

Megalosaurid Dinosaurs from the Late Jurassic Morrison Formation of Eastern Wyoming

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Abstract

The lower levels of the Morrison Formation of Wyoming have produced what may be some of the last known representatives of the Family Megalosauridae. *Edmarka rex* is one of the largest carnivores found so far at this level, and may have grown to the size of *T. rex*, up to 45 feet long and five tons body weight. At least one other megalosaurid has been found in the same quarry as *Edmarka rex*. Most of the skeletal parts recovered so far are from a second, allosaur sized megalosaurid.

This new animal has much stronger and shorter hind legs, relative to the body weight, than did the allosaurids, the most common contemporary large predators. This animal has similarities to the Morrison megalosaur, *Torvosaurus tanneri*, but differs in the pelvis, especially the ilium, which has advanced features approaching the condition seen in allosaurs and tyrannosaurs. The remains of this animal, some additional bones of a larger but presumed sub-adult *Edmarka* are described herein and compared to other theropods. In the Como Bluff area, megalosaurids may have been one of the earliest dinosaur families to disappear from the region since none have been found in higher levels of the Morrison.

INTRODUCTION

Megalosaurus bucklandi (see Owen, 1856), is the first carnivorous dinosaur discovered and one of the earliest dinosaurs to be named and described. All specimens that can be assigned with any confidence to the genus *Megalosaurus* date back 169 to 185 million years, to the Bathonian Epoch, the Middle Jurassic of England. Other fragments from the Middle Jurassic, found mainly in Europe, have been referred to *Megalosaurus* making it appear to have been the dominant predator of that age. However, by 1880, *Megalosaurus* had become a "dustbin" for any large theropod remains from the Jurassic or even Early Cretaceous (Norman, 1985). Part of the difficulty in deciding exactly what to include under the term "megalosaurid" comes from the incomplete nature of the type sample: The type specimen *M. bucklandi* is usually taken to be a fragmentary lower jaw from the Stonesfield Slate Quarries. From the same quarry and from quarries nearby came an ilium, sacrum, scapula, femur, tibia, and vertebrae from every part of the column attributed to *Megalosaurus*. However, none of these bones were found in natural articulation, and existing quarry records are not good enough to tell how many individual *Megalosaurus* are represented by these remains. Furthermore, there may well be more than one species of big carnivore mixed together in the Stonesfield quarries.

One articulated skeleton of a species close to **Megalosaurus** was found in the Middle Jurassic of Normandy - **Poekilopleuron bucklandi** - and this skeleton, fully described by Eudes-Deslongchamps (1838), helps to define the Family Megalosauridae (see discussion in Galton and Jensen, 1979).

In the 1880's and '90's European scholars often used "megalosaurid" to include the best-known large carnivores from the North American Late Jurassic Morrison Formation, **Ceratosaurus** and **Allosaurus**. This practice ceased about 1900, when nearly all paleontologists recognized the Family Allosauridae and the Family Ceratosauridae. One might conclude that the apparent absence of true megalosaurids in Morrison times was because the formation dates from last ten million years of the Jurassic, some 35-25 million years later than the classic European megalosaur localities. Therefore the megalosaurids, if not totally extinct, seem to have been displaced by allosaurids and ceratosaurids as the common top predators.

In this century, all large Morrison theropods have been referred either to allosaurids or ceratosaurids, prior to the discovery of **Torvosaurus tanneri** in western Colorado in the 1970's (Galton and Jensen, 1979; Britt, 1991). Galton and Jensen showed that **T. tanneri** shared with **Poekilopleuron** an unusually short forearm, wrist and fingers. Most paleontologists have accepted Galton and Jensen's decision to place **T. tanneri** in the Megalosauridae.

Animals from the Middle to Upper Jurassic of China have also been referred to megalosaurids. **Yangchuanosaurus hepingensis** (Gao, 1992) was thus referred. Currie and Zhao (1993) have since suggested the animal should be renamed **Sinraptor hepingensis** and that it and **Sinraptor dongi** are members of a new genus **Sinraptor**. An earlier theropod from the Middle Jurassic of China, **Gasosaurus constructus**, has also been referred to megalosaurid (Dong and Tang, 1985). This animal has a very different pelvic structure from that of **T. tanneri** and the animals described here.

In the past five years, more material referable to **Megalosaurus** has been found in three southeast Wyoming quarries in the Morrison Formation. A new large theropod, **Edmarka rex** was previously defined from some of this material (Bakker et al, 1992). **Edmarka** was assigned to the Megalosauridae because the left scapula found at Nail Quarry resembled that of megalosaurs from Stonesfield: the scapular blade was wide, had an unexpanded upper end and a slight expansion midway up the shaft, while the coracoid had an evenly rounded posterior end in lateral view. The jugal attributed to **Edmarka** differs from **T. tanneri** in shape and thickness (Bakker, et al. 1992). It is normal in that it is thin side-to-side rather than thickened to the enormous degree seen in **T. tanneri**. Since the adult ribs and jugal are as large as those of adult **Tyrannosaurus rex**, the animal could be as much as 45 feet long with a live weight of three to five tons.

The discoveries of **Torvosaurus** and now **Edmarka**, thought to represent as many as nine individuals from four quarries, suggest that the megalosaurids may have been more common in the Morrison than previously suspected. This paper describes the additional material recovered from Nail quarry in 1993 through 1996 and identified as megalosaurid. Most of this material probably refers to the same animal as the small coracoid TATE 0012-11 (formerly CPS 1003, Bakker et al., 1992) and first assumed to be that of a sub-adult **Edmarka**. In 1993 and '94, new material assigned to a megalosaurid included five caudal vertebrae, a chevron, a sacrum, a right coracoid matching TATE 0012-11, a right scapula, both ilia and femora, a left tibia and fibula, a right pubis and ischium and a number of ribs. Most of the new material has been assigned to TATE 0012. A left pubis and ischium of a larger megalosaurid was found amongst these bones. The 1995 digging season produced an atlas and axis assigned to TATE 0012. However, the axis and atlas could belong to a sub-adult **Edmarka**. In the 1996 season, six more caudal vertebrae and five chevrons attributed to TATE 0012 were found. A small theropod right ilium was found nearby that is not clearly allosaurid but is quite different from those of TATE 0012 also.

The relative locations of most of the Nail Quarry finds are mapped in Figure 1. Theropod ribs and rib fragments are not shown. A few small parts of other animals were scattered among the megalosaur parts. The bone bed has not yet been excavated to the floor in this area of the quarry. Number 9 and 18 are the left pubis and partial ischium of a larger megalosaurid. This pubis is 30 % longer than the right pubis and gracile compared to it. The size difference alone means that it is something other than TATE 0012 even though it is from the opposite side. Number 13 has been tentatively identified as a sternal plate of a sub-adult diplodocus. The vertebrae and chevrons found in 1996 were within 1.5 m of the sacrum. The recovery of three megalosaurid coracoids assures that there are the remains of at least two animals in the quarry.

The **Edmarka** scap-coracoid reported by Bakker et al. (1992) was found about 3.5 m northeast of the ilium of figure 1 and the coracoid and jugal, TATE 1003 and 1005 respectively, were found about 3.5 m east. The

posterior caudal vertebra referred to TATE 0012 was found about 8.5 m west-southwest of the sacrum. The small ilium was unearthed approximately 3 m northwest of the sacrum of TATE 0012. The axis and atlas were found about 8 m west of the sacrum.

Much of the material referred to TATE 0012 was localized, some to the point of being nearly articulated. For example, the ilia lay parallel to each other while the sacrum lay as if it were just pushed out from between them in the dorsal direction. The first caudal vertebra lay directly behind the sacrum. The right pubis and ischium were adjacent and beneath the transverse process of this vertebra. Vertebrae # 8 and 9 were articulated. Number 7 was adjacent to #8 but flipped 180 degrees.

In addition to the megalosaurids, at least three allosaurids are present in the quarry as indicated by pubae and ischia so far recovered. This collection makes the Nail quarry population about half large predators. This paper describes the bones found and assigned to megalosaurs since those described by Bakker et al. (1992) and compares them to other theropods.

TATE 0012

Provenance: Middle to Late Tithonian, Late Jurassic, Morrison Formation of the Como Ridge Anticline. The quarry is located in Southeastern Wyoming near the SE corner of the NW Quarter of the SW Quadrant of Section 1 of Township 22 N Range 77 W.

DESCRIPTION OF NEW MATERIAL

TATE 0012

No skull parts found so far have been assigned to TATE 0012. The recently discovered atlas and an axis are the only pre-sacral vertebral parts so far assigned to TATE 0012. The existence of a scapula and a pair of coracoids are a hopeful sign that dorsal vertebrae and forelimb material will be recovered. Much more work remains to finish the excavation just in the area from which most of the bones described here were recovered.

Vertebral Column

In the 1995 digging season, an axis and atlas judged to be theropod were uncovered. The atlas was found within a meter of the axis and they articulate well enough to suggest that they most likely belong to the same animal. Their size is compatible with TATE 0012 and they have been tentatively so assigned. The two were found west of the region shown in figure 1, in the vicinity of the most distal caudal attributed to TATE 0012. The axis was located less than a meter north of the distal caudal or about 7.8 m west and somewhat south of the sacrum. The axis, located about 8.2 m west of the sacrum of figure 1, was less than a meter northwest of the axis.

Atlas (Fig. 2)

The atlas shown in figure 2 has a squarish cross section viewed axially, like the other Jurassic theropods. The neurapophyses are fused to it though the sutures are still discernible. The neurapophyses close anteriorly but do not meet at the centerline. The posterior ventral edge of the atlas has facets for the attachment of cervical ribs. The anterior face of the atlas is 80 mm in width and approximately 75 mm in height. The overall dorso-ventral height is 130 mm. Its centrum centerline length is 60 mm. The anterior rim of the clearance for the odontoid has a distinct V-shape, viewed axially, in contrast to the others which are circular.

The neurapophyses of *T. tanneri* (Britt, 1991) are likewise fused to the atlas. The neurapophyses are not fused to the atlantal intercentrum in three other large late Jurassic theropods for which the atlas is known, *Allosaurus fragilis* (Gilmore, 1920), *Sinraptor dongi* (Currie and Zhao, 1993) and apparently not in *Ceratosaurus* (Gilmore, 1920) though he does not say this explicitly nor does he figure them separated from the intercentrum. He describes the suture surfaces, however, which indicates the neurapophyses are separate. It is not noted whether rib facets are present on the atlas of *T. tanneri*. Of the three other upper Jurassic theropods above and TATE 0012, only *Allosaurus* lacks the rib facets on the atlas.

The atlas of figure 2 is 1.5 to 2 times longer relative to its width than those of the other four contemporary theropods above. The posterior extension of the neurapophyses is greater than that of *T. tanneri* if the one shown is complete and the postzygapophyses seen to face more directly ventrally. The neurapophyses of the atlas of figure 2 only extend very slightly posterior to the posterior of the centrum where those of the other three theropods above have extensions well posterior. The neurapophyses in figure 2 are more L-shaped in lateral view like those of *Ceratosaurus* than triangular like those of *Allosaurus* and *Sinraptor dongi*. Though the atlas of figure 2 is similar to that of *Ceratosaur* there are several differences. The neural canal, figure 2, has a much larger opening relative to that for the odontoid. The posterior extension of the neurapophyses is much less, the intercentrum length relative to its width is greater and the rib facets more prominent.

Since the quarry also contains fossils of several sauropods of modest size, it is a possibility that the atlas could belong to one of them. The atlas of sauropods are not often recovered judging from the few descriptions in the literature. Marsh (1896) figures the atlas of *Diplodocus longus*. The neurapophyses are fused to the intercentrum and the atlas in axial view is very nearly circular. The atlas of *Apatosaurus louisæ* (Gilmore, 1936) was recovered also. It is tightly fused to the axis which is apparently not typical for sauropods. This fusion may be due to an injury. The atlas of figure 2 differs from those assigned to sauropods.

Axis (Fig. 2)

The centrum of the axis is approximately 150 mm long at the centerline including the odontoid which is fused to the centrum. The suture between the axis and the axial intercentrum is not visible. The posterior cup is 75 mm in height and 80 mm in width. The height from the ventral edge of the cup to the top of the neural spine is 220 mm. The greatest lateral width, at the postzygapophyses, is 125 mm. The axial centrum has large pleurocoels. The width of the middle of the centrum on the ventral side of these pleurocoels is quite narrow, 30 mm. The anterior face of the axial intercentrum angles dorsally with respect to the centrum centerline. The postzygapophyses are separated from the neural spine by deep notches. The cervical ribs did not fuse to the axis. The diapophyses and parapophyses suggest that the cervical rib appear to have retained flexibility at the attachment points throughout life.

The only sauropod with an axis with any similarity axis is that of *Camarasaurus supremus* (Osborn and Mook, 1921). It has similarly large pleurocoels. However, the neural spine differs from that of *C. supremus* (Osborn and Mook, 1921). The postzygapophyses of the figure 2 axis separate more from the neural spine and are placed posterior to the plane defined by the rim of the posterior cup of the centrum. The diapophyses extend laterally farther and extent down and not posterior like those of *C. supremus*. The neural spine of *C. supremus* appears to have a central stiffening rib down the posterior side that the axis of figure 2 does not. The neural arch of *C. supremus* has a wider and squarer neural spine than that of figure 2, a more anteriorly extended odontoid, lacks the cup on the anterior end of the axis and the keel on the ventral surface of the centrum (Ostrom and McIntosh, 1966). The zygapophthial articulation between the axis and atlas appears strong rather than weak like the articulation noted for *C. supremus*.

The axis, which is the correct size to be TATE 0012, has features in common with both allosaurids and *Ceratosaurus* but also differs in several details from both and other known Jurassic theropods. The proportions appear to be closer to those of the contemporary large theropods *Allosaurus* (Madsen, 1976; Gilmore, 1920) and *Ceratosaurus nasicornis* (Gilmore, 1920). Both the figure 2 axis and that of *C. nasicornis* have large, open pleurocoels. According to Currie and Zhao (1993) the Jurassic theropods, with the exception of *Syntarsus* and *Dilophosaurus*, all have pleurocoels but with small openings into them. The axial intercentrum is fused so completely to the axis of figure 2 and *C. nasicornis* that the suture is invisible. The axial intercentrum of *Allosaur*, *Sinraptor* and apparently for *Piatnitzkysaurus* do not fuse but remain visible. The axis of figure 2 is keeled though less strongly than that of *Ceratosaurus*. The axis of *Carnotaurus*, *Syntarsus* and *Dilophosaurus* are also keeled according to Currie and Zhao (1993). The posterior cup of axis of the centrum of both figure 2 and *C. nasicornis* angles up dorsally with respect to the centrum axis. This also occurs for *Yangchuanosaurus* and *Carnotaurus* again according to Currie and Zhao (1993). The posterior cup of *Allosaurus* is perpendicular to the axis. The anterior part of the neural spine of the axis in figure 2 is thin laterally. That of *C. nasicornis* is somewhat thicker. That of *Allosaurus* is even thicker.

The neural arch of the axis of figure 2, like *Allosaur* has the postzygapophyses extending out laterally from the neural spine with the narrowed spine extending above. The postzygapophyses of *Ceratosaurus* do not

separate from the neural spine. Like the axis of *Allosaurus* (Madsen, 1976) the epiphyses are almost indistinguishable from the postzygapophyses of the figure 2 axis. The figure 2 axis is more lightly constructed than those of *Allosaurus* and *Ceratosaurus*, the ventral center of the centrum is more pinched laterally. The neural spine of the axis of figure 2 is also narrower laterally. The diapophyses, in contrast, appear to be more robust and extend out farther laterally. As a result, the anterior end of the figure 2 axis appears to be as wide laterally on the anterior end as it is on the posterior end in dorsal view.

Sacrum (Fig. 3)

The sacrum from Nail Quarry is well preserved with only slight post-depositional distortion. It lacks the right sacral rib and transverse process from the 5th sacral, which had been broken off against the right ilium, and the upper ends of the neural spines, which extended into the weathered zone at the surface of the quarry and had weathered away. The 5th neural arch has been somewhat crushed dorso-ventrally partially closing the neural canal. The sediments at Nail Quarry are fine grained mudstone rich in expanding clays; many bones are undistorted, but some elements show plastic flow that occurred when the overlying strata compressed the clays. The portion of the sacrum above the transverse processes has not been illustrated in figure 3 because it still remains in the jacket. The jacket still covers the neural spines and dorsal surfaces of the transverse processes.

The contacts between the sacral centra are tight and apparently completely fused with the possible exception of the joint between the 1st and 2nd. The contacts between the centra and the neural arches appear to be fused as well.

The first sacral vertebra centrum is approximately circular in cross section overall but has a very faint keel on the ventral side. This keel probably marks the attachment of the right and left halves of the **longus** muscle, which runs underneath the centra along nearly the entire vertebral column, from the neck to near the tail tip. The front face of the centrum angles downward from the vertical at about 16 degrees. Centrum dimensions are given in Table I.

The 2nd sacral centrum is so compressed laterally that its height at its center is twice the width (Table I). The mid centra of sacra 3 and 4 are successively less compressed laterally. The centrum of the 5th sacral is nearly round again with a faint keel; its posterior face is tilted upward about 8 degrees from the centerline of the centrum axis and is mostly flat. However, there is a pronounced depression, just below the neural canal, about 10 mm deep at the maximum depth and approximately 50 mm in diameter; the first caudal centrum has a corresponding bulge to fit into this depression. The fit appears to be tight suggesting that little movement occurred between these vertebrae. A similar depression is not shown in illustrations of allosaur sacra (Gilmore, 1920; Madsen, 1976). It could be a feature of only this one animal. The five articulated sacral centra arch slightly. The arch is convex dorsally. Whether this arch is typical of other theropod sacra is not known since most are not figured in a way to show the sacrum in full lateral view. The sacrum of *A. fragilis*, USNM 4734 (Gilmore, 1920) appears to have a similar arch.

In most early carnivorous dinosaurs, cavities developed on the sides of the centra and arches. In birds, these pleurocoels are filled by air-sacs connected to a huge system of air-chambers that permits the avian lung to operate at a much higher efficiency than any mammalian or reptilian lung. In TATE 0012, the centrum of the 1st sacral vertebra has deep and long horizontal cavities just below the neural canal. Similar but much shallower cavities occur on the left but not the right sides of sacra 2 and 3. Such asymmetry in the development of air chambers in the vertebrae is very common among other carnivorous dinosaurs and brontosaurus too. Perhaps the asymmetry is caused as follows: the air-sac system in birds consists of a pair of long connecting tubes that runs down the vertebral column, one on each side. Usually an enlarged chamber buds off the tube opposite each centrum, and part of this chamber usually invades the space occupied by centrum bone. However, in meat-eating dinosaurs, where the vertebral sacs are in a process of rapid evolutionary shifts, the degree of inward invasion of bone by the sac is not tightly controlled by developmental processes.

Cavities larger than those on 2 and 3 occur again on both sides of sacral 4. On sacral 5, the sacral ribs attach at the point where these cavities would otherwise be found. Such pleurocoels are much less well developed in allosaurs.

The joints between centrum 1 and 2 and between 3 and 4 are noticeably wider than those between 2 and 3 and 4 and 5. This pattern seems to be true for *Allosaurus* (Gilmore, 1920, Plate 9). Since the sacral centra compose the main compression member of the entire hind limb apparatus, these changes in the size of the centrum-centrum contacts possibly reflect significant differences in how the stresses of locomotion were absorbed among the successive sacral vertebrae.

In general, the connections between the sacral vertebrae and the ilia of TATE 0012 are not as rigid and thoroughly fused as they are in an adult *Ceratosaurus* or *Coelophysis*. This condition is evidence that the Nail specimen may not have been fully adult when it died. On the other hand, the sacrum vertebrae are tightly fused so that the sacrum was fossilized in one piece, an occurrence not often found for large Jurassic theropods. The fused sacrum suggests an adult animal.

The 1st transverse processes are hollowed underneath so as to give them an inverted U cross-section. Their span side-to-side is greater relative to the centrum width than for allosaurs (Gilmore, 1920; Madsen, 1976). The 1st transverse processes of the Nail megalosaur are similar in shape to those of the posterior dorsal vertebrae and look as if they supported a normal rib rather than acting as a transverse process or modified sacral rib.

There is no sacral rib wedged against the first sacral centrum and arch; the first true sacral rib attaches to the sacra at the junction between the 1st and 2nd sacral centra, corresponding to what Madsen (1976) has called the "2nd sacral rib" in allosaurs. Madsen's (1976) numbering system for sacral ribs will be used here.

The transverse process above rib 2 of TATE 0012 extends outward from the junction of neural spines 1 and 2 and is attached to the sacral rib by lamina over the full width of the rib. Above this transverse process, a second blade-like transverse process (shown in Fig. 3C only) extends out horizontally towards the ilium. This blade does not reach the ilium but rather ends short of it in a horizontal knife edge. In life a sheet of connective tissue may have extended from the knife-edge of the transverse process to the inner surface of the ilium; this bone+ligament sheet is an example of a tensional member that would prevent the ilium from being pulled off the sacrum.

The 3rd sacral ribs are slightly more strongly attached to sacral centrum 2 than centrum 3. The transverse process is also more strongly attached to sacral 2 but continues well back on to 3. A lamina connects the front edges of the transverse process and the rib beneath. The attachment to the ilium for this rib + transverse process unit has the form of a "C", opening posteriorly. The posterior edge of the 3rd sacral rib is fused to the anterior edge of rib 4 at the distal end on the right side. On the left the anterior edges of 3 and 4 contact but do not fuse. The attachment to the ilium of the rib + transverse process of sacral 4 also has a "C" shape, opening anteriorly. Together, sacral rib attachments 3 and 4 make the strongest attachment for the ilium, with their ribs and transverse processes making a low "U"-shaped yoke that would attach to the ilium above the acetabulum. Such a strong union is to be expected, since the thrust of the femur into the acetabulum would stress the pelvic structure at this point.

The 4th sacral ribs are the lowest and most robust of the four sets. The transverse processes are fused along their full width by a lamina to sacral rib 4. These transverse processes are strongly attached to the neural arch of sacral 3. The transverse processes angle back at about 60 degrees to the axis of the centra.

The fifth sacral rib connects almost entirely to the 5th sacral centrum and arch. The outer end expands anteriorly but not far enough to attach to the 4th rib. The upper portion of this rib constitutes a 5th transverse process. It is strongly connected to the 5th rib over its full length by a thick lamina. The surface of the fused transverse process and caudal rib attaching to the ilium is large and triangular, with the apex pointing to the rear. This surface fits against the ilium and extends below the medial blade of the *brevis* shelf (Fig. 3, 15, 18). This extension of the 5th sacral rib attachment below the ilium does not appear to be a common feature in other dinosaurs.

The neural spines in the Nail megalosaur were set tightly together at their bases and appeared to be fused together, as is the case in the megalosaur sacrum from Stonesfield (Owen, 1856). In many primitive theropods (the Triassic *Coelophysis*, for example) and allosaurs the pre-zygapophyses surfaces have two distinct articular planes: 1) the primary zygapophysis, a surface facing mostly upward and inward; and 2) a hypantrum, a surface facing mostly inward and downward. The right and left hypantra enclose a narrow triangular space below and between the primary joint surface of the zygapophyses. Into this space fits the

hyposphene on the posterior of the preceding vertebra. Hyposphene-hypantra joints increase the backbone rigidity - the vertebra can flex side-to-side and up-and-down but cannot twist at all. Like other theropods, the Nail sacrum has a hypantrum on the 1st sacral vertebra. The angle between the right and left surfaces of the hypantrum is about 90 degrees.

This hyposphene-hypantrum articulation continues into the caudal vertebrae but the angle between surfaces of the hypantra changes from 90 degrees on the first sacral to 25 degrees on the first caudal vertebra. Contemporary theropods such as *Allosaurus* have this articulation back to the first caudal at least (Gilmore, 1920; Madsen, 1976).

TATE 0012 Sacrum Dimensions in mm. Overall length of centra - 620. Span, 1st sacral vertebra transverse processes - 290. Span, second caudal ribs - 235. Span, 3rd caudal ribs - 240. Span, 4th caudal ribs - 245.

Caudal Vertebrae (Fig. 4, 6-9)

The first caudal vertebra identification is quite certain because the centrum, figure 4, has a slightly concave anterior face with a bulge near the top that fits into the depression on the posterior face of the 5th sacral.

The caudal ribs of the anterior caudal vertebrae are back swept like those of *T. tanneri*, *Ceratosaurus nasicornis* and *Poekilopleuron bucklandi*. Like the first caudal rib of *T. tanneri*, the caudal ribs expand on their distal ends. Like *C. nasicornis*, the back sweep of the caudal ribs disappears on the posterior caudals well before the caudal ribs disappear judging from the most distal vertebra assigned to TATE 0012. The caudal ribs of *Poekilopleuron*, in contrast, continue to be back swept almost to the point they disappear.

The anterior face of the centrum is circular. The posterior face is sub-circular, being slightly depressed in the dorso-ventral direction. In most other Jurassic meat-eating dinosaurs the first caudal centrum is not nearly as wide as high, thus TATE 0012 seems to have a tail that was exceptionally wide at its base. The posterior face is convex. These joint surfaces indicate that very little movement was possible between the sacrum in front and the second caudal centrum behind.

The center of the centrum is pinched laterally. The anterior opening of the neural canal is partially enclosed within the circle defined by the front face of the centrum. The canal appears to rise relative to the centrum axis so the posterior opening is somewhat raised relative to the posterior centrum face. Actually, the posterior vertebral interface is lower than the anterior interface relative to a centerline drawn perpendicular to the anterior face. In other words, the vertebral faces are not perpendicular to a line passing through their centers. The anterior angle from the centerline to the face is usually smaller than the angle to the posterior face giving the vertebrae a keystone shape, longer at the top than the bottom. The skewing continues but to a lesser degree to the most posterior of the eleven caudal vertebrae thus far with the exception of #5. The anterior caudals of *Allosaurus*, *Dilophosaurus*, *Monolophosaurus*, *Yangchuanosaurus*, and tyrannosaurids are similarly skewed. For *Sinraptors*, the posterior face is higher (Currie and Zhao, 1993).

In most theropods, chevrons descend from the spaces between the centra of the tail. These chevrons provide attachment for the muscles that move the thigh backwards and move the tail sideways and downwards. Usually, the first chevron occurs between caudal 2 and 3. Caudal 1 of TATE 0012 shows no obvious attachment sites for a chevron.

The neural arch is tightly attached to the centrum but the joint has opened up, after death, on the anterior end, just below the pre-zygapophyses. This weak joint is another suggestion that the Nail megalosaur may not be fully adult.

Pleurocoels are developed on each side of the centrum below the caudal ribs. Pleurocoel-like cavities are also formed under both the anterior and posterior edges of the caudal ribs. The anterior cavities are bordered by the caudal rib, the brace between the caudal rib and the neural arch and the strut supporting the pre-zygapophyses. The posterior cavities are bordered by the lamina from the post zygapophysis to the top of the centrum, the caudal rib and the posterior side of the rib brace. The posterior cavities are below and anterior from the post-zygapophyses. These may be caudal air-chambers or perhaps interspinous ligament attachments. They are much better developed than those in allosaurs but are close to those in ceratosaurs. This vertebra has both a hypantrum and a hyposphene.

The ribs of the first caudal vertebra of TATE 0012 are exceptionally strong and complex, indicating a tail musculature of great size; the girth of the caudo-femoralis longus below the rib must have been relatively larger than in most other theropod dinosaurs (Fig. 18). The centerline of the caudal ribs are swept back at 45 degrees with respect to the axis of the centrum; the ribs are pointed on their ends and slightly "S" shaped as seen from above. The central third of the ribs angle posteriorly more than the distal and proximal thirds. The dorsal surfaces of the caudal ribs have a slight keel, the left more so than the right, indicating very powerful attachment of the tail flexing muscles here. The ribs are nearly horizontal in anterior and lateral views. Ventrally the caudal ribs have a heavy stiffening keel near the anterior edge of the ventral surface. This keel fades rapidly toward the distal end of the rib. The anterior edge of the ribs continue as laminae onto the lateral edge of the pre-zygapophyses. This linking of the caudal ribs to the zygapophyses by laminae is a primitive feature according to Norman (1990).

The anterior edge of the neural spine is split into two sharp ridges for about 30 mm on the proximal end; these ridges probably mark the attachment of ligament sheets that connected the first caudal to the last sacral; in between the sheets would be the contractile fibers of the **interspinalis** muscle. The posterior edge splits into two ridges about two thirds of the way down from the top that widen into the post-zygapophyses. The neural spine angles about 16 degrees back with respect to the plane of the anterior face of the centrum. This first caudal vertebra is quite distinct from those of **Allosaurus** (Fig. 5). The neural spine of the TATE 0012 vertebra is thinner, the caudal ribs are longer, more back swept and do not angle up. The hypantrum and hyposphene are not features found on contemporary allosaurs beyond the anterior of the first caudal vertebra. On TATE 0012 a hyposphene is found on the posterior of the first caudal.

A vertebra identified as the 2nd caudal, figure 6, was found immediately behind and above the first caudal. The anterior face of this vertebra is again higher than the posterior face. The caudal vertebrae of **Monolophosaurus** appears to carry this feature back through several of the anterior caudals (Zhao and Currie, 1993). The caudal of figure 6 has been identified as the second caudal based mainly on its size though the differences from the first caudal, such as the narrowness of the neural spine, suggests a more posterior position for it. It has a hypantrum. The hyposphene has broadened but still remains. This vertebra is similar to the first caudal in that the neural spine is thin and slightly back sloped especially on the front edge. The caudal ribs are horizontal, tilted slightly down from the front to rear and backswept, though slightly less so than those of the first caudal. The ventral keels remain. This vertebra differs from the first in that the ribs are shorter and relatively more broadened at the distal ends. The ribs are asymmetric. The left is shorter and wider than the right. Both the first and second caudals are somewhat distorted which probably accounts for the fact that the left ribs appear to overlap in dorsal view when the two are articulated. The neural spine is set back somewhat from the anterior end of the centrum and does not show a vertical groove for the interspinous ligament on either the anterior or posterior edge. The pleurocoel-like cavities found beneath the leading edges of the caudal ribs of the first caudal are not retained but the other four remain.

Drawings of the lateral views of the first and second caudals articulated to each other and the sacrum (Fig. 6) suggest that they either are tangential to or perhaps continue the arch of the sacral vertebrae. There is no obvious kink in the centerline of the vertebrae. The upward tilt of the posterior face of the fifth sacral vertebra reduces the decrease in tail elevation otherwise introduced by the offset of the articulating faces of the caudal centra. Though no chevron facet is obvious on the first caudal vertebra, a large notch is present on the ventral side between the articulating faces of the first and second caudal vertebrae suggesting that some form of a chevron was present there.

The 6 additional vertebra recovered in 1996 were found in two groups of three each. The two groups were close together. The most posterior three vertebrae were in one group with the most posterior two articulated. The third of the group appears to be from just anterior to the first two. It was turned 180 degrees with respect to the first two and the centrum was nearly touching the adjacent centrum. They were oriented in the matrix with their axes nearly vertical. They were complete and appear to have suffered very little distortion. They were located slightly below and northeast of the second group.

The three in the second group were more anterior. They are also considerably more damaged and distorted. The one identified as #4 was set with the centrum axis at about 45 degrees from vertical with the anterior face down. Though mostly complete, it shows evidence that both the neural spine and both caudal ribs have been bent forward and are quite fractured proximally. The vertebra identified as #3 was oriented neural spine down. The right rib was broken against the centrum of #4. The neural spine is complete but bent toward the right rib and broken off. The left caudal rib, though nearly complete, was bent back to an angle less than 45 degrees and is quite distorted as a result. The vertebra identified as #5 appears to be

undistorted but the neural spine was broken off against the centrum of #3 and the right rib was broken and perhaps slightly distorted against the centrum of #4.

As noted earlier, the caudal ribs of #1 have a complex shape while the ribs of #2 have more simple rounded ends. The vertebra identified as #3 appears to have a more complex rib like #1, suggesting that these vertebrae might represent a second megalosaur tail. The quarry map, however, shows that these vertebrae are intimately mixed with the previously removed vertebrae, especially the one identified as #2. Possibly, the vertebrae #2 and #3 are interchanged in the placement suggested here.

To better establish that these vertebrae represent one tail and their order in the tail, the lengths, widths and heights of the centra and the overall heights of the anterior ten vertebra were plotted. The centrum anterior and posterior widths are plotted in figure 8G. The posterior of one vertebra is plotted on the same abscissa value as the anterior of the vertebra following. The dimensions could be expected to decrease continuously toward the posterior though not necessarily at a constant slope. Plots showing 0, 1, 2 and 3 vertebrae missing after #5 are shown in figure 8G. The curves suggest what could be considered a reasonable agreement between the widths of the mating ends. There are no large width mismatches. The slopes show a fairly constant slope except around the 8th and 9th position region depending on the vertebra placement assumed. Most of the discrepancy in the dimensional change is in the anterior width. These vertebrae were articulated or close to it so location error is an unlikely cause. In addition, a similar plot for centra heights shown in figure 8 H lacks a similar discrepancy and the overall vertebrae heights, figure 8I, decrease smoothly also. The width differences could result from an injury to this section of the tail or perhaps natural random variation in the vertebrae. An alternative to these possible explanations is suggested by a similar plot for the caudal of *Allosaur* 8367 (Gilmore, 1920), figure 8H, lower left. A very similar discrepancy is present in the anterior widths of vertebrae #5 and 6 for 8367. Perhaps this is a point of attachment or the extent of the attachment of leg driving muscles and tendons. If so, they attach farther back on TATE 0012 than on the *allosaur* 8567. This could occur to produce greater forces to drive the heavier legs of TATE 0012.

A rather large discrepancy would occur at joint 5, the #5 to #6 joint of TATE 0012 in both width and height if it is not assumed that the #6 vertebra, at least, is still missing. We will assume that it is missing in the discussion here.

Figure 8I shows the overall heights of the vertebrae as a function of order. Eight of the ten had complete neural spines. The heights are constant to #3 then decrease in a smooth progression after #3. In figure 8I, the caudal centrum lengths of TATE 0012, #8367 and *Ceratosaurus nasicornis* #4735 (Gilmore, 1920) are plotted as a function of position. The caudal centrum lengths of TATE 0012 show more variance with position

The vertebrae assigned to positions 10 and 11, figures 7 and 8, were found before to 1996 in close contact to the vertebra identified as the #2 caudal. The positions of these two caudals prior to 1996 were estimated from a normalized plot of the widths and heights of the faces of the caudal vertebrae of *allosaur* as figured by Madsen (1976). Though no compelling reason exists to believe the tail of a megalosaurid would or should taper at the same rate as *allosaur*, little other information on theropod tail dimensions is available in the literature that could be used to identify positions of megalosaur caudal vertebrae. The positions of #10 and 11 were first estimated using Madsen (1976) to be #11 and #13. The two appear to be nearly adjacent if not adjacent. When they are placed against each other, the zygapophyses prohibit the centra from aligning properly. This misalignment might result from some distortion of the of the zygapophyses though the vertebrae show little obvious distortion. The fact that they were interred against each other, and that the centrum width and height curves, figure 8G and 8H and the neural spines, figure 8I, have a more continuous slope if they are adjacent leads to the assumption they are adjacent. The new estimate using 1996 additions then suggests that the positions of these last two of the string of caudals are no more anterior than #10 and #11. Thus the taper of the tail does appear similar to *allosaur*.

The caudal ribs of #10 and 11 caudals of TATE 0012 are asymmetric and are sometimes incomplete on the distal ends. They are back swept at about 45 degrees, and keeled on the proximal end so that the rib, its keel and the neural arch form the walls of two pleurocoel-like cavities below and anterior to the post zygapophyses. These cavities can be seen on the caudals of *Torvosaurus* (Britt, 1991). Shallow depressions are still found on either side of the centra below the caudal ribs. Again the neural spines are thin, have no dorsal lateral expansion and no grooves on either the anterior or posterior edges. The neural spine is more back swept than that of an *allosaur* and the anterior portion of the spine, still prominent on the

#13 vertebra of allosaur (Madsen, 1976), has faded to a low ridge on the #11 caudal of TATE 0012. The spine of #11 curves slightly toward the anterior like those of *Poekilopleuron bucklandi* (Eudes-Deslongchamps, 1838) but the curvature is less pronounced.

Of the new vertebrae, #4, 5, 7, 8 and 9 have caudal ribs that expand distally. Numbers 7, 8, and 9 differ from the earlier found #10 and 11 in that their neural spines and caudal ribs are less back swept. The back sweep of #7, 8 and 9 are only about 22 degrees. The ribs of #5, however, have a back sweep approaching 45 degrees. These differences could be from the positions in the tail, the varied orientations of interment or both. The centrum axis of #10 and 11 were lying more horizontal while those of #5, 7, 8 and 9 were vertical. Number #3 and 4 caudals were badly distorted by the matrix.

The ventral side of the caudal ribs split into two distinct keels from #7 and on back as the ribs approach the attachment to the neural arch. A faint trace of this division appears on #5 and perhaps even on #4.

The hyposphene-hypantrum articulation continues on back into the caudals of TATE 0012. A hyposphene appears on the caudal identified as #3 and a hypantrum is present on the one identified as #4. The posterior of #4 does not appear to have a hyposphene but the vertebra has sufficient damage to make this uncertain. The prezygapophyses are spread widely apart on the vertebra assumed to be #5 and it shows no sign of a hypantrum.

The most distal caudal assigned to TATE 0012, figure 9, has been estimated to be #20 again from a plot of the centrum dimensions of allosaur (Madsen, 1976). The shift of the vertical position of the caudal ribs with respect to the neural canal is closer to that found on the #16 allosaur caudal suggesting that the tail of TATE 0012 with this vertebra included might have tapered more rapidly posteriorly than that of allosaur. However, the #20 identification will be retained for the discussion below.

Though further posterior than #10 and #11, the structure of #20 is more complicated. The caudal vertebrae of allosaurs which become progressively less complicated posteriorly. While the anterior and posterior ends of the centra of the more anterior vertebrae of TATE 0012 are nearly equally concave, the anterior end of #20 is much more concave than the posterior. Also, a groove is present on the ventral side of the centrum that the more anterior vertebrae lack. The anterior segment of the neural spine is at least three times the height of the same portion of the spines of #10 and #11 and thicker laterally. This differs from allosaurids where the anterior segment rapidly and monotonically fades away posteriorly (Madsen, 1976). The differences of #20 relative to caudals vertebrae #10 and #11 suggests that this vertebra may not belong to TATE 0012 but rather to some other animal. This vertebra, like the atlas and axis, was found about 8 m west of the site containing the majority of the TATE 0012 bones. However, no other parts identifiable as another animal of similar size have been recognized to date and since the length of the centrum certainly fits TATE 0012, we will assume it belongs to TATE 0012 until more evidence is found to the contrary.

The 20th caudal also differs from the preceding caudals in that the caudal ribs are only slightly back swept. This change of rib angle has been observed in *Ceratosaurus nasicornis* (Gilmore, 1920). The ribs of *C. nasicornis* make a transition from back swept to straight between about #8 and #10. This transition appears to occur farther back in the tail of TATE 0012 if #20 belongs to it. The caudal ribs of TATE 0012 are much narrower than those of *C. nasicornis*. The caudal vertebrae of *T. tanneri* may be similar to those of TATE 0012. That isn't clear from the photographs.

TATE 0012 1st Caudal Vertebra Dimensions in mm. Full height - 390. Width, caudal ribs - 390. Neural spine, height - 190; width - 110; thickness, middle, - 12; top - 16. Centrum length - 105. Anterior width - 145; posterior width - 162; mid centrum width 92. Anterior height - 140; posterior height - **130**.

TATE 0012 2nd? Caudal Vertebra Dimensions in mm. Full height - 390. Width, caudal ribs - 380. Neural spine, height - 200; width, base - 100; top - 70; thickness - 13. Centrum, length - 113. Anterior width - 160; posterior width - 140; Mid centrum width - 89; Anterior height - 140; posterior height - 140.

TATE 0012 3rd? Caudal Vertebra Dimensions in mm. Full height - 390. Width, caudal ribs - ?. Neural spine, height - 210; width, base - 80; top - ?; thickness - 15; centrum, length - 121. Anterior width - 143; posterior width - 142; Mid centrum width - 88; Anterior height - 128; posterior height - 132.

TATE 0012 4th Caudal Vertebra Dimensions in mm. Full height - 380. Width, caudal ribs - 400 estimated. Neural spine, height - 210; width - 65; thickness - ?; centrum, length - 112. Anterior width - 144; posterior width - 136; Mid centrum width - 65; Anterior height - 124; posterior height - 124.

TATE 0012 5th? Caudal Vertebra Dimensions in mm. Full height - ?. Width, caudal ribs- 340 estimated. Neural spine, height - ?; width - ?; thickness - ?. Centrum, length - 113. Anterior width - 129; posterior width - 113; Mid centrum width - 60; Anterior height - 126; posterior height - 119. One vertebra, possibly two are appear to be missing here.

TATE 0012 7th? Caudal Vertebra Dimensions in mm. Full height - 335. Width, caudal ribs- 325. Neural spine, height - 185; width - ?; thickness - ?. Centrum, length - 111. Anterior width - 107; posterior width - 106; Mid centrum width - 52; Anterior height - 106; posterior height - 105.

TATE 0012 8th? Caudal Vertebra Dimensions in mm. Full height - 310. Width, caudal ribs- 325. Neural spine, height - 170; width - ?; thickness - ?. Centrum, length - 118. Anterior width - 85; posterior width - 81; Mid centrum width - 45; Anterior height - 91; posterior height - 91.

TATE 0012 9th? Caudal Vertebra Dimensions in mm. Full height - 250. Width, caudal ribs- 240 estimated. Neural spine, height - 135; width - 45; thickness - 9. Centrum, length - 118. Anterior width - 85; posterior width - 81; Mid centrum width - 45; Anterior height - 91; posterior height - 91.

TATE 0012 10th? Caudal Vertebra Dimensions in mm. Full height - ?. Width, caudal ribs- 270 estimated. Neural spine, height - ?; width, base - ?; top - ?; thickness - 9. Centrum, length - 119. Anterior width - 94; posterior width - 92; Mid centrum width - 47; Anterior height - 98; posterior height - 93.

TATE 0012 11th? Caudal Vertebra Dimensions in mm. Full height - 250. Width, caudal ribs- 240 estimated. Neural spine, height - 135; width - 45; thickness - 9. Centrum, length - 118. Anterior width - 85; posterior width - 81; Mid centrum width - 45; Anterior height - 91; posterior height - 91.

TATE 0012 Approximately 20th? Caudal Vertebra Dimensions in mm. Full height - 230 estimated. Width, caudal ribs- 260 estimated. Neural spine, height - ?; width, base about - 40; top - 33; thickness - 11. Centrum, length - 118. Anterior width - 85; posterior width - 78; Mid centrum width - 39; Anterior height -84; posterior height - 74.

Chevrons (Fig. 10)

The first chevron recovered that has been referred to TATE 0012 was 215 mm long. Superficially, it appears to be similar to those of *Torvosaurus* in the region of #10 to #11 though more curved. Closer examination shows that it is uniquely concave ventrally and anteriorly whereas the chevrons of allosaur (Madsen, 1976) and pictured chevrons for other dinosaurs are concave dorsally and posteriorly. The curvature of the TATE 0012 vertebra is not a bending of the shaft but is rather due to the expansion of the distal end of the chevron only in the anterior direction. Like the chevrons of *Torvosaurus*, the shaft is straight but the distal ends of the chevrons of *Torvosaurus* expand posteriorly. The chevron is more robust, especially in the transverse direction, than those of *Torvosaurus* for a similar length.

The haemal canal appears to be slightly deeper than that of the 11th chevron figured in Britt (1991) for *Torvosaurus*. The chevron of TATE 0012 is quite asymmetrical laterally on the proximal end.

In 1996 five more chevrons were recovered in close proximity to the six caudal vertebrae. Their lengths are 305, 285, 265, 245 and 210 mm. The shortest was lying against one caudal rib of #8. Unlike the first chevron found, these five all curved slightly to the posterior. The expansions of the distal ends of the five found in 1996 vary. Some expand caudally, others expand both cranially and caudally. The cranial expansion noted with the first one is apparently not diagnostic of a chevron of TATE 0012.

The articulation of the chevrons to the caudal vertebrae has not been illustrated in the papers detailing theropods. Using the present material, a suggested articulation for the TATE 0012 chevron is presented in figure 10 E. Because *Torvosaur* is of similar size, the chevron lengths can be expected to be similar. Assuming this to be true, the TATE 0012 chevron would come from the region of the eighth to twelfth caudal

vertebrae. We will assume here that it adequately represents a chevron from the region of vertebrae #10 to #11 for the discussion below. The chevrons change appearance slowly on the anterior part of the tail. The chevron is shown articulated between #10 and 11 vertebrae in figure 10 E. The chevron notch is symmetric to the plane of the joint between the vertebrae. The pictured articulation places the peduncle on the proximal end of the chevron symmetrically with respect to the chevron facets. The extensions on the proximal anterior end match up to shallow depressions in the anterior ventral surface of the posterior vertebral flange. The articulating surface of the proximal end of the chevron would fit symmetrically against the disc between the vertebrae. Positioned thus, the shaft of the chevron makes an angle of approximately 40 degrees with the axis of the two vertebrae in this illustration.

Figure 10 F is an articulation of *Torvosaurus* vertebra #10 through #13 and their three associated chevrons. The articulation here is similar to that of TATE 0012. The main difference is that the notches formed by the chevron facets appear to be less symmetric. The angle of the chevrons with respect to the axis of the centra as shown is about 45 degrees.

The projections on the anterior and posterior of the proximal end of the chevrons of the megalosaurids *Torvosaurus* and TATE 0012 suggest that the attachment of the chevron to the vertebral column allowed only limited flexure front to back. Figure 10 G shows an articulation of an allosaur chevron to a pair of vertebrae derived from Madsen (1976). Since Madsen illustrated only every 3rd caudal vertebra and every 5th chevron, it was necessary to use nearby components to illustrate the articulation shown. A #12 allosaur caudal is shown articulated with itself and the chevron is that of a #10 vertebra. The chevron facets of the caudal vertebrae of allosaur seem to be smaller than megalosaur and on some vertebrae almost non-existent (Madsen, 1976). The articulating surface of the proximal end of an allosaur chevron seems slightly wider laterally and more curved than for megalosaurs. It appears that the articulating surface of this chevron fits against the edge of the disc between the vertebrae. The proximal end of the chevron in Figure 10 F makes an angle of about 70 degrees with the axis of the vertebrae. The proximal end of the chevron would appear to allow much more anterior-posterior motion of the distal end than the attachment of the chevrons of *Torvosaurus* and TATE 0012. The extensions on the anterior proximal end of the allosaur chevron appear to be well away from the centrum. The chevrons of the megalosaurids are thicker laterally on the distal ends than those of the allosaurids. The groove from the haemal canal down the posterior of the chevron of these megalosaurids is similar to that of allosaurs but the anterior groove down the shaft, short in allosaurs (Madsen, 1976), extends further down toward the distal end of the chevron for megalosaurids.

Scapula-coracoid (Fig. 11)

A disarticulated right scapula and coracoid was found at the locations near the ilium as shown in figure 1. The scapula is nearly complete, missing only a small portion of its distal end. It had been flattened so that the natural curve in the long dimension had been removed. The estimated chord length of this scapula+coracoid is 835 mm with the curve restored.

The presence of at least two and possibly more disarticulated megalosaurids in Nail quarry raises questions as to the assignment of some of the bones, especially the scapulae and coracoids. The larger scapula-coracoid was previously assigned to *Edmarka rex* (Bakker et al., 1992). The assignment of the scap-coracoids might be made by comparing scap-coracoid length to femur length. Ratios of the lengths of scap-coracoids to the femurs for some other theropods and the two scap-coracoids from Nail quarry with the TATE 0012 femur are:

Sinraptor hepingensis..... 900/980 = 0.92

Sinraptor dongi. 895/876 = 1.02

Allosaurus fragilis..... 795/850 = 0.94

Piatnitzkysaurus floresi. 505/552 = 0.92

TATE 0012:

Large scap.-cor./femur.....1091/830 = 1.31

Small scap.-cor./femur.....835/830 = 1.01

The coracoid of *S. dongi* is not known but the scapula of *S. hepingensis* (Gao, 1992) is the same length so a coracoid of similar size has been assumed for *S. dongi*. The ratios are close to the same for all the other animals except *S. dongi* which is about 10 percent larger. If the large scap-coracoid were assigned to TATE 0012, the ratio would be 30 to 40 percent larger than any of the others. The large scap-coracoid seems quite unlikely to belong to TATE 0012. It better fits the larger *Edmarka rex* as originally assumed (Bakker, et al., 1992). The smaller scap-coracoid to femur length ratio is close to *Sinraptor dongi* and is only about 10 % greater than other Jurassic theropods. The small scapula-coracoid seems more likely to be that of TATE 0012.

The scapula is straight sided like that of *Edmarka* (Bakker, et al., 1992) but expands toward the distal end. It also shows the weak expansion on the posterior edge near the middle of the shaft. The sutural spine on the coracoid is present, as is the conical wedge on the scapula that fits the wedge shaped notch on the coracoid (Bakker et al., 1992). The smaller scapula is robust compared to that of *Edmarka*. Though it is about 25 percent shorter, it is only 8 percent narrower at the minimum shaft width. The angle of the glenoid notch relative to the axis of the blade is set more like that of allosaurs than that of the larger scap-coracoid.

The coracoid of TATE 0012 is large, measuring 198 by 291 mm. It is appreciably larger than that *Allosaurus* (Bakker et al., 1992), for example, and of *S. hepingensis* which is only 160 by 250 mm. This difference in size is even greater if they were compared at equal femur length. While the femur of *S. hepingensis* is 980 mm the femur of TATE 0012 is only 830 mm.

The scapula and two coracoids are all the forelimb components attributed to TATE 0012 that have been recovered so far.

Ilium (Figure 12, 13, 18)

The right ilium of TATE 0012, illustrated in figure 12 lay horizontally in the quarry on top and in contact with the left tibia and fibula. The left ilium lay between the sacrum and right ilium with its plane vertical as it would be in the living animal. That these bones have suffered some crushing is evident from the condition of the left ilium. The weight of the overburden has obviously crushed it down in the dorsal-ventral direction as evidenced by folds in the blade from compression in the vertical direction. The right ilium was interred with the blade in a horizontal plane in the matrix and appears to have very little distortion in the lateral and medial views. An examination of the left ilium shows that some significant distortion is present in the right ilium in dorsal and ventral views. For example, the maximum width of the brevis notch of the right ilium is 80 mm compared to 130 mm for the left ilium. The caudal end of the right ilium was apparently crushed laterally. It was also bent in the medial direction over the proximal end of the tibia. Some of the distortion remains in the drawing. Probably, the forces from the dorsal direction on the left ilium caused some spreading of its brevis notch. The true width is probably closer to 130 mm than 80 mm.

The pubic peduncle of the right ilium has obviously been crushed laterally by a nodule. The surface connecting to the pubis is 150 mm in length in the anterior to posterior direction and averages about 50 mm wide. The length of the articulating surface of the left pubic peduncle is only about 110 mm and the width is about 70 mm. The pubic peduncle of the left ilium is apparently bent forward and upward but its cross section does not appear to be distorted. The distortion the right pubic peduncle in the lateral direction probably expanded it in both anterior and posterior directions. Thus, the acetabulum of the right ilium should perhaps be wider. The prominent flange closing the medial side of the right ilium is little evident in the left. Crushing action on the right ilium may have enhanced the extent that this flange closes the medial side of the acetabulum. On the other hand, crushing of the left ilium in the dorso-ventral direction may have reduced the extent that it closes the acetabulum on the medial side.

The rugose surface of the pubic peduncle extends back to form a rugose protrusion into the otherwise smooth acetabular surface on both ilia. It is much more prominent on the right one.

The anterior blade of the right ilium had been broken away though some fragments remained. The dorsal edge of the ilium is quite robust to the break. Some fragments ventral part of the anterior blade found nearly in place in the broken area suggest that the anterior blade thinned considerably. Part of the lower anterior blade remains on the left ilium showing that the ventral portion of the blade narrows rapidly as it extends

cranially. Fragments of the right ilium show the thin anterior ilia became ribbed on the medial side, similar to what is shown for *Sinraptor dongi* (Currie and Zhao, 1993). The medial surface of the anterior of an allosaur ilium found in Nail quarry has a similarly ribbed surface on the anterior blade. A portion of the posterior end of the right ilium is shown restored by the dotted line. The length of the left ilium from the ischial peduncle is about the restored length and appears to be complete.

The psoas notch viewed laterally is barely open based on the left ilium. This apparently narrow psoas notch probably results from the dorso-ventral distortion suffered by this ilium though the notch might be narrow in lateral view even for an undistorted ilium.

The right ilium of TATE 0012 is restored in Figure 12 and 13 with a rather squared anterior blade, though the megalosaurids seem to have curved anterior blades and the anterior dorsal edge. The ilium of TATE 0012 shows no evidence of a sudden downward curvature. However, the ilium of TATE 0012 differs enough from the other megalosaurids that there can be no certainty that the anterior end was not squared off more like that of allosaurs, figure 13.

The ilia of TATE 0012 are described below by comparison to the ilia of other theropods as shown in figure 13 where a number of ilia are shown drawn to an equal length scale. To facilitate comparison of the ilia, a reference line has been defined. It extends from the most posterior point of the pre-acetabular (psoas) notch to the posterior ventral corner of the posterior blade. Various dimensions are defined in figure 13. Most are based on this line.

A line passing through the center of the anterior face of the 1st sacral and the posterior face of the 5th would probably be a better choice for a reference line. The line defined in figure 13 does not parallel the sacrum centerline if TATE 0012 is a typical example. The chosen reference line slopes up posteriorly relative to a sacrum line for TATE 0012. Unfortunately, sacra, especially articulated sacra, are not often found with ilia so that a "standard" reference line based on the center line of the sacral centra is not usually possible to define.

Comparison of Ilii

Based on ilia alone, *Sinraptor* and *Marshosaurus* seem to relate to the allosaurids as does *Piatnitzkysaurus* (except for the vertical pubic peduncle). *Stokesosaurus* and *Monolophosaurus* are also similar to allosaurids. The megalosaurids, *M. bucklandi*, *Torvosaurus* and *Edmarka sp.* are similar. Neither TATE 0012 nor *Ceratosaurus* are similar to others or to each other.

As defined in figure 13, the acetabular notch is relatively wider for *M. bucklandi* and *Torvosaurus* than for TATE 0012 though that of TATE 0012 may be closed some by distortion of the pubic peduncle. All the megalosaurids appear to have peduncles of similar lengths as defined in figure 13 with relatively flat suture surfaces that are perpendicular to the centerline of the peduncle. All the megalosaurids but TATE 0012 have a pubic peduncle that angles strongly forward. The pubic peduncle of TATE 0012 is angled more directly downwards like that of tyrannosaurids (Fig. 13). This is based on the right ilium of TATE 0012 that is assumed little distorted in the antero-posterior direction at least in terms of the peduncle orientation. The peduncle of TATE 0012 angles less forward than all the Jurassic animals except for the Middle Jurassic *Piatnitzkysaurus* (Fig. 13). While the peduncles of allosaurids angle anteriorly also, they are longer, and the suture surfaces are directed downward and curved. The anterior blades (or flare) are all similar in length as defined in figure 13.

The relatively straighter dorsal edge of the allosaurids compared to the megalosaurids results mainly from the considerably more rounded antero-dorsal corner of the anterior blade. Here again TATE 0012 differs from the other megalosaurids by having a straight dorsal edge even though the anterior blade may still be rounded. It differs from all the other ilia of Figure 13 in that the medial blade extends posterior to the posterior blade in lateral view. Also, the ventral edge of the medial blade appears to be visible in lateral view over most of its length. The posterior blade obscures the medial blade slightly on the posterior end. The brevis notch of TATE 0012 thus opens outwardly rather than inwardly like other theropods.

The blade heights defined from the reference lines are similar for all the ilia of figure 13 (A) to (F) except for AMNH 5753, which is higher. The point of greatest height is further anterior on allosaurids and TATE 0012 than the other megalosaurids. If the height were measured from the ventral surface of the acetabulum, the allosaurids have greater dorso-ventral heights than the megalosaurids. The ventral edges of the posterior

blades slope upwards or downwards toward the posterior relative to the reference line with no particular preference for either allosaurids or Megalosaurids.

The TATE 0012 ilium appears to be similar to that of the other megalosaurids in height to length ratios. It differs from the other megalosaurids in its much straighter dorsal edge, a feature also characteristic of the allosaurs, the laterally open brevis notch and in the shallower posterior blade. The nearly vertical angle of the pubic peduncle differs from the anteriorly sloping angles of *Megalosaurus* and *Torvosaurus*.

The acetabular notches of allosaurids and other megalosaurids are shown with smooth ventral surfaces extending from the medial surface out to the lateral edge of the shelf or hood extending out over the femur head (Gilmore, 1920; Madsen, 1976). *Sinraptor dongi* has a similarly smooth ventral surface shown for its acetabulum. TATE 0012's acetabulum retains this smooth surface in its anterior dorsal quadrant but a large step is found in the posterior dorsal quadrant that raises the ventral surface of the hood over the acetabulum well above the ventral surface of the medial portion of the notch.

TATE 0012 - Ilium Dimensions in mm. Ilium length, unrestored - 860. Ilium length, restored on the posterior from left ilium with a squared anterior edge - 910. Ilium length if restored with a rounded anterior edge - 950. Height above pubic peduncle - 420. Height above ischial peduncle - 350.

The size of the ilia relative to the torso can be expressed by the ratio of ilium to sacrum length. Sacra were not associated with all the ilia of Figure 13. The two allosaurs have the same ilium/sacrum ratio. The two ratios for TATE 0012 are for the square and rounded anterior end reconstruction.

TATE 0012 - Ratio of Ilium Length to Sacrum Length

Stonesfield *Megalosaurus* (Owen 1856) - 1.25 (assuming the ilium and sacrum were from the same animal). *Allosaurus fragilis* USNM 4734 - 1.34. *Allosaurus sp.* AMNH 5753 - 1.33 using a restored sacrum. TATE 0012 TATE 0012 - 1.47 to 1.53 depending on shape of anterior blade.

Pubis (Fig. 14, 15, 18)

The right pubis assigned to TATE 0012 was found with its distal end almost straight down. The proximal end was under the left caudal rib of the first caudal vertebra and in contact with it. The relatively small expansion of the distal end of the pubis and the enclosed obturator foramen differentiate it from allosaurids. Though a portion of the flange is missing in the vicinity of it, there appears to be a fenestra below the obturator foramen of TATE 0012. The presence of this fenestra differentiates the pubis of TATE 0012 from the other theropods with enclosed obturator foramina, such as *T. tanneri*, *Piatnitzkysaurus*, *Ceratosaurus nasicornis*, *Monolophosaurus* and *Sinraptor hepingsis*.

The shaft of the pubis is wider in the medial-lateral direction than in the anterior-posterior direction, figure 14. The distal end of the shaft enlarges to a boot about 170 mm in length which is similar in size to that of *T. tanneri*. In places in the quarry, nodules of matrix on the bone have partially destroyed the bone. The distal end of the pubis is one of the places that some of the bone surface has apparently been destroyed though the shape of it appears to be retained.

The shaft of the pubis curves slightly forward on the distal end, unlike *T. tanneri*, (figure 15 B), and the expansion is confined more to the distal end of the shaft. The pubis differs from *T. tanneri* in that the proximal end of the pubis bends more sharply around the channel for the alimentary canal and curves back medially over the top of this channel. The lateral extension of the bulge formed by this curvature is greater than that illustrated for *A. fragilis* (Gilmore, 1920) and more tightly constricts the alimentary canal. The articulation to the ilium appears to be crushed down somewhat in a ventral-medial direction. This crushing appears to increase toward the cranial end of the articular surface. This crushing appears to have increased the apparent constriction of the canal, the medial extension of the articular surface and shortened the pubis slightly. A medial symphysis is present immediately ventral to the channel for the alimentary canal. Part of this surface may be missing but it probably did not exceed about 100 mm in length. The first 20 to 30 mm of this suture extends in a cranial-caudal direction. A distal symphysis about 120 mm long was present, Figure 14H. A gap of about 230 mm in length appears to have been present between the two symphyses. The medial symphysis is straight and much longer for *A. fragilis*. The medial symphysis extends nearly to the distal symphysis for *T. tanneri*. Because of missing bone, the point that the medial symphysis of TATE 0012

ends relative to the articulating surface to the ischium is not known. It presumably stops short of the ischiac articulation in the caudal direction as no proximal symphysis appears between the ischia.

The pubis is short. The ratio of the pubis length to femur length is less for TATE 0012 than for other Jurassic theropods for which information is available even though the TATE 0012 femur is short for the size of the animal:

Ceratosaurus nasicornis..1.08

Piatnitzkysaurus floresii...0.82

Sinraptor dongi.....0.80

AMNH 5753.....0.79

TATE 0012.....0.74

Ischium (Fig. 14,15,18)

The right ischium was in contact with the pubis with distal end angling down about 45 degrees. The pubis and ischium were in nearly articulated position in terms of the angle between them but both were rotated 180 degrees about their shafts. The shaft of the ischium is similar to that of ***T. tanneri*** (Galton and Jensen, 1979) and ***Megalosaurus bucklandi*** (Owen, 1856) in that it curves downward but the curvature is much less. This curvature may be diagnostic of megalosaurids. Some older theropods, ***Coelophysis*** for example, have the downward curvature of the ischium (Galton and Jensen, 1979).

In contrast to the pubis, the ischium shows only a very slight curvature around the channel for the alimentary canal. Since the plane of the proximal end of the ischium was vertical in the matrix, it is unlikely that distortion by the matrix removed the curvature. Matrix distortion would act to increase curvature. The ischium shows no evidence of distortion. The ischia of TATE 0012 can only have a distal symphysis since the ilia must separate far enough proximally to allow space between the ilia for the sacrum. The distal symphysis can only be about 200 mm long to permit sufficient separation. The ischium shows no apparent articulating surfaces to the left ischium closer than about 200 mm from the distal end. The proximal two thirds of the ischia of TATE 0012, then, must form more of a "V" looking in the cranial direction than the "Y" as do the ischia of ***A. fragilis***, ***T. tanneri*** and ***C. nasicornis***.

The ventral edge of the ischium starts to thicken in the lateral direction about 70 mm from the articulation to the pubis. It thickens to about 10 mm at 130 mm distance from the joint where upon it thins suddenly back to a thin edge. The ventral surface appears broken suggesting that something like an obturator process may have extended ventrally from this thickened section.

The lack of a sheet of bone between the pubae and ischia extending from the distal ends of one to the distal end of the other distinguishes TATE 0012 from ***T. tanneri***. The presence of an obturator process also separates the two animals.

Pelvic Girdle (Fig. 15)

The size and close association of this pubis and ischium to the other parts of TATE 0012 leave little doubt that they belong to TATE 0012. An articulation of the right pubis and ischium with the right ilium of TATE 0012 is shown reversed in figure 15 A to facilitate comparison to figure 15C to H. The approximately 1 cm gap shown between the pubis and the pubic peduncle of the ilium has been left as a correction for the presumed axial crushing of the proximal pubis and the presumed missing articular surface of the pubic peduncle.

The pelvis of ***T. tanneri***, ***Megalosaurus bucklandi***, the Hubbel brothers allosaur AMNH 5753 and USNM 4734, figures 15 B, C, and D respectively are illustrated for comparison with TATE 0012, figure 15 A. The angle between the shaft of the pubis and ischium of TATE 0012 is about 67 degrees in figure 15 versus

about 65 degrees for *T. tanneri*, measured at the proximal end of the shaft (Galton and Jensen, 1979). The angles between the pubes and ischia of the two allosaurids as shown in figures 15 D and E are just under 60 degrees. However, the narrow connections of the ischium to the pubis and the ilium and the rocker shape of the joint surface of the pubic peduncle suggests the possibility of more flexure of the angle between the pubis and ischium for allosaurids than would be allowed by the longer suture between the pubis and ischium of TATE 0012 and *T. tanneri*. The proximal ends of both pubis and ischium of all the megalosaurids are more expanded than those of the allosaurids of figure 15. Unlike *T. tanneri*, the suture line between the pubis and ischium is straight for TATE 0012. This suture is not known for *M. bucklandi*.

The pubis of TATE 0012 appears much more robust than the ischium in lateral view. Both the other megalosaurs and the allosaurs, as illustrated in figure 15, have ischia that appear to be nearly as robust as the pubes in lateral view. In lateral view, the pubis of allosaurs are more gracile than TATE 0012. The pubis and ischium of TATE 0012 are similar to *T. tanneri*, *Sinraptor dongi* and *Piatnitzkysaurus floresi* in that the pubis and ischium are nearly the same length while for other Jurassic theropods, the pubis is longer. For 5753, the ischium is 90 percent the length of the pubis but for 4734 the ischium is a little more than 80 percent.

When the sacrum axis of the animals (estimated from the ilia) are aligned horizontal, the distal ends of the allosaur ischia are considerably elevated relative to the distal end of the pubae. The ischia of the megalosaurids are less elevated because of their curvature and their greater length relative to the pubes. The lower curvature of the ischium of TATE 0012 raises the distal end relative to *T. tanneri*. The distal ends of the pubis of *M. bucklandi* has been restored in figure 15 from *T. tanneri*. A solid sheet of bone closes the gap between the pubae of *T. tanneri*, and continues on back to close the space between the ischia (Galton and Jensen, 1979). This has not been observed in TATE 0012.

Though *Sinraptor hepingensis*, like TATE 0012, has a closed obturator foramen (Gao, 1992) and no fenestra, it is differentiated from TATE 0012 by a pubis that is much less robust than the ischium. *S. dongi* (Currie and Zhao, 1993) is similarly differentiated from TATE 0012. TATE 0012 may have had an obturator process like the prominent obturator process on the ischium found on sinraptors.

Piatnitzkysaurus is differentiated from TATE 0012 by having a robust ischium compared to the pubis. It lacks the fenestra in the proximal pubis.

Monolophosaurus is differs from TATE 0012 by virtue of the ischial fenestra, the lack of a fenestra in the proximal pubis, the strong curvature of the pubis, and the relative lengths of the pubis and ischium.

Ceratosaurus nasicornis differs in overall robustness as well as lacking a proximal pubic fenestra. If any single feature, such as the presence of fenestra, is not sufficient to distinguish the various taxa, the differences of the pubes and ischia combined with the very different ilium sets TATE 0012 apart from the other known species.

Gasosaurus constructus not only differs from TATE 0012 but from most other theropods by the configuration of the proximal pubis. In most theropods, a load applied along the axis of the pubis is absorbed mostly by the pubic peduncle. In *Gasosaurus*, however, the axis of the pubis is aligned relative to the iliac and ischial articulations such that a load applied along the axis is distributed about equally between the pubic peduncle and the pubic articulation to the ischium.

The expanded pubic boot of allosaurs and other theropods may have been used to support the animal's weight when it was resting (Marsh, 1896). The orientation of the pubic peduncle, more specifically the direction of the normal to the suture surface may indicate the direction of the forces imposed upon the ilium-pubis joint and therefore should reflect the posture of the animal at rest. In tyrannosaurs the peduncle, pubis and the pubic boot are oriented almost directly downwards, so the animal might rest with its torso horizontal. In *Deinonychus*, the peduncle, pubis and pubic boot slant downwards and backwards, so the animal might sit upright, with the torso erect (Ostrom, 1969). The allosaur pelvis of figure 15 have the peduncle slanting downwards and forwards but the angle of the pubis to the anterior spinal column appears to be 80 to 90 degrees like *T. rex*. The same angle for *T. tanneri* and TATE 0012 appears to be just under 80 degrees. Though the pelvic geometry of allosaurids and megalosaurids do not appear to differ greatly, the large difference between the pubic boot of megalosaurids compared to those of allosaurids and tyrannosaurids suggests some functional differences.

TATE 0012 Length of pubis and ischium in mm. Pubis - 610 at least, ischium to acetabular notch - 590.

Femur (Figure 16, 18)

The femur of TATE 0012 is extraordinarily massive and thick in the shaft, relative to its length. Its shaft circumference to length ratio, 0.45, is greater than the ratio of 0.4 of the adult type specimen of *Tyrannosaurus rex*, AMNH 973 (Osborn, 1906). Among the Morrison allosaurs listed in Madsen (1976), the ratio varies between 0.30 and 0.40 and is 0.37 for AMNH 5753. This ratio for the Stonesfield *Megalosaurus*, estimated from the drawings of Owen (1856), is about 0.4. The femora of 5753 and 973 compared at equal lengths in figure 16 illustrate the relative massiveness of TATE 0012.

The head of the left femur of TATE 0012 has a flange on the ventral margin of the medial end that produces a pronounced downward hook. This hook has the form of a circular disc that is attached to the medial end of the femur head and centered below the axis of rotation of the head. The disc may represent the attachment of an especially strong ligament holding the femur into the acetabulum. As seen in front or back view, the head of the femur of TATE 0012 does not turn inward as abruptly from the femur shaft as it does in allosaurs (Madsen, 1976; Gilmore, 1920), resembling the Stonesfield *Megalosaurus* femur in this respect.

The center of the 4th trochanter of TATE 0012 is located about 40 percent of the way down the femur, about the same location seen in the Stonesfield *Megalosaurus*. In allosaurids, the center of the trochanter is located 30 to 36 percent of the way down the shaft (Madsen, 1976; Gilmore, 1920). The center of the trochanter of AMNH 5753 (Fig. 16 I and J) is 39 percent of the way down the femur. On the average, the megalosaurids appear to have had greater leverage than the allosaurs, but the similar position of the 4th trochanter on 5753 means that the trochanter position cannot be used to diagnose megalosaurids.

Viewed from the distal end, the femur has the two condyles common to theropods. As in birds, the outer condyle fits in the notch between the fibula on the outside and the tibia on the inside; the inner condyle fits onto the flat surface on the posterior-inner corner of the tibia. The inner condyle of the left femur especially of TATE 0012 extends below the outer condyle. This suggests that the leg below the knee bent out relative to the axis of the femur. The femur of *Megalosaurus bucklandi* has this same feature. *Sinraptor* may also but the other theropods do not. The knees would need to be moved in toward the centerline of the animal to make the lower leg perpendicular to the ground in the lateral direction. The femur head is set on the shaft so that it slopes down laterally. The weight of the animal could be carried on the medial end of the femur head only so the distal end can swing in under the body. If the weight is distributed along the femur head instead, the femur would have to angle laterally out and down which would seem an awkward stance. Varying cartilage thickness may have shaped both the hip socket and knee to produce a more vertical configuration of the leg.

Only a very slight notch is present on the anterior of the distal end of the femur, figure 16 F, in contrast to the femora of *T. rex* and AMNH 5753, which have deep notches at that location. The scarring on the anterior face in conjunction with this notch is much less on the femur of TATE 0012 indicating that the associated bursa, if present, was smaller.

The head of the femur of TATE 0012 is rotated about 105 degrees with respect to the condyles, figure 16 H. This angle appears to be closer to 90 degrees for *T. rex* and AMNH 5753 judging from the views transverse to the shafts.

The ratio of the sacrum length to the length of the femur is 0.75 for both TATE 0012 and the isolated sacrum and ilium from Stonesfield (which may not belong to the same individual). Allosaurs have smaller sacra relative to femur length: the ratio of sacrum to femur ranges from 0.63 for USNM 4734 to 0.67 for USNM 8423.

Figure 16Q shows circumference of the femur divided by length, C/L, for a number of theropods. TATE 0012 had femurs that were much thicker relative to length, than allosaurs of similar size. In fact, the C/L of TATE 0012 is greater than even a giant theropod like *Tyrannosaurus*.

TATE 0012 Femur Dimensions in mm. Femur length - 830. Circumference of shaft - 376. Diameter - 120. Length from head to center of 4th trochanter - 330. Circumference/length ratio (C/L) - 0.45.

Tibia (Figure 17, 18).

The tibia of TATE 0012 is very thick for its length and resembles that of *Torvosaurus*. We estimate from Owen (1856) that the circumference to length ratio for the Stonesfield tibia was 0.38, a value similar to that of allosaurs, and the shaft was nearly circular. In *Torvosaurus* and TATE 0012 this ratio is about 0.44. The lower shaft is much more compressed front-to-back in TATE 0012 and *Torvosaurus* than in *Megalosaurus*. For TATE 0012, the cranial-caudal width is 0.71 of the medial-lateral width; in *Torvosaurus* this ratio is 0.67.

The articulated tibia and fibula of AMNH 5753 is shown in figure 17 H and I for comparison. Though 5753 is a larger animal, the tibia and fibula of TATE 0012 are more robust. The cnemial crest of TATE 0012 is shorter and less robust than that of 5753.

Carnivore tibiae have a flange on their outer surface that contacted the fibula. (In life this bony flange was embedded within a stout sheet of ligament that filled the space between the two bones). In allosaurs the flange is more strongly protuberant than in the megalosaurs, including TATE 0012. A 16 mm long by 6 mm wide foramen is present at the base of the fibular ridge on the TATE 0012 tibia as well as allosaur tibiae (Madsen, 1976). A plaster patch on the tibia of *Torvosaurus* near that location may cover a similar foramen (Britt, 1991).

In carnivorous dinosaurs, the astragalus is firmly attached to the lower end of the tibia; there is a triangular notch in the front surface of the tibia for the ascending process of the astragalus. In allosaurs this notch is tall, figure 17 H. In ceratosaurs and megalosaurs, including TATE 0012, the notch is low, figure 17 E, a primitive condition.

In TATE 0012, as in dinosaurs in general, there is a wide, shallow groove on the posterior surface of the lower end of the tibia. In birds, this groove supports the ankle cartilage, over which the calf muscle tendon passes (**ankle cart** in Fig. 18). The ankle cartilage functions very much like the knee cap in mammals in keeping the tendon away from the center of rotation, thus increasing the leverage.

Fibula (Figure 17)

The proximal end of the TATE 0012 fibula is less expanded in the cranial-caudal direction than in most other Late Jurassic carnivores, including *T. tanneri*. The shaft of the fibula is much more robust in the lateral direction (figure 17 E) than that of the allosaur AMNH 5753 (figure 17 E). The inner surface of the fibula head is flat and does not have the deep excavation seen in allosaurs.

The fibula apparently laid at more of an angle from a caudal position on the proximal end of the tibia to a cranial position on the distal end of the tibia, figure 17 E, than for allosaur. The fibula of AMNH 5753 parallels the tibia shaft, figure 17 I.

TATE 0012 Tibia and Fibula Dimensions in mm. Tibia length - 700. Circumference/length (C/L) - 0.44. Tibia shaft thickness, front to back - 80; side to side - 112. Fibula length - 650. Circumference/length - 0.21. Fibula length/ tibia length - 0.93.

Musculature (Fig. 18)

TATE 0012 shows a typical theropod notch between the anterior blade of the ilium and the pubic peduncle (**psoas notch** in Fig. 18). Through this notch would pass the psoas muscle, running from the underside of the trunk vertebrae to the anterior-external edge of the femur head.

(In this paper muscles are identified, where possible, by simple functional terms - such as "outer knee flexor" - **out flx** in Fig. 18. In addition, the megalosaur muscles are identified by their equivalents in human anatomy - for example, the "gluteal" - **glut** in Fig. 18. Most dinosaur anatomists use nomenclature derived from studies on lizards and crocodiles (Romer 1923; 1927a and b), and this system is listed in Fig. 18 in parentheses if the terms differ from those of human anatomy. In general, it is assumed that the human anatomical terms are preferable, since the vast majority of people who take anatomy courses are instructed in that system.)

The Nail ilium shows a low but sharp vertical ridge on the outer surface, just above the acetabulum; this ridge probably marks the posterior limit of the short muscles running from ilium to the outer surface of the femur head (equivalent to the gluteal muscles of human anatomy - **glut** in Fig 18). Some reconstructions show these muscles extending far posterior to the vertical ridge on the blade of the ilium (Romer, 1923). However, dissections show that the muscles in birds end just above the acetabulum, and therefore we interpret the ridge as the posterior limit of muscle origin.

The outer surface of the Nail ilium is raised all along the upper edge, and this raised zone has strong muscle attachment ridges and grooves that converge towards the acetabulum. Dissections show that the outer knee extensor attaches here in birds (equivalent to the **rectus femoris** in humans, **out ext** in Fig. 18). On the posterior part of the ilium, this raised zone is expanded downwards; the long knee flexor must have attached here (equivalent to the **biceps femoris** in humans; **out flx** in Fig. 18).

The sacral-hip attachments are much stronger posterior to the hip socket than anterior to the hip socket. It may be that the posterior sacral attachments brace the hip against the force of contraction of the muscles running from the brevis shelf on the ilium to the femur. This muscle, the short caudal-femoral division - **brevis** in Fig. 18 - would have been one of the thickest and strongest in the thigh. When the brevis contracted, it would pull the femur backwards. It also would tend to pull the posterior part of the ilium towards the thigh, and thus threaten to dislocate the ilium off the posterior sacral ribs. The wide, strong attachments of sacrals 3, 4 and 5 would oppose such dislocation.

The well developed brevis shelf in the lower edge of the posterior ilium of TATE 0012 opens outwardly rather than inwardly like other theropods since the posterior blade does not cover the medial blade in lateral view. This may mean that the brevis muscle may have pulled the femur somewhat inward.

The "lesser trochanter" (**les tro** in Fig. 18) is a thin prong that rises from the outer-anterior edge of the femur head. In birds, part of the deep knee extensor muscles (vastus anterior of human anatomy - **deep ext** in Fig. 18) attach to the outer surface of the trochanter. Short muscles from the ilium (**glut** and **psoas** in Fig. 18) attach to the outer surface of the femur head and behind the trochanter. The upper end of the trochanter of TATE 0012 is less expanded than those of allosaurs (Madsen 1976; Gilmore 1920) and resembles that of the Stonesfield megalosaur. A small trochanter implies that the deep knee extensor muscles were not as powerful as they were in allosaurs.

The "fourth trochanter" is the best developed muscle attachment site on the femur of carnivorous dinosaurs (**4th tro** in Fig. 18). The strongest muscle in the body, the **caudo-femoralis longus**, attaches to the inner surface of the fourth trochanter. This muscle originates from the underside of the caudal ribs and the lateral surfaces of the centra and chevrons. A shorter division, the **caudo-femoralis brevis**, attaches to the posterior edge and outer surface of the fourth trochanter; its origin is from the brevis notch, a pocket along the underside of the ilium posterior to the acetabulum.

The leverage these muscles have for pulling the hind limb backwards is determined in part by how far down the shaft the fourth trochanter is located. The further down the attachment site, the greater the leverage. That the center of the 4th trochanter of TATE 0012 and *M. bucklandi* is located so far down the femur relative to most allosaurids suggests the megalosaurids have greater leverage than the allosaurs. The leverage of the short caudal-femoral muscle and the long knee flexor in megalosaurs is further increased by the length of the origin on the lower edge of the ilium, which extends posteriorly more than it does in allosaurs. In general, greater leverage means a stronger but less swift movement of the leg.

Yet another way TATE 0012 shows greater muscular strength than allosaurs, relative to femur length, is the greater length of the upper edge of the ilium. This edge controls the width of the outer knee extensor (= rectus femoris of human anatomy, the **out ext** (Fig. 18)). Therefore the cross-section of the outer knee extensor of TATE 0012 must have been larger than that of an allosaur with the same femur length.

The TATE 0012 femur has a shallow groove below the fourth trochanter, on the posterior-outer edge of the femur, just above the knee joint. In birds and crocodiles the adductor muscles running from the ischium attach here (**ad** in Fig. 18).

In all allosaurids and tyrannosaurs there is a huge scar on the inner part of the anterior femur surface, just above the knee. In mammals a fluid-filled extension of the knee joint (bursa) lies here, as well as a short

muscle that runs to the knee extensor tendon; a similar condition probably occurred in allosaurs and tyrannosaurs. In TATE 0012, as in ceratosaurs and the Stonesfield megalosaur, there is only a faint depression in this region, indicating that the knee joint structures were not well developed here.

There is a faint scar on the outer surface of the fibula for the outer knee-flexing muscle (equivalent to the biceps femoris of human anatomy; **ext flx** out flx. Fig. 18).

The lateral foot flexor (**peroneus, lat foot flx** in Fig. 18) must have originated from the upper part of the outer fibular surface, as it does in birds and crocodiles. The anterior foot extensor (**tibialis anterior, foot ext** in Fig. 18) must have originated from the anterior-outer surface of the tibia, as it does in reptiles and birds. The main calf muscle, the **gastrocnemius (gas** in Fig. 18) must have originated from the upper part of the posterior and inner tibia surfaces, as it does in birds.

BONES OF MEGALOSAURIDS OTHER THAN TATE 0012

A much longer left pubis of a megalosaurid was unearthed near the right pubis and ischium of TATE 0012, Fig. 1. A partial left ischium that articulates to the large pubis was found within 2 meters east of the pubis. A third ilium may be that of a small megalosaurid.

Pubis (Fig. 19)

At 790 mm length, this pubis is 30 percent longer than the pubis of TATE 0012. Like TATE 0012, it has an enclosed obturator foramen with a fenestra below it. Upon comparison with the pubis of TATE 0012, the most obvious difference is that the large pubis is much more gracile. While the shaft width of the longer pubis in lateral view is the same as that of TATE 0012; in anterior view, the shaft width is actually more than 5 percent smaller than the pubis of TATE 0012. The pubic boot of TATE 0012 appears to be more robust. The proximal end of the large pubis appears to have suffered some compression in the antero-posterior direction.

Ischium (Fig. 19)

A large left ischium lacking the distal end of the shaft was found about 1 m east of the of the large pubis. This ischium differs in structure from TATE 0012 in that the proximal plate has a fenestra. Also, the mid-shaft cross section is much larger than that of TATE 0012. This ischium, even though missing the expanded part of the distal end, is nearly as long as the ischium of TATE 0012. This ischium is sufficiently large to belong with the large pubis and the joint surfaces of the two do match. The suture line between the pubis and ischium has a bend like that of *T. tanneri*. This suture is straight for TATE 0012.

The large pubis and ischium are shown articulated in figure 20. The distal end of the ischium has been restored so its length relative to the pubis is about 5 percent less than the pubis, like TATE 0012. The angle the axis of the pubis cannot be specified because the connection to the ischium was crushed and has been reconstructed in figure 20. The large pubis and ischium differ from those of TATE 0012 in that the ischium of the larger animal relative to the pubis is much more robust. The large pubis is more gracile than that of TATE 0012 with a smaller distal end. This pubis and ischium do not represent those of any known non-allosaurid theropods for many of the same reasons that those of TATE 0012 do not. The fenestra in the proximal ischium differentiates the large pubic bones from all except *Monolophosaurus*. The relatively straight pubis in conjunction with the second fenestra distinguish this animal from *Monolophosaurus*. The closest relative of this large theropod may be TATE 0012.

Ilium (Fig. 21)

The ilium differs from *T. tanneri* and *Megalosaurus* in that the acetabular notch is narrow like those of allosaurids and TATE 0012. The hood over the acetabulum drops on the lateral edge like that of *T. tanneri* but the posterior and medial blades are more similar to allosaurids. The curvature of the dorsal edge and especially that of the anterior blade of the ilium and the angle and suture surface of the pubic peduncle suggests a megalosaurid. If only the posterior portion of the ilium up to the acetabulum were available, the ilium would be identified as an allosaurid. If only the remaining portion only were available, the animal would be labeled something other than allosaurid. Since the anterior portion has features similar to *Megalosaurus*

and *T. tanneri*, it may be megalosaurid. It differs from TATE 0012 in that it is shorter relative to its height and considerably more curved on the dorsal edge.

On the other hand, of the three allosaurids known to be in the quarry, the ilia of only one have been recovered thus far. Since the ilium of Fig. 21 has some similarities to those of allosaurids, it could as well be the ilium of an allosaurid. More parts of the theropods are needed to assign the small ilium.

DISCUSSION

.Since three coracoids attributed to megalosaurids have been recovered, at least two megalosaurids must be present in the quarry site. The length of the larger scapula-coracoid (Baker et al. 1992) and the larger pubis both exceed those assigned to TATE 0012 by 30 %. These two probably represent one animal. However, the estimated length of the skull of *Edmarka rex*, based on the jugal found, (Bakker, et al. 1992) would appear to be too large to belong to the same animal that had the larger pubis and ischium. Larger presumed megalosaurid pubae, those of CEUM 3301 found near Price, Utah by the staff of the College of Eastern Utah Museum would be a more appropriate size to be that of *Edmarka rex*. They could be pubae of an adult *Edmarka*.

If the ilium of figure 21 is megalosaurid, it is too small to fit the large Nail pubis and ischium. This raises the possibility that remains of as many as four megalosaurids could be present in the quarry.

The larger Nail pubis and ischium differ from those of TATE 0012 in the distal end expansion and is much more gracile. The larger scapula differs from that attributed to TATE 0012 in that it does not expand toward the distal end (Bakker, et al. 1992). The 30% longer bones translates to an animal whose weight is around twice that of TATE 0012 even though it is relatively gracile. The neural arches of the caudal vertebrae of TATE 0012 were fused to the centra suggesting that it had reached adult size.

The difference between TATE 0012 and the animal belonging to the larger pubis, ischium and scapula could be sexual dimorphism, variation or that they are different species. Differences resulting from variation and sexual dimorphism within species of dinosaurs has been explored but not yet defined, see Carpenter and Currie (1990). The difference in size and in features between the bones common to both seem great enough that the two represent different species at least. The larger bones are tentatively assigned to *Edmarka* as the large scapula-coracoid were previously. *Edmarka rex* has been described by Baker, et al. (1992) as a megalosaurid of different genus than *T. tanneri*.

As discussed in detail above, some of bones attributed to TATE 0012 that are common to those assigned to *Megalosaurus bucklandi* are similar. However, the dorsal edge curvature and the posterior end of the ilia differ. The pubae differ in the number of foramen and TATE 0012 lacks the strong curvature seen in the ischium of *M. bucklandi* and *T. tanneri*.

Some of the bones of TATE 0012 are similar to those of *T. tanneri*. The chevrons, the tibia and the fibula from Nail Quarry are sufficiently similar to suggest that they could be the same species. The caudal vertebrae of TATE 0012, where they overlap, are similar in appearance judging from photographs of the vertebrae of *T. tanneri* but comparison via photographs is not satisfactory.

The pelvic bones all differ from those of *T. tanneri*. The pelvic structure of *T. tanneri* preserves the basic ilium shape developed back in the Middle Jurassic. But TATE 0012 evolved an ilium that had strong resemblance to that of allosaurs for some features (straight upper edge) and to tyrannosaurids in others (vertical pubic peduncle). In some features, such as the shape of brevis shelf, TATE 0012 seems unique among large theropods. The function of the hind limb may have been quite different in TATE 0012 based on the robustness of the femur, and differences in the ilium and acetabulum. Though TATE 0012 retains features similar to *T. tanneri*, the components of the pelvis do not.

The Pubis differs from that of *T. tanneri* in the apparently short length of the of the medial symphysis and the relatively small channel for the alimentary canal. The ischium lacks a medial symphysis and apparently has an obturator process. The nearly complete symphysis barrier of *T. tanneri* does not exist in TATE 0012.

The differences suggest that TATE 0012 must be a different species from *T. tanneri*, at the minimum but it seems much more likely to be a different genus. In fact, Tate 0012 was given the genus name *Brontoraptor* in earlier versions of this paper. However, at the suggestion of Ken Carpenter, Denver Museum of Natural History, we will wait to claim a new genus until we have made better comparisons to the *Torvosaurus tanneri* material. Also, the quarry is still being worked and we may find more material.

Museum Abbreviations AM, AMNH - American Museum of Natural History, New York, New York; BYUVP - Brigham Young University Vertebrate Paleontology, Provo, Utah; TATE - Tate Museum, Casper Wyoming; USNM - United States National Museum, Washington DC; UUV - University of Utah Vertebrate Paleontology, Salt Lake City, Utah.

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TABLE I

TATE 0012 Sacral Vertebrae Dimensions (mm)

Cent #	Length Ctrline	Anterior Height	Anterior Width	Post. Height	Post. Width	Centrum Width
1	130	135	169	120*	125	65
2	130	120*	125	110*	105	47
3	120	110*	105	110*	124	62
4	120	110*	124	110*	118	64
5	120	110*	118	135	145	71

* Estimated dimension

FIGURE CAPTIONS

Figure 1. Quarry map showing relative positions of the bones of TATE 0012 and *Edmarka rex*. TATE 0012: Fibula (1), tibia (2), right and left ilium (3) and (4), sacrum (5), 1st caudal (6), left femur (7), coracoid (8), 2nd caudal (10), 10th and 11th caudals (11) and (12), right pubis (14), right ischium (15), right femur (16), right scapula (17) and a chevron (19). 1996 season: 3rd caudal (20), 4th caudal (21), 5th caudal (22), 7th caudal (23), 8th caudal (24) under (25), 9th caudal (25), chevrons (26) to (30) numbered in increasing length. *Edmarka rex*?: partial left ischium (9) and left pubis (18). Unidentified origin: sternal plate? (13).

Figure 2. TATE 0012? atlas in anterior (A), posterior (B), left lateral (C) and ventral (D) view without the neuropophysis. A ventral view of the right neuropophysis and a cross section of the atlantal intercentrum is shown at (E). A dorsal view of the intercentrum with the dorsal portion of the neuropophyses remove is shown at (F) and the ventral side of the dorsal expansion of the neuropophyses at (G). TATE 0012? axis in left lateral (H) posterior (I), ventral (J) and dorsal (K) views. The postzygapophyses are shown in ventral view in (L).

Figure 3. Sacrum of TATE 0012. Left lateral view (A), ventral view (B). Diagram of left lateral view (C) SR - sacral ribs, TR -transverse processes. Sacrum in left lateral view attached to the ilium. Outline of sacral ribs (dashed lines) positioned on the outline of the ilium (solid line) (D). Ventral view of restored pelvis of TATE 0012 (E).

Figure 4. First caudal vertebra TATE 0012 in anterior (A), posterior (B), right lateral (C), ventral (D) and anterior centrum (E) views. Also shown: axial cross section through the mid centrum (F), dorsal cross section through centrum pleurocoels (G) and enlargements of dorsal (H) and anterior (I) views of the prezygapophyses.

Figure 5. First caudal vertebra of AMNH 5753 in anterior (A) and left lateral view (B). The centrum is 113 mm in length at the centerline.

Figure 6. Views of the second caudal vertebra of TATE 0012: anterior (A), posterior (B), right lateral (C) and ventral with a cross section of the mid centrum (D). The first and second caudal vertebrae articulated to the sacrum.

Figure 7. Views of the # 10? caudal vertebra of TATE 0012: anterior (A), posterior (B), right lateral with cross sections (C), and ventral with a cross section of the mid centrum (D) and enlargements of lateral (E) dorsal (F) views of prezygapophyses.

Figure 8. Views of the # 11? caudal vertebra of TATE 0012: anterior (A), posterior (B), right lateral with cross sections (C) and ventral with a cross section of the mid centrum (D) and enlargements of lateral (E) dorsal (F) views of prezygapophyses.

Figure 8G. TATE 0012. Width of the anterior-most caudal vertebrae centra as a function joint number assuming various vertebrae missing. Top Left: complete from vertebrae #1 to 12 missing # 11. Top right: complete from #1 to 12 missing #6 and 11. Bottom left: complete to 13 missing #6, 7 and 12. Lower right: complete to # 11 missing #6.

Figure 8H. TATE 0012. Height of the anterior-most caudal vertebrae centra as a function joint number assuming various vertebrae missing. Top Left: complete from vertebrae #1 to 12 missing # 11. Top right: complete from #1 to 12 missing #6 and 11. Lower right: complete to # 11 missing #6.

. Bottom left: *Allosaurus* #8367, widths and heights of the anterior ends of the first 7 caudal vertebrae.

Figure 8I Top TATE 0012. Full heights of the caudal vertebrae assuming # 1 to 11 missing #6. The dotted line shows #1 to 12 missing #6 and 11, #5 and 10 are incomplete.

Bottom: Lengths of the first 12 caudal vertebrae of TATE 0012, assuming # 6 and 11 are missing, compared to an *Allosaurus* USNM 8367 and *Ceratosaurus Nasicornis* USNM 4735.

Figure 9. Views of the # 20? caudal vertebra of TATE 0012: anterior (A), posterior (B), right lateral with cross sections (C), ventral with a cross sections of the caudal centrum, (D). Enlargements of lateral (E) and dorsal (F) views of prezygapophyses.

Figure 10. Views of an anterior chevron of TATE 0012, probably from the vicinity of the 10th caudal: posterior (A), anterior (B), right lateral (C) and proximal looking perpendicular to the attachment surface. The chevron is shown articulated to the paired # 10 and 11 caudal vertebrae of TATE 0012 in reversed view (E). Chevrons # 10 through 12 of *Torvosaurus tanneri* are shown articulated to caudal vertebrae 10 through 13 (F) and an allosaur chevron of the # 11 caudal is shown articulated to two repeated # 13 allosaur caudals (G).

Figure 11. Right Scapula and coracoid of TATE 0012 in lateral view (A), and enlarged lateral view of proximal end (B). The scap-coracoid in ventral view (C) and an enlarged ventral view of the proximal end (D); enlarged view of the scapular suture surface (E). The left scap-coracoid of AMNH 5753 in lateral (F) and ventral (G) views. The left scap-coracoid of *Coelophysis?* in lateral view.

Figure 12. Right ilium of TATE 0012, in lateral (A), medial (B) and ventral view (C). (D) Outline (heavy line) of TATE 0012 superimposed on outline of *Torvosaurus* (dashed line), taken from Britt, 1991.

Figure 13. Iliia of some Jurassic theropods normalized to equal lengths. TATE 0012, reversed right (A); *Megalosaurus* (Owen, 1856) (B); *Torvosaurus* BYUVP 4977 (Britt, 1991) (C); *Edmarka sp.* (D); *Allosaurus fragilis* USNM 4734 (Gilmore, 1920) (E); allosaur AM 5753, (Christman, 1994) reversed right (F); *Ceratosaurus nasicornis* USNM 4735 (Gilmore, 1920) (G); *Piatnitzkysaurus floresi* PVL 4073 (Bonaparte, 1986) (H); *Sinraptor dongi* IVPP 10600 (Currie and Zhao, 1993) (I); *Syntarsus rhodesiensis* (Raath, 1977) (J); *Marshosaurus* (Madsen, 1976b) (K); *Stokesosaurus* (Madsen, 1974) (L);

Monolophosaurus, (Zhao and Currie, 1993) (M); ***Albertosaurus sarcophagus*** (Osborn, 1905) (N); ***Albertosaurus libratus*** (Osborn, 1905) (O); and ***Tyrannosaurus rex*** (Osborn, 1906) (P).

Figure 14. Right pubis of TATE 0012 in lateral view (A), posterior view with cross sections (B), anterior view (C) and medial view (D). Right ischium of TATE 0012 in dorsal view (E), lateral view with cross sections (F) and medial view (G).

Figure 14H. The right pubis reflected and paired to illustrate the fit.

Figure 15. Lateral view of right pubis and ischium of TATE 0012 shown in articulation with the reversed left ilium (A). Lateral views of articulated left ilium, pubis and ischium (Pelvis) of ***Torvosaurus tanneri*** (B), ***Megalosaurus bucklandi*** (C), and two allosaurs AMNH 5753 (D) and USNM 4734 (E).

Figure 16. Left femur of TATE 0012. Lateral (A), anterior (B), posterior (C), ventral (D), Proximal (E) and distal (F) views. Cross sections of the femur are shown in (G). The angular orientation of the condyles to the femur head is shown in (H). The shaft is hollow as shown by cross section E from B to F though the hollow decreases in diameter towards the proximal end. Left femur of allosaur AMNH 5753 in medial (I) and anterior (J) views. Posterior (K), lateral (L), medial (M), and anterior (N) views of the left femur of AMNH 973, the ***Tyrannosaurus rex*** type specimen. The femur of AMNH 5753 in proximal (O) and distal (P) views. The femur of AMNH 973 in proximal view Q.

Figure 16R. Ratio of Femur circumference to length as a function of length for some large Mesozoic theropods. The miscellaneous theropods are, highest to lowest, C/L, ***Pianitzkysaurus***, ***Sinraptor dongi*** and ***Ceratosaurus nasicornus***.

Figure 17. Left tibia and fibula of TATE 0012. Lateral view (A), lateral view of fibula articulated to tibia (B), medial view with cross sections (C). Fibula, medial view (D), Articulated tibia and fibula, anterior view (E), proximal view (F), and cross section of articulated shafts (G) at G in (B). Articulated tibia and fibula of AMNH 5753 in anterior view (H) and lateral view (I).

Figure 18. Reconstruction of the major musculature of the hip and hind leg of TATE 0012. Lateral view of ilium, thigh and shin bones, with ischium and pubis restored after *Megalosaurus* - (A). Deep muscles - (B). Superficial muscles - (C). Abbreviations (usual terms for muscles given in human anatomy in parenthesis; terms used for lizard-crocodile muscles also given if different from terms of human anatomy): **ad** - femur adductors (=adductor magnus). **ankle cart** - cartilage pulley at ankle, over which gastrocnemius tendon passes. **brev** - caudo-femoralis brevis. **brevis shelf** - origin of **brev** muscle. **foot ext** - anterior foot extensor (=tibialis anterior). **4th troc** - fourth trochanter. **gas** - gastrocnemius. **glut** - gluteal (=ilio femoralis of lizards). **il-is lig** - ilium-ischium ligament. **in flx** - inner knee flexor (=hamstrings of human anatomy; pubo-ishio femoralis of lizards). **lat foot flx** - lateral foot flexor (=peroneus longus). **les tro** - lesser trochanter. **long** - caudo-femoralis longus. **out ext** - outer knee extensor (=rectus femoris of human anatomy; ilio-tibialis of lizards). **out flx** - outer knee flexor (=biceps femoris of human anatomy; ilio-fibularis of lizards). **psoas** - psoas (=pubo-ishio femoralis internus of lizards). **pub** - pubic peduncle. **pub-is lig** - pubis-ischium ligament (Bakker, 1994)

Figure 19. Medial (A), posterior (B), lateral (C) and anterior (E) views of the Left pubis assigned to ***Edmarka rex***. The transverse views are not orthogonal to the longitudinal views. The partial left ischium assigned to ***Edmarka rex***. Dorsal (E), lateral (F), and medial (G) view.

Figure 20. An articulation of the pubis modified to correct for antero-posterior crushing of the proximal end and the ischium of figure 19. The ischium has been restored by extending it to where it is 96 percent of the length of the pubis.

Figure 21. The ilium attributed to a juvenile ***Edmarka*** in ventral view.