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A JUVENILE PLESIOSAUR (REPTILIA: SAUROPTERYGIA) ASSEMBLAGE FROM THE SUNDANCE FORMATION (JURASSIC), NATRONA COUNTY, WYOMING

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ABSTRACT

The predominance of juveniles from one taxon is rarely found in faunal studies. However, the presence of seven juveniles in a sample of ten cryptocleidoid plesiosaurs from the Redwater Shale Member of the Sundance Formation of Natrona County, Wyoming may be such a paleocommunity. Juvenile characters are recognized by the lack of facets and ossification on the distal ends of the propodials and by cross-sections of the limbs. Juveniles have dense pachyosteosclerotic bone structures whereas adults have more spongy, osteoprotic bone. The dense bone of the juveniles suggests a difference in environmental preference between juvenile and adult plesiosaurs.

INTRODUCTION

The Sundance Formation (Bajocian-Oxfordian) was the last and most extensive transgressive sequence 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 presence of the small cardiocerid ammonite, *Quenstedtoceras colleri,* establishes the lower Redwater Shale as latest Callovian. This Callovian age was further confirmed by the identification of the coleoid belemnite, *Pachyteuthis densa*, and the pelecypods *Camptenectes bellestrius* and *Ostrea strigilecula* (Kvale et al., 2001).

The upper Redwater Shale Member is Oxfordian in age (Kvale et al., 2001). It represents a shallow, open shelf environment dominated by silty to shaley mudstone, occasional bioturbated shale, and ripple-dominated, glauconitic fine-grained calcareous sandstone (Figure 1; Andersson, 1979; Specht and Brenner, 1979; Kvale et al., 2001). It has been compared to the Callovian lower Oxford Clay of England (Wahl, 1997, 1999). The Sundance Seaway was affected by the Arctic or Boreal Seaway that connected to the Tethys Seaway of Europe, of which the Oxford Clay was included (Doyle, 1987; Martill, 1991). This connection is indicated by the identification of the coleiod family Cylindroteuthidae (belemnites), notably the species *Pachyteuthis densa*, which exhibited provincialism with notable migrations southwards related to sea-level change or possible seasonal migration (Doyle, 1987, 1995). The presence of belemnites in various sizes may indicate seasonality during deposition of the Redwater Shale (Imlay, 1980, Kvale et al., 2001; Wahl 1998).

The water depth during the Redwater Shale sequence was estimated to be 40 m (Specht and Brenner, 1979). The 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 a high-energy environment (Specht and Brenner, 1979). The presence of storm damaged bioherms consisting of bits of fragmented *Camptonectes* and *Gryphaea* and winnowed sandstones are further evidence of a rough depositional environment in the Redwater Shale (Specht and Brenner, 1979).

Remains of fish are extremely rare in the Sundance paleoenvironment (Schaeffer and Patterson, 1981). The marine reptile fauna is dominated by ichthyosaurs. Specimens collected in recent years suggest a fauna comprised of 80 % ichthyosaurs, 18 % plesiosaurs and only 2 % pliosaurs. Currently, a single species of ichthyosaur, *Opthalmosaurus natans* is recognized from the Sundance (McGowan and Montani, 2003). A single specimen of the giant pliosaur (13m), *Megalneusaurus rex* as well as two genera of cryptocleidoid plesiosaurs, *Pantosaurus striatus* and *Tatenecktes laramiensis* have also been reported (O'Keefe and Wahl 2003a, b). This is the first report of a plesiosaur fauna from one locality in the Sundance Formation where a majority of the specimens are juveniles.

Institutional Abbreviations—LEIUG, Leicester University, Department of Geology, Leicester, England; UW, University of Wyoming, Laramie, WY; WDC, Wyoming Dinosaur Center, Big Horn Basin

Foundation, Thermopolis, WY; YPM, Yale Peabody Museum, New Haven, CT.

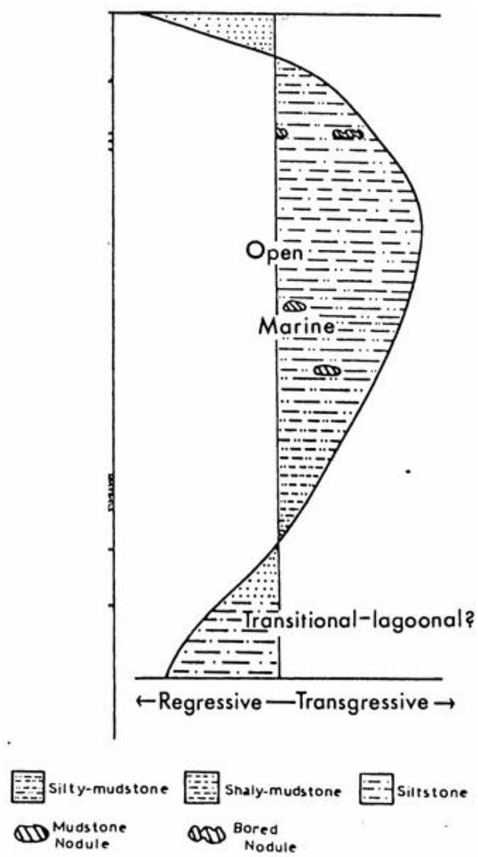

FIGURE 1. Sea level changes during Redwater Shale deposition, with generalized lithostratigraphy. Modified from Specht and Brenner, 1979.

JUVENILE PLESIOSAUR OSTEOLOGY

Juvenile plesiosaurs in large numbers are found in Cretaceous marine formations in Antarctica, New Zealand, and Australia as well as elsewhere in the United States (Martin et al., 1994; Wiffen et al, 1995). Diagnostic characteristics of juvenile plesiosaurs have been debated by several authors (Brown, 1981; Wiffen et al., 1995; O'Keefe and Wahl 2003b). Smaller sizes of particular elements are not always a good parameter in recognition of juveniles. Evidence of delayed ossification such as differential fusion in the vertebral column, is a better indicator in plesiosaurs. The vertebral column may also show some bone remodeling with a lack of fusion of the centrum to the neural arch, another good indicator of a juvenile specimen (Wiffen et al, 1995).

Poorly ossified and faceted epipodials are also a common occurrence in juveniles. Features such as lack of ossification in cartilage contact and incomplete articulation on several portions of the distal surface of propodials are thought to be another indicator of the juvenile stage of plesiosaurs (Figure 2A; Andrews, 1910; Wiffen et al, 1995). Adult plesiosaurs are identified based on the rigidly faceted distal portions of the limbs and the neural arches fused with the vertebral centra. In adults, these facets were most likely used to rigidly support the epipodials to make a stiff flipper for swimming (Brown, 1981).

However, as Wiffen et al. (1995) noted, juvenile plesiosaur material can also be identified by general aspects of bone cross-sections, with thick dense cortex bone structures in juveniles and open cancellous bone structures in adults (Figure 2B). In contrast to the spongy, woven cancellous bone in an adult propodial, the juvenile propodial will have up to 65% compact bone in the radius with a gap region of highly compacted bone structures (Figure 2B; Wiffen et al., 1995). The end of the propodials in juveniles contains periosteal cortices that are generally compact bone with only moderate vascularization (Figure 2C). The pachyosteosclerotic condition of the juveniles, compared to the osteoprotic-like condition of the adults, had an effect on the mass of the limb bones (Wiffen et al., 1995). The rapid periosteal accretion visible on the limbs of plesiosaurs from the New Zealand Cretaceous suggests a high, sustained growth rate in the juveniles. Adult plesiosaurs, however, are described as having skeletons with cancellous bone displaying abundant, intense remodeling by repeated cycles of reabsorption and accretion (Wiffen et al, 1995).

MATERIALS

Between 1992 and 2003 articulated specimens and isolated limb elements of plesiosaurs were collected from surface finds in both lower and upper Redwater Shale member, Sundance Formation, Natrona County, WY. (UW locality V-95010). Specimens from the same locality, although not necessarily from the same stratigraphic horizon, were examined for this study. The majority of the material was found disarticulated and mostly in the form of isolated propodials and vertebral centra. The few articulated specimens were found in fine-grained limestone and limey mudstone layers. The Redwater Shale plesiosaur specimens do not appear to have been buried quickly as there is some shell encrustation on the surface of several limb elements.

From this collection 7 out of 10 individual specimens were identified as juveniles based on the lack of defined facets on the distal edges of the propodials. Several limb bones also lack any deltaic

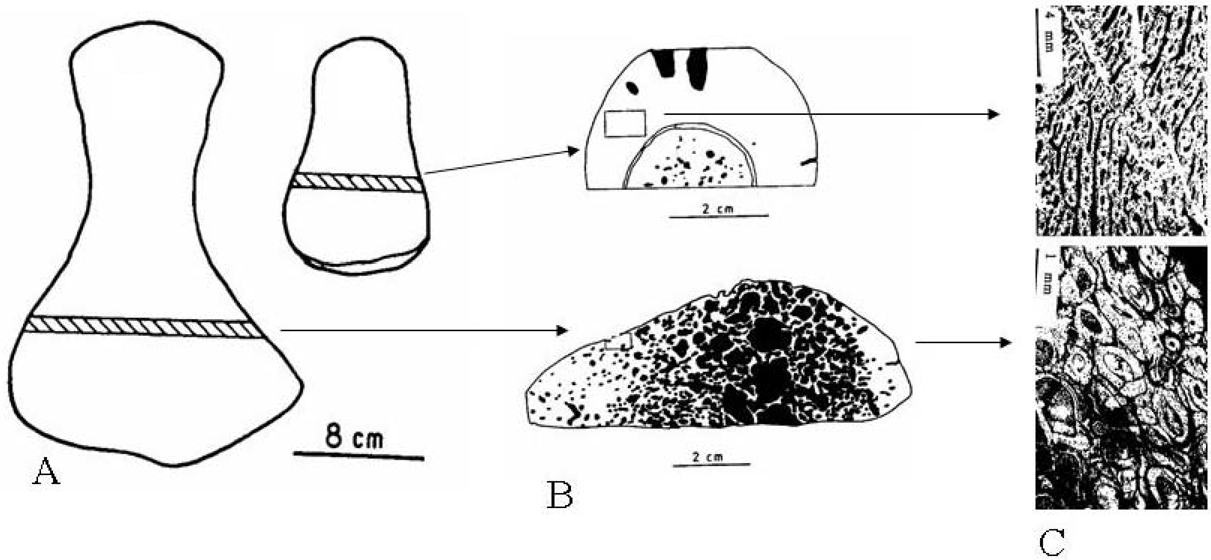

FIGURE 2. Illustration of adult and juvenile plesiosaur propodials. Lower diagram of each pair is the adult; upper diagram is the juvenile. A, Propodials. Note facets present for epipodials on adult. B, Cross-section through radius. C, Polished photomicrograph of cross-section of radius. Figure modified from Wiffen, et al., 1995.

ridge definitions on the proximal end of the propodials. Cross-sections show dense pachyosteosclerotic bone and a demarcation between the core and the outer bone (Figure 3). I consider specimens UW 24217, 24219, 24236, 24239, 24240, 24243 and 24244 to be juveniles (Figure 4; Table 1). In addition to what is in the photograph, UW 24219 also includes several isolated neural arches found with the limb. The limb elements of the seven specimens could not be determined to be femora or humeri as the ridges are rounded off and would have been supported by a cartilage sheath in juveniles. Adult plesiosaurs from this location are cryptocleidoid plesiosaurs (O'Keefe and Wahl, 2003a, b), so it is assumed that the juveniles are also. The specific taxon cannot be determined. Although not from this locality, the holotype of *Pantosaurus striatus* (YPM 543), a partial skeleton that includes articulated vertebrae, ribs, pectoral girdle, and limb fragments, is also a juvenile (O'Keefe and Wahl, 2003a). There is no evidence of juvenile plesiosaurs from the Sundance Formation other than those of the Redwater Shale.

PALEOBIOLOGY OF JUVENILE PLESIOSAURS

Why is there a high proportion of juveniles relative to adults at this location? A reliable food source for juveniles in the form of coleoid cephalopods would be one possibility. The Arctic Boreal and Atlantic Callovian-Oxfordian realm had achieved a maximum diversity and areas such as shelf seas and provincial interior seaways preserve mass accumulations of belemnite rostra indicating they were relatively common (Imlay, 1980; Kvale et al., 2001). Predation on coleoids by marine reptiles has been well documented (Pollard, 1968; Ulrichs et al, 1994). A seasonal migration of belemnites might be an important food source for both plesiosaurs juveniles and adults in a lagoonal, provincial seaway such as that of the Redwater Shale. Coleiod hooklets have been found as gastric contents in several adult plesiosaurs (Martill, 1992; Wahl, 1998) including some from the Sundance Formation: *Pantosaurus striatus* (UW 24215), *Tatenecktes laramiensis* (UW 24801) and in a juvenile (WDC SS01; Figure 5). Coleiod hooklets were also found in a Sundance ichthyosaur (UW 34653; Massare and Young, 2005). Thus belemnites were a significant source of food for the marine reptiles in the Redwater Shale.

Juveniles co-occurring, but in larger proportions to adult specimens, may identify a Jurassic nursery paleoenvironment. The survival rate of juveniles may have been greatly increased by association with adults as some juveniles are found with evidence of predation. UW 24219 has numerous bite marks in the bone surface at the distal end of the propodial (Figure 6A). A plesiosaur propodial from the Oxford Clay has also been found with similar bite marks (Figure 6B; Martill et al, 1994). Although cannibalism could have been a danger, no gastric evidence has been found to support this hypothesis. Social structure and group association for protection and perhaps coordinated feeding occur in some extant groups of marine mammals, specifically

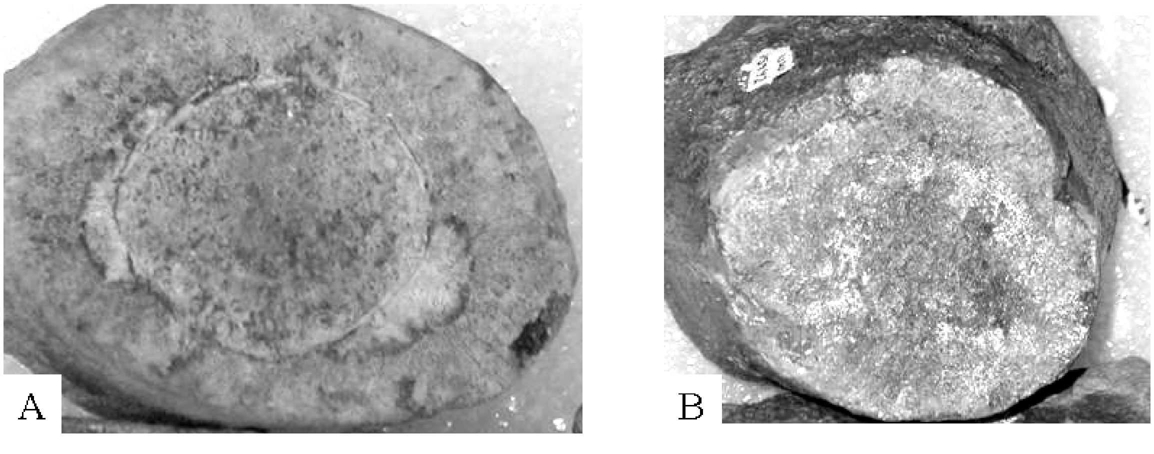

FIGURE 3. Cross-sections of Sundance plesiosaur limb material. A, Dense juvenile bone (UW 24239) showing delineation of core from outer bone; B, Spongy adult bone with no delineation (UW 24801). Scale bar equals 3 cm.

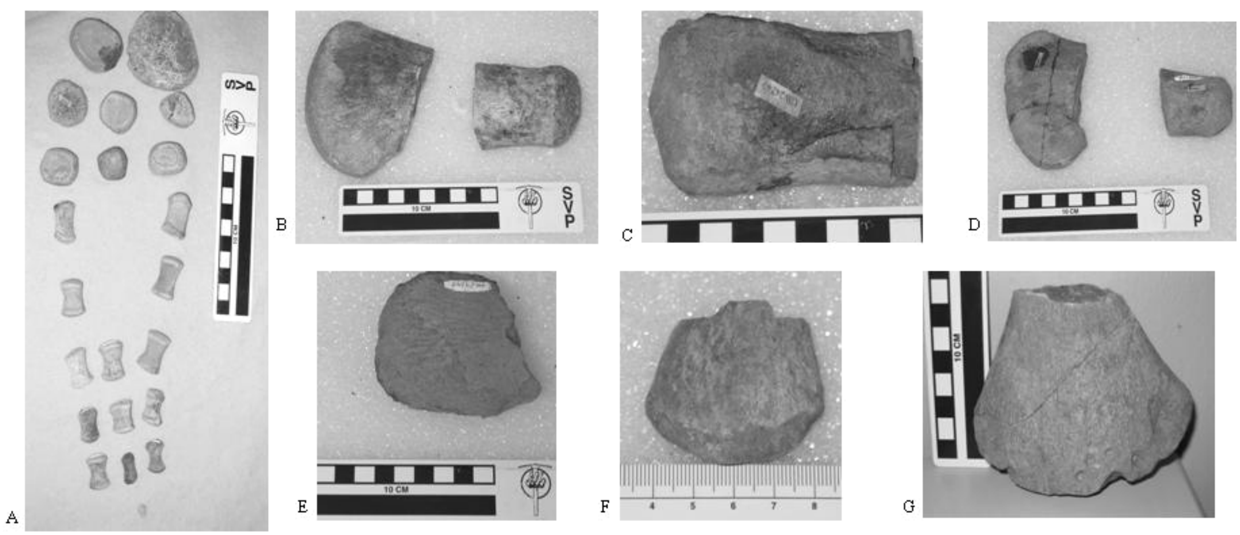

FIGURE 4. Juvenile plesiosaur limb material A, UW 24217. Note rounded unfaceted ends of metapodials. B, UW 24244. C, Linear cross-section of juvenile limb UW 24240, D, UW 24243. E, UW 24236. F,UW 24239. G, UW 24219. Scale bar in cm.

seals and sea lions (Young, 1972; Clarke and Trillmich, 1980; Nilssen et al, 2002; Craig and Ragen, 1999). Such behavior could have occurred in plesiosaurs.

Martin (1994) suggested that extremely small juvenile plesiosaurs may indicate evidence of live birth. However, the material found in the Sundance Formation is not embryonic, nor small enough to suggest that the Jurassic environment was a plesiosaur breeding ground. Extremely small juveniles have been reported from the Cretaceous Pierre Shale. These may indicate some aspect of parental care because the chances of survival of such a small animal so far from shore would have been increased by the presence of associated adults (Martin, 1994). However, although the juvenile material in the Sundance Formation is found associated with adults, this does not provide any evidence of parental care.

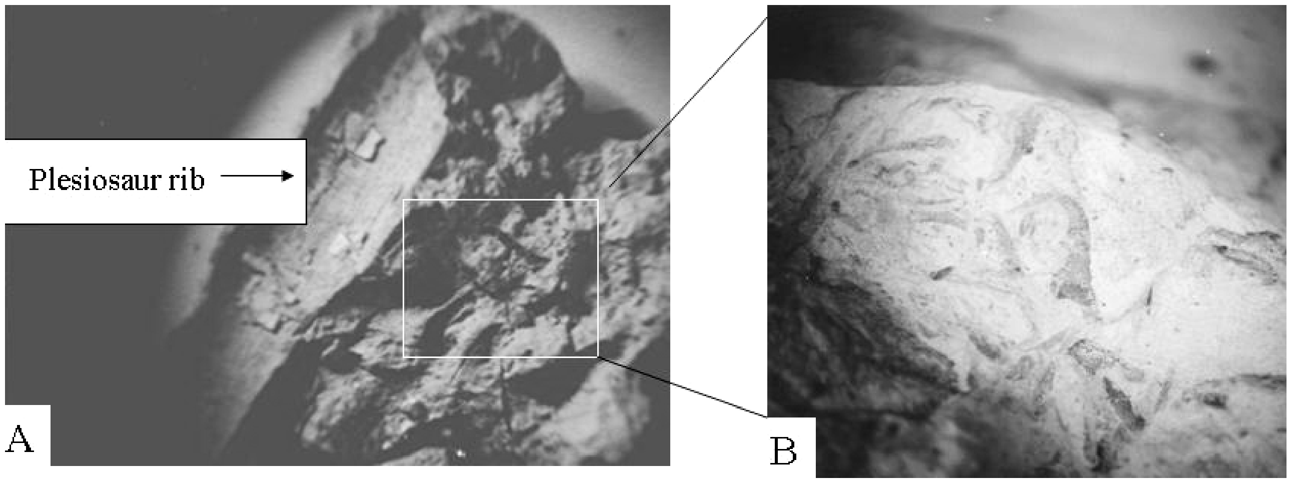

FIGURE 5. Juvenile plesiosaur gastric contents including coleiod hooklets, WDC SS-01. Scale bar equals 1 cm.

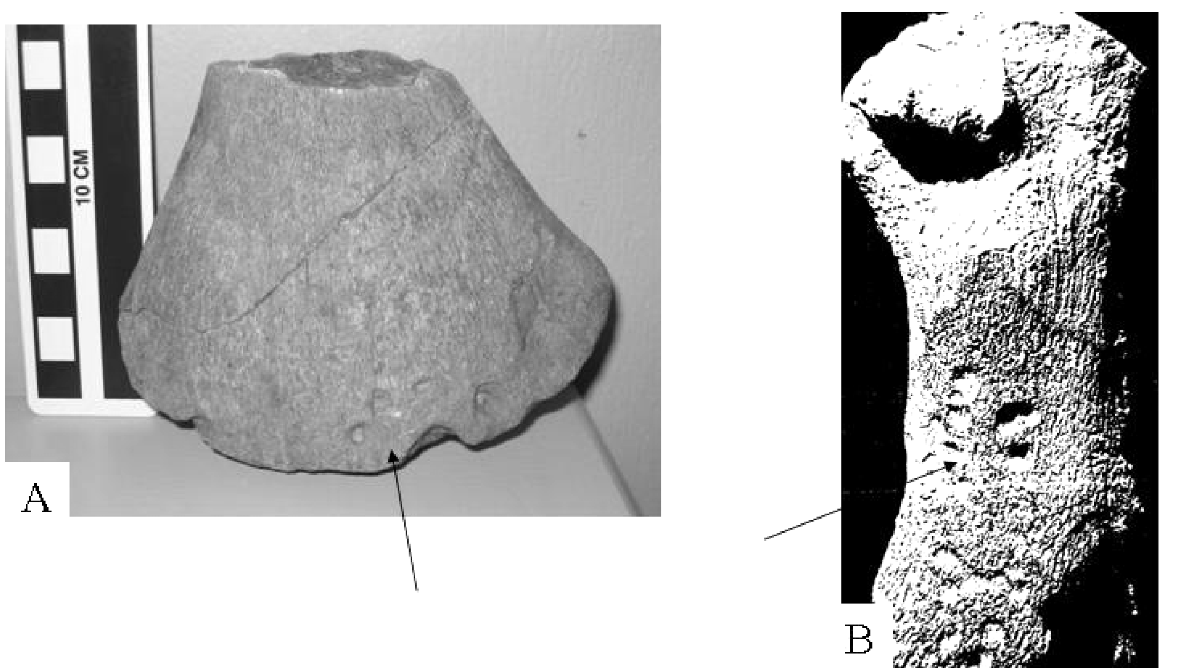

FIGURE 6. A, Bite marks on distal end of Redwater Shale plesiosaur propodial UW 24219. Scale bar in cm. B, plesiosaur propodial from Oxford Clay, LEIUG 114205 from Martill et al, (1994). Scale bar equals 10cm.

Another possibility was that the differences in the bone mass density between juveniles and adults, as previously mentioned, might have had consequences on their swimming abilities and respective paleobiology. Wiffen et al. (1995) suggested that juveniles and adults lived in separate environments. Taphonomic processes can produce size or shape biases, but rarely ontogenetic systematic biases (Wiffen et al, 1995). Discoveries of juveniles from non-marine deposits thought to be estuaries suggest a shallow water habitat separation for juveniles or perhaps a nursery site for plesiosaurs (Sato et al.,2005). The shallow water of the Sundance Formation may have been such a habitat.

Table 1. Plesiosaur specimens identified as juveniles. Measurements in cm.

Specimen number	Material Preserved	Width (cm)
UW 24217	vertebra, neural arch pieces, epipodials and phalanges	
UW 24219	distal end of propodial	9.8
UW 24236	distal end of propodial	6.0
UW 24239	distal end of propodial	4.7
UW 24240	broken propodial	5.7
UW 24243	proximal and distal ends of propodial	4.0 (proximal) 10.0 (distal)
UW 24244	proximal and distal ends of propodial	5.0 (proximal) 9.7 (distal)

CONCLUSION

The presence of a large number of juvenile plesiosaurs is unusual especially as adult plesiosaurs are not as common as the juveniles in the study area. Unfortunately, known material is not sufficiently complete to identify which taxa are represented. Chances of survival of juveniles may have been improved by association with adults as there are several juveniles found to every adult. Alternately, the predominance of juvenile plesiosaurs in the provincial seaway could be explained by environmental controls such as a food source in the form of belemnite migrations into transitional lagoonal areas.

Another possibility is that juvenile plesiosaurs may have been limited to lagoonal or shoreline shelf areas whereas the adults would have been more adapted to the open sea. The dense bone of juveniles made the skeleton displace more mass, limiting swimming speed and capabilities of rapid maneuvers for small dense bodies (Wiffen et al, 1995). Depositional evidence of rough, shallow water in the Redwater Shale Member of the Sundance Formation, may have made the bone mass difference useful for stabilization in the wave-agitated water.

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