



Figure 1 Skull of *Allosaurus fragilis* (after ref. 7). **a**, Ventral view. **b**, Detail of the basal joint between the twin basipterygoid processes of the braincase and the paired pterygoid bones of the palate. Note that the palate is part of a complex that involves the upper jaw bones as well as the side and roofing bones of the skull, the strength of which is unexpectedly high in the model proposed by Rayfield *et al.*⁴.

closure of the jaws onto active quarry^{6,9}. These modern animals have a complex form of kinesis that is related to their loss of the lower temporal bar of the skull. This loss is not necessary for the less complex kinetic movements of many other tetrapods¹⁰.

A hatchet-like attack would bring the anterior axial skeleton — including the braincase — forcefully down upon the prey, with the basal joint intervening between the braincase and jaws. This flexible synovial joint would diminish the penetrating force of the lunge transmitted through the upper teeth, while creating a large stress load on the basal joint itself. However, the basal joint in *Allosaurus* is not unusually robust or reinforced.

If *Allosaurus* used a more usual method of attack, however, the FEA results might be explained by the high torque and shear stress generated by struggling prey held by a very narrow-headed predator (Fig. 1). The allosaur skull has an open design, owing to its large fenestrae and narrow, bony struts. This greater opening of the skull, which weakens it further, requires structural com-

pensation, particularly if the struts are to withstand the pull of the muscles that they support. Hence, the ‘overengineering’ relative to bite forces may represent a compensation for just such functional factors. A chop/slash interpretation⁴ is therefore questionable on biomechanical grounds, and the FEA results could be explained more simply.

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Rayfield et al. reply — Our analysis showed that the cranial strength of *Allosaurus* far exceeded the stresses that could have been generated by its jaw-closing muscles, and we suggested that this disparity might be explained if this dinosaur had adopted a ‘slash-and-tear’ mode of attack. Frazzetta and Kardong raise three points in criticism of this suggested mode of feeding.

First, they point out that no living tetrapod (lizard) attacks prey in quite this way. However, there are no living equivalents of the 1–2-tonne, bipedal, very large-headed predators. Given that *Allosaurus* was the top predator in the Late Jurassic period¹ and its prey included a range of large, herbivorous dinosaurs (ornithomimids, stegosaurs and sauropods), its feeding strategies may not have conformed to those of small, modern lizards or even the largest of snakes.

Concerning the tooth and jaw morphology of *Allosaurus*, the upper teeth show significant size variation as they emerge in a staggered tooth-eruption sequence, presenting a discontinuous, coarse profile. This arrangement is ideally suited to creating a deep, lacerating wound. Furthermore, the upper tooth row is longer than the lower and contains more teeth, whereas the lower jaw is relatively slender and tapers towards its tip. These features of the lower jaw are concordant with our interpretation that the upper jaw is the primary weapon of attack.

Assuming that subsequent dismemberment of prey requires lower-jaw dentition, on what basis should the teeth be multi-

regional in *Allosaurus*? Strong ‘regionalization’ of teeth is a trademark of heterodont synapsids. Also, contrary to the claims of Frazzetta and Kardong, there are significant differences between many theropods in terms of tooth shape, head shape and body size^{2,3}. *Allosaurus* is the only taxon to which FEA has been applied, so it is not currently possible to compare feeding strategies among theropods.

Frazzetta and Kardong argue that cranial flexibility (kinesis) requires a transverse hinge across the top or back of the skull. The skull roof and back of the skull of *Allosaurus fragilis* are not hinged transversely and there is a complete lower temporal bar. The authors note that the basal articulation is flexible and imply that it was involved in fore–aft intracranial sliding, as seen in kinetic lizard skulls. In fact, the basal articulation is not capable of sliding in this sense, but allows the palate to rotate safely against the braincase when the skull is subjected to vertical bending forces⁴.

Furthermore, intracranial displacement between the palatal bones and the cheek region reduces stress at the basal articulation during an impact bite⁴, so ‘basal robusticity’ at this joint is not required. The conditions required for pro-, meso- or metakinesis are not met in the allosaur skull, and modern lizards and snakes cannot be considered as an appropriate analogue.

Frazzetta and Kardong’s comments on our analysis erroneously apply lepidosaur cranial mechanisms to theropod dinosaur skulls. A vertically deep, narrow-headed predator would find its head structurally compromised by high torque when wrestling with large prey⁵. As we pointed out, shear stresses are insignificant and fenestrae strengthen, rather than weaken, the skull when it is subjected to large vertical forces. Recent analysis⁴ shows the lower jaw to be substantially weaker than the upper jaw. ‘Slash-and-tear’ feeding rather than ‘predator–prey struggling’ best explains this disparity.

Although our attack strategy was proposed cautiously as an interpretation in the light of the original FEA analysis, we find no evidence here to make us radically revise our initial suggestion.

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