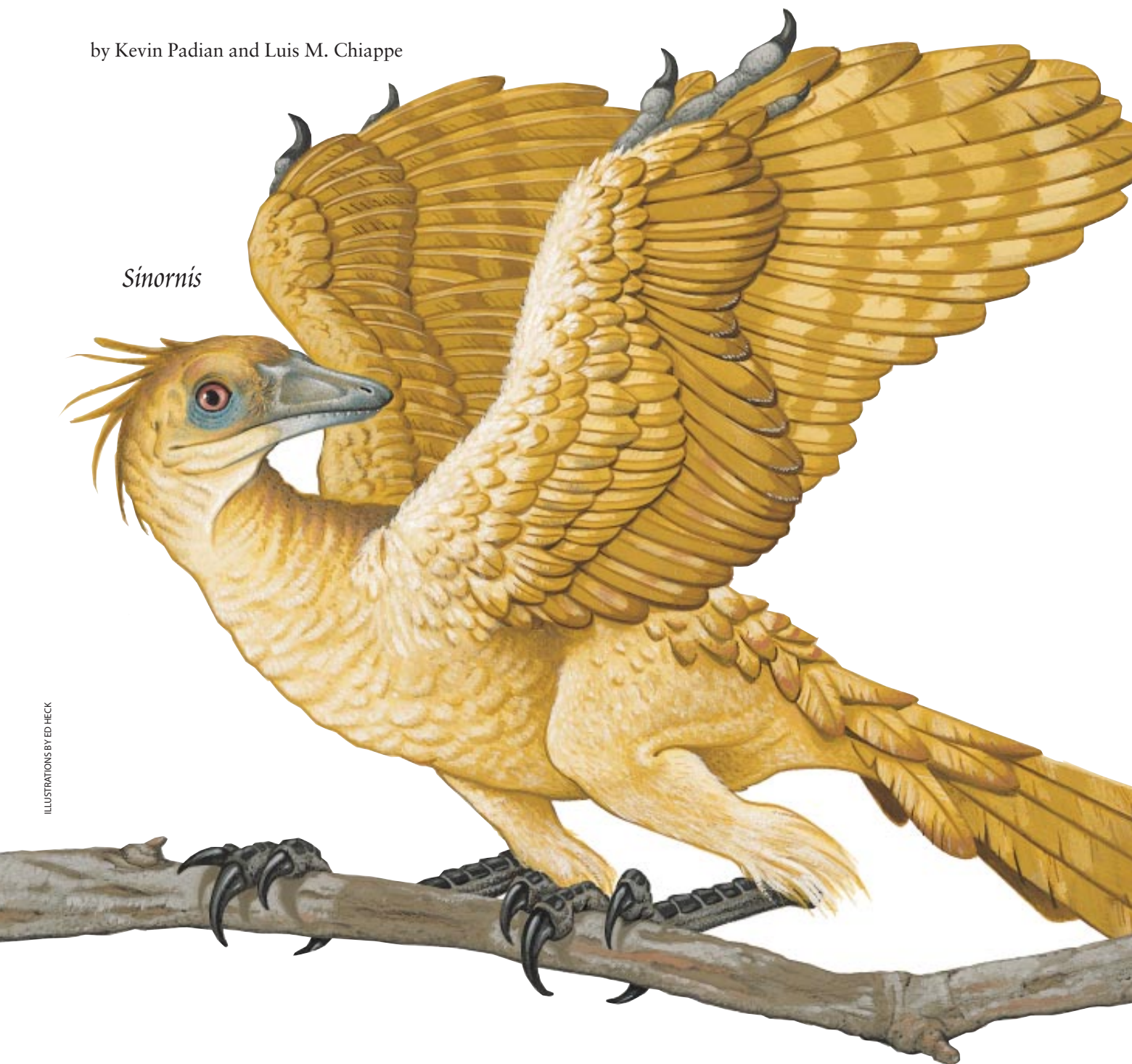


The Origin of Birds and Their Flight

Anatomical and aerodynamic analyses of fossils and living birds show that birds evolved from small, predatory dinosaurs that lived on the ground

by Kevin Padian and Luis M. Chiappe

Sinornis



ILLUSTRATIONS BY ED HECK

Until recently, the origin of birds was one of the great mysteries of biology. Birds are dramatically different from all other living creatures. Feathers, toothless beaks, hollow bones, perching feet, wishbones, deep breastbones and stumplike tailbones are only part of the combination of skeletal features that no other living animal has in common with them. How birds evolved feathers and flight was even more imponderable.

In the past 20 years, however, new fossil discoveries and new research methods have enabled paleontologists to determine that birds descend from ground-dwelling, meat-eating dinosaurs of the group known as theropods. The work has also offered a picture of how the earliest birds took to the air.

Scientists have speculated on the evolutionary history of birds since shortly after Charles Darwin set out his theory of evolution in *On the Origin of Species*. In 1860, the year after the publication of Darwin's treatise, a solitary feather of a bird was found in Bavarian limestone deposits dating to about 150 million years ago (just before the Jurassic period gave way to the Cretaceous). The next year a skeleton of an animal that had birdlike wings and feathers—but a very unbirdlike long, bony tail and toothed jaw—turned up in the same region. These finds became the first two specimens of the blue jay-size *Archaeopteryx lithographica*, the most archaic, or basal, known member of the birds [see “*Archaeopteryx*,” by Peter Wellnhofer; SCIENTIFIC AMERICAN, May 1990].

Archaeopteryx's skeletal anatomy provides clear evidence that birds descend from a dinosaurian ancestor, but in 1861 scientists were not yet in a position to make that connection. A few years later, though, Thomas Henry Huxley, Darwin's staunch defender, became the first person to connect birds to dinosaurs. Comparing the hind limbs of *Megalosaurus*, a giant theropod, with those of the ostrich, he noted 35 features that the two groups shared but that did not occur as a suite in any other animal. He concluded that birds and theropods could be closely related, although whether he thought birds were cousins of theropods or were descended from them is not known.

Huxley presented his results to the Geological Society of London in 1870, but paleontologist Harry Govier Seeley contested Huxley's assertion of kinship between theropods and birds. Seeley suggested that the hind limbs of the ostrich and *Megalosaurus* might look similar just because both animals were large and bipedal and used their hind limbs in similar ways. Besides, dinosaurs were even larger than ostriches, and none of them could fly; how, then, could flying birds have evolved from a dinosaur?

The mystery of the origin of birds gained renewed atten-

tion about half a century later. In 1916 Gerhard Heilmann, a medical doctor with a penchant for paleontology, published (in Danish) a brilliant book that in 1926 was translated into English as *The Origin of Birds*. Heilmann showed that birds were anatomically more similar to theropod dinosaurs than to any other fossil group but for one inescapable discrepancy: theropods apparently lacked clavicles, the two collarbones that are fused into a wishbone in birds. Because other reptiles had clavicles, Heilmann inferred that theropods had lost them. To him, this loss meant birds could not have evolved from theropods, because he was convinced (mistakenly, as it turns out) that a feature lost during evolution could not be regained. Birds, he asserted, must have evolved from a more archaic reptilian group that had clavicles. Like Seeley before him, Heilmann concluded that the similarities between birds and dinosaurs must simply reflect the fact that both groups were bipedal.

Heilmann's conclusions influenced thinking for a long time, even though new information told a different story. Two separate findings indicated that theropods did, in fact, have clavicles. In 1924 a published anatomical drawing of the bizarre, parrot-headed theropod *Oviraptor* clearly showed a wish-

Iberomesornis



Eoalulavis



EARLY BIRDS living more than 100 million years ago looked quite different from birds of today. For instance, as these artist's reconstructions demonstrate, some retained the clawed fingers and toothed jaw characteristic of nonavian dinosaurs. Fossils of *Sinornis* (left) were uncovered in China; those of *Iberomesornis* and *Eoalulavis* (right) in Spain. All three birds were about the size of a sparrow. *Eoalulavis* sported the first known alula, or “thumb wing,” an adaptation that helps today's birds navigate through the air at slow speeds.

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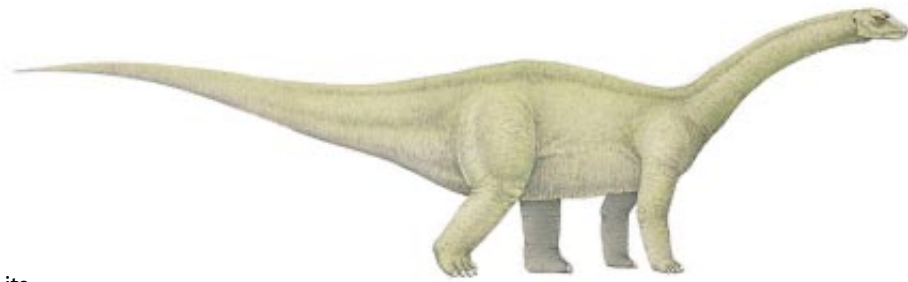
Tracking the Dinosaur Lineage Leading to Birds

The family tree at the right traces the ancestry of birds back to their early dinosaurian ancestors. This tree, otherwise known as a cladogram, is the product of today's gold standard for analyzing the evolutionary relations among animals—a method called cladistics.

Practitioners of cladistics determine the evolutionary history of a group of animals by examining certain kinds of traits. During evolution, some animal will display a new, genetically determined trait that will be passed to its descendants. Hence, paleontologists can conclude that two groups uniquely sharing a suite of such novel, or derived, traits are more closely related to each other than to animals lacking those traits.

Nodes, or branching points (*dots*), on a cladogram mark the emergence of a lineage possessing a new set of derived traits. In the cladogram here, the Theropoda all descend from a dinosaurian ancestor that newly possessed hollow bones and had only three functional toes. In this scheme, the theropods are still dinosaurs; they are simply a subset of the saurischian dinosaurs. Each lineage, or clade, is thus nested within a larger one (*colored rectangles*). By the same token, birds (*Aves*) are maniraptoran, tetanuran and theropod dinosaurs.

—K.P. and L.M.C.



Titanosaurus

DINOSAUR LINEAGES
THAT DID NOT LEAD
TO BIRDS

DINOSAURIA

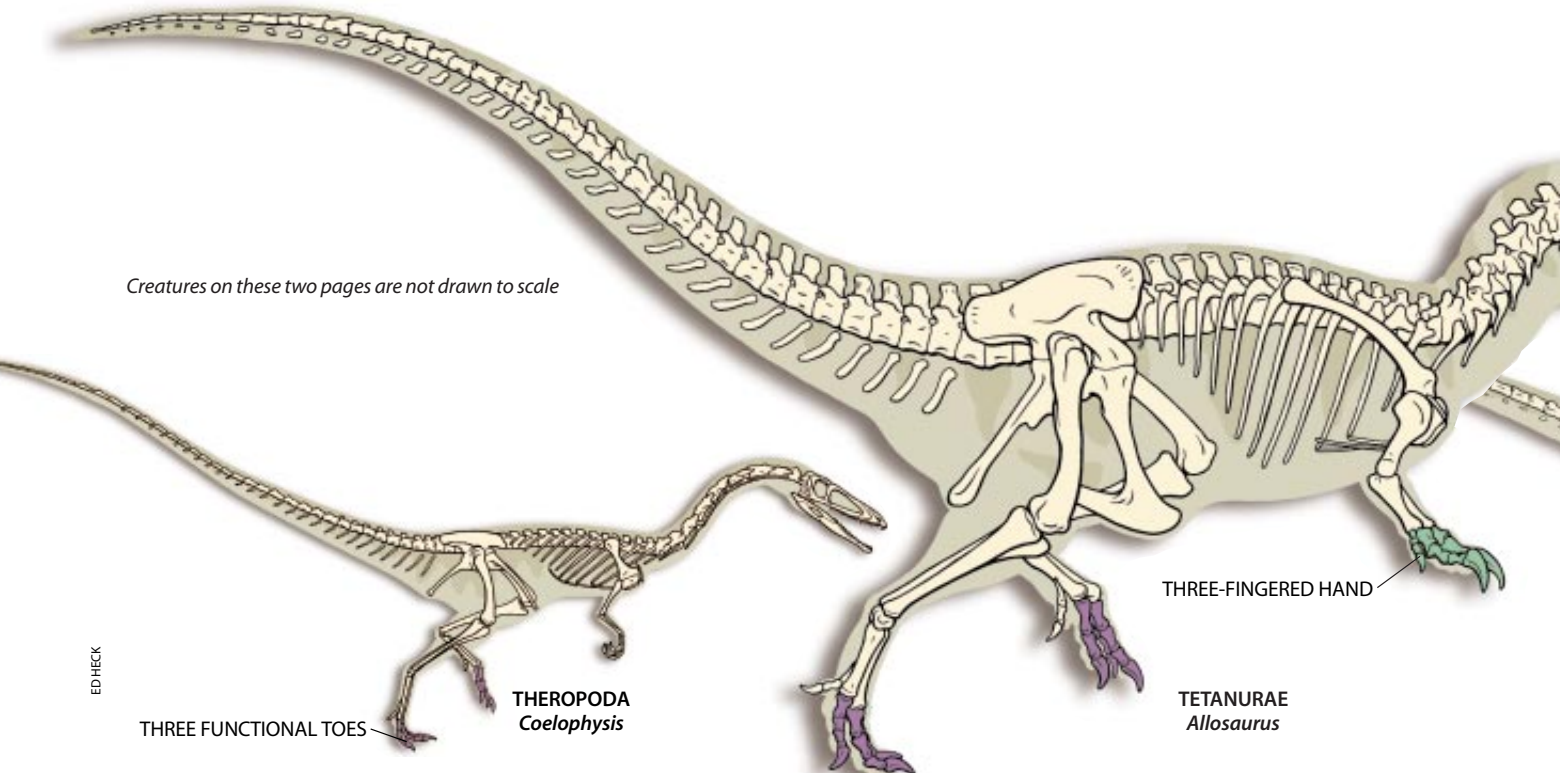
SAURISCHIA

bone, but the structure was misidentified. Then, in 1936, Charles Camp of the University of California at Berkeley found the remains of a small Early Jurassic theropod, complete with clavicles. Heilmann's fatal objection had been overcome, although few scientists recognized it. Recent studies have found clavicles in a broad spectrum of the theropods related to birds.

Finally, a century after Huxley's disputed presentation to the Geological Society of London, John H. Ostrom of Yale

University revived the idea that birds were related to theropod dinosaurs, and he proposed explicitly that birds were their direct descendants. In the late 1960s Ostrom had described the skeletal anatomy of the theropod *Deinonychus*, a vicious, sickle-clawed predator about the size of an adolescent human, which roamed in Montana some 115 million years ago (in the Early Cretaceous). In a series of papers published during the next decade, Ostrom went on to identify a collection of features that birds, including *Archaeopteryx*, shared

Creatures on these two pages are not drawn to scale



THREE FUNCTIONAL TOES

THEROPODA
Coelophysis

THREE-FINGERED HAND

TETANURAE
Allosaurus

THEROPODA Three functional toes; hollow bones

TETANURAE Three-fingered hand

MANIRAPTORA Half-moon-shaped wristbone

AVES Reversed first toe;
fewer than 26 vertebrae in tail

Coelophysis

Allosaurus

Velociraptor

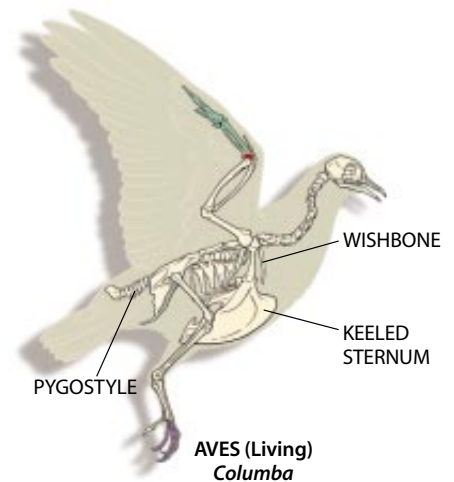
Archaeopteryx

Columba
(pigeon)

TOMO NARASHIMA

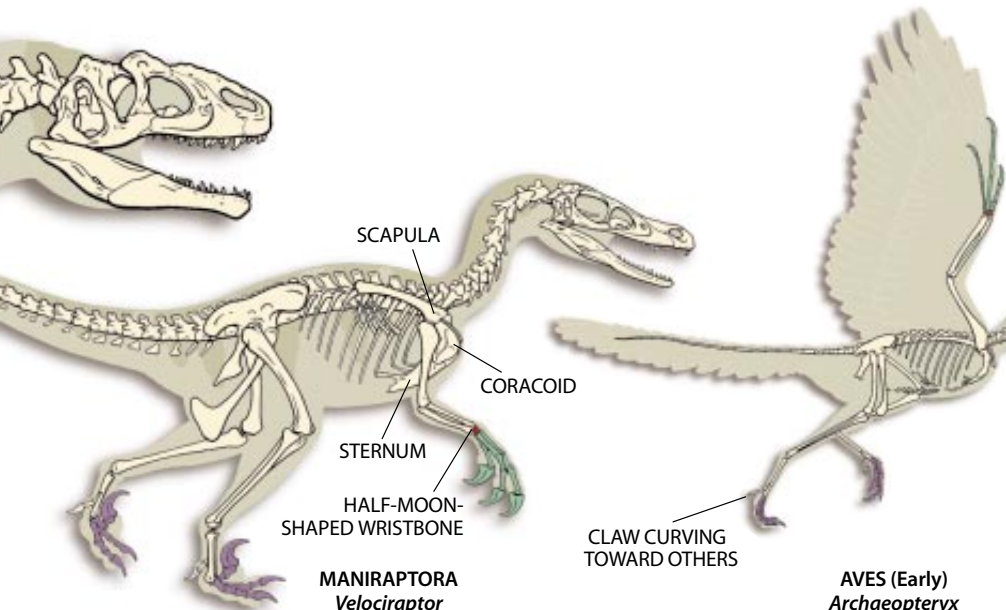
with *Deinonychus* and other theropods but not with other reptiles. On the basis of these findings, he concluded that birds are descended directly from small theropod dinosaurs.

As Ostrom was assembling his evidence for the theropod origin of birds, a new method of deciphering the relations among organisms was taking hold in natural history museums in New York City, Paris and elsewhere. This method—called phylogenetic systematics or, more commonly, cladistics—has since become the standard for comparative biology, and its use has strongly validated Ostrom's conclusions.



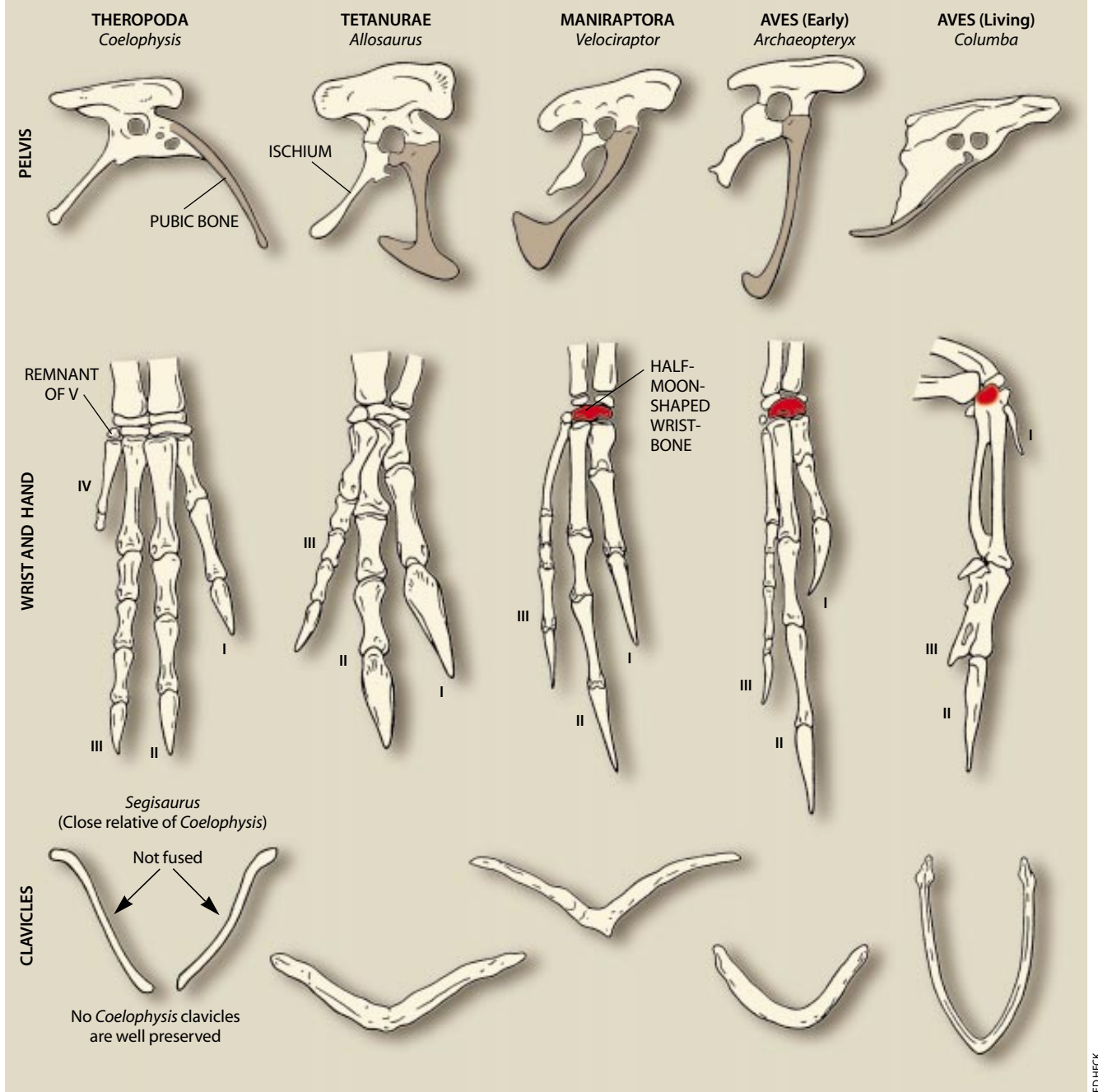
AVES (Living)
Columba

REPRESENTATIVE THEROPODS in the lineage leading to birds (Aves) display some of the features that helped investigators establish the dinosaurian origin of birds—including, in the order of their evolution, three functional toes (*purple*), a three-fingered hand (*green*) and a half-moon-shaped wristbone (*red*). *Archaeopteryx*, the oldest known bird, also shows some new traits, such as a claw on the back toe that curves toward the claws on the other toes. As later birds evolved, many features underwent change. Notably, the fingers fused together, the simple tail became a pygostyle composed of fused vertebrae, and the back toe dropped, enabling birds' feet to grasp tree limbs firmly.



MANIRAPTORA
Velociraptor

AVES (Early)
Archaeopteryx



ED HECK

COMPARISONS OF ANATOMICAL STRUCTURES not only helped to link birds to theropods, they also revealed some of the ways those features changed as dinosaurs became more birdlike and birds became more modern. In the pelvis (*side view*), the pubic bone (*brown*) initially pointed forward (toward the right), but it later shifted to be vertical or pointed backward. In the hand (*top view*), the relative proportions of the bones re-

mained quite constant through the early birds, but the wrist changed. In the maniraptoran wrist, a disklike bone took on the half-moon shape (*red*) that ultimately promoted flapping flight in birds. The wide, boomerang-shaped wishbone (fused clavicles) in tetanurans and later groups compares well with that of archaic birds, but it became thinner and formed a deeper U shape as it became more critical in flight.

Traditional methods for grouping organisms look at the similarities and differences among the animals and might exclude a species from a group solely because the species has a trait not found in other members of the group. In contrast, cladistics groups organisms based exclusively on certain kinds of shared traits that are particularly informative.

This method begins with the Darwinian precept that evolution proceeds when a new heritable trait emerges in some organism and is passed genetically to its descendants. The precept indicates that two groups of animals sharing a set of

such new, or "derived," traits are more closely related to each other than they are to groups that display only the original traits but not the derived ones. By identifying shared derived traits, practitioners of cladistics can determine the relations among the organisms they study.

The results of such analyses, which generally examine many traits, can be represented in the form of a cladogram: a treelike diagram depicting the order in which new characteristics, and new creatures, evolved [*see box on preceding two pages*]. Each branching point, or node, reflects the emergence

of an ancestor that founded a group having derived characteristics not present in groups that evolved earlier. This ancestor and all its descendants constitute a “clade,” or closely related group.

Ostrom did not apply cladistic methods to determine that birds evolved from small theropod dinosaurs; in the 1970s the approach was just coming into use. But about a decade later Jacques A. Gauthier, then at the University of California at Berkeley, did an extensive cladistic analysis of birds, dinosaurs and their reptilian relatives. Gauthier put Ostrom’s comparisons and many other features into a cladistic framework and confirmed that birds evolved from small theropod dinosaurs. Indeed, some of the closest relatives of birds include the sickle-clawed maniraptoran *Deinonychus* that Ostrom had so vividly described.

Today a cladogram for the lineage leading from theropods to birds shows that the clade labeled Aves (birds) consists of the ancestor of *Archaeopteryx* and all other descendants of that ancestor. This clade is a subgroup of a broader clade consisting of so-called maniraptoran theropods—itself a subgroup of the tetanuran theropods that descended from the most basal theropods. Those archaic theropods in turn evolved from nontheropod dinosaurs. The cladogram shows that birds are not only *descended* from dinosaurs, they *are* dinosaurs (and reptiles)—just as humans are mammals, even though people are as different from other mammals as birds are from other reptiles.

Early Evolutionary Steps to Birds

Gauthier’s studies and ones conducted more recently demonstrate that many features traditionally considered “birdlike” actually appeared before the advent of birds, in their preavian theropod ancestors. Many of those properties undoubtedly helped their original possessors to survive as terrestrial dinosaurs; these same traits and others were eventually used directly or were transformed to support flight and an arboreal way of life. The short length of this article does not allow us to catalogue the many dozens of details that combine to support the hypothesis that birds evolved from small theropod dinosaurs, so we will concentrate mainly on those related to the origin of flight.

The birdlike characteristics of the theropods that evolved prior to birds did not appear all at once, and some were present before the theropods themselves emerged—in the earliest dinosaurs. For instance, the immediate reptilian ancestor of dinosaurs was already bipedal and upright in its stance (that is, it basically walked like a bird), and it was small and carnivorous. Its hands, in common with those of early birds, were free for grasping (although the hand still had five digits, not the three found in all but the most basal theropods and in birds). Also, the second finger was longest—not the third, as in other reptiles.

Further, in the ancestors of dinosaurs, the ankle joint had already become hingelike, and the metatarsals, or foot bones, had become elongated. The metatarsals were held off the ground, so the immediate relatives of dinosaurs, and dinosaurs themselves, walked on their toes and put one foot in front of the other, instead of sprawling. Many of the changes in the feet are thought to have increased stride length and running speed, a property that would one day help avian theropods to fly.

The earliest theropods had hollow bones and cavities in

the skull; these adjustments lightened the skeleton. They also had a long neck and held their back horizontally, as birds do today. In the hand, digits four and five (the equivalent of the pinky and its neighbor) were already reduced in the first dinosaurs; the fifth finger was virtually gone. Soon it was completely lost, and the fourth was reduced to a nubbin. Those reduced fingers disappeared altogether in tetanuran theropods, and the remaining three (I, II, III) became fused together sometime after *Archaeopteryx* evolved.

In the first theropods, the hind limbs became more birdlike as well. They were long; the thigh was shorter than the shin, and the fibula, the bone to the side of the shinbone, was re-

Bones of Contention

Although many lines of evidence establish that birds evolved from small, terrestrial theropod dinosaurs, a few scientists remain vocally unconvinced. They have not, however, tested any alternative theory by cladistics or by any other method that objectively analyzes relationships among animals. Here is a sampling of their arguments, with some of the evidence against those assertions.

Bird and theropod hands differ: theropods retain fingers I, II and III (having lost the “pinky” and “ring finger”), but birds have fingers II, III and IV. This view of the bird hand is based on embryological research suggesting that when digits are lost from the five-fingered hand, the outer fingers (I and V) are the first to go. No one doubts that theropods retain fingers I, II and III, however, so this “law” clearly has exceptions and does not rule out retention of the first three fingers in birds. More important, the skeletal evidence belies the alleged difference in the hands of birds and nonavian theropods. The three fingers that nonavian theropods kept after losing the fourth and fifth have the same forms, proportions and connections to the wristbones as the fingers in *Archaeopteryx* and later birds [see middle row of illustration on opposite page].

Theropods appear too late to give rise to birds. Proponents of this view have noted that *Archaeopteryx* appears in the fossil record about 150 million years ago, whereas the fossil remains of various nonavian maniraptors—the closest known relatives of birds—date only to about 115 million years ago. But investigators have now uncovered bones that evidently belong to small, nonavian maniraptors and that date to the time of *Archaeopteryx*. In any case, failure to find fossils of a predicted kind does not rule out their existence in an undiscovered deposit.

The wishbone (composed of fused clavicles) of birds is not like the clavicles in theropods. This objection was reasonable when only the clavicles of early theropods had been discovered, but boomerang-shaped wishbones that look just like that of *Archaeopteryx* have now been uncovered in many theropods.

The complex lungs of birds could not have evolved from theropod lungs. This assertion cannot be supported or falsified at the moment, because no fossil lungs are preserved in the paleontological record. Also, the proponents of this argument offer no animal whose lungs could have given rise to those in birds, which are extremely complex and are unlike the lungs of any living animal.

—K.P. and L.M.C.

THEROPOD FOSSILS recently discovered in China suggest that the structures that gave rise to feathers probably predated the emergence of birds. *Sinosauropteryx* (left) sported a filamentous fringe along its back that could have consisted of precursors to feathers. And *Protarchaeopteryx* (right) bore true feathers, such as the cluster that is magnified in the top detail; the smaller detail highlights part of one feather.

duced. (In birds today the toothpicklike bone in the drumstick is all that is left of the fibula.) These dinosaurs walked on the three middle toes—the same ones modern birds use. The fifth toe was shortened and tapered, with no joints, and the first toe included a shortened metatarsal (with a small joint and a claw) that projected from the side of the second toe. The first toe was held higher than the others and had no apparent function, but it was later put to good use in birds. By the time *Archaeopteryx* appeared, that toe had rotated to lie behind the others. In later birds, it descended to become opposable to the others and eventually formed an important part of the perching foot.

More Changes

Through the course of theropod evolution, more features once thought of as strictly avian emerged. For instance, major changes occurred in the forelimb and shoulder girdle; these adjustments at first helped theropods to capture prey and later promoted flight. Notably, during theropod evolution, the arms became progressively longer, except in such giant carnivores as *Carnotaurus*, *Allosaurus* and *Tyrannosaurus*, in which the forelimbs were relatively small. The forelimb was about half the length of the hind limb in very early theropods. By the time *Archaeopteryx* appeared, the forelimb was longer than the hind limb, and it grew still more in later birds. This lengthening in the birds allowed a stronger flight stroke.

The hand became longer, too, accounting for a progressively greater proportion of the forelimb, and the wrist underwent dramatic revision in shape. Basal theropods possessed a flat wristbone (distal carpal) that overlapped the bases of the first and second palm bones (metacarpals) and fingers. In maniraptorans, though, this bone assumed a half-moon shape along the surface that contacted the arm bones. The half-moon, or semilunate, shape was very important because it allowed these animals to flex the wrist sideways in addition to up and down. They could thus fold the long hand, almost as living birds do. The longer hand could then be rotated and whipped forward suddenly to snatch prey.

In the shoulder girdle of early theropods, the scapula (shoulder blade) was long and straplike; the coracoid (which along with the scapula forms the shoulder joint) was rounded, and two separate, S-shaped clavicles connected the shoulder to the sternum, or breastbone. The scapula soon became longer and narrower; the coracoid also thinned and elongated, stretching toward the breastbone. The clavicles fused at the midline and broadened to form a boomerang-shaped wishbone. The sternum, which consisted originally of cartilage, calcified into two fused bony plates in tetanurans. Together these changes strengthened the skeleton; later this strengthening was used to reinforce the flight apparatus and support the flight muscles. The new wishbone, for instance, probably became an anchor for the muscles that moved the forelimbs, at first during foraging and then during flight.



In the pelvis, more vertebrae were added to the hip girdle, and the pubic bone (the pelvic bone that is attached in front of and below the hip socket) changed its orientation. In the first theropods, as in most other reptiles, the pubis pointed down and forward, but then it began to point straight down or backward. Ultimately, in birds more advanced than *Archaeopteryx*, it became parallel to the ischium, the pelvic bone that extends backward from below the hip socket. The benefits derived from these changes, if any, remain unknown, but the fact that these features are unique to birds and other maniraptorans shows their common origin.

Finally, the tail gradually became shorter and stiffer throughout theropod history, serving more and more as a balancing organ during running, somewhat as it does in today's road-runners. Steven M. Gatesy of Brown University has demonstrated that this transition in tail structure paralleled another change in function: the tail became less and less an anchor for the leg muscles. The pelvis took over that function, and in maniraptorans the muscle that once drew back the leg now mainly controlled the tail. In birds that followed *Archaeopteryx*, these muscles would be used to adjust the feathered tail as needed in flight.

In summary, a great many skeletal features that were once thought of as uniquely avian innovations—such as light, hollow bones, long arms, three-fingered hands with a long second finger, a wishbone, a backward-pointing pelvis, and long hind limbs with a three-toed foot—were already present in theropods before the evolution of birds. Those features generally served different uses than they did in birds and were only later co-opted for flight and other characteristically avian functions, eventually including life in the trees.

Evidence for the dinosaurian origin of birds is not confined to the skeleton. Recent discoveries of nesting sites in Mongolia and Montana reveal that some reproductive behaviors

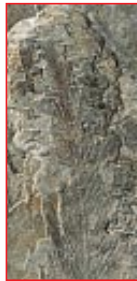


PHOTOGRAPHS BY MICK ELLISON

will depend on a fuller description of its anatomy. Nevertheless, the Chinese finds imply that, at the least, the structures that gave rise to feathers probably appeared before birds did and almost certainly before birds began to fly. Whether their original function was for insulation, display or something else cannot yet be determined.

The Beginning of Bird Flight

The origin of birds and the origin of flight are two distinct, albeit related, problems. Feathers were present for other functions before flight evolved, and *Archaeopteryx* was probably not the very first flying theropod, although at present we have no fossils of earlier flying precursors. What can we say about how flight began in bird ancestors?



Traditionally, two opposing scenarios have been put forward. The “arboreal” hypothesis holds that bird ancestors began to fly by climbing trees and gliding down from branches with the help of incipient feathers. The

height of trees provides a good starting place for launching flight, especially through gliding. As feathers became larger over time, flapping flight evolved, and birds finally became fully airborne.

This hypothesis makes intuitive sense, but certain aspects are troubling. *Archaeopteryx* and its maniraptoran cousins have no obviously arboreal adaptations, such as feet fully adapted for perching. Perhaps some of them could climb trees, but no convincing analysis has demonstrated how *Archaeopteryx* would have climbed and flown with its forelimbs, and there were no plants taller than a few meters in the environments where *Archaeopteryx* fossils have been found. Even if the animals could climb trees, this ability is not synonymous with arboreal habits or gliding ability. Most small animals, and even some goats and kangaroos, can climb trees, but that does not make them tree dwellers. Besides, *Archaeopteryx* shows no obvious features of gliders, such as a broad membrane connecting forelimbs and hind limbs.

The “cursorial” (running) hypothesis holds that small dinosaurs ran along the ground and stretched out their arms for balance as they leaped into the air after insect prey or, perhaps, to avoid predators. Even rudimentary feathers on forelimbs could have expanded the arm’s surface area to enhance lift slightly. Larger feathers could have increased lift incrementally, until sustained flight was gradually achieved. Of course, a leap into the air does not provide the acceleration produced by dropping out of a tree; an animal would have to run quite fast to take off. Still, some small terrestrial animals can achieve high speeds.

The cursorial hypothesis is strengthened by the fact that the immediate theropod ancestors of birds were terrestrial. And they had the traits needed for high liftoff speeds: they were small, active, agile, lightly built, long-legged and good runners. And because they were bipedal, their arms were free

of birds originated in nonavian dinosaurs. These theropods did not deposit a large clutch of eggs all at once, as most other reptiles do. Instead they filled a nest more gradually, laying one or two eggs at a time, perhaps over several days, as birds do. Recently skeletons of the Cretaceous theropod *Oviraptor* have been found atop nests of eggs; the dinosaurs were apparently buried while protecting the eggs in very birdlike fashion. This find is ironic because *Oviraptor*, whose name means “egg stealer,” was first thought to have been raiding the eggs of other dinosaurs, rather than protecting them. Even the structure of the eggshell in theropods shows features otherwise seen only in bird eggs. The shells consist of two layers of calcite, one prismatic (crystalline) and one spongy (more irregular and porous).

As one supposedly uniquely avian trait after another has been identified in nonavian dinosaurs, feathers have continued to stand out as a prominent feature belonging to birds alone. Some intriguing evidence, however, hints that even feathers might have predated the emergence of birds.

In 1996 and 1997 Ji Qiang and Ji Shu’an of the National Geological Museum of China published reports on two fossil animals found in Liaoning Province that date to late in the Jurassic or early in the Cretaceous. One, a turkey-size dinosaur named *Sinosauropteryx*, has fringed, filamentous structures along its backbone and on its body surface. These structures of the skin, or integument, may have been precursors to feathers. But the animal is far from a bird. It has short arms and other skeletal properties indicating that it may be related to the theropod *Compsognathus*, which is not especially close to birds or other maniraptorans.

The second creature, *Protarchaeopteryx*, apparently has short, true feathers on its body and has longer feathers attached to its tail. Preliminary observations suggest that the animal is a maniraptoran theropod. Whether it is also a bird

to evolve flapping flight, which cannot be said for other reptiles of their time.

Although our limited evidence is tantalizing, probably neither the arboreal nor the cursorial model is correct in its extreme form. More likely, the ancestors of birds used a combination of taking off from the ground and taking advantage of accessible heights (such as hills, large boulders or fallen trees). They may not have climbed trees, but they could have used every available object in their landscape to assist flight.

More central than the question of ground versus trees, however, is the evolution of a flight stroke. This stroke generates not only the lift that gliding animals obtain from moving their wings through the air (as an airfoil) but also the thrust that enables a flapping animal to move forward. (In contrast, the “organs” of lift and thrust in airplanes—the wings and jets—are separate.) In birds and bats, the hand part of the wing generates the thrust, and the rest of the wing provides the lift.

Jeremy M. V. Rayner of the University of Bristol showed in the late 1970s that the down-and-forward flight stroke of birds and bats produces a series of doughnut-shaped vortices that propel the flying animal forward. One of us (Padian) and Gauthier then demonstrated in the mid-1980s that the movement generating these vortices in birds is the same action—sideways flexion of the hand—that was already present in the maniraptorans *Deinonychus* and *Velociraptor* and in *Archaeopteryx*.

As we noted earlier, the first maniraptorans must have used this movement to grab prey. By the time *Archaeopteryx* and other birds appeared, the shoulder joint had changed its angle to point more to the side than down and backward. This alteration in the angle transformed the forelimb motion from

a prey-catching one to a flight stroke. New evidence from Argentina suggests that the shoulder girdle in the closest maniraptorans to birds (the new dinosaur *Unenlagia*) was already angled outward so as to permit this kind of stroke.

Recent work by Farish A. Jenkins, Jr., of Harvard University, George E. Goslow of Brown University and their colleagues has revealed much about the role of the wishbone in flight and about how the flight stroke is achieved. The wishbone in some living birds acts as a spacer between the shoulder girdles, one that stores energy expended during the flight stroke. In the first birds, in contrast, it probably was less elastic, and its main function may have been simply to anchor the forelimb muscles. Apparently, too, the muscle most responsible for rotating and raising the wing during the recovery stroke of flight was not yet in the modern position in *Archaeopteryx* or other very early birds. Hence, those birds were probably not particularly skilled fliers; they would have been unable to flap as quickly or as precisely as today's birds can. But it was not long—perhaps just several million years—before birds acquired the apparatus they needed for more controlled flight.

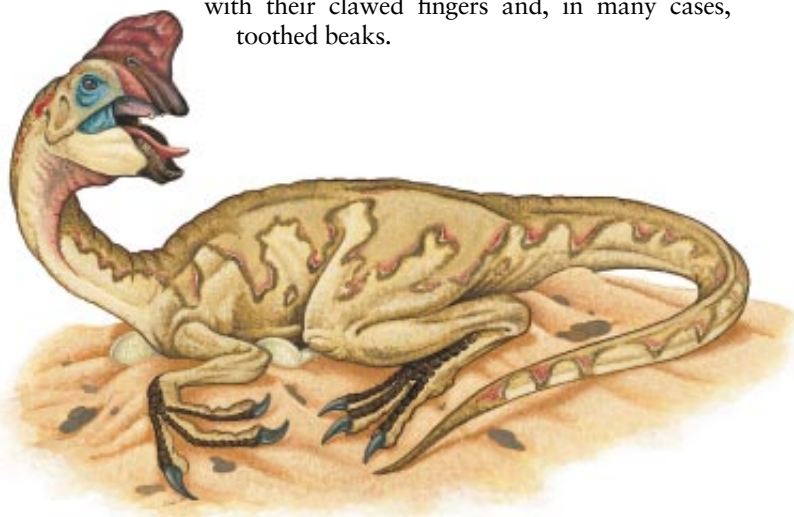
Beyond *Archaeopteryx*

More than three times as many bird fossils from the Cretaceous period have been found since 1990 than in all the rest of recorded history. These new specimens—uncovered in such places as Spain, China, Mongolia, Madagascar and Argentina—are helping paleontologists to flesh out the early evolution of the birds that followed *Archaeopteryx*, including their acquisition of an improved flying system. Analyses of these finds by one of us (Chiappe) and others have shown that birds quickly took on many different sizes, shapes and behaviors (ranging from diving to flightlessness) and diversified all through the Cretaceous period, which ended about 65 million years ago.

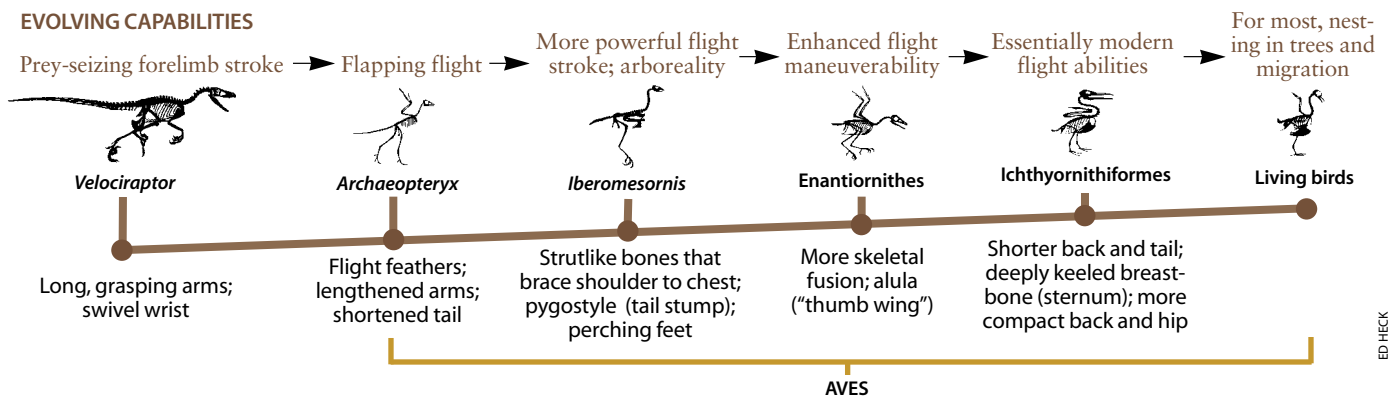
A bird-watching trek through an Early Cretaceous forest would bear little resemblance to such an outing now. These early birds might have spent much of their time in the trees and were able to perch, but there is no evidence that the first birds nested in trees, had complex songs or migrated great distances. Nor did they fledge at nearly adult size, as birds do now, or grow as rapidly as today's birds do. Scientists can only imagine what these animals looked like. Undoubtedly, however, they would have seemed very strange, with their clawed fingers and, in many cases, toothed beaks.



OVIRAPTOR, a maniraptoran theropod that evolved before birds, sat in its nest to protect its eggs (*left drawing*), just as the ostrich (*right drawing*) and other birds do today. In other words, such brooding originated before birds did. In the fossil that served as the basis for the *Oviraptor* drawing (*photograph, above*), the position of the claws indicates that the limbs were drawn in around the eggs (*large ovals*), to protect them.



EVOLVING CAPABILITIES



ED HECK

CLADOGRAM OF BIRD EVOLUTION indicates that birds (Aves) perfected their flight stroke gradually after they first appeared approximately 150 million years ago. They became ar-

boreal (able to live in trees) relatively early in their history, however. Some of the skeletal innovations that supported their emerging capabilities are listed at the bottom.

Underneath the skin, though, some skeletal features certainly became more birdlike during the Early Cretaceous and enabled birds to fly quite well. Many bones in the hand and in the hip girdle fused, providing strength to the skeleton for flight. The breastbone became broader and developed a keel down the midline of the chest for flight muscle attachment. The forearm became much longer, and the skull bones and vertebrae became lighter and more hollowed out. The tailbones became a short series of free segments ending in a fused stump (the familiar "parson's nose" or "Pope's nose" of roasted birds) that controlled the tail feathers. And the alula, or "thumb wing," a part of the bird wing essential for flight control at low speed, made its debut, as did a long first toe useful in perching.

Inasmuch as early birds could fly, they certainly had higher metabolic rates than cold-blooded reptiles; at least they were able to generate the heat and energy needed for flying without having to depend on being heated by the environment. But they might not have been as fully warm-blooded as today's birds. Their feathers, in addition to aiding flight, provided a measure of insulation—just as the precursors of feathers could have helped preserve heat and conserve energy in nonavian precursors of birds. These birds probably did not fly as far or as strongly as birds do now.

Bird-watchers traipsing through a forest roughly 50 million years later would still have found representatives of very primitive lineages of birds. Yet other birds would have been recognizable as early members of living groups. Recent research shows that at least four

major lineages of living birds—including ancient relatives of shorebirds, seabirds, loons, ducks and geese—were already thriving several million years before the end of the Cretaceous period, and new paleontological and molecular evidence suggests that forerunners of other modern birds were around as well.

Most lineages of birds that evolved during the Cretaceous died out during that period, although there is no evidence that they perished suddenly. Researchers may never know whether the birds that disappeared were outcompeted by newer forms, were killed by an environmental catastrophe or were just unable to adapt to changes in their world. There is no reasonable doubt, however, that all groups of birds, living and extinct, are descended from small, meat-eating theropod dinosaurs, as Huxley's work intimated more than a century ago. In fact, living birds are nothing less than small, feathered, short-tailed theropod dinosaurs. SA

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Further Reading

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- THE ENCYCLOPEDIA OF DINOSAURS (see entries "Aves" and "Bird Origins"). Edited by Philip J. Currie and Kevin Padian. Academic Press, 1997.
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