

velocity, mean acceleration and mean agility as the smallest set of parameters that explained significant variation in all the others. I therefore used these as independent measures of flight performance. These three variables were not significantly correlated with each other.

For all three of these independent flight parameters, the manipulation group and the interaction between manipulation group and manipulation type/year significantly influenced flight performance. The reduction and elongation manipulations influenced performance in the same direction for all three parameters in the streamer-manipulation experiment (1996) and for two of the three parameters in the basal manipulation experiment (1995) (Fig. 1). This produces the 'U-shaped' pattern (with fitness costs on the y axis plotted against manipulated-streamer length on the x axis) predicted by the natural selection alone hypothesis and is different to the positive slope predicted by the sexual selection alone hypothesis. As it is the streamer rather than the basal part of the tail that shows significant sexual dimorphism², the results from the streamer manipulation are probably more biologically meaningful⁶.

The results of this study oppose the predictions made from the sexual selection alone hypothesis. The tail streamers of male swallows could have evolved through natural selection alone but cannot have evolved entirely through sexual selection. However, it is possible that sexual selection has been involved in elongating the tail by less than the 20-mm manipulation used. Therefore, sexual selection could be responsible for the sexual dimorphism seen in this species (streamer length differs by about 15 mm between the sexes²).

The results of Møller and colleagues indicate that sexual selection may be operating at some level on male tail-feather length. My results indicate that sexual selection is probably responsible only for increasing male tail length beyond a naturally selected aerodynamic optimum; sexual selection can be responsible for a maximum of 27% of the streamer length.

Matthew R. Evans

Department of Biological and Molecular Sciences,
University of Stirling, Stirling FK9 4LA, UK
e-mail: MRE2@stir.ac.uk

1. Andersson, M. *Sexual Selection* (Princeton Univ. Press, Princeton, 1994).
2. Møller, A. P. *Sexual Selection and the Barn Swallow* (Oxford Univ. Press, Oxford, 1994).
3. Darwin, C. *The Descent of Man, and Selection in Relation to Sex* (Murray, London, 1871).
4. Smith, H. G. & Montgomerie, R. *Behav. Ecol. Sociobiol.* **28**, 195–201 (1991).
5. Norberg, R. Å. *Proc. R. Soc. Lond. B* **257**, 227–233 (1994).
6. Evans, M. R. & Thomas, A. L. R. *Proc. R. Soc. Lond. B* **264**, 211–217 (1997).
7. Rayner, J. M. V. & Aldridge, H. D. J. N. *J. Exp. Biol.* **118**, 247–265 (1985).
8. Lessells, C. M. & Boag, P. T. *Auk* **104**, 116–121 (1987).

The oldest coelurosaurian

We report here the discovery of a therizinosaur from the Early Jurassic Lower Lufeng Formation (Sinemurian stage) of Yunnan, China. This discovery extends the age range of these unusual animals, previously known only from the Cretaceous period (Albian–Maastrichtian stage¹), back by another 94 million years. This is the oldest definitive record of a coelurosaurian theropod, which therefore minimizes the divergence time for members of the group. Most important, it contradicts the

theory that the non-avian Coelurosauria occur too late in the fossil record to be related to birds.

This specimen (V11579, held at the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing), consisting of most of the left dentary and part of the splenial (Fig. 1), was collected from the bottom of dull, purplish beds of the Lower Lufeng Formation of Eshan County, Yunnan. The Lower Lufeng Formation was initially thought to have been formed in the Late Triassic² but it is now widely accepted to be of Early Jurassic origin on the basis of the invertebrate (such as coelocod, pelecypod and gastropod) and vertebrate (for example, prosauropod and the tritylodontid *Bienotherium*) fossils it contains³.

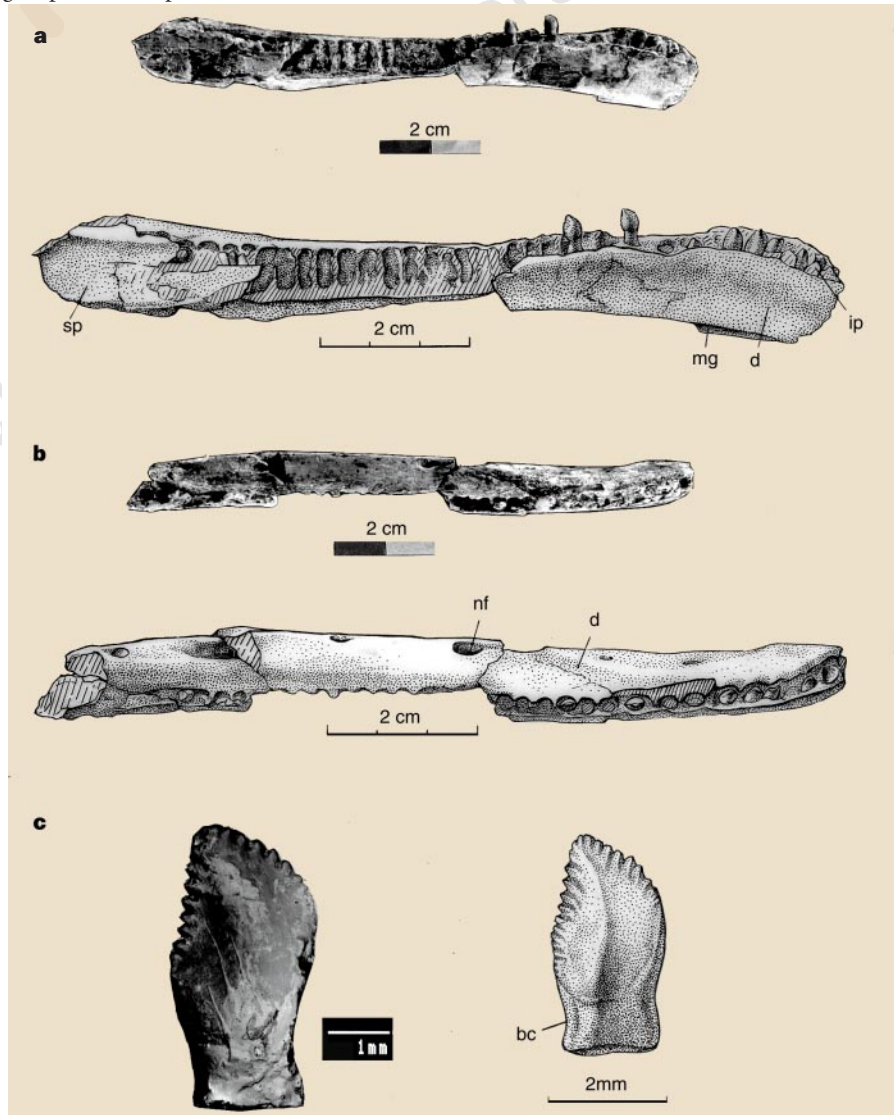


Figure 1 The left mandible of the specimen (V11579). **a**, Medial view. The downturned dentary and numerous small teeth are shared with therizinosaurids and a few other coelurosaurian theropods (troodontids and ornithomimosaurs), whereas the posterior decrease in size of the teeth and the morphology of the teeth are unique to therizinosaurids. **b**, The dorsal view shows a lateral shelf on the dentary. This is also present in ornithischians but is never so broad and flat as in this specimen and therizinosaurids. **c**, Tooth crown in lateral view. The tooth morphology, although superficially similar to that of some ornithischians and basal sauropodomorphs, is also unique to therizinosaurids in its combination of a basal constriction, circular roots, and lanceolate crown. bc, basal constriction; d, dentary; ip, interdental plate; mg, meckelian groove; nf, nutrient foramina; sp, splenial.

The therizinosauroid affinities of the specimen are indicated by the presence of a broad and flat shelf lateral to the tooth row and the few, large nutrient foramina below it; the downturned anterior end of the dentary; the decrease in the size of teeth posteriorly; the large number and small size of the teeth; and the morphology of the teeth (Fig. 1).

Therizinosauroidae ('segnosaurs') are a poorly known group of Asian dinosaurs with an unusual combination of features that, until recently, obscured their relationships. Recent hypotheses link segnosaurs with therizinosaurid theropods¹ and the group as a whole is placed in the Coelurosauria^{1,4}, which includes birds and all other theropods more closely related to birds than to Carnosauria⁵.

Previously, the oldest definitive records of Coelurosauria were *Ornitholestes* and *Coelurus* from the Late Jurassic Morrison Formation and *Compsognathus* from the Late Jurassic of Germany and France⁶. The oldest of these specimens are from beds correlated with the Kimmeridgian marine stage. Isolated teeth tentatively identified as dromaeosaurid have been found in Middle Jurassic deposits⁷. The Late Triassic *Protoavis texensis* may also belong to this group⁸, but questions have been raised about the association and interpretation of the material⁹. The new specimen is therefore the oldest fossil definitively referable to Coelurosauria, extending the record of this group back by roughly 30 million years.

The fossil record of Coelurosauria has been interpreted as inconsistent with a close relationship between birds and other members of this group¹⁰, in that most of the diversity of the non-avian Coelurosauria occurs much later in the fossil record than *Archaeopteryx* in the Late Jurassic. The presence of a non-avian coelurosaurian in the Early Jurassic indicates that by the Late Jurassic the major clades of this group must have already diverged, well before *Archaeopteryx* appears in the fossil record.

Xijin Zhao, Xing Xu

*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xizhimenwai Street, Beijing 100044, People's Republic of China
e-mail: xxu@sun.midwest.com.cn*

1. Russell, D. A. & Dong, Z. *Can. J. Earth Sci.* **30**, 2107–2127 (1993).
2. Bien, M. N. *Bull. Geol. Soc. China* **20**, 225–234 (1940).
3. Luo, Z. & Wu, X.-C. in *In the Shadow of the Dinosaurs* (eds Fraser, N. C. & Sues, H.-D.) 251–270 (Cambridge Univ. Press, New York, 1994).
4. Clark, J. M., Perle, A. & Norrell, M. A. *Am. Mus. Novit.* **3115**, 1–39 (1994).
5. Currie, P. J. in *Encyclopedia of Dinosaurs* (eds Currie, P. J. & Padian, K.) 241 (Academic, San Diego, 1997).
6. Norman, D. B. in *The Dinosauria* (eds Weishampel, D. B., Dodson, P. & Osmolska, H.) 280–305 (Univ. California Press, Berkeley, 1990).
7. Evans, S. E. & Milner, A. R. in *In the Shadow of the Dinosaurs* (eds Fraser, N. C. & Sues, H.-D.) 303–321 (Cambridge Univ. Press, New York, 1994).

8. Chatterjee, S. *Phil. Trans. R. Soc. Lond. B* **332**, 277–346 (1991).
9. Ostrom, J. H. *Archaeopteryx* **14**, 39–42 (1996).
10. Feduccia, A. *The Origin and Evolution of Birds* (Yale Univ. Press, New Haven, 1996).

Seal whiskers detect water movements

How do pinnipeds orientate themselves under water? As most pinniped species feed in conditions under which visibility is drastically reduced, for example at night, at great depths or in murky waters, it has been particularly unclear how they succeed in finding food. Here we show that harbour seals (*Phoca vitulina*) can use their whiskers to detect minute water movements. The high sensitivity of this sensory system should allow a seal to gain hydrodynamic information resulting from movements of other aquatic animals, such as prey, predators or conspecifics.

In the wild, blind but well-nourished seals have often been observed¹, showing that these marine mammals can orientate themselves and hunt successfully without vision. As pinnipeds do not possess an active sonar system², the kind of sensory information used for prey detection and spatial orientation remained unknown until now. In the aquatic environment, one usable source of sensory information consists of water disturbances caused by moving organisms. Consequently, hydrodynamic sensory systems have evolved many times in aquatic animals³. But, although marine mammals are highly adapted to their aquatic environment, hydrodynamic sensory systems have

never before been described in this animal group.

The whiskers of pinnipeds have been proposed to be useful for detecting water movements⁴. These whiskers are heavily innervated by slowly and rapidly adapting afferent fibres that respond to tiny deflections of the hair shaft^{5–7}. Like rats⁸, seals and sea lions use their whiskers for active touch discrimination^{4,9}, and probably for obstacle avoidance¹⁰. However, it was unknown whether they can also use these tactile hairs for the detection of low-amplitude water movements, thus sensing distance from other objects.

Using a 'go/no-go' response paradigm, we determined detection thresholds of hydrodynamic stimuli (in the range 10–100 Hz) for a male harbour seal. Stimuli were generated by a sinusoidally oscillating sphere (diameter 10 cm, oscillation axis vertical) attached to a Ling vibrator. Electronic signals driving the vibrator were computer-generated (stimulus duration 3 s, rise and fall times 300 ms), converted from digital to analog and power-amplified.

We trained the seal to place its head in a hoop opposite to the sphere (Fig. 1a). Here, the animal pressed the tip of its lower jaw on a knob screwed on a jib that was welded to the lower edge of the hoop. In this way a defined distance (adjustable from 5 to 50 cm) between the tip of the whiskers and sphere was guaranteed (Fig. 1a). By knowing the exact distance between the whiskers and the sphere, we could calculate the effective stimulus amplitude¹¹. Optical and acoustic cues were excluded by placing removable eye caps and headphones (pink noise masking, 151 dB rel. 1 mPa) on the seal. The seal indicated the detection of a

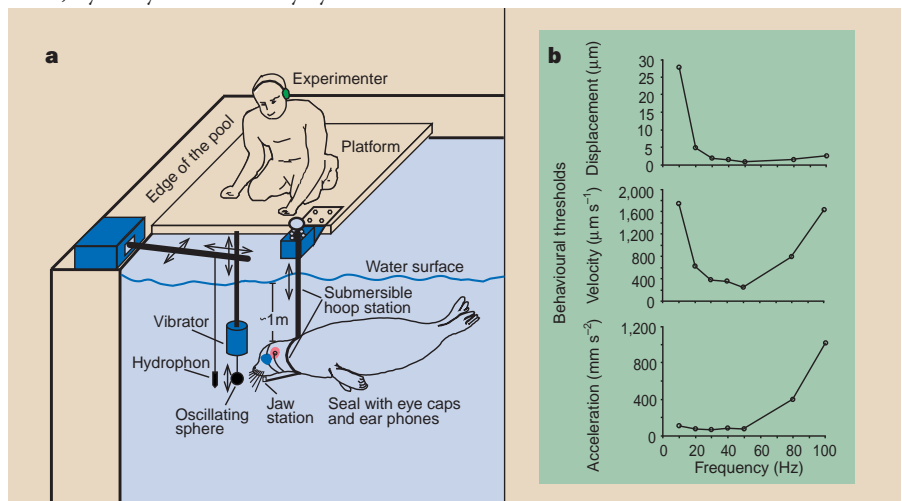


Figure 1 Detection of water movements by the harbour seal. **a**, Experimental set-up. At the beginning of a trial the hoop station was above the water surface, where the seal was stationed and supplied with eye caps and head phones, or, during whisker-exclusion tests, with a muzzle of wire mesh. Then the hoop was submerged with the seal to the final test position. The seal was trained to correct the position of its lower jaw whenever it lost contact with the knob of the jaw station. **b**, Behavioural displacement (top), velocity (centre) and acceleration (bottom) thresholds (defined as 50% correct decisions) of a harbour seal to sinusoidal water movements. Each threshold value is interpolated from 40 measurements with the last stimulus amplitude above threshold, and 40 measurements with the first stimulus amplitude below threshold.