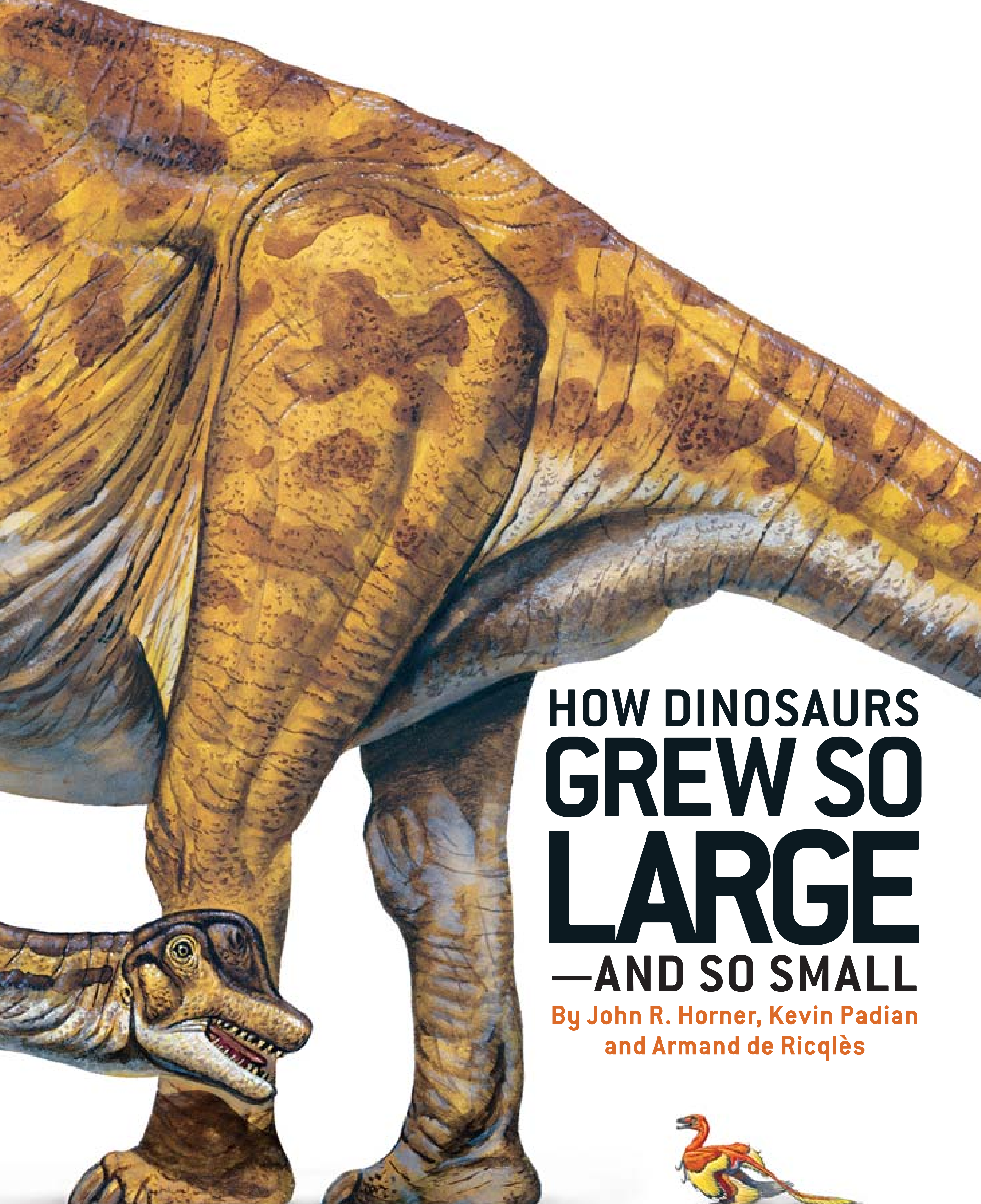
ONE OF THE LARGEST dinosaurs, *Brachiosaurus* reached adulthood in less than 20 years and the chicken-sized *Microraptor* in far less time. Scientists can measure the age of extinct animals by examining annual growth lines in the ancient bones and calculating rates of bone tissue growth in living animals.



HOW DINOSAURS GREW SO LARGE —AND SO SMALL

By John R. Horner, Kevin Padian and Armand de Ricqlès

Most people can stand comfortably under the jawline of a mounted *Tyrannosaurus rex* or walk under the rib cage of a *Brachiosaurus* without bumping their heads. *T. rex* is as big as the largest known African elephant, and *Brachiosaurus,* like other great sauropods, was much larger than any land animal alive today. We are so used to the enormous size of dinosaurs that we almost forget to think about how they grew to be so large. How long did it take them, and how long did they live? And does the way they grew tell us about the way their bodies worked?

Until recently, we had no way to measure age in a dinosaur. Paleontologists had generally assumed that because dinosaurs were reptiles, they probably grew much as reptiles do today—that is, rather slowly. Thus, the thinking went, large dinosaurs must have reached very old ages indeed, but no one knew how old, because no living reptiles attain anything near the size of a dinosaur.

This attitude can be traced back to English paleontologist Sir Richard Owen. When he named the Dinosauria in 1842, he was putting a label on a very small, poorly known group of very large, unusual reptiles. Not only were they big, he said, but they were terrestrial, unlike the seagoing ichthyosaurs and plesiosaurs that had been known since the early 1800s. They had five vertebrae (backbones) connected to the hips, not two like living reptiles. And they held their limbs underneath their bodies, not sprawled out to the sides. Despite these differences, he continued, the anatomical features of their bones—the shapes, joints and muscle attachments—showed them to be reptiles. So they must have had a reptilian physiology—that is, a typically "cold-blooded," slow metabolism. The image stuck, and well into the 1960s dinosaurs were portrayed as sluggish, lumbering beasts that must have grown slowly to great size in a sort of benign hothouse where huge beasts reigned and raged.

Yet evidence for the ages of dinosaurs, and so for how they must have grown, was there all the time—locked inside the bones themselves. Although paleontologists had known for many years that the bones of dinosaurs contain growth lines, something like the circumferential growth rings we see in trees, it was only in the second half of the 20th century that they began to use these growth lines and other structures inside the bones to figure out how these extinct animals actually grew.

The Bones Tell the Story

LIKE THE RINGS in trees, the lines in the bones of dinosaurs were annual. But they aren't quite as simple to interpret. A tree carries nearly the entire record of its growth inside its trunk. Cut it down, and you can count the rings one by one from the center to the bark. Only the outer layer is making new wood; the inside is really deadwood. The center of a bone, in contrast, is a busy place. Cells called osteoclasts hollow out the center of a long bone, such as the femur (thigh) or tibia (shin), by breaking down existing bone and allowing its nutrients to be recycled. This center, or marrow cavity, is also the factory that produces red blood cells [*see box on opposite page*].

To accomplish these tasks, the whole bone constantly grows and changes throughout life. As a bone grows, new tissue is deposited on the outside, and in the long bones growth also occurs at the ends of the shafts. Meanwhile, in the marrow cavity, osteoclasts are eroding the bone that was deposited early in life, and other cells are making secondary bone tissue along the perimeter of the cavity or invading the cortex (outer layer) of the remaining bone to remodel it.

This activity at the center of the bone often erodes the record of growth during the youngest stages of an individual's life. Consequently, it is difficult to cut open the bone of a dinosaur and find a complete record of growth just by counting the rings. So we reconstruct the early history of the bone in several ways. One is to use the bones of younger individuals to fill in the missing record. These younger bones contain the tissues that have been eroded in older bones. By examining these tissues and counting the growth lines, we can approximate the number of years that are missing from the older bones. When we have no juveniles available, we can "retrocalculate" the number of growth lines by examining distances between growth lines that are preserved.

We recently tried retrocalculation on the most famous dinosaur of all: *T. rex*. The Museum of the Rockies at Montana State University has a dozen specimens of this giant carnivore, and seven of them have reasonably well preserved hind-limb bones that allowed us to make thin sections—slices of the bone that are so thin they can be examined under a microscope.

The microscopic slides of *T. rex* limbs revealed only four to eight preserved growth lines. Others, near the

Overview/*Growing Fast to Great Size*

- Until recently, we had no way to measure the age of dinosaurs and thus to figure out how they grew.
- It turns out that this information has been locked in the animals' bones all along—many of the bones contain growth lines, something like the rings in trees.
- Using these lines and other structures within the bone, scientists have now shown that dinosaurs grew to full size quickly—much in the way that birds and mammals do today and not at all like the more slowly growing living reptiles.
- This fast growth implies that these ancient creatures had a high metabolic rate closer to that of warm-blooded animals than to cold-blooded reptiles.

MARK HALLETT [*preceding pages*]

center, had been obscured by the growth of secondary bone tissue. Even more striking, the marrow cavity is so large in these dinosaurs that two thirds of the original bone cortex is eroded away. We also noticed that in some individuals the space between the growth lines suddenly became very small toward the outermost surface of the bone. We had seen this before in other dinosaurs, such as the plant-eating duckbill *Maiasaura*. It signifies the end of active growth, essentially the point at which the animal reached full size.

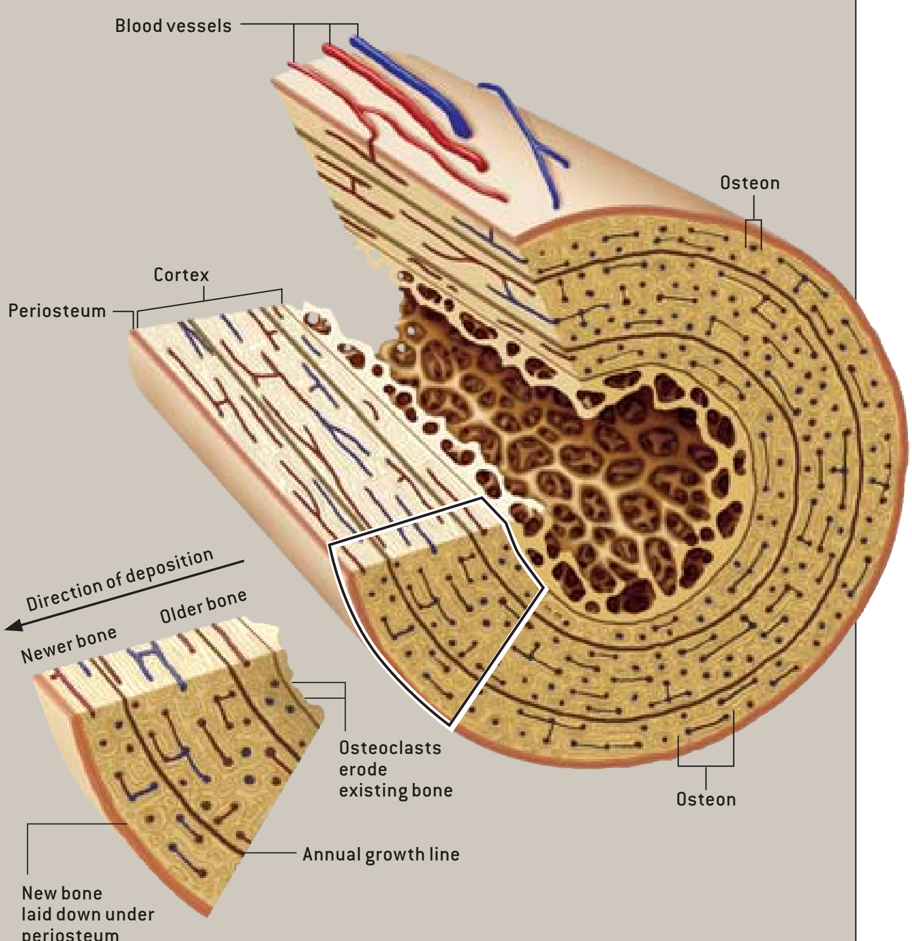
Our retrocalculations estimated that *T. rex* took 15 to 18 years to attain full size, which is to say a hip height of three meters (10 feet), a length of 11 meters (34 feet), and a weight of 5,000 to 8,000 kilograms (five to eight tons). (We were pleased to see that our estimates matched those of Gregory M. Erickson of Florida State University and his colleagues, which were completed at about the same time.) If that seems like rapid growth, it is. At least, for a reptile. It turns out that dinosaurs grew much faster than other living or extinct reptiles do.

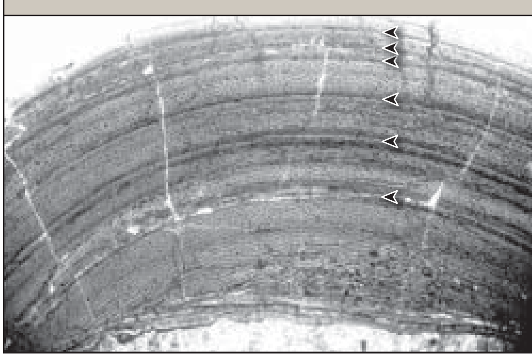
For example, Erickson and Christopher A. Brochu of the University of Iowa charted the growth of the giant crocodile *Deinosuchus,* which lived during the Cretaceous period, some 75 million to 80 million years ago [*see illustration on next page*]. These huge reptiles reached estimated lengths of 10 to 11 meters. Examining the growth lines in the skin armor of the neck, Erickson and Brochu determined that such an animal required nearly 50 years to reach this length—three times as long as it took *T. rex* to reach the same size. A closer comparison for *T. rex* proves to be the African elephant, which reaches about the same mass (5,000 to 6,500 kilograms) in 25 to 35 years. So *T. rex* grew to its adult size even faster than an elephant does.

Further research showed that *T. rex* is not unusual for dinosaurs—except that it actually grew a little bit more slowly for its size than other large dinosaurs did. Anusuya Chinsamy-Turan, now at the University of Cape Town in South Africa, found that the plant-eat-

READING A DINOSAUR BONE

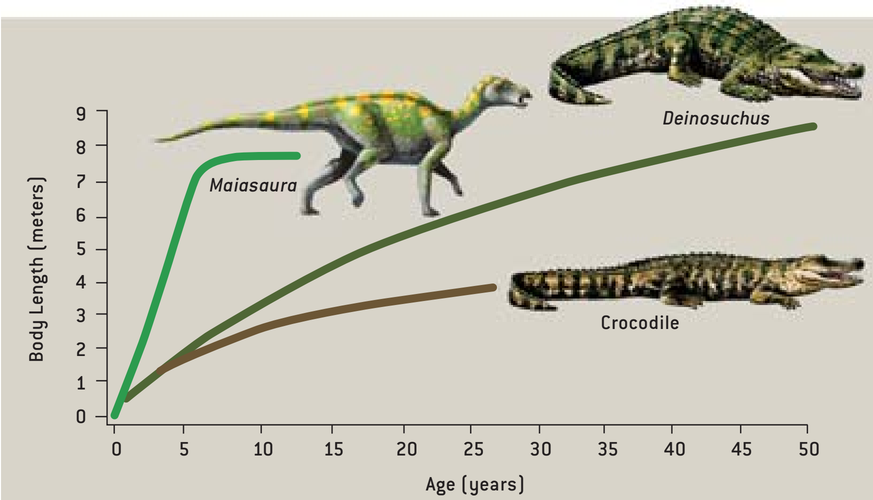
The bones of dinosaurs contain growth lines, somewhat similar to the annual rings in trees, although they are more complicated to interpret. The cortex of bone is built by minerals such as calcium phosphate and proteins such as collagen, which are carried by blood vessels. When the vascular canals, which contain the blood vessels, begin to deposit bone along their insides in concentric layers, they are called osteons. In the femur, or thighbone, and other long bones, growth is concentrated just underneath an outer membrane, the periosteum. Meanwhile the inner margin of the bone is being eaten away by osteoclast cells. A secondary series of osteons may invade preexisting bone, eroding it and depositing new bone. Because of all this activity, researchers cannot simply slice open a dinosaur bone and determine the age of the animal, but they can gain such information by performing various analyses of the rings and other features.





GROWTH LINES
The annual growth lines in the diagram above left can be seen in the photograph of the inside of the femur of *Troodon*, a small carnivorous dinosaur. These lines (*arrows*) become more closely spaced toward the outside of the bone, which was deposited in the later period of growth when the animal was slowing its growth, as we all do with age.

SHAWN GOULD (*illustrations*); JOHN R. HORNER, KEVIN PADIAN AND ARMAND DE RICQLÈS (*photograph*)



GROWTH CURVES show that even the largest dinosaurs were actually teenagers when they reached their huge sizes. They grew to adult size far faster than conventional reptiles do.

ing *Massospondylus* took about 15 years to reach a length of two to three meters. Erickson and Tatanya A. Tumanova of the Paleontological Institute in Moscow found that the small ceratopsian (horned) *Psittacosaurus* was mature at 13 to 15 years. And we calculated that the duckbill *Maiasaura* reached adulthood at between seven and eight years, by which time it was seven meters long. The giant sauropods ("brontosaur" types) outdo all the others, though: Martin Sander of the University of Bonn in Germany discovered that *Janenschia* reached maturity at about 11 years, although it continued to grow substantially after that. Frédérique Rimblot-Baly and her colleagues at the University of Paris VII determined that *Lapparentosaurus* attained full size before it was 20 years old. Kristina Curry Rogers of the Science Museum of Minnesota found that *Apatosaurus* (more familiarly known as *Brontosaurus*) matured in eight to 10 years—an annual weight gain of nearly 5,500 kilograms.

Inside a Dinosaur Bone

WHY SHOULD dinosaurs grow more like elephants than like giant crocodiles? And what does this mean for other aspects of their biology? To answer these questions, we have to look inside a dinosaur bone at the kind of tissues it laid down.

The tissue in a typical long bone of a dinosaur is primarily a type called fibrolamellar: it is highly fibrous or "woven" in texture, and it forms around a matrix of poorly organized collagenous fibers that is well supplied with blood vessels. In contrast to what we would expect in conventional reptiles, this is the same kind of tissue that predominates in the bones of large birds and large mammals,

EARLY BIRDS

Do new insights about the rapid pace at which extinct dinosaurs grew give us any new information about the evolution of birds, the living dinosaurs? Why, for example, are birds so much smaller than extinct dinosaurs? Did they change their growth rates somehow? We began looking into these questions by examining the bone tissues of *Confuciusornis*, an ancient bird from the Early Cretaceous (125 million years ago) of China that appears on the avian family tree shortly after *Archaeopteryx*, the first known bird. The inner part of the bone tissues of the crow-sized *Confuciusornis* is of a fast-growing, fibro-lamellar type (like those of other dinosaurs), but toward the outside it becomes a slower-growing type—a sign that the growth rate waned after a short, youthful spurt. We compared these tissues with those of *Troodon*, a small raptorlike dinosaur about 1.5 meters long, which David J. Varricchio of Montana State University had studied. *Troodon* tissues indicate faster growth overall.

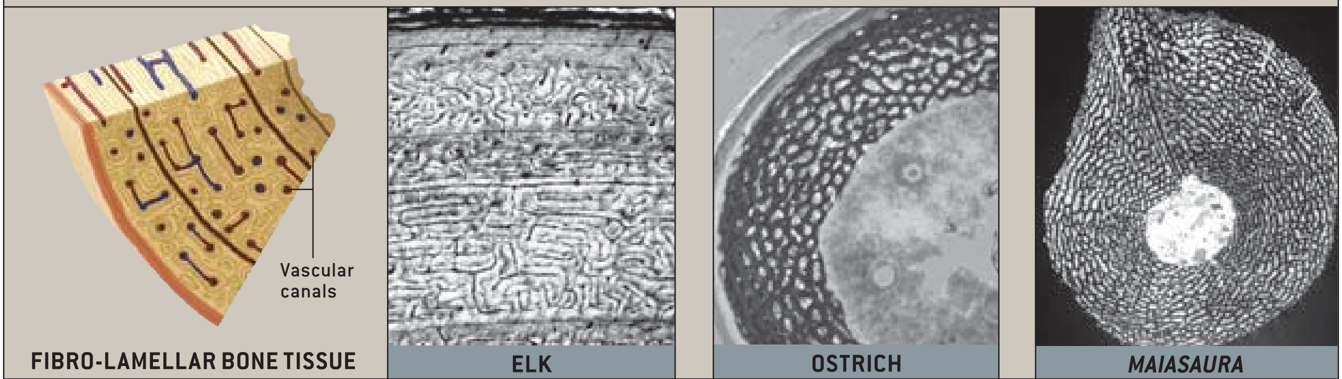
As *Confuciusornis* shows, to become small these ancient bird species truncated the juvenile burst of growth that was most rapid in other dinosaurs, which caused the birds in effect to become miniaturized. Miniaturization had an important influence on locomotion, because the feathers that were present on the forelimbs of the closest dinosaurian relatives of birds would have been more likely to help these smaller animals become airborne. Small animals can flap their wings faster than large ones, and in a smaller animal the wing loading (the ratio of weight to wing area, or how much a given unit of area has to carry) will be proportionally smaller and so aerodynamically more advantageous.

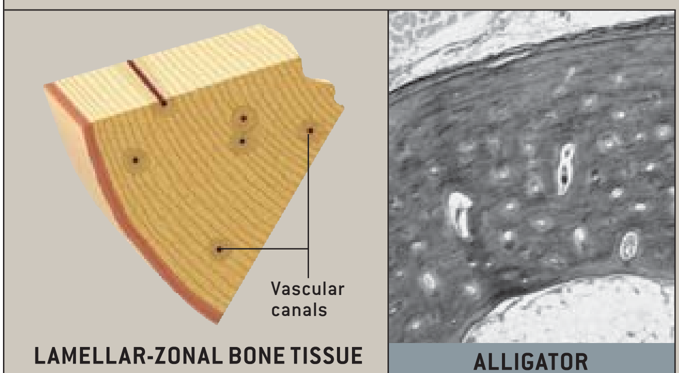
But birds today reach full size quickly, usually in weeks to months. What changed? It appears that after slowing early in their evolution, birds over time sped up their growth rate again—to rates that are often even faster than those in extinct dinosaurs. Some years ago Anusuya Chinsamy-Turan, now at the University of Cape Town, and her colleagues studied the bone tissue of early birds a bit farther along the evolutionary tree than *Archaeopteryx* and *Confuciusornis*. These Late Cretaceous birds included a primitive enantiornithine, the flightless *Patagopteryx*, the diving *Hesperornis*, and the ternlike *Ichthyornis* [*see box on pages 62 and 63*]. They, too, grew more slowly than dinosaurs, but the forms closer to living birds had tissues that indicated somewhat more rapid growth than in the very early birds.

Close to the Cretaceous-Tertiary boundary, about 65 million years ago, growth rates increased substantially, so much so that all living birds—even the ostrich—attain full size within less than a year (seven days in the case of the sparrow). Only examination of birds from the Early Tertiary will tell us whether the living groups of birds acquired their habit of rapid growth to adult size gradually or relatively suddenly. *—J.R.H., K.P. and A.d.R.*

SHAWN GOULD (*illustrations*); JEN CHRISTIANSEN (*graph*)

DINOSAURS DIDN'T GROW LIKE REPTILES





Dinosaur bones, on the inside, look much like the bones of large birds and mammals (*above*). These animals, unlike reptiles (*left*), lay down a type of bone tissue called fibro-lamellar, which grows on a scaffold of minerals and collagen fibers that are produced in discrete layers. Their bone tissue is usually very well vascularized. Lots of blood vessels imply rapid deposition of tissue, and so rapid growth. The elk and alligator bones shown here are of nearly mature individuals. Toward the outside of the bone are far fewer vascular canals, reflecting a slowing of growth. The *Maiasaura* and ostrich bones are from near-hatchling individuals. The vascular spaces in their bones are copious, indicating very rapid growth that has not yet settled into the fibro-lamellar pattern.

SHAWN GOULD (*illustrations*); JOHN R. HORNER, KEVIN PADIAN AND ARMAND DE RICQLÈS (*photographs*)

which grow to full size faster than typical reptiles do. A crocodile bone, on the other hand, is formed mostly of lamellar-zonal tissue—compact, highly mineralized bone that contains more regularly organized fibers and much sparser, smaller vascular canals. Furthermore, the growth lines in crocodile bones are more tightly spaced than those in dinosaur bones, another indication that crocodile bones grow more slowly [*see box above*].

Rodolfo Amprino of the University of Turin in Italy recognized in the 1940s that the type of tissue laid down in a bone at any given place or time during growth was mainly a function of how fast the tissue was growing at that point. Fibro-lamellar tissue, no matter where or when it is deposited, reflects locally rapid growth, whereas lamellar-zonal tissue signals slower growth. An animal can lay down either of these tissues at different times—as the growth strategy warrants. The type of tissue that predominates through the animal's life provides the best guide to its growth rate.

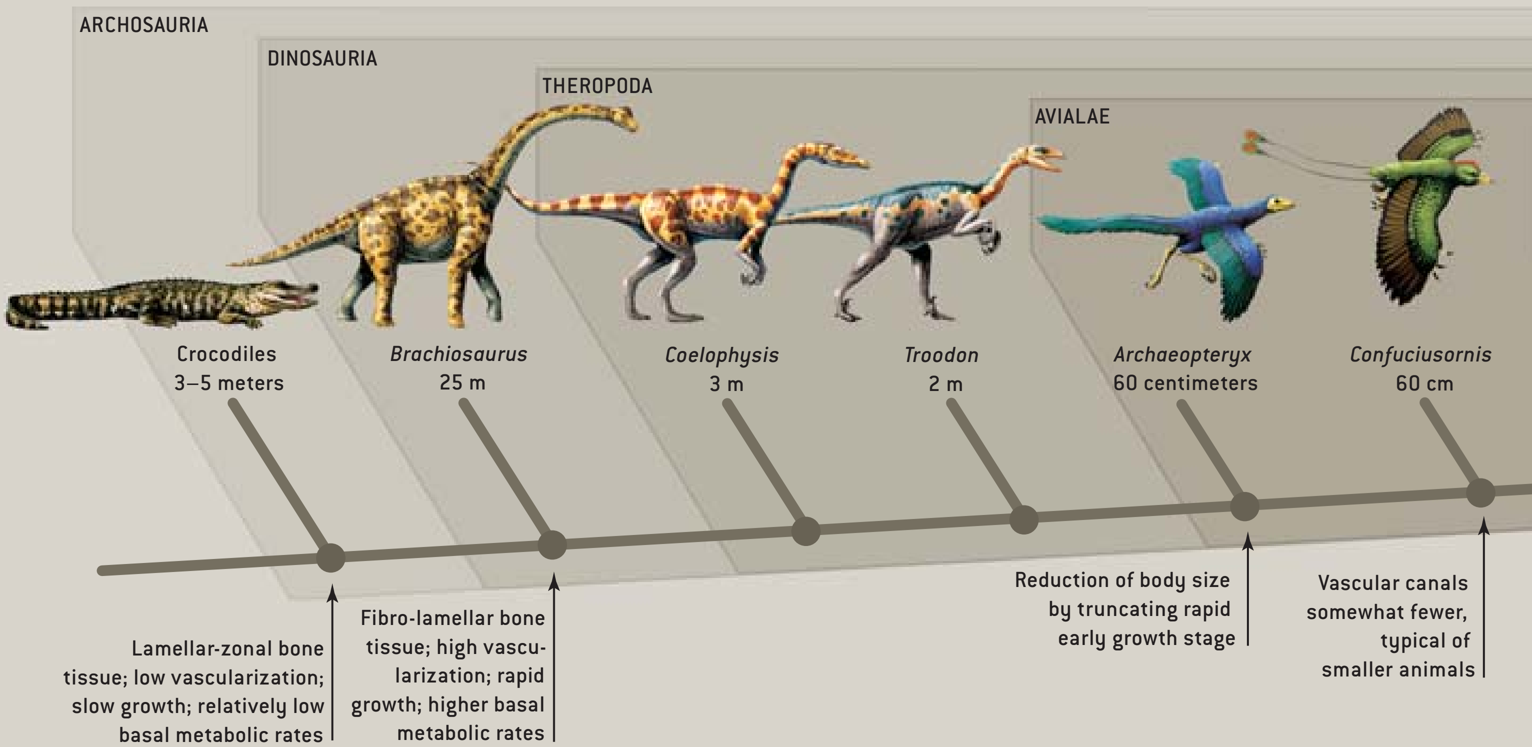
One difference between dinosaurs, on the one hand, and crocodiles and other reptiles, on the other, is that dinosaurs deposit fibro-lamellar tissue all through growth to adult size, whereas other reptiles switch very soon to lamellar-zonal bone. We inferred from this that dinosaurs sustained more rapid growth until the adult stage, because there would be no other good explanation for the persistence and predominance of fibro-lamellar tissue.

The pace at which dinosaurs grew was assessed in a different way by Erickson, Rogers and Scott A. Yerby of Stanford University. Using estimates of the body mass of dinosaurs, they plotted the animals' mass against time to derive growth curves for a variety of species and compared the curves with those for other groups of vertebrates. They found that all dinosaurs grew faster than all living reptiles, that many dinosaurs grew at rates comparable to those of living marsupials, and that the largest dinosaurs grew at rates comparable to those of rapidly maturing birds and large mammals. We confirmed their results for body mass with our own studies using length.

THE AUTHORS

JOHN R. HORNER, KEVIN PADIAN and *ARMAND DE RICQLÈS* have worked together on investigations of dinosaur bones for more than 12 years. Horner is curator of paleontology at the Museum of the Rockies and Regents Professor of Paleontology at Montana State University. Padian is professor of integrative biology and curator of the Museum of Paleontology at the University of California, Berkeley. De Ricqlès is professor at the Collège de France in Paris, where he occupies the chair in historical and evolutionary biology; his CNRS research team at the University of Paris VII works on the formation of bone and other skeletal tissues.

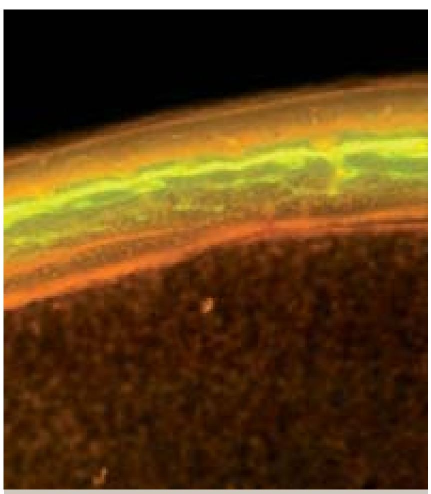
BONE GROWTH AND EVOLUTION IN BIRDS



In one sense, such findings were not unexpected. Many years ago Ted J. Case of the University of California at Los Angeles showed that within any group of vertebrates (fishes, amphibians and so on), larger species grow at absolutely higher rates than smaller species do; so, although larger species reach adult size in a longer time, they grow more quickly to do so. What was surprising is that dinosaurs grew as fast as they did.

We were curious about when in the course of their evolution dinosaurs acquired this habit of rapid growth, so we plotted our estimated growth rates on a cladogram, or diagram of relationships, that was built on hundreds of independent characteristics from all parts of the skeleton. We added the estimated growth rates for pterosaurs (flying reptiles closely related to dinosaurs, which grew much like them), crocodiles and their extinct relatives, and lizards. We put birds among the dinosaurs, because birds evolved from dinosaurs and so are technically included with them [see "The Origin of Birds and Their Flight," by Kevin Padian and Luis M. Chiappe; SCIENTIFIC AMERICAN, February 1998].

For added help in estimating the growth rates of dinosaurs, we looked at



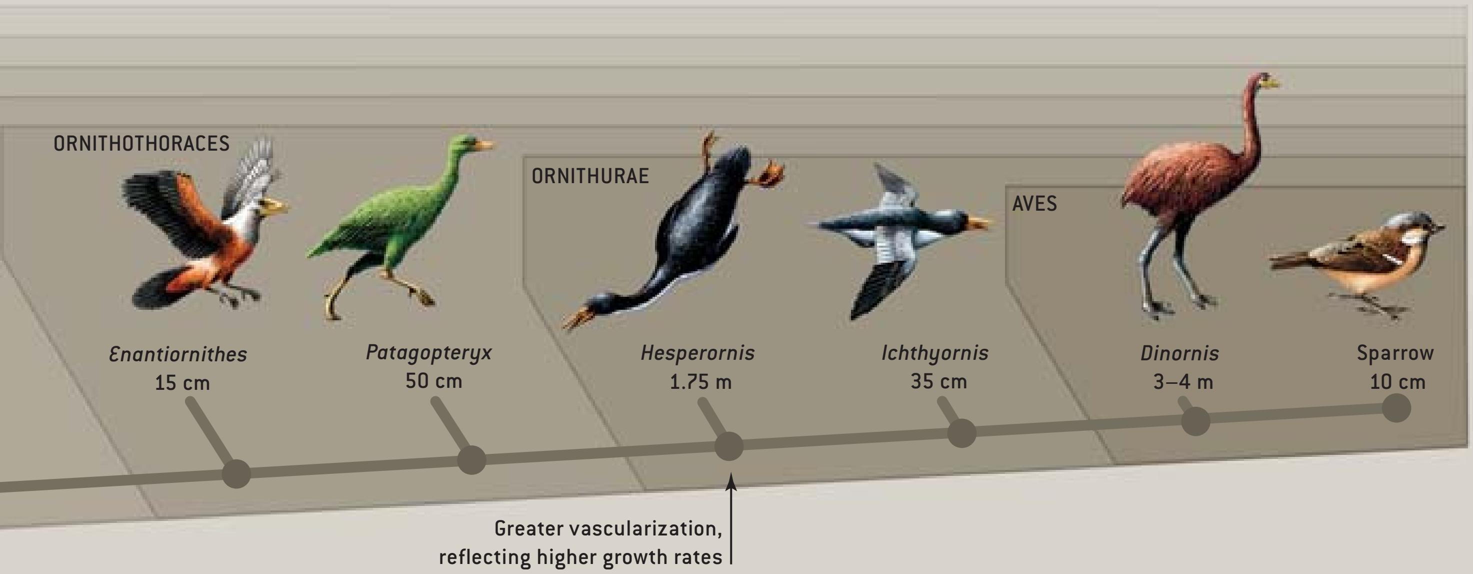
DISCRETELY DEPOSITED BONE layers are revealed by green, yellow and orange fluorescent dyes, injected weekly into a mallard duck. These dyes show exactly how much growth occurred each week.

living birds, which show the same range of tissues expressed in dinosaur bones. Jacques Castanet and his colleagues at the University of Paris VII injected mallard ducks with solutions that would stain the growing bones. By using different colors at different times, they were able to measure rates of weekly growth in the sacrificed birds [*see illustration at left*]. Using these calibrations, we determined that, without exception, dinosaurs and pterosaurs grew at much higher rates than other reptiles. We did find considerable variation among the dinosaurs and pterosaurs, a variation mirrored by Castanet's findings in birds: the animals that grew relatively more slowly than others were the smaller ones—just as Ted Case's patterns would predict.

Unconventional Reptiles

THE STUDY OF dinosaur bones has told us a great deal about the evolution of some of the major features of these animals. About 230 million years ago,

SHAWN GOULD (*illustrations*); JEN CHRISTIANSEN (*cladogram*); JACQUES CASTANET (*photograph*)



Dinosaurs, from their beginning, had bone tissues that differed greatly from those of other reptiles. Their bones grew more rapidly, as in birds and mammals of today. When the first birds (Avialae) evolved, their substantial reduction in size was a result of slower growth of their bone. But their growth was still more rapid than in other reptiles. Then, as the living bird groups (Aves) began to emerge, growth accelerated again, so that pigeon-sized birds matured in weeks instead of months. All birds today, even the ostrich, reach adult size within a year, and most do so much more quickly—the sparrow in seven days. When birds evolved, they slowed down their growth rates at exactly the time when growth is highest in their dinosaur ancestors, their juvenile period, effectively miniaturizing them as adults.

in the early part of the Triassic period, the lineage that would produce dinosaurs, pterosaurs and their relatives split from the lineage that would produce crocodiles and their relatives. The dinosaurian lineage soon acquired sustained elevated growth rates that set them apart from other reptiles. This speedy growth may have played a role in the success that dinosaurs and pterosaurs enjoyed toward the end of the Triassic, when so many crocodile relatives and other archaic groups with more typical reptilian bone structure became extinct.

The high growth rates of dinosaurs also give us a firmer idea about their metabolic features. The higher the metabolic rate—that is, the more energy devoted to building up and breaking down bone and other tissues—the faster the tissues will grow. So evidence of sustained rapid growth, even into late juvenile and subadult stages, implies that the animals in question had relatively high basal metabolic rates. Because dinosaurs were not like living reptiles in the way they grew, but much like birds and mammals, their basal metabolic rates were probably more like those of birds and mammals than like those of today's reptiles. This suggests that they were much more likely to have been warm-blooded, in a general sense, than cold-blooded, but it is difficult to know the details, such as body temperature and how much it varied, or how much body heat dinosaurs could acquire from (or needed to shed to) the air around them. Clearly, many questions remain. Dinosaurs were perhaps even more unusual creatures than we had previously thought—not exactly like any animals of today and certainly not conventional reptiles. If anyone ever discovers a five-ton living bird, a lot of these questions will be settled. SA

MORE TO EXPLORE

Dinosaurian Growth Rates and Bird Origins. K. Padian, A. J. de Ricqlès and J. R. Horner in *Nature,* Vol. 412, pages 405–408; July 26, 2001.

Dinosaurian Growth Patterns and Rapid Avian Growth Rates. G. M. Erickson, K. Curry Rogers and S. A. Yerby. Ibid., pages 429–433.

Age and Growth Dynamics of *Tyrannosaurus rex.* J. R. Horner and K. Padian in *Proceedings of the Royal Society of London, Biological Sciences,* Vol. 271, No. 1551, pages 1875–1880; September 22, 2004.

Growth in Small Dinosaurs and Pterosaurs: The Evolution of Archosaurian Growth Strategies. K. Padian, J. R. Horner and A. de Ricqlès in *Journal of Vertebrate Paleontology,* Vol. 24, No. 3, pages 555–571; September 2004.

What's Inside a Dinosaur Bone? K. Padian in *UCMP News* (University of California, Berkeley); September 2004. Online at **www.ucmp.berkeley.edu/museum/ucmp_news/2001/5-01/dinosaur1.html**

Physiology. K. Padian and J. R. Horner in *The Dinosauria.* Second edition. Edited by D. Weishampel, P. Dodson and H. Osmólska. University of California Press, 2004.

Dinosaur bone histology: **http://ltc.smm.org/histology/**