

function of t . A steady state can be attained only when $V_p=0$ (and so $F=0$), because only then does the energy dissipation due to friction at P vanish.

For example, suppose that the body is the uniform spheroid $a^2(x^2 + y^2) + b^2z^2 = a^2b^2$. The principal moments of inertia at its centre, O , are $A = M(a^2 + b^2)/5$ and $C = 2Mb^2/5$. The function $h(\theta)$ is easily determined in the form $h(\theta) = (a^2\cos^2\theta + b^2\sin^2\theta)^{1/2}$, and from equation (11) we obtain the remarkable simplification

$$V_p = -(J/4Ah^2)(a^2 - b^2)\sin 2\theta \quad (13)$$

Gyroscopic balance occurs provided that

$$\Omega^2 \gg \frac{5g|a^2 - b^2|}{(a^2 + b^2)\min(a, b)} \quad (14)$$

As regards the frictional force, there are two obvious possibilities. First, we may assume a Coulomb law, $F = -\mu MgV_p/|V_p|$; then equation (12) integrates to give

$$\tan\theta = -(a/b)\tan\mu q(t - t_0) \quad (15)$$

where $q = Mgab(a - b)/|a - b||J|$ and t_0 is a constant of integration. Here we may take $J = A\Omega^*(a^2 + b^2/2)^{1/2}$, where Ω^* is the value of Ω when $\theta = \pi/4$. For the prolate spheroid ($q > 0$), this describes a monotonic decrease of θ from $\pi/2$ to 0 over the time interval $[t_0 - \pi/2\mu q, t_0]$; for the oblate spheroid ($q < 0$), it similarly describes a monotonic increase of θ from 0 to $\pi/2$ over the time interval $[t_0, t_0 + \pi/2|\mu q|]$. In either case, equation (15) thus represents a transition from the unstable to the stable state over a finite time interval $\Delta t = \pi/2|\mu q|$.

Alternatively, if we assume a 'viscous'

friction law $F = -\mu MgV_p$, then equation (12) becomes $\dot{\theta} = -(\mu q/2)\sin 2\theta$, where now $q = 5g(a^2 - b^2)/2(a^2 + b^2)$. This integrates to give

$$\tan\theta = e^{-\mu q(t - t_0)} \quad (16)$$

which again describes monotonic transition from unstable to stable states (whether $q > 0$ or $q < 0$) on the secular time scale $|\mu q|^{-1}$. Numerical integration of the exact equations (without use of the gyroscopic approximation) confirms the validity of this description.

The key to the above analysis lies in the fact that the Jellett constant (equation (10)) exists for arbitrary bodies of revolution as an adiabatic invariant when the condition described by equation (7) is satisfied, and not only for the previously analysed bodies with part-spherical forms.

Finally, we may note that a raw egg does not rise when spun, simply because the angular velocity imparted to the shell must diffuse into the fluid interior; this process dissipates most of the initial kinetic energy imparted to the egg, the remaining energy being insufficient for condition (14) to be satisfied and for the state of gyroscopic balance to be established.

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1. Braams, C. M. *Physica* **18**, 503–514 (1952).
2. Hugenholtz, N. M. *Physica* **18**, 515–527 (1952).
3. Gray, C. G. & Nickel, B. G. *Am. J. Phys.* **68**, 821–828 (2000).
4. Jellett, J. H. *A Treatise on the Theory of Friction* (Macmillan, London, 1872).

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Hox expression from the mandibular arch of gnathostomes may have facilitated the evolution of jaws.

In gnathostome embryos, cranial neural-crest cells migrate from the overlying mid- and hindbrain into the pharyngeal arches^{5,6}, where they give rise to the pharyngeal skeleton, including the jaw. With the exception of those destined for the mandibular arch, cranial neural-crest cells express specific combinations of *Hox* genes, which reflect their site of origin in the segmented hindbrain^{5,6}. In lamprey embryos, the branchial skeleton also develops from cranial neural-crest cells^{7,8} but, in contrast to gnathostomes, the lamprey mandibular arch fails to form separate dorsal and ventral cartilage condensations^{4,9}. Instead of forming a Meckel's cartilage, the lamprey first arch forms the velum, a muscular pumping organ

with a small, solitary cartilaginous condensation⁴ (Fig. 1a).

To investigate whether modulation of *Hox*-gene expression in the mandibular arch could be associated with the evolutionary origin of jaws, I cloned lamprey *Hox* genes and analysed their expression patterns during embryogenesis. Two overlapping genomic cosmids (MPMGc05511883 and MPMGc055J22138) were found to contain three *Hox* genes with orthology to the *Hox5-6-7* cognate group. During lamprey embryogenesis, the *HoxL6* (GenBank accession no. AY089982) expression domain spreads anteriorly from the blastopore and extends into the cranial mesoderm (see supplementary information), where I detected transcripts from the onset of mandibular-arch formation prior to colonization of this region by neural-crest cells⁹ (Fig. 1b).

HoxL6 continues to be expressed strongly in the mandibular and posterior arches as these become individually defined (Fig. 1c), and in two stripes in the dorsal hindbrain (see supplementary information), where the neural crest originates⁷⁻⁹. In older embryos, *HoxL6* expression was detected within each pharyngeal arch, and in the upper and lower lips (Fig. 1d). *HoxL6* transcripts co-localize with *Dlx*, a marker of the lamprey cranial neural crest^{10,11}, and were later detected in hypertrophic chondrocytes, indicating that *HoxL6* is expressed by neural-crest cells in the pharyngeal arches (compare Fig. 1d and e, and see supplementary information).

Within the mandibular arch, however, I detected *HoxL6* transcripts and *Dlx* protein in mutually exclusive ventral and dorsal domains, respectively (Fig. 1d, e). Comparison of *HoxL6* and *HoxL5* (GenBank accession no. AY089981) expression revealed that the *HoxL6* domain extends anterior to the boundary of *HoxL5* expression (see supplementary information), suggesting that spatial collinearity¹² has been broken. These findings identify lampreys as the only known vertebrate in which *Hox* genes are expressed in the mandibular arch.

To determine whether the breakage of *Hox6* collinearity is a derived condition of lampreys, I analysed expression of the single *Hox6* orthologue *AmphiHox6* in the cephalochordate amphioxus. *AmphiHox6* expression was detected throughout the neural tube, up to the base of the cerebral vesicle, and in endoderm up to the first gill slit (Fig. 1f). *AmphiHox6* expression extends anterior to the *AmphiHox3* and *AmphiHox4* domains¹² and, like *AmphiHox2*, does not respect spatial collinearity. Thus, in cephalochordate and lamprey embryos, *Hox6* genes are expressed anterior to their 3' neighbours, indicating that this could be a general feature of non-

Evolutionary biology

Lamprey *Hox* genes and the origin of jaws

The development of jaws was a critical event in vertebrate evolution because it ushered in a transition to a predatory lifestyle, but how this innovation came about has been a mystery. In the embryos of jawed vertebrates (gnathostomes), the jaw cartilage develops from the mandibular arch, where none of the *Hox* genes is expressed; if these are expressed ectopically, however, jaw development is inhibited¹⁻³. Here I show that in the lamprey, a primitively jawless (agnathan) fish that is a sister group to the gnathostomes⁴, a *Hox* gene is expressed in the mandibular arch of developing embryos. This finding, together with outgroup comparisons, suggests that loss of

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 diet¹⁻³. 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 joint⁷ (Fig. 1). Kinetic skulls occur widely among non-mammalian tetrapods, including the earliest⁸. 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

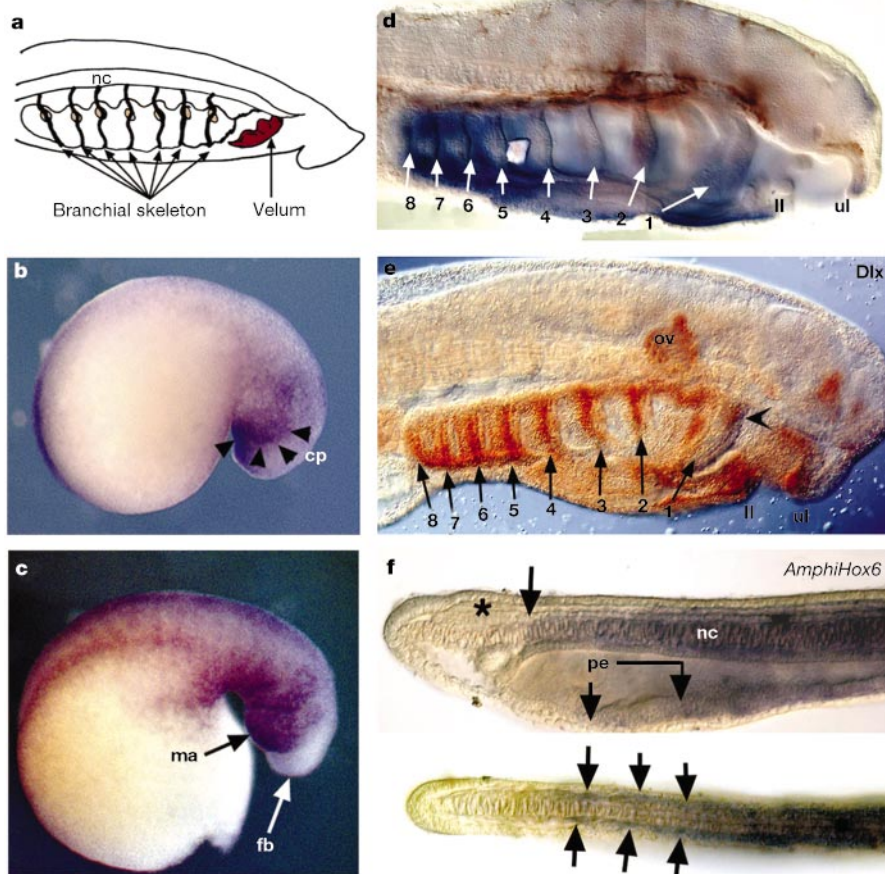


Figure 1 Expression of *Hox6* genes in lamprey and amphioxus embryos. Anterior is to the right in **a–e** and to the left in **f**. **a**, Diagram of the lamprey head. **b–d**, Whole-mount *in situ* hybridization showing *HoxL6* expression in lamprey embryos at stage 21 (**b**), 22 (**c**) and 26.5 (**d**). Note the expression 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 lampreys⁴. 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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- Alexandre, D. *et al. Development* **122**, 735–746 (1996).
- Pasqualetti, M. *et al. Development* **127**, 5367–5378 (2000).
- Grammatopoulos, G. A. *et al. Development* **127**, 5355–5365 (2000).
- Janvier, P. *Early Vertebrates* (Oxford Scientific, New York, 1996).
- Trainor, P. A. & Krumlauf, R. *Nature Rev. Neurosci.* **1**, 116–124 (2000).
- Schilling, T. F. *et al. Dev. Biol.* **231**, 201–216 (2001).
- Langille, R. M. & Hall, B. K. *Development* **102**, 301–310 (1988).
- Newth, D. R. *J. Exp. Biol.* **28**, 247–260 (1951).
- Horigome, N. *et al. Dev. Biol.* **207**, 287–308 (1999).
- Neideet, A. H. *et al. Proc. Natl Acad. Sci. USA* **98**, 1665–1670 (2001).
- Myojin, M. *et al. J. Exp. Zool.* **291**, 68–84 (2001).
- Wada, H. *et al. Dev. Biol.* **213**, 131–141 (1999).
- Ogasawara, M. *et al. Dev. Biol.* **223**, 399–410 (2000).

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