Spring 2011

An Allosaurus From The Morrison Formation (Late Jurassic) Of Converse County, Wyoming

Dennis D. Roth
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AN *ALLOSAURUS* FROM THE MORRISON FORMATION (LATE JURASSIC) OF
CONVERSE COUNTY, WYOMING

being

A Thesis Presented to the Graduate Faculty
of the Fort Hays State University in
Partial Fulfillment of the Requirements for
the Degree of Master of Science

by

**Dennis D. Roth**

B.S., Fort Hays State University

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GRADUATE COMMITTEE APPROVAL

The Graduate Committee of Dennis D. Roth approves this thesis as meeting partial fulfillment of the requirements for the Degree of Master of Science.

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Date ____________________________
ABSTRACT

I describe a partial skeleton of a theropod from the Later Jurassic Morrison Formation of Converse County, Wyoming. Collected material included 17 vertebrae, three ribs, two associated left metatarsals and an incomplete ilium of an *Allosaurus* in a gray silty-mudstone containing conchostraca. Several vertebrae are deformed with transverse processes broken and pressed against the neural spine, or twisted transverse processes from lateral or dorso-ventral compression. The material has evidence of erosion prior to deposition, as well as during postfossilization. I propose the deformation of the vertebrae is due to a demineralization of the bones. The flattened surfaces appear to have been exposed prior to deposition while residing in a low energy alkaline lacustrine environment; causing the vertebrae to become malleable and susceptible to deforming under their own weight. There is also evidence of interaction between two of the vertebrae, where one was resting on top of the other, causing the transverse processes to become twisted. Examination of the neurocentral sutures and length of metatarsal IV indicate this *Allosaurus* is a maturing sub-adult. This specimen represents the first documented occurrence of *Allosaurus* in Converse County and the third dinosaur documented from the property.
ACKNOWLEDGMENTS

This project was possible due to the support and comments from the following:
William Wahl for informing me of the specimen, Kate Banghard, Jordi Sunjuan Rubio, and Jeff McCoy for removal of the specimen from the quarry; the landowners (who wish to remain anonymous) for allowing me to continue work in the quarry during the summers of 2008-2010; Greg Wilson and the employees of the Wyoming Dinosaur Center for their help; the Big Horn Basin Fossil Foundation for allowing me the opportunity to work on the specimen; the Sternberg Museum of Natural History for space and tools for the preparation; Mike Calvello for discussions, help, and venting about our work; my advisers, professors, and committee members, Drs. Richard J. Zakrzewski, Greg H. Farley, Kenneth R. Neuhauser, and S. Christopher Bennett for their helpful “pressure,” and always getting me to think of the problem from another angle; and of course, my family and friends, who without their love and support, I would never have gone as far as I have.
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INTRODUCTION

The Morrison Formation is a widespread unit that was deposited in the Western Interior of North America during the Late Jurassic (Fig. 1). A clastic-wedge deposit, it is interpreted as an extensive floodplain with smaller lake and fluvial channels. It is one of the most well documented and studied fossil-bearing formations in the United States with studies ranging from biogeographic (Engelmann, 1999), paleohydrologic (Dunagan and Turner, 2004), paleoenvironmental (Turner and Peterson, 2004; Good, 2004; Parrish et al., 2004), paleoecologic (Engelmann et al., 2004; Hasiotis, 1998; Foster, 2003), and biodiversity (Chure et al., 2006).

WDC-DMP-002 (Wyoming Dinosaur Center) is a partial skeleton, mostly vertebrae, sacral material, several ribs, and two metatarsals of an *Allosaurus*. The material was collected during the field seasons of 2005 to 2010 in the southern portion of Converse County, Wyoming. WDC-DMP-002 was discovered in 2005 on private property with permission from the landowners, while work was continuing at the *Supersaurus vivinae* site, (WDC-DMJ-021; Lovelace, 2006). Members of the team prospected for other potential fossil sites on the property. Another site, approximately 300 m from the larger *Supersaurus* quarry, was discovered by tracing weathered fossil material from an eroded gully. The team's main concern was the excavation of the *Supersaurus*, however collected what they could from the new locality. Before the end of the season they had placed a field jacket over the material they could not remove.

Material recovered included fragmented sacral vertebrae, one mostly complete left
metatarsal IV, the proximal end of left metatarsal III, and sections of the left ilium of a large theropod dinosaur. These first collected pieces of WDC-DMP-002 show high amounts of post-fossilization weathering (Fig. 2) with the sacral material exhibiting the most weathering. WDC-DMP-002 is the first large theropod documented from Converse County, but the third dinosaur described from the same property. *Supersaurus vivinae* and an unnamed maniraptorian (WDC-DML-01, Wahl, 2006) also come from this property.

The remainder of the specimen would be removed three years later in the dig season of 2008 by a team from the Wyoming Dinosaur Center led by William Wahl. Inside the jacket were six vertebrae in a calcareous mudstone. After removal it was transported to the WDC before being brought to the Sternberg Museum of Natural History for further preparation in Fall 2008.

During the field season of 2009, three more vertebrae were discovered and removed from the site. These additional vertebrae were from the middle to posterior-most caudal section. In the 2010 season, another distal caudal vertebra was recovered from the quarry. The site has continued to produce more material with every season, prompting continual visits in subsequent years. Although the material consists mostly of vertebral elements, there is still the possibility for finding other skeletal remains as work continues.

**MATERIALS AND METHODS**

Only exposed fragmented material was originally collected in 2005. Based on
field notes from 2005 the field jacket was originally thought to cover only six vertebrae in sequence. After transporting WDC-DMP-002 to the Sternberg Museum of Natural History in Fall of 2008, preparation began using pneumatic air-scribes and a pocket knife to remove the specimen from the jacket. Individual bones of WDC-DMP-002 are numbered according to the order in which they were discovered and do not correlate with a vertebral sequence.

Photographs were taken during every stage of the preparation process, then combined into a composite image. Using this image and notes taken during the removal process, the specimen locations were reconstructed. An in depth look at this reconstruction method can be found in Roth (2010).

The number of vertebrae included in the jacket was nearly twice that originally reported. Field notes indicated there were six vertebrae within the jacket; however, a total of 11 vertebrae were recovered, including three cervical and nine caudal vertebrae.

There was a noticeable difference in the texture of the matrix around the specimen. The texture of the lower layer was calcareous and nodular in nature. It was resilient, and broke apart with conchoidal fracturing only when the air-scribe was used (Fig. 3). The upper layer was more friable and broke apart with little effort. This noticeable change in matrix texture may be due to exposure prior to being covered in the jacket.

Lastly, there are conchostraca, small pollypod crustaceans, found in the lower calcareous layer (Fig. 4). Work by Lucas and Kirkland (1998) suggests that the
conchostracans associated with the WDC-DMP-002 material are similar to the *Liostheria* found at the *Supersaurus* site (Lovelace, 2006). Conchostracans have a chitinous carapace similar to bivalves in appearance and their presence with the material suggests an alkaline lacustrine environment for the site.

**LOCALITY**

The Morrison Formation is exposed throughout the state and *Allosaurus* has been reported from several other locations (Fig. 5). *Allosaurus* is the most commonly encountered theropod in the Morrison; its geographic distribution is primarily in Wyoming, Colorado, and Utah, but specimens have also been reported from Montana, New Mexico, South Dakota, Oklahoma, and Portugal (Mateus, et al., 2006).

Lovelace (2006) described the geology and stratigraphy of the study area in some detail. My own measurements and field notes match his and therefore the same stratigraphy. The WDC-DMP-002 site is in a section of the Morrison Formation 21 m above the contact with the Sundance Formation, and 49 m below the contact with the Cloverly Formation (Fig. 6).

**DESCRIPTION**

**SAURISCHIA**

**THEROPODA**

**ALLOSAURIDAE**

*ALLOSAURUS* sp.

WDC-DMP-002 consists of three cervical, 12 caudal, and two fragmentary sacral
vertebrae, an incomplete left ilium, three incomplete ribs, and two left metatarsals (III and IV) of an *Allosaurus*. The vertebrae are dark red, possibly due to a high iron or phosphate concentration in the surrounding mudstone, whereas the sacral material is a cream-blue. The cream-blue is likely due to exposure after fossilization, whereas the dark red is the original color (pers. obs). The ilium shows both colors, and is primarily darker on the most posterior section, whereas the anterior section exhibits weathering.

The identification was based upon comparative morphology between WDC-DMP-002, *Allosaurus*, and *Ceratosaurus*, which are two common theropods found in the Morrison. The cervicals in both groups are opisthocoelous, however, the anterior centrum surface is flattened in *Ceratosaurus*, whereas it is more pronounced in *Allosaurus* (Fig. 7). The caudal vertebrae between the two groups differ in shape and nature of the ventral groove. The ventral groove is present in both *Ceratosaurus* and *Allosaurus*; however, the groove in *Ceratosaurus* caudal vertebrae is much deeper and wider (Fig. 8). *Allosaurus* vertebrae take on a pinched, hour-glass shape, whereas *Ceratosaurus* vertebrae are wider.

The metatarsals provide the best evidence for placing WDC-DMP-002 into *Allosaurus*. Metatarsals are fused at the astragulus-calcaneum articulation and WDC-DMP-002 shows no signs of fusion along the proximal articulation of metatarsals III and IV (Fig. 9)

Cervical Vertebrae

There are three cervical vertebrae associated with the specimen. The three are
separated, laterally and dorso-ventrally deformed, and were found in the eastern section of the quarry (Fig. 10). All three cervicals show a degree of compression, opisthocoelous centra, and pre-depositional weathering.

**WDC-DMP-002-02** – The left lateral transverse process is missing and there is evidence of weathering along the left side (Fig. 11). The articular processes of the ribs are present on both sides; the left is weathered, but mostly intact, the right sustained damage during removal from the plaster jacket. Directly dorsal to the articular process of the ribs are the pleurocoels. The left lateral pleurocoel is hidden due to the compression and erosion of that side, whereas the right lateral pleurocoel is well preserved. Shallow uniform grooves are noticeable along the sides of the centrum rim, a sign of possible muscle attachment.

The neural spine is stout when compared to analogous cervical vertebrae (Fig. 7). Although there is no obvious break along the neural spine, there is obvious weathering to the bone, suggesting that the decrease in height is due to predepositional weathering. Despite the degree of weathering, the pre- and postzygapophyses are complete, with wide surfaces for articulation with anterior and posterior vertebrae.

The vertebra is compressed laterally, showing distortion with a slight right lateral twist towards the far ventral portion of the centrum. The right lateral surface shows no obvious weathering. The transverse process sweeps posterioventrally, running from the prezygapophysis. There is no distortion in the right lateral pre- or postzygapophyses and transverse process.

The weathering on the left side is not extensive. There is erosion of the left
transverse process, the articular process of the rib, far left curve of the centrum, and distal most dorsal portion of the neural spine. I hypothesize that this is the fifth vertebra in the cervical sequence.

**WDC-DMP-002-03** - Considerably larger than the previous vertebra, this cervical is also not as laterally compressed, and the right portion has a large amount of evident weathering and distortion (Fig. 12). The left surface shows a more complete articular process for the rib, deep pleurocoel, and fossae under the pre- and postzygapophyses, with the transverse process swinging posterioventraly and longer than the previous vertebra. The neural spine is thinner and higher than WDC-DMP-002-03, however, it is missing the far ventral portion. Vertebra 03 follows in sequence with 02, and is cervical six.

Exhibiting a high degree of weathering, the right surface was flattened during predepositional events. The transverse process is broken and cemented close to the centrum within the matrix. The anterior section of the centrum shows extensive weathering and the pleurocoel is almost unrecognizable. There is also a degree of shearing (Fig. 12D), which has pulled the anterior section of the centrum at an angle to the medial plane of the vertebrae. The posterior section of the centrum does not show such a compression, suggesting that the anterior half of this vertebra was exposed at the surface.

**WDC-DMP-002-06** – Unfortunately, WDC-DMP-002-06 was one of the more damaged bones during preparation. Transport and removal of WDC-DMP-002-01, 02, 04, and 05
had put 06 through considerable stress. The neural canal walls and various parts of the
transverse processes, pre- and postzygapophyses were shattered into pieces too small to
be realistically fixed. However, the remaining material can still be useful.

The articular processes of the rib are mostly intact and do not appear to have been
damaged before preparation. Both pleurocoels are only deformed from the process that
compressed the vertebra and appear to be intact. The various fossae of the processes
cannot be determined, as much of that area is fragmented. Mostly intact, the
prezygapophyses are as wide as those in 02, though the length of the process is
incomplete. The most distal portion of the postzygapophyses is rounded, unlike 02 and
03.

The centrum is opisthocoelous and had been compressed dorsoventrally prior to
deposition. This compression is at an angle, where it almost looks like anterior-posterior
compression, as the anterior face and the posterior face are in very close proximity to
each other. The degree of dorsoventral compression can be seen in the posterior portion
of the centrum, which is deformed into a wide horizontal oval. The anterior portion of
the centrum, however, is not distorted in such a way and is more circular.

It appears as if the posterior-dorsal portion of the vertebra was exposed before
deposition. There is an eroded posterior portion of the neural spine and the left
postzygapophysis has a small break that is filled with matrix. The degree of compression
can also be seen when comparing the neural canal and the posterior keel to the previous
vertebrae (Fig. 13).
Due to the degree of deformation and structural damage to the specimen, placing it into the cervical sequence is difficult. In WDC-DMP-002-02 and 03, there are enough of the vertebrae that are undeformed to determine their placement in the cervical sequence. When considering WDC-DMP-002-06 and its placement, one can presume that because 02 and 03 are close within the sequence that 06 is relatively close and represents cervical 7. Their proximity in the quarry should be considered because both 03 and 06 were removed as a single section of the jacket during preparation. That section required extensive work to separate both vertebrae without increasing the damage to 06.

Sacral Vertebrae

The sacral region is highly fragmented and had the highest degree of postfossilization exposure. Fragments recovered nearby may belong to the ilium or the two sacral vertebrae associated with the specimen. Currently collected pieces are not enough to realistically complete either the ilium or the sacral vertebrae.

Caudal Vertebrae

The caudal vertebrae make up the largest section of the specimen. Out of 15 vertebrae recovered, 12 are from the caudal series. Several have some kind of deformity, from being flattened, to erosional surfaces along one side. Due to the high number of caudal vertebrae in theropod dinosaurs and the condition of several of these vertebrae, it is not possible to give an accurate sequence number for these remains. However, one can place them in specific regions.

For placing the vertebrae into relative sections of the tail, I establish an anterior-
most, middle, and posterior-most section of the tail. Characteristics of these sections are based on the nature of the neural spine, pre- and postzygapophyses, and angle of the transverse process relative to the centrum. Madsen (1976) mentioned such changes along the caudal sequence in *Allosaurus* (Fig. 14). Collectively, the caudal vertebrae all share the following characteristics; pinched hourglass shape when viewed ventrally, amphicoelous centra, and a shallow ventral groove.

The anterior-most section of the caudal sequence is characterized by high neural spines and wide transverse processes. The transverse processes have a posterior sweeping feature whereas the neural arch has not begun a posterior tilt and is higher than the distal edges of the transverse processes. In the mid-section the neural spine shows a posterior tilt and the transverse processes are reduced in size and pulled posteriorly to a higher degree than in the anterior-most section. The posterior-most vertebrae have a reduced neural spine with the dorsal edge below the transverse processes. Proportionally, the length of the centrum is three times the width of the vertebrae, with the pre- and postzygapophyses extending beyond the anterior and posterior faces of the centrum and articular faces rotated to a vertical position.

**WDC-DMP-002-01** – This vertebra has no evidence of deformation (Fig. 15). The neural spine is shortened, with evidence of weathering along the posterio-dorsal part. From the prezygapophyses, the neural spine sweeps backwards with the postzygapophyses merging with it. The inter-spinous ligament scar is well preserved at the anterior end and the posterior surface seems to have been weathered along with the
neural spine. Both transverse processes sweep posteriorly and dorsally, with the distal left lateral process broken.

The neural spine seems to sweep posteriorly from the prezygapophyses suggests that this vertebra is within the middle section of the caudal series. It shares close proximity with WDC-DMP-002-04, 07, 13, and 14 found the following year.

**WDC-DMP-002-04** – A vertebra from the middle section of the tail, there is little deformation, save for a slight lateral shear (Fig. 16). The neural spine inclines posteriorly, with a small process at the anterior surface before it curves back into the main portion. Weathering is evident along the postzygapophyses and very distal dorsal portion of the neural spine, whereas the prezygapophyses are well preserved. The anterior portion of the vertebra is well preserved, with missing fragments resulting from the recovery and preparation processes.

**WDC-DMP-002-05** – Highly deformed, this vertebra is missing the right transverse process, possibly lost when the jacket was removed from the quarry. The left process, however, has been broken near the centrum and pushed up against the neural spine (Fig. 17). Such a deformation was probably initiated by weathering and then the break filled in with sediment. The vertebra is extremely laterally compressed, missing part of the right anterior portion of the centrum, which is reshaped into a vertical ellipse.

**WDC-DMP-002-07** – Found in close proximity to vertebrae 04 and 05 (Fig. 18), 07 is deformed anterior-posteriorly, with the posterior section off of the median line. Other than this shift, there is no noticeable deformity in 07. The transverse processes extend
outward and slightly dorsally. There is a posterior swing of the neural spine, with a noticeable anterior protrusion before the spine, which has missing fragments.

The right transverse process is broken, the distal end is still encased in matrix with a portion of another transverse process. Fractured, partly broken, the left process is missing small portions and the far distal end.

**WDC-DMP-002-08** – Like 06, this vertebra suffered considerable damage during preparation and was sitting in proximity to 09. The centrum is broken into three pieces and the neural spine suffered several fractures (Fig. 19). The vertebrae shows an anterior-posterior shear, though not similar to 10 or 11. Of the transverse processes, the right process shows a ventral bend towards the distal edge and the distant left process has a slight dorsal bend. Although the neural spine is fragmented, the completed pieces show that the distal dorsal anterior end is broken to the left at a low angle. The break is matrix filled, suggesting that this feature is a product of predepositional weathering and breakage.

**WDC-DMP-002-09** – Other vertebrae have varying degrees of deformation associated with their position, 09 is no exception. The most striking deformation is a dramatic twisting of the transverse processes (Fig. 20). There are obvious breaks along the length of the transverse process, where it starts to twist. The left transverse process curves dorsally and is twisted to a high degree. The dorsal surface of this transverse process is intact, with small breaks due to preparation. In contrast, the ventral surface of this transverse process is broken and filled with matrix. Preparation of this vertebra
suggested that this break was caused post mortem.

The right transverse process is intact and twisted postero-ventrally. Although the degree of twisting is not as profound as in the left transverse process, there is a noticeable break filled with a mix of matrix and fragments. Ventrally there is more aggregated matrix in contact with the process and due to the nature of the specimen, additional matrix could not be removed.

The specimen is also broken and pieces are missing due to transport and preparation. The neural arch is short, has possible weathering along the ventral edge, and is tightly encased in the mudstone. Preparation, although precarious, did reveal the neural canal mostly intact and undeformed throughout despite such stress on the vertebra.

On the anterior surface of the centrum, was a thin wide bone, possibly a chevron (Fig. 21). There is evidence of predepositional weathering and erosion along the edges.

**WDC-DMP-002-10** – Unlike other vertebrae belonging to WDC-DMP-002, WDC-DMP-002-10 does not appear to have any weathering associated with it. The most distinctive feature, however, is a lateral shear (Fig. 22). This shear pulls the right surface posteriorly to a higher extreme than would be expected this early in the caudal sequence. The centrum resembles a soda can that was compressed at an angle, such deformation was noted by Jennings and Hasiotis (2006) in a sauropod caudal being crushed underfoot. This vertebra still retains the neural spine, both transverse processes, and pre-, and postzygapophysis, despite the compression.

Surface characteristics of this vertebra are difficult to see. Much of the surface
was covered by particles of matrix during preparation and glued trying to keep the bone together. There are multiple fractures running through the bone, further preparatory work was not undertaken due to the seeming fragility of this vertebra.

**WDC-DMP-002-11** – The final vertebra collected in the field jacket. Similar to 10, this vertebra is distorted with an anterior to posterior shear (Fig. 23). The right transverse process is mostly intact with the most distal edge missing. On the opposite side the left transverse process is broken at a right angle. Matrix has filled in around the break, mixing with fragments. This break occurred postdeposition, but before fossilization. The neural spine is also broken in a similar way and 70% is missing.

**WDC-DMP-002-12** – Discovered the summer after the field jacket was removed from the quarry, this vertebra is different from the others. It is much smaller, the transverse processes are reduced to small ridges that join with the prezygapophyses that are extended into long protrusions that run anterior-posteriorly (Fig. 24). The postzygapophyses are extended slightly posteriorly but are much smaller than the prezygapophyses (Fig. 24c). The characteristics of 12 place it in the posterior most portion of the caudal sequence.

Although the centrum is amphicoelous, there is a slight bulge present in the concavity at the posterior end of the centrum. This bulge may be a nodule of matrix, as it seems to be similar in texture, however, there is heavy mineralization through part of this nodule. This vertebra is one of the few that has no visible signs of distortion.

**WDC-DMP-002-13** – This vertebra is mostly complete, save for the distal portions of the
right transverse process and a posterior portion of the left transverse process. Like most other vertebrae, this one is deformed. However, it is deformed with a lateral shear (Fig. 25) with the ventral portion being sheared to the left. The right transverse process has been placed higher than the left. Along the ventral portion of the centrum is the small groove, however, it is difficult to see with the leftward distortion of the centrum.

Despite the distortion, the neural spine is unaffected, pulled back, with a small protrusion resting anterior. This characteristic of the neural spine is indicative of the mid-section of caudal vertebrae, placing this vertebra was along the mid part of the tail in WDC-DMP-002.

**WDC-DMP-002-14** – Also found during the field season of 2009, this vertebra is in the distal third section of the caudal sequence. Mostly complete, it is compressed dorso-ventrally (Fig. 26), giving the anterior section of the centrum a d-shape. The postzygapophyses are fragmented within the matrix, a result of predepositional weathering. A groove is noticeable along the ventral side.

**WDC-DMP-002-16** – During the summer of 2010, another vertebra was found at the quarry by a field crew from the WDC (Fig. 27). This vertebra is from the distal third section of the caudal sequence and is the most posterior of all the caudal vertebrae found thus far. The prezygapophyses are elongated far beyond the edge of the centrum, half the length, whereas the postzygapophyses are shorter and stouter. The vertebra has no visible deformation aside from the artifacts of preparation; however, there is evidence of an erosional surface along the anterior edge of the centrum.
Ribs

Three ribs have been recovered from the site. The first is a cervical rib collected when the specimen was found, it is an anterior cervical rib with a preserved capitulum, partial shaft, and surrounded in matrix (Fig. 128A). The second rib is another cervical rib that was against the centrum of one of the vertebrae and recovered within the field jacket. There is a possibility that it articulated with the right parapophysis of 03. The two cervical ribs (Fig. 28B), are incomplete. One of these ribs is still mostly encased in matrix, the other is mostly uncovered. Due to the fragile nature of these ribs, preparation work has not proceeded in order to protect the specimen.

Whereas the first two ribs are cervical, the third appears to belong to an anterior-most dorsal vertebra, approximately 85% complete (Fig. 28C) and is 27.0 cm long. There is a wide separation between the articular process and it is longer than the two cervical ribs. It was thought to be another vertebra when recovered from the quarry and was given the collection number WDC-DMP-002-15.

Pelvic Girdle

There is one large posterior portion of the ilium that has survived. Postfossilization weathering is noticeable along the median side of the ilium. The bone is from the left side of the animal and there is progressively severe weathering along the anterior portion. Pieces of the ilium and sacral vertebrae were the first pieces collected in 2005 and had greatly weathered (Fig. 29).

Ilium reconstruction indicates that it is broad and mostly flat, with a change in
thickness dorsoventrally. Such a difference in bone thickness may be a result of postfossilization weathering, because the anterior portion of the ilium is currently recovered only in fragments. The acetabulum is deep and shows weathering along the medial surface anteriorly, covering the ischiac peduncle. This weathering is more pronounced on the medial surface and noted on the lateral surface and on the two sacral vertebrae.

Metatarsals

There are two pieces of the appendicular skeleton represented in the material. Both pieces were found in 2005 when parts of the sacrum were collected and a field jacket placed over the rest of the specimen. These pieces are both left metatarsals.

The largest and most complete is metatarsal IV with a length of 28.1 cm (Fig. 30). The shaft is triangular, with a sharp ridge running from the proximal end down to the distal end. The far distal end has a small depression along one surface by the articulation point with the phalanges. The other metatarsal is the proximal articulation surface of metatarsal III, and is missing approximately 80% of the shaft (Fig. 31).

TAPHONOMY

One of the most unusual characteristics of WDC-DMP-002 is the deformation of the vertebrae. Transverse processes from several vertebrae are either missing, broken or were cemented against the neural spine, or the vertebra is flattened laterally with a heavily damaged side whereas the opposite one remains seemingly undamaged. There is an absence of any dorsal vertebrae, ribs, and very little limb material associated with
WDC-DMP-002; it is either destroyed or undiscovered as of yet.

The deformation of the vertebrae is puzzling. Suggestions for the deformation vary from genetic causation, pathologies, and even fault activity during the uplift and formation of the anticline south of Douglas, Wyoming where the property is located. Although these are interesting possibilities, I do not feel they are very plausible. Fault activity would have a similar shear effect on all the vertebrae present at the site, not just a few and there would be a noticeable orientation of that shear in all of the material. A pathology is also plausible, however, none of the vertebrae show evidence of regrowth around areas where the bone is damaged,. This is particularly apparent in 09, which is the most drastically deformed of the specimen elements. I doubt a genetic cause, because such an effect would not only affect one vertebra, but most, if not all, of the vertebrae in a similar manner. It is my interpretation that the deformation is due to the depositional environment in which the vertebrae were resting prior to being covered.

The environment at the quarry was a low-energy ephemeral lacustrine as evidenced by the fine-grained carbonate siltstone-mudstone and conchostraca at the site. Discovery of conchostraca during preparation as well as the carbonate nature of the matrix suggests that the environment was alkaline in nature. Behrensmeyer (1975) noted that bones that have had their hydroxyapatite and other minerals removed become malleable, and humid environments tend to demineralize bone.

The vertebrae of WDC-DMP-002 are deformed in varying ways, mostly by lateral or dorso-ventral compression. When the cervicals 02 and 03 are compared both have one
flattened lateral side and the opposite side undamaged. The flattened sides are articulated and do not match, with 02 having a flattened left side and 03 with a flattened area on the right side. Vertebrae 05 is extensively flattened laterally, more so than 03 and 02, with the broken transverse process resting against the neural spine. Specimens 10 and 11 are both laterally compressed, but with a slanted shear as both of their deformities.

When bones are exposed to the environment, there are different degrees of weathering that can affect them. When Behrensmeyer (1978) looked at the effects of weathering on bones, she noted that bones that had portions exposed to the environment weathered faster than those that were not, and many bones could have two different stages of weathering. The flattened sections of WDC-DMP-002 were weathered as exposed surfaces of the vertebrae lay in a shallow alkaline lacustrine environment.

To test this, vertebrae 01-14, and 16 were placed in their orientation in situ (Fig. 10). The flattened surfaces of the vertebrae, that had the distortions aligned with the surface facing up and the undeformed surfaces down (Fig. 32). The portions of the vertebrae exposed suggest that they were either fully or partially submerged.

Vertebrae 02 and 03 both have flattened areas but on opposite sides; the opposite side being undeformed. Vertebra 06 is flattened from a postero-dorsal to antero-ventral angle, and 05 has a extreme degree of lateral compression. The neural spine of 08 has a low angle break at the most distal dorsal portion and there is no similar feature on the rest of the vertebrae. This surface lines up with the flattened surface of other vertebrae and such an orientation is supported by the dorsal curving nature of the right transverse
process, suggesting that 08 was resting on its side with the neural spine exposed when the vertebra deformed under its own weight. Other vertebrae that exhibit this feature of being deformed while laying on the lateral side include 10, 11, and 13. Vertebrae 01, 04, 07, and 12 show evidence of resting on either a posterior or anterior centrum face with no lateral compression. Vertebra 16 was found laying on its side, however, there is no noticeable compression, but there is a weathered surface on the anterior edge of the centrum.

In situ, 08 and 09 were very closely associated. This close association would account for the unusual distortion found in the transverse processes of 09. This orientation had 08 resting on 09, the anterior centrum face of 08 cupping the left lateral transverse process of 09 almost precisely and the right transverse process was twisted around the left transverse process of 08. This relationship suggests that 08 was oriented on top or against 09, causing it to twist under the weight (Fig. 33). Because the vertebrae likely settled in an alkaline lacustrine environment, they were demineralized and softened, explaining the deformation of several of the vertebrae.

Contraction of the muscles after death would have caused the spine to curve back, from neck to tail. The classic death pose of many dinosaur finds shows that the tail and neck often curve dorsally (pers. obs), towards each other, which would explain the close association of cervical and caudal vertebrae of WDC-DMP-002. As the *Allosaurus* decomposed, the right side of the animal was most likely scavenged and transported away from the main body, leaving the remains exposed to the environment. This could explain
the absence of appendicular, thoracic, and pectoral material.

The Morrison environment is considered to have been analogous to a semi-arid savannah with seasonal rainfall. However, fossil invertebrates and plants can indicate local environments that are more humid than other geographic ranges (Engelmann et al., 2004). Conchoidal fracturing of the matrix and the presence of conchostraca suggest that the locality of WDC-DMP-002 was wetter than other Morrison deposits (Lovelace, pers comm).

There is evidence suggesting fluvial movement in the system. The caudal vertebrae are in close association with the three cervicals found at the site. Specimen 16 is a caudal vertebra from the most posterior section of the tail but lays at the eastern portion of the quarry, far removed from the other posterior-most caudal elements (Fig 10). Work by Lovelace (2006) mentions a river that flowed through the locality during the early deposition of the Morrison, migrated through the study site. There are intermittent crevasse splays suggesting periodic flooding associated with seasonal rainfall. Such flooding would be responsible for the movement of water within the WDC-DMP-002 locality, causing the vertebrae to be dispersed after the soft tissues had decomposed.

ONTOGENETIC AGE

In many reptiles, size is often correlated with age, therefore the size of the animal could be an indicator of age. This is not always accurate. Another indicator would be the closure of the neurocentral sutures of the vertebrae (Brochu, 1996). Brochu defined the
nature of the sutures as such; in an open suture the neural arch and centrum can be easily
separated, whereas the neurocentral suture is no longer visible in a closed suture. Of the
material vertebrae 02, 03, and 06 show signs of an open suture using this definition.
Vertebrae 01, 10, 11, 12, 13, 14, and 16 show a closed suture, and the remaining caudal
vertebrae show partial sutures.

Brochu (1996) used the closure of the neurocentral suture as an indicator of
maturity in extant archosaurs. The neurocentral suture closes in an posterior-anterior
pattern and presumed this would apply to extinct archosaurs as a basal trait. Irmis (2007)
disagreed, and suggested that the fusion of the suture is distinct across different taxa and
examined distinct groups of archosaurs and several species of theropods. _Allosaurus_
neurocentral sutures appeared to close from posterior to anterior. Some theropod
specimens seem to have anterior-posterior suture closure, such as _Nqwebasaurus_ and
_Eustreptospondylus oxoniensis_. Irmis found the pattern of neurocentral closure in non-
avian dinosaurs was ambiguous, suggesting more work focusing on this aspect of
dinosaur ontogeny.

WDC-DMP-002's age cannot be accurately determined with the vertebrae
currently recovered. The pattern of neurocentral suture closure suggests the specimen is
still maturing and could be a juvenile to sub-adult. Growth studies of _Allosaurus_ have
investigated the proportions of the hind limb materials, particularly the femur, tibia, and
fibula (Foster and Chure, 2006). WDC-DMP-002 is missing all of such hindlimb
material, with only a recovered metatarsal IV and broken III.
Foster and Chure (2006) looked at ratios between metatarsal IV, the tibia, fibula, and femur to distinguish the allometry of *Allosaurus* from juvenile to adult (Table 1). WDC-DMP-002 is missing most of the hindlimb material, however the lengths for metatarsal IV from their specimens were provided. Using that information, I plotted the length of the metatarsal IV from WDC-DMP-002 in comparison to their samples (Fig. 34).

WDC-DMP-002 plots close to the specimens MOR 3897, DINO 3984 and USNM 4734. MOR 3897 is a sub-adult from Wyoming, DINO 3984 is a sub-adult from Dinosaur National Monument, whereas USNM 4734 is an adult from the Marsh-Felch quarry. While this suggests that *Allosaurus* sub-adults would have metatarsal IV lengths between 300 to 250 mm, it is inconclusive. Proportions of the femur, tibia and fibula were plotted, not just metatarsal IV, and USNM 4734 plots closer with adult specimens than with sub-adults (Foster and Chure, 2006: Fig. 3-5). There is a distinct difference between juvenile, sub-adult, and adult specimens in the proportion of hindlimb elements, this is noted by Foster and Chure, suggesting that juveniles occupied a different ecological niche than did adults. Juveniles being more agile cursorial predators than the adults, hunting smaller, more agile prey. WDC-DMP-002 appears to be a sub-adult based upon the length of metatarsal IV. However, while there is a possibility it could represent an adult animal, without the rest of the hindlimb material, it cannot be conclusively stated.
CONCLUSIONS

WDC-DMP-002 is an interesting specimen represented vertebrae with very little appendicular material and evidence of pre- and postfossilization weathering. The lacustrine environment in which it rested was low energy and alkaline, with a shallow water table. Deformation of the vertebrae indicates a partly submerged orientation in the surrounding environment, demineralizing them, and deforming under their own weight. Several vertebrae show such demineralization, as well as weathering and exposure prior to deposition. Based on comparative anatomy, the size of metatarsal IV, and the pattern of the neurocentral closure, WDC-DMP-002 represents a still maturing sub-adult Allosaurus.
REFERENCES


TABLE 1
Length of Metatarsal IV of *Allosaurus* Specimens

<table>
<thead>
<tr>
<th>Specimen by Institution</th>
<th>Length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH 612</td>
<td>325</td>
</tr>
<tr>
<td>USNM 4734</td>
<td>275</td>
</tr>
<tr>
<td>AMNH 680</td>
<td>342</td>
</tr>
<tr>
<td>DINO 3984</td>
<td>254</td>
</tr>
<tr>
<td>MOR 693</td>
<td>286</td>
</tr>
<tr>
<td>MCZ 3897</td>
<td>159</td>
</tr>
<tr>
<td>SDSM 30510</td>
<td>148</td>
</tr>
<tr>
<td>WDC-DMP-002</td>
<td>281</td>
</tr>
</tbody>
</table>

FIGURE 1. Distribution of the Morrison Formation with reported *Allosaurus* localities (modified from Turner and Peterson 1999).
FIGURE 2. Post-fossilization exposure of fragmented pieces from the ilium (A-C) and the specimen just removed from the matrix (D) of WDC-DMP-002. A) exposed for the longest time, a cream-blue coloration with sections of the fragment eroded away. B) exposed but has not begun to deteriorate aside from previous exposure. C) still has the dark coloration associated with the material, with the discoloration on the far side. D) a piece of a transverse process that was broken during preparation, showing the dark red color. Scale bar is 10 cm.
FIGURE 3. Conchoidal fracturing in the lower matrix of the WDC-DMP-002 quarry.

Scale bar is 5 mm.
FIGURE 4. Examples of conchostraca found in the lower mudstone layer. Scale is in mm.
FIGURE 5. Wyoming with Converse County shaded in gray showing the location of WDC-DMP-002 and other known *Allosaurus* localities (modified from Turner and Peterson, 1999).
FIGURE 6: Stratigraphy of the study site, indicating where WDC-DMP-002 was found in Zone 1, along with WDC-DMJ-021 (Supersaurus vivinae), and WDC-DNL-01 (unamed maniraptoran) both found in Zone 2 (modified from Lovelace, 2006).
FIGURE 7. Comparative morphology of the cervical vertebrae of A) *Allosaurus* (modified from Madsen, 1976), B) *Ceratosaurus* (modified from Gilmore, 1920), and C) WDC-DMP-002-02. Scale bar is 10 cm.

Scale bar is 10 cm.
Sacral material excluded from reconstruction due to lack of collection information. Scale bar is 10 cm.
FIGURE 11. Cervical vertebra of WDC-DMP-002-02. A) right lateral, B) left lateral, C) posterior, and D) anterior views. Scale bar is 10 cm.
FIGURE 12. Cervical vertebra of WDC-DMP-002-03. A) left lateral, B) right lateral, C) posterior, and D) anterior views. Scale bar is 10 cm.
FIGURE 13. Cervical vertebra of WDC-DMP-002-06 showing posteriordorsal to anteriorventral compression and weathering surface on the posteriordorsal faces. A) right lateral, B) left lateral, C) posterior, and D) anterior faces. Scale bar is 10 cm.
FIGURE 14. Breakdown of the caudal sequence in *Allosaurus* showing the characteristics of the vertebrae. A) anterior most caudal (WDC-DMP-002-05), B) Mid caudal (WDC-DMP-002-07), and C) posterior most caudal (WDC-DMP-002-12). Image modified and used with the permission of Scott Hartman.
FIGURE 15. Caudal vertebra of WDC-DMP-002-01, showing A) right lateral, B) left lateral, C) anterior, and D) posterior surfaces. Scale bar is 10 cm.
FIGURE 16. Caudal vertebra of WDC-DMP-002-04 showing A) right lateral, B) left lateral, C) anterior and D) posterior views. Scale bar is 10 cm.
FIGURE 17. Caudal vertebra of WDC-DMP-002-05 showing A) right lateral, B) left lateral, C) anterior, and D) posterior views. Scale bar is 10 cm.
FIGURE 18. Caudal vertebra of WDC-DMP-002-07 showing A) right lateral, B) left lateral, C) posterior, and D) anterior views. Scale bar is 10 cm.
FIGURE 19. Caudal vertebra of WDC-DMP-002-08 showing A) right lateral, B) left lateral, C) posterior, and D) anterior views. Scale bar is 10 cm.
FIGURE 20. Caudal vertebra of WDC-DMP-002-09 showing A) right lateral, B) left lateral, C) posterior, and D) anterior views. Scale bar is 10 cm.
FIGURE 21. Bone found in the centra of WDC-DMP-009; fragment of a possible chevron. Scale bar is 10 cm.
FIGURE 22. Caudal vertebra of WDC-DMP-002-10 in A) right lateral, B) left lateral, C) posterior, and D) anterior views. Scale bar is 10 cm.
FIGURE 23. Caudal vertebra of WDC-DMP-002-11 showing A) right lateral, B) left lateral, C) posterior, and D) anterior views. Scale bar is 10 cm.
FIGURE 24. Caudal vertebra of WDC-DMP-002-12. Showing the A) left lateral, B) right lateral, C) posterior with nodule circled (see text for details), and D) anterior surfaces. Scale bar is 10 cm.
FIGURE 25. Caudal vertebra of WDC-DMP-002-13 showing A) left lateral, B) right lateral, C) anterior, and D) posterior views. Scale bar is 10 cm.
FIGURE 26. Caudal vertebra of WDC-DMP-002-14 showing A) right lateral, B) left lateral, C) posterior and D) anterior views. Scale bar is 10 cm.
FIGURE 27. Caudal vertebra of WDC-DMP-002-16 showing A) left lateral, B) right lateral, C) anterior, and D) posterior views. Scale bar is 10 cm.
FIGURE 28. The three ribs associated with WDC-DMP-002. A) found when the specimen was recovered and still encased in matrix, B) discovered during the main preparatory stage, and C) discovered in the field and originally believed to be another vertebra, given the collection number WDC-DMP-002-15. Scale bar is 10 cm.
FIGURE 29. Left ilium A) lateral surface, B) medial surface, and C) associated sacral vertebrae. Scale bar is 10 cm.
FIGURE 30. Metatarsal IV of WDC-DMP-002, A) posterior and B) anterior views.

Scale bar is 10 cm.
FIGURE 31. Proximal end of metatarsal III from WDC-DMP-002. Missing ~80% of the shaft. Scale bar is 10 cm.
FIGURE 32. Orientation of WDC-DMP-002 in situ. Flattened surfaces correspond to exposed surfaces while opposing sides remain intact, suggesting partial submersion.
FIGURE 33. The dynamics of WDC-DMP-002-08 (in blue) and 09 (in red). A) the specimen articulated in the position they were discovered in. B) artist rendering to show the two vertebrae intermingled. C) Side view of 08 laying on 09 and causing the transverse processes to twist as the vertebrae were demineralized. D) The final position of 08 and 09 as found in situ. Scale bar is 10 cm for A and B.
Metatarsal IV length of various *Allosaurus* specimens

![Graph showing size distribution of metatarsal IV of selected Allosaurus specimens](image)

**FIGURE 34.** Size distribution of the metatarsal IV of selected *Allosaurus*. WDC-DMP-002 (▲) plots along with two known sub-adults (♦) and a smaller adult (▼), known juveniles (■) are shown to plot below the mature animals. Abbreviations: AMNH, American Museum of Natural History, New York; DINO, Dinosaur National Monument, Jensen; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts; MOR, Museum of the Rockies, Bozeman, Montana; SDSM, South Dakota School of Mines and Technology, Rapid City, South Dakota; USNM, National Museum of Natural History, Washington, D.C; WDC, Wyoming Dinosaur Center, Thermopolis, Wyoming (modified from Foster and Chure, 2006).