

This article has been accepted for publication and will appear in a revised form, subsequent to editorial input by Cambridge University Press, in **Geological Magazine** (published by Cambridge University Press).

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[Geological Magazine / FirstView Articles](#)

DOI: <http://dx.doi.org/10.1017/S0016756813000472> ,

Published online: 03 July 2013

Please check the online publication for revisions to this article before citing it.

Palaeoecology of the Marine Reptiles of the Redwater Shale Member of the Sundance Formation (Jurassic) of central Wyoming, USA

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Abstract

The Redwater Shale member (Oxfordian) of the Sundance Formation was deposited in the foreland basin of the Cordillera during the last and largest marine transgression of the Jurassic in North America. One ichthyosaur (*Ophthalmosaurus natans*), two cryptocleidoid plesiosaurs (*Tatenectes laramiensis*, *Pantosaurus striatus*), and one pliosauroform (*Megalneusaurus rex*) are known from the Redwater Shale member. Ichthyosaurs are much more abundant than plesiosaurs, making up almost 60% of the fauna. No actinopterygian fish have been found, although four species have been identified from the lower Sundance Formation. At least one hybodont shark and one neoselachian are known from rare isolated teeth. The main food source for the marine reptiles were belemnoids, as indicated by preserved gut contents for all four species. In comparison, the better known and slightly older Peterborough Member of the Oxford Clay Formation of England, has a much higher taxonomic and ecological diversity, especially in the plesiosaurs, marine crocodiles, and fish. The lower diversity in the Redwater Shale probably reflects a much lower primary productivity in the Sundance Sea, as well as restricted migration from the open ocean to the north.

Key words: ichthyosaur, plesiosaur, *Pantosaurus*, *Ophthalmosaurus*, *Tatenectes*, *Megalneusaurus*, Oxford Clay Formation

1. Introduction

During the Jurassic, the North American plate drifted northward, such that by middle Callovian to middle Oxfordian time, central Wyoming was approximately 23-25° N latitude (Kocurek & Dott, 1983). The Middle and Upper Jurassic strata of the western interior of the U.S. record a series of marine cycles of transgression and regression (Brenner & Peterson, 1994; Kvale *et al.*, 2001). The Sundance Sea was the southern portion of a boreal 'pocket' sea, with an outlet to the north. It extended from central South Dakota to western Utah, and from northern New Mexico to the Arctic (Figure 1; Brenner & Davies, 1974). On the eastern and southern shorelines, the low relief land shed sediments into the basin. The western shoreline was along highlands that became more tectonically active throughout the Oxfordian. With increasing tectonic activity, coarser sediments were deposited and eventually the basin was filled (Brenner & Davies, 1974).

The upper Sundance Formation records the last incursion of the sea during the Oxfordian, the fourth marine cycle of the Jurassic in North America. It is bounded by the J4 and J5 unconformities (Pipiringos & O'Sullivan, 1978; Brenner & Peterson, 1994). Ammonites, ostracodes, and foraminifera suggest that this interval lasted approximately 8 million years (Brenner & Peterson, 1994), but Kvale *et al.* (2001, figure 5) estimated about 4 million years. The sediments, which now make up the Redwater Shale member of the Sundance Formation, record the largest Jurassic transgression and a regression, both of which occurred during a eustatic rise in sea level (Brenner & Peterson, 1994). The transgression was controlled by the global sea level rise, but the regression occurred because increased tectonic activity to the west caused a high sedimentation rate that exceeded the rise in sea level (Brenner & Peterson, 1994). More recently, Kvale *et al.* (2001) recognized three smaller-scale shallowing episodes within the upper Sundance Formation strata in north-central Wyoming (Bighorn Basin). These are punctuated by coquinas, which we have recognised in our field area as well. They have been attributed to storm deposits (Brenner & Davis, 1974) but have more recently been interpreted as sand waves generated by storm and tidal currents (Brenner *et al.*, 1985).

This report is based in large part on our work in the upper Sundance Formation of central Wyoming. Our study area encompasses northern Natrona County and adjacent areas, including Alcova Reservoir (southern Natrona County) and the Gas

Hills (eastern Fremont County; Figure 2). Central Wyoming was far from the shoreline, in a deeper area of the Sundance Sea, and accumulated predominantly muddy facies of the Redwater Shale. The purpose of this paper is to describe the vertebrate fauna of the Redwater Shale member based on more than a decade of field work and collecting in central Wyoming, and to present our interpretation of the palaeoecology of this interval of the Sundance Sea. We also compare the Redwater Shale vertebrate fauna to the more diverse and better known fauna of the Peterborough Member of the Oxford Clay Formation of England.

1a. Institutional abbreviations

TATE Tate Geological Museum, Casper College, Casper, WY; **USNM** U.S. National Museum, Smithsonian Institution, Washington, DC; **UW** University of Wyoming, Laramie, WY; **WDC** Wyoming Dinosaur Center, Thermopolis, WY.

2. Stratigraphy

The Sundance Formation ranges in age from middle Bathonian to Oxfordian (Kvale *et al.*, 2001). It lies unconformably on the Triassic Gypsum Springs Formation and is overlain by the Morrison Formation, river channel and floodplain deposits famous for a diverse dinosaur assemblage. The Windy Hill Sandstone (Pipiringos, 1968) occurs discontinuously between the terrestrial strata of the Morrison Formation and the marine Redwater Shale. It is a marine sandstone, oolitic in some locations, with cross-bedding, oscillation and current ripple marks, and pterosaur tracks (Johnson, 1992; Connelly, 2006). It indicates shallow marine deposition where the sedimentation rate could not keep up with the eustatic sea level rise (Brenner & Peterson, 1994). Until recently, the Windy Hill sandstone was included in the upper Sundance Formation (Pipiringos, 1968; Johnson, 1992), but its occurrence above the J-5 unconformity and an interfingering relationship with the lower Morrison strata have led to its reassignment to the Morrison Formation (Brenner *et al.*, 1985; Peterson, 1994). However, the lower Morrison strata are terrestrial, whereas Windy Hill strata are marine and thus at least environmentally more similar to the Sundance Formation.

In south-central and northeastern Wyoming, the Sundance Formation has been subdivided into six members, from lower to upper: Canyon Springs Sandstone, Stockade Beaver Shale, Hulett Sandstone, Lak Member, Pine Butte Sandstone, and Redwater Shale (Figure 3; Imlay, 1947; Robinson *et al.*, 1964; Pipiringos, 1968;

Johnson, 1992). The Redwater Shale has been recognized in central and north-central Wyoming by Imlay (1980) and Johnson (1992), and in Natrona County by Specht & Brenner (1979). We have identified both the Pine Butte Sandstone and the Redwater Shale members in Natrona County, although the former varies greatly in thickness. Pipiringos (1968) noted that belemnites are absent in the strata below the Redwater Shale, and this is consistent with the belemnite-bearing strata that we identify as the Redwater Shale member.

The Redwater Shale is a medium to dark gray, glauconitic shale with many thin beds of glauconitic sandstone. In northern Natrona County, three limestone coquinas occur, comprised of *Camptonectes* and/or *Ostrea* or *Gryphaea* shells, along with other bivalves, belemnites, and rare bone material. A thicker layer of green-gray crossbedded, thin-bedded glauconitic sandstone occurs in the lower part of the Redwater Shale. Another distinctive tan to olive green fine sandstone with abundant trace fossils occurs higher in the section. Sandstones become more common towards the top of the Redwater Shale, reflecting shallower water of the regressive phase. The soft shales of the Redwater Shale weather quickly to form vegetated slopes with outcrops of the resistant sandstones and limestone coquinas. Layers of iron-rich concretions also occur, and some of these concretions encase bone material, most often vertebrae and ribs.

The Redwater Shale is younger than the well known marine reptile fauna of the Peterborough Member of the Oxford Clay Formation (middle Callovian), England (Martill *et al.*, 1994; Martill & Hudson, 1991, text-fig. 1.2). Brenner & Peterson (1994) have suggested an early to at least middle Oxfordian age for the Redwater Shale. Imlay (1982) correlated the Redwater Shale member in northeastern and southeastern Wyoming with the *Cardioceras cordatum* zone (upper lower Oxfordian). The Redwater Shale member in the Bighorn Basin of north-central Wyoming, however, spans the *Cardioceras cordatum* and *Perisphinctes plicatilis* zones (upper lower Oxfordian to lower middle Oxfordian; Imlay, 1982). More recently, Kvale *et al.* (2001, figure 5) and McMullen (Unpublished M.S. thesis, University of Georgia, 2012, figure 9) suggested a middle Callovian to middle Oxfordian age for the “upper” Sundance Formation in north-central Wyoming (Bighorn Basin), but they included strata from the J3 to the J5 unconformities. The ammonites *Cardioceras* and *Quenstedtoceras* occur in the Redwater Shale at Alcova Reservoir in southwestern

Natrona County (MR, pers. obs.), more in keeping with the Oxfordian age of Imlay (1982).

3. Taphonomy of the marine reptiles

Reptilian remains are not confined to specific horizons. We have found specimens throughout the Redwater Shale, to within a couple of meters of the Windy Hill Sandstone (UW 34786; Massare *et al.*, 2006). Thus the fauna represents an accumulation of skeletons over a fairly long interval of time. Most *in situ* material that we have found is ichthyosaurian. No complete skeletons have been found, although we have excavated a well-preserved skull and articulated anterior skeleton of an ichthyosaur (UW 24216). The skull was at nearly right angles to the bedding plane on which the articulated vertebral column rested, suggesting that the carcass landed on the sea floor in a “nose dive”, with the skull penetrating the soft substrate (Wahl, 2007b). Articulated partial skeletons of both ichthyosaurs and plesiosaurs have been found (e.g., ichthyosaur UW 34653; plesiosaurs UW 15943, WDC SS01), although they are not common. Strings of articulated vertebrae and ribs, sometimes a substantial portion of the vertebral column, are more common (e.g. ichthyosaurs UW 15936, UW 24235, UW 19686, UW 34786). Disarticulated, associated bones have been collected *in situ* (e.g., ichthyosaurs UW 15936, TATE v-2038, UW 24802) and as float (e.g., plesiosaurs UW 15943, UW 24217; and ichthyosaurs UW 24234, UW 2). Isolated limb bones, pectoral elements, centra, and ribs have also been collected as float.

The Redwater Shale does not typically form good outcrops, except for the limestone coquinas and thicker sandstone layers. Most areas in which it occurs are vegetated, and bones are often found as weathered float. Many of the more complete specimens are in irregularly shaped carbonate concretions within dark to medium gray shale layers or in sandstone lenses (F. R. O’Keefe, pers. comm. 2013). Some of the concretions include coarse shell hash (e.g., encasing UW 15936 and UW 34653), but a few are micritic (e.g., encasing UW 24216 and WDC SS-019). These concretions are distinct from the iron-rich concretions previously mentioned, which tend to be more ellipsoidal in shape and occur in distinct horizons. Both kinds of concretions can encase bone.

Burrows, probably by crustaceans, are associated with some specimens. UW 24216 had burrows running through the concretion along the ribs, and lobster

carapace fragments (*Eryma?*) were found within the burrows by WRW as the specimen was prepared. One ichthyosaur (TATE v-2038) had sand-filled burrows in shale adjacent to the bones, as well as serpulid worm tubes in fine sediment immediately below the bones.

4. Palaeoenvironment

Based on the bivalve fauna, Wright (1974) considered the Redwater Shale to be a shallow, open shelf environment. The presence of belemnoids and crinoids would suggest normal marine salinity. Tang & Bottjer (1996) gave a depth estimate of less than 100 m. We suggest, however, that the depth was much less, on the order of 40-50 m, comparable to the 30-50 m depth that has been suggested for the Peterborough Member of the Oxford Clay Formation (Hudson and Martill, 1991).

McMullen (Unpublished M.S. thesis, University of Georgia, 2012) recognized two facies of the Redwater Shale in north-central Wyoming (Bighorn Basin), an offshore mudstone facies and a transitional facies of interbedded sandstone and mudstone. The former was interpreted as a low energy offshore environment that was below storm wave base. The latter was interpreted as a subtidal environment closer to the shoreline and frequently disturbed by waves (McMullen, Unpublished M.S. thesis, University of Georgia, 2012). In northern Natrona County, layers of thin-bedded, cross-bedded sandstone occur in at least two horizons, and thin glauconitic sandstones occur throughout in the shale. Concretions around some ichthyosaur skeletons (UW 34653, UW 15963) contain coarse shell hash. So although shale is the dominant deposit, suggesting a quiet water environment below wave-base, frequent layers of fine sandstones and shell hash around skeletons indicate that the depths were near wave base. McMullen (Unpublished M.S. thesis, University of Georgia, 2012) indicated that the offshore facies had a higher abundance and diversity of vertebrates, but we have found vertebrates throughout the section in Natrona County, often immediately above (e.g., UW 15936; UW 19686) or below (e.g., UW 34786) thin beds of sandstone.

The Redwater Shale interval was a fairly rough water environment. Water-worn belemnites are fairly common, and water-worn bones or bone fragments occur as well. Andersson (1979) described cobble layers of reworked concretions some of which were encrusted or bored by bivalves. He suggested that other cobble layers might be lag deposits from an interval of erosion. We have found cobbles that are

encrusted by bivalves on the top and bottom, indicating currents or waves that were strong enough to turn them over. The limestone coquinas may also indicate rough water, or at least higher energy conditions. The coquinas have been interpreted as episodic storm deposits (Brenner & Davis, 1974), as storm-winnowed deposits on the higher areas of an irregular sea floor (Specht & Brenner, 1979), and as sand waves moved by tidal and storm currents (Brenner *et al.*, 1985). All of those interpretations imply episodes of wave and current agitation reaching the seafloor.

Sedimentation rates were variable, but generally low as indicated by abundant glauconite throughout the Redwater Shale. Large carcasses on the sea floor may have served as baffles, accumulating coarser sediments within the shale. On one side of the limbs of the pliosaur *Megalneusaurus rex*, a thick sandstone lens occurs in the shale. It is possible that the carcass was exposed on the sea floor for some time before burial, blocking water flow so that coarser sediment was deposited on the leeward side. Concretions with shell hash suggest that this could have occurred with smaller carcasses as well. We have not, however, seen encrustations on bones of articulated vertebrate specimens, although encrusted belemnites occur. Another possible explanation is that the carcasses interfered with the movement of sand waves along the sea floor.

5. Fauna of the Redwater Shale

5. a. Macroinvertebrates

The invertebrate fauna of the Redwater Shale is dominated by mollusks. By far the most common invertebrate is the belemnoid *Pachyteuthis densus*. It occurs throughout the Redwater Shale, and has been found in the same horizons as vertebrate remains. A second, large belemnoid with a very deep phragmacone has been found (WDC JSI-22), and may represent a second, rare species. Doyle (1987) suggested that *Cylindroteuthis* is also present. Belemnoids of the Redwater Shale have not been adequately studied, and so they may be more diverse than is currently thought. Belemnite guards with diameters of 1-2mm, found in harvester ant mounds, suggest that the belemnoids could have been reproducing in the Sundance Sea. The lower Redwater Shale, in particular, has high concentrations of *Pachyteuthis*, and it is in these horizons where the anthills are covered with tiny guards. Belemnoids were a major food source for the reptiles because an ichthyosaur (UW 34653), both plesiosaur species (UW15943, UW 24215, and WDC SS-01), and the pliosaur (UW

4602) have been found with coleoid hooklets as gut contents (Massare & Young, 2005; Wahl *et al.*, 2007; Wahl, 2012).

The ammonites *Cardioceras* and *Quenstedtoceras* occur in the Redwater Shale of central Wyoming. A cardiocerid ammonite jaw has been reported in the gut contents of a cryptocliedoid plesiosaur (WDC SS-001) from Hot Springs County (Wahl, 2012). Ammonite protoconchs can occasionally be found in harvester ant mounds in the lower Redwater Shale in northern Natrona County.

Wright (1974) identified seven bivalve species from the Redwater Shale in Wyoming and South Dakota, listed here in decreasing abundance: *Camptonectes bellistriatus*, *Ostrea strigilecula*, *Gryphaea nebrascensis*, *Pleuromya newtoni*, *Tancredia sp.*, *Meleagrinnella curta*, and *Tancredia transversa*. *Camptonectes*, *Ostrea*, *Gryphaea*, and *Meleagrinnella* were epifaunal suspension feeders. *Pleuromya* and the two *Tancredia* species were infaunal, siphonate suspension feeders (Wright, 1974). Kvale *et al.* (2001) reported *Ostrea strigilecula*, *Vaugonia sturgisensis*, *Modiolis sp.*, *Idonarca sp.* as well as *Meleagrinnella curta* and the two *Tancredia* species from the Redwater Shale equivalent in the north-central Wyoming (Bighorn Basin). In both assemblages, the bivalve fauna are all suspension feeders, and a large proportion of them (*Ostrea*, *Gryphaea*, *Meleagrinnella*, *Camptonectes*, *Modiolis*) are epifaunal (Wright, 1974).

Pentacrinoid crinoids are the most common echinoderm in the Redwater Shale. We have found star-shaped crinoid columnals and stem pieces on harvester ant mounds in the lower the Redwater Shale as well as elsewhere in the member. Crinoid fragments also make up the sediment of starved ripples and an encrinite in the lower Redwater Shale near Alkalai Creek in northern Natrona County (Wahl, 2007a). Connely & Talbot (2008) reported a well preserved *Isocrinus* specimens in the Redwater Shale in southern Johnson County. *Chariocrinus* and *Isocrinus* have been identified from the Stockade Beaver Shale in the lower Sundance Formation (Hunter & Zonneveld, 1982; Koch, 1972). Other echinoderms are rare. The starfish *Eokainaster pewei* has been reported from what might be the lower Redwater Shale of the Owl Creek Mountains (Miller & Unklesbay, 1943; Blake, 1971) and from the Redwater Shale in the southern Bighorn Mountains (Connely & Talbot, 2008). Sea urchin spines can also be found in harvester ant mounds in the lower Redwater Shale. Sea urchin plates were found in the crinoid hash in the lower Redwater Shale and/or Pine Butte member from Johnson County (Connely & Talbot, 2008) and at Como

Bluff in southeastern Wyoming (MVC, pers. obs.). In addition, brittle stars are also known from the Stockade Beaver Shale (lower Sundance Formation) from these localities (Pipiringos, 1957; MVC, pers. obs.).

Crustaceans were also a component of the benthic fauna of the Redwater Shale. WRW has found small pieces of crustacean carapaces (WDC JSI-10), which may be either *Mecochirus* or *Eryma*, in burrows associated with an ichthyosaur skeleton, UW 24216 (Wahl, 2008). A large piece of an *Eryma* carapace was found in the lower Redwater Shale (Wahl, 2004), and it has been reported from the equivalent Redwater Member of the Stump Formation in Utah (Feldman & Titus, 2006).

5. b. Vertebrates

At least two kinds of chondrichthyan were present in the Sundance Sea. Wahl (2005, 2007a) described teeth, dermal denticles, and dorsal fin spine denticles of a hybodont shark (UW 24218), possibly *Hybodus* or *Asteracanthus*, associated with the skeleton of a cryptocleidoid plesiosaur (UW 24215). Schaeffer & Patterson (1985) reported *Hybodus* from the Stockade Beaver Shale of the lower Sundance Formation. A hybodont shark tooth, as well as a long, thin tooth of a neoselachian shark, have been found in the coarse sands of starved ripples in the lower Redwater Shale (Wahl, 2007a). Another single shark tooth was found in an encrinite in southern Johnson County (Connely & Talbot, 2008). Shark teeth are extremely rare, but it appears that at least two kinds of chondrichthyans were present.

The osteichthyans *Hulettia americana*, *Caturus dartoni*, *Lepidotes* sp., and *Occithrissops willsoni* occur in the Stockade Beaver Shale (lower Sundance Formation; Figure 3), *Hulettia* being the most common (Schaeffer & Patterson, 1985). Dense, dark coloured bone and teeth, which can be attributed to some kind of osteichthyan fish, have been found in harvester ant mounds in the lower Redwater Shale (WRW, pers. obs.). Similar dense bone fragments occur in the gut contents of *Megalneusaurus rex* (UW 4602) and *Pantosaurus* (WDC SS-01), and are associated with a partially articulated fragmentary skeleton of an ichthyosaur (TATE v-2038). Such fragments are neither common nor taxonomically identifiable, but they are clearly not reptilian bone fragments. The rough water environment and slow sedimentation rate may have inhibited preservation of small fish skeletons.

The most common vertebrate in the Redwater Shale is the ichthyosaur *Ophthalmosaurus natans* (Marsh, 1879). The ichthyosaur was first described as *Sauranodon natans* and later changed to *Baptanodon natans* when the genus name

was found to be preoccupied (Marsh 1880a). Andrews (1910) argued that *Baptanodon* was synonymous with *Ophthalmosaurus*, and most subsequent workers have agreed (but see Appleby, 1956). Recent phylogenetic analyses, however, have failed to recover a monophyletic *Ophthalmosaurus* (Druckenmiller & Maxwell, 2010; Fischer *et al.*, 2012). Early workers recognized four additional species: *B. discus* (Marsh, 1880b), *B. marshi*, Knight, 1903; *B. robustus*, Gilmore, 1906; and *B. reedi*, Gilmore, 1907. Presently, only *O. natans* is considered valid (McGowan & Motani, 2003; Maisch & Matzke, 2000), and we have not found any evidence to the contrary in the material that we have collected. *Ophthalmosaurus natans* can be distinguished from the closely related British species, *O. icenicus*, by the pattern of centrum shape change along the vertebral column. In particular, *O. natans* has longer centra relative to their height in the posterior dorsal and anterior caudal region than does *O. icenicus* (Massare *et al.* 2006). Appleby (1956) also noted a difference in braincase features, especially the relative contribution of the supraoccipital and exoccipitals to the foramen magnum (but see discussion in McGowan & Motani, 2003, p. 111).

Specimens of *Ophthalmosaurus* fall into a range of size classes, including centra of a presumably voided embryo found as gut contents of a cryptocleidoid plesiosaur (O'Keefe *et al.*, 2009). The largest specimen we have collected has a skull length of 80 cm (Figure 4), which would correspond to a total length, from the tip of the snout to the base of the tail fluke, of 3.2 m if we assume the same body proportions as *O. icenicus* (Andrews, 1910, text-figure 42). Massare *et al.* (2006) estimated a preflexural length of the vertebral column of a large, composite specimen as 2.8 m. Again assuming proportions similar to *O. icenicus*, this would suggest a length of about 3.5 m including the skull. Most specimens, however, are considerably smaller.

Two long-necked cryptocleidoid plesiosaurs are known from the Redwater Shale, *Pantosaurus striatus* and *Tatenectes laramiensis* (O'Keefe & Wahl, 2003a, b). Both species are endemic to the Sundance Sea. Juvenile plesiosaur material has also been collected, although the material is insufficient for taxonomic identification (Wahl, 2006). It is likely, however, that at least one species of plesiosaur was breeding in the Sundance Sea.

The plesiosaur *Tatenectes* was originally described as '*Cimoliosaurus*' *laramiensis* by Knight (1900), but the holotype is lost. It is the same taxon as '*Tricleidus*' *laramiensis* (Mehl, 1912). O'Keefe & Wahl (2003b) created a new genus for the species, erected a neotype based on the original description, and noted its close

relationship to *Kimmerosaurus*. The relationship was confirmed by O’Keefe & Street (2009), who placed *Tatenectes* within the “Aristonectidae”, with *Kimmerosaurus* as a sister taxon. O’Keefe *et al.* (2011) estimated the adult body length as just under 3 m, although the length of the neck is uncertain. They noted that *Tatenectes* has a strongly dorsoventrally compressed body and the pelvic girdle has shifted anteriorly, reducing the distance between the limbs. The extreme compression and anteroposterior shortening gave *Tatenectes* an unusual body shape for a plesiosaur (O’Keefe *et al.*, 2011).

Pantosaurus striatus (Marsh, 1891), the second cryptocleidoid plesiosaur from the Redwater Shale, was originally described as *Parasaurus striatus*, but the generic name was changed because it was preoccupied (O’Keefe & Wahl, 2003a). The holotype (YPM 543) originally included teeth and cranial material, but that portion of the specimen has been lost (O’Keefe & Wahl, 2003a). The taxonomic affinities are made more difficult to ascertain because the holotype is a juvenile (O’Keefe & Wahl, 2003a). Overall, the taxon is less well known than *Tatenectes*. The cervical centra are ‘waisted’, where the middle of the centrum has a smaller diameter than the articular faces, and the centra are almost as long as they are wide, two features that are among those diagnostic of the species (Wilhelm & O’Keefe, 2010). O’Keefe & Wahl (2003a) noted that the centrum morphology was similar to that of *Muraenosaurus*, but specimens are too incomplete for a phylogenetic analysis. *Muraenosaurus reedi* Mehl, 1912, described from the Sundance Formation, is considered to be a junior synonym of *P. striatus* (O’Keefe & Wahl, 2003a), suggesting that earlier workers also noted a similarity to *Muraenosaurus*. *Pantosaurus* has more robust limb bones than *Tatenectes* (O’Keefe & Wahl, 2003a) and so may have been a somewhat larger species.

Megalneusaurus rex is the only pliosauromorph in the Redwater Shale, although the rhomaleosaurid *Borealonectes* is known from the Callovian of northern Canada (Sato & Wu, 2008). The type specimen (UW 4602) was collected in 1895 and provisionally assigned to *Cimoliosaurus* (Knight, 1895), but subsequently assigned to a new genus, *Megalneusaurus* (Knight, 1898). Two hind limbs, one articulated and one disarticulated, are all that remain of the original holotype. A poorly preserved but articulated forelimb of the same individual was collected in 2008 from the original site (Wahl *et al.*, 2010). The limbs do not provide useful taxonomic information, but the shape of the limbs suggest that *Megalneusaurus* may be a pliosaurid. It is the

rarest of the marine reptiles, with only three other specimens known from the Redwater Shale, all of which are isolated, weathered bones collected as float (UW 24238-neural arch; WDC SS-019-propodial fragment; USNM 536978). The only *in situ* specimen of *Megalneusaurus* (UW 4602, the type specimen) occurs in the upper Redwater Shale, within 10 m of the top of the unit (Wahl *et al.*, 2007), and so the plesiosaur seems to have appeared during the regressive phase of the Redwater Shale. If we assume the same body proportions as for *Liopleurodon* (Robinson, 1976, figure 10A), the 106 cm partial forelimb that we collected (Wahl *et al.* 2010) would suggest a total length of 9.2 meters for the holotype individual. *Megalneusaurus* appears to have been more wide ranging than the other plesiosaurs, being known from the Alaskan peninsula (Weems & Blodgett, 1994), as well as from Wyoming.

6. Palaeoecology of the vertebrates

Ophthalmosaurus natans was a pursuit predator, but had a more undulatory swimming style than *O. icenicus*, based on the shape of the centra (Massare *et al.*, 2006). It may not have been as fast and efficient a swimmer as *O. icenicus* of comparable size, but it was probably more maneuverable (Massare, 1994; Massare *et al.*, 2006). *O. natans* has slender, fairly pointed, but small teeth (Figure 5), characteristic of the Pierce I guild of Massare (1987). For UW 24216, with a skull length of 80 cm, tooth crown heights range from 0.5 mm to 2 cm, with the largest preserved tooth being 3.5 cm high, including the root. The largest teeth appear to be anterior to the maxilla, and are smaller at the anterior end of the rostrum. Gut contents of UW 34653 confirm that the species consumed coleoid cephalopods, fairly soft prey as would be predicted from the tooth form (Massare, 1987; Massare & Young, 2005). UW 24216 preserves teeth throughout the entire rostrum, although most are dislodged from their natural position. *O. natans* had a complete dentition as an adult, as asserted by Gilmore (1905, p. 99). Teeth can be seen along the entire length of the jaw in UW 24216. The specimen preserved teeth because the skeleton landed head first on the sea floor and the rostrum was driven into the sediment (Wahl, 2007b). The encasing sediment held the teeth in place, even at the anterior end of the rostrum that was split open (Figure 4). The reported lack of teeth or only anterior teeth in *Ophthalmosaurus natans* specimens (e.g., McGowan & Motani, 2003, p. 110) is probably an artifact of preservation.

The bone microstructure of *O. natans* suggests an animal that was adapted for life in rough, shallow water (Sheldon, 1997), as would be expected of an animal living in the relatively shallow Sundance Sea. Rib cross-sections of UW 24216 show a thick layer of cortical bone and thick trabeculae (Figure 6), somewhat similar to what has been reported for another ophthalmosaurid, *Mollesaurus* (Talevi & Fernández, 2012). Animals living in shallow water are continuously subjected to waves and current, which provide the stress to maintain and increase bone density (Sheldon, 1997). Bone microstructure thus suggests that *O. natans* was inhabiting the Sundance Sea, not migrating in for breeding or feeding. It also implies that it was not a deep diving species.

However, the exceptionally large eye of *Ophthalmosaurus natans* has been interpreted as an adaptation for low light levels encountered in deep diving, perhaps as deep as 600 m or more (Motani *et al.*, 1999). Although *O. icenicus* may have been a deep diver, bone microstructure and the environment of the Sundance Sea suggest that it was not the case for *O. natans*. Humphries & Ruxton (2002) argued that visual acuity, the ability to resolve fine details, is as important as sensitivity to low light levels. They suggested that ichthyosaurs may have been selective hunters of small prey at moderate depths, needing large eyes to distinguish among prey species. So possibly the large eye of *O. natans* allowed it to hunt in low light conditions at dawn or dusk, perhaps coinciding with a time of day when belemnoids were active. Nilsson *et al.* (2012), however, suggested that an eye size of about 9.0 cm diameter (3.0 cm pupil diameter) was the upper limit for optimal sensitivity and acuity. Larger eyes did not substantially improve either and so selection was probably for another aspect of vision. In the largest *Ophthalmosaurus* that we have found (UW 24216; Figure 4), the outer diameter of the sclerotic ring is about 20 cm and the inner diameter (diameter of the opening) is 8 cm. Nilsson *et al.* (2012) hypothesized that selection for such very large eyes was to enhance long-range recognition of large objects, such as predators or potential mates. Or large eyes may have evolved to use visual signals to coordinate group hunting or for recognition of other ichthyosaurs (Humphries & Ruxton, 2002). In any event, an exceptionally large eye, as seen on *O. natans*, need not imply deep diving.

The cryptocleidoid plesiosaurs were about the same size as the ichthyosaurs. With its highly dorso-ventrally flattened body (O’Keefe *et al.*, 2011), *Tatenectes* was not a fast swimmer, and because of its long neck may have favored an ambush strategy

(Massare, 1988; 1994). *Tatenectes* had large gastralria that are pachyostotic along their midline, adaptations for stability in shallow water (Wahl, 1999; Street & O'Keefe, 2010). Thus like *O. natans*, *Tatenectes* was a shallow water species, and was probably living in the Sundance Sea rather than migrating in from the open ocean to the north. Its teeth were small, slender and pointed (O'Keefe & Street, 2009), and it occupied the Pierce I guild (Massare, 1987). Coleoid hooklets were found associated with a partial *Tatenectes* skeleton (UW 15943), so belemnoids probably made up a major portion of its diet.

The body shape of *Pantosaurus* is not known, but if it had the typical cryptocleidoid body shape (small head and fairly long neck), *Pantosaurus* would have also tended towards an ambush style of attack, or at least slower swimming speeds (Massare, 1988; 1994). *Pantosaurus* may have been a more opportunistic predator than *Tatenectes*, as specimens have been found with gut contents that include coleoid hooklets (UW24215 and WDC SS-01), an ammonite jaw (WDC SS-01), small fragments of fish bone (WDC SS-01), and a scavenged ichthyosaur embryo (O'Keefe *et al.*, 2009). However, its tooth form is unknown.

The pliosaur *Megalneusaurus* was much larger than the other reptiles. It was the fastest predator in the sea, if for no other reason than its large size. It could have easily consumed juveniles and subadults of the other reptiles. Bite marks are known on a small plesiosaur propodial (UW 24219, Figure 7; Wahl, 2006), although neither the species of the victim nor the predator can be determined. Stomach contents have been recovered for the type specimen (UW4602) of *Megalneusaurus*, and these consist of coleoid hooklets, as occurs with the other reptiles, along with a few rare fish bone fragments (Wahl *et al.*, 2007). *Megalneusaurus* appeared towards the end of the Redwater Shale deposition, when the Sundance Sea was experiencing the last regressive phase. Because it is so rare, it may be that the pliosaur was a visitor rather than an inhabitant of the area, but this is impossible to determine with any certainty. However, *Megalneusaurus* is the only marine reptile in the Redwater Shale fauna to occur outside of Wyoming (Weems & Blodgett, 1994).

7. Comparison with the Peterborough Member, Oxford Clay Formation

One of the best known and diverse marine vertebrate fauna of the Jurassic is that of the Peterborough Member of the Oxford Clay Formation. It is mainly Middle Callovian in age (upper Calloviense Zone through the Athleta Zone; Martill &

Hudson, 1991, text-fig.1.2), older than the Redwater Shale by a few million years. The deposition of the Peterborough Member was estimated to have been a period of just 2 million years, based on the average duration of ammonite zones (Martill *et al.*, 1994). By comparison, the Redwater Shale spans one ammonite zone (Imlay, 1982) but the duration has been estimated as at least 4 million years, and perhaps as much as 8 million years (Kvale *et al.*, 2001; Brenner & Peterson, 1994, respectively). In spite of the shorter time frame, the Peterborough Member has a much higher diversity of vertebrates and invertebrates, although some of the same genera are present in both faunas. This discussion will focus on the vertebrates.

A major difference between the Redwater Shale and the Peterborough Member is that the latter has a much more diverse fish fauna, with 27 genera, including both chondrichthyans and osteichthyans (Martill *et al.*, 1994). In fact, fish remains are the most abundant vertebrate in the Peterborough Member (Martill & Hudson, 1991). Even if we assume that all of the fish species in the Stockade Beaver Shale survived to Redwater Shale time, only five fish genera are known (Schaeffer & Patterson, 1985). Four of the lower Sundance Formation genera, *Caturus*, *Lepidotes*, *Hybodus*, and *Ischyodus* are also found in the Peterborough Member, and the first two genera are among the most common fish fossils (Martill *et al.*, 1994). The most common fish in the lower Sundance Formation is *Hulettia*, which appears to be endemic to the Sundance Sea (Schaeffer & Patterson, 1985). Notably, remains of the giant suspension feeding fish, *Leedsichthys*, which are frequent in the Peterborough Member (Martill *et al.*, 1994), are absent in the Redwater Shale. Thus fish made up a much more significant component of the food web in the Peterborough Member, and probably were prey for many marine reptiles. Additionally, the relationships among the fish species themselves were quite complex (Martill *et al.*, 1994, figure 7). In contrast, it appears that belemnoids were the major food source for the reptiles in the Redwater Shale, as indicated by preserved gut contents and their abundance compared to other possible prey species.

An ophthalmosaurid ichthyosaur is a major component of both faunas. Based on the collection of specimens from the Thirty-three Mile Road area in northern Natrona County (Figure 2), ichthyosaurs make up at least 58% the Redwater Shale fauna (Table 1), whereas they are only about a quarter (23%) of the Peterborough Member fauna (Martill & Hudson, 1991, text-figure 8.1). Only one species, *Ophthalmosaurus icenicus*, is recognized from the Peterborough Member (Kirton,

unpublished Ph.D. dissertation, Newcastle upon Tyne, 1983; but see Appleby, 1956). With its deep caudal fin and streamlined body, *O. icenicus* was an efficient pursuit predator and could probably sustain higher speeds than *O. natans* of comparable size (Massare, 1988; Massare *et al.*, 2006). *Ophthalmosaurus natans* had a more flexible vertebral column that suggests greater maneuverability but slower sustained swimming speed (Massare *et al.*, 2006). The difference in swimming styles suggests a difference in how prey was located and captured. Although no gut contents are preserved, Martill *et al.* (1994) argued that the diet of *O. icenicus* was likely soft cephalopods, in part because of the very slender, elongate rostrum. Preserved gut contents indicate that *O. natans* also fed on cephalopods, specifically belemnoids, although *O. icenicus* had many more species to select from. Martill *et al.* (1994) considered *O. icenicus* to be a deep diving form and thought that it may have been a migrant, ranging well beyond the Oxford Clay basin. This is in contrast to our interpretation of *O. natans* as predominantly shallow water species that was endemic to the shallow Sundance Sea.

A major difference in diversity occurs in the Plesiosauria, with more than three times as many species in the Peterborough Member than in the Redwater Shale (Martill & Hudson, 1991). The Peterborough Member preserves six species (assigned to four genera) of long-necked plesiosaurs, compared to two species in the Redwater Shale. The long-necked plesiosaurs are 38% of the Peterborough fauna (Martill & Hudson, 1991, text-figure 8.1) about the same proportion as in the Redwater Shale (39%; Table 1). Martill *et al.* (1994; table 1) reconstruct the Peterborough plesiosaurs as surface dwelling invertebrate feeders (*Cryptoclidus*, *Tricelidus*) and more generalist surface feeders (*Muraenosaurus*). In addition, the very rare plesiosaur *Pachycostasaurus* has been interpreted as a slow swimmer that fed on nekto-benthic prey such as arthropods, cephalopods, or ganoid fish (Cruickshank *et al.*, 1996). The Redwater Shale is similar to the Peterborough Member in the two common feeding types of long-necked plesiosaurs, although it had far fewer species.

In addition, the Peterborough Member includes six species of pliosauromorphs, representing five genera and comprising 12% of the fauna (Martill & Hudson, 1991, text-figure 8.1; Ketchum & Benson, 2011). These include large opportunistic carnivores (*Liopleurodon*, *Simolestes*) as well as generalists, fish and cephalopod feeders (*Peloneustes*, '*Pliosaurus*'; Martill *et al.*, 1994), and a rare, gracile longirostrine form (*Marmornectes*; Ketchum & Benson, 2011) that may have been a

more specialized feeder. The Redwater Shale preserves a single rare species of pliosaur, comprising less than 3% of the fauna (Table 1). By virtue of its size, *Megalneusaurus* was probably an opportunistic predator that was capable of preying upon the other marine reptiles, although the only preserved gut contents indicate a diet of mainly cephalopods (Wahl et al., 2007). Overall, the Plesiosauria, especially the pliosaumorphs, were much more ecologically and taxonomically diverse in the Peterborough Member than in the Redwater Shale. Moreover, the plesiosaurs comprise 50% of the reptilian fauna of the Peterborough Member, twice as abundant as the ichthyosaurs. In the Redwater Shale, the ichthyosaurs are much more abundant than the plesiosaurs (Table 1).

The most noticeable difference between the reptilian faunas, however, is the lack of marine crocodiles in the Redwater Shale. Two families of marine crocodiles, metriorhynchids and teleosauroids, make up 22% of the Peterborough Member specimens (Martill & Hudson, 1991 text-figure 8.1). Martill & Hudson (1991) listed two species of the teleosaurid genus *Steneosaurus*, but a recent phylogenetic analysis by Young *et al.* (2012) suggested that there are at least three species. The metriorhynchids include four species, representing the genera *Metriorhynchus*, *Gracilineustes*, *Suchodus*, and the rare hypercarnivore *Tyrannoneustes* (Young *et al.*, 2013). The marine crocodiles occupied the Crunch, Pierce II, and Cut guilds of Massare (1987; Young *et al.*, 2010), and thus were quite ecologically diverse. The complete absence of these ambush predators in the Redwater Shale fauna is puzzling, especially as they also occur in the Middle Jurassic of South America (e.g., Gasparini *et al.*, 2005; Fernández & Herrera, 2009). A metriorhynchid crocodile has been reported from the Middle Jurassic (Aalenian-Bajocian) Snowshoe Formation of eastern Oregon, however, the area is part of the Izee terrane, which was accreted in the Upper Jurassic (Wilberg, Unpublished Ph.D. dissertation, University of Iowa 2012). Thus a marine crocodile inhabited the eastern Pacific in the Middle Jurassic, but it did not necessarily inhabit the North American coast.

Possibly the marine crocodiles were excluded because of cool temperatures associated with the flow of water from the northern boreal ocean. Ploynoi (unpublished M.S. thesis, Wichita State College, Kansas, 2007) estimated an average water temperature of 15-17°C from oxygen isotope measurements on belemnites. Hudson & Martill (1991) cited temperatures of 17-20°C for the Peterborough Member, similarly based on pelagic species. More recently, Anderson et al. (1994)

calculated a mean temperature of 15°C from belemnites, 17°C from the bivalve *Gryphaea*, and 21°C from the ammonite *Kosmoceras*, although the latter may be 3-4°C too high because of possible fractionation. Thus oxygen isotope analyses do not indicate a substantially different water temperature for the Redwater Shale compared to the Peterborough Member. Although the Redwater Shale might have been a few degrees cooler, it is unlikely to have affected the distribution of crocodiles. Crocodiles can tolerate those temperatures, although a mean annual temperature of 25-35°C is the preferred range (Markwick, 1998). Young et al. (2010) suggested that the Oxfordian expansion of the metriorhynchids failed to reach the Sundance Sea before the final regression occurred. Or perhaps the Redwater Shale was too far from the shoreline to be a suitable habitat for marine crocodiles (Hudson & Martill, 1991, fig. 3).

Five percent of the fauna of the Peterborough Member are terrestrial species, dinosaurs, that washed in, and an additional 1% are pterosaurs (Martill & Hudson, 1991, text-figure 8.1). No bones of terrestrial animals have been found in the Redwater Shale, although pterosaur tracks occur in the overlying Windy Hill Sandstone (Connely, 2006). Wood fragments occur in Natrona County, but they are extremely rare. They have also been reported from western nearshore strata (Brenner & Peterson, 1974). This probably indicates that the Redwater Shale environment, at least in central Wyoming, was an open but shallow ocean, much farther from the shoreline than the Peterborough Member.

Figures 8 and 9 depict the trophic structure of the Redwater Shale and the Peterborough Member, respectively. Belemnoids form the basis of the food web for marine reptiles in the Redwater Shale (Figure 8), whereas fish are a major component, if not the most important food source for the reptiles, in the Peterborough Member (Figure 9). This difference in the trophic structure probably contributed to the difference in diversity of the marine reptiles. The marine reptiles are much more diverse in the Peterborough Member because of the more diverse and abundant assemblage of potential prey. Not only were there more fish, but there were more belemnoid and ammonoid species as well. Of course, this does not address the question as to why so many more prey species were available in the Peterborough Member (see below).

8. Conclusion

A number of non-biological factors may contribute to the lower diversity of vertebrates in the Redwater Shale compared to the Peterborough Member. The Redwater Shale lacks any quarry or shoreline exposures, but instead forms vegetated slopes with few outcrops. Moreover, the Redwater Shale has not been collected for as long a time by as many workers as the Peterborough Member. Our research and that of O'Keefe and his students represent the first focus on the marine reptiles of the Sundance Formation since pioneering work in the late 19th and early 20th century by O. C. Marsh, W. C. Knight, W. Reed, and C. W. Gilmore. Martill and Hudson (1991, text-figure 8.1) estimated the relative proportions of marine reptiles of the Peterborough Member from over 1000 museum specimens. By comparison, the number of reptilian specimens from the Redwater Shale is probably less than 20% of that number. Thus the limited exposures and limited collecting may contribute to the lower diversity of the Redwater Shale. Preservation bias may come into play as well, especially in terms of the fish preservation. The Sundance Sea was probably close to wave base depth for much of its duration, and rough water, frequent storm deposits, and erosion may have reduced the likelihood of preservation of articulated skeletons of small vertebrates such as fish.

These factors, however, are inadequate to explain the difference in diversity. The Redwater Shale has a depauperate fauna even taking the aforementioned biases into account. Fewer prey species limited the diversity of the large reptilian predators. It is not uncommon for physically stressful environments to have lower diversity, although low habitat heterogeneity could also reduce diversity (Therriault & Kolasa, 2000). The rough-water environment of the Sundance Sea may have exceeded the tolerances of potential prey species. More likely, however, the outlet to the north limited the number of species that could migrate into the Sundance Sea. Martill et al. (1994) thought that at least some of the Peterborough fauna were migrants from deeper water (see also Hudson & Martill, 1991, fig.3). A more extensive connection to the open ocean may have allowed a greater variety of species to frequent the Oxford Sea. By comparison, the Redwater Shale fauna includes mainly shallow water species, and the relatively narrow outlet to the north may have been a bottleneck for open ocean species trying to enter the Sundance Sea.

The low diversity of pelagic invertebrates, fish, and benthic invertebrates in the Redwater Shale is probably indicative of low primary productivity in the pocket sea, perhaps due to poor circulation, distance from the shoreline, or low sedimentation

rates. By comparison, the Peterborough Member is dominated by bituminous shales, and the high carbon content, up to 10% in some strata, indicates very high primary productivity (Duff, 1975; Hudson & Martill, 1991). Notably, vertebrate remains occur in shales with the highest carbon content, suggesting an association with times of highest primary productivity (Hudson & Martill, 1991). It is probably this higher primary productivity that allowed the Peterborough Member to attain a very high diversity of both invertebrates and vertebrates. The low diversity in the Redwater Shale probably reflects a much lower primary productivity, as well as restricted migration from the open ocean to the north.

Acknowledgements

Field work has been aided by an army of Tate Museum volunteers, several undergraduate field assistants from SUNY Brockport and Wellesley College, and more recently, volunteers from the Wyoming Dinosaur Center. Colleagues have joined us in the field over the years, and we greatly appreciated their company, assistance, and discussions. We thank the Bureau of Land Management for supporting our research through permits for surface collection and excavations, including PA02-WY-075, PA02-WY-076, PA05-WY-130, PA05-WY-131, and PA08-WY-165 issued to JAM. We are grateful to the University of Wyoming and the Tate Geological Museum for serving as repositories for the specimens collected on BLM administered land. We also thank the Wyoming Dinosaur Center for the use of their fossil preparation lab. Finally we thank Erin Maxwell, Mark Young and Robin O'Keefe for their thoughtful reviews and suggestions. Some field work by JAM was partially funded by Scholarly Incentive grants from SUNY Brockport.

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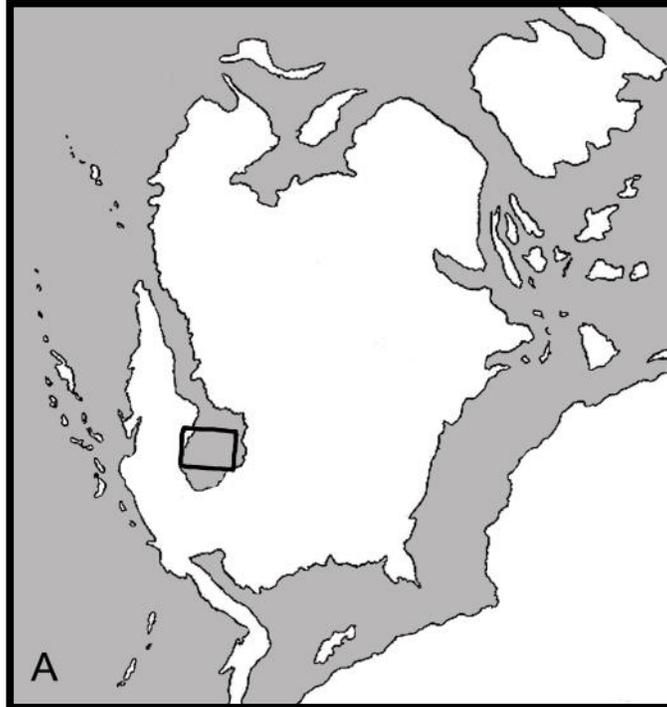


Figure 1: Paleogeography of North America during the Upper Jurassic, showing the Sundance Sea. Continental areas in white; marine areas in gray. Rectangular outline shows the location of Wyoming. Modified from the *Geologic Atlas of the Rocky Mountains*, p. 184, and online paleogeographic map by Ronald Blakey (<http://cpgeosystems.com/namJ150.jpg>).

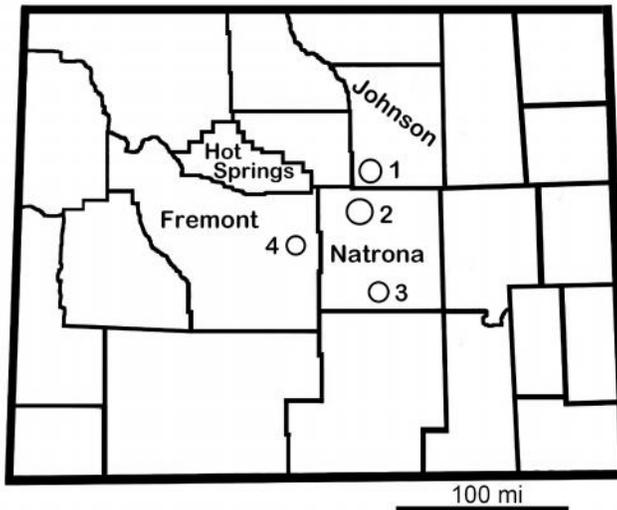


Figure 2: Outline map of Wyoming showing county boundaries. Our field areas included portions of Johnson, Fremont and Natrona counties. 1. Wold Ranch; 2. Thirty-three Mile Road area; 3. Alcova Reservoir; 4. Gas Hills. Scale bar = 100 miles.

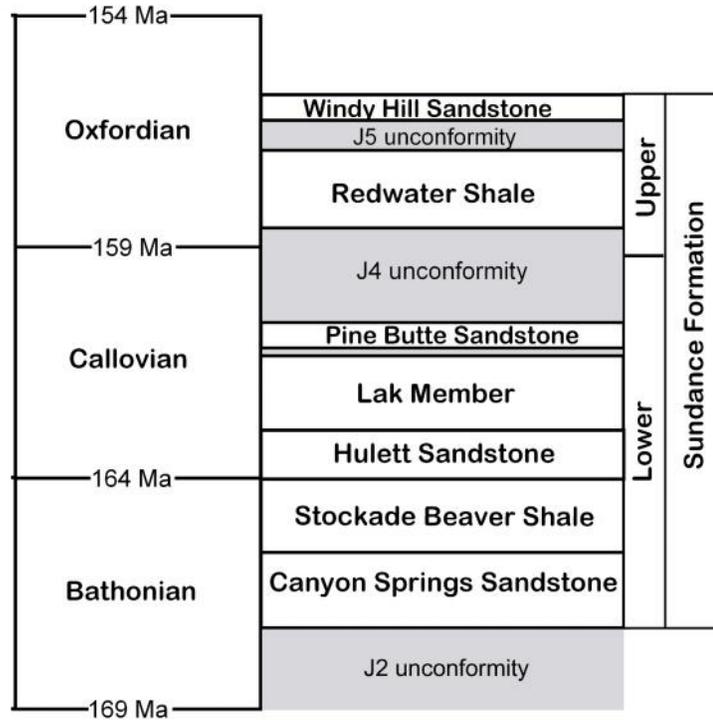


Figure 3: Members of the Sundance Formation showing the stratigraphic position of the Redwater Shale (Oxfordian), bounded by the J4 and J5 unconformities (modified from Johnson, 1992). The Windy Hill Sandstone is included as the upper member of the Sundance Formation, but others have included it in the overlying Morrison Formation (e.g., Peterson, 1994).



Figure 4: UW 24216 *Ophthalmosaurus natans* skull, approximately 80 cm long. The specimen settled to the sea floor apparently in a nose dive as the skull was at nearly a right angle to bedding and the post-cranial skeleton. Scale bar = 10 cm.

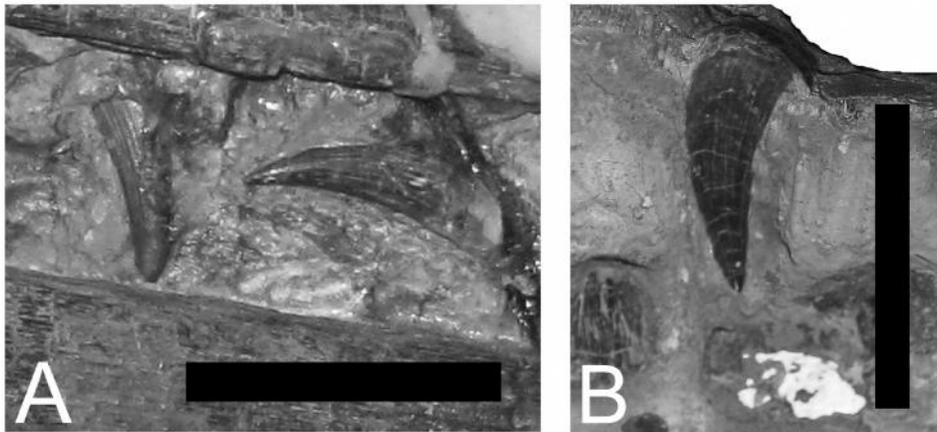


Figure 5: UW 24216 *Ophthalmosaurus natans* teeth. A. Teeth from the posterior portion of the rostrum (but anterior to the nares). Scale bar represents 3 cm. B. Tooth from the anterior portion of the rostrum. Scale bar = 2 cm.



Figure 6: UW 24216 *Ophthalmosaurus natans* cross-section of ribs showing thick trabeculae. Rib cross-section changes shape from the head to the distal end. A is from a more proximal location on a rib than B. Scale bars = 1.5 cm

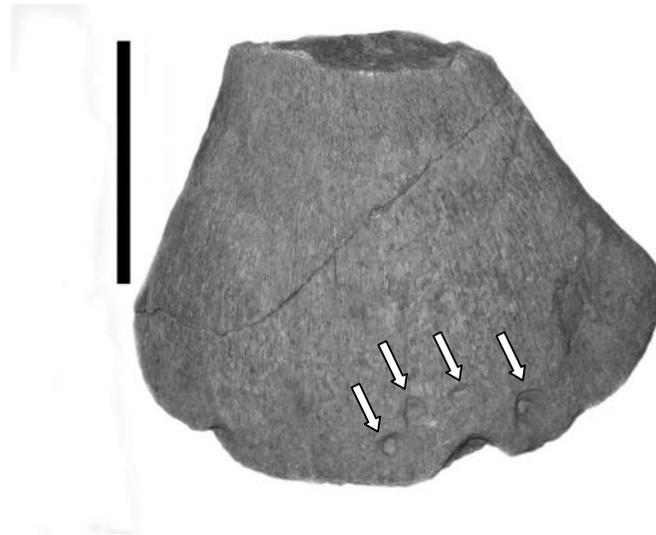


Figure 7: UW 24219, a portion of a small plesiosaurian propodial showing bite marks, four circular depressions, at the distal end indicated by the arrows. Specimen on display at the Tate Geological Museum, Casper College, Casper, WY, USA. Scale bar = 5 cm.

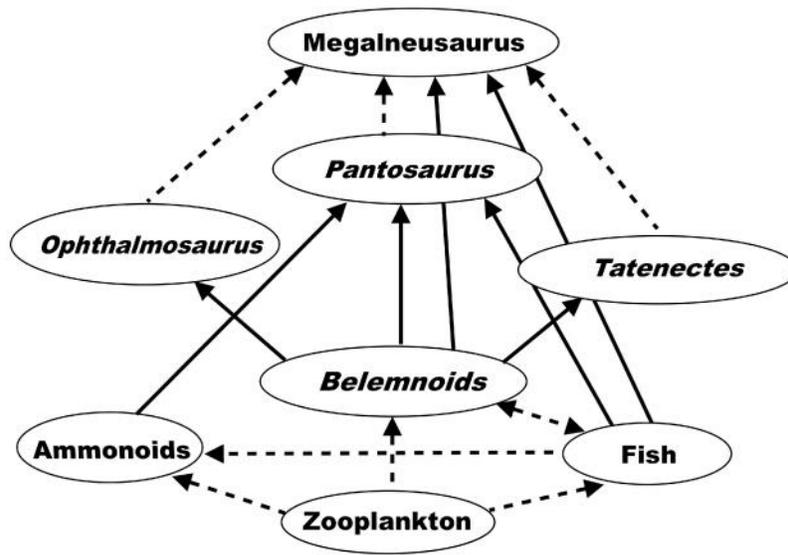


Figure 8: Food web for the Redwater Shale member of the Sundance Formation. Dashed lines indicate inferred relationships. Solid lines indicate relationships supported by preserved stomach contents.

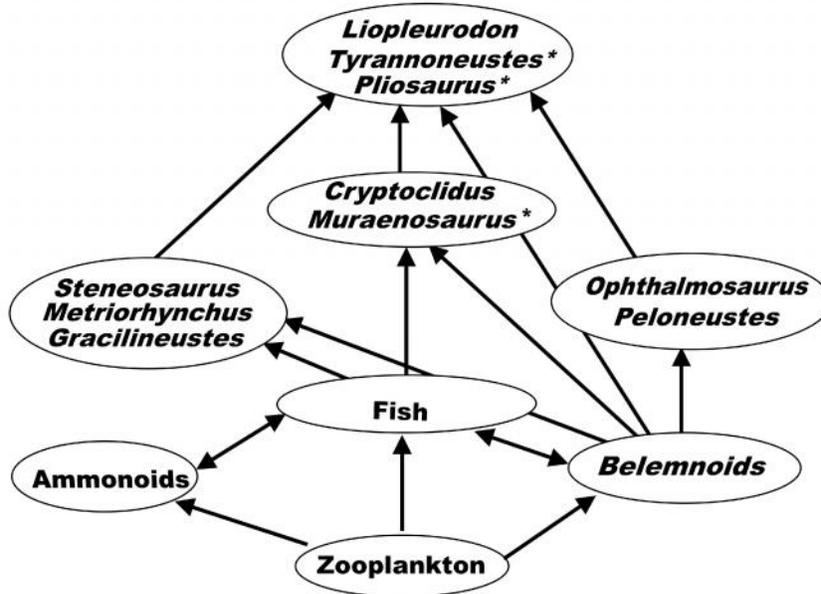


Figure 9: A simplified food web for the Peterborough Member of the Oxford Clay Formation, modified from Martill *et al.*, 1994. Unlike Figure 8, solid lines do not indicate relationships supported by preserved stomach contents. All relationships are inferred. Star indicates a rare taxon. Very rare taxa (e.g. *Simolestes*, *Pachycostasaurus*, *Marmornectes*) are omitted.

Supplemental Material Online

Table 1: Specimens from the Thirty-three Mile Road area from Alkalai Creek to Roughlock Hill, Natrona County, discovered and/or collected by the Tate Geological Museum, Casper. This is a fairly unbiased collection from approximately 1992-2000, during which time nearly everything that was found was collected and catalogued.

Specimen	Taxon	Preservation	Description
UW 2	ichthyosaur	float	limb elements and vertebral fragments
UW 3	<i>Pantosaurus</i>	float	distal propodial and limb fragments
UW 11586	ichthyosaur	float	limb fragments
UW 15936	<i>Ophthalmosaurus</i>	in situ	anterior articulated vertebral column
UW 15937	<i>Ophthalmosaurus</i>	in situ	partly articulated posterior skeleton
UW 15938	<i>Pantosaurus</i>	float	basioccipital, vertebra fragments
UW 15939	ichthyosaur	float	limb fragments
UW 15943	<i>Tatenectes</i>	in situ	articulated partial skeleton
UW 19686	<i>Ophthalmosaurus</i>	in situ	articulated vertebral column
UW 24212	ichthyosaur	float	a few phalanges
UW 24213	<i>Ophthalmosaurus</i>	float	fragments of large forefin
UW 24216	<i>Ophthalmosaurus</i>	in situ	skull and anterior articulated skeleton
UW 24217	plesiosaur	float	limb fragments
UW 24219	plesiosaur	float	limb fragments
UW 24229	plesiosaur	float	propodial fragment
UW 24230	plesiosaur	float	vertebra and epipodial
UW 24231	plesiosaur	float	propodial fragment
UW 24234	<i>Ophthalmosaurus</i>	?in situ	whole and partial vertebrae
UW 24235	<i>Ophthalmosaurus</i>	float	articulated vertebral column
UW 24236	plesiosaur	float	three fragments of propodial
UW 24237	<i>Ophthalmosaurus</i>	float	vertebral and limb fragments
UW 24238	<i>Megalneusaurus</i>	float	very large neural arch
UW 24239	plesiosaur	float	vertebral and limb fragments
UW 24240	plesiosaur	float	weathered limb fragments
UW 24241	<i>Ophthalmosaurus</i>	float	vertebral and limb fragments
UW 24243	plesiosaur	float	one limb fragment
UW 24244	plesiosaur	float	three limb fragments
UW 24246	ichthyosaur	float	limb elements
UW 24249	ichthyosaur	float	a few vertebrae and bone fragments
UW 24250	ichthyosaur	float	three limb fragments
UW 24252	ichthyosaur	float	a few vertebra
UW 24804	<i>Ophthalmosaurus</i>	in situ	partial skeleton, skull pieces
UW 34651	ichthyosaur	float	limb elements
UW 34652	<i>Pantosaurus</i>	float	humerus, radius

UW 34653	<i>Ophthalmosaurus</i>	in situ	articulated vertebral column, ribs
UW 34682	plesiosaur	float	unknown
UW 34684	ichthyosaur	float	rib and vertebra fragments
UW 34708	ichthyosaur	float	vertebral fragments
