

Are birds dinosaurs?

There is heated debate over the phylogenetic position of birds. Cladistic analysis^{1,2} nests birds within the theropod dinosaurs, but recent papers in successive issues of *Science* argue strongly against that view. Firstly, Burke and Feduccia³ present developmental evidence that the digits of the avian hand (II, III, IV) are not homologous with the digits of theropods (I, II, III). Secondly, Ruben and colleagues⁴ present fossil evidence that theropods had a crocodile-like respiratory system that could not sustain endothermic oxygen requirements, and could not have evolved into the through flow system of modern birds because intermediates would have suffered a debilitating diaphragmatic hernia.

In accord with Huxley's⁵ and Ostrom's⁶ suggestions, cladistic analysis¹ of avian phylogeny places them within theropod dinosaurs – specifically the dromaeosaurs (medium sized fast bipedal predators including the late-Cretaceous *Velociraptor*). But some evolutionary biologists have argued that many of the characters supporting this phylogenetic position are convergent, not homologous, and that the large bodies, short forelimbs, and cursorial habits of theropods make them singularly unlikely bird ancestors.

Developmental analysis by Burke and Feduccia³ supports the suggestion of convergence by attacking a fundamental homology. Birds' and theropods' hands are reduced to three digits. In theropods the digits can be identified as I, II and III (thumb, forefinger and middle finger), because early theropods such as *Herrerasaurus* retain the primitive five-fingered state, but with vestigial digits, IV and V. The theropod pattern of reduction is apparently unique – other amniotes reduce digit number by losing digits I, or V. *Archaeopteryx* had been assigned the theropod formula of I, II, III, because it had the appropriate number of phalanges in each digit (the generalized archosaur hand has 2,3,4,5,3), so this was the assumed pattern in birds.

Burke and Feduccia³ studied the formation of cartilaginous precursors of limb elements in amniote embryos. It appears that birds conform to the stereotypical amniote pattern of limb development, with the primary axis of cartilage condensation aligned with digit IV. Birds have apparently reduced digit number by the standard amniote pattern of elimination of digits I and V, not the unique theropod pattern of elimination of IV and V.

The late-Cretaceous theropod *Sinosauropteryx*⁷ has added fuel to both sides

of the debate. *Sinosauropteryx* is extraordinarily well preserved, with soft body parts evident, and a line of filamentous structures along its back that might be proto-feathers⁷. However, the detailed structure of bird feathers is lacking and the filamentous structures could simply be the remains of the skin or tendons of the dinosaur's back.

Ruben and colleagues⁴ describe a clear curved line across the thoracic cavity of *Sinosauropteryx* that appears to mark the boundary between two distinct thoracic compartments. Crocodiles and other reptiles have a similar thorax separated into two cavities by an airtight diaphragm. The septate lungs of such reptiles act like simple elastic bellows. Lizards fill their septate lungs by pumping movements of the ribcage, but crocodiles fill their lungs by pulling the piston-like liver out of the upper thoracic cavity using muscles attached to the pelvis and the forward-pointing pubis. Ruben and colleagues⁴ argue that the pelvis design of *Sinosauropteryx*, combined with the outline of the diaphragm, suggest that this advanced theropod had crocodile-like hepatic ventilation and a simple septate lung.

In a septate lung the tidal volume is small (only a small proportion of the air in the lung is renewed at each breath), and diffusion is the main mechanism that transports fresh air to the respiratory surface, limiting the rate of gas exchange to below that needed by active endotherms⁸.

Ruben and colleagues⁴ argue that the backward directed pubis of *Archaeopteryx*, and all other birds is 'broadly inconsistent' with a hepatic-pump ventilation mechanism. Instead the unique rib design

of modern birds allows the ribcage to move fore and aft during ventilation. To inhale, the ribs rotate pushing the sternum away from the backbone, sucking air into the abdominal air sacs. *Archaeopteryx*, and the enantiornithine birds lacked this adaptation of the ribs. Ruben and colleagues⁴ suggest that these early birds therefore also lacked the air-sac system, efficient ventilation, and endothermic metabolism of modern birds.

The modern bird system requires a single thoracic cavity, whereas the crocodile and theropod system require the thorax to be divided into two separate airtight chambers. Ruben and colleagues⁴ argue that the earliest stages in the evolution of avian respiration from the theropod system would have required selection for a diaphragmatic hernia in the intermediates. This would have prevented the animal from breathing, and is therefore unlikely to have been the subject of strong favourable selection.

These new findings add to a growing list of characters weighing against the bird–dinosaur link – such as the relatively large body size and small forelimbs of theropods (making them unlikely precursors for flight), and the rarity of the semi-lunate carpal in theropods (found in only four species).

But the greatest difficulty of all is the problem of timing: the most bird-like theropods did not appear until the late Cretaceous – 70 million years after *Archaeopteryx*, and 50 million years after the divergence of the modern bird orders according to the best recent molecular estimates⁹. The most bird-like theropods would have been living fossils when they were alive.

Nevertheless, cladistic analysis, supported by a wealth of apparent morphological synapomorphies, puts the birds firmly in the theropod camp. Furthermore,

Cambrian explosion blown out of the water

The fossil record of metazoan animals no longer starts with the Cambrian explosion 544 million years ago. Recent papers in *Nature*¹ and *Science*² describe fossils of metazoan embryos from 570 million-year-old phosphorites of the Doushantuo province, southern China. The fossil embryos are constant in size irrespective of whether they are divided into 2, 4 or 8 cells. The divisions seem to represent successive stages in the cleavage of a blastomere, and the tetrahedral pattern of division resembles that seen in modern nematode and flatworm embryos.

These stunning fossil embryos are consistent with recent molecular clock estimates that suggest that the metazoans originated long before the Cambrian explosion³. Darwin⁴ seems to have been quite correct in suggesting that '... before the lowest Cambrian stratum was deposited, long periods elapsed, as long as, or probably far longer than, the whole interval from the Cambrian age to the present day; and that during those vast periods the whole world swarmed with living creatures.'

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we may see precursors of the avian air-sac system in the non-vascularized sections of the septate lung that are set aside to act as pumps and ventilate the vascularized sections of the lung, and one has to wonder whether the primary axis of cartilage development in the unique circumstances of the three fingered limb of a theropod, lacking the proximal elements of digit IV would look exactly like that in birds.

The debate over the phylogenetic position of birds seems far from any conclusion – the two camps seem as implacably opposed as ever. Why? Perhaps because where natural selection meets the strict constraints of biomechanics, convergence is inevitable, and separating common inheritance from common function may

be near-impossible in a system so highly derived.

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Sex discrimination before birth

Sex-allocation theory describes how parents should bias investment in sons and daughters when male and female offspring give different fitness returns¹. Often, studies of sex allocation are based on species where a mechanism influencing sex allocation is known to exist, for example haplodipoidy in some insects. Among birds, unusual physiological or genetic mechanisms of sex determination are not known; however, accumulating studies attribute skews to primary sex-ratio adjustment^{2,3}.

Although very little is known about the sex-determining mechanism (other than that it is chromosomally based), female birds have the potential to control the primary sex ratio, as they are the heterogametic sex. The few papers reporting skews in avian sex ratios often refer to secondary sex ratios and concentrate on adaptive rather than the proximate explanations for such biases. Now three^{4–6} new papers indicate that female birds can detect offspring sex in the reproductive tract. Furthermore, females are capable of making decisions concerning investment in sons and daughters based on this information⁶.

Heinsohn and colleagues report that in the parrots *Eclectus scroatus* females are capable of extreme skewing of the sex ratio⁴. Data from aviculturalists' records of fledglings from successive breeding attempts showed that females produce much longer runs of one sex than expected if sex was determined by chance; in one case, 20 sons were produced before a daughter. *Eclectus* females usually lay two eggs but fledge only one young. Although it is possible that both eggs hatch and females

then selectively kill chicks according to sex, the authors use statistical models to show that infanticide alone could not account for the observed sex biases. Moreover, where two young do fledge, they are very likely to be of the same sex: only six of 41 two-chick broods comprised young of both sexes. Rejected eggs were not found in the aviaries (R. Heinsohn, pers. commun.). In the absence of dump laying of 'wrong'-sexed eggs, or infanticide, the mechanisms generating these sex ratios must involve manipulation of sex before egg-laying.

Female zebra finches (*Taeniopygia guttata*)⁵ similarly adjust the sex ratio of their eggs. In an elegant study, Kilner showed that females with experimentally restricted food intake produced significantly more male-biased sex ratios than when experiencing high food availability. The reduction in proportion of daughters produced was predicted, since some studies show that the reproductive success of females reared when food is scarce is more adversely affected than that of males. In addition to this overall sex ratio adjustment, Kilner found that early-laid eggs, which tended to hatch first, produced significantly more daughters than sons, regardless of food availability. Hence, females were manipulating not the overall ratio of sons to daughters, but also the order in which they produced males and females.

A description of avian reproductive physiology is needed to put these results into context. Female birds have only a single functional oviduct and ovary. In the ovary of a newly hatched chick there are millions of oocytes, most of which die

during growth. Of the surviving fraction, a few develop each breeding attempt when layers of yolk are deposited sequentially around them. At maturity, the ovary contains a hierarchy of follicles, the largest being next to ovulate. Once released from the ovary, the follicle passes to the end of the oviduct and is fertilized by sperm waiting in folds at the top of this structure. The fertilized egg then spends a day passing through the oviduct, where albumen and shell is secreted around it before laying.

In principle there are at least three ways in which female birds could alter offspring primary sex ratio. They might either determine the sex of the follicle they ovulate through pre-ovulation control of chromosome segregation, differentially provision oocytes of different sexes to determine the order in which they will be released from the ovary, or detect the sex of the ovulated follicle and reabsorb follicles of the 'wrong' sex. The last explanation would result in delays in production of eggs (possibly reflected in the pronounced hatching asynchrony recorded in *Eclectus* parrots). Whatever the mechanism, these papers report strong evidence that females can recognize the sex of a follicle before laying.

Research on American kestrels (*Falco sparverius*)⁶ demonstrates that females are not only capable of recognizing the sex of a follicle, but also of provisioning the egg accordingly. Anderson and colleagues found that eggs producing males were larger than eggs producing females, irrespective of laying order. The authors explain this in terms of an adaptation to enhance the competitive ability of sons competing with larger sisters in the nest. In this case, the female may either determine which size of egg she is preparing to lay and then adjust the sex accordingly, or perhaps more likely detect the sex of the