrate any specimens, and it is difficult to determine if the cirripeds settled on the scaphites while the ammonites were still alive. The cirripeds also occur on inoceramids and rudists in this formation, leading Hattin (1982) to argue that the cirripeds were benthic and, therefore, probably only settled on the scaphite shells after the ammonites sank to the bottom.

The distribution of *Discinisca* on the specimen of *Hoploscaphites crassus* suggests, in contrast, that the brachiopods may have settled on the scaphite while it was still alive. They are only present in the apertural furrow on the ventral side of the scaphite, which may have provided an ideal niche for settlement. If they had encrusted the scaphite after it had died, either while it was floating or resting on the seafloor, they presumably would have covered a larger part of the shell.

The presence of *Discinisca* along the apertural margin of the scaphite yields insights into the paleobiology of these ammonites. The fact that the brachiopods are attached just below the apertural margin implies that the soft body of the scaphite probably did not cover this area. If it did, it would have prevented the epizoans from settling there. Instead, the soft body may have rested against the flared apertural lip, forming a delicate web funneling food to the mouth. Landman *et al.* (2012) reached similar conclusions about the morphology of the scaphite soft body in their larger study of the mode of life of these ammonites. They further argued that scaphites did not possess long muscular arms. They pointed out that impressions of such features have never been reported and that the mature aperture is contracted, not expanded, which would have impeded unconstrained movement of the arms. In addition, in modern cephalopods, such appendages only appear in rapid swimmers that use the tentacles to capture prey. In modern *Nautilus*, epizoans are also rare at the apertural margin (Landman *et al.* 1987). This may be due to the fact that the hyponome in *Nautilus* occasionally extends backward along the outside surface of the shell, effectively discouraging the settlement of epizoans.

The furrow at the apertural region of the scaphite shell must have provided a perfect perch for the larvae of *Discinisca* to settle, although it is curious that this is the only specimen of *Hoploscaphites* ever observed with *Discinisca* encrusted on it. The fact that six specimens occur in the same area is unlikely to be coincidental. It is possible, as mentioned above, that the rest of the shell was covered with periostracum that prevented them from settling elsewhere. The furrow may also have afforded a cryptic or protected micro-habitat in which to thrive. Slight movements of the scaphite soft body and jaw may have produced water currents that serendipitously transported food particles toward the brachiopods, enhancing their filter feeding (for a discussion of filter feeding in modern *Discinisca*, see Paine [1962] and LaBarbera [1985]).

The longevity of *Discinisca* can potentially yield insights into the longevity of the scaphite but, unfortunately, little is known about the life span of these brachiopods (Williams and Rowell 1965). The specimens of *Discinisca* on the scaphite cluster into two size groups, 1 mm and 2-3 mm. If these two groups represent two generations and if recruitment is annual, it implies that the ammonite may have lived at least one year after reaching maturity. It further implies that the ammonites may not have spawned only once, but spawned several times prior to their death. Indeed, modern coleoids exhibit a range of reproductive strategies, with

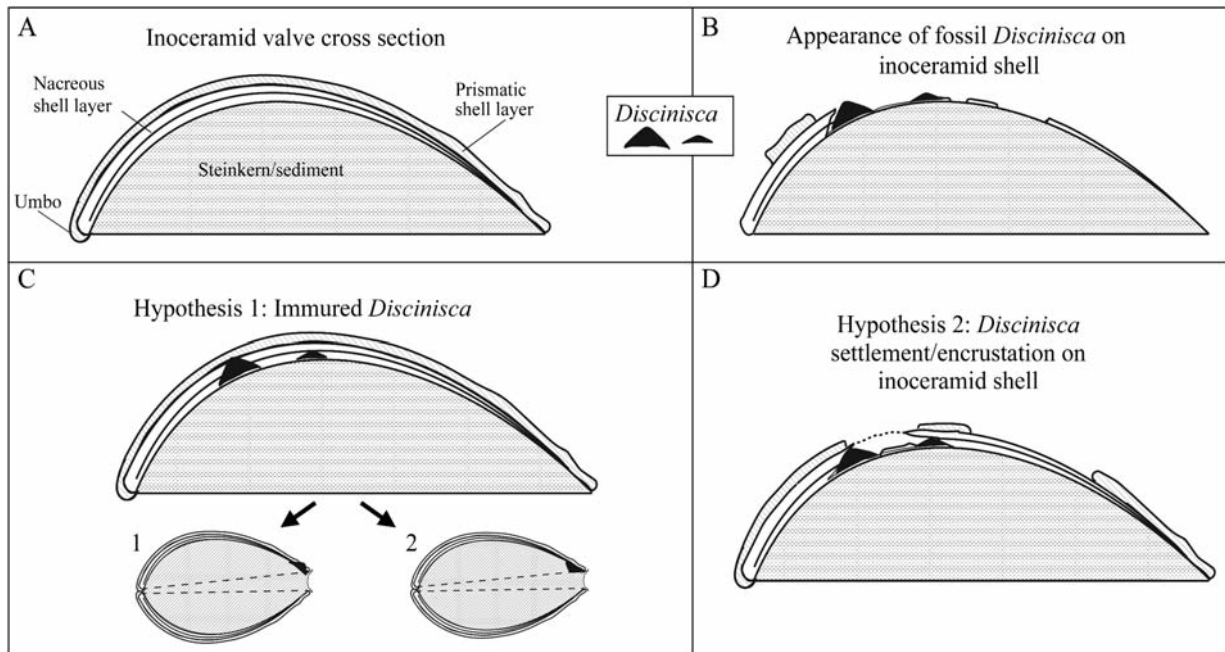
many variations on the theme of multiple spawning (Rocha *et al.* 2001).

The number of years that ammonites lived after reaching maturity has been estimated from two other studies of epizoans. Meischner (1968) described a complicated case of encrustation of an adult specimen of Middle Triassic *Ceratites semipartitus* by the bivalve *Placunopsis ostracina*. He identified six spatfalls. According to him, four of them settled on the last whorl of the ammonite while it was alive and two of them settled after the ammonite died. He therefore concluded that the ammonite did not live more than one year after reaching maturity. In another study, Seilacher (1960) described a case of encrustation of Late Cretaceous *Buchiceras bilobatum* by *Ostrea* sp. He inferred that the oysters may have grown after the ammonite was mature but before it died. Based on the age of the oysters, he concluded that the ammonite lived 0.5 to 3 years after reaching maturity.

Encrustation of the inoceramids: Several of the brachiopods appear to be covered with a thin layer of nacreous shell suggesting that they settled on the inoceramids while the bivalves were still alive (Text-fig. 7.1, 7.2). Wilson and Taylor (2001) stated that overgrowth of *Discinisca* by other shell producing organisms is fairly common. In our specimens, this would have required one of two scenarios: 1) the *Discinisca* would have had to settle directly on the soft mantle tissue near the outer lip of the bivalve (Text-fig. 9C1), but this contradicts the fact that modern representatives of *Discinisca* prefer to settle on hard substrates or 2) the *Discinisca* would have had to settle on the inside surface of the inoceramid shells (Text-fig. 9C2), but this contradicts the fact that the brachial valves in our specimens are facing outward (Text-fig. 9B).

The other, more likely explanation, is that the *Discinisca* settled on the shells after the death of the inoceramids (Text-fig. 9D). The prismatic and nacreous layers of the inoceramid shells may have begun to break down and delaminate as a result of the decomposition of the organic matrix holding the shell together. This would have allowed the *Discinisca* to attach and grow within small crevices in between the decomposing and exfoliating shell layers. This scenario is consistent with the orientation of the brachiopods, with the brachial valves facing outward. However, it is difficult to determine the extent of the breakdown of the prismatic and nacreous layers prior to burial because parts of the shell were damaged in the process of preparation.

The sizes of the *Discinisca* vary among the inoceramid specimens, ranging from 1.5 to 4.1 mm. This size



Text-fig. 9. Competing hypotheses to explain the encrustation of *Cateceramus? barabini* by *Discinisca*. A – Cross-section of the inoceramid shell. B – The specimens of *Discinisca* are lodged in fractures and crevices on the inoceramid shell. C – 1. If the specimens of *Discinisca* settled on the inside surface of the shell, they would have been oriented with the brachial valves facing inward, just the opposite of what we observe. 2. If the specimens of *Discinisca* settled directly on the soft mantle tissue near the outer lip of the bivalve, they would have been oriented with the brachial valves facing outward, which is consistent with what we observe. However, modern representatives of this genus prefer to settle on hard substrates. D – The most likely explanation is that the specimens of *Discinisca* settled and grew in small crevices on the outer surface of the inoceramid shell as it began to break down and delaminate

variation may indicate either multiple settlement events or that some individuals lived longer than others. For example, in AMNH 102489, two larger *Discinisca* are present on an older ruga (Text-fig. 6.4D, I) and four smaller individuals are present on a younger ruga (Text-fig. 6.4E–H). This pattern of distribution suggests two recruitment events. The alternative possibility is that the smaller individuals died before the larger ones. This scenario is unlikely because the pedicle of the brachiopods decays rapidly after death leading to the detachment of the shells.

SUMMARY

Discinisca is a small and inconspicuous faunal element in the Upper Cretaceous of the U.S. Western Interior but may be more abundant than previously thought. Our examples document its occurrence on scaphites and inoceramids in the lower Maastrichtian Pierre Shale of east-central Montana and east-central Wyoming. The encrustation on the scaphite is a rare example of epizoans on scaphites. The brachiopods may have become attached to the scaphite while it was

still alive, with implications for the paleobiology of the scaphite. In contrast, the brachiopods probably attached to the inoceramids after their death. However, they occur in crevices on the surfaces of the shells, suggesting that the shells had begun to break down and delaminate on the sea floor as a result of the decomposition of the organic matrix holding the shells together.

The appearance of *Discinisca* may be a useful indicator of low oxygen conditions or environments with few predators or competitors. The faunal assemblage at the inoceramid locality is depauperate and may imply low oxygen levels. The abundance of inoceramid shells littering the muddy sea floor probably provided ample hard ground for attachment of the brachiopods. The faunal assemblage at the scaphite locality is much more diverse, implying higher levels of oxygen on the bottom. Nevertheless, the site of attachment on the scaphite lip may have served as a cryptic habitat for *Discinisca*, discouraging potential competitors and predators. In addition, if the encrustation occurred during the lifetime of the scaphite, the mobile mode of life of the ammonite would have further protected the brachiopods from predation.

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APPENDIX

Table 1. Faunal list at AMNH loc. 3270, Pierre Shale, Dawson County, Montana (alphabetical within larger grouping) (reprinted from Landman *et al.* 2015). Uncommon: 1–5 specimens; common 6–20 specimens; abundant: 21–30 specimens; very abundant: >30 specimens

Species	Habitat	Feeding Strategy	Abundance
CEPHALOPODA			
<i>Baculites</i> sp. cf. <i>B. baculus</i> Meek and Hayden, 1861	Nektonic	Planktivore	Uncommon
<i>Hoploscaphites crassus</i> (Coryell and Salmon, 1934)	Nektonic	Planktivore	Very abundant
<i>Hoploscaphites plenus</i> (Meek, 1876)	Nektonic	Planktivore	Very abundant
<i>Hoploscaphites saltgrassensis</i> (Elias, 1933)	Nektonic	Planktivore	Abundant
coleoid	Nektonic	Carnivore	Uncommon
BIVALVIA			
<i>Anomia gryphorhyncha</i> Meek, 1872	Epifaunal	Sessile suspension feeder	Uncommon
<i>Crenella elegantula</i> Meek and Hayden, 1861	Epifaunal	Mobile deposit feeder	Uncommon
<i>Cucullaea nebrascensis</i> Owen, 1852	Infaunal	Mobile suspension feeder	Common
<i>Cuspidaria moreauensis</i> (Meek and Hayden, 1856a)	Infaunal	Burrowing carnivore	Common
<i>Cuspidaria ventricosa</i> (Meek and Hayden, 1856a)	Infaunal	Burrowing carnivore	Common
<i>Cymbophora warrenana</i> (Meek and Hayden, 1856b)	Infaunal	Mobile suspension feeder	Uncommon
<i>Endocostea typica</i> Whitfield, 1877	Epifaunal	Suspension feeder	Common
<i>Limopsis striatopunctata</i> Evans and Shumard, 1857	Epifaunal	Mobile suspension feeder	Uncommon
<i>Malletia evansi</i> (Meek and Hayden, 1856a)	Infaunal	Mobile deposit feeder	Common
<i>Modiolus galpinianus</i> (Evans and Shumard, 1854)	Semi-infaunal	Suspension feeder	Uncommon
<i>Modiolus meeki</i> (Evans and Shumard, 1857)	Semi-infaunal	Suspension feeder	Common
<i>Nucula cancellata</i> Meek and Hayden, 1856a	Infaunal	Mobile deposit feeder	Very Abundant
<i>Nucula percrassa</i> Conrad, 1858	Infaunal	Mobile deposit feeder	Common
<i>Nucula planomarginata</i> Meek and Hayden, 1856a	Infaunal	Mobile deposit feeder	Common
<i>Nuculana (Jupiteria) scitula</i> (Meek and Hayden, 1856a)	Infaunal	Mobile deposit feeder	Common
<i>Nuculana (Nuculana) grandensis</i> Speden, 1970	Infaunal	Mobile deposit feeder	Uncommon
<i>Nymphalucina occidentalis</i> (Morton, 1842)	Infaunal	Siphonate suspension feeder	Abundant
<i>Oxytoma (Hypoxytoma) nebrascana</i> (Evans and Shumard, 1857)	Epifaunal	Suspension feeder	Common
<i>Pecten (Chlamys) nebrascensis</i> Meek and Hayden, 1856a	Epifaunal	Mobile suspension feeder	Abundant
<i>Phelopteria linguiformis</i> (Evans and Shumard, 1854)	Epifaunal	Epibyssate suspension feeder	Uncommon
<i>Pholadomya deweyensis</i> Speden 1970	Deep infaunal	Mobile suspension feeder	Uncommon
<i>Protocardia subquadrata</i> (Evans and Shumard, 1857)	Infaunal	Mobile deposit feeder	Very Abundant
<i>Solemya subplicata</i> (Meek and Hayden, 1856a)	Infaunal	Siphonate suspension feeder	Uncommon
<i>Tenuipteria fibrosa</i> (Meek and Hayden, 1856a)	Epifaunal	Epibyssate suspension feeder	Uncommon
<i>Yoldia rectangularis</i> Speden, 1970	Infaunal	Mobile suspension feeder	Uncommon
GASTROPODA			
<i>Aporrhais biangulata</i> Meek and Hayden, 1856a	Semi-infaunal	Detritivore	Common
<i>Atira? nebrascensis</i> Meek and Hayden, 1856a	Epifaunal	Grazer	Very Abundant
<i>Cylindrotruncatum demersum</i> (Sohl, 1964)	Epifaunal	Carnivore	Common
<i>Drepanochilus evansi</i> Cossman, 1904	Epifaunal	Carnivore	Very Abundant

<i>Euspira obliquata</i> (Hall and Meek, 1856)	Epifaunal	Carnivore	Abundant
<i>Oligoptycha concinna</i> (Hall and Meek, 1856)	Epifaunal	Carnivore	Common
<i>Pyrifusus subdensatus</i> Conrad 1858	Epifaunal	Carnivore	Uncommon
<i>Rhombopsis intertextus</i> (Meek and Hayden, 1856a)	Epifaunal	Carnivore	Uncommon
SCAPHOPODA			
<i>Dentalium gracile</i> Hall and Meek, 1856	Semi- infaunal	Detritivore	Very Abundant
<i>Dentalium pauperulum</i> (Meek and Hayden, 1860)	Semi- infaunal	Carnivore	Very Abundant
COELENTERATA			
<i>Microbacia americana</i> Meek and Hayden, 1860	Epifaunal	Suspension feeder	Uncommon
BRACHIOPODA			
<i>Discinisca</i> Dall, 1871 <i>sp.</i>	Epifaunal/ infaunal	Suspension feeder	Uncommon
MISCELLANEOUS			
burrows			Uncommon
bryozoans	Epifaunal	Suspension feeder	Uncommon
circular fossils			Uncommon
crustacean	Epifaunal	Carnivore	Uncommon
echinoids	Epifaunal	Carnivore	Common
epibiont			Common
fish	Nektonic	Carnivore	Abundant
“seed”			Uncommon
tubes			Uncommon
wood/bone			Uncommon

Table 2. Faunal list at AMNH loc. 3836 at the informal Pierre Shale reference section (Gill and Cobban, 1966) exposed along the Old Women Creek Anticline near Red Bird, Niobrara County, Wyoming (alphabetical within larger grouping). Uncommon: 1–5 specimens; common 6–20 specimens; abundant: 21–30 specimens; very abundant: >30 specimens

Species	Habitat	Feeding Strategy	Abundance
BIVALVIA			
<i>Cataceramus? barabini</i> (Morton, 1834)	Epifaunal	Suspension feeder	Very abundant
<i>Dosiniopsis deweyi</i> (Meek and Hayden, 1856a)	Infaunal	Suspension feeder	Uncommon
<i>Malletia evansi</i> (Meek and Hayden, 1856a)	Infaunal	Deposit feeder	Uncommon
<i>Ostrea translucida</i> Meek and Hayden, 1857	Epifaunal	Suspension feeder	Uncommon
GASTROPODA			
<i>Drepanochilus</i> <i>sp.</i>	Epifaunal	Grazer	Common
<i>Euspira obliquata</i> (Hall and Meek, 1856)	Epifaunal	Carnivore	Uncommon
SCAPHOPODA			
<i>Dentalium gracile</i> Hall and Meek, 1856	Semi-infaunal	Detritivore	Uncommon
BRACHIOPODA			
<i>Discinisca</i> Dall, 1871 <i>sp.</i>	Epifaunal/infaunal	Suspension feeder	Abundant