THE MUSCLE-POWERED BITE OF *ALLOSAURUS* (DINOSAURIA; THEROPODA): AN INTERPRETATION OF CRANIO-DENTAL MORPHOLOGY

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ABSTRACT

The skull morphology of *Allosaurus* has been the subject of functional interpretations which imply a predatory behaviour radically different from that recorded in any predatory land vertebrate. Those interpretations imply the use of the skull and maxillary dentition as analogues of hand-held, man-made weapons, incorporating the inertia of the predator´s dash toward prey to add to the effect of the impact, and using wide jaw gapes as a way to keep the mandible out of the way of such blows. We re-interpret the evident adaptations for gape and for recruitment of neck muscles in head depression of *Allosaurus* in terms of a muscle-powered bite directed at surfaces with moderate convexity, such as the bodies of very large pres. In our model, the forces leading to penetration of the teeth are generated in the context of the opposition between the maxillary and the mandible. This interpretation allows us to incorporate all the observed adaptations of the *Allosaurus* skull, while avoiding the problems created by previous models.

Key words: *Dinosauria; Theropoda;* Allosaurus; *Predatory Behaviour.*

RESUMEN

La morfología craneal de *Allosaurus* ha sido objeto de interpretaciones funcionales que implican un comportamiento depredador radicalmente distinto para el inferido para cualquier vertebrado depredador terrestre. Esas interpretaciones implican el uso de la dentición superior e inferior como análogos de cuchillos o dagas manufacturadas por el hombre, incorporando la inercia del golpe del depredador contra la presa para añadir el efecto del impacto, y usando amplias aperturas mandibulares para mantener la mandíbula fuera de la línea de acción del impacto. Reinterpretamos las evidentes adaptaciones para amplias aberturas mandibulares, y para la utilización de la musculatura cervical en la depresión de la cabeza de *Allosaurus* en función de una mordida basada en la fuerza muscular dirigida a superficies moderadamente convexas, como el cuerpo de una gran presa. En nuestro modelo, las fuerzas que producen la penetración son generadas en el contexto de una oposición entre el maxilar y la mandíbula. Esta interpretación nos permite incorporar todas las adaptaciones observadas en el cráneo de Allosaurus, al mismo tiempo que se evitan los problemas creados por modelos alternativos.

Palabras clave: *Dinosauria, Theropoda,* Allosaurus, *Comportamiento depredador.*

Introduction

Allosaurus is a nonavian Avetheropoda, a clade comprised of all descendants of the most recent common ancestor of *Allosaurus* and Neornithes (Holtz Jr., 1994; Holtz Jr., 1998; Padian *et al.*, 1999), from the Upper Jurassic of North America and Europe (Paul, 1988; Pérez-Moreno *et al.*, 1999). Allosauroidea comprises the Allosauridae, formed by the genus *Allosaurus, Neovenator, Acrocanthosaurus, Giganotosaurus* and *Carcharodontosaurus*, plus the Sinraptoridae, formed by *Yangchuanosaurus* and *Sinraptor* (Holtz Jr., 1998; Padian *et al.*, 1999; Sereno, 1999) (Fig. 1). A single species, *Allosaurus fragilis* MARSH, 1877 has normally been recognized, and is accepted in this

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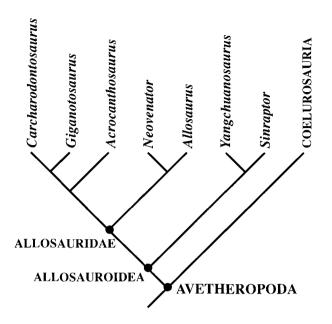
Fig. 1.—Cladogram reflecting the phylogenetic relationships within the Avetheropoda clade, showing the position of *Allosaurus*. Cladogram after Holtz Jr (1998), Padian *et al.*, (1999) and Sereno (1999).

paper. The most abundant remains of this large theropod (about 7,5-7,9 meters long; Paul 1988) come from the giant sauropod fossil faunas of the Upper Jurassic, like the Morrison Formation (USA) (Molnar *et al.*, 1990). In the times of the Morrison, *Allosaurus* shared their habitat with the large cer-atosaur *Ceratosaurus*, the megalosaur *Torvosaurus* and the very large and less known allosaur *Saurophaganx* (Van Valkenburgh & Molnar, 2002); all of these species of nonavian theropods are believed to have been the top predators of these faunas. The available prey for that kind of large eat-meating dinosaur ranged from the little hyp-silophodont *Othniellia* and the medium sized iguanodontians *Camptosaurus* and *Dryosaurus*, to the large stegosaur *Stegosaurus* and the giant sauropods of the genus *Diplodocus*, *Apatosaurus*, *Barosaurus*, *Seismosaurus*, *Brachiosaurus* and *Camarasaurus*. The question of how such predators like the allosaurs, megalosaurs and ceratosaurs killed the very much larger sauropods, or whether they could even attempt to take the adults, is still a matter of debate, as is the way in which large predatory nonavian theropods used to bring down their prey.

A recent effort to compare dinosaurian and mammalian predators (Van Valkenburgh and Molnar, 2002) has found that all the large toothed nonavian theropods appear to have been hypercarnivorous, displaying much less morphological variation than mammalian predators. While the latter manage to partition the available resources thanks to a considerable variety of feeding adaptations, it would appear that theropods were competing intensely for a very concrete resource - dinosaur meat. How they managed to partition the resources with such apparently homogeneous feeding adaptations is something of a mystery. In general, theropod species within a guild tend to differ a little more markedly in size than species of mammalian predators, but nonetheless, there are examples of pairings and trios of species with clearly overlapping body mass, as in the case of allosaurs, ceratosaurs and megalosaurs in the Morrison formation (Van Valkenburgh and Molnar, 2002).

There are, however, several morphological traits of the skull of *Allosaurus* which differ from all other Jurassic large theropods, and which have led some paleontologists to produce interpretations of their predatory behavior that differ markedly from those of all known terrestrial vertebrate predators. The features in which the *Allosaurus* skull differs from other theropods include the following: it has downward pointing paroccipital processes, where head turning and depressing muscles insert; an antero-posteriorly shortened temporal fenestra where jaw-adducting muscles were housed; postero-inferior displacement of the articular area of the quadrate for the mandible; reinforced basitubera in the base of the skull for insertion of ventral neck muscles; presence of a small element, the antarticular (not known in other species), placed at the medial end of the articular-surangular junction (Madsen, 1976; Molnar *et al.*, 1990); and maxillary teeth that are smaller than would be expected for a theropod of its size. Allosaurs share with tyrannosaurids the possession of an enlarged transverse crest in the back of the skull, for the insertion of powerful extensor muscles from the neck (Bakker, 1998; Paul, 1988). Bakker, (1998) interpreted all these features as adaptations for large gape and for recruitment of the neck musculature in head elevation and depression, which in turn would allow allosaurs to use their skull and maxillary dentition for what he termed a sort of "Samoan war-club", violently hitting the body of the prey animal with a downward motion of the neck and skull. Such features were seen as an adaptation to killing very large prey animals such as giant sauropods, a habit termed "brontophagy" by the author.

More recently, Rayfield *et al.* (2001) used a Finite Element Analysis (FEA) to study the constructional morphology of the cranium of *Allosaurus fragilis*, and concluded that it was capable of withstanding large vertical forces, while employing a conventional analysis of muscle forces based on the positions of attachment areas to argue that the jaw adductors were relatively weak. The authors concluded that this combination of "a weak muscle-driven bite
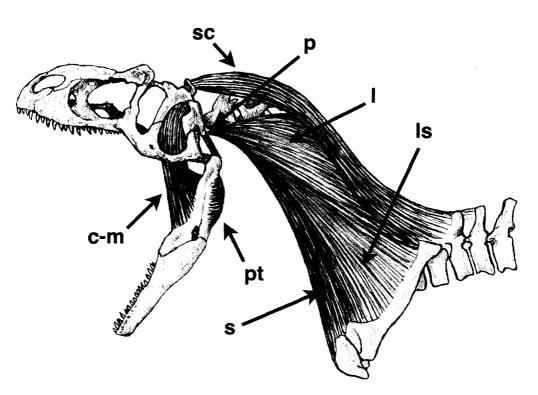
Fig. 2.—Skull and cervical vertebrae and reconstruction of selected muscles in *Allosaurus*. cm capiti-mandibularis; l: longissimus; ls: levator scapulae; p: paroccipital process; pt: pterigoideus; s: sternomastoideus; sc: spinalis capitis.

force...and unusually high cranial strength" implies the involvement of a non-muscular force during the attack, and infer use of the inertia of the predator's rush toward its prey. In this "high-velocity impact" scenario, the mandible plays no active role, at least during the initial contact, and the action of the cranium and upper dentition hitting the body of prey is likened by the authors to "a person wielding a large, heavy hatchet". Such predatory behavior is seen as contrasting with the crushing bite of *Tyrannosaurus rex* (Hurum and Currie, 2000), which is thought by them to have had "a specialization towards carcass dismemberment and possibly tackling larger, heavily armoured prey". By contrast, *Allosaurus* is seen as a hunter of lighter and more agile forms such ornithopod dinosaurs, but occasionally able to hunt larger prey like sauropods using a "devastating, high-impact attack before the prey may retaliate". Frazzetta and Kardong (2002) have already criticised that interpretation and suggested that the FEA results are better explained by the biomechanical demands of prey seizure and retention, although Rayfeld, *et al.* (2002) have rejected that argument in favour of their initial viewpoint.

The interpretations offered by Bakker (1998) and more recently by Rayfeld *et al.* (2001) differ in the size of preferred prey for allosaurs, but they agree

in viewing the use of the maxillary dentition by analogy with man-made weapons, instead of a muscle-powered bite based on the opposition between maxillary and mandibular dentition as seen in the immense majority of terrestrial vertebrate predators. We believe that both explanations are open to serious question, and propose a different interpretation, one accounting not only for the evident adaptations for wide gape and recruitment of neck musculature in head depression, but also for the FEA results and for estimations of muscle force. We contrast our interpretation with the hatchetting scenario, and consider the question of prey capture and retention in *Allosaurus* within the wider context of skull morphology and function in other vertebrate predators.

Cranial and cervical musculature in *Allosaurus*

Insertions and action of neck muscles attaching to the skull.

Several features of the allosaur skull are related to modifications in the insertions of cervical muscles. Bakker (1998) has shown that the paroccipital process of allosaurs projects clearly downwards instead of laterally as in other theropods (Fig. 2). The paroccipital process serves for insertion of the
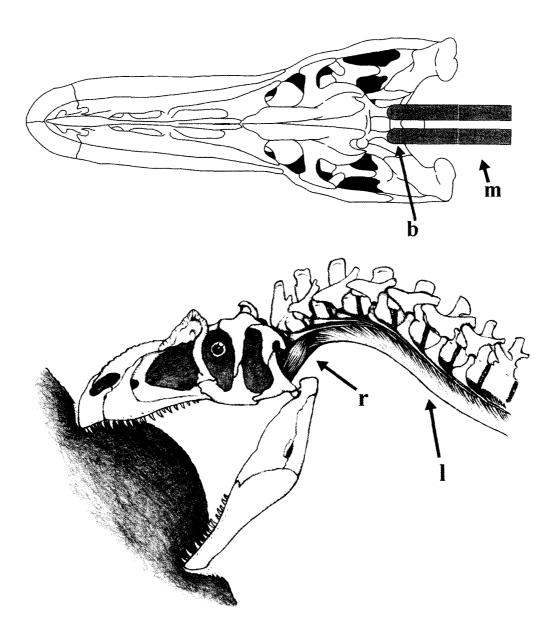
Fig. 3.— *(Top)* Cranium of *Allosaurus* in ventral view showing basitubera (b) and fibers of the *longus colli* and *rectus capitis* muscles (m). The basitubera are present in other members of the Archosauria, including extant crocodilians and birds, and prominence in nonavian theropods is widely accepted as evidence for the power of these head-depressing muscles (Bakker *et al.* 1988). The *rectus capitis* and the anterior fibres of the *longus colli* depress the head on the atlanto-occipital joint, while the posterior fibres flex the neck and contribute to the backward motion that sinks the teeth deeper into the prey and finally pulls out flesh. *Allosaurus* teeth are actually relatively smaller than those shown in images of the FEA (Rayfield *et al.*, 2001), and the dental battery very reminiscent of varanid lizards (Paul, 1988) and thus fit for a similar biting mode of attack, while one would expect huge teeth in a "hatchetting" theropod. *(Bottom)* Skull and cervical vertebrae of *Allosaurus* in biting position, showing the trajectory of the *rectus capitis* (r) and *longus colli* (l) muscle fibres. This drawing corresponds to an intermediate (not initial) stage of the bite, when the mandible has already started to close around the bitten section of the prey body and a fold of skin and flesh is beginning to form.

transversarius muscle, which in turn transmits the contracting force of a bundle of more posterior muscles including the levator scapulae, sternomastoideus and scalenes. Such a muscle arrangement is evident in modern crocodilians (Chaisson, 1962;

Grenard, 1991). Bakker (1998) convincently argued that the reorientation of the paroccipital process in *Allosaurus* increases the head-depressing action of these muscles, which in other theropods function more as lateral rotators of the head.

The great development of a paired process called the basitubera in the base of the cranium of theropods indicates the presence of strong head depressor muscles, and their enhanced vertical action is shown by the ventral projection of those processes (Fig. 3). Bakker (1998:152) observed the presence of "a set of transverse thickenings in the bone boxwork behind the basitubera", which he interpreted as evidence showing that "unusual stresses were incurred during head ventral-flexing". The relationship between the basitubera and the insertion of head-depressing muscles was also considered in detail by Bakker *et al.* (1988) who established the relationship in modern crocodiles and birds through dissection, and discussed the relevance of the disposition of the basitubera for head carriage in the Tyrannosauridae. The relationship between the basitubera and the insertions of the rectus capitis muscles is well established in modern crocodilians (Iordansky, 1973), and in fact the relative orientation of these processes is seen as an indicator of the predominant type of head movement, either horizontal as in fish-catching crocodiles, or vertical as in meat-eating species (Langston 1973). Involvement of the head depressing muscles in the bite is known in modern vertebrates (Gorniak and Gans, 1980), and inferring its presence in an extinct taxon is entirely reasonable.

The anterior position and hypertrophy of the insertions for neck and head extensors such as the spinalis capitis in the top of the braincase of *Allosaurus* (Fig. 2) suggest considerable ability to elevate the snout, fitting with Bakker's suggestion that the animals attacked with their snout tilted upwards, as modern crocodiles often do.

Adaptations for wide gape

As Bakker (1998) has shown, the shape of the cranio-mandibular articulation in *Allosaurus* allows the jaw to rotate along a wider arc than is possible for other theropods without disarticulation of the mandible. In addition, the insertion area in the skull for the jaw closing muscles, as defined by the temporal fenestra, is antero-posteriorly more narrow in *Allosaurus*, and the mandible is vertically deeper in the area around the joint between the dentary and post-dentary bones, where the same muscles attach. The consequence of these changes is that the fibres of these muscles are longer and oriented more vertically, allowing the jaw to open more widely without over-stretching the muscle fibres, but providing a weaker bite in the process (Fig. 1).

The antarticular, placed at the articular-surangular junction, probably acted as a stop to prevent cau-

dal disarticulation of the jaw joint (Madsen, 1976; Molnar *et al.*, 1990), and this is an important feature in a wide-gape predator.

Functional implications

Rayfield *et al.* (2001) suggest that their inferred hatchetting action would be aided by a "powerful neck musculature", but in order to have contributed to such an action those muscles would have had to act like those of a person wielding a weapon. Just as the arm of the stabbing person turns around the shoulder and elbow articulations to gather strength for the blow, so the neck and head of the allosaur would have had to turn around the cervico-thoracic articulation (Fig. 4), or even the whole body would have had to turn around the pelvic articulations in order to power that downward stroke. We propose instead a radically different combination of mechanics and timing for the action of neck muscles.

In our hypothesis (Fig. 5), the initial contact of *Allosaurus* with its prey would be a conventional muscle powered bite, and all forces transmitted to the cranium via the maxillary dentition would be generated in opposition to the mandible. The inertia of the dash towards the prey would play no relevant role in the penetration of the upper teeth into its flesh. Instead, the allosaur would likely seek a relatively convex part of the prey's body, such as the neck, a leg, or the fold of skin between thigh and belly, where its jaws had something to seize. Such parts would require a more careful approach, with the neck rotating at precise angles to orientate the head for the bite, rather than pulling it down in a violent, blind stroke (Fig. 6). Once the upper and lower dentition were positioned around the bitten area, the force of the jaw adductors would be supplemented by the action of the head depressor musculature, which would rotate the cranium around the atlanto-cranial articulation and add to upper teeth penetration, while the mandible remained anchored to the body of prey and acted as support. The action of the cervical head depressors, plus the violent motions of the struggling prey, would account for additional stress to the allosaur cranium as adequately as the supposed hatchetting motion.

The contribution of neck musculature to the bite was especially important when biting at surfaces with little convexity, such as the body of very large prey, because when the jaws opened at the gapes necessary to encompass such surfaces, the cranio-mandibular jaw adducting muscles were in a disadvantageous position to provide a strong bite.

Once initial contact with the prey had been established, it is likely that the reduced but still powerful
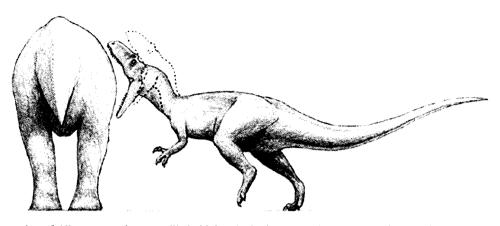
Fig. 4.—Reconstruction of *Allosaurus*, using an unlikely high-velocity impact against a sauropod, which is shown in posterior view. The mandible is shown at the unlikely gape necessary to prevent it from hitting the body of the prey and thus forcing the mouth to shut violently, although any mandible hitting a solid object with such a wide gape is likely to have been dislocated. The profile of the head and neck in the extremely dorsiflexed neck position previous to the impact is shown with a dotted line. For the sake of simplicity the body axes of predator and prey are shown as being at right angles, but it is more likely that the prey would be actively trying to escape, and thus the approach would be partly from behind. This would detract from the impact, since only the teeth from one side would hit the prey, but probably still be damaging to the mandible.
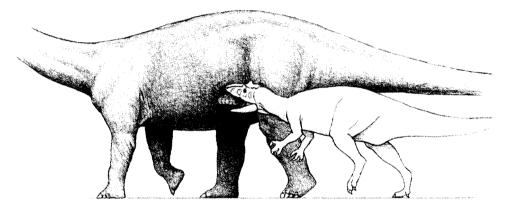

Fig. 5.—Reconstruction of *Allosaurus* biting its prey according to our hypothesis. The prey is bitten in a convex part of its body, and the neck of the allosaur rotates laterally to orientate the head for the bite. Such complex rotation excludes a violent "hatchetting" motion, and the bite is powered by the jaw closing and head-depressing muscles.
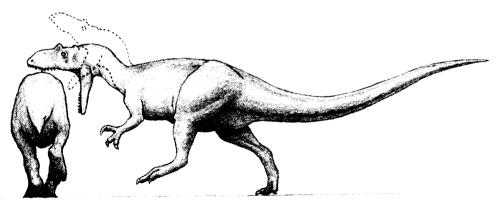

Fig. 6.—*Allosaurus* using a hatchetting motion against a medium-sized ornithopod. This scenario would require a less extreme dorsiflexion of head and neck, but the gape would have to be enormous anyway. One additional problem with this scenario would be that the teeth of *Allosaurus* would very likely encounter bone when hitting the dorsal or the sacral area of a medium-sized prey. This would surely imply breakage of a large part of the predator's dental battery with every hunting episode, something that would be too costly even for a reptile with continuously replacing teeth.

forelimbs with their three-clawed hands would have played a major role in maintaining stable control, particularly with prey of similar or smaller size than *Allosaurus*. The presence of such powerful arms itself argues against any tendency to relinquish contact with the prey after the initial attack as suggested by Bakker (1998), and also calls in question the need for a single devastating attack as implied in the hatchetting scenario of Rayfeld *et al*. In fact it would make more sense to see the need for such a devastating attack by *Tyrannosaurus rex*, which lacked the forelimbs necessary for any significant manipulation of its prey.

Further problems with the hatchetting interpretation

Rayfield *et al*. (2001) provided no comparative data to establish whether the crania of other theropods or even extant predators using a muscle-powered bite without recourse to any hatchetting motion to kill prey have similarly reinforced or "over-engineered" skulls, a point made in initial comment on their paper (Erickson, 2001). We do not, for instance, know how much force the cranium of say a lion could withstand according to an FAE, in which case claiming that *Allosaurus* had a predatory behavior radically different from any existing land predator on the basis of a character that may equally well be present in an undetermined number of other taxa seems unjustified. However, our criticisms of the hatchetting scenario for *Allosaurus* fall into a number of more specific areas.

In the first place, Rayfield *et al*. (2001) propose an analogy with "a person wielding a hatchet", but then claim that the allosaur could have incorporated the inertia of attack into the force of the bite (a "high-velocity impact). In order to make the analogy more complete, we would need to envisage the person with the hatchet running toward a victim, and suppose that the hatchet would strike harder because the person was running. However, the claim that the inertia of the allosaur's dash toward prey could be incorporated into the bite, and generate vertical forces (which in turn transmitted stress to the cranium), is contradicted by the simple fact that the force of the allosaur's rush would logically have been directed forwards, and would have required the teeth and the whole maxilla to be oriented anteriorly instead of ventrally in order to benefit from such kinetic energy (Fig. 4). Despite the ability to elevate the snout implied by morphometric analysis of the cranium discussed above, this would appear to require and excessive lifting of the cranium, but in any event more valid analogies for

an attack that incorporates inertia would be a running soldier using a bayonet or a white shark accelerating towards prey, and in both cases the weapon's point is directed anteriorly (see below).

Even ignoring these problems of the high-velocity impact scenario, one must remember that the teeth of *Allosaurus* are relatively small for such a large theropod. Looking at the relative sizes of the elements of Fig. 4, one wonders if hitting the side of a large sauropod with such a set of teeth would be a "devastating blow" as Rayfield *et al*. propose, especially since the jaws would be near the point of dislocation and hardly able to bite with any effectiveness. The likely consequence of such an impact on the body of a prey animal would rather be a line of punctures with the shape of an allosaur toothrow. This leaves aside the likely problem of tooth breakage in such a scenario. Rayfeld *et al*. acknowledge that the teeth of *Allosaurus* were adapted for slashing or slicing, unlike the stouter conical and D-shaped teeth of *Tyrannosaurus rex*, and thus argue that this reinforces the case for a weak muscle-driven bite. But if the teeth were relatively unsuited to a strong bite then they were even less suited to a hatchette like attack, and even continuous, lifelong replacement would be of little help if significant numbers of teeth were damaged in nearly every encounter.

Even if we ignore the problem of the inertia and try to imagine the hatchetting as a result of the downward motion of the head, we still would have to face the problem of the enormous gapes neccesary to clear the mandible from the path of the cranium and maxillary teeth. The problem is especially acute because the FEA analysis shows that the greatest strengthening of the cranium is at the level of the central rather than the anterior maxillary dentition. To allow for this with the craniodental morphology of *Allosaurus* a gape of well over 90 degrees would be neccesary (Fig. 6).

Wider comparisons

The Komodo dragon analogy

Rayfield *et al.,* mention the extant Komodo dragon, *Varanus komodoensis*, as a modern analogue for allosaur predatory behavior, but reports on the behavior of these varanids and observation of footage of wild dragons attacking large mammals like deer and pigs show that they use a muscle-powered bite to sink their teeth into the flesh of prey (Auffenberg, 1981). Komodo dragons do not attack their prey with jaws open at enormous gapes while using their own heads as "hatchets", nor do they

incorporate the inertia of the attack to increase the power of penetration of their upper teeth. They do indeed approach their prey at high speed, but this is simply a means of contacting it before it can flee. It is also clear that the dragons only open their jaws wide enough to incorporate the bitten portion of flesh between the upper and lower dentitions. The superficial similarity in overall craniomandibular achitecture between varanids and allosaurs and even the shape of the individual teeth (Molnar & Farlow, 1990), is strongly suggestive that the latter would use a muscle-powered bite in just the same way as the former.

Slash and tear and the case of the great white shark

The hatchetting motion is seen by Reyfield *et al.* (2001) as the initial stage of a "slash and tear" killing and feeding method, but the two stages are not clearly separated in their explanations and they seem to assume that one thing neccesarily goes with the other. But that is not the case, and while various modern predators appear to use a "slash and tear" attack method, none can be said to use a hatchetting motion to sink its upper teeth into the prey without the contribution of the opposing force of the mandible. The image of a predator like a wolf biting prey as it runs may give the wrong impression that speed is adding to the power of the bite, but in fact it is the muscle-powered bite that causes the "slashing", and the pull of the prey trying to escape, or that of the predator trying to hold it, which causes the "tearing" of the flesh. Speed of impact has nothing to do with the whole process.
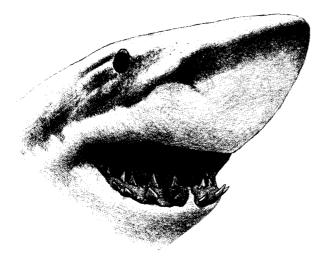

Fig. 7.—The head of the great white shark, *Carcharodon carcharias*, in anteroventral view, showing the triangular shape and anterior orientation of the mandibular teeth.

There is however one example of a modern predator that appears to incorporate the inertia of its approach to prey as part of a "slash and tear" method, but it is a marine species: the great white shark, *Charcharodon carcharias*. The shark's attack method is radically different from that of any land predator because it goes torpedo-fashion into its prey and uses that contact to inflict severe wounds, carrying the prey in the jaws before tearing out a great chunk of meat, in most cases the entire head of the pinniped, or until the prey is dead due to exsanguination (Klimley *et al.*, 1996). The lower teeth of *Charcharodon* (Fig. 7) hit the prey first, and in fact those in the outermost rows are directed anteriorly, and have the right shape and orientation to produce large wounds (not to mention shock) during initial contact. The upper teeth, and the more internal rows of lower teeth, are oriented posteriorly like those of predatory reptiles and contribute to tearing chunks of flesh, and their action is powered by the jaw muscles of legendary strength which close in a reflex action when any solid object is contacted. Even in the white sharks, such action of the jaw closing muscles and the lateral movements of the head are the main ways of tearing flesh, and the speed of impact is not primarily a way to inflict greater damage but a mere consequence of the quick approach. The breaching behavior for which some great whites are notorious (Klimley *et al.*, 1996) is just a way to catch their fast pinniped prey by surprise. Lamnid sharks, such as Great Whites and Makos, are adapted to catch very fast prey such as tuna, swordfish and, in the particular case of Great Whites, sea mammals like phocids, otariids or cetaceans (Klimley *et al.*, 1996; Douglas and Jones, 1996), and they need to get to their prey quickly if they want to get to it at all. That need for speed has affected both their morphology and their attack strategies.

The use of a shark example may sound farfetched in this context, but it emphasizes the fact that theropods were not designed to throw themselves teeth-first into prey.

The sabertooth debate

For the purpose of illustration we may mention that a theory not unlike the "hatchetting" scenario was proposed to explain the morphology of mammalian sabertooth cats, namely the "stabbing" theory (Simpson, 1941). Like allosaurs, sabertooths had relatively weak jaw adductors (Simpson, 1941; Akersten, 1985; Bryant, 1996; Turner and Antón, 1987; Antón and Galobart, 1999), apparently not strong enough to drive their long canine teeth into

the flesh of prey, and it was proposed that they would attack with a stabbing motion that incorporated the inertia of the predator's leap. That model is currently discredited in favour of the more convincing "canine shear bite" (CSB) model (Turner and Antón, 1987; Antón and Galobart, 1999), but the similarities with the hatchetting model are striking, and may be founded on a common, intuitive tendency toward interpreting the structure of extinct predators in terms of man-made weapons. Even taking into account the great structural differences between both groups, it is interesting to note that, in the case of the sabertooths, the currently accepted hypothesis, the "canine shear-bite", implies the recruitment of head-depressing muscles to add to the strength of the bite.

It is important to bear in mind that mammalian sabretooths, as well as the sabretoothed therapsids, had very high crowned canines, so they needed to open their jaws at very wide gapes in order to get clearances between canine tips comparable to those possible for their non-sabretoothed counterparts. Extended gape should not be seen as an adaptation to attacking much larger prey, but rather for a different kind of bite leading to bleeding instead of crushing, tearing or strangling. Allosaurs, on the other hand, had lower-crowned teeth than other theropods of comparable size, implying that an increased gape actually meant the possibility of biting at less convex surface and thus suggesting larger prey.

Resource partitioning

In the absence of any true modern analogue for the predatory dinosaurs, it is essential that studies are done which compare them with other vertebrate predators and put their adaptations in perspective. As stated by Van Valkenburgh and Molnar (2002.527): "..there is reason to believe that some of the same processes that shape mammalian predators and their communities were important to dinosaurian predators as well". In this context, the preliminary comparisons undertaken by these authors are a welcome contribution. One interesting result of that work is the surprisingly low morphological diversity among large theropods within guilds. This begs the question of how several species of hypercarnivorous predators with essentially similar morphologies, and in some cases with considerable overlap in size, managed to partition their resources. If our interpretation of the adaptations of *Allosaurus* is correct, then their adaptations to a large-gape bite set them apart from sympatric large nonavian theropods such as ceratosaurids and megalosaurids, allowing them to bite the bodies of

larger prey. It is possible that detailed re-interpretation of the cranial morphology of theropods from other faunas will also show subtle differences not detectable for more "coarse-grained" comparisons, and indicative of further resource partitioning within Mesozoic predator guilds.

Some attempts to interpret the diversity of large theropods at the Morrison fomation have largely centered around the relaitve size of the dentition.. Paul (1988) suggested that the large teeth of *Ceratosaurus* might make it, and not *Allosaurus*, the more apt sauropod killer, at least unless allosaurids hunted in packs. But the same author admitted that the ceratosaur was the smaller of the two predators, and the one with a weaker skull and more fragile teeth. More recently, Henderson (1998) split the Morrison *Allosaurus* into two "morphs", and pointed to morphological similarities between one of them,. the "*Allosaurus* morph", and the ceratosaurs, while seeing the other (the "*Antrodemus* morph") as markedly different from the others. The author interpreted the differences as indicators of different feeding strategies, but it was not made clear which "morph" was adapted to taking the larger prey, or even if the observed differences were related with prey size at all.

However, and for reasons expalined above, it is likely that in spite of its impressively high-crowned teeth, and in part because of them, *Ceratosaurus* was capable of smaller absolute clearances between teeth tips than *Allosaurus*, implying biting at more convex surfaces and hence smaller prey.

Closing comments

In their response to the criticisms of their interpretations of the FEA offered by Frazzetta and Kardong (2002), Rayfeld *et al* (2002) suggested that their attack strategy for *Allosaurus fragilis* was proposed cautiously. Nevertheless, the entire emphasis of their original argument was based on the notion that such a quantified analysis effectively reduces the conjectural or qualitative aspects of palaeontological interpretation. As they argued, "our results provide quantitative evidence to suggest that during attack or feeding, *Allosaurus* generally used a high velocity impact of the skull into its prey" (Rayfeld *et al.*, 2001).

However, while sophisticated techniques like FEA have a clear part to play in palaeontology both the results and the interpretations must make biological as well as structural sense. In experimental sciences, any hypothesis can be promptly falsified by experimentation, but in historical sciences (and paleontology is likely to remain an historical sci-

ence, no matter how many *Jurassic Park* sequels are released), nothing can take the place of logic and common sense. A quantitative assessment of the strength of a skeletal element does not remove judgement from interpretation of the result, however much we may wish to harden the science of palaeontology, and the fact that the cranium of *Allosaurus fragilis* could absorb high stresses in a particular way does *not* mean that it did. Without a comparative framework in which to assess the results, the information provided by any quantitative structural analysis is ambiguous, and we must avoid letting complex analyses lead us into the trap of the Panglosian paradigm (Gould and Lewontin, 1979) when it comes to interpretation. The human brain that devised Finite Element Analysis might appear similarly "overengineered", but that hardly implies a routine, everyday requirement for genius during the Pleistocene. The skull of *Allosaurus fragilis* was undoubtedly strong, and no doubt had to be so in order to withstand everyday stresses and strains when a large predator dealt with its prey, but we can see no necessity to explain any over strengthening that may have resulted in terms of a high velocity impact or any other such extreme prey capture strategy.

Conclusions

The skull of *Allosaurus*s shows a series of morphological features indicating adaptation for wide gape and recruitment of the neck musculature for head depression during the bite. These features, as well as the structural strengthening of the maxilla, have been interpreted previously as indicative of unusual predatory behavior, with the skull and maxillary dentition seen as analogues of man-made weapons such as hatchets or war-clubs. We re-interpret those features within the context of a muscle-powered bite aimed at slightly convex surfaces, such as the bodies of very large prey animals. The comparatively low-crowned *Allosaurus* teeth allow encompassing of large objects without the need for an additional gape that would be required by higher teeth. The decreased bite force of the jaw adductors, imposed by the adaptations for gape, is compensated by the emphasised contribution of neck muscles to head depression. These muscles would depress the head during the bite, contributing to penetration of the teeth into the flesh of prey while the mandible had a supportive role based on the action of the jaw adductors. The action of head depressing muscles during the bite would account for additional vertical forces acting on the maxillary teeth, beyond those produced by the jaw adductors, thus

explaining the additional reinforcement of the maxilla detected by Finite Element Analysis. This model also explains why the FEA results show the highest reinforcement to be at the level of the middle of the maxillary tooth row, rather than in the anterior-most portion as would be expected in a "hatchetting" action This model agrees with the interpretation of *Allosaurus* as hunters of very large prey, and suggests resource partitioning within late Jurassic large theropod guilds, with the large but morphologically more conservative ceratosaurs and megalosaurs taking relatively smaller prey.

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