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REDISCOVERY OF WILBUR KNIGHT'S *MEGALNEUSAURUS REX* SITE: NEW MATERIAL FROM AN OLD PIT

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ABSTRACT
We report the rediscovery of Wilbur Knight's 1895 excavation site of the large Jurassic (Oxfordian) pliosaur *Megalneusaurus rex* from the Sundance Formation. The type specimen (UW4602) is housed at the University of Wyoming and is the only known pliosaur from the Sundance Formation. Recent examination of the excavation site has uncovered new fossil material including possible gastric contents. We can now verify that *Megalneusaurus rex* was collected from the upper Redwater Shale member of the Sundance Formation, about 10 m below the Windy Hill sandstone of the Morrison Formation. It appears that *M. rex* frequented the shallower portions of the Sundance Sea during the last regressive phase. The discovery of the site is significant in establishing the stratigraphic context of this largest member of the Sundance marine reptile fauna.

INTRODUCTION

The Sundance Formation was deposited during the last and most extensive transgressive episode of the Jurassic in North America (Kvale et al., 2001). The majority of the vertebrate fossils have been collected from the Redwater Shale Member. The Redwater Shale is Oxfordian in age (Imlay, 1980; Kvale et al., 2001). It represents a shallow, open shelf environment dominated by silty to shaley mudstone, with occasional bioturbated shale, and ripple-dominated, glauconitic, fine-grained calcareous sandstone (Andersson, 1979; Specht and Brenner, 1979; Kvale et al., 2001).

In the last decade or more, exploration of the Sundance Formation in Natrona County, Wyoming, has resulted in the discovery of many isolated bones and several partial skeletons of ichthyosaurs and juvenile and adult plesiosaurs (Drake and Wahl, 1994; Wahl, 2006; Massare et al., 2006; O'Keefe and Wahl, 2003a, b). A survey of the specimens in museums and those recently collected suggests a local Sundance Formation fauna comprised of about 70% ichthyosaurs and 30% plesiosaurs. Currently, a single species of ichthyosaur, *Opthalmosaurus natans* is recognized from the Sundance (McGowan and Motani, 2003). Two genera of cryptocleidoid plesiosaurs, *Pantosaurus striatus* and *Tatenectes laramiensis* have also been reported (O'Keefe and Wahl 2003a, b).

The large pliosaurid, *Megalneusaurus rex*, is the only known pliosaurid from the Sundance Formation (O'Keefe and Wahl 2003a). Wilbur Knight excavated the partially articulated, but incomplete, skeleton near the town of Ervay, Wyoming in 1895 (Knight, 1895, 1898). Knight (1898) described a specimen that included a complete forelimb, portion of the pectoral girdle, ribs, and "cervical, dorsal and caudal vertebra". Part of a second limb was found but not explicitly described by Knight (1898). Since Knight's initial description, only a cursory mention of *M. rex* has been made in the literature (Brown, 1981; Weems and Blodgett, 1996; O'Keefe and Wahl, 2003a; Wahl, 2006). With the exception of an isolated neural arch (UW24238) from the Upper Redwater Shale of the Sundance Formation, and pieces of a humerus from the Naknek Formation of Alaska (Weems and Blodgett, 1996), no other North American Jurassic pliosaurid material has been referred to this taxon. As *M. rex* represents the largest pliosaurid from North America and the only one from the Sundance Formation, new information on this giant predator would be useful.

A locality believed to be Wilbur Knight's lost site was identified during the summer of 1996 while surveying outcrops of the Sundance Formation near the western border of Natrona County. Relocation of the excavation was undertaken to establish how the initial excavation was performed as well as to ascertain a more precise stratigraphic position for *Megalneusaurus* *rex*. The purpose of this paper is to present evidence demonstrating the successful relocation of the site and to describe new material that was collected there in 2005 and 2006.

Institutional Abbreviations—UW, University of Wyoming, Laramie, WY; **WDC**, Wyoming Dinosaur Center, Big Horn Basin Foundation, Thermopolis, WY; **AMNH**, American Museum of Natural History, New York, NY.

RELOCATION OF THE EXCAVATION SITE

In the course of developing a museum display of Sundance marine reptiles at the Tate Geological Museum, Casper, WRW was given permission for additional preparation, molding, and casting of the holotype of *Megalneusaurus rex* (UW4602) in 1995. Interest in the specimen spurred a search for the type locality, with the hope of finding more material. The rediscovery of the excavation site was the fulfillment of several years of searching using clues provided in Wilbur Knight's correspondence with many paleontologists of his era. As a professor of Geology and Mining Engineering, as well as Curator of the Museum at the University of Wyoming, Wilbur Knight was a prolific letter writer. Copies of his letters, in the form of carbon film sheets, are preserved in the American Heritage Collections at the University of Wyoming, donated by Wilbur Knight's son, Samuel E. Knight. The letters are identified in the collection by book and page number, and are referred to here in the same way.

The excavation of the specimen and general geology of the site of interest are mentioned in two letters and the specimen, called "the Megalneusaur", "pliosaur" or "large plesiosaur" is specifically referred to in six letters. Knight mentioned the excavation, done during a geological resources survey, in a letter to J. E. Ervay (Book 1, p.141), where he described the excavation site as being located "7 or 10 miles from the Ervay post office". In later letters, it is referred to as "70 miles west of Casper" (Book 1, p. 55) and "90 miles from the Union Pacific rail-head at Rawlins" (Book 1, p.161).

The most personal and revealing letters from Knight were written after the publication of his paper on *Megalneusaurus* (Knight, 1898). Knight wrote to H. F. Osborn in December 1898 about the specimen, requesting the return of the pliosaur bones and shark teeth from the Cope collection at the American Museum of Natural History (Book 2, p. 154). He again addressed the same issue in a letter to J. M. Garrett of New York, asking for return of collected material "…that one of Prof. Copes [sic] collectors stole from me in the year 1895" (Book 2, p. 191). This letter is useful in that it mentions both the year of the discovery and the *Megalneusaurus rex* type locale:

> "Prof. Cope arranged to spend a summer with me in the field; but at the last moment he had to remain at home and sent a young man by the name of Stewart in his place. I took Mr. Stewart in to the field and spend 30 days with him and left him in an excellent field with two good men to help him and turned my horse homeward. On my way in I went and examined the Dutton Oil Basin and while at work in the field found the Megalneusaurus. I was short of packing and had to go to the ranchers to get boxes and tools as well as a wagon to take the remains in. On account of packing material I had to bury considerable of the animal in the quarry. Later Stewart landed in the same locality and the rancher told him what I had found, and that I had buried a portion of it and would come up later and get the rest. Stewart then concluded that he would take what I had been obliged to leave behind. He told his two men of the find and that he intended to go and take the remainded [sic] of the skeleton. Since he insisted on doing this his men quit working for him and went to Casper…" (Book 2, p. 191);

Knight referred to the general geology of the Dutton Oil Basin in a later report (Book 1, p.325) with a rough geologic cross-section and map, later used in publication (Knight, 1901). An oil seep was reported by Knight in the Dutton Oil Basin (Knight, 1901), and an oil seep is still present there. The *Megalneusaurus rex* type locality was rediscovered in the Gas Hills area (T33N, R90W), near the Dutton Oil Basin and the original western border of Natrona County. This region has been resurveyed since Knight's 1898 description, and now lies just inside of the eastern border of Fremont County. Our site identification was reinforced using Knight's (1901) published map identifying shallow oil basins of Wyoming.

The original triangular excavation pit is not much larger than the described specimen itself (Figure 1). It is near a uranium test pit that exposes the uppermost Sundance Formation and the overlying Windy Hill Sandstone of the Morrison Formation. A spoil pile may have existed, as evidenced by the badly weathered bone fragments that occur in patches, mixed into the topsoil and scattered over several square meters surrounding the excavation pit (Figure 2). The patchiness of the bone fragments suggests they are not *in situ*. The presence of a broken knife blade at the excavation may be the only evidence of any work that

FIGURE 1. *Megalneusaurus* excavation site in the Dutton Basin, Fremont County, WY. Excavation pit with person standing in it is within the oval. Dashed line marks the bottom of the Morrison Formation. Note the uranium test pit on the left edge of the photo and the open pit uranium mine site in the distance to the far right.

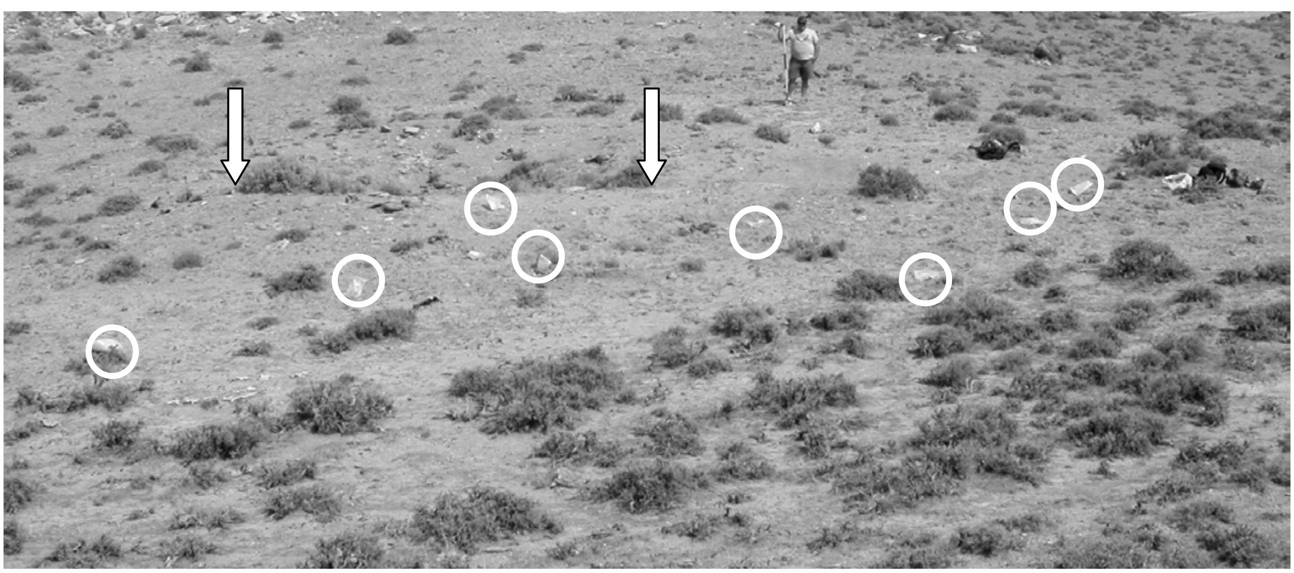

FIGURE 2. *Megalneusaurus* excavation site in the Sundance Formation delimited by arrows. Plastic collection bags (circled) show locations of scattered bone fragments occurring in patches around the pit.

went on there. This artifact has not been dated as yet, but artifacts at historic paleontological sites can help identify both the time of excavation and possible parties involved (Tanke, 2006). It is hoped that a further search with a metal detector will find more evidence such as nails or other tools.

STRATIGRAPHY

A careful reading of the literature indicates that *Megalneusaurus* is from the upper Sundance Formation, but there has been some confusion (see Weems and Blodgett, 1996 for a complete discussion). Knight (Book 2, p. 154) noted that the marine reptile remains could be found below the "*Atlantosaurus* beds". *Atlantosaurus* (a *nomen dubium* of *Apatosaurus*) was included in Marsh's (1878) description of the large sauropods from the Morrison Formation. In his publication describing the pliosaur, Knight (1898) referred to the "…uppermost band of marine beds of the Jurassic" and suggested these beds be named the "Como group", unaware that a similar name, "Como beds" had been proposed for the Morrison Formation (Weems and Blodgett, 1996). In a later publication, Knight referred to the marine Jurassic as the Shirley stage, and referred to *Megalneusaurus* as a "Shirley" fossil (Weems and Blodgett, 1996). Knight (1901) also mentioned the "Shirley marine Jurassic" below the "Como" in the description of the Dutton Oil Basin. This older terminology still persists on old museum labels, including a cast of the holotype forelimb (AMNH4992).

To add to that confusion, after Knight's death in 1903, in an unsigned 1905 letter written to S. W. Williston at the University of Chicago, the writer (most likely W. H. Reed who had taken over the curation of the museum at the University of Wyoming after Knight's death) redefined the *Megalneusaurus* excavation as in the marine beds "down in the sand in the same position as the belemnites below where the *Baptanodons* [sic] are mostly found" (Book 2, letters after 1903 are not listed by page number). *Baptanodon* is the genus to which the North American Jurassic ichthyosaur *Opthalmosaurus natans* was originally assigned (McGowan and Motani, 2003). Recently collected marine reptile specimens are from the Redwater Shale, and the older collections almost certainly are as well. Glauconitic (green) sand, however, is not found below the Redwater Shale, contrary to what Reed's letter suggests.

We can confirm that *Megalneusaurus* was collected in the upper Sundance Formation. The type locality lies in the upper Redwater Shale approximately 10 m below the Windy Hill Sandstone of the Morrison Formation. The lithology at the site consists of a glauconitic, fine- to medium-grained sandstone. The presence of siltstone rip-up clasts in the area, though not in contact with the bone fragments, suggests a high-energy environment (Specht and Brenner, 1979). No shell encrustation or epibionts occur on the surface of the pliosaurid limb elements, although this has been reported on other marine reptiles (Massare et al., 1999) and occurs on cobble-size rip-up clasts elsewhere in the Redwater Shale. Similar sandstones, however, occur near the top of the Redwater Shale elsewhere in Natrona County.

A comparison matrix sample was collected during the preparation of the epipodials of the holotype UW4602 for molding and casting in 1997. The articulated distal ends of the holotype limbs were unprepared and retained some of the original matrix. Matrix surrounding UW4602 is distinctive, with green glauconitic grains mixed with orange iron-stained sand grains. This matches the matrix surrounding the bone fragments found at the excavation site. Additionally, the sandy, glauconitic matrix matches material mixed into the original plaster filler used by Knight to reconstruct the pliosaur limb. This lithology does not occur in many other outcrops at which marine reptiles have been found. The articulated specimens of marine reptiles from the Redwater Shale collected recently by the authors and specimens in older museum collections mostly occurred in carbonate concretions of fine micrite or fossil hash that would not be confused with the sandy-matrix in contact with the pliosaurid bone fragments. One exception is the posterior portion of an ichthyosaur vertebral column (UW34786), which was collected from an area near the Alcova Reservoir by JAM in 2005. This specimen occurred in a sandy matrix in the uppermost Redwater Shale, within a few meters of the Windy Hill sandstone.

The bone preservation of UW4602 is distinctly different from the typical preservation of bones from the Redwater Shale. The bones of UW4602 show extensive recrystallization, giving them a pearly or milky appearance at the dense bone surface of recognizable fragments such as the ribs. This milky appearance is less noticeable at the spongy epipodial contacts. The preservation of bone fragments at the site matches that of the mounted, articulated paddle of UW4602 at the University of Wyoming Geological Museum, as well as the disarticulated limb bones of the specimen (Figure 3). The weathered bone found at the site, discolored from recrystallization, fits Knight's description of "yellow in color" (Book 2, p. 192), whereas other bones from the Redwater Shale are typically tan to reddish brown, including the aforementioned specimen (UW34786) from Alcova Reservoir.

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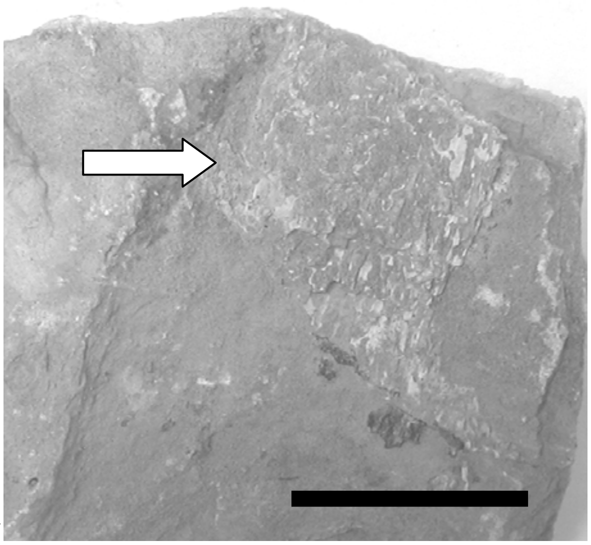

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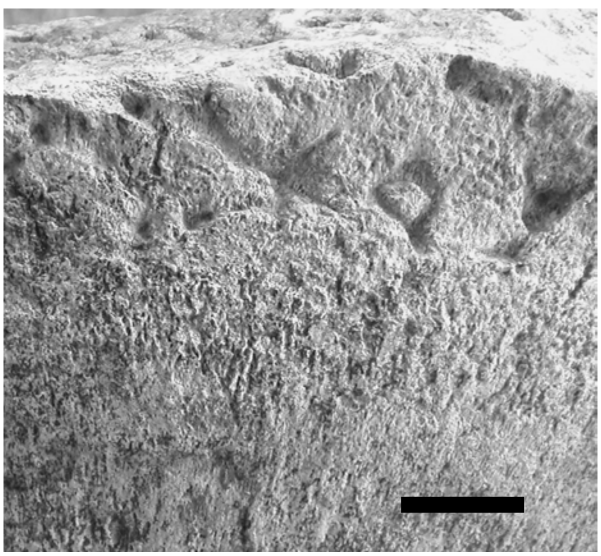

FIGURE 3. A. Preservation of the recently found bone fragment (arrow), shown here in contact with the sandy matrix. Preservation matches that of B. the original holotype material. Scale bars equal 2 cm.

MATERIAL

Type Specimen—*Megalneusaurus rex* is known only from the type specimen (UW4602). Presently, holotype material includes a complete propodial and two sets of articulated epipodials (Figure 4A,B). The bone dimensions (articulated propodial and epipodials plus phalages) indicate a limb length of approximately 2 m. The vertebrae and "pectoral" material mentioned by Knight (1898), however, could not be located and may have been lost in the past century. In letters to both H. F. Osborn and S. W. Williston (Book 1, p.164 and Book 1, p.327), Wilbur Knight referred to the limbs as femora. Though he did not mention the specimen by genus name, their extraordinary size (2 m) could only be from the holotype. In publication, however, Knight (1898) referred to the complete limb as a forelimb and gave a 2.209 m length.

The type specimen is also mentioned by Knight in letters written in 1897 to E. D. Cope in Philadelphia, PA (Book 1, p.78) and to H. F. Osborn of the American Museum of Natural History (Book 1, p.164). He mentioned the plesiosaur again in 1898 (Book 1, p.327), stating the length of the bone, identified in this letter as a femur, as "…being the largest known at 39 inches". He also mentioned it in 1898 to S. W. Williston at the University of Kansas, in a letter concerning the mounting angle of the large plesiosaur limb (Book 1, p.195). A letter to R. S. Tarr of Cornell College, Ithaca, NY in 1899 mentions the plesiosaur's limb length of 995mm (Book 1 p.271).

Diagnostic ontogenetic characteristics of plesiosaurs have been described by several authors (Brown, 1981; Wiffen et al., 1995; Wahl, 2006), and indicate that the *M. rex* specimen was an adult. The facets of the limb elements at articulation points on the proximal and distal surfaces of propodials and epipodials may be a common occurrence in adult plesiosaurs. We estimate a length greater than 10 m for *Megalneusarus rex* based on comparisons of the complete articulated limb described by Knight (1898) and published reconstruction of the large pliosaurids *Pliosaurus brachyspondylus* and *Liopleurodon ferox* (Andrews 1913; Tarlo, 1960; Martill and Hudson, 1991).

New Skeletal Material—The surface around the excavation pit was examined for "float" by scraping down several inches to the estimated level of the original excavation. The ventral portion of at least one vertebral centrum was found (Figure 5A), as well as the paired bases of three neural arches, in-filled with a distinctive silty glauconitic sediment (Figure 5B). Compared to the surrounding rock, the infilling is a finer-grained with a lower percentage of glauconite. No other vertebral material was found aside from the scattered, fragmentary material mentioned above. It is unclear from Knight (1898) whether the vertebrae he found were articulated. Knight (1898) provided some vertebral measurements and the new material falls within the expected size range. Many strings of articulated vertebrae have been found from smaller plesiosaurs (O'Keefe and Wahl, 2003a, b) and ichthyosaurs (Massare et al., 2006; and UW24235, UW24216, UW19686, UW15936). However, the rough environment of deposition may have selectively disarticulated the *Megalneusaurus* specimen. Although the UW4602 skeletal elements could have been disarticulated by scavenging in the depositional

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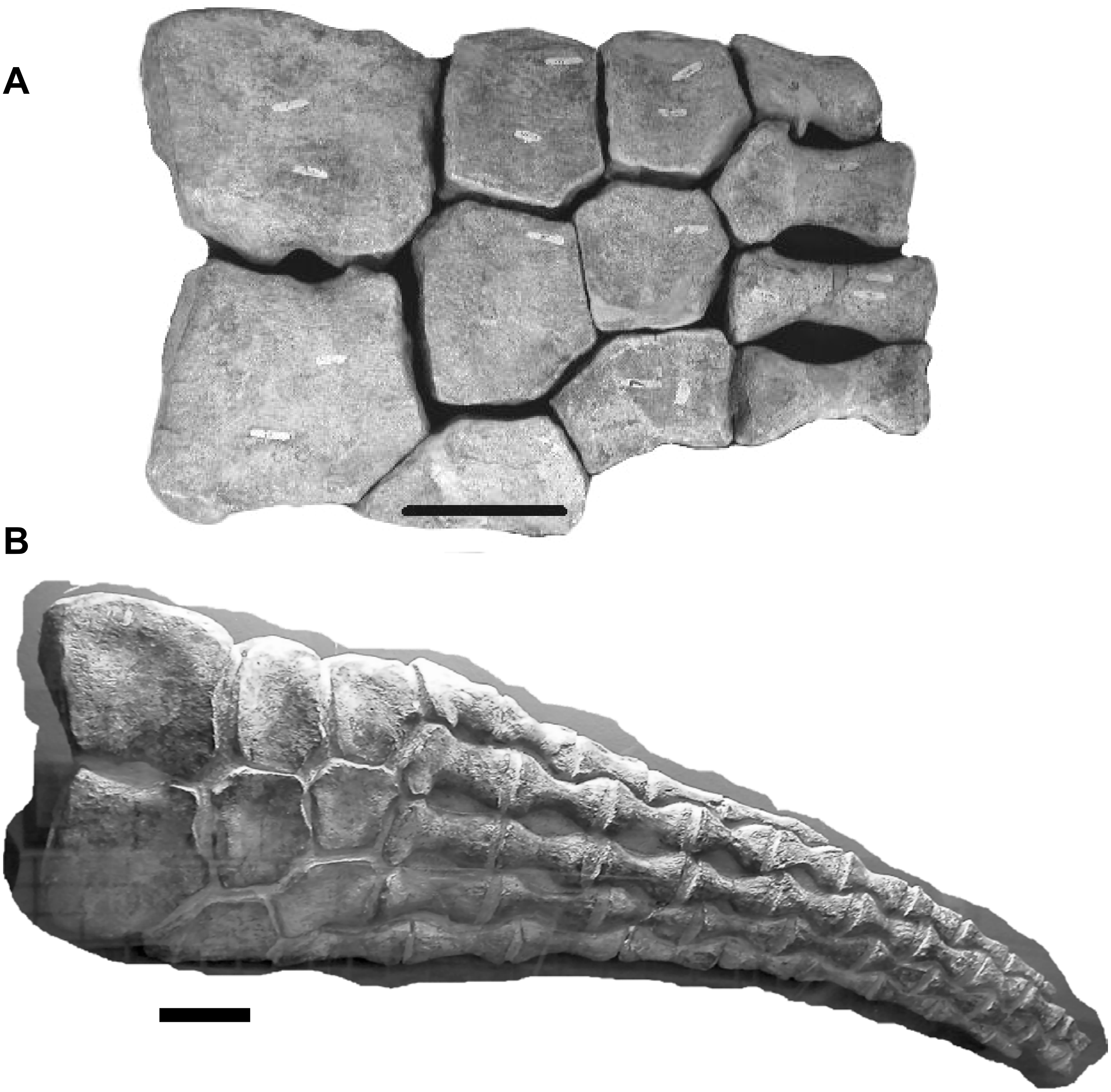

FIGURE 4. UW 4602 limb material found by Wilbur Knight. A. Disarticulated limb in the Vertebrate Paleontology Collections of the University of Wyoming. B. Articulated limb on display at the Geological Museum, University of Wyoming. Scale bars equal 10cm.

environment, no evidence such as bite marks or tooth scratches has been recognized.

Rib material is fairly abundant but in small, weathered sections and very few connect together. Rib heads have not been found to date, although possible gastralia have been identified mainly on the basis of oval shape and a smaller size compared to the rib sections.

A large bone fragment (37 cm by 22 cm), probably from the pectoral or pelvic girdle, was found approximately 20 meters from the original excavation pit (Figure 6 A, B). This is significant as pectoral material was described by Knight in both letter and publication (Book 2, p.154; Knight, 1898). Part of an epipodial was also discovered (Figure 7). The new girdle and epipodial material were identified by pitting,

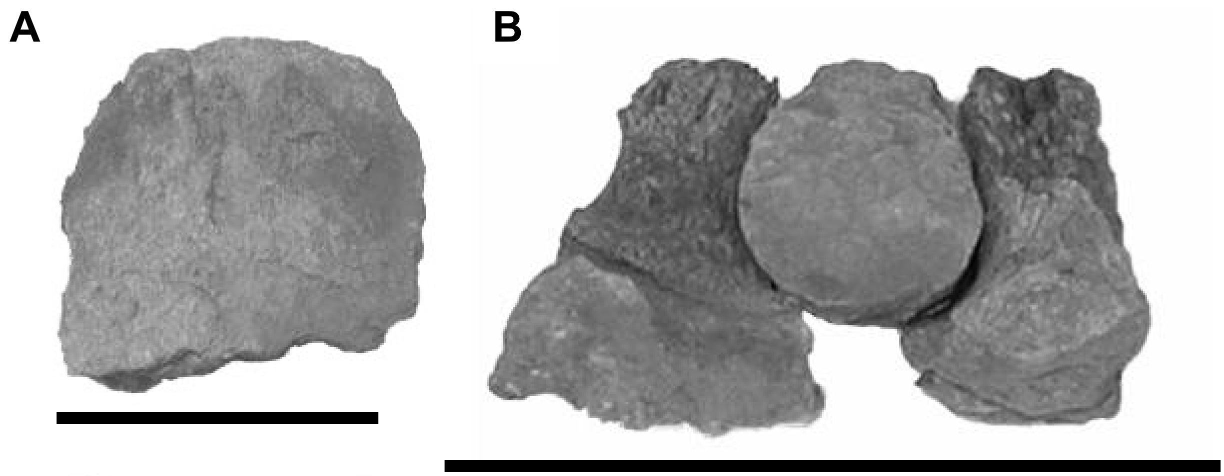

FIGURE 5. New material identified from the Dutton Basin site included: A. ventral portion of a vertebral centrum, and B. matrix filled neural arch. Scale bars equal 10 cm.

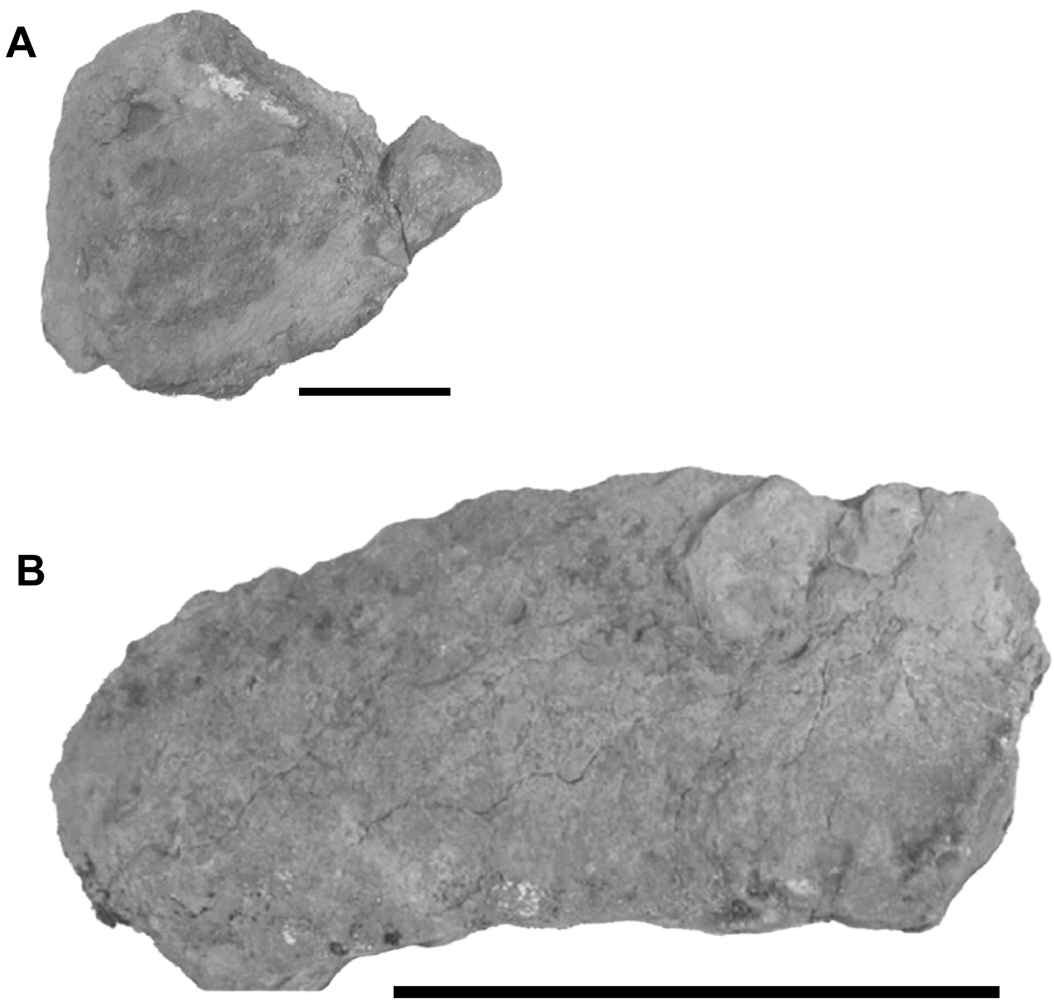

FIGURE 6. A. Portion of possible limb girdle material from the Dutton Oil Basin site. B. Side view of same bone fragment, showing cartilage pitting. Scale bars equal 10 cm.

most likely from the cartilage sheath that occurred at bone contacts, suggesting articulation (Figure 6B, 7). Similar pitting can be seen on limb elements of UW4602.

Preserved Gut Contents—Sections of the excavation facies had a hard, limey matrix containing dense amounts of coleoid (belemnite) cephalopod tentacle hooklets that occur in contact with bone (Figure 8). The matrix around the hooklets is coarse to medium, sub-rounded sandstone with some large (>1.0mm) quartz clasts, and lacks glauconite, so it is distinctly different from the surrounding glauconitic sandstone. Knight (1898) however, did not mention such material. These hooklets are not found associated with large numbers of belemnites and therefore are not likely the result of masses deaths of cephalopods (Wahl, 1998). Also the jaw structures have been identified within the hooklet masses and this suggests predation (Wahl, 1998). Predation on coleoids by marine reptiles has been well documented (Pollard, 1968; Martill, 1992; Ulrichs et al, 1994) and has been reported for an ichthyosaur from the Sundance Formation (Massare and Young, 2005). Similar gastric contents also occur in Sundance plesiosaurs *Pantosaurus striatus* (UW24215), *Tatenectes laramiensis* (UW24801), and an unidentified juvenile plesiosaur (WDCSS01; Wahl, 1998, 2006). In the Sundance Formation, hooklets have only been found associated with marine reptiles, even though belemnites are abundant in many strata. A juvenile plesiosaur (UW 24219) has been found with numerous bite marks in the bone surface at the distal end of the propodial (Wahl, 2006). So cephalopods may not have been the only prey of the Sundance marine reptiles.

FIGURE 7. Epipodial element showing cartilage pitting. Scale bar equals 10 cm.

DISCUSSION

No evidence in publication or correspondence available to the authors indicates any attempt to relocate the excavation prior to the present investigation. The excavation is in close proximity to uranium mine sites. Several access roads remain in the area and uranium test pits are common. The presence of the uranium test pits may have confused any earlier attempt to identify the original excavation. A spoil pile may have existed, but could have either been reworked or scattered by heavy equipment in the course of industrial excavation. Or, as the remains of a "Hercules Blasting Powder" canister was found nearby, any excavated but uncollected bone material could have been disturbed by the use of explosives in the immediate area. The large piece of what may be limb girdle material (Figure 6) was found far away from any other bone fragments, as float above what appears to be the level of the original excavation. It may have been dropped during collection by Knight or Stewart or left behind at a bone float sorting point. Lichen growth on the bone surface is heavier than on the rock fragments on the soil, suggesting that the material had been on the surface longer. However, the porous surface of the exposed bone could also be responsible for the thicker lichen growth. As this large girdle fragment was found 20 m away from the original excavation, it is possible that scavenging in the depositional environment could have scattered portions of the articulated carcass; however, no evidence of bite marks or tooth scratches have been found on the bones to support this scenario.

CONCLUSION

Information gained from an analysis of the stratigraphy of the site and the new bone material sheds new light on *Megalneusaurus*. The sandy matrix occurring ten meters below the Windy Hill Sandstone suggests that *Megalneusaurus rex* frequented shallower portions of the Sundance Sea during the final regressive phase of Redwater Shale deposition. There has been no other pliosaurid material collected or identified from below this layer.

As the reexamination of the site continues, new material may enhance the knowledge of the phylogenetic relationships of this pliosaur to the better known Jurassic pliosaurs from Europe and South America. So far a cladistic analysis of *M. rex* has not been warranted with so little available material. We will continue to look for more of this rare component of the Sundance ecosystem.

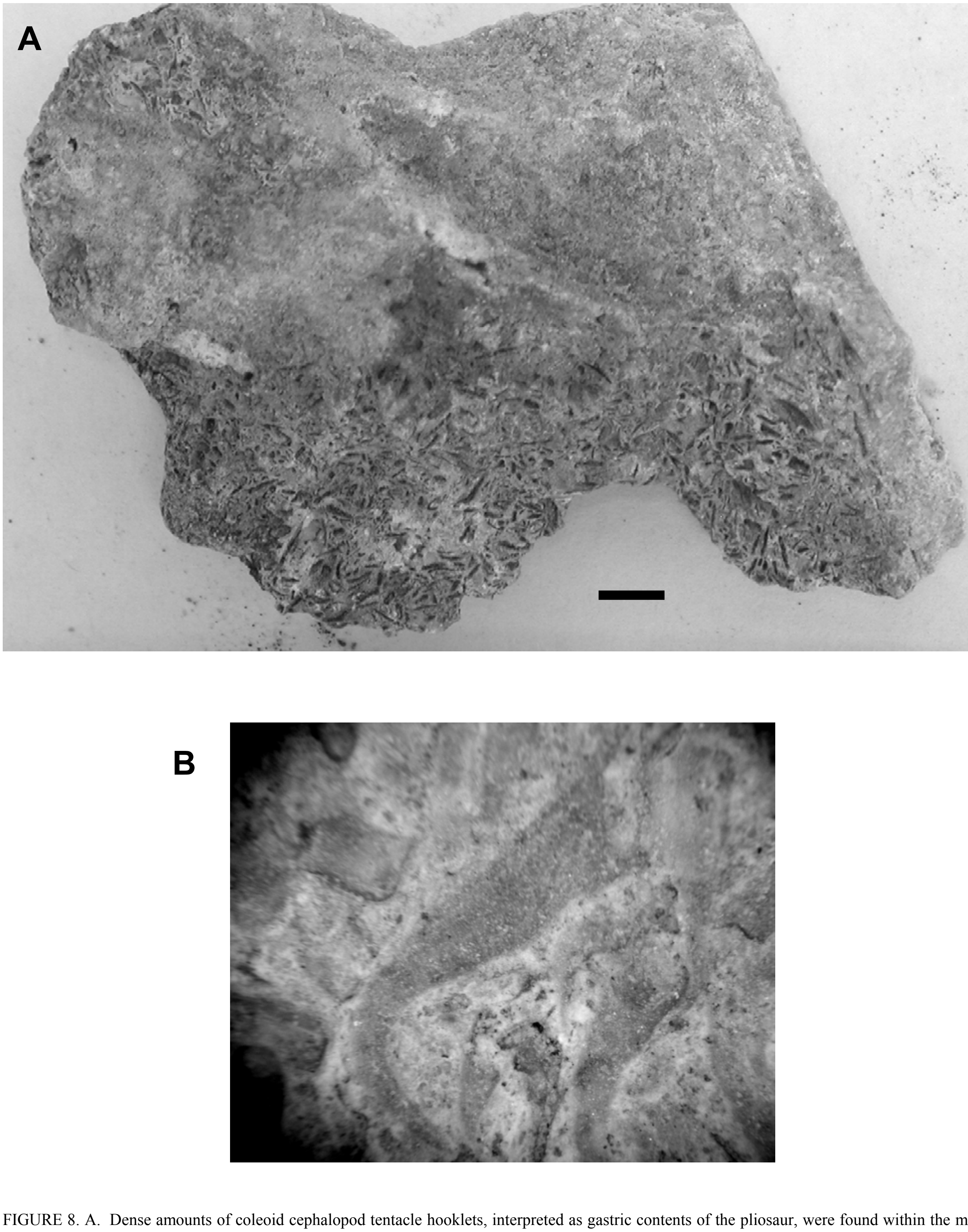

FIGURE 8. A. Dense amounts of coleoid cephalopod tentacle hooklets, interpreted as gastric contents of the pliosaur, were found within the matrix. The hooklets were preserved with the original chitin intact in the sandy matrix. Scale bar equals 5 mm. B. Hooklets also preserved as calcite-filled molds in the matrix. Field of view approximately 5 mm wide.

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