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OBSERVATIONS ON THE MORPHOLOGY AND PATHOLOGY OF THE GASTRAL BASKET OF *ALLOSAURUS*, BASED ON A NEW SPECIMEN FROM DINOSAUR NATIONAL MONUMENT

Daniel J. CHURE

Dinosaur National Monument, Box 128, Jensen UT 84035, USA
dan_chure@nps.gov

Abstract: A well preserved and complete gastral basket of *Allosaurus* (DINO 11541) corrects a number of earlier misinterpretations of this structure in *Allosaurus*. The basket consists of eighteen rows of gastralia. The first row has only one element per side and these do not overlap medially but rather form a cranially facing notch. All other rows have two elements per side, the medial one being the longer. The right and left median elements overlap at the midline of the basket. *Allosaurus* has only four elements per gastral row.
Previous interpretations for *Allosaurus* have been as high as nine elements per row. The supposed fused, V-shaped median gastral element is now known to be a furcula. The supposed four lateral elements in USNM 4734 are actually all part of a single median element injured during life and healed as a series of pseudoarthroses. The presence of pseudoarthroses and calluses in other median gastral elements of USNM 4734 further support this interpretation.
The presence of similar pathologies in the gastralia of another specimen of *Allosaurus* (USNM 8367) as well as in the dorsal ribs of a specimen of *Acrocanthosaurus atokensis* (SMU 74646) suggests that such injuries were not uncommon in allosauroid theropods. These injuries may be the result of either struggles with prey or intraspecific behavior, such as kicking or head-flank butting.

Key words: Dinosauria, Theropoda, Osteology, Allosaurus, Gastralia, Jurassic, Morrison, Pathology

Observations sur la morphologie et les pathologies de la cage gastrale d'*Allosaurus* basées sur un nouveau spécimen du *Dinosaur National Monument*, Etats-Unis d'Amérique

Résumé : Une cage gastrale complète en bon état de préservation d'*Allosaurus* permet de corriger d'anciennes interprétations de cette structure chez ce dinosaure. Le cage en question consiste en 18 rangées de gastralia. La première rangée présente un seul élément par côté ; les deux éléments de cette paire ne se recoupent pas médialement mais forment une encoche dirigée cranialement. Les autres rangées possèdent deux éléments par côté, le médian étant le plus long. Les éléments médians gauches et droites se recoupent sur l'axe de symétrie. *Allosaurus* ne possède que quatre éléments par rangée gastrale.
Les anciennes interprétations pour *Allosaurus* ont proposé jusqu'à 9 éléments par rangée. L'élément gastral supposé fusionné en forme de V s'est révélé être une furcula. Les quatre éléments latéraux supposés de USNM 4734 sont en fait les fragments d'un unique élément central fracturé durant la vie de l'animal et cicatrisé sous forme d'une série de pseudarthroses. La présence de pseudarthroses et de cals sur d'autres éléments de la série gastrale de USNM 4734 soutient cette interprétation.
La présence de pathologies similaires sur les gastralia d'un autre spécimen *d'Allosaurus* (USNM 8367) et sur les côtes d'un spécimen d'*Acrocanthosaurus atokensis* (SMU 74646) indique que de telles blessures n'étaient pas rares chez les théropodes allosauroides. Ces blessures peuvent être le résultat de luttes avec des proies ou de comportements intraspécifiques tels que des ruades ou des coups de tête contre les flancs.

Mots clés : Dinosauria, Theropoda, Ostéologie, Allosaurus, Gastralia, Jurassique, Morrison, Pathologie

INTRODUCTION

Allosaurus is the most abundant theropod in the Late Jurassic Morrison Formation (Foster & Chure, 1998, 2000 ; Chure *et al.*, 2000). As a result of this rich fossil record it is one of the best known theropods and has been the subject of several monographic studies (Gilmore, 1920; Madsen, 1976; Chure, 2000). Because of this *Allosaurus* is a critical taxon in many phylogenetic analyses of the Theropoda.

However, the discovery of a spectacularly complete and articulated specimen of *Allosaurus* in Dinosaur National Monument has clarified several aspects of *Allosaurus* morphology; namely the presence of a furcula, the composition and morphology of the wrist, and the gastral basket. Both the wrist and the furcula have already been described (Chure & Madsen, 1996; Chure, 1999, and in press). The present report focuses on the gastral basket.

INSTITUTIONAL ABBREVIATIONS

AMNH = American Museum of Natural History, NY.
BYU = Earth Sciences Museum, Brigham Young University, UT.
CMNH = Carnegie Museum of Natural History, PA
DINO = Dinosaur National Monument, UT.
MOR = Museum of Therockies, MT.
SMU = Southern Methodist University, TX.
USNM = United States National Museum, Washington, D.C.

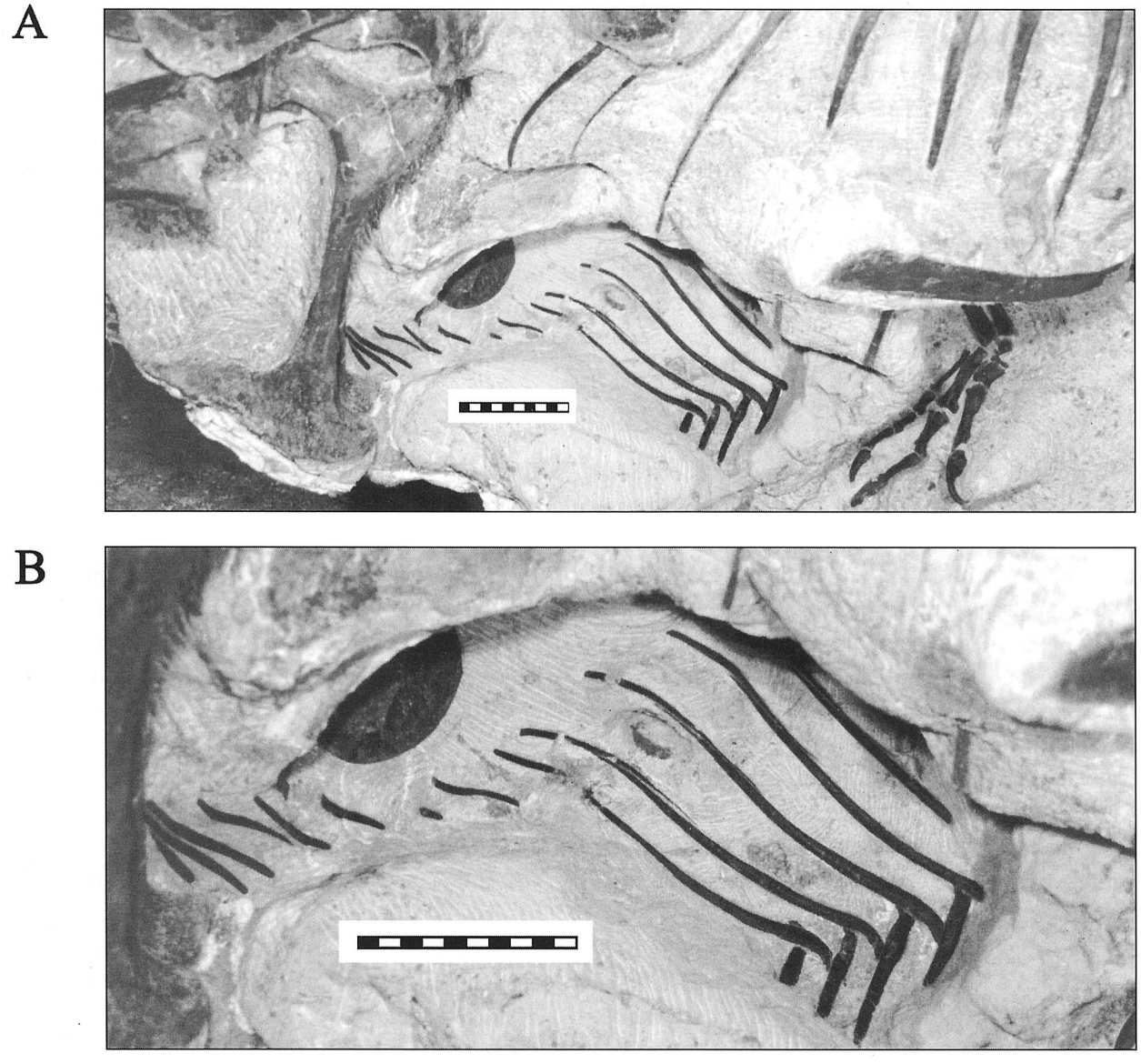

Figure 1. Gastral basket of *Allosaurus* (DINO 11541) in dorsal view.
A. Position of basket between pectoral and pelvic girdles. B. Close up of median and lateral elements. Scale bar in cm.

DESCRIPTION

The specimen (DINO 11541) is a new species of *Allosaurus*, currently under description (Chure, 2000). It was found in the upper portion of a 60 cm. layer of conglomerate at the base of a 1.4 m deep paleochannel in the Salt Wash Member of the Morrison Formation of Dinosaur National Monument (Hubert & Chure, 1992). The skeleton was in the hyperdorsoflexed attitude strongly suggestive of desiccation of the body before burial (Gradzinski, 1969; Weigert, 1927), which probably explains how the skeleton remained articulated in the high energy river environment. Part of the right (stratigraphically up) forelimb and hindlimb and the right side of the skull is missing, along with the middle part of the tail. The right side of the gastral basket was damaged before discovery and many of the lateral elements are missing or incomplete. However, the gastral basket was in-place between the pectoral girdle and pelvis (fig. 1).

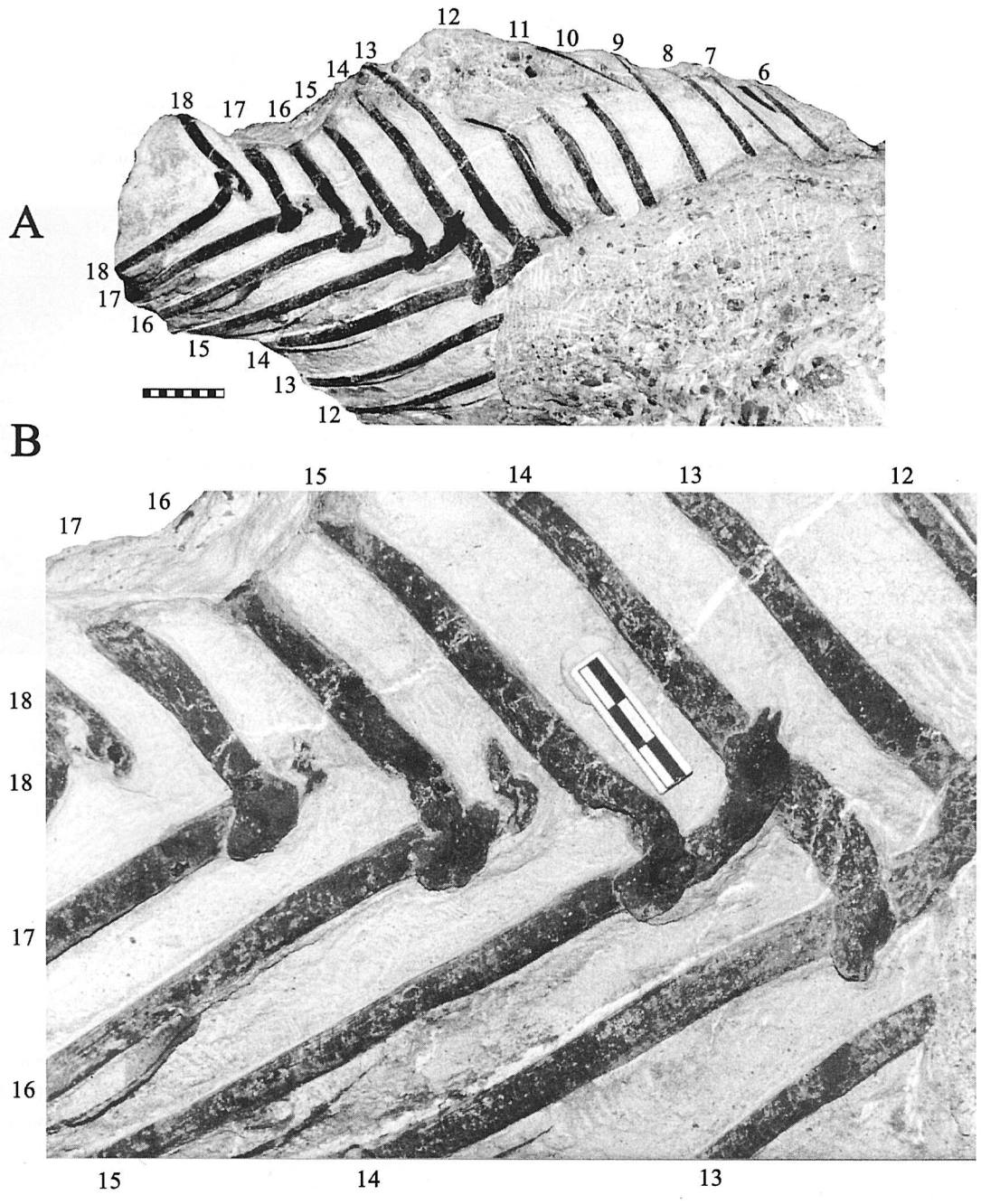

Figure 2. Gastral basket of *Allosaurus* (DINO 11541) in ventral view. A. View showing narrowing of basket towards caudal end. B. Close up showing displacement of contact between median elements. Numbers refer to gastral row, numbered from front of basket. Scale bar in cm.

The basket is in a large block of sandstone along with the vertebral column, left dorsal ribs, the left scapula, and the left femur. As a result, the cranial half of the basket is exposed in dorsal view and the caudal half in ventral view. The cranial half of the cuirass is broad and flat (possibly due in part to postmortem dorsoventral flattening), with a gentle dorsal curvature. The caudal part is narrower and more V-shaped in cross-section (figs. 1, 2) and on the better preserved left side the caudal part of the basket can be seen to be lateral to the pubic boot (fig. 3).

The basket contains eighteen rows of gastralia. The first row is different than the rest of the cuirass in several ways (fig. 4). In the first row there is only one element on each side, rather than two. These elements do not overlap medially. Instead, the medial end of each is a vertical, oval surface and the right and left gastralia meet such that their medial faces form a cranially facing right angle notch (fig. 4A, C). There are no grooves on the cranial margin of these elements for contact with lateral gastralia, further confirming that the first row consists only of the median elements (fig. 4B).

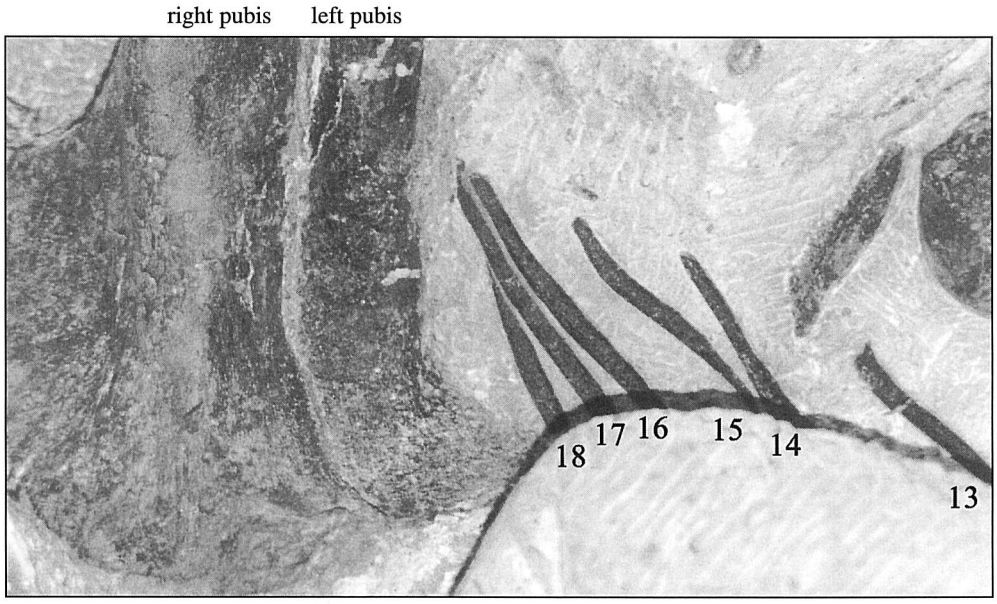

Figure 3. Medial view of left lateral elements of gastral basket in DINO 11541. Note their position lateral to distal end of left pubis. Numbers refer to gastral row, numbered from front of basket.

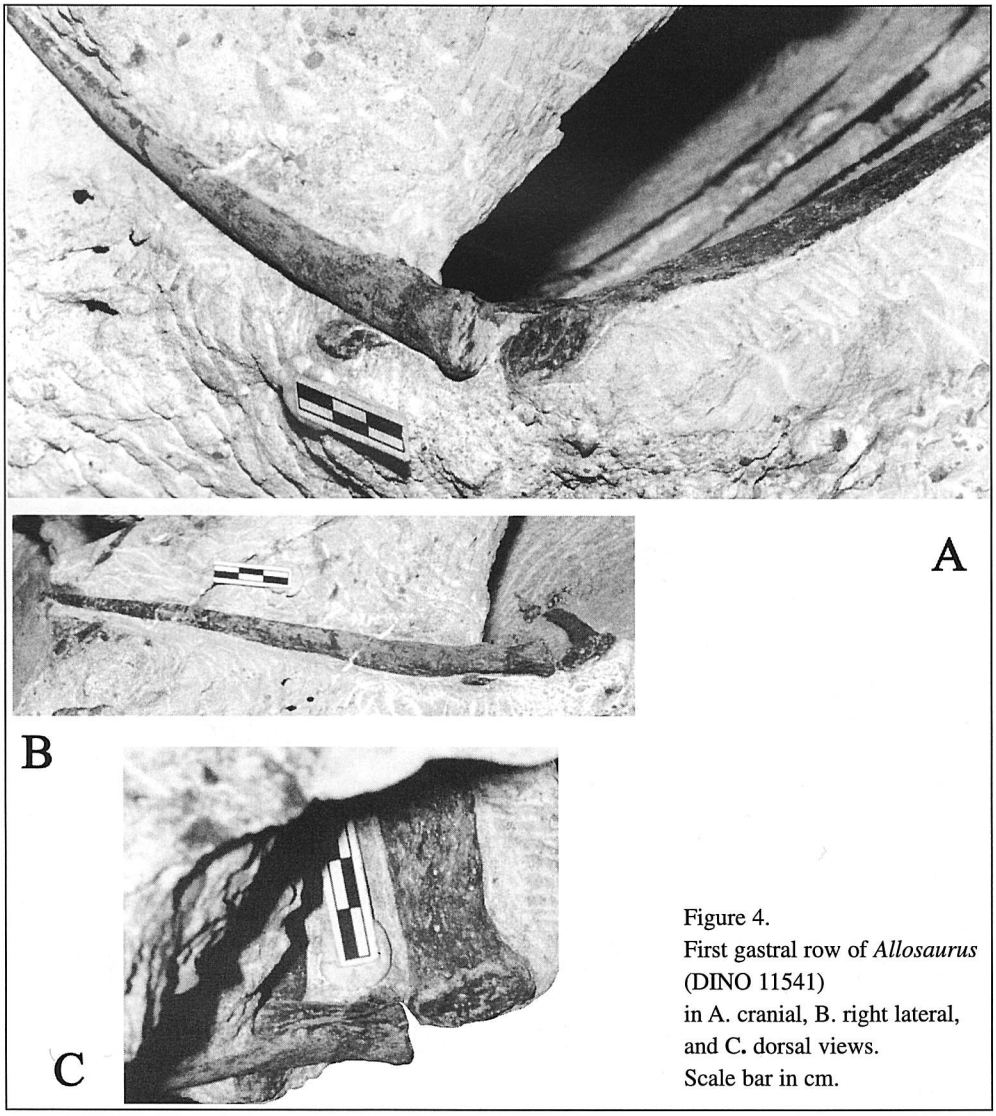

Figure 4.
First gastral row of *Allosaurus* (DINO 11541)
in A. cranial, B. right lateral, and C. dorsal views.
Scale bar in cm.

In gastral rows two through eighteen there are four gastralia per row, two median and two lateral (fig. 5). There is no median V-shaped element like the one reported by Gilmore (1920) in USNM 4734. The median elements are longer and more robust than the lateral ones and slightly sinuous in dorsal or ventral view (fig. 1). The medial end is caudally curved and expanded (fig. 2). The medial ends overlap such that in ventral view the right median gastralium is ventral to the left. The ventral surface of the medial end of the left gastralium is convex and this fits into a concavity on the dorsal surface of the medial end of the right gastralium (fig. 2B). Laterally the median elements taper to a point (fig. 5B). A groove on the cranial face of the median gastralia is for the contact with the lateral element (figs. 5B, 6).

There has been postmortem separation between the median elements of the cuirass (fig. 5).

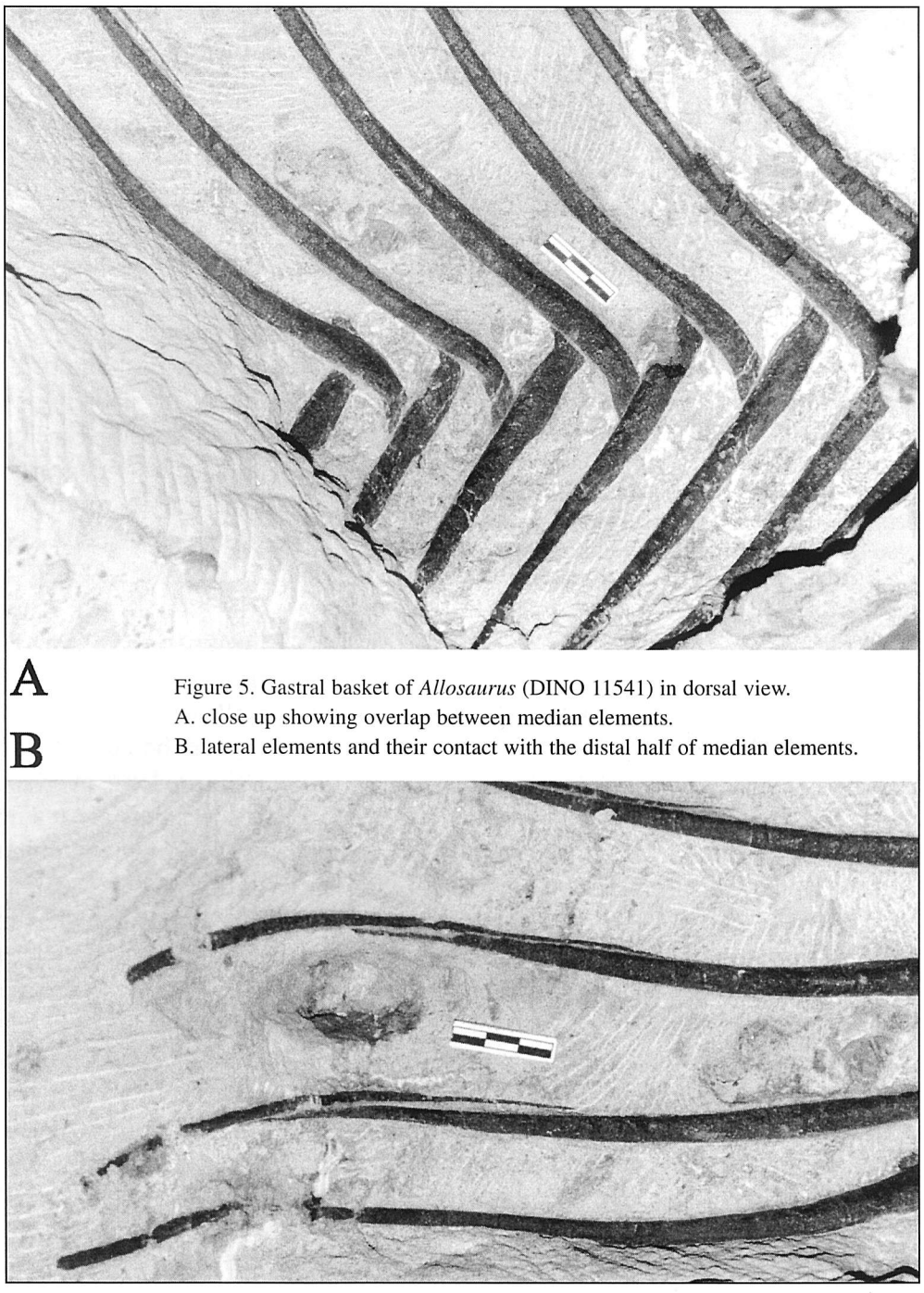

Figure 5. Gastral basket of *Allosaurus* (DINO 11541) in dorsal view.
A. close up showing overlap between median elements.
B. lateral elements and their contact with the distal half of median elements.

The ventral overlapping of the right median elements is best seen in median gastral pair 17. There has been slight disarticulation of this contact in segments 18 and 16. In segments 13, 14, and 15 there has been considerable cranial shifting of the left median elements, to the extent that, for example, the medial end of left median gastralium 15 overlaps the shaft of right median gastralium 14. This offset continues, to a varying degree, through gastral segment 2.

The lateral elements are shorter than the median gastralia (figs. 1A, B, 5B). This is typical for theropods, although the condition is reversed in some maniraptorans (Norell & Makovicky, 1997). Each lateral element has a wide, truncated lateral edge and tapers medially (fig. 5B). Each lateral element has a groove and fits in a groove on the craniodorsal edge the medial element (fig. 6). This overlap between median and lateral elements was not strong, as there is some separation along this contact in all gastral rows in DINO 11541.

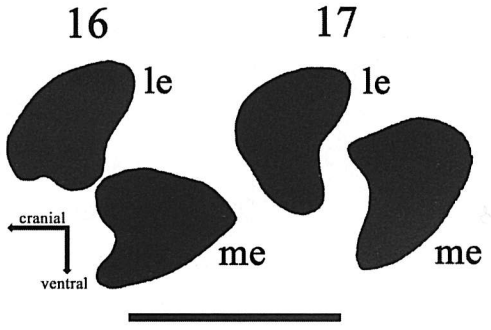

Figure 6. Cross section of median and lateral pairs of right gastralia in rows 16 and 17 of DINO 11541, drawn from a broken surface. Cross section of row 16 at about 185 mm lateral from midline of basket. Cross section of row 17 at about 160 mm lateral from midline of basket. Spacing between rows 16 and 17 reduced for illustrative purposes. le = lateral element, me = median element Scale bar = 1 cm.

DISCUSSION

The gastral cuirass of DINO 11541 is the most complete and best preserved for any non-coelurosaurian theropod. Gastralia in *Allosaurus* are usually isolated and incomplete (Cleveland-Lloyd Dinosaur Quarry collections in the University of Utah, MOR 693, AMNH 5753, CMNH 33903, USNM 8367). An exception is a partial basket in USNM 4734 described by Gilmore (1920). However, in light of DINO 11541 several errors of interpretation can now be identified in that work.

The gastral basket of USNM 4734 is still in matrix, in three blocks which fit together. It has been dorsoventrally flattened and retains none of its original curvature. The basket is exposed in ventral view, although some of the elements have been rotated along their long axis and some are displaced. Most of the elements preserved are median and lateral elements of the right side, although there are a few scattered left median elements present.

Based on his study of USNM 4734 and 8367 Gilmore (1920) estimated that there were at least seven, and possibly nine, gastralia per row (at least three, and possibly four, laterals and a V-shaped median element). This is an exceptionally high count, the highest for any theropod. Gilmore (1920: p. 54) found support for this high count in one gastral row in USNM 4734 which he thought preserved four laterals on one side (figs. 7, 8A, B).

However, the V-shaped element in USNM 4734, of which only one was found, is now known to be a furcula, based on the in-situ furcula found in DINO 11541 (Chure & Madsen, 1996). This drops Gilmore's count to six or possibly eight. Examination of the row which Gilmore thought to preserve four lateral gastralia shows that the three proximal segments are likely to be parts of a single, medial gastralium, which was damaged during life and healed pathologically.

The gastralia of USNM 4734 show a number of breaks and pathologies. Some are green breaks which occurred at the time of death or post-mortem (fig. 7) and need not concern us any further. Other pathologies are the result of injuries sustained during life which subsequently healed. These are of two types. The first are healed fractures indicated by calluses (fig. 8C, D, E). The second are pseudoarthroses, breaks which during healing formed moveable joints (fig. 8A, B). Several of these pseudoarthroses have well formed ball and socket articulations. In all theropods the contacts between medial and lateral gastralia are long, overlapping, sliding contacts. Ball and socket joints are unknown in gastral baskets, further supporting the interpretation that these are pseudoarthroses.

Thus, anomalies in the gastral basket of USNM 4734 can best be interpreted as being the result of an injury during life to the median gastral elements. The subsequent regular movement of the gastral basket during breathing and locomotion resulted in the development of a number of pseudoarthroses. This interpretation, coupled with the recognition that Gilmore's median element as a furcula, reduces the count in USNM 4734 to four elements per row, a median and lateral element on each side. This is consistent with what is now known based on DINO 11541 and is typical for theropods (Claessons, 1996).

There is a growing interest in how broad patterns of pathologies may provide insight into vertebrate paleobiology at various taxonomic levels (Rothschild & Martin, 1993; Rothschild & Tanke, 1992). Among dinosaurs such analyses have been done for ornithischians but not yet undertaken on the same scale for theropods. Nevertheless, it may be significant that calluses and pseudoarthroses in the gastralia like those in USNM 4734 are also are present in the scattered gastralia of another *Allosaurus fragilis* specimen,

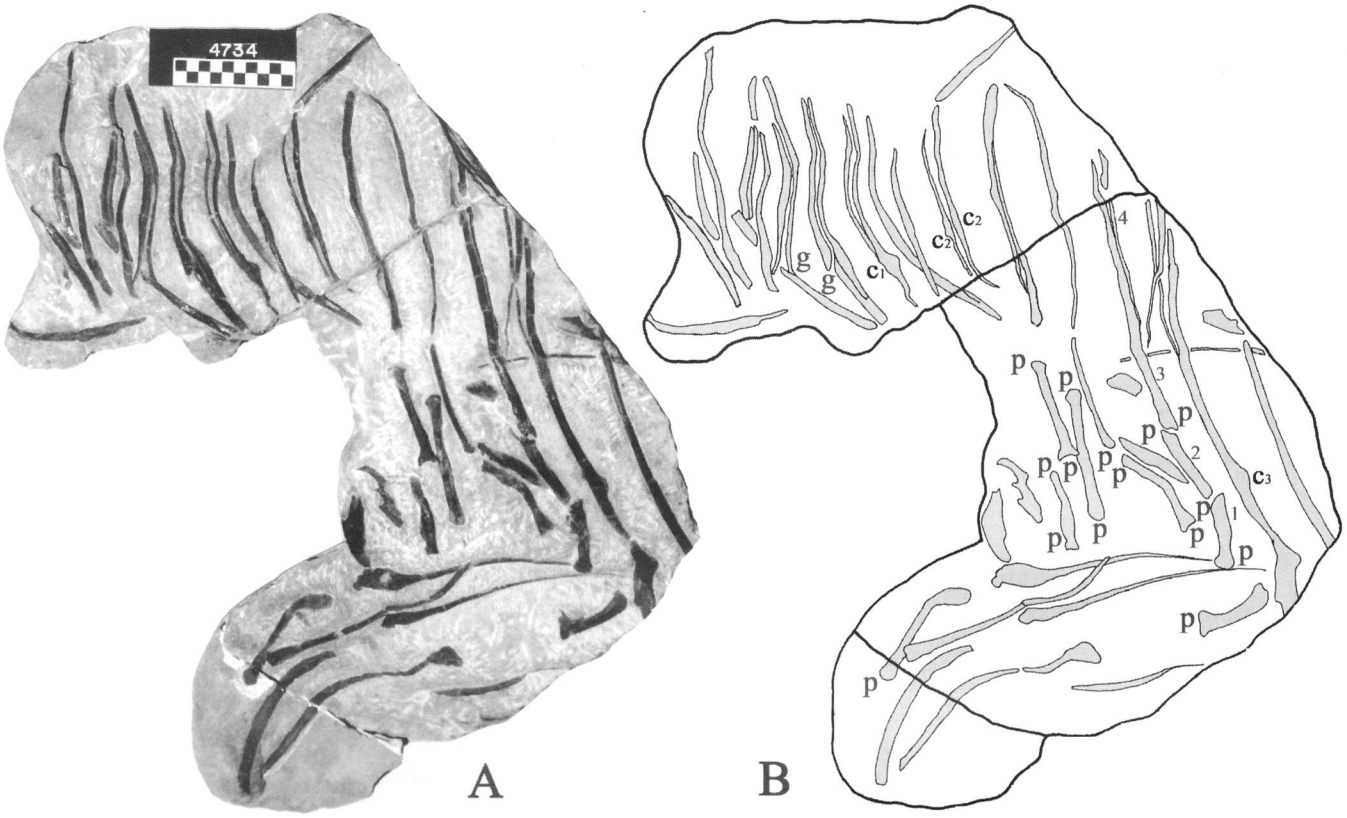

Figure 7. Gastral basket in *Allosaurus fragilis* (USNM 4734). A. Photograph of basket in ventral view. B. Explanatory line drawing. c1, c2, c3 = calluses on medial gastral elements, g = green breaks, p = peudoarthroseal surfaces on median gastral elements, 1,2,3,4 = 4 lateral gastral elements as identified by Gilmore (1920). Scale bar in cm.

USNM 8367 (Gilmore, 1920: fig. 38). This suggests that injuries to the flanks and belly region may not have been uncommon in *Allosaurus* and that those injuries were not always fatal. These injuries may be the result of intraspecific behaviors, such as head-flank butting or kicking (Paul, 1988), or possibly from struggles during the subduing of prey, although we have no direct knowledge of what *Allosaurus* preyed on or even if it was a predator. Flank injuries may be of broad behavioral significance, at least among allosauroids, as Harris (1998) has reported a series of calluses and pseudoarthroses on the dorsal rib shafts of *Acrocanthosaurus atokensis*.

Finally, the discovery of an in-place furcula in DINO 11541 led to the identification of a furcula in a number of specimens of *Allosaurus*, both described and undescribed (Chure & Madsen, 1996). Alcober *et al.* (1998) reported a furcula in an unnamed carcharodontosaurid allosauroid from Argentina. However, one can not jump to the conclusion that any V-shaped element is a furcula, because the few gastral baskets known in basal tetanurines show significant morphological variation between genera, including the presence of V-shaped median elements.

The gastral basket in *Acrocanthosaurus atokensis* has at least four V-shaped median elements in the caudal region but only paired overlapping median elements are present in the cranial region (Harris, 1998). These V-shaped elements are clearly fused median gastralia as they have grooves along their cranial margins for contact with the medial part of the the lateral gastralia. Thus *Acrocanthosaurus* retains the general theropod pattern of four elements per row.

In *Poekilopleuron bucklandi* (Eudes-Deslongchamps, 1838) there are at least seven V-shaped median elements but, in contrast to *Acrocanthosaurus*, they are in the cranial half of the basket and are more sinuous than in *Acrocanthosaurus*. The only known specimen of *P. bucklandi*, including the gastralia, was destroyed in an Allied bombing raid on Caen in 1944 (Taquet 1998). Fortunately, a cast of the basket has recently been rediscovered in Paris (Ronan Allian, pers. comm. 2000), and is currently inder study.

Finally, two V-shaped median gastral elements have been collected from the Dry Mesa Quarry in the Morrison Formation of Colorado (fig. 9). While these elements are not referable to *Allosaurus*, large specimens of the neoceratosaurian *Ceratosaurus* sp. and the spinosauroid *Torvosaurus tanneri* are known from the site (Britt, 1991). This suggests that median V-shaped gastral elements may have a wide distribution in basal tetanurines.

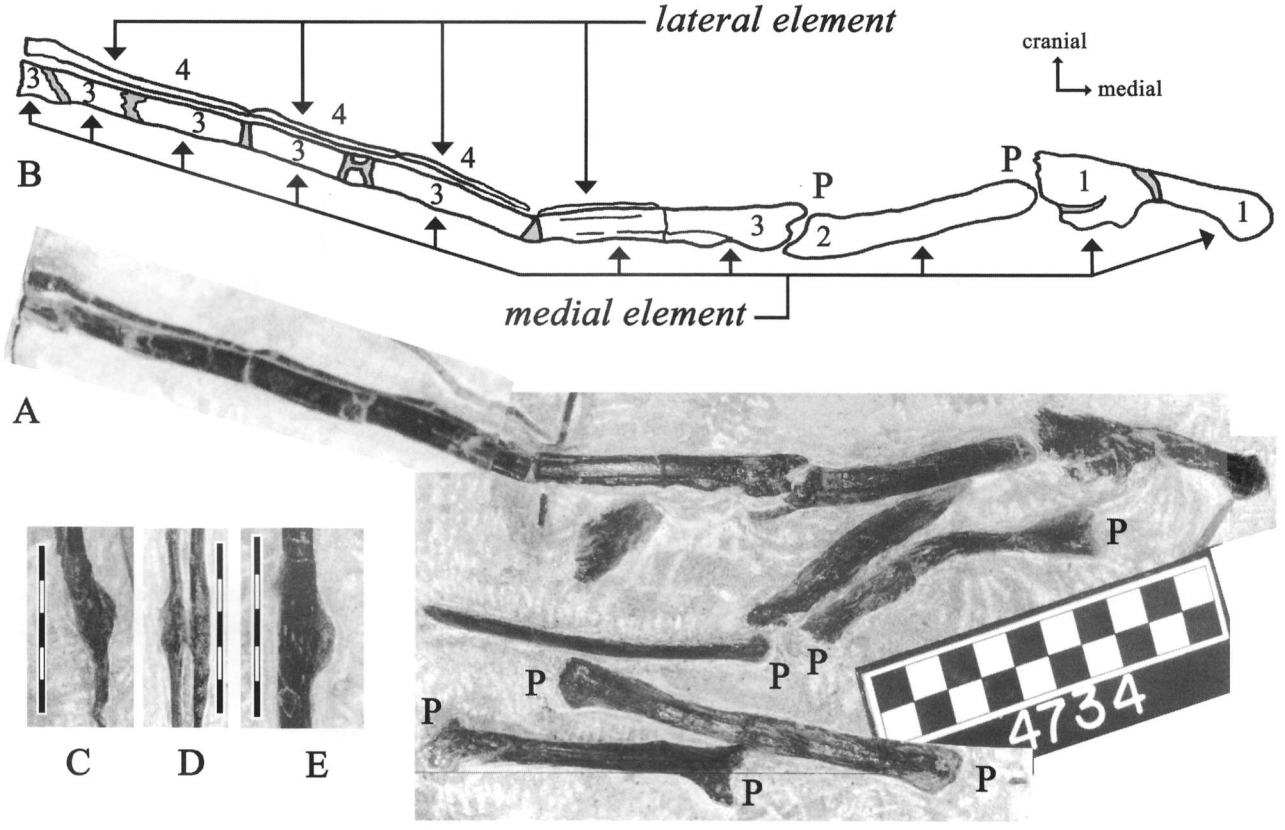

Figure 8. Pathologies in the the gastralia of *Allosaurus fragilis* (USNM 4734). A. Close up of the element interpreted by Gilmore (1920) as showing four gastralia on one side of basket, as well as several segments of median elements with pseudoarthroseal surfaces. B. Explanatory drawing of A. C. Close up of callus (c1 in fig. 7B). D. Close up of paired calluses (c2 in fig. 7B). E. Close up of callus (c3 in fig. 7B). 1,2,3,4, = Gilmore's interpretation of four elements on one side of basket. Lateral element, median element = identification in this work of Gilmore's elements.

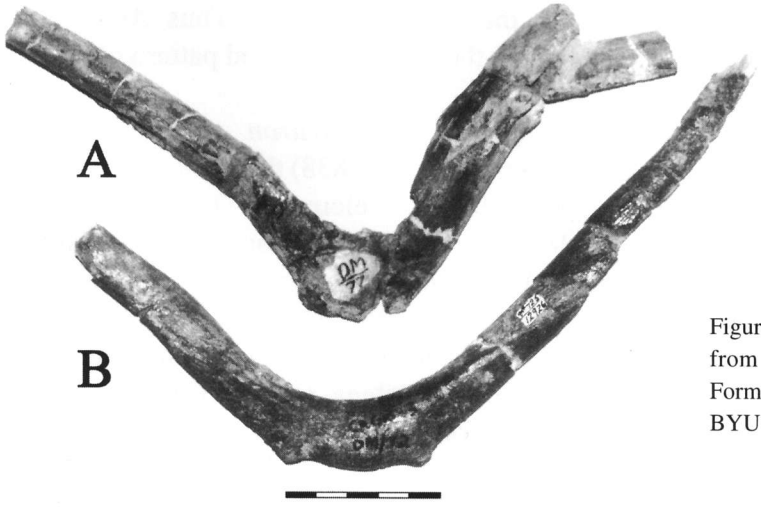

Figure 9. Likely V-shaped median gastral elements from the Dry Mesa Quarry in the Morrison Formation of CO. Ventral view. A. BYU 5115 B. BYU 12926. Scale bar in cm.

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