A Pleasing Discovery from North Dakota's Ancient Seas

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In today's oceans there are a wide variety of mammals that have adapted to living at least part of their lives in the water. Millions of years ago during the Mesozoic Era, better known as the "Age of Dinosaurs," none of those mammals were yet in existence. Instead, many different types of reptiles were adapted to aquatic lifestyles and filled the ecological roles that are today filled by mammals. Nearly all of the aquatic reptiles from the Mesozoic Era are part of a broad group known as Sauropterygia, with only the mosasaurs falling outside this group as they are closely related to monitor lizards. The first sauropterygians arose in the Triassic Period, and the group persisted until the end of the Cretaceous Period when they went extinct along with the non-avian dinosaurs. Within that group you can find the dolphin-like ichthyosaurs, the walrus-like placodonts (similar feeding style, but lack the large tusks), and the seal-like nothosaurs. While those animals had similar body shapes and/or diets to modern aquatic mammals, one highly successful group of sauropterygians had a unique body shape that is not seen in any living animal today: the plesiosaurs.

Plesiosaurs (a term here used to refer to the superfamily Plesiosauroidea) were massive animals of the ancient seas, spanning up to 50 feet in length in the largest species, which is about the length of a modern-day humpback whale. Unlike the whales of today, or the other swimming reptiles of the Cretaceous like the mosasaurs, plesiosaurs had elongate necks with relatively small heads at the end (fig. 1). They were fully aquatic, unable to return to land given the structure of their body and their large size. They had no gills, so they had to return to the surface to breathe like most secondarily aquatic animals (for example, whales, penguins, seals, sea turtles, etc.). Plesiosaurs are most commonly known in popular culture as the inspiration behind sea monster myths

Figure 1. Reconstruction of the sea that covered much of North Dakota in the Late Cretaceous. Long-necked elasmosaurid plesiosaurs are seen in the water through a cresting wave while pterosaurs (flying reptiles) soar overhead.

Art by Douglas Henderson.

like the "Loch Ness Monster." These iconic animals are easily recognizable but tend to be relatively rare as fossils and most species are only known from a few or even a single specimen, making each new discovery important.

How They Lived

Plesiosaurs differed from other aquatic reptiles that lived during the Cretaceous in their swimming style. Most of the swimming reptiles that lived during the Cretaceous powered their swimming by strong side to side movement of large tails, much like how modern sharks swim. However, plesiosaurs had small tails compared to their overall body size that could not have propelled them through the water in the same way. Instead, plesiosaurs had four large flippers that they used to move through the water, though exactly how they used those flippers has been a matter of great debate over the years. One of the early ideas was that they used them like oars to row through the water, moving their flippers forward and backward in a horizontal plane. While such a motion works well for moving a boat along the surface of the water because the oars leave the water on the forward stroke and then reenter the water for the powerful backwards stoke, performing the same motion entirely under the water is highly inefficient. Additionally, as paleontologists learned more about the anatomy of plesiosaurs it became clear that the shoulder and hip joints were not well suited for horizontal movement, but were better adapted to vertical, up and down movements. Most marine animals that swim using flippers (for example, sea turtles, penguins, seals, etc.) use some type of vertical movement of the flippers to swim. However, among modern animals only sea turtles have two sets of flippers like the extinct plesiosaurs. In sea turtles the back flippers are used for maneuvering, while the front flippers provide the thrust for swimming, and a similar swimming method was proposed for plesiosaurs by some authors (Lingham-Soliar, 2000). One problem with this idea is that the rear flippers of sea turtles tend to be much smaller than the front flippers, while the front and rear flippers of plesiosaurs are roughly the same size and shape, suggesting both were being used for a similar purpose.

So, if both sets of flippers were being used for swimming, how exactly was that accomplished? Some paleontologists suggest that the front and rear flippers would work in opposition to each other, with the rear flippers moving down as the front flippers moved up, and vice versa, allowing thrust to be constantly generated (Riess and Frey, 1991). While this may make some intuitive sense, when that motion is modeled it is clear that offset movement of the rear flippers would disrupt the water current generated by the front flippers, making that swimming motion highly inefficient. So, were the rear flippers used for swimming or maneuvering? A recently published study that modeled the efficiency of several different swimming methods in plesiosaurs found that the four flipper swimming method was likely correct, but that the flippers would not have worked completely in opposition to each other as previously proposed, nor would they have moved perfectly in sync with each other. Instead, the rear flippers would be just slightly delayed behind the front flippers, creating a strong and thin jet of water behind the flippers that would have propelled them through the water (fig. 2) (Muscutt et al., 2017).

So how fast were plesiosaurs? As it turns out, the answer was likely: not very fast at all. Their large size, unique body shape, and use of flippers instead of a tail to swim all work against them in the speed department. If plesiosaurs were cold-blooded animals like most other reptiles, then they likely had a cruising speed of around one mile per hour. If they were warm-blooded, their cruising speed may have been elevated to between three and four miles per hour (Motani, 2002). For reference, that latter speed is about the feeding speed of a blue whale, which then speeds up to a cruising speed of around 12 miles per hour. However, estimates of cruising speed for the other large marine reptiles known from the end of the Cretaceous, mosasaurs, finds that they swam at approximately the same cruising speed (Motani, 2002). The top speed of an extinct animal is difficult to accurately calculate, but it is likely that mosasaurs could move at a higher top speed over short distances than plesiosaurs based on their body shape and method of swimming, allowing them to undertake brief bursts of speed to catch prey items.

This discussion raises another interesting question: were plesiosaurs cold-blooded or warm-blooded? One of the best ways to answer that question in extinct animals is to estimate their resting metabolic rate by studying the histology, or microstructure, of their bones. Different types of bone tissues are known to grow

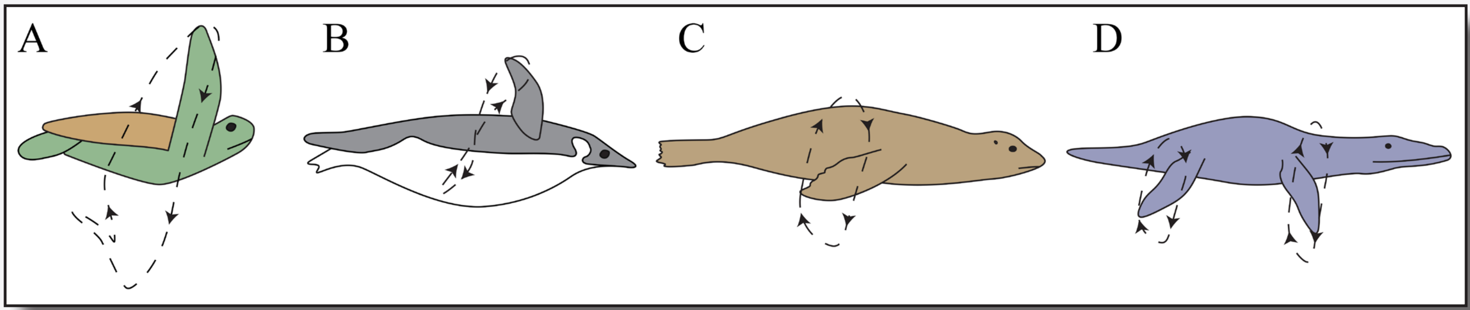

Figure 2. Different methods of flipper powered swimming seen in sea turtles (a), penguins (b), seals (c), and that interpreted for extinct plesiosaurs. The dashed lines indicate the motion of the flippers and the arrowheads denote the direction of movement along the path. Figure modified from Muscutt et al. (2017: fig. S1).

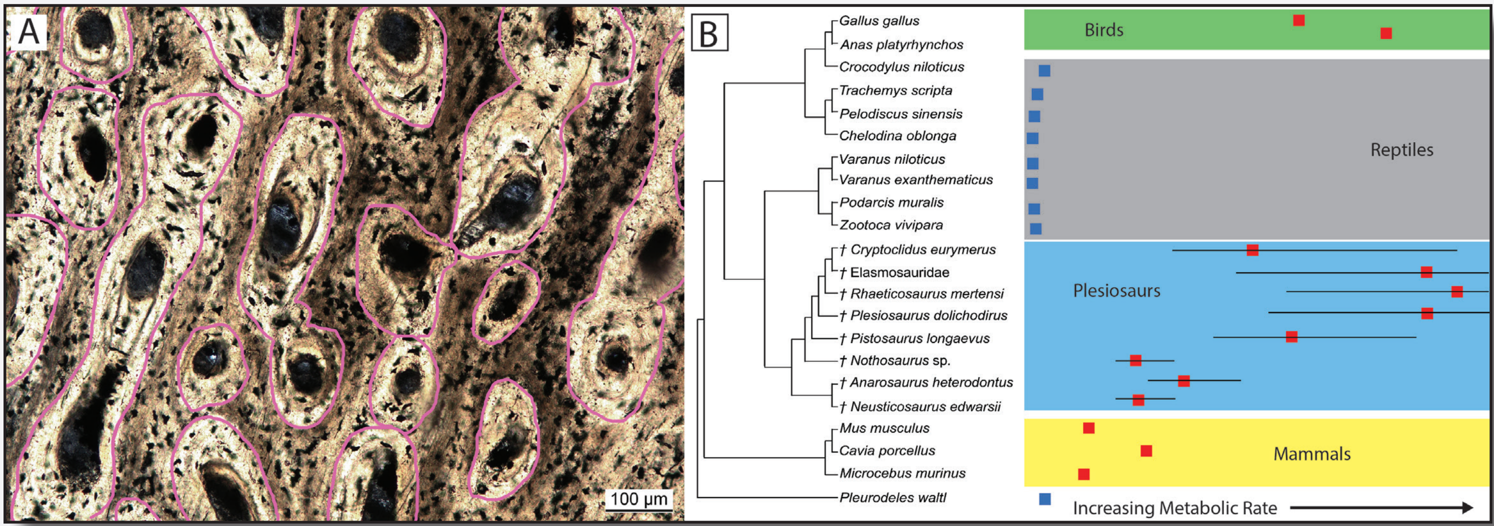

Figure 3. Evidence that plesiosaurs were endothermic (warm blooded). A thin section of plesiosaur bone viewed under polarized light (a) shows the density of primary osteons which contained blood vessels (outlined in pink). A high density of blood vessels indicates faster growing tissues that need high blood supply to support an elevated metabolic rate. In (b), we see the distribution of observed resting metabolic rates of various modern birds, reptiles and mammals compared to that inferred for extinct plesiosaurs. An evolutionary tree is shown to the left of the names to highlight the relationships of these animals. Red boxes indicate warm blooded animals, while blue boxes indicate cold blooded animals. For plesiosaurs, the red boxes are placed at the average estimate metabolic rate and black lines indicate the 95% confidence intervals for those values. Modified from Fleischle et al. (2018: figs 2 and 3).

at different rates in living animals, with some tissues typically only seen in slower growing, cold-blooded animals and others typically only seen in faster growing, warm-blooded animals. A recent study looking at the bone histology of many different types of plesiosaurs found that their resting metabolic rate was as high as seen in modern mammals (fig. 3), and the large-bodied, long-necked elasmosaurid plesiosaurs were closer to the very high metabolic rates seen in living birds (Fleischle et al., 2018). Thus, it was likely that plesiosaurs were endothermic (warm-blooded), fast growing, active animals. A similar conclusion was previously reached for mosasaurs, but in that case it was based on studying the chemistry of their bones and not the tissue types (Harrell et al., 2016). All of that evidence indicates that the top predators of the Cretaceous seas were fast-growing, active animals that would have needed to consume quite a bit of food each day to survive.

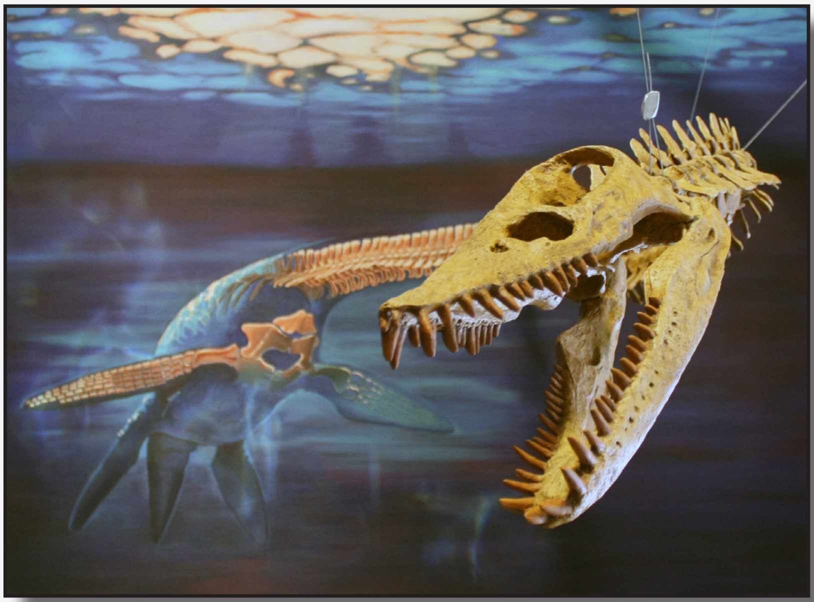

Figure 4. Close up view of the skull of a plesiosaur now on display in the Adaptation Gallery in the State Museum at the North Dakota Heritage Center in Bismarck. Note the shape of the teeth, which were specialized for grabbing fish. Photo courtesy of the State Historical Society of North Dakota.

Thanks to some well-preserved fossils, we have a good idea of what plesiosaurs were eating to feed that high metabolic rate. Several plesiosaur specimens are known to preserve stomach contents from the animal's last meal. Those meals typically consisted of various species of small to medium sized fish (Cicimurri and Everhart, 2001), though in some cases there were also parts of squid, pterosaurs, sharks, and even a specimen with part of a mosasaur in its stomach. This diet fits with the shape and placement of teeth in plesiosaurs, which are tall, narrow, straight, and interlock (fig. 4), morphologies often seen in animals that specialize in eating fish. The presence of the pterosaur and mosasaur bones could either indicate that plesiosaurs were farther up the Cretaceous food chain than is typically accepted, or that they supplemented their fish-heavy diet by scavenging from dead carcasses they encountered in the sea. Another interesting piece of evidence provided by these fossilized stomach contents is the presence of gastroliths, or stomach stones, in plesiosaurs. Those stones were swallowed by plesiosaurs to help break down their food, as seen in many different types of animals today. In one case a plesiosaur specimen found in Kansas included numerous gastroliths of pink or grey Sioux Quartzite (Cicimurri and Everhart, 2001), which would have had to have been picked up almost 500 miles to the northeast of where the specimen was found, likely near islands along the eastern shore of the seaway. That discovery indicates the individual plesiosaurs roamed over large areas, perhaps migrating to different areas of the Western Interior Seaway seasonally or for mating purposes.

One more interesting aspect of plesiosaur ecology is their method of reproduction. Many secondarily aquatic vertebrates return to land to reproduce, either by laying eggs (sea turtles and penguins) or by bearing live young (seals, sea lions, walruses, etc.). However, cetaceans (whales, dolphins, and porpoises) give live birth in the water, typically to a single, large offspring. Given that sea turtles and plesiosaurs are both reptiles that have enlarged flippers for swimming and that sauropterygians and turtles are often considered to be closely related, it used to be thought that plesiosaurs likely returned to land to lay eggs, much like sea turtles do today. Although this may have been possible for some of the earliest (and smallest) plesiosaurs, the large-bodied elasmosaurids would have had extreme difficulty moving onto land with their extremely long necks and portly bodies and would be easy prey for predators. The discovery of an exceptionally preserved plesiosaur specimen in Kansas in 1987 resolved this question of plesiosaur reproduction (fig. 5). A beautifully preserved specimen of the plesiosaur *Polycotylus latippinus* revealed a pregnant female plesiosaur with a single, large fetus present within the abdominal cavity (O'Keefe and Chiappe, 2011). This indicated that plesiosaur reproduction was most similar to that seen in modern cetaceans, and that plesiosaurs did not venture up onto land for reproduction. That discovery may also indicate a certain level of parental care was present in these animals as well to help ensure the survival of their lone offspring.

Plesiosaur Fossils from North Dakota

As I mentioned above, plesiosaur fossils in general are uncommon, and that fact holds true for the rocks in North Dakota. Plesiosaurs were alive during the time of deposition of the oldest rocks exposed at the surface in North Dakota: the Carlile, Niobrara, Pierre, and Fox Hills Formations. To date, plesiosaur fossils have only been found in North Dakota in two of those formations, the Pierre and Fox Hills Formations. The first discovery of plesiosaur bones in North Dakota may have been made by a team led by the famous paleontologist Edward Drinker Cope on behalf of the Academy of Natural Sciences of Philadelphia in 1893 (Daeschler and Fiorillo, 1989). In July and August of that year, Cope and his team were collecting fossils in north-central South Dakota and south-central North Dakota, largely in areas adjacent to the Missouri and Grand rivers. During much of that time they were based out of Fort Yates, North Dakota. One of the specimens collected on that expedition is a single vertebra (back bone) from a plesiosaur, most likely from either the Fox Hills or Pierre Formations that was sent back from Fort Yates. There is no exact location

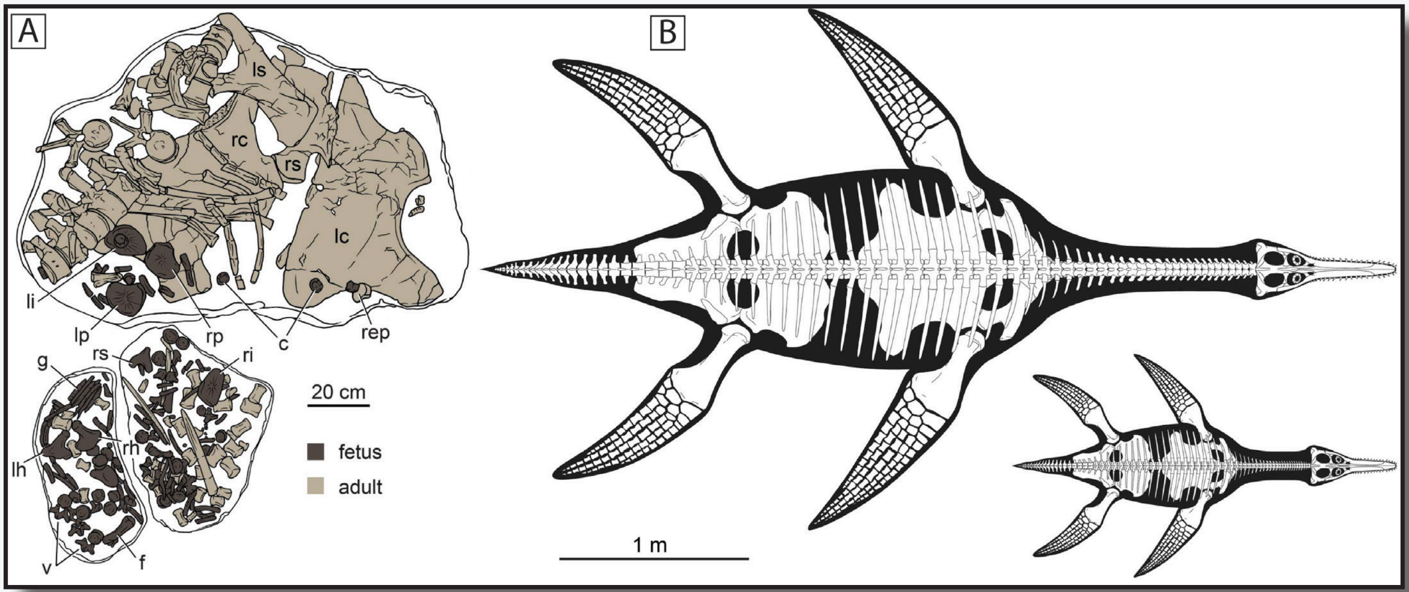

Figure 5. Interpretation of a fossilized pregnant female plesiosaur. Illustration of the actual specimen (a), which was collected in three blocks outlined in the illustration, and reconstructed sizes of the mother and fetus (b). Modified from O'Keefe and Chiappe (2011, figs. 2 and 3). In (a), adult bones are in light brown, and fetal bones are in dark brown. Most of the adult skeleton was found with this specimen except the skull and neck, but only the parts immediately adjacent to the fetus are shown in (a). Abbreviations: c, centra; cm, centimeter; f, femur; g, gastralia; lh, left humerus; li, left ischium; lp, left pubis; m, meter; rep, right epipodial; rh, right humerus; ri, right ischium; rp, right pubis; rs, right scapula; and, v, vertebrae.

information preserved with that specimen, but it is very possible it came from North Dakota.

The North Dakota State Fossil Collection only has four plesiosaur specimens from North Dakota. Two of them are isolated plesiosaur vertebrae that were collected along the banks of the Missouri River south of the Bismarck-Mandan area. Those vertebrae are very similar in size and shape to the one collected by the Cope expedition in 1893. They were collected in different years by different people, likely from the Fox Hills Formation. Attempts to locate more of those specimens have been unsuccessful. Another isolated vertebra was found on private land near the Pembina Gorge in Cavalier County from the Pierre Formation. A cast of that vertebra was graciously donated to the North Dakota State Fossil Collection to document the discovery. Whereas those specimens are enough to note the presence of plesiosaurs in North Dakota, they are far too fragmentary to determine exactly what species were present.

North Dakota's Best Plesiosaur

In 1994 a volunteer field crew from the Pioneer Trails Regional Museum in Bowman, North Dakota was prospecting rocks of the Pierre Formation on land managed by the Bureau of Land Management (BLM) south of Rhame, North Dakota (fig. 6). That work was being conducted as part of an agreement between the BLM and the North Dakota Geological Survey (NDGS) to survey BLM lands and document fossil sites, and the Pioneer Trails Regional Museum has a long history of working with the NDGS to find and protect North Dakota's fossil resources. That crew discovered a new site where plesiosaur bones (vertebrae, parts of the flippers, and a single tooth) were exposed on the surface and a partially eroded, articulated string of vertebrae continued into the rock.

Figure 6. Photographs of the collection of a partial plesiosaur skeleton from southwestern North Dakota in 1994. In (a), a mostly volunteer field crew (NDGS paleontologist John Hoganson [now retired] on the left) excavate part of the neck of the plesiosaur. In (b), seven of the neck vertebrae [white arrow pointing to each one] that were uncovered in the rock at the site. Removal of the specimen from the ground required a large plaster jacket with boards for support (c) to be constructed around the bones, and heavy machinery (d) was required to lift the plaster jacket out of the ground for transport back to the Pioneer Trails Regional Museum in Bowman, ND.

After cleaning up the surface, they followed the vertebrae into the ground, eventually exposing fifteen vertebrae from the neck that stretched for about six feet. For reference, the entire neck of this plesiosaur would contain on average 70 vertebrae and be over twenty feet long. The bones were stabilized with glues, encased in a protective layer of burlap soaked in plaster, and then removed from the ground and transported back to the Pioneer Trails Regional Museum. Volunteer Terry Schaffer oversaw the first phase of cleaning on the specimen, removing most of the surrounding rock and providing stabilization to the fragile bones that were damaged from sitting so close to the surface prior to being discovered.

In 2016 the specimen was transferred to the North Dakota State Fossil Collection for further cleaning and study. The significance of the specimen as the most complete plesiosaur yet found in North Dakota was immediately recognized and planning began to get the specimen on display in the Adaptation Gallery in the State Museum at the North Dakota Heritage Center in Bismarck. NDGS paleontologist Becky Barnes spent weeks performing the detailed preparation work that was needed to get the specimen ready for display. The size and shape of the vertebrae (they look like elongated soda cans lying on their side) indicate this specimen is from one of the species within the family Elasmosauridae, a group that includes the largest species of plesiosaur. Study thus far conducted on this specimen suggests the preserved string of vertebrae comes from the middle portion of the neck and likely is referable to an animal called *Styxosaurus*.

The limited outcrops in the area where the fossil was collected makes it hard to tell what portion of the Pierre Formation it was collected from and approximately how old the specimen is. Another way of determining the age of a fossil site during the Late Cretaceous is by identifying the invertebrate fossils found at the site. The invertebrates (clams and squids, especially) are well studied from this time period, and there are detailed charts that document the age and duration of each species that can be used to narrow down the age of a fossil site. Several well-preserved shells of the extinct squid *Baculites eliasi* (J. Slattery, pers. comm.) were collected along with the plesiosaur specimen. The presence of that squid species indicates the site is positioned within the upper portion of the Pierre Formation and dates to either the end of the Campanian Stage or the very beginning of the Maastrichtian Stage (Cobban et al., 2006), making these fossils approximately 72 million years old (Cohen et al., 2013).

The discovery of this plesiosaur specimen adds an important piece of information to our knowledge of the fauna and environment of the Cretaceous seaway in North Dakota. That work continues throughout the state, aided in large part by the Public Fossil Digs program, which will return again this summer to work in outcrops of the Pierre Formation in the Pembina Gorge. Every new discovery gives us a clearer idea into this long-lost world that was dominated by voracious sea monsters unlike anything we can see in the oceans of today.

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