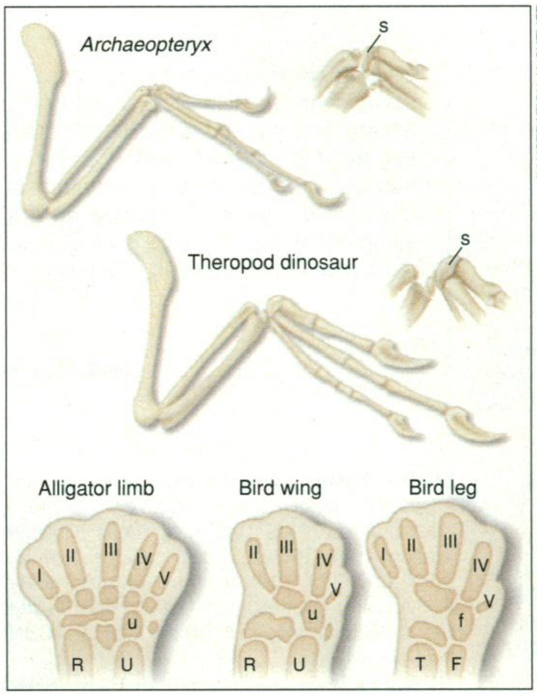
EVOLUTION

The Forward March of the Bird-Dinosaurs Halted?

Richard Hinchliffe

"Birds are dinosaurs." This is the provocative beginning to the chapter on the origin of birds in a recent book on dinosaur evolution (*1*). That it is by now the conventional view, repeated in student text books of vertebrate zoology, is a tribute to the success over the last 20 years of John Ostrom in persuading many biologists that *Archaeopteryx*, the first bird, is a feathered dinosaur (*2*, *3*). But in reality, the bird-dinosaur link remains contentious and a report by Burke and Feduccia on page 666 of this issue reopens this question (*4*).



They look alike, but... The similarity of the forelimbs of *Archaeopteryx* (**top**) and the theropod dinosaur *Deinonychus* (**middle**) may be due to convergence, not a common evolutionary line. Probably, the three dinosaur digits are I-II-III, whereas bird wing digits are II-III-IV, on the basis of evidence from embryos. The pattern of development of digits is very similar in bird wing and leg (**bottom middle** and **right**) and in the alligator (**bottom left**), an archosaur reptile and the birds' closest living relative (*4*, *11*, *13*). F, fibula; f, fibulare; R, radius; s, semilunate; T, tibia; t, tibiale; U, ulna; u, ulnare. Digit rays are numbered; phalanges are not drawn.

The first two *Archaeopteryx* fossils were found in the mid-19th century in the 150-million-year-old Jurassic limestone of Bavaria, both displaying remarkably preserved feathers and a reptilian skeleton. Such a convincing mosaic of bird-reptile features was a gift of the evolutionary gods to those such as Thomas Huxley who were trying to establish the transformation of members of one vertebrate class into another in evolution. Huxley saw a close dinosaur-*Archaeopteryx* relation (*5*), but until the 1970s the prevailing view was that *Archaeopteryx* (and therefore modern birds) derived from the thecodonts, relatively unspecialized basal archosaurs from which the dinosaurs probably radiated. A dinosaur origin was ruled out (*6*) because modern birds and *Archaeopteryx* were thought unlikely to have regained the clavicle or wishbone that the thecodonts possessed but the dinosaurs had apparently lost. When some dinosaurs were then discovered with clavicles, the way was open for the return of the "dinosaur origin" hypothesis. Ostrom proceeded to draw attention to many similarities in the skeletons of *Archaeopteryx* with those of a particular dinosaur group, the theropods (*2*, *3*). Later these similarities were formalized into a list of synapomorphies, or shared derived characters, by Gauthier in a cladistic analysis (*7*) supporting the dinosaur origin hypothesis.

Particularly convincing was the evidence of similarity in limb structure (see figure). Like *Archaeopteryx*, theropods have a wing/fore-limb digit number that is reduced from five to three. Some dromaeosaur theropods such as *Deinonychus* have the three main digits showing similarity in claw structure and in the number of elements (and their form) in each digit, while a wrist bone (the semilunate) appeared similar to one in the same position in *Archaeopteryx*. By the 1990s, the once heterodox "dinosaur origin" theory had become orthodox.

Orthodox theories always act as irritants, and a group of nonbelievers includes L. Martin (*8*), M. Hecht (*9*), and S. Tarsitano (*10*). Another dissident is A. Feduccia, who has published two marvelously illustrated books on bird origins and evolution (*11*) and is an author of the report published here. This new work addresses a question that has been on the table for 150 years: the identity in modern birds and *Archaeopteryx* of the three major digits of the wing, a highly specialized form of the pentadactyl limb. Are the bird digits the first, second, and third (I-II-III), or are they the second, third, and fourth (II-III-IV) (*12*)? How this question is answered affects in an important way the interpretation of the evolution of birds. In dinosaurs there is good evidence for the I-II-III formula since primitive theropods such as *Herrarasaurus* have two posterior vestigial digits (x) and thus a I-II-III-x-x structure. If the interpretation is that birds have digits II-III-IV, this presents a real problem for the theory of their theropod dinosaur origin.

The authors of the report carefully compare the fore- and hindlimb development patterns of an archosaur (an alligator, representing the birds' closest living relatives), a primitive reptile (the chelonian *Chrysemys*), and the chick (and other bird species). The striking Alcian blue photomicrographs demonstrate clearly the very similar developmental pattern in all three amniotes. The sequence of digit formation is posterior to anterior, with digit IV being the first formed in alligator and turtle where it appears to continue a connected axis from the more proximal ulna/ulnare through its distal carpal IV. Because the alligator and turtle have five digits, there can be no difficulty in identifying digits in these species. In the chick wing-bud, the first formed digit is in the same position as the first formed digit in alligator, with the same connections. This digit, the most posterior in the definitive wing, must therefore be number IV, as previously argued on purely avian embryological evidence (*12*). Convincing additional evidence is based on serial homology and the similarity of the bird wing-bud with the leg-bud in which the similarly positioned first formed digit can be identified with certainty as number IV since in the leg all five digits are present. This result makes the authors' interpretation that the first wing digit to form is number IV entirely reasonable and supports their assertion that in the wing the definitive bird digits are II-III-IV. This conclusion of identity on the basis of developmental evidence relies on classical homology and the principles of position and connections. But there is also support for this viewpoint from studies on limb reduction patterns (including mutants and experiments) in amniotes in general (*13*).

The report makes a very forceful statement of the II-III-IV theory, by assessing both fore- and hindlimb in chelonian-archosaur-bird material. Some of this evi-

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dence has been published in a different context by Muller (*13*), who argued for a very similar overall pattern of development in these three groups (and therefore probably in birds and reptiles in general), with differences explained by heterochrony (differences in the relative timing of developmental events) or by fusion of adjacent skeletogenic elements. But the present report gives the developmental evidence a sharp focus that makes it a timely contribution to current debate on bird origins. It represents a different methodology in ascertaining homology from that adopted by many paleontologists, who use multiple synapomorphies. However, increasingly, vertebrate morphologists are turning to development for information on the generation of diversity in evolution.

This convincing evidence of II-III-IV wing digit identity will not be to the liking of the cladistic supporters of a dinosaur origin of birds. For them, it introduces the possibility of convergence (rather than common origin) as an explanation of the similarities between the structure of the forelimb (and, indeed, of other structures) of theropods and the wing of *Archaeopteryx*.

Doubts about homology between theropod and bird digits remind us of some of the other problems in the "dinosaur-origin" hypothesis (*11*). These include the following: (i) The much smaller theropod forelimb (relative to body size) in comparison with the *Archaeopteryx* wing. Such small limbs are not convincing as proto-wings for a ground-up origin of flight in the relatively heavy dinosaurs. (ii) The rarity in theropods of the semilunate wrist bone, known in only four species (including *Deinonychus*). Most theropods have relatively large numbers of wrist elements, difficult to homologize with those of *Archaeopteryx*. (iii) The temporal paradox that most theropod dinosaurs and in particular the birdlike dromaeosaurs are all very much later in the fossil record than *Archaeopteryx*.

In reality, there is no easy solution to this question of bird origins, and for the moment the theropod dinosaur origin holds sway. Its supporters can point to some very striking theropod similarities with *Archaeopteryx*. But many of these could be due to convergence, with the birdlike dinosaurs appearing in the Cretaceous often some 75 million years after *Archaeopteryx*. Opponents of the orthodoxy are less united, but the thecodont origin still has support (*10*, *11*). The problem for this view is the long evolutionary gap, with no convincing intermediates. What we need is a proto-*Archaeopteryx* find to complement the numerous post-*Archaeopteryx* finds that are now being made (*14*). But for the time being this important developmental evidence that birds have a II-III-IV digital formula, unlike the dinosaur I-II-III, is the most important barrier to belief in the dinosaur-origin orthodoxy.

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ECOLOGY

Mass Extinction and Evolution

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On pages 689 and 692 of this issue, two reports by Hughes and his colleagues (*1*) and by Nee and May (*2*) consider aspects of the mass extinction that is now overtaking the world's biodiversity. The new results indirectly throw light on an overlooked but significant angle of the biotic crisis: its grossly disruptive impact on the future course of evolution.

Hughes and her colleagues discuss the elimination of populations—the geographical or genetic subdivision of species—by human activity rather than the more commonly analyzed elimination of species. Indeed, populations are readily examined; whole species are not. The authors estimated global numbers of populations by evaluating diversity within species from the literature and calculated that, whereas a median estimate for the species total is 14 million, populations could well number over 3 billion. They find that in tropical forests alone, populations could be disappearing at a percentage rate three to eight times the rate for species extinctions (conservatively reckoned). This is a significant loss for the ecosystem services supplied to humankind by populations—for instance, soil generation, watershed functions, pest control, regulation of weather and climate—valued recently (*3*) at $33 trillion per year.

This raises critical questions for the foreseeable future. If we lose, say, half of all species plus 90% of the populations of surviving species, which will be more detrimental for the biggest service of all, environmental maintenance of the biosphere?

Equally significant, which will have the greater impact on future evolution? What counts is not only how many populations disappear, but also which populations disappear, with which functions. Do evolutionary processes such as speciation and origination stem largely from core populations within a species' range, or do they derive more from peripheral populations (which tend to be at greater risk through habitat loss)? In support of the second viewpoint is the notion that populations in border zones may contain greater genetic variability, because they have to adapt to environmental pressures that often arise in greatest measure among the semiforeign areas at the limit of a species' range. Or could it be that the richest resources for natural selection occur in the heartland zone, whereas natural selection pressures are greatest in the peripheries? These are vital questions (*4*) for a biosphere in extreme turmoil from human activities.

As an indication of how far a species can lose populations while still flourishing as a species, consider the case of wheat. The current crop with an expanse of more than 250 million hectares comprises at least 500 trillion individuals, probably a record. (For proportion, figure out how long a period of time is represented by 1 trillion seconds.) As a species, wheat is the opposite of endangered. But because of a protracted breeding trend toward genetic uniformity, the species has lost the great bulk of its populations and most of its genetic variability. This highlights the urgent need to conserve populations as well as species, in light of the many benefits supplied by populations but not by species.

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