

GASTRIC CONTENTS OF A PLESIOSAUR FROM THE SUNDANCE FORMATION (JURASSIC), HOT SPRINGS COUNTY, WYOMING, AND IMPLICATIONS FOR THE PALEOBIOLOGY OF CRYPTOCLEIDID PLESIOSAURS

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ABSTRACT

The discovery of a semi-articulated partial skeleton of a plesiosaur from the Redwater Shale Member of the Sundance Formation of the Bighorn Basin, Wyoming, may represent the most complete cryptocleidid found to date from this formation. Though poorly preserved, the specimen comprises portions of the pectoral region; dorsal, sacral, caudal vertebrae and the first complete posterior appendicular region ever found for a Sundance plesiosaur, including largely articulated hind flippers. The reported specimen (WDC-SS01) has concentrated gastric contents consisting of a mass of coleoid hooklets as well as disarticulated cardiocerid ammonite jaws; the latter is the first described from a Jurassic plesiosaur. The gastric mass appears to be intact as opposed to the scattered coleoid hooklets found in other Sundance plesiosaurs and was located posterior to the gastralia and anterior to the pelvic girdle. The find has implications for feeding, ecology and food processing capabilities and provides further evidence of the importance of both coleoid and ammonite cephalopods in the diets of Sundance marine reptiles and may suggest a more complex ecology than previously thought.

INTRODUCTION

Exploration of the Sundance Formation, Wyoming, has resulted in the discovery of both juvenile and adult ichthyosaurs and plesiosaurs, however most material consists of isolated bones, making partial skeletons important discoveries (Marsh, 1891, 1895; Massare and Young, 2005; Wahl, 2006b; O'Keefe and Wahl, 2003a, b; Wahl et al, 2007). The Sundance Formation fauna is comprised of about 70% ichthyosaurs and 30% plesiosaurs. This includes two genera of cryptocleidoid plesiosaurs, *Pantosaurus striatus* and *Tatenectes laramiensis* (O'Keefe and Wahl 2003a, b). The specimen, WDC-SS01, reported here is a poorly preserved but semi-articulated partial skeleton of a juvenile plesiosaur and maybe the most complete *Pantosaurus striatus* collected thus far. Partial skeletons of *Pantosaurus* have been described by O'Keefe et al (2009) and identification of WDC-SS01 to this taxon is based on the morphology of the vertebrae, the wide pelvic bones and the gracile gastralia (Wilhelm and O'Keefe, 2010).

Although collection of articulated vertebrate remains from the Redwater Shale Member is noteworthy, identification of intact gastric material is a bonus. Gastric material of Sundance plesiosaurs, in the form of coleoid material, shark remains, and portions of an embryonic ichthyosaur, have been previously noted (Wahl et al, 2007; Wahl, 2008; O'Keefe et al, 2009), however, this paper is the first report of a

predator-prey relationship between a Jurassic plesiosaur and cardiocerid ammonites.

GEOLOGICAL SETTING

The majority of the vertebrate fossils have been collected from the Redwater Shale Member of the Upper Sundance Formation (Bajocian-Oxfordian), which was deposited during the last and most extensive transgressive sequence of the Sundance seaway (Pipiringos, G. N. and R. B. O'Sullivan, 1978; Kvale, et al, 2001; Feldmann, R.M. and A. L. Titus. 2006). The presence of the small cardiocerid ammonite, *Quenstedtoceras colleri*, establishes the lower Redwater Shale as of latest Callovian age (Kvale et al., 2001), which is further confirmed by the identification of the coleoid belemnite, *Pachyteuthis densa*, and the bivalve mollusks *Camptonectes bellestrius* and *Ostrea strigilecula* (Kvale et al., 2001). The overlying upper Redwater Shale Member is Oxfordian in age (Pipiringos, G. N. and R. B. O'Sullivan, 1978; Kvale, et al, 2001; Feldmann, R.M. and A. L. Titus. 2006).

Depositional Environment—The Redwater Shale paleoenvironment represents a shallow, open shelf 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). The Sundance Seaway was affected by the Arctic or Boreal Seaway that connected it to the Tethys Seaway of Europe, of which the Oxford Clay

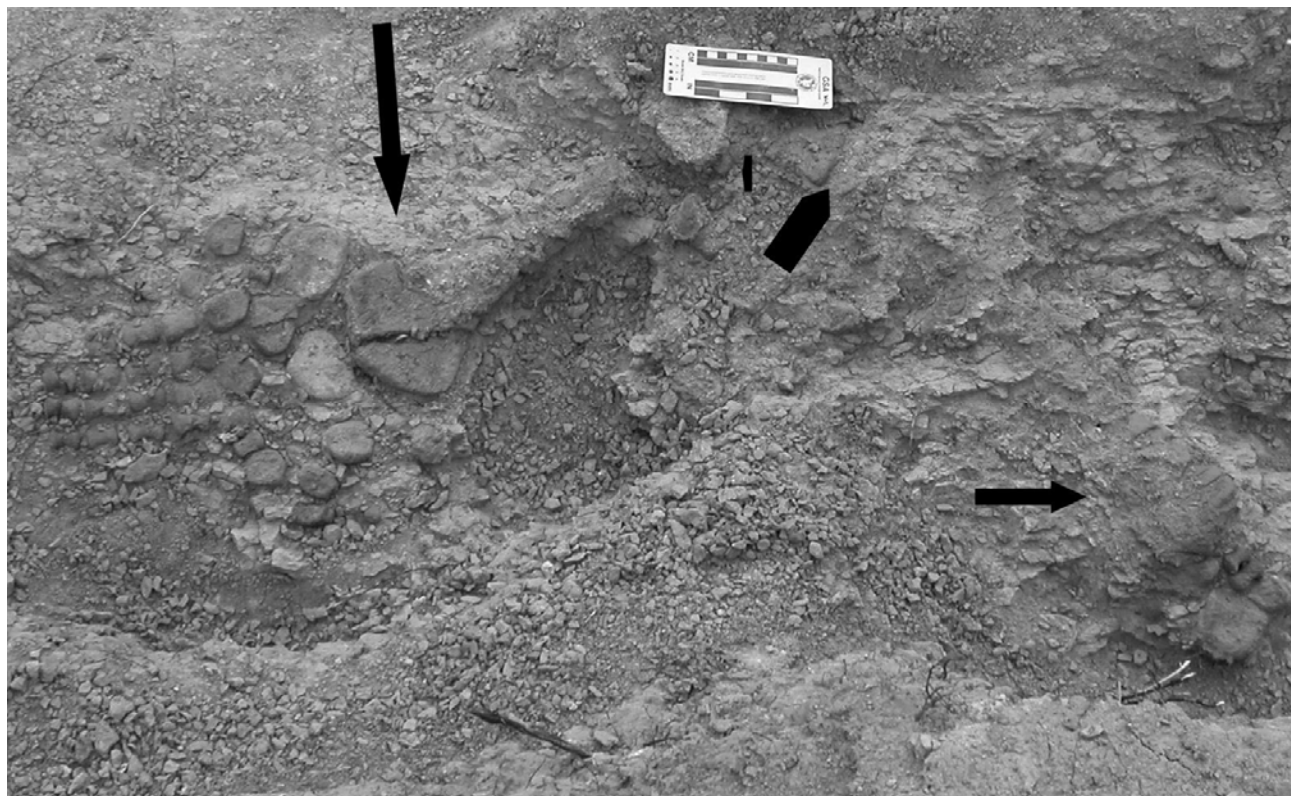


FIGURE 1. The intact posterior of WDC-SS01 (*Pantosaurus striatus*) prior to collection in the field. Note the partially articulated hind-limbs (arrows) and articulated ischia (block arrow). Scale bar = 10cm.

Formation was a part (Doyle, 1987; Martill, 1991). This connection is indicated by the identification of the coleoid (belemnite) family *Cylindroteuthidae* and notably the species *Pachyteuthis densa*, which exhibited provincialism with migrations southwards at times of sea-level change or possibly during seasonal migration (Doyle, 1987, 1995). Thus the presence of belemnites of various sizes may indicate seasonality during deposition of the Redwater Shale Member (Imlay, 1980; Kvale et al., 2001; Wahl 1999).

Water depth during the Redwater Shale deposition was estimated to be 40 m (Specht and Brenner, 1979), and this relatively shallow depth made storm action on paleocommunities very destructive (Tang and Bottjer, 1996). The presence of glauconitic grains and siltstone rip-up clasts is evidence of this high-energy environment (Specht and Brenner, 1979), and the presence of storm damaged bioherms consisting of fragmented *Camptonectes* and *Gryphaea* bivalves and winnowed sandstones are further evidence of a high energy depositional environment in the Redwater Shale (Specht and Brenner, 1979). A prevalence of juvenile marine reptiles and adult plesiosaurs such as *Tatenectes laramiensis* with adaptations for the rough, shallow water

paleoenvironment have been noted before (Wahl, 2006b; O'Keefe et al, 2011).

Institutional Abbreviations—UMUT, University Museum University of Tokyo, Tokyo, Japan; UW, University of Wyoming, Laramie, Wyoming; WDC, Wyoming Dinosaur Center, Big Horn Basin Foundation, Thermopolis, Wyoming; YPM, Yale Peabody Museum, New Haven, Connecticut; USNM, Smithsonian Institution, Washington, D.C.

MATERIALS

The articulated plesiosaur specimen WDC-SS01 was found partially encased in a fine-grained limestone concretion, with the skeleton extending into limey mudstone layers with abundant shell hash. (Figure 1). The collection area was a mixed siltstone and shell hash facies containing the semi-articulated plesiosaur skeleton. It sloped outward to a more resistant sandstone flat ridge crossed by numerous game trails. The flat surfaces of the game trails collected much of the bone fragment float associated with WDC-SS01. Gypsum crystal growth causing splintered bone surfaces made preparation of specific elements of

WDC-SS01 difficult; thus complete bones such as some vertebrae are not available for study

The discovery of the juvenile plesiosaur WDC-SS01 is unusual as partially articulated plesiosaurs are less common than isolated bones in the study areas (Wahl, 2006b; Wilhelm and O'Keefe, 2010). Isolated limbs elements are common finds but identification of isolated epipodials to species is difficult. It is anticipated that the articulated, associated elements from WDC-SS01 will make future identification of plesiosaur finds easier. Adult cryptocleidoid plesiosaurs have been collected from the Sundance formation (O'Keefe and Wahl, 2003a, b; O'Keefe et al 2011, Wilhelm and O'Keefe, 2010), so it is assumed that the recovered juveniles are also cryptocleidoids. Likewise, there is no evidence of other juvenile plesiosaurs in the Sundance Formation, other than those found in the Redwater Shale. The holotype of *Pantosaurus striatus* (YPM 543) is also a juvenile (O'Keefe and Wahl, 2003a).

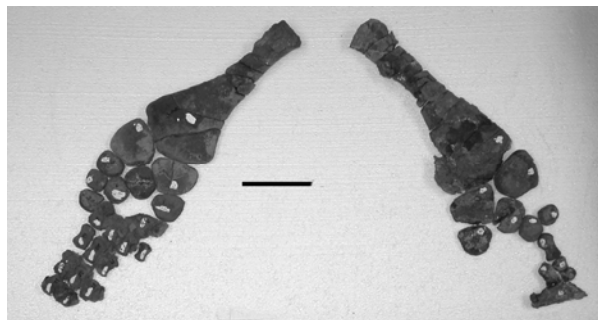


FIGURE 2. WDC-SS01 (*Pantosaurus striatus*) prepared, articulated hind flippers. Scale bar = 10cm.

Osteology of WDC-SS01—The plesiosaur skeleton WDC-SS01 comprises 34 vertebrae including dorsals, sacrals and caudals; a complete pelvis; femora with all tarsals and associated but disarticulated distal phalanges (Figure 2), and numerous ribs and gastralia. The vertebral column within the concretion was found articulated, whereas the sacral material was scattered in the matrix surrounding the pelvis. A near complete but poorly preserved vertebral caudal series was also recovered scattered but distal to the pelvic region (Figure 3). The pelvic elements were in articulation with the exception of the ilia. Ribs were associated with the articulated dorsal vertebrae, and gastralia were scattered anterior to the pelvic bones. Some isolated elements and broken bone fragments, including portions of the pectoral region, humeri, epipodials and phalanges, occurred as float. The proximal and distal ends of the propodials and epipodials exhibit spongy ridges which are sub-faceted or rounded and would have been supported by a cartilage sheath as noted in other juveniles (Wahl, 2006b). The femoral heads are

distinct, with pitting for the cartilage contact points and with ridges at the edges but with the shaft lacking definition. Cross-sections show dense pachyosteosclerotic bone and a clear demarcation between the core and the cortical outer bone.

Although poorly preserved and a juvenile, WDC-SS01 must be one of two plesiosaurs found in the Sundance Formation, *Pantosaurus striatus*, Marsh, 1895 or *Tatenectes laramiensis* Knight, 1900. Recently discovered specimens of both plesiosaurs with complete pelvic regions allowed the identification of WDC-SS01 as *Pantosaurus*, as indicated by the articulated pelvic bones including the distinctive ilia and gracile gastralia. (O'Keefe and Wahl, 2003a; Wilhelm and O'Keefe, 2010).



FIGURE 3. Dorsal (top) and lateral view of reconstructed caudal vertebrae of WDC-SS01 (*Pantosaurus striatus*). Scale bar = 10cm.

Pantosaurus striatus has been described as a small cryptocleidoid plesiosaur with 35-40 cervical vertebrae, which are as long as wide and waisted, with an elongate cervical rib facet mounted on a pedestal. Foramina subcentralia are small and placed close together with well ossified rims (Wilhelm and O'Keefe, 2010). Two specimens have been referred to *Pantosaurus striatus*, (USNM 536965 and USNM 536967, Wilhelm and O'Keefe, 2010); USNM 536965 was found with an intact pelvis and associated ribs and gracile gastralia.

The *Pantosaurus* specimen USNM 536965; preserves four dorsal, three sacral, and eight caudal vertebrae (Wilhelm, 2010). All centra are waisted, wider than tall, and taller than long (Wilhelm, 2010). Wilhelm (2010) also mentions that the sacral vertebrae have stout sacral ribs at a 90° angle to the neural spine. The sacral ribs are constricted at their midpoint and then widen again at the distal articulation with the ilia. Unfortunately the ribs of WDC-SS01 were disarticulated, however, when the centra are articulated there is a slight downward bend of the tail beginning at the fourth caudal (Wilhelm, 2010). Though the exact position of the caudal series for WDC-SS01 cannot be determined by placement of the post-sacral vertebrae, the bend is present in 18 vertebrae centra of descending

size from 4.3cm to 8mm in diameter. The peripheral elements of most of the vertebrae of WDC-SS01 were disarticulated; the neural arches and chevrons of the caudal vertebrae of WDC-SS01 were poorly preserved, associated but not articulated, and were mixed with porous matrix. As such, small neural arches as well as associated ribs were not preserved.

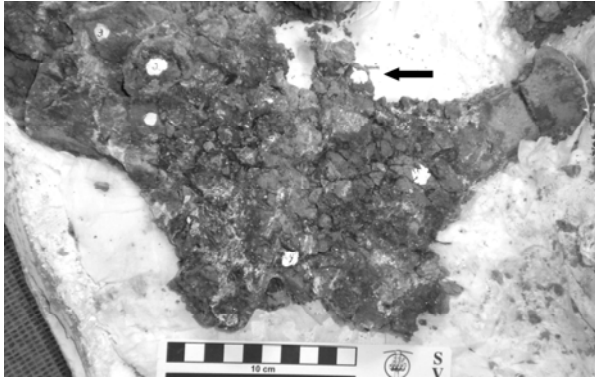


FIGURE 4. WDC-SS01 (*Pantosaurus striatus*) partially prepared pelvic region including separate ischia. Note the hook flange extension at the anterior end of the ichium symphysis (arrow). Scale bar = 10cm.

This poor preservation is unfortunate, because the position and angle of the neural spines of *Pantosaurus* are distinctive (O'Keefe and Wahl, 2003a; Wilhelm, 2010). In the *Pantosaurus* holotype (YPM 543), USNM 536963, and USNM 536965, the neural spines of the cervical, dorsal, sacral, and caudal vertebrae are posteriorly directed to differing degrees (O'Keefe and Wahl, 2003a; Wilhelm, 2010). Determining which elements were associated with which vertebrae in this poorly preserved juvenile specimen, WDC-SS01, has proven difficult.

Tatenectes specimen USNM 536976 consists of an articulated vertebral column comprising 22 vertebrae; 16 dorsals, four sacrals, and two caudals, as well as a complete pelvis with numerous associated ribs and gastralia. USNM 536976 was referred to *Tatenectes laramiense* based on its possession of diagnostic pachyostotic midline gastralia and lateral gastralia with an autapomorphic "J shape" (Street and O'Keefe, 2010). Neither of these features could be seen on WDC-SS01, which preserves the same body portion, a complete rear end of the plesiosaur.

The large flat pelvic bones of WDC-SS01 generally resemble the same bones in the other cryptocleidoid plesiosaurs from the Redwater Shale. For example, the width of the pubes exceeds their lengths in both taxa (Wilhelm, 2010; O'Keefe et al, 2011). However, the ischia of WDC-SS01 appear to retain the distinctive hooked flange extension at the anterior of the ichial symphysis (Figure 4) as noted by

Wilhelm and O'Keefe (2010). The most useful comparative elements for identification of WDC-SS01 were the ilia of USNM 536965. The distinctive ilia of *Pantosaurus striatus* (USNM 536965) have a large head at the acetabulum where they contact the ischia and a reduced head where they join with the sacral ribs (Wilhelm, 2010; O'Keefe et al, 2011). The shaft is curved and sub-triangular to oval in cross-section as it rises to the ilial blade. This iliac blade (articular surface) is compressed mediolaterally as in similar cryptocleidoids (Andrews, 1910). The ilia of USNM 536965 are widest at the acetabular end and approximately the same width at the midpoint of the shaft and the iliac blade (Wilhelm, 2010; O'Keefe et al, 2011). The ilia of WDC-SS01 resemble those of USNM 536965; although, as WDC-SS01 is a juvenile, the ilial head appears smaller and less well-defined. (Figure 5).

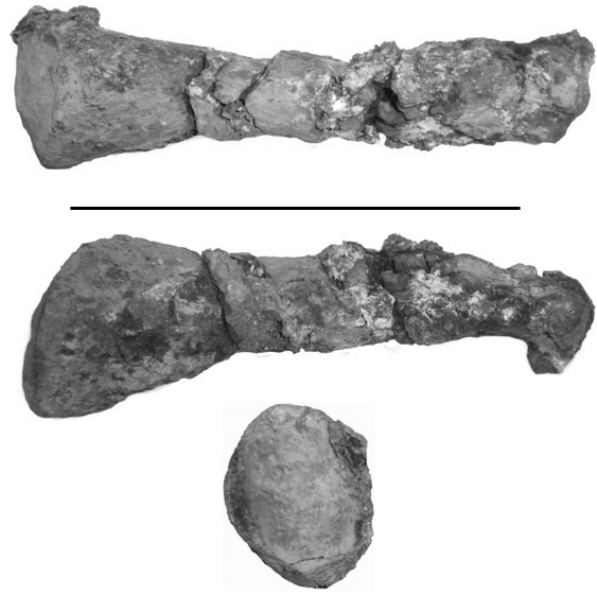


FIGURE 5. Medial (top) and posterior (center) views of left ilia; acetabular head (bottom) from WDC-SS01 (*Pantosaurus striatus*). Scale bar = 10cm.

PALEOBIOLOGY OF WDC-SS01

Diagnostic characteristics of juvenile plesiosaurs have been debated by several authors (e.g Brown, 1981; Wiffen et al., 1995; O'Keefe and Wahl 2003b; Wahl, 2006b). Smaller sizes of particular elements are not always a good parameter in recognition of juveniles, however, evidence of delayed ossification such as differential fusion in the vertebral column or remodeling with a lack of fusion of the centrum to the neural arch is a better indicator of a juvenile specimen (Wiffen et al, 1995). The lack of ossification and lack

of well-defined facets on the distal ends of the propodials and epipodials are other characteristics of juveniles (Brown, 1981; Wiffen et al, 1995). Likewise ontogenetic age in plesiosaurs can be determined by the bone as seen in cross-sections of the limbs; juveniles have dense, pachyosteosclerotic bone whereas adults have spongy, osteoprotic bone (Wiffen et al, 1995).

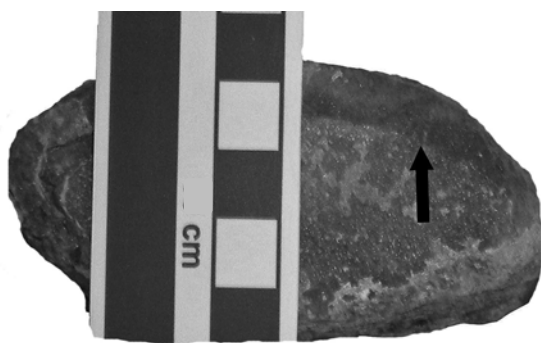


FIGURE 6. Cross-section of complete femur of WDC-SS01 (*Pantosauros striatus*). Differentiation of dense (arrow) to cancellous bone within limb shaft suggests a juvenile stage of plesiosaur. Scale bar = 5cm.

Bone cross-sections were used to identify WDC-SS01 as a juvenile plesiosaur. The femora have notable thick, dense cortical bone to core contrasting structures (Figure 6). The dense bone of juveniles results in relatively heavier bones and this may consequent a difference in lifestyles compared to adults, such as limitations on swimming speed and/or capabilities of rapid maneuvers (Wiffen et al, 1995). This difference would manifest itself in swimming abilities and subsequent prey pursuit. Also the rapid periosteal accretion visible on the limbs of plesiosaurs suggests a high, sustained growth rate in juveniles as compared to adult plesiosaurs, with cancellous bone displaying remodeling by repeated cycles of re-absorption and accretion (Wiffen et al, 1995). Such a rapid growth rate may require more frequent food consumption. The juvenile plesiosaurs apparently maintained a conservative ecology suggesting that they were limited to lagoonal or shoreline environments in contrast to the adults whose larger body sizes were better more adapted to the open sea (Wiffen et al, 1995; Wahl, 2006b).

Gut Contents—Coleiod hooklets have been found as gastric contents in several adult plesiosaurs (Martill, 1992; Wahl, 1999; Wahl et al., 2007) including some from the Sundance Formation: *Pantosauros striatus* (UW 24215), *Tatenectes laramiensis* (UW 24801), the pliosaur *Megalneusaurus rex* (UW 4602), and in the juvenile reported here,

WDC SS01. With regards to shelled cephalopods, evidence of predation comprises bite marks on shells or jaw structures (aptychi) of cephalopods in the gastric contents (Sato and Tanabe, 1998). More fragile parts of belemnite cephalopods such as tentacle hooklets and jaws are more rarely preserved (Wahl, 1999). Two sections of disarticulated cephalopod aptychi indicate that cardiocerid ammonites (possibly *Quenstedtoceras colleri*) were a part of the diet of WDC-SS01 (Figure 7). These jaws are distinctly different from the leaf shaped jaws of belemnites also found in plesiosaurs (Sato and Tanabe, 1998; Wahl, 2006a). This may also suggest that these plesiosaurs fed in a nekto-benthic lifestyle. Sato and Tanabe (1998) noted ammonite jaws in the gastric contents of a polycotylid plesiosaur from the Upper Cretaceous of Japan (UMUT MV 19965), the first firm evidence of a plesiosaur predator-prey relationship with ammonites. It was also suggested that small desmoceratid ammonites were the

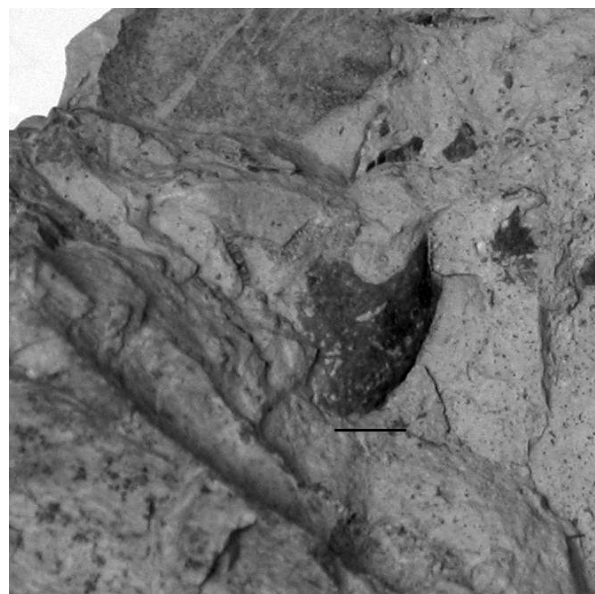


FIGURE 7. The disarticulated cephalopod jaw associated with WDC-SS01 (*Pantosauros striatus*). Scale bar = 5mm.

prey of plesiosaurs and the lack of shells in the gut content was due to strong stomach acids or gastroliths (Sato, and Tanabe, 1998). Unfortunately as no skull was recovered with UMUT MV 19965, and the tooth morphology is unknown. However the small size of the ammonites, as suggested by the small jaws (<15mm), may indicate that they were swallowed whole (Sato and Tanabe, 1998). Were the shelled cephalopods swallowed whole by WDC-SS01 as well? The small size of the ammonite jaws in WDC-SS01 also suggests a small size of ammonite that may have allowed for indiscriminant or selective feeding on

cephalopods. The ammonite which most likely produced the scattered jaws in UMUT MV 19965 was a desmoceratid, which had a flat to slightly rounded shell but retained prominent ribs (Sato, and Tanabe, 1998). The ammonite most likely to have produced the jaws found in WDC-SS01 was a cardiocerid, possibly *Quenstedtoceras colleri*, which had a round, wide shell shape that was wide at the apex of the shell, possibly suggesting a wide bite in the cryptocleidoids. The alternative would be to suggest potential scavenging on dead or dying ammonites in which the flesh of the cephalopod could conceivably be hanging outside the shell (Wahl, 2008).



FIGURE 8. Matrix surrounding the bones of WDC-SS01 (*Pantosaurus striatus*) contains large amounts of scattered individual hooklets of belemnites. Scale bar = 5mm).

Gastric Mill—The hooklets within WDC-SS01 occur individually in the matrix surrounding the bones (Figure 8) and as a concentrated mass located directly anterior and within the pelvic bones, surrounded by associated gastralium (Figure 9). This mass is made up of crushed hooklets, compacted to a point that individual hooklets cannot be distinguished. This suggests a “gastric mill” that crushed the hooklets as they passed through some point in the viscera (Taylor, 1994; Wings, 2007). O’Keefe et al (2009) noted the presence of small gastroliths within USNM 536965. The bones were enmeshed in a “coherent mass of sand and grit whose lithology differs markedly from the surrounding shale” (O’Keefe et al, 2009). The mass was reported to include sand and grit particles, invertebrate shell fragments, vertebrate bone fragments, and fish scales (O’Keefe et al, 2009). The presence of gastroliths as small as sand sized particles has been noted in other plesiosaurs (Sato and Wu, 2006; Thompson et al, 2007). The gastric contents of crushed hooklets and sand and grit, with some particles ranging from 2mm to 7mm, have been identified in

WDC-SS01, as well as in the Sundance plesiosaur, UW 4602 *Megalneusaurus rex* (Wahl et al, 2007).

In the pelvic region of *Tatenectes laramiensis*, USNM 536976, O’Keefe et al (2011) noted “the ventral dishing of the pubes, presumably to accommodate pelvic viscera” (O’Keefe et al, 2011). In WDC-SS01 the gastric mass of dense broken hooklets occurs anterior to the pelvic bones and the referred “dishing” aspect of the pubes may suggest the retention of the gastric mass and the position of the “gastric mill” anterior of the viscera.

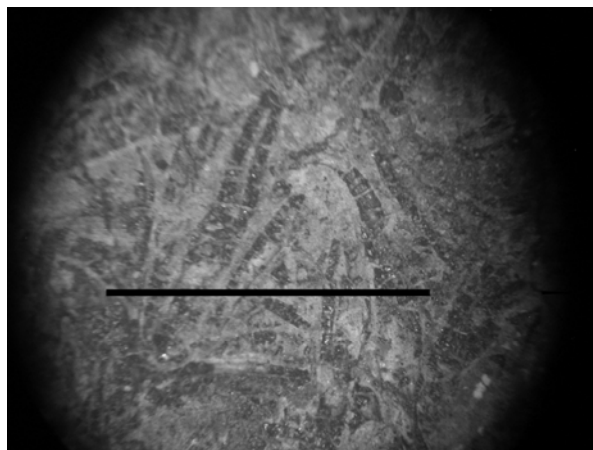


FIGURE 9. A mass of concentrated crushed hooklets from plesiosaur WDC-SS01 (*Pantosaurus striatus*). Scale bar = 5mm.

CONCLUSION

A partial skeleton tentatively referred to *Pantosaurus striatus* has been found with preserved gut contents. Although a juvenile, WDC-SS01 includes articulated vertebrae from the tail and pelvic region as well as partially articulated, semi-complete hind-flippers, making it one of the most complete *Pantosaurus striatus* specimens known. The completeness of the limb material may prove useful in the identification of isolated limb elements found elsewhere in the Redwater Shale.

A wide variety of food items as gut contents have been documented in plesiosaurs, including coleoid hooklets and beaks (Martill, 1992; Wahl, 2006a), fish and shark fragments (Cicimurri and Everhart, 2001; Wahl, 2005), and curiously whole bivalves (McHenry et al., 2005). WDC-SS01 is notable in preserving both a scattered and concentrated gastric mass containing coleoid hooklets and the disarticulated jaws of a cardiocerid ammonite, possibly *Quenstedtoceras colleri*, further evidence for the consumption of ammonites by plesiosaurs. WDC-SS01 is thus revealing a more complex paleobiology than previously known for cryptocleidoids. For example,

the presence of the ammonite jaws in WDC-SS01 and the ichthyosaur embryo in *Pantosaurus striatus* USNM 536965 may suggest an opportunistic feeding style. Likewise, the suggestion of scavenging on a dead ichthyosaur embryo by Wilhelm and O'Keefe (2010) would equally apply to the soft body parts of an ammonite, or is there the possibility that *Pantosaurus striatus* specialized on hard shelled prey. Teeth or skull material of *Pantosaurus* is not yet known; however, the disarticulated cardiocerid jaws found in the gastric mass suggest an interesting feeding problem. Would a smashing or piercing type of tooth as described by Massare, (1987) have been more useful in feeding on a cardiocerid type of ammonite, which is round in cross-section? Evidence from a shark bitten ammonite would suggest a tearing type tooth is just as useful (Vullo, 2010). Alternatively, would tooth shape not matter at all in scavenging on a dead ammonite carcass?

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