Figure 1 Expression of *Hox6* genes in lamprey and amphioxus embryos. Anterior is to the right in **a–e** and to the left in **f**. **a**, Diagram of the lamprey head. **b–d**, Whole-mount *in situ* hybridization showing *HoxL6* expression in lamprey embryos at stage 21 (**b**), 22 (**c**) and 26.5 (**d**). Note the expresssion in the cheek process (**b**) and mandibular arch (**c**) and the absence of expression from forebrain (**c**). In **d**, *HoxL6* expression is shown in pharyngeal arches (numbered). Expression in the mandibular arch (1) is strongest in the ventral region. **e**, Distal-less (Dlx) immunostaining of a larval lamprey head. Note the dorsal restriction in the mandibular arch (arrowhead). **f**, Lateral (top) and dorsal (bottom) views of amphioxus early larvae, showing *AmphiHox6* expression. Top arrow, anterior expression boundary in neural tube and notochord, posterior to cerebral vesicle (asterisk); arrows marked 'pe', expression boundary in pharyngeal endoderm of first gill slit; paired arrows in bottom image, segmental expression in anterior neural tube. cp, cheek process; ma, mandibular arch; fb, forebrain; ll, lower lip; ul, upper lip; ov, otic vesicle; nc, notochord.

gnathostome chordates and that posterior retraction of *Hox6* expression may have occurred in gnathostomes after their divergence from agnathans.

Comparison of gene expression in lamprey and gnathostome arches has highlighted a surprising conservation between them[10,11,13], but has revealed few differences that can account for the evolution of jaws. Given the inhibitory effects of *Hox* genes on jaw formation, loss of *Hox* expression from the first arch and the associated neural crest of early gnathostomes may have facilitated ventral chondrification of the first arch crest, and thus formation of ventral mandibular cartilage.

Previous work proposed that jaws originated either by modification of pre-existing gill arches or by augmentation of a dorsal mandibular structure that resembled the velum of osteostrachans and modern lampreys[4]. My results identify a potential developmental mechanism for the latter hypothesis, and raise the possibility that the ventral mandibular skeleton was added onto an evolutionarily ancient, velar-like cartilage after *Hox* expression was eliminated from the first pharyngeal arch.

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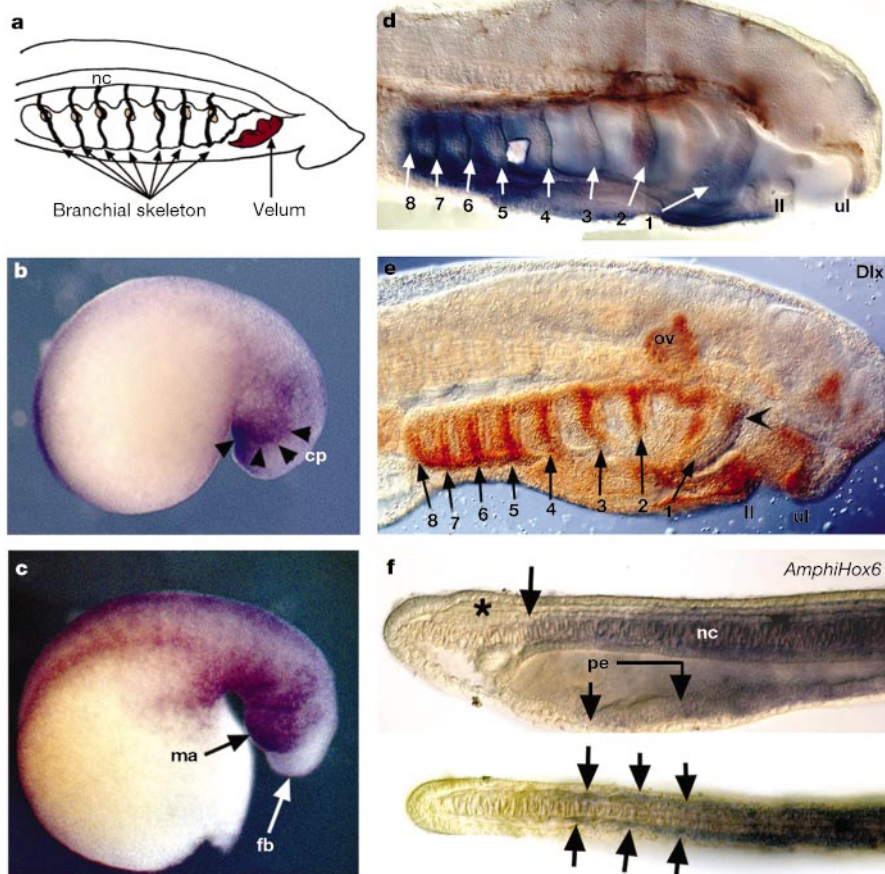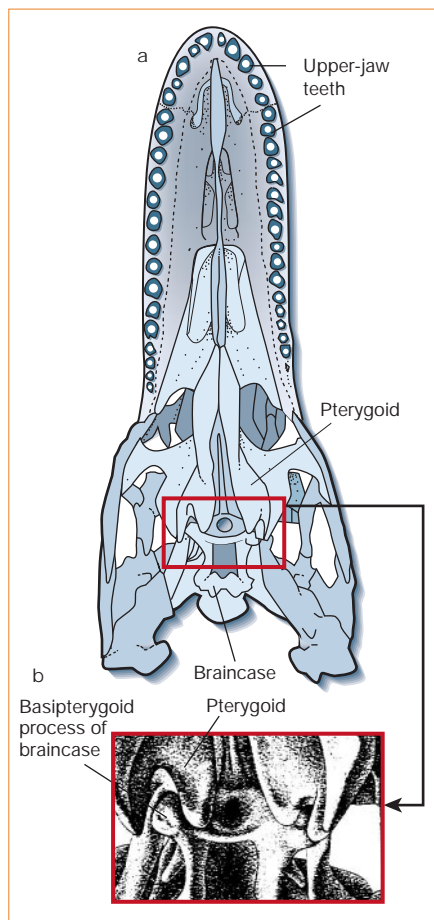
COMMUNICATIONS ARISING
Biomechanics

Prey attack by a large theropod dinosaur

Prey-capture strategies in carnivorous dinosaurs have been inferred from the biomechanical features of their tooth structure, the estimated bite force produced, and their diet[1–3]. Rayfield *et al.*[4] have used finite-element analysis (FEA) to investigate such structure–function relationships in *Allosaurus fragilis*, and have found that the skull was designed to bear more stress than could be generated by simple biting. They conclude that this large theropod dinosaur delivered a chop-and-slash 'hatchet' blow to its prey, which it approached with its mouth wide open before driving its upper tooth row downwards. We argue that this mode of predation is unlikely, and that the FEA results, which relate to an 'overengineered' skull, are better explained by the biomechanical demands of prey capture. Understanding the mechanics of predation is important to our knowledge of the feeding habits of carnivorous dinosaurs and for accurate reconstruction their lifestyles.

First, we note that no living carnivorous tetrapod attacks prey in quite the way that the authors contend. For example, in lizards that grasp their prey without the aid of the tongue, the attack depends upon careful and precise jaw closure, which may be followed by a shaking or lateral flailing of the prey; it does not depend on an initial high-impact collision[5,6].

Second, if *Allosaurus* is unusual in using such a biomechanically stressful chop/slash attack, then its tooth morphology, and possibly its tooth regionalization, should reflect this, and its jaw and tooth design should be substantially different from that of other carnosaurs. This is not the case, however, as allosaur teeth are unremarkable among theropod dinosaurs[2,7]. In fact, the teeth of the upper jaw (which would deliver the blow) are not much different from those of the lower jaw (which would not). The modest tooth regionalization in the allosaur specimen cited by Rayfield *et al.*[4] is comparable to that of other carnosaurs, including *Tyrannosaurus*, *Albertosaurus* and *Velociraptor*, that presumably do not use a hatchet-like attack.

Third, and perhaps most revealing, the skull of *Allosaurus* was kinetic — equipped with a movable basal joint[7] (Fig. 1). Kinetic skulls occur widely among non-mammalian tetrapods, including the earliest[8]. In its simplest form, cranial kinesis requires a transverse 'hinge' across the top or back of the skull, and a sliding basal joint, producing a functional separation between upper jaws and braincase. In modern lizards and snakes, cranial kinesis helps to align the teeth and jaws when grasping prey, and to synchronize

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 tetrapods[10].

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 interpretation[4] 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 period[1] and its prey included a range of large, herbivorous dinosaurs (ornithopods, 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 forces[4].

Furthermore, intracranial displacement between the palatal bones and the cheek region reduces stress at the basal articulation during an impact bite[4], 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 prey[5]. 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 analysis[4] 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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