Paludicola 12(2):68-82 June 2019

VERTEBRATE TRACE FOSSILS IN THE MOWRY SHALE (LOWER CRETACEOUS) OF WYOMING, USA

Melissa V. Connely

Department of Earth and Environmental Science, Casper College, Casper Wyoming
mconnely@caspercollege.edu

ABSTRACT

The upper contact of the Mowry Shale Formation (Cretaceous) contains a variety of trace fossils in several locations throughout Wyoming. Over the past several years, new discoveries of trace fossils have been investigated by students and faculty at Casper College, Wyoming. Some of the trace fossils discovered are those of vertebrate animals. These trace fossils resemble swimming and resting marks including claw marks, foot prints, and tail and/or fin drags. These very unique and poorly known trace patterns may have been produced by marine fish and/or reptiles. At the same level, some impressions have been identified as the invertebrate *Asterichnites octoradiatus*. The presence of these trace fossils can aid in understanding vertebrate behavior and the paleoecology of the Mowry Sea, as well as provide insight into the paleoenvironmental conditions of the Cretaceous marine ecosystems of the Western Interior.

INTRODUCTION

The Cretaceous Mowry Shale Formation was deposited in an epicontinental sea, covering much of the Western Interior of North America. The sea extended along the east side of the Cordillera, as far south as Utah and Colorado, but did not connect to the Tethyan Ocean to the south (Bremer, 2016; Plint et al., 2009). The Mowry Sea supported a variety of marine reptiles including ichthyosaurs (Nace, 1939; McGowan, 1972; Maxwell and Kear, 2010), plesiosaurs, and crocodiles (Massare and Dain, 1986; Massare, 1998; Stewart et al., 1994). Invertebrates are known mainly from trace fossils. Clark (2010) described the ichnofossil *Planolites* from near the uppermost layer of the Mowry Shale at Alkali Anticline in the Bighorn Basin, near one of the study sites. Invertebrate trace fossils from other localities include *Protovirgularia*, *Cylindrichnus*, *Lockeia*, *Planolites*, navichnia and *Zoophycos* (Clark, 2010). Although trace fossils are known from the Mowry Shale, they are uncommon (Clark, 2010; pers. obs.).

Trace fossils are important indicators of past animal behavior and can be applied to understand the activity of extinct species (Bennett et al., 2014). How an animal interacts with their environment such as the sea floor can provide clues to paleoecology (Rhoads, 1975). Generally, vertebrate traces in a marine ecosystem are rare (e.g., Manni et al., 1999; Zhang et al., 2014). At the study sites, however, vertebrate traces were the dominant ichnofossil. Those described in this study are on the top-most surface of the Mowry Shale. This study is an attempt to investigate known ichnofossils localities in the Mowry Shale Formation in Wyoming and to describe new discoveries. The well-preserved trace fossils provide evidence of behavior of various vertebrates and cephalopods. Study of the sediments, along with description of the trace fossils, can provide a picture of the fauna interacting with their environment, and can increase the understanding of ecosystems of the Mowry Sea.

STRATIGRAPHY

At the study sites, the Mowry Formation contains thinly laminated, dark gray siliceous shale that weathers to a silver-grey. Unlike the shales above and below the formation, it often hosts small pine forests, which take advantage of the hard siliceous shale as a water reservoir. This feature makes it easier to find the formation in the field. The Mowry Shale Formation includes a shale interval from which the formation gets its name, and the overlying, and much thinner layer, the Clay Spur bentonite. Stratigraphically the study sites are located at the topmost layer of the Mowry Shale and just below a sharp contact with the Clay Spur bentonite, the uppermost bed of the Mowry Shale Formation (Figure 1). A hiatus between the Mowry Shale and the Clay Spur bentonite is not present, indicated by the clarity and detailed preservation of the surface traces, which imply the absence of erosion and a rapid burial. Weathering features indicating subaerial exposure such as desiccation cracks are not present.

The Mowry Shale Formation marks the transition between the Lower and Upper Cretaceous (Albian/Cenomanian transition) units in Central Wyoming. Cobban and Reeside (1951) and Reeside, and Cobban (1960) placed the Mowry Shale on the

Cenomanian/Albian boundary based on ammonite assemblages. Based on biostratigraphic and sequence stratigraphic correlations of North Texas and European sections, along with radiometric dating of bentonite beds in the Western Interior sediments of North America, the Albian/Cenomanian boundary has been set at 97.2 Ma (Scott et al., 2009). However, the International Commission on Stratigraphy (2018) currently places the boundary at 100.5 Ma. Researchers radiometrically dated the "Clay Spur" bentonite at ~98 Ma (Obradovich et al., 2002; Obradovich, 2005, pers. comm,), making it Cenomanian in age. George et al. (2014) placed the boundary between the Upper and Lower Cretaceous at the base of the Mowry Shale (Figure 1), making all of the Mowry Shale Formation Cenomanian in age.

Overlying the Clay Spur bentonite is the Frontier Formation (Watson, 1980) west of the Powder River Basin, and the Belle Fourche Shale (Hosterman and Patterson, 1992; Massare, 1998) east of the basin, both of which are Cenomanian in age (George et al., 2014; International Chronostratigraphic Chart, 2018; Figure 1). The contact between the Mowry Shale Formation and the Frontier Formation is typically placed at the top of the Clay Spur bentonite bed (Nixon, 1973; Burtner and Warner, 1984). Underlying the Mowry Shale is the Muddy Sandstone, which is Albian in age (George et al., 2014; International Chronostratigraphic Chart, 2018).

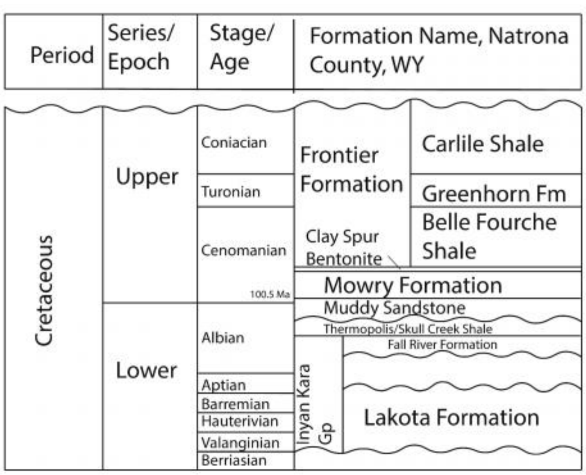

FIGURE 1. Stratigraphic chart of Cretaceous units associated with the Natrona County, Wyoming. Taken in part from the Wyoming Stratigraphic Nomenclature Chart (George et al., 2014).

LOCALITIES WITH TRACE FOSSILS

History of the Sites.—Vokes (1941) first reported trace fossils of unknown origin in the Mowry Shale. These were later described and named by Brown and Vokes (1944) as a cephalopod trace fossil, *Asterichnities octoradiatus.* However, Vokes (1941, p. 452) also showed an image he described as a "…groove-like gastropod (?) trail,…" These trails have been noted in other areas and are the focus of this report. Davis (1963, p. 143), mentions "…long, sinuous, groove-like depressions about one-half to one inch across, one-half inch deep, and up to sixty feet long wind across this bedding plane surface…" in the upper contact of the Mowry Shale from Weston County, Wyoming. Burford (1985) described similar markings at a site located in the Bureau of Land Management's (BLM) Off Highway Vehicles (OHV) Park in Natrona County, Wyoming (Hanson and Connely, 2006). Burford (1985) mentioned that these trace fossils could possibly belong to a marine crocodile.

Some of the trace fossils mentioned by Burford (1985) have now been re-described as belonging to the ichnotaxa *Asterichnites octoradiatus* (Figure 2). However, the other trace fossils from the OHV Park were not identified. In 2004, trace fossils from the OHV Park were reported to the Tate Geological Museum by local citizens. Upon further investigation, it was determined that this was the same stratigraphic interval as those reported from Johnson County (Figure 3) and in Big Horn County, in an outcrop of the Alkali Anticline in the Bighorn Basin (i.e. uppermost layers of the Mowry Shale). These reports were presented as undergraduate research projects (Connely and Talbot, 2005; Trumbull and Connely, 2010).

FIGURE 2. *Asterichnites octoradiatus* trace fossils at the OHV Park, Natrona County, Wyoming. Scale = 15 cm.

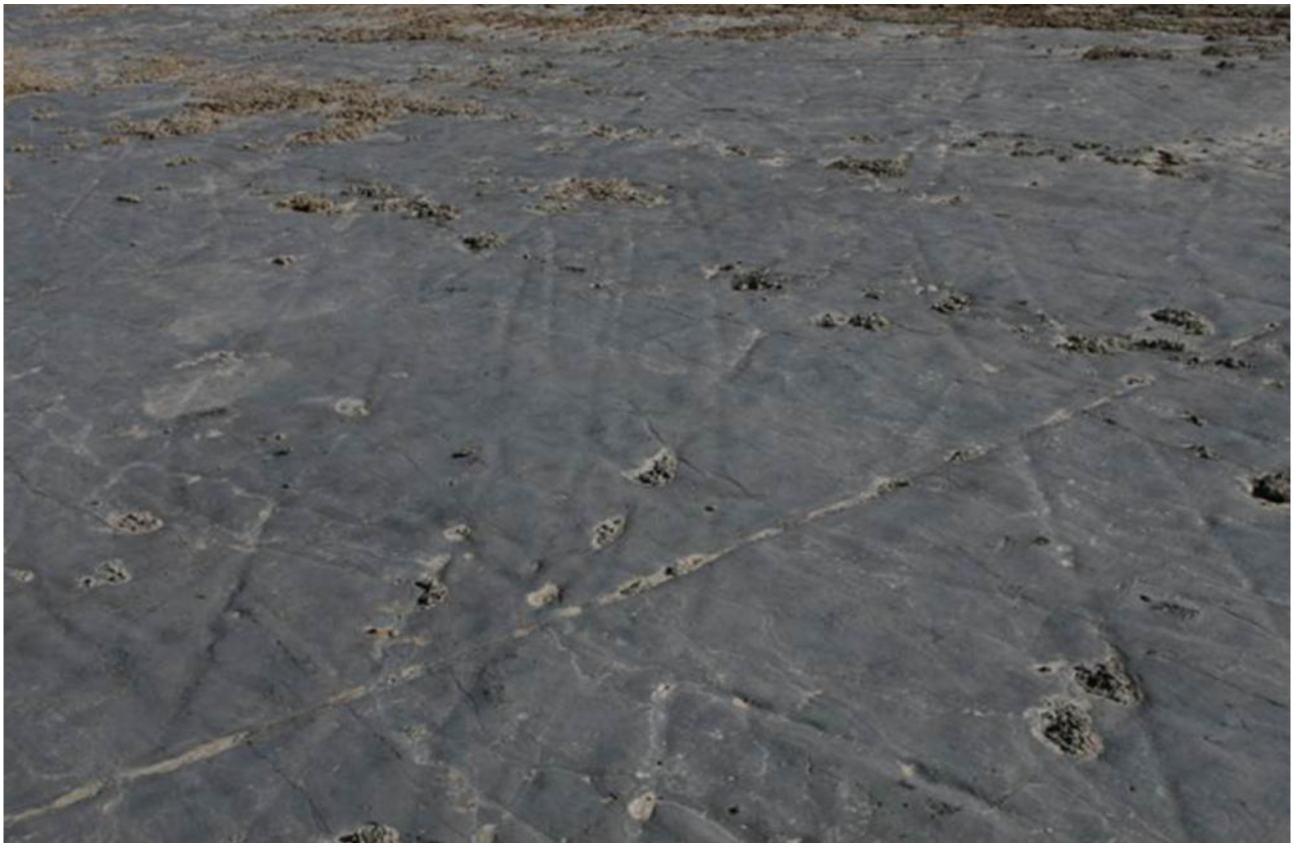

FIGURE 3. Trace fossils reported from Johnson County, Wyoming by Lawson (2009). This site did not have the protective “sandpaper” surface and was destroyed by weather shortly after this image was taken. Notice several parallel grooves and one single groove cutting across from lower left to upper right.

Location of the Sites.—A total of six sites throughout Wyoming and surrounding states have an assemblage of trace fossils on the top surface of the Mowry Shale, presumably the same stratigraphic level (Figure 4). The site with the most diverse collection is the BLM OHV Park in Natrona County, west of Casper. The original discovery site containing trace fossils was described by Vokes (1941) from an area southwest of Billings, Montana. Brown and Vokes (1944) described similar tracks to an area northwest of Cody, Park County. Davis (1963) reported his observations from Weston County. The exact locations of the historic sites are unknown. The fifth site is located in Johnson County in an active bentonite mine (Lawson, 2009, pers. comm.). Here numerous trace fossils were reported (Figure 3). However, shortly after the site was identified, the surface was destroyed by winter weather conditions and thus could not be studied in detail. The sixth and most recently discovered site is located in the Alkali Anticline in Big Horn County (Trumbull and Connely, 2010).

The outcrop that contains the OHV Park site is on the eastern flank of a northwest, southeast trending structure known as the Immigrant Gap Anticline, northwest of Casper. The surface containing the trace fossils was uncovered by the mining of the Clay Spur bentonite. This exposed shale surface was protected by a sandpaper–like layer described as a “crystalline ash” at another nearby locality (Corbett et al., 1985). The surface contains a single layer of light colored, angular, course sand-sized grains mostly of quartz, biotite, and sanadine over a layer 1 to 4 mm thick of similar material but much finer grained. This single layer of the sandpaper surface appears to cover all of the tracks and traces and was likely deposited shortly after the traces were made. Fragmentary vertebrate remains, possibly an ichthyosaur, were present at the surface of the OHV Park. Unfortunately they were too weathered for a positive identification.

Methods.—The study was started in 2004 and continues to this day. The surface of the outcrops containing the trace fossils was mapped using a grid system. The data was transferred onto Mylar grid paper

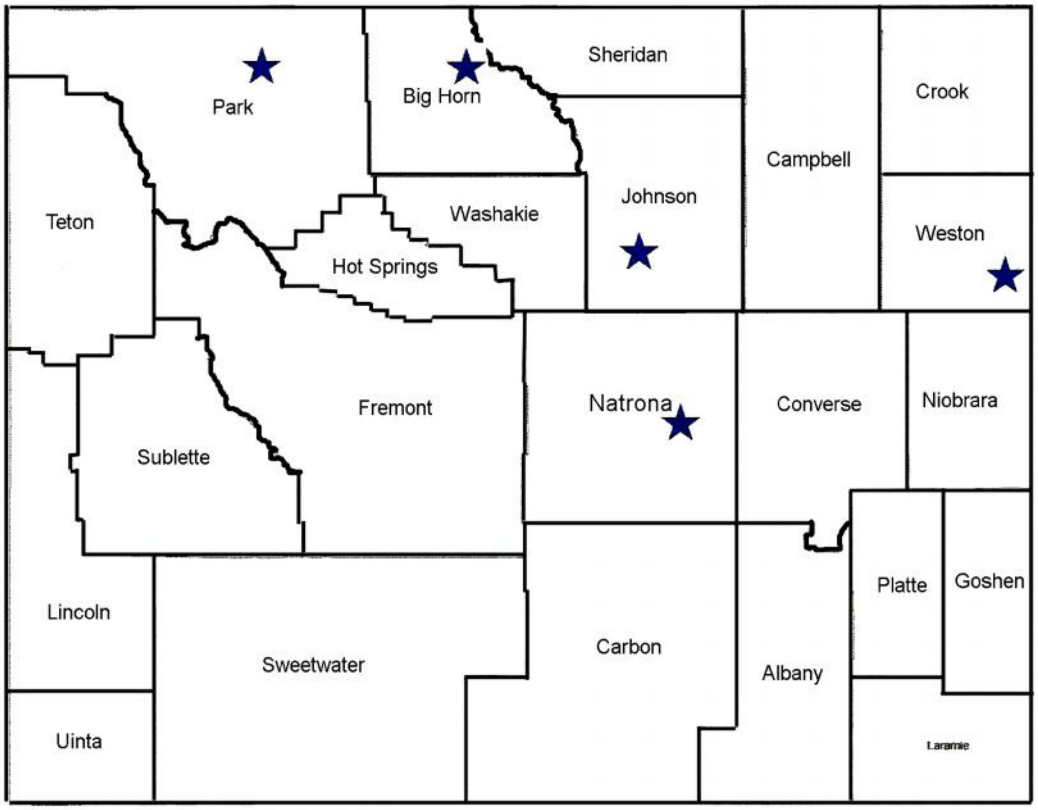

FIGURE 4. Locations of Wyoming sites reported in this study.

to illustrate the morphology and orientation of traces. In some cases, latex molds were made in the field. These molds are curated at the Tate Geological Museum, Casper College, Wyoming. Ongoing studies are incorporating photogrammetry to record trace morphology.

MOWRY SHALE PALEOENVIRONMENT AND FOSSILS

The Mowry Shale represents high stand deposition (Long et al., 2000) with a depth of 15m to 150m at the OHV Park site about the time that these traces were created. Further west, the maximum depth was 300m (Costanzo, 2006). The identified ichnofossils represented by *Zoophycos* and *Cruziana* ichnofacies and the lack of sedimentary structures suggests water depths beneath fair-weather wave base to beneath storm-wave base (Bremer, 2016). At the maximum depths, the water would have been aerobic to dysaerobic (Elzea and Murray, 1990).

Fossils are known from the Mowry Shale, but are fragmentary (Druckenmiller, 2002), including vertebrates, invertebrates, plants, and ichnofossils. Although rare, ammonoids and bivalves are the most common invertebrates observed in the Mowry Shale in Natrona County. At the upper most surface containing the trace fossils, ammonoids were present only at the Johnson County site. Vuke (1982) described some well-preserved angiosperm leaf fossils from the Galalatin Ranges of Montana, which could be some of the earliest examples known. Various pollens and other microfossils are also known and were used in biostratigraphic studies (Vuke, 1982; Scott et al., 2009). However, the stratigraphic position of these reports is unclear.

Vertebrates reported from the Mowry Shale include fish such as *Hypsodon sp.*, *Leucicthy sp.*, *Erythrinolepis sp.*, and *Halecodon sp*. (Cockerall, 1919; Anderson and Kowallis, 2005). Most fish are identified through abundant scales in the shale. Stewart and Hakel (2006) collected eight types of

Actinopterygii from the Mowry Shale in Natrona County. Turtles, crocodiles, and sharks (Paull, 1957) were found in the underlying Muddy Sandstone, and marine crocodiles are also known from the Mowry Shale (Mook, 1934). Plesiosaurs and ichthyosaurs are well known from the Mowry Shale (Nace, 1939; Romer, 1968; Massare and Dain, 1989; Stewart, et al, 1994), the latter being the most common marine reptile in the fauna (J. Massare, 2019, pers. comm.). At the OHV Park, a partially articulated ichthyosaur skeleton was collect from a hard ironstone concretion only a few hundred meters from the trace fossil sites by the staff of the Tate Geological Museum, Casper College, Wyoming. Other unidentified bones were found within the trace layer. Scattered bones of marine, flying, and even terrestrial reptiles were found in concretions in the Mowry Shale, but details of the species have not been described (Kirschbaum and Roberts, 2005).

DESCRIPTION AND INTERPRETATION

Several fossil tracks, traces, and impressions were identified at the OHV Park and three other sites in Wyoming. Five of these morphotypes (herein referred to as A – E) are most likely from vertebrates, whereas a few other morphotypes (including the ichnotaxon *Asterichnites octoradiatus)* are probably from invertebrates.

Vertebrate Traces: Trace Type A.—These trace fossils are long (1 to ~26 meters) single or two parallel grooves, ~3 cm wide and .5 to 1.5 cm deep (Figure 5). The groove vertical section is u-shaped. The sides of the grooves are slightly raised with an expulsion or displacement rim. Most grooves are straight although longer sets have a single bend to an s-shaped pattern. Parallel sets are ~ 35 to 50 cm apart (Figure 6). The grooves are not always continuous but become shallow for about a meter then reappear along the same vector. These fossils match the descriptions made by Davis (1963) from a mine in Weston County. These trace fossils appear to have been made by a swimming organism dragging an appendage in the mud. The expulsion rim along the edges supports a displacement of mud or marginal ridge and is not a depositional artifact. The little (or lack of) sinuosity suggests that the track maker used an axial oscillatory or suboscillatory mode of movement. This appendage or tail is likely not responsible for the primary propulsion of the animal but may have been used to steer or stabilize the body. The gradual skips in the trace suggest that the track maker periodically became more buoyant as it was moving through the water column, and was not a benthic creature. These traces might have been created by the pectoral fin of an ichthyosaur or the tail of a plesiosaur. Ichthyosaurs have a lunate tail, which is used for their main propulsion, whereas plesiosaurs swam using their limbs. The tail of the plesiosaur or the pectoral fins of the ichthyosaur was used for stability (Massare, 1988). Many of these trace fossils come in parallel pairs which would support a pectoral fin or appendage interpretation. The groove is long and shallow (U-shaped vertical section) created by the dragging of a blunt object. Ichthyosaurs have stiff and fairly thick forelimbs. Fish tend to have thinner blade like fins, which would create a more V-shaped impression. Crocodiles and some fish are more undulatory in their swimming movement, using much of their torso for propulsion (Massare, 1988). This type of movement would show up in a sinuous pattern (such as the inchotaxon *Undichna* Anderson, 1976). Tool marks can be ruled out because these grooves are numerous, crisscross each other with no consistent orientation, and do not vary their morphology, size and distance between each other along their course.

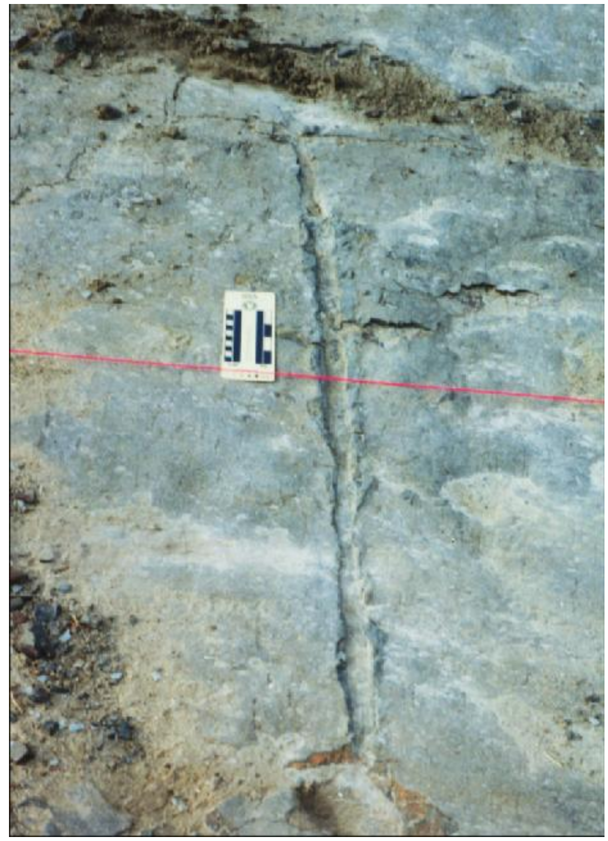

FIGURE 5. Trace fossil Type A from the OHV Park, Natrona County, Wyoming. The surface is protected by the "sandpaper"-like surface. Notice the expulsion material along the edge of the trace. Scale = 10 cm

Trace Type B.—These trace fossils are two separate but apparently related markings (Figures 7, 8 and 9). The primary trace has a broken, sinuous pattern or arcuate impression. They are thinner in width (~1cm

FIGURE 6. Two parallel traces of Type A from the OHV Park.

wide) and shallower in depth (<1cm) then those in Type A. The overall length is much shorter and with a repeated sinuous morphology. In cross section, these traces are U to V-shaped. The secondary traces are thin 3 to 4 parallel markings that can be found in a subparallel path to the primary trace. These have a similar sinuous pattern but are more continuous. This trace fossil was only observed at the OHV Park, where two occurrences were mapped. Both trace fossils can be compared to the fish swimming trace ichnogenus *Undichna* (Anderson, 1976). They also resemble the crocodile swim trace fossil *(Hatcherichnus)* from the Upper Jurassic Morrison Formation (Foster and Lockley, 1997) but without the manus or pes impressions.

These trace fossils suggest an animal swimming near the seafloor. The primary trace appears to be produced by a tail/fin that was propelling a swimming animal with axial horizontal oscillatory or suboscillatory motion. The secondary parallel grooves on the side are more likely an appendage mark generated by claws, sharp spines, or fins that drag or cut through the mud. The two trace fossils seem to be related as they occur together in both instances, however they are offset and do not overlap like those in *Undichna*. This trace fossil is interpreted as made by a single individual with a tail, which uses oscillatory or suboscillatory propulsion. Aquatic amphibians with a long tail and trailing legs (Turek, 1989) as well as aquatic reptiles (Trewin, 2000) could make similar impressions. Swimming crocodiles use their tail with suboscillatory propulsion (Massare, 1988) or faster axial swimming (Farlow, et al., 2018). Modern crocodiles use its hind limbs for balance, steering and to push off of the bottom or paddle the animal forward (Farlow, et al., 2018). This posture would allow claws to gently mark the sea floor. However, it is unlikely that dragging claws could make even parallel marks like those described in Trace Type B. With some exceptions, the trace fossil best resembles that of *Undichna insolentia* as described by Trewin (2000). *U. insolentia* displays four parallel in-phase and incised epichnial grooves. Trace Type B differs from *U. insolentia* in that the inner pair of the parallel grooves are not strongly incised and is twice the size as *Undichna* described by Trewin (2000). In addition, *Undichna* is associated with oxygenated freshwater environments instead of the more reducing, marine environment of the Mowry Shale.

Trace Type C.—These trace fossils are shallow (~1 cm deep) and longer than wide (25 cm wide and 1 to 5 meters long) troughs (Figure 10, 11, and 12). Each trace fossil has a gradual end with no apparent edge, whereas the other end may have a well-defined terminus. All appear to be impressed in a north/south direction at the OHV Park. Some have a subtle secondary central indentation in a shallow ridge down the center. The surface of the trace fossil is smooth but with uneven sides. A marginal ridge is faint and non-existent in many samples. This track was not identified at the Johnson County or the Alkali Anticline sites in Big Horn County. These may be similar to a second type of trace fossil described by Davis (1963) in Weston County.

Type C trace fossil appear to be more of a partial resting trace than that of a swimming trace. The mud is slightly disturbed as an indentation. Expulsion material is not present. The trace fossil resembles the impression made by an animal coming down to rest on the ocean bottom and coming to a complete stop as it may be inferred by the terminus end and a shallow beginning. It is unclear as to the trace maker, but it is clearly made by an animal that has a flat bottomed or slightly convex torso, with a hint of a medial furrow, and is approximately 20 to 25 cm wide. If these represent a resting trace fossil, an ambush predator would be a

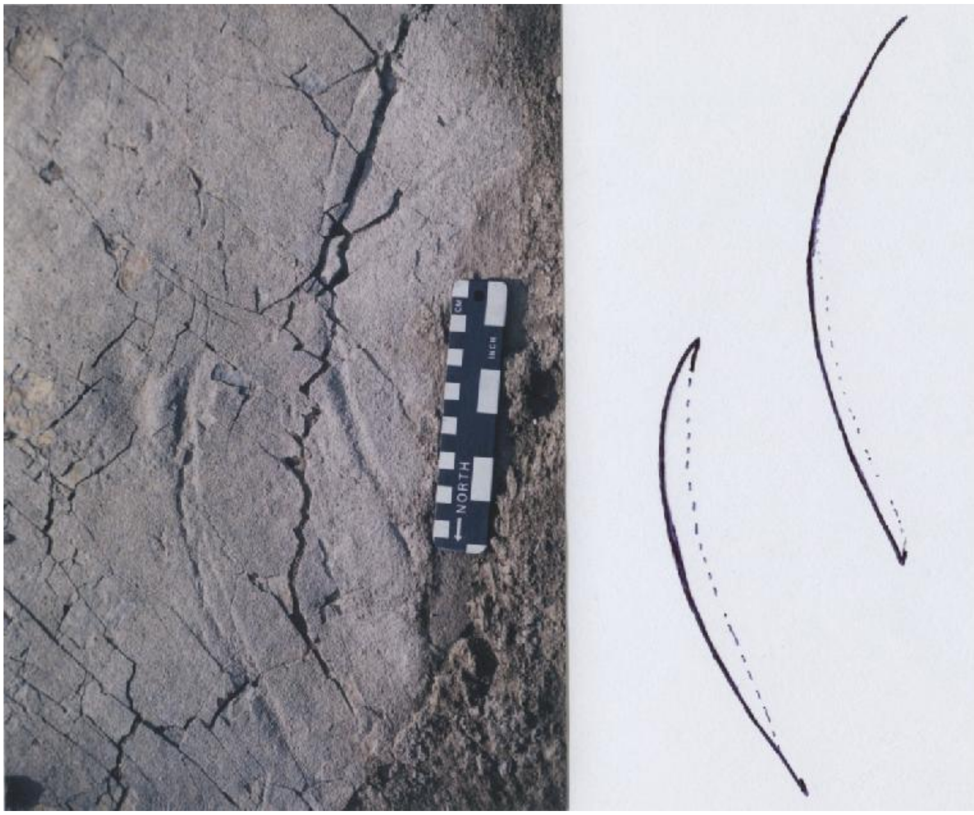

FIGURE 7. Trace fossil Type B. Primary trace with line drawing from OHV Park, Natrona County, Wyoming. Scale = 15 cm.

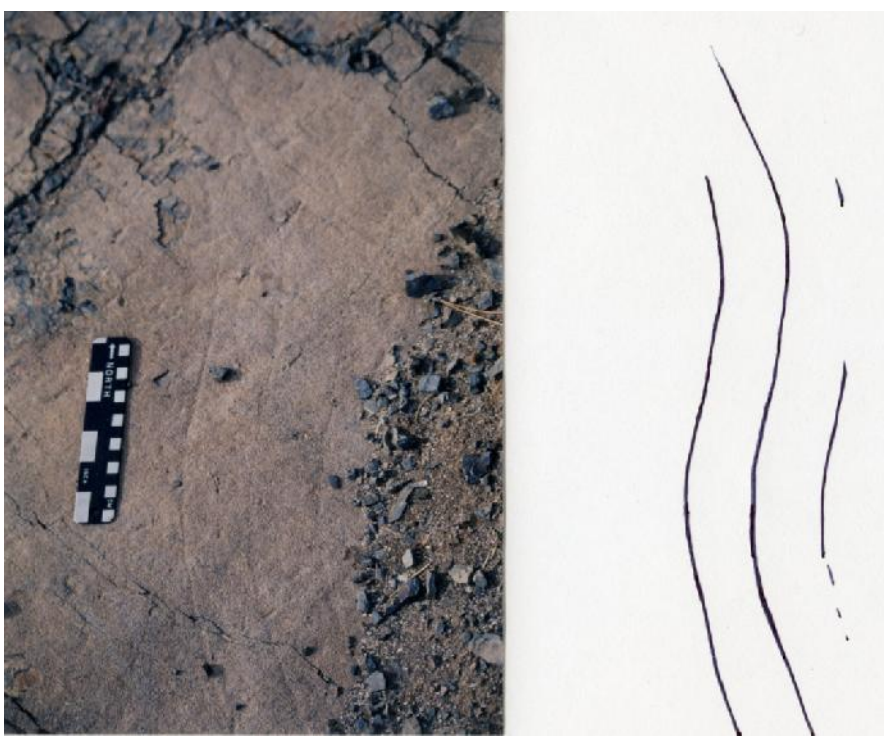

FIGURE 8. Trace fossil Type B. Secondary trace with line drawing. Scale = 15 cm.

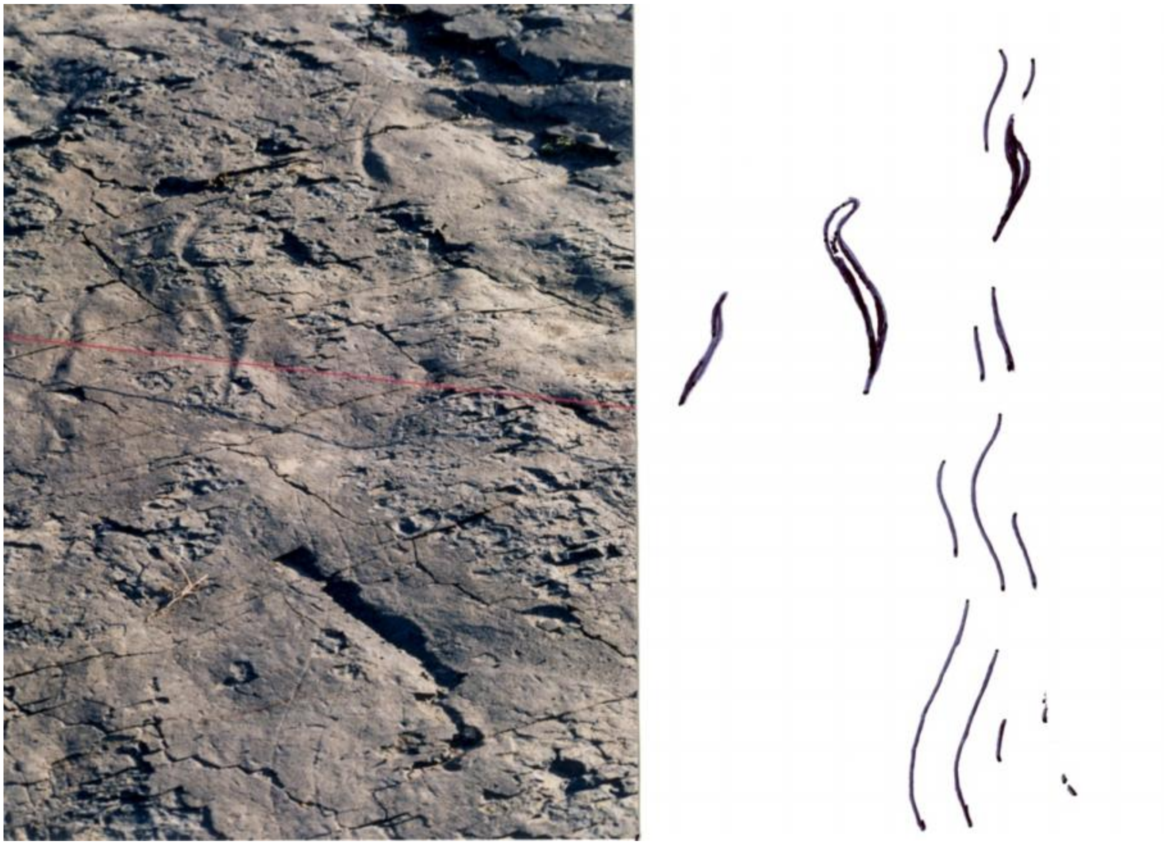

FIGURE 9. Trace fossil Type B with associated primary and secondary trace set.

FIGURE 10. Trace fossil Type C. Resting trace with no expulsion rim.

FIGURE 11. Trace fossil Type C showing terminus end (upper right). Scale = 15 cm.

likely candidate. Crocodiles, which fit the size of the trace fossil, are described as ambush predators (Massare, 1988) and could easily rest on the ocean floor to wait for food to pass by. Forrest (2003) described evidence from a plesiosaur that had been partially eaten by the crocodile *Metriorhynchus* showing related behavior. Modern species are able to submerge for up to two hours (Seebacher, et al., 2005) and at depths of several meters. Furthermore, much of their social, feeding and reproductive behavior often occurs in the water (Farlow et al., 2018). As mentioned by Forrest (2003), crocodiles are capable of exploiting a wide range of feeding sources and habitats. Other animals that could leave this type of impression would include large fish, sharks, and turtles. Invertebrates are ruled out due to the size of the trace fossil. Although ammonites are known from the Mowry Shale Formation, most are too small to create a 25 cm wide shallow trace fossil. The lack of fin marks and general size rule out most fish types. The sediments appear to be displaced but not overly disturbed. Therefore, it is doubtful that this is a feeding behavior of an animal looking for food within the mud of the ocean floor.

Trace Type D.—These trace fossils are indentations showing possibly 2 or 3 impressions (Figure 13). There is only one example of this trace so any interpretation is highly speculative. It could be an invertebrate resting trace fossil such as *Rusophycus*.

Trace Type E.—These trace fossils are irregularly sub-circular impressions (Figure 14). In cross section one edge is deeper and becomes shallow at the other end. Just outside of the deep end side are claw-like marks and a pile of ejecta. There are only two of these trace fossils, which appear to be associated and oriented in the same direction. These trace fossils resemble descriptions by Farlow et al. (2018) and Natali et al. (2019).

This trace fossil is only known from the OHV Park. However, fossil trackways of a possible dinosaur were reported from the Mowry Shale on Dinosaur Ridge, Colorado (Moklestad et al., 2018). The deep impression, claw-like marks, and ejecta from Type E suggest it was made by a clawed animal pushing off of the ocean bottom or a bottom walking and/or punting reptiles. Crocodiles and turtles are the only marine animals with claws. Crocodiles and turtles are known

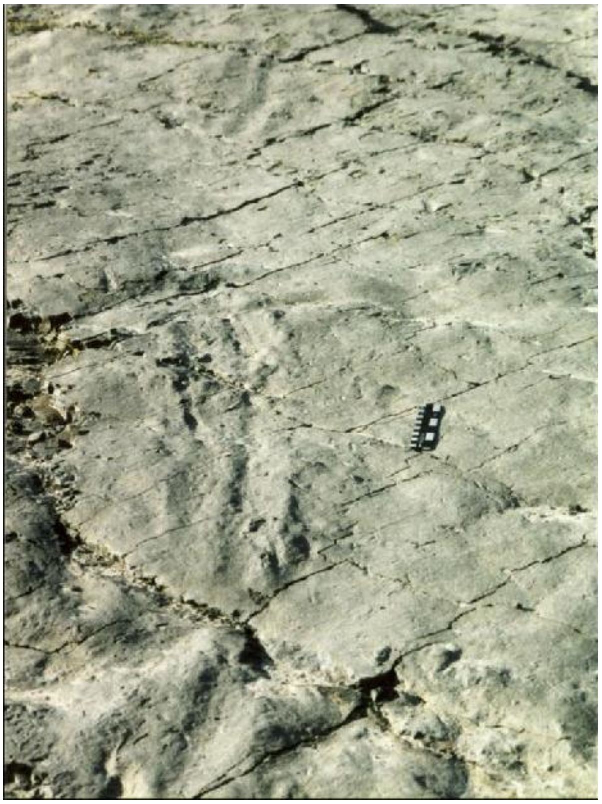

FIGURE 12. Trace fossil Type C showing medial ridge. Scale = 15 cm.

bottom walkers (Brand, 1979; Bennett et al., 2014; Xing et al., 2014; Farlow et al., 2018) and could have left this type of track morphology. Turtles are known from the underlying Muddy Sandstone, but not from the Mowry Shale, so they are a less likely candidate for the trace fossil maker. Crocodile swim traces are also known from another Cretaceous deposit, such as the Dakota Group of Colorado (Foster and Lockley, 1997; Avanzini et al., 2007; Lockley et al., 2010), and is a more likely candidate. Natali (2019) described similar traces in marine sediments of the Maiolica Formation in Italy. He specifically described tetrapod tracks that are irregularly sub-circular or elliptical shape with a displacement rim, somewhat similar to Type E. Natali (2019) suggested that these traces were made by the forelimb based on the lack of an overprint. Trace Type E appears to only represent only one side of the body if they are consecutive impressions. This feature is not uncommon, as was reported by Farlow et al., (2018).

Invertebrate Traces.—A few invertebrate trace fossils were found on the same surface as the vertebrate trace fossils. Invertebrates trace fossils are not as common at the study sites, with the exception of the supposed cephalopod trace fossil (see below). *Planolites* was described near the Alkali Anticline site (Clark, 2010). Other trace fossils observed at the site include a surface feeding trace resembling that of an unbranched or semi-spiral burrow. Vertical trace fossils were also seen but due to the laminar fracturing pattern of the Mowry Shale, finding an intact burrow was difficult and will be investigated in future studies.

Asterichnites octoradiatus (Brown and Vokes, 1944, pg 658) was found along with the vertebrate traces described above (Figure 2). These are the most common invertebrate traces in the study areas. *Asterichnites octoradiatus* are eight-limbed star-like impressions. Each has a center circular quarter-sized impression with eight thin grooves radiating away from the center. Brown and Vokes (1944) described these as being possible cephalopod impressions. They are the most common trace for all of the studied sites, but this may be due to the unique morphology that makes them easily recognizable. Upon careful inspection of one sample (TATE i419), a second set of parallel grooves inside each tentacle impression could be seen (Figure 15). The presence of the secondary grooves within the tentacle impressions could easily have been created by the hooklets found on the tentacles of a squid-like animal.

FIGURE 13. Trace fossil Type D. Scale = ~ 10 cm.

FIGURE 14. Trace fossil Type E showing mud drops or ejecta (left) and track impression on the right. Scale = 15 cm.

FIGURE 15 *Asterichnites octoradiatus* (TATE i419). A.Close up view showing secondary grooves. B. Details of groove and hooklet impressions. Scale in mm.

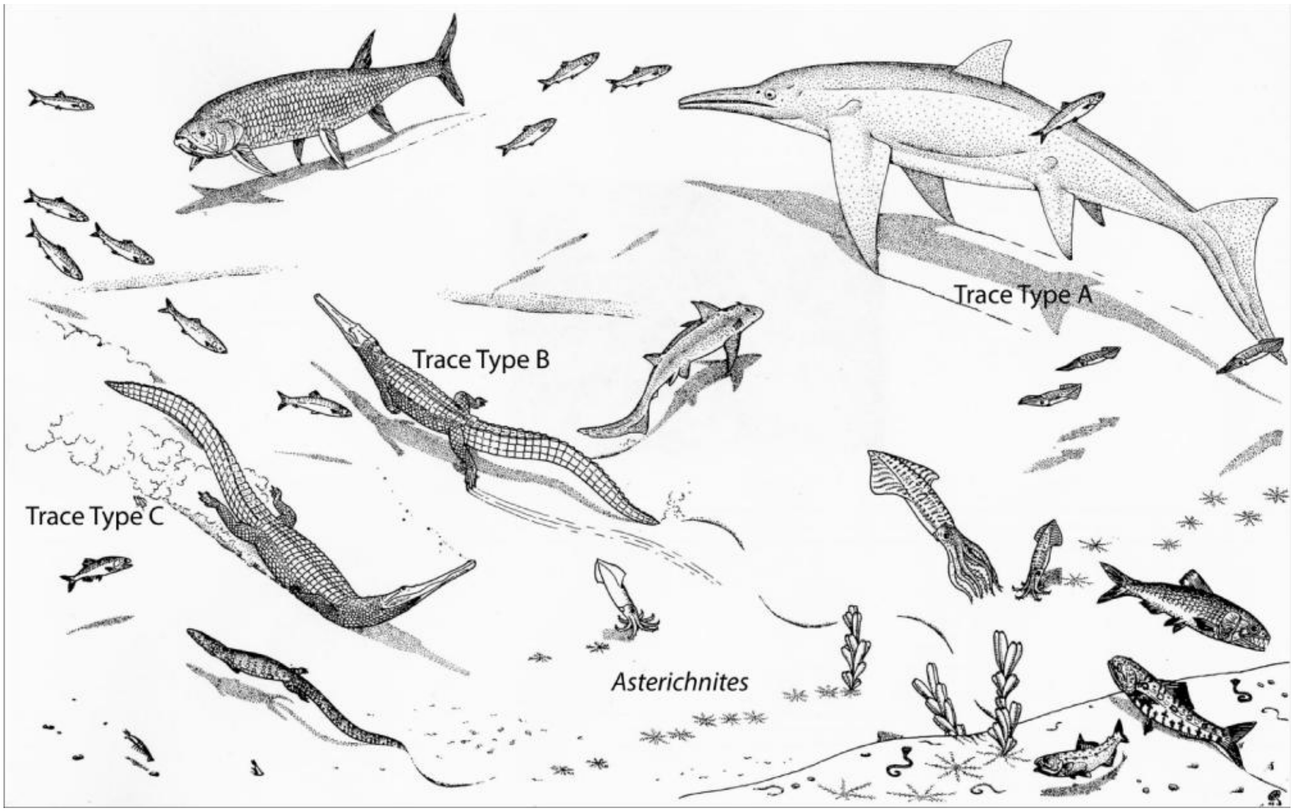

FIGURE 16. Illustration showing ecosystem interpretation. © Copyright Russell Hawley 2019.

The behavior associated with these trace fossils is unclear. Brown and Vokes (1944) suggested that the cephalopod was possibly looking for a place to attach eggs. During reproductive activity, squid deposit egg sacks on the ocean floor. In modern squid, these deposits can be communal in a "big bang" deposit or they could be singular solitary deposits (Hanlon and Messenger, 1996). Furthermore, some squid are known to migrate to shallow waters to spawn, although others will stay in deeper waters. The tracks do not seem to be random but often occur as ~10 impressions in a semi-linear pattern. This would suggest an intentional behavior such as in egg laying. Drew (1911) recorded a female *Doryteuthis münster* bouncing along the ocean bottom with only the tips of her arms just before depositing an egg string. The trace fossils at the OHV Park and those described by Vokes (1941) have rows of stellate impressions and are arranged in a semi-linear pattern, which would support the bouncing hypothesis.

A second possibility would be a feeding behavior, where the cephalopod would probe the ocean floor for invertebrates. The presence of various worm burrows in the shale, although uncommon, would support this idea. However, it seems that this behavior would produce a more random pattern in the track positions on the ocean floor. In either case, if this site was a common place for egg laying or a feeding ground for cephalopods, then it wouldn't be hard to assume that marine reptiles would find the ocean bottom a good place to find a meal (Figure 16). The preserved stomach contents of marine reptiles (Pollard, 1968; Massare and Young, 2005) suggest that squid and other cephalopods were a common food source.

CONCLUSION

The uppermost surface of the Mowry Shale in Wyoming provides researchers with well-preserved set of trace fossils from Cretaceous (Cenomanian) marine ecosystem. Ash from volcanic eruptions buried these traces, capturing a single moment in time. It appears that the Mowry had a diverse fauna of predators and prey. The trace fossils found on the ocean floor show evidence of behavior from various vertebrates and cephalopods, although interpretations are admittedly subjective. Continued studies and new discoveries will help clarify these explanations.

The current interpretation describes a scene where predators, both ambush predators and active hunters, rest and scour the ocean bottom looking for prey (Figure 16). Jurassic ichthyosaurs fed on cephalopods, as indicated by hooklets found as stomach contents (e.g., Pollard, 1968; Massare and Young, 2005) although some Cretaceous species had a different diet (Kear, et al., 2003). The presence of the cephalopod stellate impressions along with evidence of cruising behavior of ichthyosaurs, as demonstrated by Trace Type A and B, paints a picture of swimming ichthyosaurs and/or other vertebrates looking for cephalopod and/or their eggs on the seafloor. Trace fossil Types C, and E suggest a possible ambush predator resting and/or pushing off the sea floor perhaps waiting for a fish or other vertebrate to swim by.

ACKNOWLEDGMENTS

This project is dedicated to Arthur E. Burford, a professor for the University of Akron and a long time Wyoming geologist. Mr. Burford was contacted in the summer of 2004 for information about the location of the OHV Park site. Unfortunately, Mr. Burford passed away a month later before we could tell him about the finds and project that has generated from his original report in 1985.

Thanks is given for the following: The NSF EPSCoR for funding this project; the Bureau of Land Management for their financial and academic support and for providing field assistance in mapping a surveying; the Tate Geological Museum for access to the collections and as the repository for the data and samples collected; to Russell Hawley for the wonderful illustrations and reconstruction of the Mowry Sea; and to Dr. Obradovich for supplying updated radiometric dates.

LITERATURE CITED

Anderson, A. 1976. Fish trails from the Eargly Permian of South Africa. Palaeontology 19: 397-409.

Anderson, A.D., and B.J. Kowallis. 2005. Storm deposited fish debris in the Cretaceous Mowry Shale near Vernal, Utah. Pp. 125-130, in C.M. Dehler, J.L.Pederson, D.A.Sprinkel, and B.J. Kowallis (eds.), Uinta Mountain Geology, Utah Geological Association Publication 33.

Avanzini, M., L. Piñuela, J. Ignacio Ruiz-Omeñaca, and J. Carlos Garcia-Ramos. 2007. The Crocodile Track *Hatcherichnus*, From the Upper Jurassic of Asturias (Spain). Pp. 88-92, in J.Milàn, S.G. Lucas, M.G. Lockley, and J.A. Spielmann, (eds.), Crocodyle tracks and traces. New Mexico Museum of Natural History and Science, Bulletin 51.

Bennett, M.R., S.A. Morse, and P.L. Falkingham. 2014. Tracks made by swimming Hippopotami: An example from Koobi For a (Turkana Basin, Kenya), Palaeogeography, Palaeoclimatology, Palaeoecology 409: 9–23.

Brand, L. 1979. Field and laboratory studies on the Coconino Sandstone (Permian) vertebrate footprints and their paleoecological implications. Palaeogeography, Palaeoclimatology, Palaeoecology 28:25-38.

Bremer, J.M. 2016. Stratigraphy and sedimentology of the Cretaceous Mowry Shale in the Northern Bighorn Basin of Wyoming: Implications for unconventional resource exploration and development. Unpublished M.S Thesis, University of Nebraska, Lincoln 82 pp.

Brown, B. and H.E. Vokes. 1944. Fossil imprints of unknown origin; 2 Further information and a possible explanation. American Journal of Science 242:656-672.

Burford, A.E. 1985. Reptilian markings on the Upper Mowry Shale Emigrant Gap area, Natrona County, Wyoming. The Cretaceous Geology of Wyoming, Wyoming Geological Association 36th Annual Field Conference Guidebook 157-158.

Burtner, R.L. and M.A. Warner. 1986. Relationship between illite/smectite diagenesis and hydrocarbon generation in Lower Cretaceous Mowry and Skull Creek Shales of the Northern Rocky Mountain Area. Clays and Clay Minerals 34:390-402.

Clark, C.K. 2010. Stratigraphy, sedimentology, and ichnology of the Upper Cretaceous Frontier Formation in the Alkali Anticline region, Bighorn County, Wyoming. Unpublished M.S. Thesis, University of Nebraska, Lincoln 76 pp.

Cobban, W.A., and J.B. Reeside Jr. 1951. Lower Cretaceous ammonite in Colorado, Wyoming and Montana. America Association of Petroleum Geologists Bulletin 35:1892-1893.

Cockerell, T. D. A. 1919. Some American Cretaceous fish scales. United States Geological Survey Professional Paper 120I:165–188.

Connely, M.V. and B. Talbot. 2005. Trace fossils in marine sediments of the Mowry Shale (Early Cretaceous) of Wyoming are possibly vertebrate in origin. Journal of Vertebrate Paleontology, Supplement 25:47.

Corbett, R.G., Friberg. L.M., Muller, A.J., Wingard, P.S. 1985. Sandpaper surface at the superface of the Mowry Shale, Natrona County, Wyoming. Geological Society of America, Rocky Mountain Section Meeting, Abstracts 17(4):214.

Costanzo, L.A. 2006. Stratigraphy of the Lower Cretaceous Muddy Sandstone, Wind River Indian Reservation, Fremont County, Wyoming. Unpublished M.S Thesis, Colorado School of Mines 151 pp.

Davis, J.C. 1963. Origin of the Mowry Shale. University of Wyoming, Contributions to Geology 2:135-146.

Drew, G.A. 1911. Sexual activities of the squid: *Loigo pealii* (Les.): I copulation, egg laying, and fertilization. Journal of Morphology 22:327-352.

Druckenmiller, P.S. 2002. Osteology of a new plesiosaur from the lower Cretaceous (Albian) Thermopolis Shale of Montana. Journal of Vertebrate Paleontology 22:29–42.

Elzea, J.M., and H. H. Murray. 1990. Variation in the mineralogical, chemical and physical properties of the Cretaceous Clay Spur bentonite in Wyoming and Montana: Applied Clay Science 5:229-248.

Farlow, J.O., N.J. Robinson, M.L.Turner, J. Black, and S.M. Gatesy. 2018. Footfall Pattern of a Bottom-Walking Crocodile (*Crocodylus acutus*). Palaios 33(9), 406-413.

Forrest, R. 2003. Evidence for scavenging by the marine crocodile *Metriorhynchus* on the carcass of a plesiosaur. Proceedings of the Geologists Association 114:363-366.

Foster, J.R., and M.G. Lockley. 1997. Probable crocodilian tracks and traces from the Morrison Formation (Upper Jurassic) of eastern Utah: Ichnos 5:121–129.

George, L.,D. Cardinal, and G. Winter. 2014. Wyoming Stratigraphic Nomenclature Chart. Wyoming Geological Association.

Hanlon, R.T. and J.B. Messenger. 1996. Cephalopod Behavior. Cambridge University Press, 232 pp.

Hanson, D.A., and M. Connely. 2006. Mowry Shale ichnofossils; Management of a unique fossil tracksite in an off-highway vehicle recreation park. New Mexico Museum of Natural History and Science, Bulletin 34:19.

Hosterman, J.W., and S.H. Patterson. 1992. Bentonite and Fuller's Earth Resources of the United States. U. S. Geological Survey Professional Paper 1522:45pp.

International Commission on Stratigraphy. 2018. International Chronostratigraphic Chart, Available online at www.stratigraphy.org/ICSchart/ChronostratChart2018-07.pdf.

Kear, B.P., W.E. Boles, and E.T. Smith. 2003. Unusual gut contents in a Cretaceous ichthyosaur. Proceedings of the Royal Society of London. Suppl 2. Series B: Biological Science 270:206-208.

Kirschbaum, M., and L.N.R. Roberts. 2005. Stratigraphic framework of the Cretaceous Mowry Shale, Frontier Formation and adjacent units, southwestern Wyoming Province, Wyoming, Colorado, and Utah. Chapter 15, in Petroleum Systems and Geologic Assessment of Oil and Gas in the Southwestern Wyoming Province, Wyoming, Colorado, and Utah. U.S. Geological Survey Digital Data Series DDS–69–D.

Lockley M.G., S.G. Lucas, J. Milàn, J.D. Harris, M. Avanzini, J.R. Foster, and J.A. Spielmann. 2010. The fossil record of crocodylian tracks and traces: an overview. Pp. 1-13, in J. Milàn, S.G. Lucas, M.G. Lockley, and J.A. Spielmann (eds.), Crocodyle tracks and traces. New Mexico Museum of Natural History and Science Bulletin 51.

Long, M.S., S.M. Ritter, and T.H. Morris. 2000. Facies architecture and sequence stratigraphy of the Lower Cretaceous Muddy Formation in the southeastern Bighorn Basin, Wyoming: American Association of Petroleum Geology, Annual Meeting, Abstracts 2000:87.

Manni, R., U. Nicosia, and G. Nobili. 1999. An unusual tetrapod trackway from lower Jurassic marine sediments of central italy: *Accordiichnus natans* n. ichnogen., n. ichsp. Geologica Romana 35:167-187.

Massare J.A., 1988. Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. Paleobiology14:187-205.

Massare, J.A. 1998. Marine reptiles of the Mowry and Belle Fourche Shales (Cretaceous) in Northeastern Wyoming. Pp. 33, in R.A. Hunter (ed.), Life in The Late Cretaceous, Tate Geological Museum.

Massare, J.A., and L. E. Dain. 1989. The marine reptiles of the Mowry Shale (Albian) of northeastern Wyoming. Journal of Vertebrate Paleontology. 9(3 supplement): 32A.

Massare, J.A. and H.A. Young. 2005. Gastric contents of an ichthyosaur from the Sundance Formation (Jurassic) of Central Wyoming. Paludicola 5:20-27

Maxwell, E.E. and B.P. Kear 2010. Postcranial anatomy of *Platypterygius americanus* (Reptilia: Ichthyosauria) from the Cretaceous of Wyoming. Journal of Vertebrate Paleontology 30:1059–1068.

McGowan, C. 1972. The systematics of Cretaceous ichthyosaurs with particular reference to the material from North America. University of Wyoming, Contributions to Geology 11:9–29.

Moklestad, T., T. Caneer, and S. Lucas. 2018. The "Lost Tracks" at Dinosaur Ridge, Colorado, from the base of the Cretaceous (Late Albian-Early Cenomanian) Mowry Shale Member of the Benton Formation, show a swimming(?) ornithopod affected by a current. Pp. 503-511 in S.G. Lucas, and R.M. Sullivan, (eds.) Fossil Record 6. New Mexico Museum of Natural History and Science Bulletin 79.

Mook, C.C. 1934. A new species of *Teleorhinus* from the Benton shales. American Museum Novitates 702:1-11.

Nace, R.L. 1939. A new ichthyosaur from the Upper Cretaceous Mowry Formation of Wyoming. American Journal of Science 237:673–686

Natali, L., A. Blasetti, and G., Crocetti. 2019. Detection of Lower Cretaceous fossils impressions of a marine tetrapod on Monte Conero (Central Italy). Cretaceous Research 93:143-150.

Nixon, R.P. 1973. Oil source beds in Cretaceous Mowry Shale of northwestern interior United States. American Association of Petroleum Geologists Bulletin 57:136-161.

Obradovich, J., T. Matsumoto, and T. Nishida. 2002. Integrated biostratigraphic and radiometric study on the Lower Cenomanian (Cretaceous) of Hokkaido, Japan. Proceedings of the Japan Academy: Series B. Physical and Biological Sciences. 78:149–153.

Paull, R.A. 1957. Depositional history of the Muddy Sandstone Bighorn Basin, Wyoming. Unpublished Ph.D. Dissertation, University of Wisconsin. 269 p.

Plint, A.G., A. Tyagi, M.J. Hay, B.L. Varban, H. Zhang, and X. Roca. 2009. Clinoforms, paleobathymetry, and ud dispersal across the western Canada, Cretaceous Foreland Basin: Evidence from the Cenomanian Dunvegan Formation and contiguous strata. Journal of Sedimentary Research. 79:144–161.

Pollard, J. E. 1968. The gastric contents of an ichthyosaur from the lower Lias of Lyme Regis, Dorset. Palaeontology 11: 376-388.

Reeside, J.B., Jr. and W.A. Cobban. 1960. Studies of the Mowry Shale (Cretaceous) and contemporary formations in the United States and Canada: A stratigraphic and paleontologic study of five large assemblages of gastroplitine cephalopods interpreted as five species of *Neogastroplites* having an unusual degree of variability. Geological Survey Professional Paper. 355:1-126.

Rhoads D.C. 1975. The paleoecological and environmental significance of trace fossils. Pp. 147-160, in R. W. Frey (ed.) The Study of Trace Fossils. Springer, Berlin, Heidelberg.

Romer, A.S. 1968. An ichthyosaur skull from the Cretaceous of Wyoming. University of Wyoming, Contributions to Geology 7:27–41.

Scott, R.W., F.E. Oboh-Ikuenobe, D.G. Benson and J. M. Holbrook. 2009. Numerical age calibration of the Albian/Cenomanian boundary. Stratigraphy 6:17-32.

Seebacher, F., C.E. Franklin, and M. Read. 2005. Diving behavior of a reptile (*Crocodylus johnstoni*) in the wild: Interactions with heart rate and body temperature. Physiological and Biochemical Zoology 78:1-8.

Stewart, J.D., S.A. Bilbey, D.J. Chure, S.K. Madsen, and K. Padian. 1994. Vertebrate fauna of the Mowry Shale (Cenomanian) in northeastern Utah. Journal of Vertebrate Paleontology 14 (3 supplement):47A.

Stewart, J.D., and M. Hakel. Ichthyofauna of the Mowry Shale (early Cenomanian) of Wyoming. New Mexico Museum of Natural History and Science, Bulletin 35:161-163.

Trewin, N.H. 2000. The Ichnogenus *Undichna*, with examples from the Permian of the Falkland Islands. Palaeontology 43:979-997.

Trumbull, C.B. and M.V. Connely. 2010. New ichnotaxa from the Mowry Shale of Wyoming may be vertebrate in origin. Geological Society of America, Rocky Mountain Section Abstracts 42(3):41-42.

Turek, V. 1989. Fish and amphibian trace fossils from Westphalian sediments of Bohemia. Palaeontology 32:623-643.

Vokes, H.E. 1941. Fossil imprints of unknown origin. American Journal of Science 239:451-453.

Vuke, S.M. 1982. Depositional Environments of the Cretaceous Thermopolis, Muddy, and Mowry Formations Southern Madison and Gallatin Ranges, Montana. Unpublished M.S. Thesis, Indiana University. 153 pp.

Watson, J.E. 1980. Catalog of Wyoming stratigraphy, Tooke Engineering, Casper, WY

Xing, L., M. Avanzini, M.G. Lockley, T. Miyashita, H. Klein, J. Zhang, Q. He, L. Qi, J. D. Divay, and C. Jia. 2014. Early Cretaceous turtle tracks and skeletons from the Junggar basin, Xinjiang, China. Palaios 29:137-144.

Zhang, Q., W. Wen, S. Hu, M.J. Benton, C. Zhou, T. Xie, T. Lü, J. Huang, B. Choo, Z. Q. Chen, J. Liu, and Q. Zhang. 2014. Nothosaur foraging tracks from the middle Triassic of Southwestern China. Nature Communications 5, Article 3973:1-12.