



WHAT GOOD WAS ALL THE HEADGEAR?

DINOSAUR DISPUTES

In the social arena, controversies are fed by opinion and ideology. Uncomfortable facts are routinely ignored. Among scientists—ideally, at least—controversies must be grounded in facts. But merely piling up facts doesn't close a case. It's how the facts fit together that counts. That's the role of a theory: to make sense of disparate facts.

Theories excite scientists, because theories make predictions: new evidence, if it is relevant at all, should conform to the theory. If it does not, the theory must be revised.

Ever since the first discoveries of dinosaur bones, theories about the animals—how they lived and died, how their bodies functioned, why they grew so large and had such strange armament, how they were related to other animals—have occupied some of the best scientific minds.

Some of those theories have emerged as mainstream scientific thinking—most paleontologists espouse them more or less whole, though dissenting voices are usually around to highlight their imperfections. Other theories, on topics that still lack decisive evidence, remain vigorously competitive.

For this special issue, Natural History invited eleven leading investigators to present their views about four of the most important controversies in dinosaur paleontology. In some cases, the mainstream contender has proceeded with certainty, emboldened by the weight of the evidence. The challenger has largely been content poking holes in the theory. In other cases, the positions staked out are complementary.

All the participants, of course, anticipate further discoveries that will confirm, once and for all, their own theoretical predictions.

For Decoration

By Mark B. Goodwin

After prospecting for several hours one hot, dusty afternoon in the summer of 1983, I noticed a round, cracked, softball-size, and honey-colored fossil emerging from the badlands around the Judith River Formation in Montana. I was about to uncover the best pachycephalosaur (“thick-headed lizard”) skull yet found, buried in the bed of an ancient stream that had meandered across a broad coastal plain 78 million years ago.

Pachycephalosaurs first gained notoriety when the science-fiction writer L. Sprague de Camp characterized them as “bonehead” dinosaurs with a fondness for using the “bulge” of “solid bone” on top of their brains to “butt each other with these heads in fighting over the females.”

In pachycephalosaurs, the bones at the top of the skull do indeed unite to form a conspicuous round (and quite solid) dome, surrounded by

clusters of bony horns, nodes, and tubercles. Some specimens even sport multiple pairs of horns, between four and six inches long. Needless to say, all this headgear is prominently featured when charging pachycephalosaurs are portrayed. But did these dinosaurs really butt heads?

My colleague John R. (“Jack”) Horner, of Montana State University–Bozeman, and I tested the head-butting hypothesis on some thirty pachycephalosaur domes and skulls. We examined micron-thin sections of bone from the insides of the skulls under the microscope, and imaged the skulls with high-resolution computer tomography. Both juvenile and subadult pachycephalosaur domes turned out to be highly porous and filled with spaces for blood vessels, showing that the bone tissue was fast-growing and well nourished.

For decades paleontologists had as-

sumed that what they called “radiating structures” in the dome could resist compression, giving the animals a biomechanical advantage in head-butting. Our microscopic examinations proved instead that the structures were transitory, a product of the growth of the dome. Remarkably, they were absent in the skulls of adults—precisely the individuals that would have engaged in head-butting. And in the fossils we examined, we saw no evidence of fractures, healed wounds, or specialized adaptations for managing the forces generated by head-butting, such as the adaptations that occur in bighorn sheep.

So if the elaborate cranial dome was not for head-butting, what was its function? We think the “bulge of solid



Two male Centrosauruses cross horns in a fictionalized encounter. Was dinosaur headgear like theirs primarily for defense against predators or for combat over mates? Was it primarily for display? Or was it some combination thereof?

bone” and accompanying cranial protuberances were chiefly ornamental. They enabled individuals within a species to recognize each other and communicate, the way African antelope such as hartebeest, impala, and wildebeest do when they display their elaborate horns. If the modern animals are good models, most encounters among head-butting dinosaurs would have been ritualized displays of intimidation,

aggression, and submission.

Our microanalysis yielded another noteworthy discovery: collagen fibers that typically anchor tendon and ligaments to bone lay within and just below the surface of the dome. The finding indicates that the skull had an external covering, most likely of hard keratin, similar to the bills of modern birds.

Many birds display brightly colored keratin on their heads to communicate with other members of their species. The domed skulls of pachycephalosaurs may likewise have been vibrantly colored to indicate sexual maturity, attract a mate, or warn an adversary.

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For Defense

By Catherine A. Forster and Andrew A. Farke

When fossil ceratopsians, or horned dinosaurs, were first discovered in the American West in the 1870s, the enormous spikes, horns, and neck shields that sprouted from the creatures’ humongous skulls instantly captivated the public and paleontologists alike. Speculation about the purpose of these bizarre cranial appendages quickly followed. Paleontologists suggested that the long horns were used defensively, to “impale the enemy.” Even today this idea makes perfect intuitive sense. Any animal fairly bristling with long, pointed horns and spikes simply looks ready to fend off any and all would-be predators. More recently, paleontologists have suggested that other dinosaurs, notably the dome-headed pachycephalosaurs, also used

their cranial appendages defensively. Pointy headgear certainly plays a role in the defensive strategies of many modern animals. For example, the horned lizard *Phrynosoma mcalli* apparently uses the horns on its head to deter the shrike, a bird fond of impaling lizards on thorns or barbed wire for later consumption [see “The Natural Moment,” March 2005]. Longer horns make a lizard less likely to end up as a shrike’s meal. Much larger animals adopt a similar defensive strategy: some unfortunate visitors to Yellowstone National Park have experienced the use of horns by bison firsthand.

But paleontologists early on recognized that defense may not have been the sole function of cranial “weaponry.” In 1907 J.B. Hatcher and colleagues charmingly informed their

readers that “*Triceratops* was extremely deficient mentally” and likely quite docile, except during the breeding season, when “combats between rival males . . . must have been prompted and carried out by blind, unreasoning instinct.”

The “mate competition” hypothesis is borne out by research showing that the cranial headgear of most modern animals evolved not only for defense against predators, but also for ritualized jousting or just plain “showing off” among members of their own species. Male bighorn sheep with the largest horns, for instance, have the highest social rank and are more likely to mate. Similar patterns hold for many horned or antlered mammals, including African antelope, deer, and pronghorn. Among reptiles, the male Jackson’s chameleon (which looks like a

miniature *Triceratops* with three horns and a bony frill, or ruff, over its neck) also engages in horn-to-horn combat with other males of its kind.

Actual evidence of horn use in ceratopsians is circumstantial. On some *Triceratops* fossils, both on the face and on the frill (the only plate extending back over its neck), there are healed puncture wounds. Some paleontologists interpret the wounds as evidence of combat with members of the same species. Other skulls show that ceratopsians underwent rapid evolutionary change and that, in particular, the size and shape of their horns and frills responded to shifting circumstances with great plasticity. Those findings suggest that natural selection focused on diversifying the cranial appendages for use in relations with other members of the same species. Beyond that, com-

parison to modern animals is all paleontologists have to go on to infer ceratopsian behavior.

Ultimately, dinosaurs probably used their cranial appendages in whatever way they were needed. The pattern is well demonstrated in deer: even though antlers function primarily for display and for combat with rivals, they can also be used with deadly efficiency against predators. *Triceratops* likely used its horns to impress mates, shoo off rivals, or argue for territorial ownership. But it’s hard to imagine that such deadly weaponry wasn’t aimed at a menacing *Tyrannosaurus* when the need arose. If you’ve got it, use it!

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WERE DINOSAURS “COLD-” OR “WARM-BLOODED”?

“Cold-blooded”

Endothermy, or warm-bloodedness, in birds and mammals results from high rates of internal heat production, even while at rest. In the wild, metabolic rates in birds and mammals are about twenty times higher than they are in reptiles. These elevated metabolic rates also require accelerated rates of oxygen consumption and lung ventilation.

Endothermy is a highly specialized physiological strategy, whose evolutionary history, until recently, was elusive: no fossilized structures could unambiguously and exclusively prove endothermy. For example, one might think that skeletal growth rates would be higher for an endothermic animal than for an ectothermic, or cold-blooded, one. Perhaps, too, the higher growth rates would become apparent in the bone microstructure. But both those tests are inconclusive, and, in any case, those features are not causally linked to the metabolic rates

of birds or mammals. Even the possible presence of feathers in some dinosaurs is not a certain indicator of endothermy: many modern birds occasionally regulate their body temperatures ectothermically.

The entire study of metabolism in fossilized animals changed recently, with the realization of the importance of respiratory turbinates, the scroll-like structures in the nasal cavities of all terrestrial birds and mammals. Because turbinates reduce respiratory water and heat loss, they are tightly linked to high rates of lung ventilation in these terrestrial endotherms. In contrast, all living ectotherms lack respiratory turbinates. Thus the study of turbinates can open a window onto the metabolism of dinosaurs and their close relatives, the earliest birds.

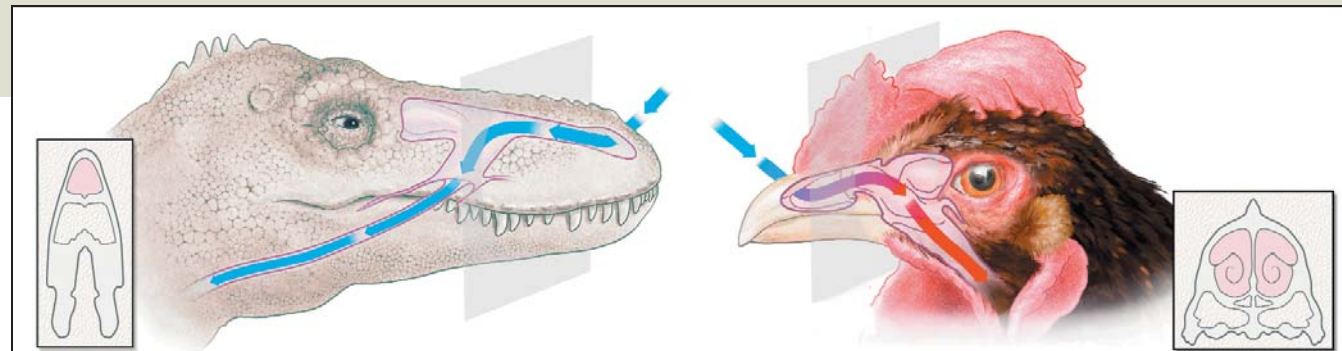
Turbinates are delicate, and so they themselves are often not preserved in fossils. But their existence can be in-

By John A. Ruben and Willem J. Hillenius

ferred in another way. We found that living endotherms have much wider nasal chambers than living ectotherms do, probably to compensate for the turbinates' extra resistance to air flow.

Multiple lines of evidence indicate that dinosaurs had relatively narrow, ectotherm-like nasal passages. When we examined several specimens, including the theropod *Nanotyrannus*, via computed tomography (CT), we could find no evidence of respiratory turbinates. In all dinosaur specimens the nasal passages are surprisingly narrow, with little room for an elaborate complex of respiratory turbinates, and proportionately nearly identical to those of extant ectotherms. The CT scans also revealed that most of the space in the animals' snouts was taken up by large, air-filled nasal sinuses, which do not function in respiration.

Together, those findings constitute strong evidence that dinosaurs and



early birds lacked the high ventilation rates associated with endothermy. The modified, enlarged “modern” avian nasal cavities first appear in certain Late Cretaceous birds, which suggests that endothermy appeared relatively late in the evolution of birds.

The metabolic status of the dinosaurs probably reveals less about their lifestyle than many investigators have supposed. For example, it would be erroneous to conclude from their relatively low metabolic rates that they were sluggish herbivores or “sit-and-wait” predators. Given the mild climates of the Mesozoic, most dinosaurs almost certainly maintained a constant body temperature, whether they were endothermic or not. And

Respiratory turbinates recycle heat and moisture during breathing, and so prevent excessive respiratory dehydration in endotherms. For example, in the chicken (right), cool, dry air (blue arrows) enters the nose. As it passes through the complex of turbinates, it is heated and humidified (red arrows). When the bird exhales, most of the moisture condenses back onto the turbinate surfaces. In contrast, modern ectotherms, such as crocodiles and lizards, lack respiratory turbinates; their ventilation rates are so low that the amount of water lost through breathing is negligible. To make room for the turbinates, endotherms have comparatively spacious nasal cavities (see inset at right). CT scans, however, indicate that dinosaurs such as *Nanotyrannus* (left) have very narrow nasal passages (see inset at left), nearly identical to those of modern ectotherms. It therefore appears that dinosaurs, and even early birds, lacked respiratory turbinates, and that their lung ventilation rates and metabolic rates were not as high as those of modern endotherms.

even if they were fully ectothermic, there are large, tropical-latitude lizards, such as the Komodo dragon, alive today that demonstrate that ectothermy by no means implies sluggishness. Had dinosaurs possessed the physiological capacities and predatory habits of the Komodo dragon, they might well have maintained large

home ranges, actively pursued and killed large prey, and, when cornered, defended themselves fiercely.

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“Warm-blooded”

By Mary Higby Schweitzer

When I was growing up, paleontologists (and virtually everyone else) regarded dinosaurs as slow-moving, stupid, ill-adapted reptiles—in short, ectothermic, or “cold-blooded.” Now all that has changed: the dinosaurs' ancestors may have been cold-blooded, but most paleontologists think that, over time, dinosaurs began to exhibit traits that we link with higher metabolic rates. Today they are portrayed as lithe, agile, intelligent animals, able to compete with the best that mammals had to offer—and probably win. The idea that metabolic rates changed over time in this group of animals brings two basic questions to mind: First, why might an animal lineage adopt the strategy of warm-bloodedness, given its steep energy

costs? Second, how—since no one can take the temperatures of extinct animals—can paleontologists tell what kind of metabolism was at work in the dinosaurs?

Natural selection favors new adaptations if, by reducing an animal's competition from other organisms for limited resources, or by helping it better survive and thrive in its environment, the animal produces more offspring. Yet, in general, a warm-blooded animal requires about ten to twenty times more food and oxygen (per unit weight, per unit time) than a cold-blooded animal. Those requirements would seem too costly for warm-bloodedness to evolve through natural selection.



Albertosaurus fossil shows the dinosaur's head and neck drawn downward over its back. The pose is struck when the muscles contract at death: the stronger muscles at the back of the neck—which hold the head upright in life—overcome the weaker muscles at the front. The death pose is characteristic of warm-blooded animals, such as birds and mammals. The fossil is in the Royal Tyrrell Museum in Alberta, Canada.

One plausible explanation is that warm-bloodedness reduced competition. If an animal's metabolic rate was just a little bit higher than that of its competitors, maybe it could be active for just a little bit longer, or could move a little bit faster. Maybe it could forage an hour earlier or an hour later than its competitors, or move a little farther from home to find food and water. Maybe, with extra speed, it could hunt prey more effectively. Those advantages would not require a great increase in body temperature (half a degree might suffice). But the benefits might be enough, statistically speaking, to pass on a higher metabolism to offspring. Other factors might then favor yet another slight

increase in body temperature. Ever so slowly, the animals in the lineage might approach what biologists consider full-blown endothermy.

The second question is slightly more complicated. By studying living animals, however, we can answer a great many questions about the metabolic rates of extinct animals. Dinosaurs had many characteristics that today occur only in warm-blooded species. Only warm-blooded animals become obligate bipeds—animals that *must* walk on two legs. Only warm-blooded animals have upright posture: legs positioned directly under their bodies, rather than splayed to the sides, as in lizards. Only warm-blooded animals have an insulating body covering, such as hair

or feathers. Warm-blooded animals are the only terrestrial creatures that live in large herds or flocks or that migrate long distances.

All those traits occur in dinosaurs. More precisely, some traits (upright posture) occur in all dinosaurs; other traits (feathers) occur only in some. Dinosaurs may not have been as fully warm-blooded as birds or people are, but all the evidence suggests their metabolic rates were substantially higher than those of living crocodiles, lizards, snakes, and turtles.

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WERE DINOSAURS THE VICTIMS OF A SINGLE CATASTROPHE?

Yes, and an Asteroid Did the Deed.

By David E. Fastovsky

The idea that a single, spectacular, catastrophic event—an asteroid impact—at the end of the Cretaceous period, 65 million years ago, obliterated all the nonbird dinosaurs (as well as many other organisms) is a simple, attractive scenario. But is it more accurately described as *simplistic*? Since not all life was wiped off our planet, there must have been winners as well as losers in the Cretaceous endgame. Surely survival occurred for better reasons than a mere roll of the cosmic dice!

Yet in the past fifteen years it has become clear that the extinction of the dinosaurs was geologically instantaneous. Geological instantaneity, however, is an inexact quantity. From a vantage point of 65 million

years after the event, paleontologists cannot resolve time spans of less than tens of thousands of years: whether the extinction took a minute or many thousands of years may never be known. Still, 10,000-year timescales rule out events that lasted millions of years, and those include a whole class of gradual, earthbound processes.

In three separate studies in western North America (the only place where these issues have been studied), the diversity of dinosaur fossils was carefully recorded, meter by meter, through rocks that record the Cretaceous-Tertiary (K/T) boundary. In each case, paleontologists failed to identify any decrease in dinosaur diversity in the 2 million years or so preceding the

boundary. In fact, every published, quantitative, field-based, stratigraphically refined study addressing this question has concluded that dinosaur diversity was unchanged up to the K/T boundary: the final extinction was thus geologically instantaneous.

When it comes to the ecology of survival, paleontologists are in refreshing agreement: your chances of surviving were pretty good if you were small and cold-blooded (correctly termed ectothermic). But your best bet was to be aquatic.

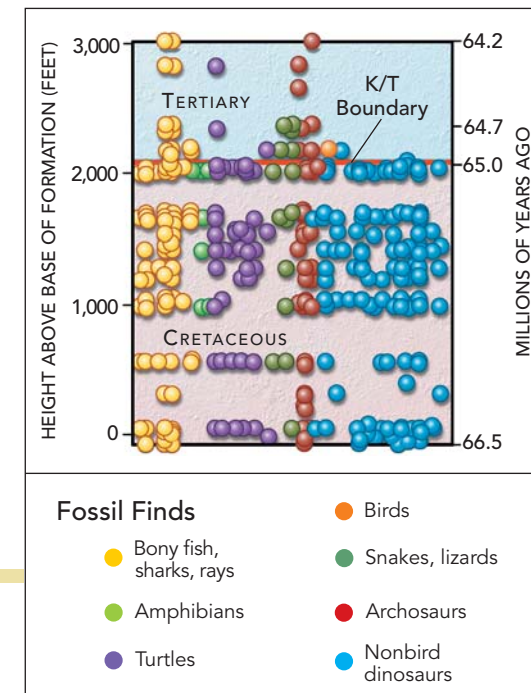
At first blush, those attributes might not seem the ideal armament against incoming asteroids. But they do seem to have been keys to survival. Although the exact effects of large-body impacts on Earth remain

uncertain, there is a general consensus that such impacts probably have two kinds of dire consequences: dust, smoke, and debris in the atmosphere blocking sunlight for several months, and an instantaneous pulse of thermal energy igniting global fires. [See “Loading the Cannon,” by Charles Liu, page 58.]

For both those effects, being small, ectothermic, and aquatic may have been the secret to survival. For as long as sunlight was blocked, photosynthesis would have ceased, reducing much of Earth’s available foodstuffs to detritus. Dinosaurs and other organisms dependent on “primary production”—fresh plants and meat—would have become effectively helpless. But aquatic animals,

which tend to feed on detritus, may have been protected. On land, many Cretaceous mammals were likely part of detritus-based food chains. Furthermore, many were small enough to have lived in burrows (as many small mammals do today), and so they could have been protected from the thermal pulse. Finally, in the face of a global heat pulse and fires, small size and aquatic refuge offered nearly ideal shelter in what had become an inhospitable world. In short, the ecology of both winners and losers reflects the imprint of the impact with surprising fidelity.

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Record of the distribution of fossil vertebrates (colored dots), excluding mammals, is shown for rocks of the Ferris Formation, in south-central Wyoming. The figure shows the approximately 1.5 million years before the Cretaceous-Tertiary (K/T) boundary, 65 million years ago, and 800,000 years after it. The red horizontal line represents a layer of rock more than twenty-six feet thick that includes the boundary. Because that layer is largely devoid of fossils, the exact location of the K/T boundary within those twenty-six feet is uncertain. Nonbird dinosaurs disappear dramatically within the twenty-six-foot-thick layer. The data are from J.A. Lillegraven and J.J. Eberle, *Journal of Paleontology* 73:691–710, 1999; the figure is based on a graph in D.E. Fastovsky and P.M. Sheehan, *GSA Today* 15:3, 4–10, 2005.

No, It Only Finished Them Off.

By J. David Archibald

Some 65 million years ago, Murphy’s Law applied—almost everything that could have gone wrong did: A huge bolide, or asteroid, struck Earth. Globally, the seas receded. Fissures on the Indian subcontinent spewed forth thousands of cubic kilometers of material. All three events took place in rapid succession, toward the end of the Cretaceous period. Each of them is thought to have been the largest event of its kind in the past 250 million years, and each is thought to have played a role in the demise of the nonbird dinosaurs. Each event left obvious physical and chemical proof of its occurrence in the rock record. That much is clear. But how can paleontologists measure the effects of such events on the creatures living at that time?

The most powerful method is simply to read, in the fossil record,

which animals survived and which did not. Only western North America, though, preserves a reasonably continuous fossil record of the land and freshwater vertebrates for the last 10 million years of the Cretaceous and on through the Cretaceous-Tertiary (K/T) boundary. In those last 10 million years of the Cretaceous, but well before the K/T-boundary events, the most recent compilations show an unequivocal decline in the diversity of dinosaur species. In fact, before the time of the boundary is reached, between one-third and one-half of all dinosaur species—mostly such relatively common groups as the duck-billed and horned dinosaurs—had already disappeared.

The analysis of the final million years of the Cretaceous is more problematic, because the precision required is far greater than is discernible in the fossil record. A re-

cent study in North Dakota noted little or no change in the vertebrate fauna throughout the thickness of the Hell Creek Formation. Those data were cited to argue that a bolide impact must have suddenly terminated the nonbird dinosaurs at the top of this formation.

Yet in the uppermost five meters of the formation only two dinosaurs could be identified well enough to specify their generic name. What happened to the other eighteen or so nonbird dinosaur species present in the Hell Creek Formation? No one knows whether they survived to the time of the boundary or became extinct thousands of years before it.

Apart from the problems of detecting rates of dinosaur extinction, we can examine the pattern of total vertebrate extinction. Of 107 species of vertebrates known from Hell Creek, about half had disappeared

by the time corresponding to the K/T boundary. Of those extinctions, 75 percent are concentrated in just four groups: lizards, marsupials, sharks (and their relatives), and nonbird dinosaurs. The lizards may have faced habitat loss from increasing rainfall in the Hell Creek region near the end of the Cretaceous. As sea levels fell, the Bering land bridge enabled the precursors of modern hoofed mammals to enter North America and outcompete other mammals, notably the marsupials. The sharks, too, lost their habitat as the seas retreated. And the nonbird dinosaurs? With the loss of inland seas, the low coastal plains, from which almost all of the fossils of these animals are known, shrank and fragmented.

Then the bolide struck Earth. Many consequences of this impact have been proposed—global wild-

fire, extended periods of darkness, sharp temperature increases, tsunamis, and hurricanes. Other suggested effects—notably acid rain and a sharp drop in the temperature—now seem extremely unlikely, given the fossil record. The most recent proposed consequence has been sudden infrared heating. That might explain why large creatures such as dinosaurs died, whereas smaller species survived by taking refuge in holes, crevices, or under a thin layer of water.

Whatever the results of the impact, though, it only finished a job that earthbound factors had already begun. The dinosaurs and other vertebrate species had already become vulnerable to extinction.

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HOW DID DINOSAURS BEGIN TO FLY?

From the Trees Down

A century-old controversy over whether avian flight began in the trees (trees-down theory) or on the ground (ground-up theory) finally appears to be settled. Hundreds of small, exquisitely preserved feathered theropod dinosaurs were discovered just as they were some 125 million years ago when they were smothered in the “Cretaceous Pompeii” of China. These fossils show various transitional stages—from wingless, tree-dwelling theropods to fully winged, active flyers.

The central theme of the trees-down theory is that gravity was the source of energy: a small climbing dinosaur first parachuted down, then began to stay aloft longer by gliding, and finally acquired powered flight. As those abilities developed, feathers became larger and more specialized, providing greater lift and thrust. In

contrast, a theropod struggling toward flight directly from the ground up, without any gliding stage, had gravity working against it.

We developed a computer model to simulate the flight performance of these Chinese theropods and an early bird, *Archaeopteryx*. All these animals had acquired adaptations for quadrupedal climbing similar to those of the modern young hoatzin, a bird native to tropical South America. They were small, with highly recurved claws; their fingers and toes were long for grasping bark; their wrist joints were swiveled so they could flex their hands during climbing; and their stiffened tails supported them as they climbed upward.

At first, small theropods such as *Sinosauropteryx* invaded arboreal habitats to elude predators. Their bodies were covered with downy feathers,

which provided insulation in the cooler environment of the trees.

Caudipteryx and *Protarchaeopteryx* typify the next stage in the evolution of flight. Symmetrical contour feathers on their hands and tails provided lift during parachuting, but offered little control over the flight stroke.

Microaptor, which exemplifies the third stage of flight, was a glider; its two sets of wings, one over the other, functioned much like the fixed wings of a biplane. But the creature’s most unusual feature was a set of long, asymmetric feathers with hooked barbs on its hind limbs and forelimbs. The leading edge of each long feather was narrower than the trailing edge, which helped streamline the body in flight, and the hooked, interlocking barbs gave strength and flexibility to the feather and prevented air from passing through it in flight.

By Sankar Chatterjee and R. Jack Templin

Such asymmetric feathers are essential for flight—and their presence in a fossil this old contradicts the ground-up theory: *Microaptor* had them even on its metatarsals, or “toes,” which would have made running on the ground nearly impossible. Our analysis suggests that *Microaptor* held its hind legs tucked under its body in a Z shape during gliding, which gave the animal a configuration strikingly similar to that of a biplane.

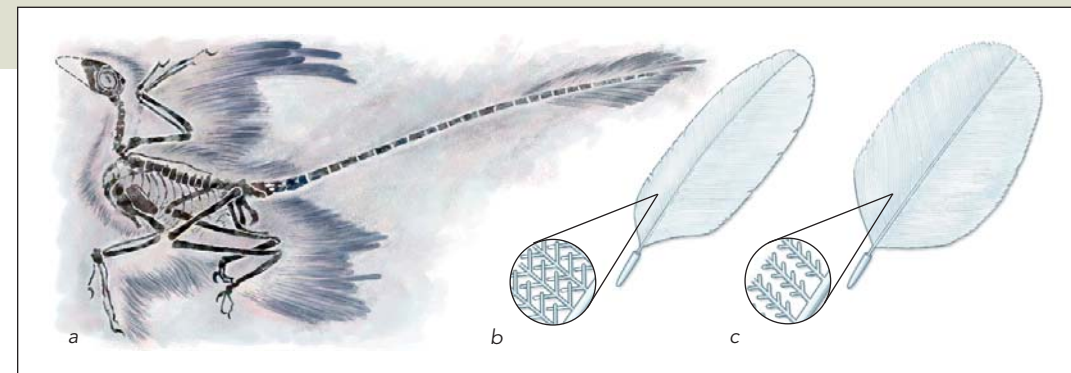
Sinornithosaurus represents the fourth stage of flight. Its forewings were even larger than *Microaptor*’s, forming, in essence, a gliding monoplane. The feathers on the metatarsals were lost on the back wings.

Finally, *Archaeopteryx* achieved fully

powered flight, as its wings became even larger than those of *Sinornithosaurus*. *Archaeopteryx* retained the hindlimb feathers of the gliders, but the feathers were now much shorter, more like the “trousers” of modern raptors that streamline the legs just before an aerial attack or during a flight with a captive prey. It is intriguing to contemplate that perhaps avian

flight, like aircraft evolution, went through a biplane stage before the monoplane was introduced.

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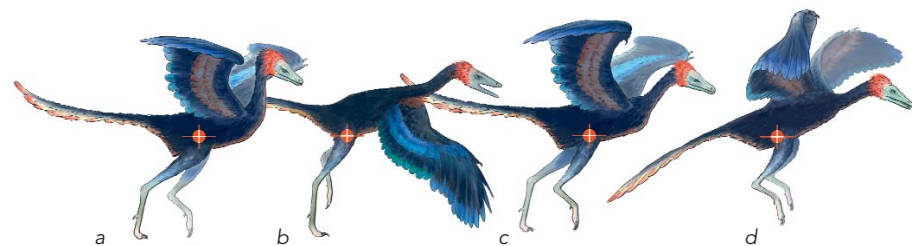
Fossil of *Microaptor* (a) has preserved traces of the animal’s feathers. The long digits and sharp claws of the fore- and hind limbs equipped the animal both for climbing trees and perching in them. The long feathers on its wings and legs had evolved for flight: they were asymmetric, with interlocking barbules (b); less developed feathers, such as the symmetric feathers with noninterlocking barbules (c), cannot sustain flight. The long flight feathers on *Microaptor*’s back legs limited its ability to run in preparation for takeoff; to launch its flight, it would first have had to climb a tree and take off gliding, assisted by gravity.

From the Ground Up

Early on a windy December morning, slightly more than a hundred years ago, the Wright brothers’ *Flyer* made a short takeoff run, then took to the air. The airplane was aloft for only 120 feet, but the flight was epoch-making: the first time a powered, heavier-than-air flying machine got off the ground to make a successful, controlled flight.

More than 150 million years earlier, another first took place in aviation: a small dinosaur flapped its feathered arms as it ran, perhaps fleeing a predator. Slowly it rose above the ground, escaping its pursuer, and then lived long enough pass its genes on to the next generation. The era of avian flight had begun.

Making such a parallel between the Wright *Flyer* and the first dinosaur flight may seem far-fetched.



Primitive bird—or a theropod dinosaur—could have increased its thrust, or force in the direction of its run, by flapping its wings (a,b). The enhanced thrust would have boosted its running speed and, at the same time, increased its lift, the upward force created by the air moving across the wings. As lift increased, the forward force between the bird’s hind limbs and the ground would have been reduced until it reached zero and the bird took off (d). The bird’s center of gravity (red crosshairs) would not move up or down until the bird left the ground, because the vertical components of all the forces would have remained in equilibrium.

But new evidence has given fresh credibility to the idea that flight originated “from the ground up.”

Since the late 1800s, two antagonistic theories have competed to explain the onset of avian flight. Some investigators have argued that birds became

airborne “from the trees down,” as their theropod forerunners mastered tree-climbing, then parachuting and gliding, and finally powered flight. Others have countered that small land-dwelling dinosaurs learned to fly without ever developing arboreal

By Luis M. Chiappe

habits: no trees were needed. The fact that gravity-aided flight seems easier to achieve than its opposite has always lent a kind of intuitive advantage to the trees-down theory. Yet neither direct evidence of the hypothetical tree-climbing stage, nor convincing arguments that the meat-eating precursors of birds developed specialized adaptations for climbing or gliding, have ever materialized.

In contrast, the fossil record makes it clear that theropod dinosaurs lived a terrestrial existence. Their long legs and short toes were well suited for running. Fossils of bipedal, bird-like dinosaurs such as the parrot-headed oviraptorids, the lightly built troodontids, and the sickle-toed dromeosaurids have been discovered in positions that indicate they were brooding their eggs, but always in

habitats: no trees were needed. The fact that gravity-aided flight seems easier to achieve than its opposite has always lent a kind of intuitive advantage to the trees-down theory. Yet neither direct evidence of the hypothetical tree-climbing stage, nor convincing arguments that the meat-eating precursors of birds developed specialized adaptations for climbing or gliding, have ever materialized.

Furthermore, these animals evolved the skeletal framework necessary for flapping their feathered forelimbs—the functional precursors of powered flight. Fossils spanning the evolutionary transition from theropod to bird also detail how the wings of these animals became larger as their bodies became smaller. Aerodynamic studies have documented how, by flapping their wings, the animals could have boosted their running speed. Taken together, the evidence suggests that flight could have evolved as a by-product of wing-assisted running in animals that were becoming lighter even as their wings were becoming bigger.

Does all this evidence prove conclusively that birds evolved their flight from the ground up? With wing-assisted running the theropod forerunners of birds could have ascended inclines, including trees. But if they did, why didn’t they take advantage of that more protective environment when they were nesting or resting—that is, when they were most vulnerable to predators?

Theories about the origin of flight will continue to be conjectural. Yet aerodynamics, the potential for locomotion, and the documented habits of birds’ predecessors all make the ground-up hypothesis the less conflicted of the two conjectures.

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