Bird's-eye View

By Matthew T. Carrano and Patrick M. O'Connor

The array of the dinosaurs that flourished during the Mesozoic era was as dazzling as any bestiary ever imagined; not even medieval fantasies of griffins and unicorns could compete with the fabulous record of fossils in rock. Yet with a single exception, the entire dinosaur lineage was obliterated 65 million years ago. The sole dinosaurian representatives to survive the cataclysm were the birds, a group that has since radiated into virtually every environment on the planet.

The suggestion of an evolutionary link between dinosaurs and birds originated with several late-nineteenth-century biologists, most notably Darwin's friend Thomas Henry Huxley. At first welcomed, the hypothesis was later disregarded by most biologists and treated with skepticism through much of the twentieth century. But in the past three decades, the hypothesis has roared back to life, with almost overwhelming support. The latest evidence for the link has come from the spectacular recent discoveries of a number of feathered dinosaurs in China.

To many a casual eye, the case is made by the presence of feathers on the fossils. But feathers only highlight one of the most visible similarities between the two groups. Biologists classify birds among the dinosaurs not only because both groups have (or had) feathers, but also because they share a suite of other, characteristic anatomical traits. One of those important traits is the "pneumaticity" of the skeleton: certain dinosaurs possessed bones riddled with air pockets, which during life were linked with the pulmonary, or breathing, system of the animal. Much the same is the case with many birds today.

The classification of birds as dinosaurs also implies that many other so-called avian features are better thought of as dinosaurian. And similar anatomies could imply that the bodies of birds and dinosaurs functioned similarly. Moreover, one may also learn a great deal about dinosaur biology by contrasting their features with the anatomical and biomechanical characteristics of other, more distantly related vertebrates. It is the birds, though, that have carried the torch of dinosaurian biological heritage from the Mesozoic through global calamity to the present day. Modern paleontologists, in large part by the light of that torch, are elucidating the paleobiological characteristics of those long-dead, long-buried, long-obscured animals.

To understand what one can learn about dinosaurs from the study of birds, it is useful to sketch how the two groups are related. A discipline of biology known as cladistics, or phylogenetic systematics, investigates the evolutionary relationships among organisms by charting their anatomical similarities. Cladistic hypotheses about such interrelations often take the form of a branching diagram called a cladogram. Each junction on the cladogram indicates an evolutionary event that split one lineage into two. Each of the two descendant lineages shares one or more features inherited from the ancestor at the most recent junction, and those shared features define different groups. To examine the relations within and between groups of organisms is also to chronicle the sequence by which those groups' features evolved.

According to the leading cladistic hypotheses, birds are descended from within the group of theropod dinosaurs. Theropods are quite familiar to most people, if not necessarily by that name: members include giant *Tyrannosaurus,* sickle-clawed *Velociraptor,* and birdlike *Ornithomimus.* Theropods such as *Herrerasaurus,* from the Middle Triassic are among the earliest known dinosaurs. [*For a summary chart of geologic periods, see "Up Front," page 6.*]

Theropods, like birds, were bipedal animals. All of them share several key features: thin-walled bones, a foot with three main toes, and a joint in the lower jaw. Early theropods split into two groups, the herrerasaur-like primitive theropods, and a group called the neotheropods, which included most of the familiar predatory dinosaurs [*see the branch of the illustration on pages 40 and 41 outlined in blue*]. Early neotheropods, known as the coelophysoids, were common in the Late Triassic and Early Jurassic.

As the neotheropods emerged as a separate group, they shared an important "birdlike" trait—the fur-
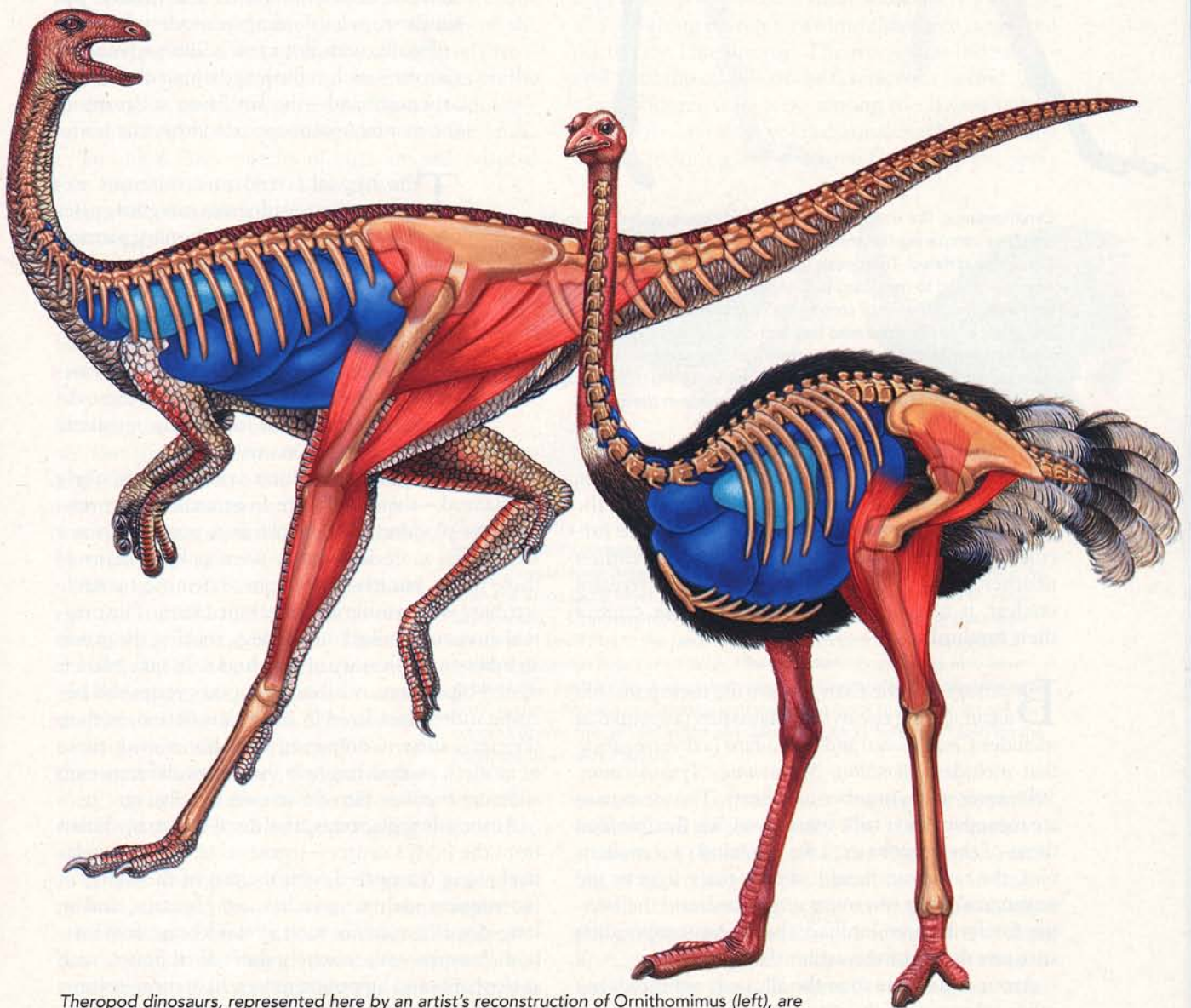
Theropod dinosaurs, represented here by an artist's reconstruction of Ornithomimus (left), are thought to comprise the group from which modern-day birds, including the ostrich (right), descended. Because common descent implies shared anatomical characteristics, comparisons of theropod and bird anatomies can provide new insights into dinosaur biology. Two particularly fruitful comparisons—of the muscles and bones of the legs, and of the animals' "pneumatized" bones—have revealed much about theropod locomotion and the theropod pulmonary system.
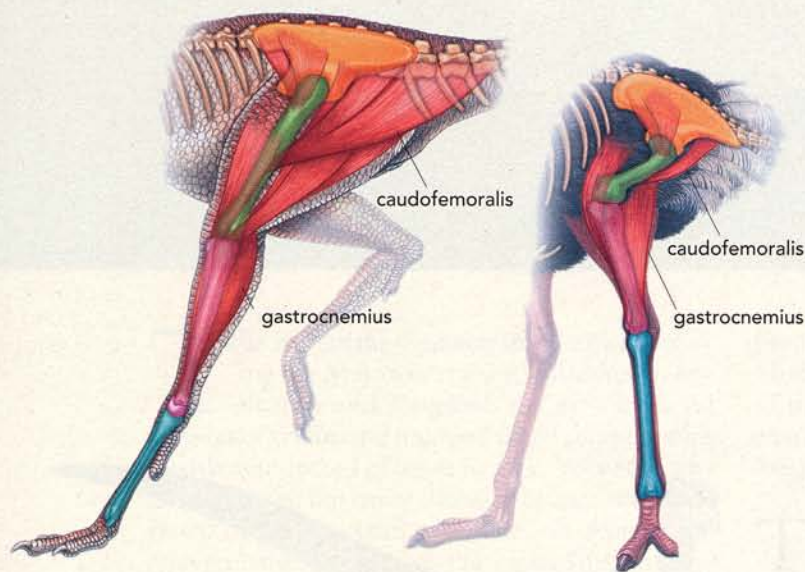
Ornithomimus, like nearly all theropods and birds, walked on its hind legs, but comparing the anatomy of the two groups shows their methods of walking differed. Theropods (left) had large caudofemoralis muscles, which attached to their long tails and provided power that caused much of the movement of each step to occur at the hip. Ostriches (right) and the other birds have reduced tails and correspondingly diminutive caudofemoralis muscles. But birds, for their size, have proportionately larger muscles, such as the gastrocnemius, in the lower leg than theropods did; most movement during a bird's step takes place at the knee.

cula, often (in birds) called the wishbone. The furcula is formed by the fused left and right clavicles, and in modern birds it acts as a spring between the powerful flapping wings. Clearly, though, the furcula did not function in that capacity in the earliest neotheropods. Although its original role remains unclear, it may have helped neotheropods control their forelimbs.

By the end of the Early Jurassic the theropods split again, giving rise to the ceratosaurs (a group that includes *Ceratosaurus)* and tetanurans (a diverse group that includes *Allosaurus, Spinosaurus, Tyrannosaurus, Velociraptor,* and a number of others). The tetanurans are named for their tails, which were less flexible than those of their forebears. Like the hand of a modern bird, the tetanuran hand had only three fingers; the tetanurans' wrist was more specialized, and their entire forelimb more birdlike, than the corresponding anatomy of any of the earlier theropods.

Around the same time the allosaurs appeared, another subgroup of the tetanurans, the coelurosaurs, also branched off. Coelurosaurs included both large species, such as *Tyrannosaurus rex,* and small ones, some not much bigger than a chicken. The coelurosaurs—particularly their subgroup known as

maniraptorans (to which *Velociraptor* and many other dinosaur species belonged)—show the greatest affinities with birds. Some early forms, including primitive tyrannosaurs, had a downy covering on the skin, possibly either for insulation or for display [*see "The Varieties of Tyrannosaurs," by Mark A. Norell and Xu Xing, page 34*]. Other species had distinct feathers covering nearly the entire body. Maniraptorans also had a specialized shoulder blade and a unique, curved bone in the wrist, which enabled the hand to move in just one plane. The motion was similar to wing folding in modern birds.

Finally, with just a few additional modifications—such as the lengthening of the forearm and hand—the last living subgroup of the maniraptorans appeared: the true birds.

The hypothesized interrelations expressed by a cladogram can guide paleontologists to specific evolutionary patterns that can shed light on other aspects of dinosaurian biology. For example, how did dinosaurs move? Living animals, of course, confront the same laws of physics as the dinosaurs did. By studying the biomechanics of locomotion in living animals, then, dinosaur biologists can focus more precisely on what the fossil evidence can convey.

Early theropod locomotion was not particularly specialized—theropods were, in general, neither runners nor plodders, neither climbers nor diggers nor swimmers; more likely, they were jacks of many of those trades, but masters of none. Their most notable attribute was an inherited one: bipedalism. The original dinosaurs walked on two legs, making the group an oddity in the history of vertebrates. In spite of their shared bipedalism, various theropod groups did become more specialized in their locomotion, as their skeletons attest. Comparing their bones with those of modern animals can help show how differences in anatomy translate into differences in behavior.

Among living groups, the distal—that is, distant from the body's center—segments of limbs are relatively long (compared with the rest of the body) in fast runners such as ostriches and cheetahs, and in long-distance runners such as wildebeest and caribou. Animals with relatively short distal bones, such as elephants and hippopotamuses, have more columnar legs and do little running. Between those extremes is a near-continuum of variation. The proportions of the distal limb bones in theropods were generally intermediate between the extremes of cheetah and elephant.

Another mammalian tendency is that large species typically have relatively short limbs and small species relatively long ones. The same pattern held in theropods. Some large theropods, such as spinosaurs and allosaurs, had lionlike limbs—perhaps because they hunted by stealth or covered relatively little ground in their roamings. Other species bucked the trend, though. Tyrannosaurs had a runner's limbs, despite their enormous size—indicating that they were probably adapted to running relatively fast or far.

Another way to examine theropod biomechanics is to reconstruct the musculature of the limbs. Muscle-attachment marks on fossilized theropod bones can be compared to similar marks on the dinosaur's nearest living relatives: the crocodilians—whose ancestors were quadrupedal—and the birds.

The hind-limb muscles of birds are well adapted for bipedal motion. The muscle arrangement at the hip and knee maximizes stability, yet gives the leg the ability to make wide swings fore and aft. But bipedalism in birds is a highly specialized form of bipedal motion; the large tails of birds' ancestors, which in crocodilians still anchor the leg muscles, have mostly vanished in birds. Hence, in birds, the muscles attached to the tail are also small [see illustration on opposite page]. Birds walk in a crouched posture, moving the knee more than the hip—what biologists sometimes call "Groucho running," after Groucho Marx.

An analysis of theropod fossils shows that the animal had birdlike limb muscles early in their evolution. That was certainly the case by the time the coelophysoids appeared, and perhaps even by the time of Herrerasaurus. The repositioning of the muscles changed the way theropods walked: they began moving their legs as birds do—in one plane, fore and aft—rather than as crocodiles do, waddling from side to side.

In later theropods, such as allosaurs and tyrannosaurs, several new muscle attachments appeared, which occur in birds but not in crocodilians or earlier theropods. Yet despite the rearrangement of the attachments of some leg muscles, most theropods still retained substantial attachments of the leg muscles to the tail. The Mesozoic world was probably not full of Groucho-running theropods. Rather, the leg muscles attached to the tail would have caused the upper part of the limb to move at the hip.

Although great size, as well as a great range of body sizes, are among the most familiar qualities of dinosaurs, the early theropods were both small and fairly uniform. *Eoraptor,* one of the earliest theropods, was perhaps three feet long and weighed about twenty-five pounds, more or less the dimensions of a medium-size dog. Yet even that animal was much larger than its nearest ancestors. Further change came quickly. By the Late Triassic, the dominant predators were coelophysoid theropods, a group ranging from the nine-foot-long *Syntarsus* to the fifteen-foot-long *Gojirasaurus.* But the first large theropods, animals more than thirty feet long and weighing between two and three tons, appeared during the Late Jurassic. The true giants did not arrive until the middle of the Cretaceous period. The carcharodontosaurs were among the largest terrestrial predators that ever lived, some reaching as much as forty feet long and weighing four tons. The spin-
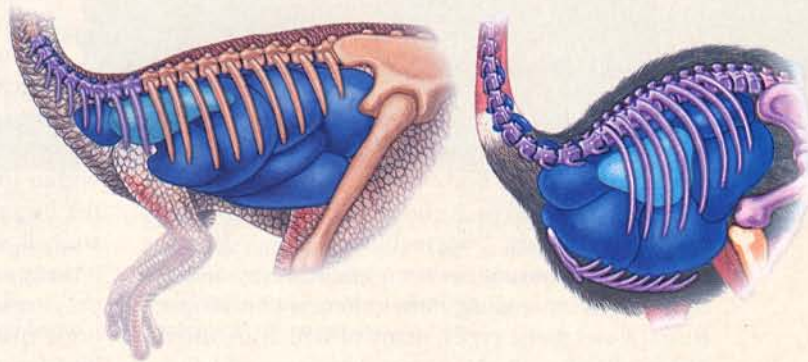
Skeletons of theropod dinosaurs and most modern birds are perforated by their pulmonary systems, a condition known as pneumaticity. Pneumatic bones (purple) have holes in them to accommodate air sacs (blue) extending from the lungs (light blue). In birds, most air sacs serve as bellows to ventilate the lungs. Ornithomimus (left) had pneumatic bones only in the vertebrae and in small ribs in the neck, whereas the ostrich (right) has air-filled bones throughout much of its body. The pneumaticity of bones may have evolved as a means of reducing their density, thereby allowing theropods to grow larger without a commensurate increase in body mass. The artist's reconstruction of the air sacs in the dinosaur outside its bones is based on the positions of air sacs in birds.

osaurs were contemporary to the carcharodontosaurs, and similar in size. The giant tyrannosaurs appeared in the latest part of the Cretaceous, reaching or exceeding the carcharodontosaurs in size.

What is interesting is not so much the absolute size of those giant predators but that at least three lineages of theropods independently evolved to almost exactly the same size. Something, it would seem, made such a size advantageous. Or perhaps something structural or ecological made any larger size a real disadvantage.

Body size affects nearly every aspect of organismal biology. The basic physics of size dictates an

animal's structure and function in a number of predictable ways. For example, when an animal doubles its linear dimensions, its volume increases eightfold. Hence processes that depend on volume, such as maintaining body temperature, are highly sensitive to changes in body size. Other physiological processes that depend on surface areas—gas exchange across a membrane, for instance—are intermediately affected by changes in body size. One consequence of those geometric relationships is that the larger the animal, the harder it becomes to adjust its body temperature. Body temperature is regulated through the body's surface area, but heat is stored in the body's volume.

To some degree, most living reptiles rely on the external environment for controlling body temper-

Lightweight bones made giant dinosaurs possible. Birds owe their bones to that earlier evolution.

ature; thus, reptiles are called ectothermic, or, somewhat erroneously, "cold-blooded." Birds, however, can fine-tune their body temperatures internally, a condition referred to as endothermy, or, also somewhat erroneously, "warm-bloodedness." But the apparent dichotomy between endothermy and ectothermy is misleading; rather, there is a broad spectrum of metabolic types, many of which are directly correlated with the anatomical form and function of the breathing apparatus.

Many reptiles have relatively simple lungs. As they expand or contract, air flows in and out of them through the same channels, just as it does in people. But the configuration of the internal cavity of the reptilian lung varies from species to species. In a few species, including some lizards, each lung is a simple sac, and gases are exchanged only around its edges. In other species, such as monitor lizards and crocodilians, the lungs are partitioned into chambers made up of an intricate net of support structures. The network provides a larger surface area, which enables higher rates of gas exchange than do the edges of a simple, saclike lung.

Modern birds have modified the basic reptilian design in such a way as to increase lung partitioning, and, consequently, the surface area for gas exchange. But unlike the reptilian lung, the avian lung changes very little in size during ventilation. Instead, birds have flexible air sacs (usually nine in number) that act as bellows to move air through the lungs. Although the air sacs are connected to the

lungs, they do not take part directly in gas exchange. Furthermore, in some parts of the bird lung, air flows almost continually in just one direction. Those specializations enable birds to exchange gases efficiently enough to sustain high metabolic rates and regulate their temperatures internally.

Although avian lungs and air sacs are made of soft tissues, they have important connections with the skeleton. Extensions from the air sacs physically invade the skeleton, a process known as pneumatization. The result can be dramatic. Imagine walking down the windpipe of a bird, into its lungs, and then on into the skeleton, including the backbone and limbs—within the pulmonary system. That's some fantastic voyage!

No other living animals have pneumatic bones like those of birds, but substantial evidence suggests that theropods, along with the flying pterosaurs and sauropod dinosaurs, had at least a superficially similar pulmonary system. Like birds, those animals had holes in the outer surfaces of many of their bones. The holes were connected to large, air-filled chambers within the bones.

Even in birds, though, the function of pneumatic bones remains unclear. No gases are exchanged within the bones, nor do the air-filled chambers in the bones help move air through the lung—bone, after all, is not a flexible bellows. One plausible idea is that pneumatic bones might have evolved because they replaced heavy (and metabolically expensive) bone marrow with air. Pneumatic bones enable a bird (or a dinosaur) to expand its overall body size without a commensurate increase in weight.

In spite of the uncertain role of pneumatic bones, their presence in theropods suggests that at least some theropods had air sacs similar to those observed in birds. Without additional evidence, though, it is probably idle to speculate any further about how theropods breathed. Nevertheless, the historical perspective provided by theropod pneumaticity may be the key to understanding the origin of air-filled, lightweight bones in birds.

Ornithologists have long sought to explain pneumatic bones in birds as an adaptation to some aspect of their lifestyle, such as the great benefit they offer for energy savings in flying. Pneumaticity clearly originated much earlier in avian history, but perhaps for a similar reason—that is, its adaptive value in relaxing the constraints on the size of theropods. One point corroborating that idea is that many of the largest theropods, such as carcharodontosaurs and tyrannosaurs, often had the most extreme pneumaticity. Many of the smaller theropods, in contrast, only pneumatized certain regions of the vertebral column.
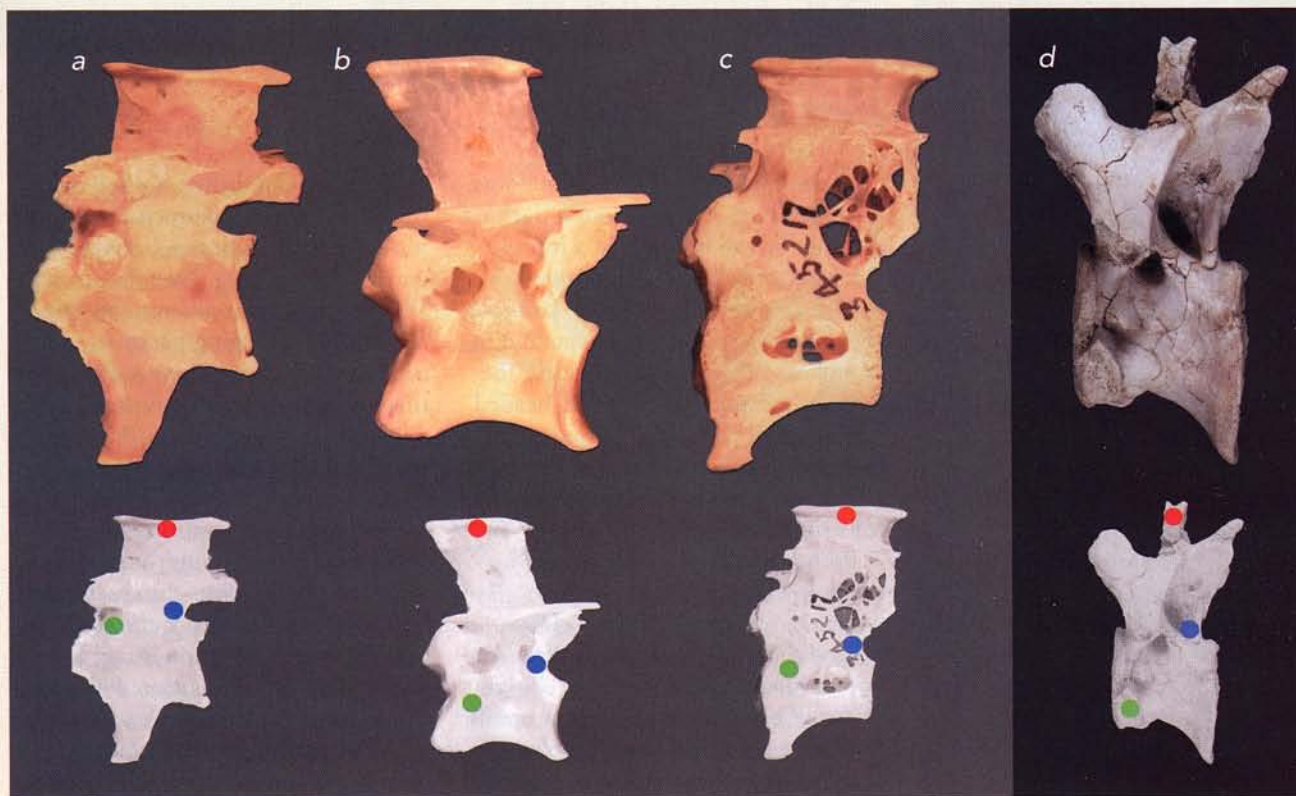
Vertebrae (top row) in three species of bird—penguin (a), owl (b), and screamer bird (c)—show varying degrees of pneumaticity. (The more air sacs in the bone, the greater its pneumaticity.) The theropod dinosaur vertebra (d) exhibits similar pneumatic openings. Large birds such as screamers likely possess such heavily pneumatized bones to reduce body weight, whereas penguins and other diving birds have no pneumatization in order to reduce their buoyancy. Medium-size birds such as owls have intermediate levels of pneumaticity. The colored circles in the line drawings (bottom row) correspond, by color, to identical anatomical structures in each bone.

Similar patterns of pneumaticity occur in birds: among flying birds, at least, the larger the bird, the more extensive its pneumaticity. Certain large-bodied flying birds, such as bustards, pelicans, and vultures, pneumatize virtually the entire skeleton, out to the tips of the wings. Many medium-size and small birds, such as ducks, pheasants, and songbirds, only pneumatize the vertebrae and limb bones closest to the lung and air sacs. Some interesting exceptions to the correlation between body size and pneumaticity occur in birds that dive underwater to feed, such as grebes, loons, and penguins. Those birds have eliminated bony pneumaticity altogether, so as to reduce their buoyancy when they dive.

The broad variation in skeletal pneumaticity among birds suggests that interactions between the pulmonary and skeletal systems alter drastically in response to a variety of physical and environmental pressures. Could similar variations in pneumaticity reflect the various physical and ecological factors theropods had to confront? With birds as a model, paleontologists should be able to frame and test hypotheses that can begin to answer that question.

Using living animals as "model organisms" for understanding dinosaur biology offers many advantages over traditional methods of paleontology. But paleobiologists must also remain cautious when making inferences related to the activities of long-dead animals. For example, as tempting as it is to read "bird" into every dinosaurian trait, it is just as important to acknowledge the limits of current knowledge, and the fact that the dinosaurs maintained their own evolutionary trajectory; they likely possessed an amalgam of traits present in modern birds and their reptilian relatives.

Ideally, paleontology integrates multiple lines of evidence, from a variety of living and extinct animals, to assess the full biological potential of long-extinct groups. That approach is not without its limits. Nevertheless, by seeking novel ways to integrate the vast array of biological subdisciplines, paleobiologists are beginning to put a modern face on some very old "terrible lizards." Those complementary studies will ultimately provide the most rigorous assessment of how dinosaurs actually lived. □