

um may have served to absorb shocks such as the one of a sudden impact on prey.

Important postcranial features include the opisthocoelous, low-spined neck-vertebrae, which must have enabled the animal to perform rapid, wide-ranged movements with its craniocervical region.

Unlike some other theropods, allosaurids retained comparatively large forelimbs and strong claws with increased body size (Bybee et al. 2006), which likely played a role in prey restraint. Furthermore, palaeopathological surveys have found an unusual rate of stressfractures in allosaurid metatarsals, indicative of prey-handling behaviour involving the feet (Rothschild et al. 2001).

Discussion & Conclusion

The lightly built, narrow skull and the inferrable morphology of its jaw adductors are contraindicative of strong bite force in *Allosaurus*. On the other hand, the morphology of its teeth and the extreme resistance of its cranium in dorsoventral direction, as well as the presence of extensively bite-marked bones of large prey in strata dominated by this taxon (Hone & Rauhut 2009), all suggest it was capable of generating large forces when attacking prey.

The adaptations for large gape angle, head ventroflexion and cervical flexibility are all most consistent with a slashing bite, that relied on the combination of high-velocity strikes with subsequent pulling motions, causing extensive internal damage through the actions of neck muscles rather than jaw adductors. Prey could furthermore be restrained using the claws of the powerful fore- and hindlimbs if such behaviour was necessary.

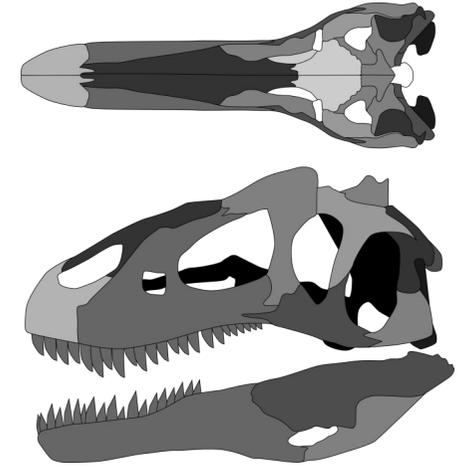
Long phases of contact with struggling prey items, that would have imposed large torsional and lateral stresses on the skull, could thus be avoided, while both retaining a very potent macropredatory weapon, and remaining suf-

ficiently nimble to catch smaller animals.

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Cranial Function in Allosaurus—a comparative Analysis



Abstract:

The Upper Jurassic carnosaur Allosaurus, known from the North American Morrison Formation and the Portuguese Lourinha Formation, displays a set of unusual craniocervical features. Its morphology has been subject to several major works, which to survey and conclude from is the purpose of this paper.

In conclusion I find that Allosaurus' functional morphology suggests it employed a slash-and-pull bite to cause deep flesh wounds and blood loss by striking rapidly at prey, which could be the key to its evolutionary success by allowing it to be a very versatile hunter that incorporated animals of various sizes and clades in its diet, consistent with preserved feeding traces on Morrison Formation bones.

Introduction

The large-bodied Upper Jurassic carnosaur *Allosaurus* has cranial, mandibular and cervical features that differ considerably from most other carnivorous dinosaurs. It has generally accepted that these reflect a killing style with a major role of post-cranial structures and a reduced role of jaw adduction, even though the particulars have been subject to debate. Here I want to outline and interpret the current state of knowledge regarding this matter.

Material

The first to notice the peculiarities in the cranial morphology of *Allosaurus* was Bakker in his 1998 monograph. He noted extreme adaptations for increasing jaw gape at the cost of bite force, such as a deepened and shortened area of attachment for the temporal musculature and a posteriorly facing, broadened and deeply notched quadrate and an antarticular in the mandible. Bakker also compared the neck musculature to other theropods and mammalian carnivores and proposed the skull to have served as a zoological analogy to a serrated warclub.

In 2001 Rayfield and colleagues employed finite element analysis to a cranium of *Allosaurus* sp. (MOR 693, 79cm skull length [Snively et al., 2006]), demonstrating that it would have been able to withstand a dorsoventral load of almost 1.9KN while biting at the mid-maxillary dentition, despite an estimated bite force at maxillary teeth 3, 4 and 5 of only 200kg. Bite force for a similar-sized specimen (SMA 0005, 79cm skull length [BHI online]) was later estimated to be considerably greater, comparable to a great white shark when correcting for body size.

This result was interpreted as an adaptation for the use of

high-velocity impacts of the upper jaw in subduing prey. Consistent with this theory and Bekker's earlier findings, the cervical musculature of *Allosaurus* displays a strong emphasis on ventroflexion, as deduced from the reinforced basal tubera and the ventrally facing paroccipital processes, providing attachment areas and ventroflexible levers for m. rectus capitis ventralis, longissimus capitis profundus and superficialis and iliocostalis capitis.

The cervical centra of *Allosaurus* are opisthocoelous and bear relatively low but long neural spines, which allows for a wide range of motion and, together with the lightly constructed, pneumatic cranium, for rapid strikes. (Snively et al 2007, 2013).

The high-velocity-impact-scenario sensu Rayfield et al./Bakker was subsequently challenged on the basis of more conservative alternative explanations. Frazzetta & Kardong (2002) explained the dorsoventral strength as a compensation for the narrow shape of the skull, a hypothesis subsequently rebutted by Rayfield et al. Antón et al. (2003) raised doubts as to whether such behaviour would not dislocate the jaws and proposed a scenario in which the predator first applied a traditional bite that was subsequently augmented by head ventroflexion, using the extant *Varanus komodoensis* as an analogy.

Snively et al. (2013) proposed a feeding model employing ventro-posterior pulling actions to dismember prey.

Morphological Comparisons

Among extant predators, the most suitable taxa for comparison with allosaurids are certain members of varanidae, falconidae and lamnidae.

Komodo dragons (*Varanus komodoensis*) are large-bodied apex predators with recurved, serrated teeth, lightly constructed skulls and relatively low bite forces. They make use of pulling forces to tear flesh, resulting in *in vivo* forces an order of magnitude greater than simulated bite forces (Moreno et al. 2008, D'amore et al. 2011). These varanids are, however, in the order of 20-40 times smaller than adult *Allosaurus*, have proportionally smaller skulls and adductor forces and have a lower profile.

Great white sharks (*Carcharodon carcharias*) are more similar in body size, hypothesized speed and they have similar bite forces (Wroe et al. 2008) to allosaurids. These predators make use of their velocity to drive their teeth into prey when ramming them from below.

Falcons (falconidae) finally are many orders of magnitude smaller than *Allosaurus*, but use their flexible necks and sharp-edged beaks to tear flesh while feeding on prey that is held by their talons, in a manner similar to that proposed for carnosaur.

Interpretation of functional anatomy

- 1) Ventrally directed paroccipital processes provide a large ventroflexive lever arm for m. longissimus capitis superficialis and m. iliocostalis capitis
- 2) reinforced basal tubera provide a robust insertion point for a strong m. l.cap. profundus and M. rectus capitis
- 3) an enlarged transverse nuchal crest provides an attachment point and lever arm for a robust dorsiflexive neck musculature
- 4) An anteroposteriorly shortened but deep temporal fenestra and a deepened posterior region of the mandible allow for long, narrow jaw muscles and a large cranio-mandibular gape angle.
- 5) A posterior tilt of the quadrate, hypertrophied, ligament-reinforced, deeply bifurcated condyles and the presence of an antarticular serve to enhance the attainable gape angle and stabilize the quadratoarticular joint under these conditions.

Other notable features of *Allosaurus*' skull are its lateral compression (which is however fairly variable between species and specimens), gracile mandible, and the relatively robust teeth by virtue of their long, low crowns, allowing for a generalist feeding style (Testin et al. 2011). The moderately kinetic structure of the theropod crani-