SKULL AND TOOTH MORPHOLOGY AS INDICATORS OF NICHE PARTITIONING IN SYMPATRIC MORRISON FORMATION THEROPODS

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ABSTRACT: The Upper Jurassic Morrison Formation of the western United States has produced a diverse assemblage of large, carnivorous dinosaurs. Analysis of the skulls and teeth assigned to two of the best preserved of these sympatric Morrison Formation genera, *Allosaurus* MARSH and *Ceratosaurus* MARSH, reveals three distinct forms. These three skull and tooth morphologies are interpreted as evidence of feeding and behavioural niche partitioning among the top Morrison carnivores. One form, represented by some members of the genus *Allosaurus*, has a shortened face, and a tall, wide skull, with short, posteriorly-directed teeth. Other *Allosaurus* specimens have a long face, a low skull profile, and longer, more vertically oriented teeth. *Ceratosaurus* also has a long face, but is distinguished from the latter allosaurid by exaggeration of the depth of the skull and by having even longer and broader teeth. Distinct lacrimals and nasal ornaments seen in the three forms would aid in interspecific recognition, and reduce incidences of direct competitive interaction. The general rarity of *Ceratosaurus* in the Morrison suggests competitive displacement of *Ceratosaurus* by the long-toothed, long-skulled allosaurs.


INTRODUCTION

Many distinct genera of large, carnivorous dinosaurs are known from quarries in the Upper Jurassic Morrison Formation. Some individual quarries have produced multiple genera of carnivorous forms: Cleveland-Lloyd Quarry in Utah has produced *Ceratosaurus* MARSH, *Allosaurus* MARSH, *Marshosaurus* MADSEN and *Stokesosaurus* MADSEN (MADSEN, 1976), Dry Mesa Quarry Marsh, in Colorado has produced *Torvosaurus* GALTON & JENSEN, *Ceratosaurus*, *Allosaurus*, *Marshosaurus*, and *Stokesosaurus* (BRITT, 1991), and Como Bluff quarries have produced associated *Allosaurus*, *Torvosaurus*, and other large carnivorous forms (BAKKER, 1996).

A review of the literature and of published skeletal illustrations and reconstructions suggests that if there are not two species of *Allosaurus* from the Morrison Formation, there is at least evidence for two 'morphs'. PAUL (1988) argued for two, possibly three, species. BRITT (1991) and CHURE (pers.
comm., 1997) also claim at least two species of Allosaurus. MADSEN (1976: pl. 2) produced a composite skull for Allosaurus based on material from the Cleveland-Lloyd quarry. This restored skull shows marked differences between right and left examples of the maxillae, lacrimal, pterygoids, and nasals suggesting that this Allosaurus is a chimera. MADSEN (1976), commenting on the variation in the number of tooth alveoli shown by his extensive sample of maxillae, states that the variation could not be explained by different growth stages of the individuals who possessed the elements. Gilmore's illustrations (GILMORE, 1920) of the reconstructed skull of "Antrodemus" LEIDY (currently regarded as a junior synonym for Allosaurus) is very different from the reconstructed skull presented by MADSEN (1976).

The dinosaur remains at the Cleveland-Lloyd, Dry Mesa, and Como Bluff quarries were all deposited within 3 million years of each other (SMITH, 1996). With several different types of large, bipedal carnivore in the Morrison environment there would have been extensive niche overlaps with resultant interspecific competition if they were living together. The competition between these sympatric carnivores would have been heightened by the fact that they were all of roughly the same body length of 6-8 m. The morphological differences within the genus Allosaurus could be interpreted as showing the effects of natural selection reducing intraspecific competition by producing two different forms of Allosaurus. The present paper aims to interpret cranial and dental morphology, as it relates to niche partitioning and feeding strategy, for three, well known, sympatric theropods - Ceratosaurus and two forms of Allosaurus. For the purposes of this paper, one form of Allosaurus, based on the MADSEN (1976) reconstruction, will be referred to as Allosaurus. The other Allosaurus, the one illustrated by GILMORE (1920), will be referred to as "Antrodemus".

CARNIVORE ECOLOGY

It is a common observation in ecology that the invisible hand of natural selection acts to reduce the physiological, morphological, and behavioural similarities between competing organisms, thus lessening the depression of fitness due to niche overlap. These reductions in similarities were termed "character displacements" by BROWN & WILSON (1956).

Evidence for character displacement in sympatric carnivores can be found in extant faunas. DAYAN et al. (1989, 1990) presented separate instances that show niche partitioning among modern carnivorous mammals. In one study (DAYAN et al., 1989), three sympatric species of weasel (Mustela sp.), from eight different localities across North America were shown to have consistent, regularly spaced groupings of mean canine diameter. In another study (DAYAN et al., 1990), small felids were also shown to fall into regularly, spaced categories with respect to mean canine diameter. PIMM & GITTLEMAN (1990), commenting on the work of DAYAN et al. (1989, 1990), noted that these small mustelids and felids form a natural guild with members of the guild sharing the same prey.

There are also examples of character displacement in fossil carnivores. WERDELIN (1996) found a regular partitioning of carassial total lengths and blade lengths in late Miocene and early Pliocene hyaenids from Eurasia and Africa. The similarity of the hyaenid partitioning to that seen in extant, sympatric canids led WERDELIN (1996) to infer similar ecological roles for these early hyaenids who filled the niches now filled by the true canids. MASSARE (1987), in a study of tooth variation in Mesozoic marine diapsids, found a range of tooth forms similar to that seen in modern carnivorous marine mammals. The material studied by MASSARE (1987) did not come from a single deposit or time plane, but her study indicates that it is possible to identify feeding specializations and niche partitioning among carnivorous diapsids.

The large theropods of the Morrison Formation form a guild, one specialized for locating, killing, dismembering, and ingesting large prey. The skulls and teeth of large theropods are their most variable features, and the best indicators of how predatory niches were divided up. In their review of mammalian carnivore teeth, VAN VALKENBURGH & RUFF (1987: 380) state that "...canine teeth of large predators are used to kill and dismember prey and to wound or threaten other individuals." and "...differences in bite power and behaviour should be reflected by differences in canine shape if teeth are designed to resist expected loads." It seems reasonable to extend these observations to other taxa such as dinosaurs to infer how their teeth, and the associated skull bones and muscles, would have functioned.

METHODS

Published illustrations of Ceratosaurus and "Antrodemus" (GILMORE, 1920) and Allosaurus (MADSEN, 1976) were used as the primary data sources. Outline drawings of the three skulls are presented in Figure 1.

Skull lengths were measured from the posterior end of the occipital condyle to the anterior margin of the premaxillae from ventral views of the three taxa. The postorbital heights were taken along lines that ran from the skull table, through the approximate center of the lower temporal fenestra, and intercepted perpendicularly with the ventral margins of the jugals. The antorbital heights were taken from...
the suture lines between the nasal and frontal bones and the ventral margins of maxillae. The antorbital widths were measured along lines that crossed the anteriormost rims of the antorbital fossae. The skull of the holotype of *Ceratosaurus* described by Gilmore (GILMORE, 1920) is severely crushed laterally, and his restoration in dorsal view is too wide. Based on the interpretations of other skull features of *Ceratosaurus* (see discussion below), the dimensions of the narrower skull restoration provided by PAUL (1988) were used for the calculation of the width/length ratios of *Ceratosaurus*. The length of the supratemporal fenestra was taken along the midline of the fenestra from the left side of the skulls.

Tooth crown heights were taken along lines oriented perpendicular to the ventral margins of maxillae. The crown height of a tooth is the distance from the maxilla margin to the ventralmost part of the tooth crown. Tooth width was measured as the fore-aft basal length of the visible portion of the crown. Tooth angle measurements represent the angle between the vertical length measuring line and a line running from the anterior base of the tooth to the distalmost tip of the crown.
VARIATIONS IN SKULL CHARACTERS AND FUNCTIONS

Table I and Figure 2 summarize the morphometric results. The most striking feature of the tabulated ratios is the closeness of the values between Ceratosaurus and Allosaurus in all but two cases. Only in relative maxillary tooth size and surangular form are Allosaurus and "Antrodemus" similar. These findings suggest that the two 'morphs' of Allosaurus, each had very different feeding strategies and, possibly, different behavioural patterns as well. There appears to be convergence between Allosaurus fragilis Marsh and Ceratosaurus nasicornis Marsh towards having a low, narrow skull, long teeth, and a wide gape. Ceratosaurus retains its morphological distance, and ecological uniqueness, by having longer teeth and more elaborate skull ornamentation. These observations, as well as functional interpretations, are expanded upon below.

TOOTH ORIENTATION

Ceratosaurus and Allosaurus have premaxillary and maxillary teeth that are more vertically oriented than are the teeth of "Antrodemus". The first two appear to be converging on applying deep bites to their prey. If the teeth of theropods are viewed as general purpose tools (Farlow et al., 1991), then the elongate teeth of Ceratosaurus and Allosaurus would correspond to multiple copies of the long, slashing teeth of canids (Van Valkenburgh & Ruff, 1987). The associated elongation of the skull in these two genera (see Skull Form below) further supports this slashing mode of attack as well.

TOOTH SIZE

Comparisons of the relative tooth sizes reveal niche partitioning among the three genera. Both Ceratosaurus and Allosaurus, with their more vertical teeth, have teeth that are a larger fraction of skull length than "Antrodemus". Ceratosaurus is distinguished from Allosaurus by having a crown height/skull length ratio 50% greater than Allosaurus.

The exceptionally long teeth of Ceratosaurus have several possible interpretations. Ceratosaurus could be feeding on different prey than the long-toothed Allosaurus. With large carcasses commonly available (Dodson et al., 1980), it could be that Allosaurus and Ceratosaurus were scavenging different portions of a large carcass, thus avoiding a potential ecological overlap. The exaggerated form of the teeth in Ceratosaurus could be related to interspecific recognition (see skull heights discussion), or could have importance in intraspecific behaviour, outside any function related to prey capture or ingestion (Coombs, 1990; Tanke & Currie, 1995).

TOOTH FORE-AFT BASAL LENGTH/LENGTH

"Antrodemus" has the broadest teeth in lateral view, when comparisons of the tooth fore-aft basal length/crown height ratios are made. This increased length in the antero-posterior direction would greatly increase the strength of the teeth about an axis oriented transversely to the jaw margin (Farlow et al., 1991). When combined with the marked posterior inclination of the teeth in "Antrodemus", it seems that the teeth have been selected to maximize their ability to withstand forces induced by the head pulling back while the teeth clamped onto the prey. A similar form of tooth is seen in the extant Komodo dragon (Varanus komodoensis) (Auffenberg, 1981). This large lizard violently tugs its head backwards with the jaws securely clamped to the prey.

SKULL HEIGHTS

The postorbital and antorbital relative heights of the skulls of Allosaurus and Ceratosaurus are both low, while those of "Antrodemus" are high. A similar pattern is seen when cat and dog skulls are compared. Dogs use their long, low skulls to deliver quick, slashing bites to wound and harass prey. Cats use their short, high skulls to deliver a deep, strong bite that holds onto the prey (Van Valkenburgh & Ruff, 1987). The longer skulls and jaws of canids have larger bending moments about the jaw articulation resulting in increased stresses within the skull when a bite force is applied. The shorter, and therefore stronger, skull of felids allows them to deliver a much stronger bite, either to hold more tightly to prey or drive the teeth deeper into the prey. By inference, the short face of "Antrodemus" suggests that it had a stronger bite than that of the long faced Allosaurus.

The relatively taller skull of Ceratosaurus, when compared with Allosaurus, could be explained in terms of resistance to bending. The longer and broader teeth of Ceratosaurus would present increased frictional resistance to penetration because of their increased surface area. More powerful jaw adductor muscles, applying forces to propel the bigger teeth, would increase the stresses experienced by the whole skull. Increasing the depth of the skull in Ceratosaurus would increase its flexural rigidity and hence its strength.

An alternate interpretation could be that the taller skull of Ceratosaurus, its apparent height further enhanced by high lacrimals and a nasal horn, would aid in species recognition. In an environment hosting several similar carnivores, these skull ornamentations can be viewed as acting to reduce niche overlap by permitting quick recognition of conspecifics without the risk of direct contact/competition. A similar case could be made for the two forms of lacrimals seen in the allosaurids: low and rounded in Allosau-
TABLE I
Comparison of ratios for three Morrison Formation theropods.

<table>
<thead>
<tr>
<th></th>
<th><em>Ceratosaurus nasicornis</em></th>
<th><em>Allosaurus fragilis</em></th>
<th>&quot;Antrodemus valens&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maxillary Tooth Orientation (Average Angle)</td>
<td>sub-vertical (31°)</td>
<td>sub-vertical (31°)</td>
<td>backwards (39°)</td>
</tr>
<tr>
<td>Maximum Maxillary Tooth Crown Height/Skull Length</td>
<td>0.127</td>
<td>0.081</td>
<td>0.072</td>
</tr>
<tr>
<td>Tooth Fore-Aft Basal Length/Crown Height Ratio</td>
<td>0.386</td>
<td>0.345</td>
<td>0.455</td>
</tr>
<tr>
<td>Skull Height/Length (Postorbital Region)</td>
<td>0.417</td>
<td>0.405</td>
<td>0.532</td>
</tr>
<tr>
<td>Skull Height/Length (Antorbital Region)</td>
<td>0.324</td>
<td>0.305</td>
<td>0.381</td>
</tr>
<tr>
<td>Skull Width/Length (Postorbital Region)</td>
<td>0.295</td>
<td>0.413</td>
<td>0.544</td>
</tr>
<tr>
<td>Skull Width/Length (Antorbital Region)</td>
<td>0.256</td>
<td>0.249</td>
<td>0.320</td>
</tr>
<tr>
<td>Supra Temporal Fenestra Length /Skull Length Ratio</td>
<td>0.108</td>
<td>0.107</td>
<td>0.136</td>
</tr>
<tr>
<td>Anterior &amp; Posterior Nasal Suture Amplitudes</td>
<td>low</td>
<td>low</td>
<td>high</td>
</tr>
<tr>
<td>Surangular Dorsal Form</td>
<td>low</td>
<td>raised</td>
<td>raised</td>
</tr>
<tr>
<td>Quadrato-Squamosal Orientation</td>
<td>inclined</td>
<td>inclined</td>
<td>sub-vertical</td>
</tr>
</tbody>
</table>

**SKULL WIDTHS**

In addition to a shorter, stronger face, "Antrodemus" has a wider postorbital skull than *Allosaurus* and *Ceratosaurus nasicornis*. Cats also have a relatively broader post orbital region relative to dogs. This wide area for the expansion of jaw adductor muscles gives felids a large jaw closing force. (Note: the wide zygomatic arches of felids, acting as origins for the masseter muscles, are also related to transverse motion of the mandible relative to the skull during feeding.) The very low postorbital width ratio of *Ceratosaurus* skull, the one with the most severe crushing, may be a result of the restoration (PAUL, 1988) being too narrow. However, this low postorbital width ratio is associated with low lateral profile and a narrow snout, and a similar association is seen in the narrow-skulled, long-toothed allosaur.

Both *Allosaurus* and *Ceratosaurus* share a more narrow snout when compared with "Antrodemus". This narrowness of the skull, when combined with the low elevation of the skull, is similar to forms seen in some extant varanids where the elongate, narrow skull is used for quick, darting movements (LOSOS & GREENE, 1988). The narrowness could also be interpreted as "focussing" the bite force onto a smaller area, thus increasing the stress applied to region where the teeth contact the prey. The longer teeth of *Allosaurus* and *Ceratosaurus* and the possible increased frictional resistance caused by increased tooth surface area, or the need for a deep bite, may have required a higher applied stress.

**ANTERIOR AND POSTERIOR NASAL SUTURES**

Other indicators of increased skull strength exhibited by "Antrodemus" are the deeply interdigitated sutural contacts between the nasals, premaxillae, and frontals. These high-amplitude sutures would increase the rigidity of the sutural contacts and increase the strength of the skull, important when applying a strong bite force and
UTFL/SL □ Allosaurus fragilis □ "Antrodemus valens" □ Ceratosaurus nasicornis

SWA/SL □ SWP/SL □ SHA/SL □ SHP/SL □ TW/TL □ TL/SL

Scaled Ratios

0.0 0.2 0.4 0.6 0.8 1.0

Fig. 2 - Skull ratio data rescaled to show the similarity between Allosaurus fragilis MARSH and Ceratosaurus nasicornis MARSH, and the differences between Allosaurus fragilis and "Antrodemus valens" (LEIDY). The largest value in ratio triple has been set to 1 and the smallest value of any triple set to 0. The remaining intermediate value has been rescaled proportional to its distance between the two extremes. Abbreviations: SHA - Skull Height Anterior, SHP - Skull Height Posterior, SKP - Skull Width Posterior, SL - Skull Length, SWA -Skull Width Anterior, TL - Tooth Length, TW - Tooth Width, UTFL - Upper Temporal Fenestra Length.

when pulling backwards to remove a portion of flesh from a prey item. A similar form of strengthening is seen in the skull roof of artiodactyls where intraspecific combat with antlers is common (HILDEBRAND, 1982). The same sutural contacts in Allosaurus and Ceratosaurus are much simpler. With only low-amplitude contact between the nasals and frontals, and much less total contact area between nasals and premaxillae, this would imply a potentially weaker, or more mobile (BAKKER, 1986), skull in these two genera.

SUPRATEMPORAL FENESTRA LENGTH RATIO

Allosaurus and Ceratosaurus have relatively smaller dorsal temporal openings when compared with "Antrodemus". The large upper temporal fenestra of "Antrodemus" correlates with the other features that indicate enhanced development of jaw adductor musculature in this animal.

SURGANGULAR DORSAL FORM

The more elevated and complex dorsal surface of the surangular in "Antrodemus" and Allosaurus suggests enhanced development of the aponeuroses associated with enhanced jaw adductor musculature. For "Antrodemus" this would tie in with the other aspects of skull and tooth form that point to a very strong bite. In contrast, the surangular in Ceratosaurus is barely elevated above the dorsal margin of the dentary and has a much less rugose surface (GILMORE, 1920: pl. 26).

The apparently weak development of the surangular and associated aponeurosis in Ceratosaurus is at odds with its big teeth and deep, strong skull. Downward movement of the head while applying a bite has been observed in domestic cats (GORNIAK & GANS, 1980) and this might have been important in Ceratosaurus as well. In Ceratosaurus the lower temporal fenestra is very large, suggesting a large muscle mass. A larger muscle mass inserting onto a larger area of the jaw might have allowed Ceratosaurus to propel its large teeth.

QUADRATE-SQUAMOSAL INCLINATION

Allosaurus and Ceratosaurus both show an anteriorly inclined postero-lateral margin to the skull, in contrast to the almost vertical postero-lateral margin shown by "Antrodemus". If bones are strongest when loaded along their long axis, the orientation of the quadrate-squamosal pair suggests differences in how jaw adductor muscle forces were applied by the three genera. Allosaurus and Ceratosaurus would appear to have applied maximum jaw force when the lower jaw was wide open, and the jaw muscles were parallel to the quadrates and perpendicular to the long axis of the mandible, similar to the configuration seen in crocodiles. "Antrodemus", with a more vertically oriented quadrate-squamosal pair, would have applied a maximum jaw force when the jaw was almost closed. This ties in with the other skull features that indicate a strong "grip-and-pull" style of jaw function.

A more anteriorly inclined quadrato-squamosal can also be viewed as posterior displacement of the jaw joint, resulting in an increased gape. Sabre-toothed cats were capable of opening their jaws very wide, and the large teeth of large theropods are similar to those of the sabre-toothed cat Smilodon (FARLOW et al., 1991). The correlation between adaptations for a wide gape and long teeth exhibited by Allosaurus and Ceratosaurus further distances their feeding style from that of "Antrodemus".

SPATIAL DISTRIBUTION

The type specimens for Ceratosaurus and "Antrodemus" are both from the same quarry, Garden Park, Colorado (GILMORE, 1920). Ceratosaurus is also known from only four other quarries in the Morrison (BRITT, 1991). From the Cleveland-Lloyd quarry in Utah are the scattered remains of an single Ceratosaurus (MADSEN, 1976). The Cleveland-Lloyd Ceratosaurus is vastly outnumbered by the remains of Allosaurus of many different sizes. The two quar-
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ries represent different environments - Garden Park is interpreted as a channel deposit in a moderately drained floodplain, while Cleveland-Lloyd is a poorly drained floodplain or delta (DODSON et al., 1980). The Cleveland-Lloyd site is interpreted to have been a predator trap with all the entombed individuals being part of a single population (PAUL, 1988; MADSEN, 1976). Ceratosaurus appears to have been a minor player in the fauna of this locality.

With both Ceratosaurus and Allosaurus representing long, narrow-skulled, long-toothed predators it is probable that the two species would have been in direct competition with each other. The rarity of Ceratosaurus at the Cleveland-Lloyd site could be explained by its being displaced by the more abundant Allosaurus. At the Garden Park site the short, wide-skulled, short-toothed form represented by Antrodemus would not be in a competitive situation with the form represented by Ceratosaurus. A similar situation exists at the Dry Mesa site, with the remains of at least two Ceratosaurus in association with allosaur remains that have the tall pointed lacrimal of Antrodemus (BRITT, 1991). Although these groupings of genera pairs are little more than random associations, it is tempting to infer a situation of more "equal abundance" when it is two morphologically dissimilar carnivores, as seen at the Garden Park and Dry Mesa sites.

BODY SIZE EFFECTS

Several trends have been identified with respect to carnivores, their prey, and their respective sizes. VEZINA (1985) notes that log (prey mass) is positively correlated with log (predator mass). The similar sizes (6-8m) of the best known, large predatory dinosaurs of the Morrison Formation can be interpreted as being a reflection of the large size of the potential prey - several genera of sauropods, stegosaurs, and camptosaurs (FARLOW, 1976; DODSON et al., 1980), but this large predator size could also be viewed as a way of reducing competition. VEZINA (1985) and GITTLEMAN (1985) both show that the range in size of prey taken by a predator increases with increasing predator size. Being large would enable a predator to take advantage of unexpected food sources while foraging at random. Increased choice of prey would increase potential prey biomass, thus lessening competition.

GITTLEMAN (1985) notes that the abundances of large prey species decrease with increasing size. A large predator has increased cursorial ability and can forage over a larger area (MOLNAR & FARLOW, 1990). This increased foraging ability would enable a large predator to find more of its large and preferred, but rarer, prey items. The destruction and ingestion of vegetation by many large dinosaurian herbivores would require the herbivores to range over a large area to find sufficient food (DODSON et al., 1980). A large carnivore, with a lowered cost of locomotion, would have a selective advantage if it was able to follow these migrating, low abundance herds. The closeness of the body sizes of the different Morrison theropods could be interpreted as convergence towards an optimal body size for tracking large, rare prey.

CONCLUSIONS

The co-occurrence of many sympatric species of large carnivorous dinosaurs within the depositional environment represented by the Morrison Formation would have led to competition between these top predators. Based on the adequate skull material from three of these species (Allosaurus, Antrodemus, and Ceratosaurus), the distinct differences in skull and tooth form suggest three different feeding strategies and/or behavioural patterns. Convergence towards similar large body size by these sympatric carnivores might have been a mechanism to reduce competition by increasing the range of potential prey. Differentiation in tooth and skull form would lessen competition brought on by similar body size and a conservative post-craniaw body plan.

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