

NEW MATERIAL FROM THE TYPE SPECIMEN OF *MEGALNEUSAURUS REX* (REPTILIA: SAUROPTERYGIA) FROM THE JURASSIC SUNDANCE FORMATION, WYOMING

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ABSTRACT

In 2008, an articulated distal forelimb of the type specimen of the large pliosauromorph *Megalneusaurus rex* (UW 4602) was discovered adjacent to the original excavation pit from which two hindlimbs had been collected in 1895. The new material includes six complete or partial carpals, four metacarpals, and nearly all of the phalanges. Although the new bones were damaged by weathering and gypsum crystal growth, the articulated arrangement of the bones is preserved. Important features include (1) broadly flared metacarpals that articulate proximally and distally with the adjacent metacarpals; (2) curved facets on phalanges that are concave proximally and convex distally; (3) laterally interlocking phalanges between digits I and II and between digits IV and V for the entire length of the outer digits; and (4) tightly articulated, interlocking phalanges among all digits distal to the 3rd phalanx. Examination of the material collected in 1895 indicates that a similar structure occurred on the hindlimb as well. The results of this arrangement are rigid, reinforced leading and trailing edges of the flipper, as well as a stiff distal end. During swimming, the limb moved as a rigid unit, with no flexibility at any articulation distal to the head of the propodial. The stiff flipper generated thrust by pushing backward and downward against the water during power stroke; and generated lift when the limb was rotated and moved forward and upward during the recovery stroke.

INTRODUCTION

In 1895, Wilbur Knight discovered the type specimen of *Megalneusaurus rex* (UW 4602; for institutional abbreviations see below), originally described as *Cimoliosaurus rex*, the only Jurassic pliosauromorph known from North America (Knight, 1895; Wahl et al., 2007). Knight collected a nearly complete, articulated limb including the propodial, most of which is presently on display at the Geological Museum, University of Wyoming. Material including cervical, dorsal, and caudal vertebrae, neural arches, a large portion of the limb girdle, and ribs were also reported in the paper which erected a new genus for the species (Knight, 1898). This material has since been lost. Knight (1898) did not mention nor figure the disarticulated second limb of the same specimen, which includes a complete set of epipodials, mesopodials, metapodials, and phalanges of the same individual, which is presently housed in the UW collections. Only two other specimens from Wyoming can be referred to *M. rex*: a weathered neural arch, collected as float from Natrona County (UW 24238), and a very weathered propodial fragment from Hot Springs County (WDC SS019). Neither specimen has been described in publications. Another specimen of *M. rex* comprising a partial propodial has been reported

from the Upper Jurassic Naknek Formation of Alaska (Weems and Blodgett, 1994).

In 1996, the excavation site of the type specimen of *Megalneusaurus rex* was relocated in the Gas Hills area of eastern Fremont County, WY (Wahl, *et al.*, 2007). The discovery revealed that UW 4602 is from the upper part of the Redwater Shale Member of the Sundance Formation, about 10 m below the Windy Hill Sandstone. The specimen is thus of Oxfordian age (Kvale, *et al.*, 2001). We report here on the discovery in 2008 of a third limb from the type specimen of *Megalneusaurus rex* (UW 4602).

Institutional Abbreviations—AMNH American Museum of Natural History, NY, U.S.A.; BMNH, British Museum of Natural History, London, U.K.; UW, University of Wyoming, Laramie, WY, U.S.A.; WDC, Wyoming Dinosaur Center, Big Horn Basin Foundation, Thermopolis, WY, U.S.A.;

MATERIAL

The new limb, which is missing the propodial and epipodials, is 106 cm long from the proximal edge of the intermedium to the distal end. The limb has five digits, with the first considerably shorter than the others. It is missing the metapodial and half of the first phalanx of digit V, but is otherwise fairly complete, but

poorly preserved. The most distal phalanges of digits II, III, IV, and V are not discernable as individual bones. Their proximal and distal ends may be inferred from slight ‘bumps’ in the brown, iron-rich matrix at the distal end of the limb. This matrix is distinct from that surrounding the limb, and we infer that it is derived from weathering of bone.

The history of the collection of UW 4602 is unusual (Wahl, *et al.*, 2007). Wilbur Knight (UW) had been in the field with a man named Stewart, who worked for E. D. Cope at the AMNH. Knight had left Stewart and was returning home when he discovered the specimen. He borrowed a wagon from a nearby rancher to take the specimen back to Laramie. He intended to return with more packing material and remove the rest of the bones, but before he could return, Stewart removed material that Knight had left behind and sent it to Cope at the AMNH (Wahl, *et al.*, 2007). We suspect that the third limb reported here had been exposed and reburied by either Knight or Stewart because we removed soil rather than *in situ* shale from the upper part of the specimen. Adjacent to the limb, shale was encountered at a shallower depth. Furthermore, the proximal limb elements were iron-stained and somewhat weathered, suggesting partial exposure, perhaps during the initial exploration of the site in 1895. In addition, after removing some of the soil, we found a broken phalanx that was missing its proximal end. The missing piece may have been collected by Knight or Stewart. At least one phalanx of UW 4602 in the UW collections was incorrectly assembled from pieces of phalanges of two different digits; thus some partial phalanges were collected in 1895. Likewise, an old nail, confidently dated to the late 1800’s, was found lying under the soil, directly on top and in contact with the elements of the new limb. This may have been accidentally dropped or intentionally left as a marker by someone expecting to return to the site.

The spoils pile from the original excavation, now reduced to a low mound, ringed the old pit. The new limb was found less than 2 m SE of the original excavation pit, with the proximal row of bones exposed at the surface. The limb was lying on its ventral surface along a bedding plane, with the long axis oriented almost N-S. It dipped into the ground at an angle of 10°–15°. A hard, irregularly cross-bedded sandstone was under and around the limb. It was about 8 cm thick under the limb and extended eastward beyond the limb, thickening to more than 20 cm. The sandstone did not occur on the west side of the limb. A similar sandstone lens is exposed on the side of the 1895 pit. We attribute its presence to the carcass acting as a baffle, causing eddies and scouring on the leeward side and collecting coarser sediments (Schafer, 1972). Stratigraphically above the limb was a dark gray shale, which was overlain by a thinly bedded, cross-bedded,

friable sandstone. A similar stratigraphy was exposed on the side of the old excavation pit.

The shallow depth of the *in situ* matrix was such that some bone surfaces were damaged by plant roots. Calcareous concretion filled some of the spaces between the limb elements. This matrix was free of cephalopod hooklets that were present in large amounts at the site (Wahl, *et al.*, 2007), possibly suggesting that the limb material had undergone some early diagenesis before the complete breakdown of the carcass. The underside of the flipper was covered with a layer of gypsum, and the articular facets of many phalanges and some of the bone surfaces have been destroyed by this crystal growth. Furthermore, space that had developed in the matrix during diagenesis was also filled with gypsum crystals. Several phalanges were stained a patchy, yellow-orange color on their surfaces because of contact with the iron-rich shale above.

TABLE 1. Measurements of individual bones of *Megalneusaurus rex* (UW 4602). All measurements in cm. Measurements and bone names of the 1895 specimens are those published by Knight (1898), although our assessment is that these specimens are hindlimbs. Note that the measurements of Knight (1898) are higher than those of the 2008 specimen described herein.

	cm	1895 specimen	2008 specimen
"ulnare"	length	9.5	5.0 ⁺ ?
	width	13.0	broken
"intermedium"	length	10.0	7.4
	width	14.0	11.5
"radiale"	length	8.5	7.5
	width	13.5	10.9

The *in situ* limb had a slight curvature to it, which we interpret as a posterior curvature, curving towards the old excavation pit where the two limbs were removed in 1895. Between the new limb and the old excavation pit is an area from which we have recovered numerous chunks of concretion containing cephalopod hooklets, including some very densely packed pieces. We interpret these pieces as stomach contents of *Megalneusaurus rex* (Wahl, *et al.*, 2007), as the preservation is similar to what has been reported for an ichthyosaur and other plesiosaurs from the Redwater Shale (Massare and Young, 2005; Wahl, 2006). The relative positions of the excavation pits and presumed stomach contents would suggest that the rear of the animal was towards the 1895 excavation pit. Thus based on the field relationships, the new discovery is most likely a forelimb.

Andrews (1913) and Tarlo (1960) indicated that the the hindlimb is larger than the forelimb for Upper Jurassic pliosaurids. More recently, O’Keefe and

Carrano (2005) suggested that all large pliosauromorphs probably had larger hindlimbs than forelimbs. Table 1 presents a comparison of individual bones, using measurements from Knight (1898) and our measurements of the new material. The new material is consistently smaller. We estimate that the new limb is approximately 15% smaller than Knight's material, further suggesting that the 2008 material is a forelimb. Knight originally described the 1895 material as a hindlimb in a brief preliminary report (Knight, 1895), but in a second, more detailed paper, he identified it as a forelimb (Knight, 1898). It now appears that his first identification was correct.

DESCRIPTION

Material Collected in 2008: Forelimb—The new limb is missing the humerus, radius, and ulna (Figure 1). From the shape of the proximal edges of the carpals, it appears that the radius articulated with both the radiale and the intermedium, whereas the ulna articulated mainly with the long, straight proximal end of the intermedium. The ulnare is broken, but was likely only half the width of the intermedium. A second row of carpals consists of three closely spaced polygonal bones (Figure 2).

Metacarpals II, III, and IV are broadly flared proximally and articulate with adjacent metacarpals (Figure 3). Although damaged, metacarpal I shows a short, shelf-like projection in contact with a projection on metacarpal II. This feature is preserved better in the 1895 hindlimb material and is figured below. Metacarpal V and the proximal end of the first phalanx of digit V are missing. Metacarpal V probably articulated with the ulnare as in other pliosauromorphs (Andrews, 1913, figs. 3, 6).

Digit I is the shortest, digits II and V are of nearly equal length, digit III is longer, and digit IV is the longest. The difference in lengths of digits II-V appears due to a variation in the size of the phalanges as well as in the number of phalanges (Table 2). The phalange count as preserved is I-5, II-8, III-9, IV-8, and V-8. Digit I is complete, although the distal phalanx is very poorly preserved. Only the proximal end of the eighth phalanx is present on digit II. The distal phalanges have been weathered to a dark brown powder possibly due to the accretion of iron-rich minerals or dissolution by plant roots. Irregularities in the brown matrix at the distal end suggest one additional phalanx in digits II, III and V, and two additional phalanges in digit IV. The 1895 hindlimbs may also be missing distal phalanges, but the relative lengths of the digits in the 2008 limb are consistent with the 1895 articulated hindlimb.

The phalanges have an hour-glass shape, and all are broken in the middle, narrowest portion of the shaft.

The articular facet between successive phalanges is a curved, sinuous surface (Figure 4), although gypsum crystal growth has damaged the ends of most phalanges of the new specimen. In three dimensions, the phalanges are irregularly concave proximally and irregularly convex distally. Thus it is possible to orient an isolated phalanx if the proximal and distal ends are well-preserved. These are not, however, ball and socket articulations; the facets are complexly curved and do not allow rotation between the bones. In addition, the cross-sectional shapes of the metacarpals and proximal phalanges vary from one digit to the next. These features are better preserved in the 1895 material and are discussed further below.

Metacarpal I is shorter than metacarpal II (Figure 3; Table 2). This causes an offset of the phalanges of digit I relative to digit II, such that the concave middle of the shaft on a phalanx fits around the contact between two phalanges on the adjacent digit (Figure 5). A similar offset occurs between digits IV and V. This produces tight, laterally interlocked phalanges on the leading and trailing edges of the flipper for the entire length of digits I and V. This is in contrast to the condition of the inner digits, where gaps occur between the shafts of the first two or three phalanges (Figure 1). The pattern of offset and interlocking phalanges is similar to the articulated hindlimb from 1895 on display at UW, but inexplicably not what is shown in Knight's (1898) reconstruction.

At the third phalanx of the three inner digits, differences in the accumulated length of the phalanges cause an offset such that the hour-glass shapes of phalanges on adjacent digits interlock (Figure 6). This is approximately the position on the limb where we infer that digit I ends. Distally the interlocking is tighter and separation between successive phalanges is reduced to no more than a 1 mm. The phalanges are all dorso-ventrally compressed and take on an oval cross-section.

Material Collected in 1895: Hindlimbs—An articulated hindlimb of UW 4602 collected in 1895 is on display at the Geological Museum at UW. It includes the tibia and fibula, but not the femur, and a nearly complete distal portion of the limb. The phalange count as mounted is I-5, II-9, III-9, IV-9, and V-8. The distal phalanges of digits II and IV are fragments only. Three phalanges on digit I have been reconstructed, but we were unable to examine the mount closely to determine if any other elements were casts or reconstructed. The mount shows the same interlocking pattern of phalanges that is preserved in the forelimb, in contrast to the published reconstruction (Knight, 1898). Because of this, we suspect that the mount is in its original articulated state rather than reconstructed, but we did not have access to the



FIGURE 1. UW 4602 *Megalneusaurus rex*. Forelimb of type specimen discovered in 2008, shown in ventral view. Scale bar = 30 cm.

specimen to confirm this. The second hindlimb of UW 4602 from 1895 is disarticulated and stored in the UW collections.

Knight (1898) indicated that the propodial was 99.1 cm long and figured it as a complete bone. No complete propodials are in the UW collections. Presently there are three pieces of propodial that do not now fit together. One piece is a trilobed head of a femur (Brown, 1981, fig. 176), with numerous holes on the surface, perhaps indicating a cartilagenous cap (Figure 7A, B). The propodial shaft cross-section is quadrate, although Knight (1898) described it as ‘prismatic’. A second piece is the well-preserved distal end of a propodial, which we also identify as a femur (Figure 8). The facets are concave and articulate with the convex surfaces of the tibia and fibula in the UW collections. A third fragment of propodial is from the distal end of the shaft, but is broken at both its distal and proximal ends (Figure 9). It is a smaller, more slender bone than the distal femur, and we suggest that it may be a portion of a humerus. Based on the orientation of the forelimb excavated in 2008, it is possible that the humerus, or a portion of it, was lying on or near the surface and could have been collected in 1895 by Knight or Stewart.

A feature noted by Knight (1898) but not described in detail, are interlocking projections on the tibia and fibula. The tibia has a bony projection on its medial margin that fits into a depression on the fibula at the proximal end of the medial margin (Figure 10; also see articulation in Figure 8). Distally, the fibula has a projection that fits into a depression on the tibia. Similar interlocking articulations occur between the tibia and fibula of *Peloneustes philarchus* (BMNH 2440) from the Oxford Clay of England (WRW pers. obs.). Andrews (1913, fig. 23) shows the articulation

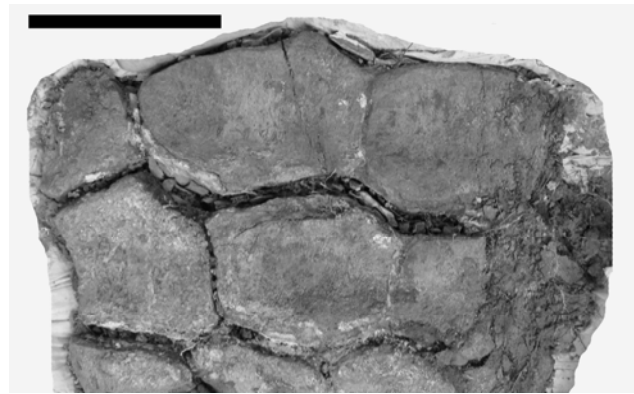


FIGURE 2. UW 4602 *Megalneusaurus rex* 2008 forelimb. Proximal end in ventral view, showing the articulated radiale (top right), intermedium, and partial ulnare (top left), as well as second row of three carpals (below), the first of which (lower right) is a fragment. Scale bar = 10 cm.

in a diagram, but he does not describe the projections and depressions.

Based on the articulated forelimb, we reconstructed the disarticulated hindlimb in the UW collection (Figure 11). The difference in size and cross-sectional shape of the metatarsals and phalanges allows the isolated bones to be put together in articulated positions with considerable confidence. Some phalanges had been broken at the narrowest portion of the shaft and reassembled. One was assembled from separate pieces of phalanges from different digits, as the proximal and distal ends have different cross-sectional shapes. When the bones are articulated, two proximal phalanges are “left over”. In addition, we have collected four badly weathered fragments of phalanges from the spoils pile

TABLE 2. Measurements of metacarpals and phalanges of 2008 material of *Megalneusaurus rex* (UW 4602). All measurements in cm. frag: only a fragment is preserved; pres: presence inferred from irregularities in the iron-rich brown matrix distal to previous element.

element	Digit I		Digit II		Digit III		Digit IV		Digit V	
	length cm	width cm	length cm	width cm	length cm	width cm	length cm	width cm	length cm	width cm
metacarpal	9.0	5.6	9.7	4.8	9.8	4.3	10.3	3.8	missing	
phalanx 1	7.7	3.5	9.0	3.4	10.1	3.3	10.2	3.3	frag	
phalanx 2	7.7	1.9	8.2	2.7	8.3	3.2	8.5	3.1	9.6	2.5
phalanx 3	6.9	1.7	8.0	2.6	8.3	2.6	8.8	2.7	9.0	2.0
phalanx 4	8.4	1.7	7.3	2.3	8.0	2.2	8.0	2.2	8.5	2.0
phalanx 5	frag		7.0	1.9	6.9	1.5	7.3	2.1	7.7	1.9
phalanx 6			6.3	1.9	5.6?		6.5	1.4	7.0	1.5
phalanx 7			5.6		5.0?		6.0		6.5	6.0?
phalanx 8			frag		frag		frag		frag	
phalanx 9			pres ?		pres		pres		pres ?	
phalanx 10					pres ?		pres ?			

surrounding the old pit. As neither hindlimb at UW appears to be missing proximal phalanges, this may be evidence that elements from more than two limbs were exposed and collected in 1895. Our reconstruction shows a gentle posterior curvature to the hindlimb, similar to that preserved in the forelimb and shown in the hindlimb on display at UW. The maximum width of the limb is located near the distal end of the femur (Figure 11). Some distal phalanges are missing.

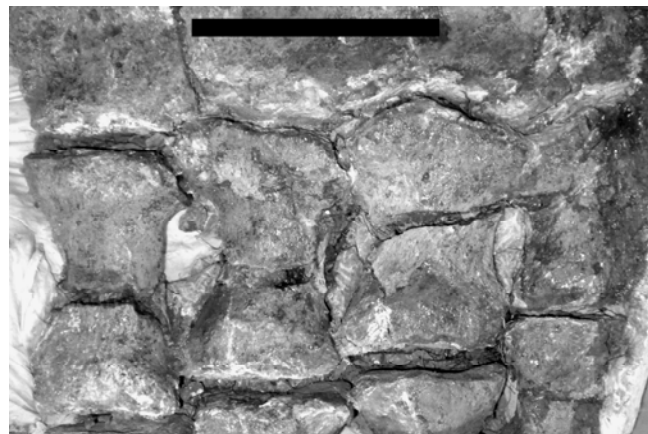


FIGURE 3. UW 4602 *Megalneusaurus rex* 2008 forelimb. Metacarpals I (left), II, III, and IV (left), illustrating the flared proximal ends that articulate with the adjacent metacarpal. Scale bar = 10cm.

The tarsals consist of six polygonal bones arranged in two rows, comparable to the forelimb. The tibiale and intermedium are wider than long, and articulate along a straight contact with the tibia and fibula. The

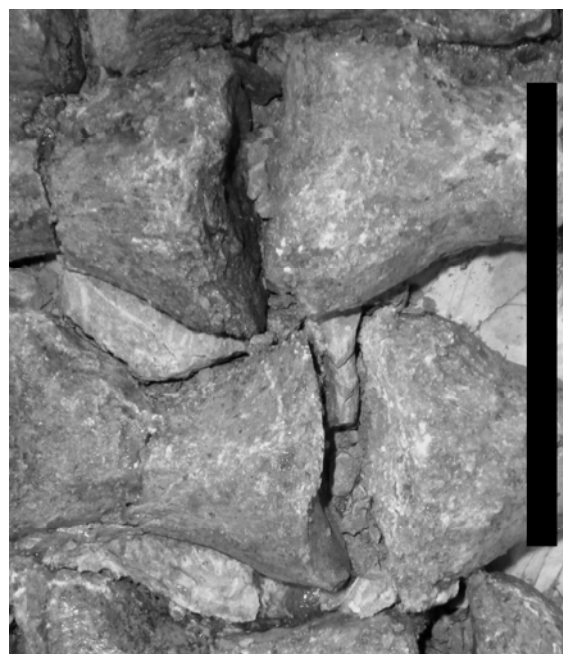


FIGURE 4. UW 4602 *Megalneusaurus rex* 2008 forelimb. Curved contact between successive phalanges, showing the convex distal end of one phalange (right) and concave distal end of the successive one (left). The distal ends of the right phalanges have been damaged by gypsum crystal growth. The proximal end of the flipper is to the right. Scale bar = 10 cm.

fibulare is longer than wide and articulates with a small facet on the trailing edge of the fibula. The second row of tarsals articulate tightly with the first. Their distal surfaces are convex and articulate with concave surfaces of metatarsals II, III, and IV. Metatarsal V

articulates with the fibulare, but the convex articular surface is on the metatarsal. Metatarsal I is smaller than the others and has a narrow, shelf-like projection that contacts the expanded proximal end of the metatarsal II (Figure 12). *Peloneustes philarchus* (BMNH 2440) also shows this feature (WRW pers. obs.), although it was not noted in Andrews (1913).

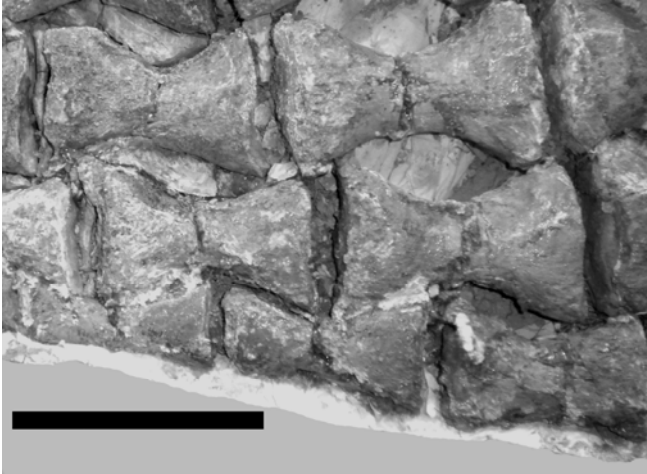


FIGURE 5. UW 4602 *Megalneusaurus rex* 2008 forelimb. Leading edge of forelimb, showing portion of digits I (bottom), II, and III (top). Note the tightly articulated phalanges of digits I and II, and the asymmetric shape of the phalanges of digit I. The proximal end of the flipper is to the right. Scale bar = 10 cm

Most of the phalanges have an hour-glass shape, and a few had been broken in the middle and reassembled. The pattern of an irregularly concave proximal facet and an irregularly convex distal facet continues for the at least the first three phalanges on digit II, III, and IV, similar to what is preserved on the new forelimb. Because metatarsal I is much shorter than metatarsal II, the phalanges of digits I and II are offset and interlock along their lateral margin as in the new forelimb. The phalanges of digit IV and digit V similarly interlock laterally because of the offset produced by the proximal shift of metatarsal V to articulate with the fibulare. Phalanges of digit V of the hindlimb are narrower and longer than those of the other digits, and some lack the pronounced hour-glass shape. They are also longer and narrower than those of digit V of the forelimb.

The metatarsals and phalanges vary in the cross-sectional shape at their proximal and distal ends (Figure 13). Digit I metatarsal and phalanges are triangular in cross-section, with the tapered end of the triangle towards the leading edge of the flipper. The cross-section is quadrate in digits II and III, triangular in digit IV, and oval in digit V, with the short axis oriented dorso-ventrally. When articulated as they

would have been in life, the resulting dorso-ventral cross-section of the flipper is a streamlined, hydrofoil shape (Figure 13). Similar differences in cross-sectional shapes of the digits occur on the forelimb, but the preservation is not as good. The articulation of the phalanges on adjacent digits form a convex upper (dorsal) surface and a slightly concave lower (ventral) surface to the flipper starting at the metapodial row. The ventral concavity becomes more pronounced distally, beginning at the 3th phalanx, where the hour-glass shaped phalanges of adjacent digits tightly interlock. Thus the limb as a whole had a slight ventral curvature and a hydrofoil shape in cross-section.

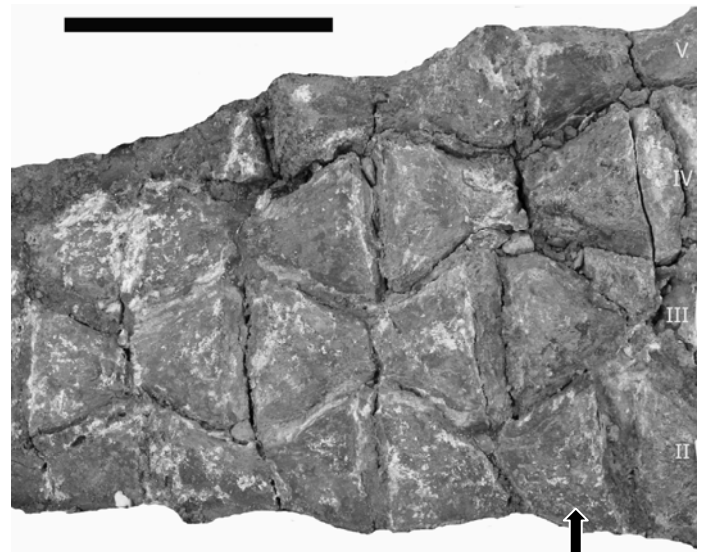


FIGURE 6. UW 4602 *Megalneusaurus rex* 2008 forelimb. Laterally interlocking hour-glass shaped phalanges of digit II (bottom), III, IV, and V (top). The proximal end of the flipper is to the right. The arrow indicates the proximal end of the fifth phalanx of digit II; above is the distal end of the fourth phalanx of digit III, above again is the fifth phalanx of digit IV, and above again is the distal end of the fourth phalanx of digit V. Scale bar = 10 cm

FUNCTIONAL SIGNIFICANCE

Based on the material collected in 2008, a new reconstruction of the distal forelimb of *Megalneusaurus rex* is presented here (Figure 14). The morphology of both the forelimbs and hindlimbs of *M. rex* show features that restrict movement between elements and reinforce the flipper as a whole. One such feature is the concavo-convex articulation of the tibia and fibula with the femur. Another is the proximal bony projection on the tibia that fit into a depression on the fibula (Figure 8). At their distal contact, a less prominent projection on the fibula fits into a slight depression in the tibia. Together these features reinforced and immobilize the

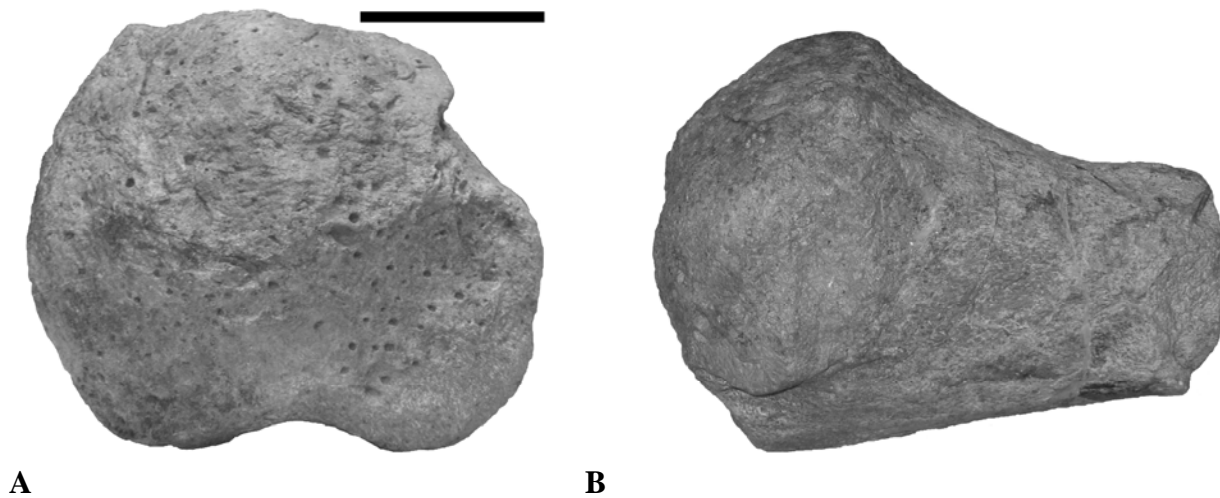


FIGURE 7. UW 4602 *Megalneusaurus rex* 1895 material. A. Proximal end of the head of the femur, collected by Knight. An outline is figured in Knight, 1895. B. Femur head in lateral view. Scale bar = 10cm.

articulation, preventing movement of elements in both the paraxial (forward and backward) and dorso-ventral (up and down) planes. The proximally flared, tightly articulated metapodials similarly prevent paraxial and dorso-ventral flexion (Figure 3). The sinuous articular facets of the phalanges (Figure 4) most likely prevented torsional rotation between successive phalanges and reduced flexion in the longitudinal plane. The laterally interlocking phalanges distal to the 3rd phalanx prevented paraxial movement of individual elements at the distal end of the limb.

The streamlined hydrofoil or blade shape of the limb was formed by the bony elements themselves, without the need of soft tissue to mold the skeleton into a hydrofoil shape. The tight packing of limb elements left little room for soft tissue between elements (Figs. 1-5). The wedge shaped cross-section of digits I and II, coupled with their tightly interlocking phalanges would prevent flexion in the dorso-ventral, paraxial, and longitudinal planes. This strengthened and stiffened the leading edge of the flipper. Similarly, the offset of phalanges and subsequent lateral interlocking of digits IV and V stiffened and strengthened the trailing edge. Distally, tightly interlocking, dorso-ventrally flattened phalanges formed a flat, rigid flipper. Thus every edge of the flipper meeting the resistance of the water was wedge shaped or flattened, with interlocking contacts of successive repeated shapes.

The cross-sectional shape is a hydrofoil, but from the first row of phalanges to the distal narrowing tip, the shape is also bow-like, with a slightly concave ventral surface. This concavity from the wedge-shaped

leading edge to the trailing edge is a by-product of the close packing of the elements (Figure 13). Such a slight 'cupping' or 'sculling' shape would reinforce the flipper against dorsal-ventral stresses.

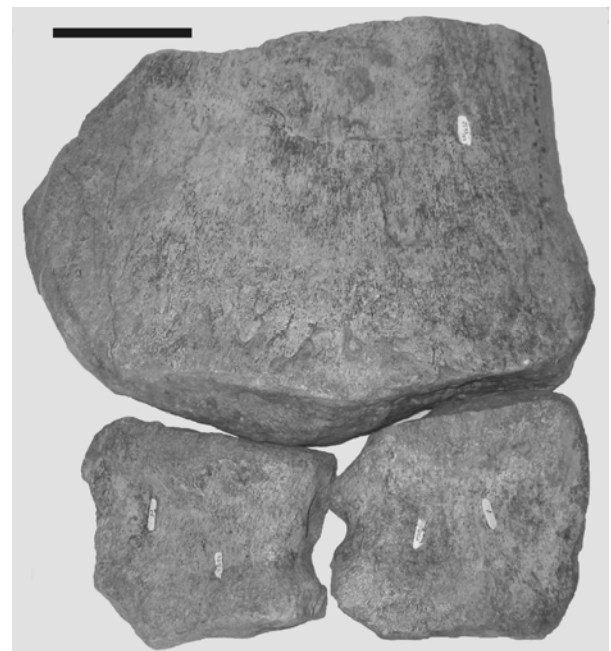


FIGURE 8. UW 4602 *Megalneusaurus rex* 1895 disarticulated material. Distal end of the femur shown articulated with tibia (right) and fibula (left) in ventral view. Scale bar = 10 cm.

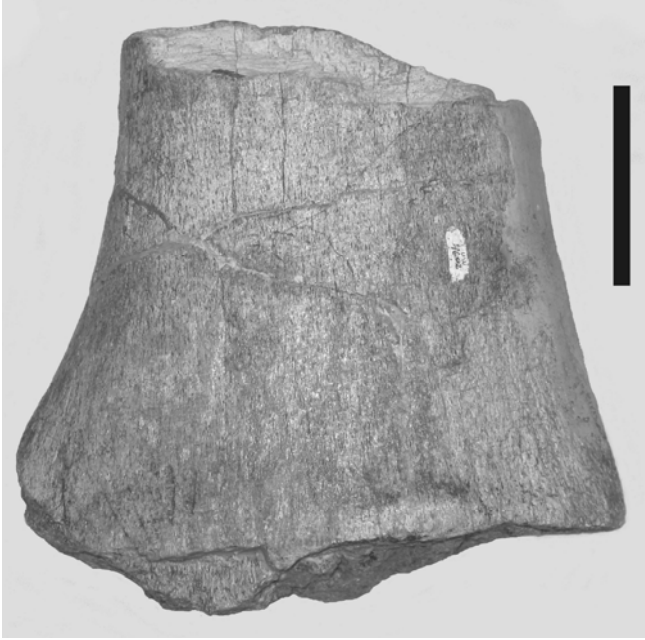


FIGURE 9. UW 4602 *Megalneusaurus rex* 1895 material. Fragment of (?)humerus. The bone is dorso-ventrally flattened, so is from the distal portion of the shaft. Scale bar = 10 cm.

Whether this flipper structure is typical of Jurassic pliosauromorphs remains to be seen, as articulated limbs preserved *in situ* are unusual. Tightly packed digits with phalanges in lateral contact has been reported in the Cretaceous pliosauromorph *Edgarosarus* (Druckenmiller, 2008, fig. 16). Two other Cretaceous pliosauromorphs, *Trinacromerum* and *Nichollssaura*, have tightly interlocking phalanges between adjacent digits, similar to *Megalneusaurus* (Adams, 1997; Druckenmiller and Russell, 2008; Druckenmiller, 2009). In addition, *Trinacromerum* has tongue and groove articulations that prevented movement at articular surfaces and stiffened the limb (Adams, 1997). Adams (1997) suggested that these features of *Trinacromerum* were adaptations for high speed swimming because they allowed the fin to lengthen (relative to body size) still maintain rigidity. In *Megalneusaurus*, the rigid flipper may likewise have been an adaptation for high speed swimming (see discussion of aspect ratio below), but it may have also been a scaling effect related to its large size.

The limbs of plesiosaurs have long been interpreted as functioning as ‘wings’ for underwater flight (Robinson, 1975; Godfrey, 1984; Reiss and Frey, 1991). Underwater flight *sensu stricto*, however, requires a figure-eight motion in a vertical plane, which was impossible in plesiosaurs because the limb could not be elevated above the horizontal (Tarsitano and Reiss, 1982; Godfrey, 1984). Instead, plesiosaur ‘flight’ comprised a backward and downward power

stroke that generated thrust, coupled with a forward, and presumably upward, recovery stroke that generated lift (Godfrey, 1984; Reiss and Frey, 1991). The construction of the limb of *Megalneusaurus rex* suggests that the limb was inflexible at every joint, and that it moved as a rigid unit from the articulation with the limb girdles. The stiffening of both the leading and trailing edges and the slight ventral curvature suggest that the power stroke of *Megalneusaurus rex* was drag-based, generating thrust by pushing against the water, consistent with earlier interpretations (Godfrey, 1984; Reiss and Frey, 1991). The streamlined cross-section and overall hydrofoil shape of the limb would have generated lift when the limb was rotated and moved forward in the water (Godfrey, 1984; Reiss and Frey, 1991). Movement of the neck and large head would have been necessary to keep the animal on a level course in the water. The locomotion of plesiosaurs was neither underwater flight nor rowing, but the limbs of *M. rex* show features advantageous to both modes. Plesiosaur locomotion, however, was unique among extant and extinct tetrapods, and a comprehensive analysis of the hydrodynamics has yet to be done.

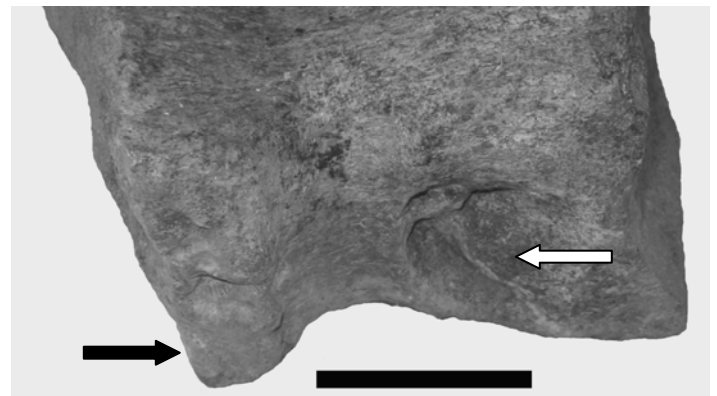


FIGURE 10. UW 4602 *Megalneusaurus rex* 1895 material. Medial edge of the fibula. (ventral view) with proximal end to the right, shows a depression (right arrow) into which a projection on the tibia fits, and a projection (left arrow) that fits into a depression on the tibia. Also note the articulation between the tibia and fibula in Fig. 7. Scale bar = 5 cm

The details of propulsion with two sets of identical limbs is not understood. Brown (1981) suggested that only the front flippers were used for propulsion, while the hind flippers were extended backward and held against the body. Recent experimental work by Long, *et al.* (2006), demonstrated that for flapping underwater flight at a steady cruising speed, using one pair of limbs is more efficient than two. Reiss and Frey



FIGURE 11. UW 4602 *Megalneusaurus rex* 1895 material. Individual flipper bones of the hindlimb in ventral view, shown in articulation, based on the morphology of the forelimb. Note the backward curvature and the interlocking phalanges on the leading and trailing edges of the limb. Scale = 30 cm.

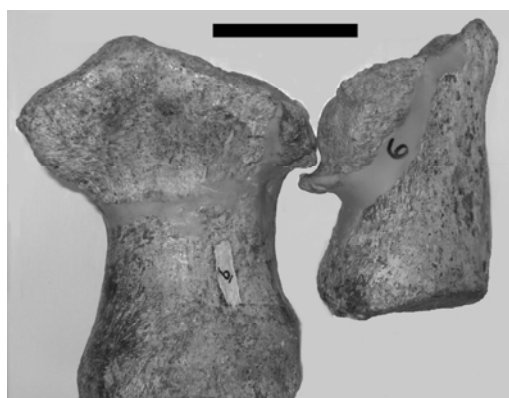


FIGURE 12. UW 4602 *Megalneusaurus rex* 1895 material. Disarticulated metatarsals of digits II (left) and I (right) show bony processes that articulated as show. Note that the shorter metatarsal of digit I would result in the phalanges of digit I being offset with respect to those of digit II. Scale bar = 5 cm.

(1991) argued that for a large animal that is not a true underwater flier, a rapid loss of momentum would occur during the recovery stroke. They suggested (Frey and Reiss, 1982; Frey and Reiss, 1991) that plesiosaurs moved their front and back pairs of limbs alternately, such that when one pair was in the power stroke the second pair was in the recovery stroke. Thus thrust generation would be continuous and the speed would not drop during the recovery phase (Frey and Reiss, 1982; Reiss and Frey, 1991). Fur seals and sea lions add a glide phase between the power stroke and recovery stroke in routine swimming (JM pers. obs.),

and this may have been another option for plesiosaurs. Any one of these gaits may have been employed for steady cruising. Long, *et al.* (2006) found that two pairs of limbs, moving in phase, were superior to one pair for rapid acceleration and quick stopping. Plesiosaurs likely employed different gaits for different swimming activities.

Knight (1898) measured the length of propodial as 99.1 cm and its distal width as 36.5 cm. The entire hindlimb of *Megalneusaurus rex* is 220.9 cm long (Knight, 1898). Using these measurements and the equation developed by O'Keefe (2001) would give an aspect ratio of 8.0 for the hindlimb. The aspect ratio of the forelimb is more difficult to estimate. From the piece of presumed humerus in the UW collection, we estimate that the distal humerus width was 85% that of the femur. The 2008 limb material is 106 cm long, but does not include the epipodials. Using these two measurements, the forelimb aspect ratio would be at least 8.2. If the length of an epipodial was included, this figure would be higher. These aspect ratios are within the typical pliosauiromorph range (O'Keefe, 2001; O'Keefe and Carrano, 2005). For comparison, *Liopleurodon*, a large pliosauiromorph from the Callovian stage Oxford Clay Formation, has an aspect ratio of 7.83 for the forelimb and 7.85 for the hindlimb (O'Keefe, 2001). O'Keefe (2001) interpreted this flipper shape as consistent with a high speed, maneuverable pursuit predator.

Cephalopod hooklets thought to be from UW 4602 suggest that belemnites were part of the diet of *Megalneusaurus rex*. Belemnites are by far the most common possible prey item in the Sundance

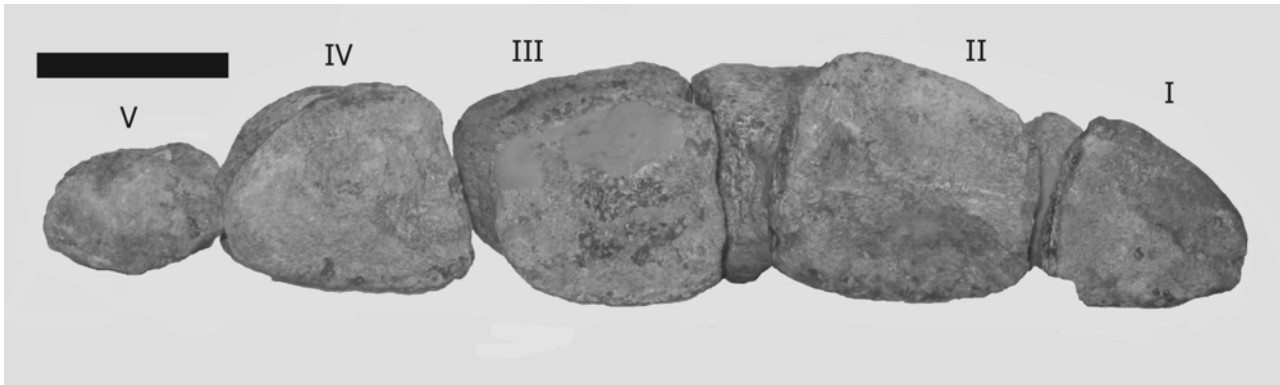


FIGURE 13. UW 4602 *Megalneusaurus rex* 1895 material. View of distal ends of the metatarsals in articulation positions, resting on their dorsal surfaces. Digit I, on the leading edge of the flipper, is to the right. The difference in cross-sectional shape also occurs in the proximal phalanges. The digit V metapodial (left) is offset proximally (into the page), as it would have been during life. Note the hydrofoil shaped cross-section. Scale bar = 5 cm.

F179ormation. Long distance cruising to locate shoals of belemnites may have been the hunting style of *M. rex*, and might explain why such a large predator was in the relatively shallow Sundance Sea. *M. rex*, however, was not as maneuverable as the cryptoclidid plesiosaurs (O’Keefe, 2001) or ophthalmosaurid ichthyosaurs (Massare *et al.*, 2006) with whom it shared the sea. It may therefore have had to rely on an ambush attack to capture these larger prey items, as suggested by the results of Long *et al.* (2006).

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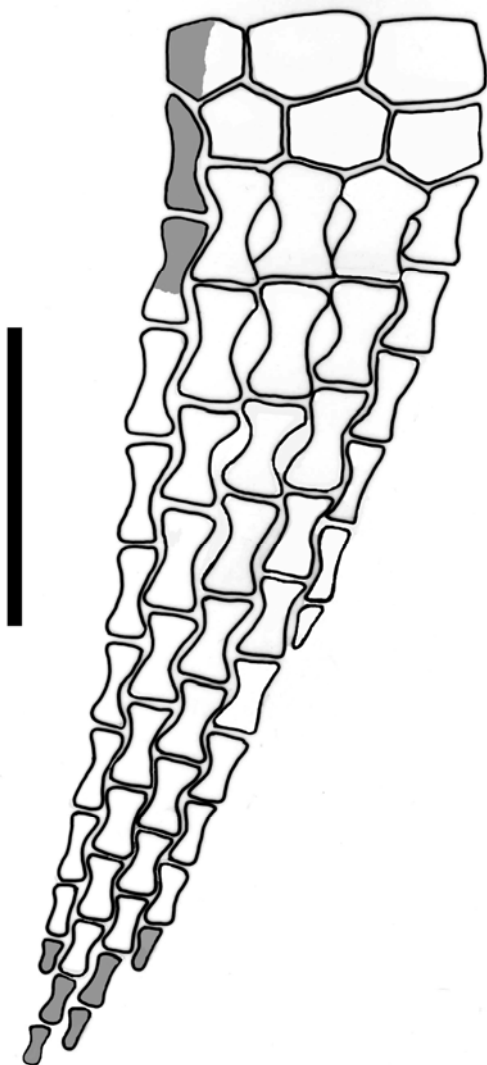


FIGURE 14: Reconstruction of distal forelimb, from carpals to distal phalanges, of *Megalneusaurus rex* (Knight, 1895), based on 2008 forelimb of the type specimen UW 4602. Shaded bones are conjectural. Scale bar = 30 cm

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