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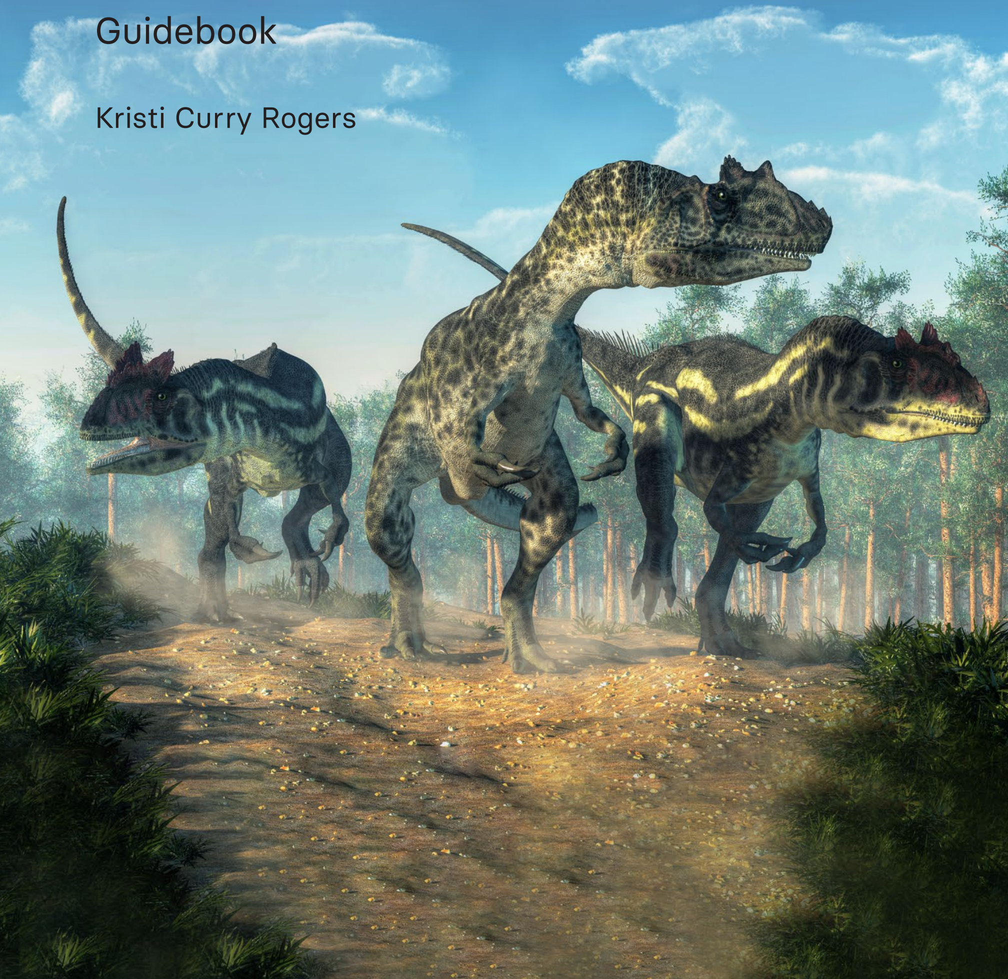
Rediscovering the Age of Dinosaurs

Guidebook

Kristi Curry Rogers



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KRISTI CURRY ROGERS

Kristi Curry Rogers is a dinosaur paleontologist and a Professor of Biology and Geology at Macalester College. She earned her PhD in Anatomical Sciences from Stony Brook University. She conducted a detailed study of sauropod dinosaurs inhabiting the island of Madagascar, which resulted in the discovery and naming of two new sauropod dinosaur genera, *Rapetosaurus* and *Vahiny*. She has published more than 45 research papers and coauthored the book *The Sauropods: Evolution and Paleobiology*.

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OUR ENDURING FASCINATION WITH DINOSAURS

This course will explore a remarkable and mysterious group of animals: dinosaurs. Sixty-six million years ago, they vanished from the earth in a cataclysm—or did they? These lectures take a deep dive into the discoveries that help paleontologists bring these beasts back to life. You'll look at the science to flesh out their origin, radiation, and downfall—and their surprising living legacy. This course will also cover the discovery of the first fossils that gave rise to the Dinosauria classification, right on up to the cutting-edge science that is changing the way people think of dinosaurs today.

ENDURING FASCINATION WITH DINOSAURS

Most people have never heard of *Deinocheirus*. This dinosaur was first discovered in the 1960s, when a pair of giant arms sporting large claws were unearthed in the Mongolian desert. The name *Deinocheirus* pays tribute to these scary appendages—derived from the Greek for "horrible hand." For the next 50 years, no additional fossils were found to piece together the rest of the story. Not until 2013 was the full picture of *Deinocheirus*'s crazy body revealed when more fossils were found. Though it is in the group of dinosaurs that includes famous predators like *Tyrannosaurus rex*, *Deinocheirus* traded out traditional sharp teeth for a duck-like beak. It walked on short, powerful hind legs; it had three fingers tipped with sharp, 18-inch-long claws; and the spines of its vertebrae formed a giant sail on its back. Even stranger, its short, stubby tail ended in a fan of long, fluffy feathers.

People of all ages have a seemingly innate fascination for dinosaurs. Interest in dinosaurs is as prevalent today as it's ever been. Most adults can name at least five iconic dinosaurs. Few other scientific disciplines enjoy the deep, nearly universal knowledge we all share about dinosaurs.

JACK HORNER

Consider some historically exciting discoveries in Montana made by a paleontologist named Jack Horner. An old coffee can full of bones in a small-town museum drew his interest. This led him to excavate the first dinosaur nesting ground found in North America. The site became known as Egg Mountain, and it yielded multiple layers of fossils that preserved tons of dinosaur nests and bone beds.

One of those discoveries was a species of duckbilled dinosaur. This was later called *Maiasaura*, or the "good mother lizard." It took care of babies in the nest and brought them food, as a modern bird might.

Horner's book *Digging Dinosaurs* was one of the popular translations of the raw science that helped us all rethink the age of dinosaurs. Paleontologists call this time the dinosaur renaissance. From the 1960s to the 1990s, a series of remarkable discoveries from around the world, combined with new interpretations of old bones, helped to pull dinosaurs from the ancient past and bring them to life.

DIGGING IN

One might imagine that dinosaur bones are found as the result of detailed, coordinated reconnaissance in an area where paleontologists know they'll find something great. There's a little bit of truth to that. But discovery is also about sheer luck—and simply being in the right place at the right time.

Paleontologists do plenty of research before heading out into the field. They read the historical literature because sometimes a brief mention in an article written more than a century ago will hold important clues on where to look. They use detailed maps and study the geology ahead of time to be sure that the rocks in the area they hope to explore are the right age—and the right type—to contain dinosaurs. Then, they organize their expedition and begin the search.

They start by scanning the rocks around them for any little glint of bone or teeth. This is when luck kicks in. If the bone fragments paleontologists find on the surface have been exposed to wind, rain, and sun for too long, then their story will be forever lost to science. However, if paleontologists show up too early, then an ancient skeleton might still be locked below the surface.

Any tiny fragment of bone that paleontologists find has the potential to lead to an entire skeleton or a bone bed filled with many skeletons. Once they find that first fragment, they sprawl out and follow the trail to the source. Usually, the skeleton that yielded those bony fragments has long since disintegrated into dust through centuries of erosion and exposure. But sometimes paleontologists get lucky. Sometimes that little trail of bony fragments they collect will lead to something more complete.

Once the fossils are in hand, the work of understanding dinosaurs moves into the museum. There, the finds are archived, cataloged, studied, and exhibited. This is where large storerooms filled with row after row of fossils are found. Some of these discoveries might remain encased in the plaster jackets that allowed for their safe transport from the expedition site. Others are cleaned and conserved, ready for study.

Fossil preparators crack open the plaster to begin the painstaking work of cleaning each bone and then piecing together all those fragments. Think of this job as the most intense jigsaw puzzle ever—where every piece in the box is roughly the same color, some edges are broken, and you don't have a picture on the front of the box to guide you. It's a job for the patient and the observant. Preparators can spot the millimeter-thin connecting points between two tiny fragments and glue them back together to systematically rebuild a skeleton or skull.

And then comes the unveiling. One day, exhibit halls will teem with people who gaze in awe at those large jaws, sharp claws, and long dinosaur necks—some with spikes, frills, or armor. Paleontologists' continually changing understanding of dinosaurs provides ample opportunities for teaching about the nature of science thanks to the behind-the-scenes diligence and creativity of curators, students, and scientists. By developing and rigorously testing a hypothesis, a single discovery—or a new way of interrogating the data researchers have had for years—can, and does, completely change old ideas.

Because of all this work, dinosaurs are no longer the wild kingdom's clunkers of the old days. Since the late 1960s, almost everything we thought we knew about them has been transformed—from their relationships to each other to their lifestyles, behaviors, and even how they looked.

US AND THEM

It is through dinosaurs that many people experience their first connection to science. When we look at the bones of extinct dinosaurs, we're faced with a seemingly endless number of questions. What did they eat? What could they see? What did they sound like? What color were they? How fast could they move? This basic sense of wonder about their lives is the reason for at least some of their irresistibility. But our connection to dinosaurs goes much deeper.

When we contemplate the size of a newly discovered dinosaur relative to a school bus or think about how many millions of years ago that dinosaur hunted, we are pulling these dinosaurs into the modern era. We are considering them in relation to ourselves and the world we know and love today. In this way, dinosaurs embody the dramatic changes that life has undergone from then to now. They open the door to understanding that our planet has a deep history—that life back then was different from life right now and that it has been changing all along. And finally, they remind us that extinction is out there.

Unlike so many things of legend in our world, we can visit dinosaurs. And even better, since we have only their bones before us, dinosaurs ignite creativity and allow our imaginations plenty of room to roam.

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FINDING THE FIRST DINOSAUR BONES

Imagine living back before humans knew how rocks are formed. If you spotted something that looks like a bone sticking out of a hillside, you'd probably wonder what it was and how it got there. At different points in human history, many kinds of explanations were suggested to demystify the unusual novelty of fossils. But when did human explanations of the fossil record become more firmly grounded in science? When did humans develop a common lexicon for the discoveries of these bones in stones? To answer those questions, this lecture heads back to the 17th century, when the first diagram of a dinosaur bone appears in the published literature.

THE FIRST FINDS

Robert Plot was a naturalist, a chemistry professor, and the first keeper of the Ashmolean Museum at the University of Oxford. He was fascinated by the burgeoning study of natural history. He was especially interested in unusual rocks that bore strange resemblances to other things—including animals and even human body parts. Plot called these bizarre structures “formed stones.” He imagined that they were the result of God’s handiwork.

One of the most unusual pieces in Plot’s collection was a “formed stone” that resembled the knee joint of a human thigh bone, or femur. But this bone of stone was large, and Plot struggled to understand the implications of his find. He ruled out the possibility that this strange object belonged to a large mammal through a series of logical steps. In the end, he concluded that the bone must have come from the leg of a giant human. He included an illustration of this mysterious giant’s bone in a report that he published in 1677. He supported his contention with examples drawn from the work of Greek and Roman philosophers, who’d written on the evidence for giant humans.

Almost a century later, Plot’s original illustration was redrawn in a scientific treatise by Richard Brookes that included the use of natural objects—including fossils—in medicine. To Brookes, Plot’s specimen bore a striking resemblance to a pair of giant testicles. Thus, he went ahead and included a Latin description that identified the fossil as *Scrotum humanum*. Once humans finally uncovered the existence of dinosaurs, paleontologists would realize that this was the femur from a large-bodied carnivorous dinosaur.

The scientific pursuit of dinosaurs took off in the early 1800s, when the first few scraps of bones and teeth, encrusted in ancient sediments, were discovered by regular people. These were the bones of dauntingly large creatures that vanished from our world. No one knew how long ago these miraculous creatures walked the earth. Whatever the first finds of bones and teeth were, the animals we’d soon come to know as dinosaurs were spectacularly different from anything alive.

The study of dinosaurs got rolling by 1815. A couple of important discoveries helped fuel the excitement. French scientist Georges Cuvier had unlocked the power of comparative anatomy. He demonstrated that each major group of organisms had its own specialized body plan and that a body's function might be predicted by a study of form. For example, a sharp, serrated tooth could point to a carnivorous lifestyle. Cuvier also pushed the idea that life had experienced periodic, sudden catastrophes that were so significant that "the Thread of Nature's operations was broken by them." Such catastrophic intervals drove mass extinctions and pointed to a past Earth that was different from the present.

Meanwhile, the fossil frenzy was growing in England. There, the public's imagination was captured by the discoveries of a young woman named Mary Anning. Anning had unearthed an incredible swimming reptile from the cliffs at Lyme Regis. Anning's famous find would later be formalized as *Ichthyosaurus*, named from the Greek words for "fish" and "lizard." Anning later discovered another marine reptile, *Plesiosaurus*, along with some of the first known pterosaurs, or flying reptiles.

DINOSAUR #1

In the meantime, Reverend William Buckland was building his own collection of fossil bones of some large unknown animals from rock quarries near Oxford. He was a professor at Oxford, one of England's most prominent geologists, and the president of the Geological Society of London. Buckland collected part of a large lower jaw full of sharp, terrifying teeth; a handful of vertebrae; some pieces of a pelvis and shoulder; and a few bones from a hind limb. These bones came from a number of creatures of varying sizes. They were all enormous, seemingly from the same type of animal, and seemed to belong to a group akin to modern lizards.

Buckland wrote a report in which he described this collection of bones. This became the first formal description of a dinosaur—though that word was not coined yet. He named his newfound beast *Megalosaurus*, or "big lizard." He conjectured that the animal may have been more than 40 feet long and heavier than an elephant. Buckland used the anatomy of the jaw, with large, serrated teeth set into sockets, to interpret this creature as a carnivore. He also noted a few key differences that set *Megalosaurus* apart from being an overgrown lizard. The thigh bone of *Megalosaurus* was shaped so that its hind legs would fall directly underneath its body. This arrangement is distinct

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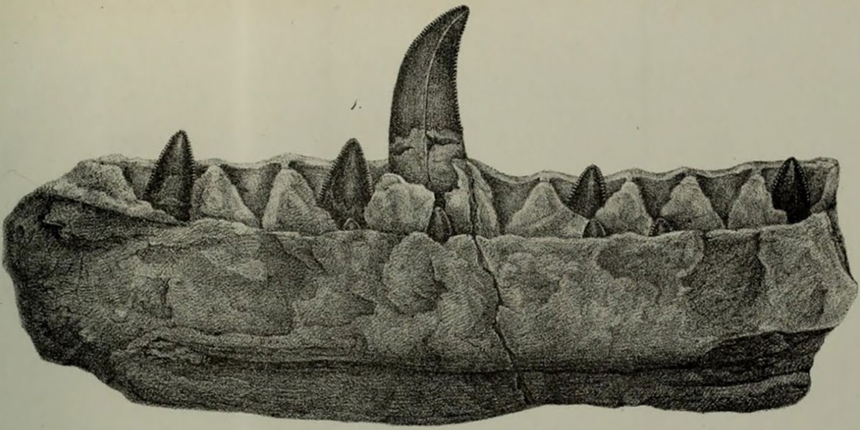

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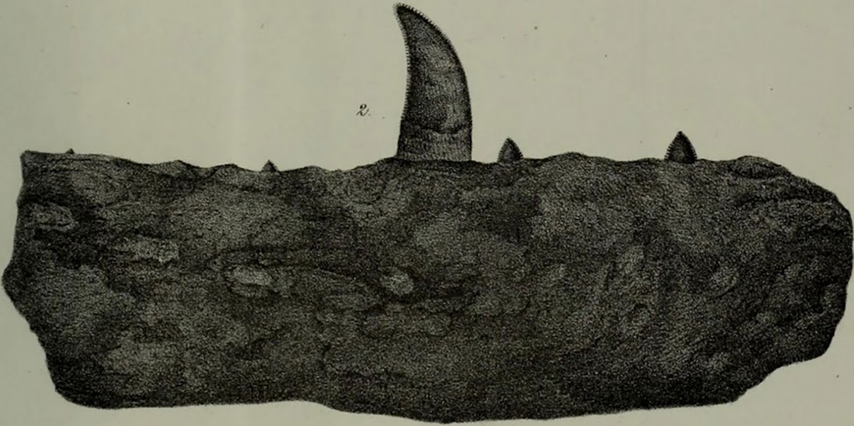

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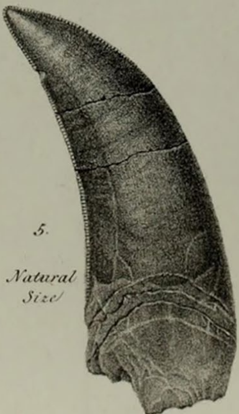

UNDER JAW AND TEETH OF MEGALOSAURUS.

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Scale 1/2 Inch to One Inch.

from living lizards, whose limbs sprawl out to the side. The legs and hips of *Megalosaurus* pointed to similarities with the more erect limb anatomy observed in living mammals and birds.

The handful of bones that Buckland described for *Megalosaurus* provided a first glimmer that something was different about this ancient, giant, land-living reptile. Plot's *Scrotum humanum* was later associated with *Megalosaurus* and given its proper genus and species designation.

DINOSAUR #2

Meanwhile, Dr. Gideon Mantell and his wife, Mary Ann, were making discoveries of their own in the English countryside. Gideon was obsessively collecting and analyzing fragments of bones for years before Buckland. The Mantells collected curious fossils in the sandstones near their home and discovered a number of bones of different fossil creatures, including a few specimens later attributed to Buckland's *Megalosaurus*.

As the story goes, the Mantells' first truly notable dinosaur discoveries occurred in 1822, when Mary Ann was killing time while her husband treated patients. The couple had recently completed work on a collaborative volume on the marine fossils they'd been finding in the area. Gideon was responsible for the descriptions, and Mary Ann provided the scientific illustrations. One day, Mary Ann spotted a couple of strange teeth in the gravel along a countryside lane. Gideon returned again and again over the next months in search of more fossil material. A few more teeth, along with a couple of bones, came to light as the summer went on. These turned out to be the teeth and bones of a second type of giant reptile, fundamentally different from the *Megalosaurus*.

Gideon spent several years tracking down comparative data and conferring with the expert comparative anatomists and geologists of the day. He noted the similarities of these strange, large, fossilized teeth to those of living herbivorous iguanas. He eventually interpreted these teeth and bones as those of a large, plant-eating reptile. He used the tools of comparative anatomy to extrapolate that an iguana with teeth of similar size would have been gigantic—maybe more than 60 feet long. Finally, in 1825, Gideon named his new fossil reptile *Iguanodon*, or "iguana tooth."

With the naming of *Iguanodon*, it became known that there had been herbivorous giant reptiles living alongside the ferocious, carnivorous *Megalosaurus*.

DINOSAUR #3

After roughly 10 years, Gideon Mantell's undying interest in fossils killed his business as a physician. His relationships with his wife and children became strained, and they eventually left him. His house was converted into a museum, but since he continually waived the entrance fee, Gideon was nearly destitute.

In 1832, Gideon purchased boulders dynamited from a quarry, each containing fossil bones. Each fragment he discovered could be reunited into a single, articulated skeleton. Until this find, all the earlier giant reptiles had been known only from isolated, fragmentary pieces. This new specimen included several spikes and plates lining the back that formed protective bony armor. Gideon called this new animal *Hylaeosaurus*, "the lizard of the wood," in recognition of the forest where the original bones were discovered. *Hylaeosaurus* indicated that another type of plant-eating creature—quite distinctive from the *Iguanodon*—roamed ancient England, providing additional food for *Megalosaurus*. Gideon's newest find represented the most complete skeleton then known.

FINALLY … DINOSAURIA!

By 1841, the ranks of ancient reptiles had swelled to include several additional creatures pulled from the rocks in England and beyond. Each newly named creature was a prehistoric tongue twister imbued with descriptive meaning: *Plateosaurus* meant "broad lizard"; *Cetiosaurus* meant "whale lizard"; and *Thecodontosaurus* meant "lizard with teeth in sockets." Enough fossil material had come to light that Richard Owen, a famous English comparative anatomist, had the requisite data to bring some order to this assemblage of ancient bones.

Owen scrutinized the fossils, paying particular attention to *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*. He observed traits in their skeletons that signaled a new, distinctive tribe of terrestrial reptiles. These reptiles walked with their legs held directly underneath their bodies, reinforced by the tight connection of the hip vertebrae to the pelvis. Owen noted that the posture of this new group of reptiles was more similar to that of mammalian quadrupeds. For this new group of animals, Owen proposed the name Dinosauria from the Greek words *deinos*, for "terrible" or "fearfully great," and *sauros*, meaning "lizard." Owen chose a word inherently signifying "lizard," though in his own estimation, these new reptiles were quite un-lizard-like. Owen even speculated that dinosaurs may have had a four-chambered heart more like those of mammals and birds and that dinosaurs exhibited "superior adaptations to terrestrial life."

A NOTE ON NAMES

The general rules for imparting a new moniker are pretty much the same for every newly named organism on Earth. They all follow some straightforward requirements that include a clear description of the features that distinguish the new organism from everything that has ever been named before. The science of naming organisms is called taxonomy. Paleontologists who are working on dinosaur taxonomy follow the rules laid out in the *International Code of Zoological Nomenclature*. Every new dinosaur name includes two parts: a genus name and a species name. Genus names are capitalized, but species names are not. When these names are written, they are italicized (or underlined).

Names say something important about how different organisms are related to one another. People usually think of the species as the smallest unit of biodiversity. A genus is a slightly more inclusive group, as it might contain multiple closely related species. For example, modern humans are of the genus *Homo* and the species *sapiens*. There are a bunch of other human species that are closely related to us that also fit within the genus *Homo*, like *Homo erectus* or *Homo neanderthalensis*. When grouping species within genera, researchers are assuming that these species are closely related to each other.

Consider this naming system in a little more detail, applied to dinosaurs. For the *Tyrannosaurus rex*, *Tyrannosaurus* is the genus name, and *rex* is the species name. Most of the time in casual vernacular, people shorten things up by calling dinosaurs by their genus names—think *Triceratops* or *Stegosaurus*. This usually works because, at least for dinosaurs, each genus often includes only a single species.

However, occasionally, researchers identify a new species that is pretty similar to one that has already been named. When that happens, they can place that new species within an already existing genus. Take, for example, the genus *Velociraptor*. The original species, *Velociraptor mongoliensis*, was first described and given a name in 1924. More recently, paleontologists identified a second, closely related animal that was distinctive enough to warrant a new species name: *Velociraptor osmolskae*. When being casual, you might call either of these closely related creatures *Velociraptor*. If you want to be more precise, however, you'd call them *V. mongoliensis* or *V. osmolskae*. This is often how people talk about *T. rex*, using the species name in casual conversation.

Those are the particulars of naming fossils. But how do scientists come up with the crazy names that they give to dinosaurs? Most paleontologists take this task super seriously. Dinosaur names have significance for the ways that scientists communicate with each other about their discoveries. They also drive public fascination and can spark new excitement about science that extends far beyond scientific circles.

Back in the olden days, it was easy to stick together Greek or Latin words that drew to mind something special or unique about the animal's anatomy, with that *-saur* suffix. Scientists often use the same method today because of the quick mental picture that a *-saurus* provides to broader audiences. That's how researchers created names like *Apatosaurus*, which means "deceptive lizard," because some of its bones reminded the scientist who named it of a different type of animal. Or *Pachycephalosaurus*, whose name refers to the solid (*pachy-*) head (*-cephalo*) of that creature.

But sometimes species are named after scientists who were key players in developing ideas in the field—like *Bonapartesaurus*, named for the prolific Argentinian dinosaur scientist José Bonaparte. Other times, dinosaurs take on species names that honor humans. *Masiakasaurus knopfleri* was named for the musician Mark Knopfler. The music of his band seemed to always be playing in the quarry when the bones of this carnivorous dinosaur were found. Dinosaur names have gotten even more creative and interesting as time has gone by. They often draw upon the languages native to the people who live in the area where the bones are discovered.

For example, paleontologists discovered two long-necked dinosaurs on the island of Madagascar. They elected to use the language of the people inhabiting the area of the discovery—Malagasy. When asked about the legendary giants in their native folklore, the inhabitants shared stories about a mischievous giant called Rapeto, so the genus name *Rapetosaurus* was given to one of the sauropods. The species name *krausei* was chosen to honor David Krause, the paleontologist who pioneered dinosaur research in Madagascar.

Evidence of the second sauropod was rare in Madagascar, so the discoverers concluded that it didn't spend as much time there as the *Rapetosaurus*. Therefore, the Malagasy word V*ahiny*, which means "traveler," was used for the genus name. Its species name, *depereti*, honors the first scientist to name dinosaur fossils from Madagascar: French paleontologist Charles Depéret. He described the first long-necked dinosaur bones from the basin way back in 1896.

ART THAT BROUGHT THE DINOSAUR WORLDS TO LIFE

Every paper that names a new dinosaur is accompanied by a press release that includes artistic representations of the animals "in the flesh." The first descriptions of dinosaurs were published in obscure publications, buried in government documents, or located in thick monographs that are almost impossible to find in the original version. The descriptive text, specificity of words, and detailed illustrations that accompany these original works are incredible. For example, when Buckland published his paper on the bones of *Megalosaurus*, he included five lithographed plates, which show every bone he described. He included imagery of both the inside and the outside of the jaw at half size. He also provided a life-size foldout of the inside view of the lower jaw to make an impression on his readers.

These technical art pieces provide paleontologists with the raw material for making their own comparisons down the road. The work of paleoartists provides a visual record of changing ideas about dinosaurs through time. Once Gideon Mantell had enough *Iguanodon* bones in hand to develop an artistic reconstruction, artist John Martin stopped by Gideon's museum and created a painting that he called *The Country of the Iguanodon*, finished in

1838. The painting is significant not only because it is the first full-body reconstruction of *Iguanodon* but also because it places *Iguanodon* within its surrounding world.

By the mid-1850s, when Dinosauria was a legitimate biological group that was widely known, Richard Owen decided that it was important for the general public to be invested in, and excited about, dinosaurs. He commissioned sculptor Benjamin Waterhouse Hawkins to create life-size concrete reconstructions of the prehistoric beasts. *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus* were included. Hawkins infused each with its own unmistakable individual style—the basic features that made each of these new celebrities recognizable to the casual observer. He included the spikes of *Hylaeosaurus*, the nose spike of *Iguanodon*, and the sharp teeth of *Megalosaurus*.

Before the exhibit opened, Hawkins hosted a dinner inside the *Iguanodon* sculpture, attended by Buckland, Gideon Mantell, and Owen. Ahead of sculpting each dinosaur, Hawkins worked closely with Owen to confirm details of the anatomy that underpinned his plans for each animal.

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THE EXTINCTION THAT LAUNCHED THE DINOSAURS

Before you can have a full understanding of dinosaurs, you have to go back to the beginning—back to the time when dinosaurs were not the rulers of their environments but were little reptiles running around at the feet of other, more dominant creatures. This lecture is all about the origin of the dinosaurs and the context in which they got their lucky break. Dinosaurs were born of multiple catastrophes, which resulted in their unlikely triumph in terrestrial ecosystems.

GEOLOGICAL TIME PERIODS

Geological time is a scale that was developed by relating layers of rock to life on Earth. These time scales are vast—on the scale of millions and billions of years. Researchers organize geological time according to major changes in life that inhabited periods before and after clear boundaries in the fossil record. In terms of dinosaurs, the most important time interval is the Mesozoic era. *Mesozoic* translates to “middle life.” The beginning and end of major intervals of time are marked by mass extinctions. These are geologically instantaneous events that wipe out many diverse life forms and change the world in a visible and tangible way in the fossil record. Major changes in the animal—or faunal—composition of life on Earth help in breaking vast periods of time into pieces that are more workable.

The Mesozoic era is divided up into three large time chunks. The oldest interval is the Triassic period. The middle interval is the Jurassic period. And the most recent, or final, interval is the Cretaceous period. Dinosaurs make their debut at the end of the Triassic period.

Time periods tend to be divided up by major mass extinction events. There have been five mass extinctions over the course of Earth’s history. Researchers call these events the big five. These are periods of time when an abnormally high number of organismal groups die off in a geological instant. The first two of the big five dramatically impacted marine life—that’s because most life on Earth at this time was living in marine ecosystems. Both of these mass extinctions resulted from rapid and intensive global cooling.

Extinction 3 occurred around 250 million years ago and marks the division of the older Permian period from the beginning of the Triassic period. That extinction is the most serious one that Earth has ever had. Around 95% of all life on the planet went extinct during this interval of time. Paleontologists call this event the Permian extinction, or the Permian-Triassic extinction. Extinction 4 occurred near the end of the Triassic period. These two mass extinctions bracket the story of the origin of dinosaurs, and they contextualize dinosaurs’ subsequent evolution.

ACT 1: MASS EXTINCTION (PART 1)

The curtain opens in the Permian period, more than 250 million years ago. During the Permian period, the supercontinent of Pangaea coalesced by bumping continents into one another and pushing up mountain ranges higher than the Himalayas are today. As those continents collided, the global climate changed dramatically. Ocean circulation patterns were altered. Land masses became more arid, more prone to drought, and much drier overall.

The animals that evolved and thrived during the Permian were pretty weird, such as sail-backed reptiles like *Dimetrodon* and *Edaphosaurus*. They are mammal-like reptiles, with skulls that have similarities on the inside linking them to humans in a long chain of evolutionary history. The Permian period was a time of large, strange amphibians, newly evolved small reptiles, and our own ancient ancestors. All these creatures were diversifying into this new world of the vast supercontinent of Pangaea.

But toward the end of the Permian period, something was brewing way up north, in what is now called Siberia. An interval of intense volcanism began to create geological features called the Siberian Traps. These ancient lava deposits are the result of flood volcanism. This occurs when magma rises close to the surface and heats up the crust, causing giant cracks to form and allowing lava to pour out over Earth's surface. These types of events have serious implications for the global climate. Similar events also warmed up Earth at two other times, including during the interval that ended up with dinosaur extinction.

Over a few tens of thousands of years, the Siberian Trap volcanism pumped out enough lava to cover more than 720,000 cubic miles in basalt deposits. Lava contains nasty chemicals—hydrogen sulfide, carbon dioxide, and ammonium—and those gases were building up in Earth's atmosphere as a result. When this happens, these types of compounds act like a thick, insulating blanket, trapping solar radiation close to Earth's surface and causing the global temperature to rise.

At the end of the Permian period, the global temperature kept rising, and that caused a cascade of events that changed living conditions everywhere. The average surface temperature of Earth got hot. The oceans got so hot that bubbles of methane gas, frozen in the mud at the bottom, thawed out and floated up to the surface. This created burps of methane, which contributed even more to the global temperature rise.

As this happened, oceans began to acidify. Thus, small marine microorganisms that built their shells out of calcium carbonate could no longer survive in the oceans. These little creatures helped to sequester carbon, but they stopped doing their job. As a result, carbon dioxide flooded the atmosphere. So many organisms went extinct in so many parts of the world that an ecological vacuum resulted.

However, there are always some organisms that survive extinction events, and they go on to repopulate all those ecological spaces that were once filled. When this happens, they undergo their own rapid evolution and diversification. These survivors form the blueprint for the life that comes later. In the case of the Permian extinction event, the recovery of animal diversity occurred relatively quickly—at least on a geological time scale. In about 5 million years, animals at the top of the food chain had emerged. But it took more than 50 million years for the underlying ecosystem to diversify.

ACT 2: WELCOME TO THE TRIASSIC

In the Mesozoic era, the Triassic period begins when the Permian period ends. The beginning of the Triassic period is marked by the survivors of the Permian extinction event radiating out into the empty world. The lack of competition made it possible for experimental body plans to evolve.

The earliest Triassic recovery fauna included some large amphibians and bizarre reptiles. It is here that the ancestors of our own lineage, the mammal-like reptiles called cynodonts, get their shot at stardom. The Early Triassic period is also where the ancestors of crocodiles, dinosaurs, and turtles first hit the scene. Among this group of strange, newly evolved reptiles were giant tusked herbivores and large, serrated-toothed carnivores. The survivors included some crocodile relatives that ran on dainty little legs. They also included others that convergently hit upon characteristics that would later make some dinosaurs famous. These included spikes on the shoulders, similar to the spikes that would later evolve in armored dinosaurs, and large, flattened, steak-knife-like teeth that would eventually evolve in carnivorous dinosaurs.

Fossilized footprints worldwide provide hints about the ways that animals walked in the postapocalyptic world of the earliest Triassic period. It seems that several beasts made footprints that demonstrate a less sprawled and slightly more upright stance than the reptiles that were most common in the Permian period. Maybe the survivors' slightly more upright posture indicates something important about their biology that helped them sneak through the extinction filter.

One of the most important and innovative groups to evolve in this decimated landscape was the archosaurs. Archosauria translates to "ruling reptiles." Archosaurs can be divided into two large "tribes." The first is the crocodilians and their close extinct relatives. This group is called the Crurotarsi—a name pointing to the crocodile-like anatomy of their hind feet and ankles. The other large group includes dinosaurs—including birds and their close relatives, the flying pterosaurs. This group is called the Avemetatarsalia, referencing the birdy nature of the feet and ankles of this lineage.

DIFFERENTIATING THE CRUROTARSI AND AVEMETATARSALIA

There are a ton of little bumps and holes in bones, and differences in bone shapes, that support the distinction of these two groups. But the most important anatomical difference lies in their ankles. These are easy to spot in the fossil record, and they also indicate different ways of locomoting that are unique to each group.

Consider the lower leg, ankle, and foot of a crocodile-line archosaur, or member of the Crurotarsi, and a bird-line archosaur, or member of the Avemetatarsalia. Both have a fibula and tibia. Below the tibia is an ankle bone called the astragalus. Then, there is a second ankle bone, called the calcaneum. Below that are a couple of other little ankle elements followed by toe bones.

There is an important distinction between the ways in which animals in each of these two tribes of archosaurs move their ankles relative to their toes. In the Crurotarsi, there is a little ball-and-socket joint that connects the astragalus and calcaneum. This joint means that they can rotate—or spin—relative to one another. This is important for the way that these animals walked. Remember, Richard Owen recognized that the key difference between dinosaurs and modern reptiles was a difference in the way their limbs move.

Consider the way that an alligator walks. It's kind of a sinuous, side-to-side slither, with all the limbs splayed out to the sides of the body. This means that every single time that a crocodilian takes a step forward, it needs to rotate its foot to continue to point forward. It does this through the rotational axis between the two ankle bones. That makes for excess flopping of the feet in crocodiles and their extinct relatives.

The Avemetatarsalia do it differently. In the ankles of dinosaurs and their close relatives, the plane of movement isn't through the ankle bones. It's beneath them—between the astragalus and calcaneum up top and the toes down below. Instead of a rotating ball-and-socket joint, the two ankle bones are essentially stuck together. There is only a tiny bit of wiggle between them. This unique organization imparts a hinge-like movement to the feet of dinosaurs and their close relatives. Along with the accompanying changes to the position of the hind limbs relative to the body, this special avemetatarsalian ankle sets these bodies up to evolve fast running.

When the Triassic gets rolling, it's the Crurotarsi that diversify rapidly and most thoroughly into the open ecological niches. These animals dominate the terrestrial ecosystems during the bulk of the Triassic. They get large and specialize. Some of them even convergently evolve features typically associated with dinosaurs. They essentially kept the dinosaur-line avemetatarsalians from controlling ecosystems—for a while.

ACT 3: MASS EXTINCTION (PART 2)

As the Triassic period drew to a close, the supercontinent of Pangaea was beginning to tear apart. When rifting occurs, volcanism ensues, and noxious greenhouse gases build up in Earth's atmosphere again. Just as Earth heated up in the Permian because of intense volcanism, the same was true during the end-Triassic period.

As South America and Africa began pulling away from North America, a tear in Earth's surface created a hot spot for volcanism known as the Central Atlantic Magmatic Province. This initial crack would eventually form the Atlantic Ocean, as the rifting created a low spot that became filled with salt water. The Atlantic today continues to get a tad wider each year. The European and African continents inch away from North and South America. New ocean crust forms at the mid-Atlantic spreading ridge, centimeter by centimeter.

The Triassic extinction event caused by increased CO_2 in the atmosphere is recorded in some interesting signatures left behind in the plant fossil record. During Late Triassic volcanism, as CO_2 built up in the atmosphere, the stomata that plants used to exchange gas were reduced in number or size. Since plants "breathe" CO_2, the more CO_2 in the atmosphere, the fewer stomata plants must have on their leaves to get the same amount of gas into their growing bodies. Thus, this extinction is recorded in the fossils of leaves from this time.

The Late Triassic global warming event signaled troubled times for the specialized, large-bodied, ecologically narrow Crurotarsi. Another mass extinction took tons of that diversity down. In the end, only one group of Crurotarsi survived in any great numbers—the crocodile ancestors that gave rise to the group that thrives on Earth today.

ACT 4: DINOSAURS ON THE LOOSE

In every extinction event so far, there were always survivors—but researchers don't usually know why. Those survivors restock the empty ecosystems with new life. The ancestors of pretty much every group known of in the modern world passed through the end-Triassic extinction. The ancestors of crocodiles, pterosaurs, dinosaurs, mammals, modern amphibians, lizards, and snakes are the new players on the stage now.

In this new world, dinosaurs become diverse quickly. In the Late Triassic period, when dinosaurs first show up, their body plans are pretty basic. They start out as small bipedal carnivores. This basic dinosaur blueprint from 230 million years ago is found in rocks in the foothills of the Andes in Argentina, in a sedimentary unit called the Ischigualasto Formation.

Not long afterward, dinosaurs with new styles of hip anatomy, a diversity of different basic body plans, and different dietary strategies emerge. Dinosaurs travel along as continents rift apart, evolving and diversifying throughout the rest of the Mesozoic. In the geological blink of an eye, it seems that dinosaurs radiate around the globe.

The immediate ancestors of dinosaurs already had some key specializations of the ankles and hind limbs for running more quickly. Early dinosaurs may also have had specializations for feeding and for breathing more efficiently than other kinds of reptiles at the time. Maybe they were warm-blooded? Maybe they grew differently than other animals? These ideas are testable with the available data gleaned directly from the bones of the earliest dinosaurs.

The basic anatomy of bones persists in the fossil record. Though the blood vessels and cells disappeared long ago, the holes and tubes that housed these soft parts remain. They reveal growth patterns that paleontologists can directly compare with the same structures in modern animals.

Considering whether the earliest dinosaurs grew differently than other kinds of animals, paleontologists have been sampling the bones of the earliest dinosaurs and their compatriots, all from the Ischigualasto Formation. The dinosaurs that inhabited this ecosystem included three smallish carnivores—*Herrerasaurus*, *Eodromaeus*, and *Sanjuansaurus*—and a few early herbivores—*Eoraptor*, *Chromogisaurus*, and *Pisanosaurus*. These animals lived side by side with many of the Crurotarsi, giant amphibians, and mammal-like reptiles. Thus, they offer a perfect opportunity to compare growth patterns recorded in the bones of various organisms inhabiting the same ecosystem. The results so far indicate that dinosaurs may have exhibited a couple of key differences in their growth strategies compared to other animals in the Ischigualasto Formation. These differences may have given them a leg up early in their evolutionary history.

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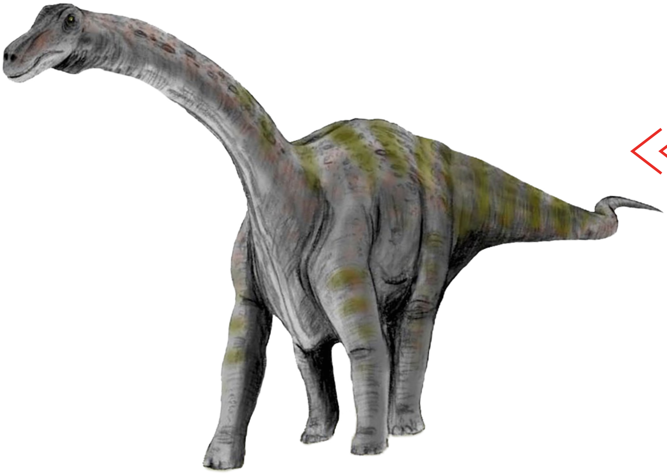

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THE SAURISCHIA: SHARP TEETH, LONG NECKS

When Richard Owen coined the term Dinosauria in 1842, he knew of only a handful of animals that fit within this new group. Since then, the number of dinosaurs discovered has ballooned to more than 300 genera and 900 species. Humans tend to look for common, shared characteristics to group together things that are most like each other. This is all a part of taxonomy. In this lecture, you will learn about the ways in which paleontologists divvy up dinosaurs.

DINOSAUR DIVERSITY

Remember that the age of dinosaurs is usually considered to be the large geological time period called the Mesozoic era. This gets further subdivided into three smaller chunks of time. The oldest time chunk is called the Triassic period. It began around 250 million years ago and ended around 200 million years ago. Dinosaurs originated in the Triassic, around 230 million years ago, and their first known fossils come from the Ischigualasto Formation in Argentina. In the Triassic world, the continents were still mostly connected together in the giant landmass called Pangaea. During the Triassic, the continents began to drift apart, gradually separating over millions of years. These rifting events were key to promoting the evolution of dinosaurs, allowing them to rapidly spread across the globe.

In evolution, the more the environment changes, the more organisms can diversify in response. The next period of the Mesozoic is the Jurassic. The Jurassic period began around 200 million years ago and concluded by about 145 million years ago. By this time, the Pangaea supercontinent has been divided into a northern-hemisphere landmass called Laurasia and a southern-hemisphere landmass called Gondwana.

Another important thing to watch while moving through these geological time periods is the amount of ocean. At the time, there were no polar ice caps. That's because the entire Mesozoic era was warmer than Earth today. Thus, there was more liquid water on Earth, which contributed to flooding of the continents. You can easily see this in Jurassic-age Europe—and it plays an important role in the Cretaceous period.

The Cretaceous period is the most recent block of the Mesozoic era. It began around 145 million years ago and ended with the mass extinction of dinosaurs 66 million years ago. The end of the Cretaceous period marks the end of the age of dinosaurs and the end of the Mesozoic era.

Regarding the continents, there were a number of changes yet to come that followed the extinction of most dinosaurs. For example, India began a rapid northward drift, eventually bumping into Asia and crumpling up the land ahead of it into the Himalayas. Moreover, North America was divided into two regions by a continental seaway. This was basically due to a little finger of the Arctic Ocean and a little finger of the Gulf of Mexico meeting up at around Kansas. All this extra ocean provided the same kind of evolutionary opportunity for marine reptiles that the ever-changing landmasses provided for dinosaurs.

Since dinosaurs originated when landmasses were stuck together, they drifted throughout their evolutionary history along with the continents. This means that paleontologists even find dinosaurs in rocks from the polar regions of the world. Dinosaurs have been found in Cuba, Romania, Russia, Tibet, China, Brazil, Madagascar, and India.

At the most recent count, there are more than 900 dinosaur species known. No doubt there are many more out there left to discover. In fact, there are probably even more dinosaurs that paleontologists will never know about. With all these dinosaurs, researchers need a way to talk about them that is clear and consistent. Thus, they focus on obvious, recognizable features.

DIVVYING UP DINOSAURS

When trying to divide this monolithic group of Dinosauria into more manageable subgroups, the best place to begin is to look at their hips. Like dinosaurs, we humans have a total of six bones in our hips—three on each side. All these bones fuse together as we age to support our hind limbs and our guts. Our hip bone is called the ilium. This bone is in the same position as in a dinosaur. The bone at the front of the hip, in the crotch area, is the pubis. Since we give live birth to our young, this bone retains a flexible cartilaginous connection to allow a baby's head to pass through on the way out. The third bone is close to our lower back—this is the ischium. In dinosaurs, the ischium is closer to the tail and points backward, but it is basically the same as it is in us. Where these three bones meet in our bodies and in the bodies of dinosaurs, they form the hip socket, where the thigh bone, or femur, plugs in.

In dinosaurs, there are two basic varieties of hips. There is the saurischian, or "lizard-hips," pelvis, where the ilium points up toward the sky, the pubis points forward toward the head, and the ischium points back toward the tail. This is a triradiate hip, where all three hip bones point in different directions. Another arrangement is where the ilium stays pointing up toward the sky.

The ischium is still pointing backward toward the tail, but the pubis has been rotated backward so that it's aligned parallel to the ischium and also points back toward the tail. This bidirectional hip style, where bones only point up and back, is the ornithischian, or "bird-hips," pelvis. As a result, there are two great "tribes" of dinosaurs that can be distinguished by looking at their hip anatomy: the Saurischia and the Ornithischia.

The anatomy of the hips is sort of similar in the Ornithischia dinosaur group and birds, but this is the result of convergent evolution. These groups independently evolved a superficially similar hip structure. In fact, the moniker Ornithischia was developed long before paleontologists knew that the true ancestors of today's birds are the lizard-hipped Saurischia. The same thing can be said for the moniker *lizard hips*. Saurischians aren't more closely related to lizards. They have a general similarity that made early scientists recall the hips of other kinds of reptiles.

In addition to their hips, saurischian dinosaurs all have several things in common. They have long necks. They have extra connections between each vertebra that impart a slight rigidity to all that length. And their neck bones are porous; thus, they're filled with air. Although some of these bones can be large and the necks of all saurischians are pretty long, they are lightweight. That makes it easier for these giant dinosaurs to have relatively lightweight bodies.

Saurischians are easy to spot among the dinosaurs. The saurischian body plan is the first body plan on the scene, showing up more than 230 million years ago, and is the most abundant one in early dinosaur evolutionary history. Saurischians include three large groups, which you can think of as predators, weird herbivores, and giants. The first is the Theropoda group, which translates to "beast foot." These are the predators, including *Megalosaurus*, *Allosaurus*, and *Tyrannosaurus*. The Theropoda group includes all meat-eating dinosaurs and nearly all feathered dinosaurs. Birds evolved from this group.

The second group is called the Prosauropoda, which translates to "before the lizard-footed." Prosauropods sometimes walked on two legs and sometimes on four legs. Some of them were herbivores, while others were omnivores. The Prosauropoda group includes famous animals like *Massospondylus*, a dinosaur that is common in Early Jurassic rocks in Africa, and *Plateosaurus*, a European prosauropod known from hundreds of well-preserved skeletons.

Finally, the third group is the Sauropoda. This name means “lizard foot” because the members of this tribe have five fingers and toes. Scientists think that sauropods evolved from one group of larger prosauropods. The sauropods are exclusively herbivorous. They are the giant, long-necked dinosaurs. Examples of these include *Apatosaurus*, *Brachiosaurus*, and *Diplodocus*.

THEROPODA

Theropods have a few key features that they share: bipedal running, grasping hands, specializations for feeding, and beautiful feathers. Theropods have adaptations in their hips, hind limbs, and feet for bipedal running. Their hands are especially well suited for grasping. This means that throughout their evolution, the number of fingers that they have tends to be reduced from the ancestral five to usually only two or three. The ends of these fingers are tipped with recurved, sharp claws, which are perfect for holding onto potential prey.

Theropods also exhibit specializations of their teeth, jaws, and faces that point to their strategy of being fearsome carnivores. First, they have serrated teeth. A theropod tooth exhibits a cutting edge with serrations that help increase the surface area of the tooth, which makes them more efficient at slicing and cutting through meat. Another important modification related to feeding occurs in the skulls of many theropod dinosaurs. Therapods—and some other dinosaurs—have a bunch of bones that can move a little bit relative to one another. This feature is especially important in theropods, which had a sliding joint in their lower jaw that allowed them to increase the gape when opening their mouths. This means that they could accommodate larger chunks of food with each powerful bite.

Finally, several groups of theropod dinosaurs—including the one that eventually gave rise to the birds—evolved feathers. Theropods have a fuzzy body covering that occasionally gets preserved in the fossil record. *Sinosauropteryx* was one of the first dinosaurs discovered that preserved evidence of feathers. Since then, many more specimens have come to light. A dinosaur from China, *Yutyrannus*, was preserved with eight-inch-long downy feathers. *Yutyrannus* was pretty large—about 30 feet long from head to tail. This indicates that feathers were present long before there were birds and that, originally, having feathers was decoupled from flying. It was only later on, when some theropods evolved smaller body sizes and true wings, that flight was possible in this lineage.

Theropods are incredibly diverse. They can be giant, and they can be tiny. If you see any dinosaur that looks like it has sharp teeth, grasping hands, running legs, or feathers, you can be pretty sure that you are looking at a member of the Theropoda group. For instance, tiny *Eodromaeus* was one of the first dinosaurs on Earth. It was discovered in the Ischigualasto-Villa Union Basin of Argentina and already exhibits the key features that place it firmly within Theropoda. Its name translates to "dawn runner." This helps paleontologists remember that early dinosaurs were tiny, bipedal, carnivorous runners.

Theropods also scale up. One of the largest is *Giganotosaurus*, discovered in Cretaceous-period rocks in Argentina. This guy was even larger than *T. rex* and is estimated to have been around 40 feet long from head to tail. Theropods also scale way down. Because all living birds are evolved theropods, technically, hummingbirds are probably the smallest dinosaur ever. But don't forget about all those other living dinosaurs, from owls to eagles to ostriches and penguins. This is the only group of dinosaurs that survived the mass extinction that snuffed out the other dinosaur groups.

Animals like *Velociraptor*, made famous by the *Jurassic Park* book and movies, were theropods. Paleontologists now think that this group of theropods likely had feathers. Another dinosaur made famous by *Jurassic Park* is *Dilophosaurus*, the venom-spitting dinosaur with the neck frills from the film. (However, there is no evidence of frills or venom in any dinosaur.) Despite the film's artistic depiction, there's no doubt that *Dilophosaurus* was an early theropod.

PROSAUROPODA

Next is the strange group of early dinosaurs called the Prosauropoda. This group includes some of the oldest dinosaurs and the first dinosaurs to get pretty large. They were also the most common herbivorous dinosaurs in the Late Triassic and Early Jurassic periods. Prosauropods share relatively small heads and long necks and tails, with a barrel-shaped body in between. They could walk on two legs or all fours. They had five fingers and evolved a large claw on their thumbs. They were the first group of dinosaurs that evolved herbivory. It's likely that for this group of animals, all these features were intertwined and related to their herbivorous lifestyle.

The skulls of prosauropods were filled with little leaf-shaped teeth. These teeth don't show any signs of chewing. Paleontologists hypothesize that their barrel-shaped bodies may have been perfect vats for digestion. The thumbs of prosauropods were nearly opposable. They may have used their large thumb claw to procure vegetation and draw it into their mouths.

One of the coolest specializations in prosauropods is facultative bipedalism. This simply means that this group of dinosaurs sometimes walked only on their hind legs but could also drop down to their hands to walk on all fours. As prosauropod body sizes increase, these animals evolve a more quadrupedal body plan. However, the most common prosauropods have skinny front arms and meatier legs, reflecting their more common bipedal stance.

One of the amazing things about prosauropods is how quickly they radiated across the planet. By the earliest part of the Jurassic period, a diverse array of prosauropods is found on continents as widespread as Antarctica, Europe, Madagascar, Asia, North America, and South America. In part, it is this worldwide distribution that makes them challenging to study. Since they tend to look pretty similar, it can be hard to distinguish the different genera and species.

Two of the most famous prosauropods, *Massospondylus* and *Plateosaurus*, are also perfect models of the prosauropod body plan. *Massospondylus* is well known in the Early Jurassic rocks of southern Africa. The first fossils of *Massospondylus* were described back in 1854 by Richard Owen. He named this animal on the basis of its comparatively long neck vertebrae. Ongoing discoveries yielded information that eventually led to speculation that *Massospondylus* didn't spend much time on all fours and that its short arms may have been particularly useful for swatting off predators. One of the most exciting *Massospondylus* discoveries was a nest of eggs containing nearly full-term embryos in South Africa. This provided new information indicating that *Massospondylus* probably cared for nest-bound hatchlings until they doubled in size.

Plateosaurus looks like *Massospondylus*—a little nondescript, with a long, slithery neck and smallish head. It's usually depicted standing on only its hind limbs. However, based on preserved tracks, it also walked on all fours. *Plateosaurus* was originally discovered back in 1834. It was only the fifth named dinosaur genus. It is well known from Europe and Asia in Late Triassic rocks. As with other prosauropods, the broad barrel chest of *Plateosaurus* provided plenty of room for a large digestive system and a serious pair of lungs.

The prosauropods went extinct during the Early Jurassic and are the first recorded extinction of a major dinosaur group. Some paleontologists hypothesize that they may have been pushed to extinction as even more efficient herbivores hit the scene.

SAUROPODA

The final group of saurischian dinosaurs is the Sauropoda. The sauropods are the behemoths of the dinosaur world—immense, long-necked, long-tailed, four-legged herbivores. All sauropods were humongous as adults, even though they hatched from eggs that were about as large as a softball. Even the smallest known adult sauropods were larger than an elephant. The Sauropoda group includes animals that grew up to 115 feet long from head to tail.

Moreover, the sauropod body plan evolved early in the reign of dinosaurs. Paleontologists find these large animals in the Late Triassic fossil record. This body plan stuck around, with only minor modifications, until the Mesozoic period ended with a bang. Even though sauropods sometimes serve as icons for extinction, they are among the most successful and most remarkable group of dinosaurs.

Even though *Sauropoda* translates to "lizard foot," sauropods are quite different than lizards. In fact, they are more like birds and mammals—in the way they grow, the way their limbs are organized, and even the way they breathe. The long necks of sauropods were permeated with air sacs that lightened the load of the lengthy neck and increased the surface area for the absorption of oxygen. Sauropods were eating machines. They had relatively simple teeth that were constantly being replaced throughout their lifetime, as they spent most of their time feeding. Interestingly, each major group of sauropods modified the standard sauropod body plan with little embellishments—including a whiplike tail, large noses, and even armor plates in the skin.

The longest animals to ever live on land are sauropods like *Diplodocus*. Known from fossils discovered in western North America, *Diplodocus* had a specialized whiplike, elongated tail. In the longest *Diplodocus* ever found, the tail alone is more than 60 feet in length. The teeth of *Diplodocus* were shaped like little pegs. This indicates that this giant creature did virtually no chewing of the vegetation that it ate. Instead, its teeth were used to rake vegetation off branches and stems before swallowing. The hard work of digestion happened in its gut rather than in the mouth.

Another great example of a sauropod is *Brachiosaurus*, which is often considered the tallest known dinosaur. Some estimates indicate that *Brachiosaurus* may have been able to hold its head nearly 60 feet up in the air. Finally, *Rapetosaurus krausei* was a member of a group of armored, globally distributed sauropods called the Titanosauria, or "titanic lizards." The group includes the largest sauropods ever to walk the earth. *Rapetosaurus* was an important discovery. For most of paleontological history, these titanosaurs were poorly understood. Though paleontologists knew they inhabited every continent, only a few fossils were found. However, working in the field in northwestern Madagascar, a group of paleontologists discovered a complete skeleton of a new species of titanosaur. Since its discovery, *Rapetosaurus* has been like a key that has opened up paleontologists' understanding of this late surviving group of dinosaurs.

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THE ORNITHISCHIA: ARMOR, THICK HEADS, HORNS

The Ornithischia dinosaurs are known for a different arrangement of their hips. They still have three bones that meet each other to form the hip socket. They still have the ilium pointing up toward the sky. And they still have the ischium pointing backward toward the tail. However, the pubis has turned and rotated backward so that it lies in parallel with the ischium and points toward the tail. This rotation of the pubis is tied to a change in the way that the tail connects to the hips in both birds and the ornithischian dinosaurs. These distantly related groups evolved this feature independently. It is probably linked to the changing muscle mass in the tails of both groups. The ornithischians are also known for their weaponry and display features, and they are super specialized for herbivory. This lecture will introduce you to the different species of Ornithischia.

THE ORNITHISCHIA

Take a simple example of how herbivory shows up in the fossil record. In ornithischians, the teeth are inset from the jaws—like in humans. Human molars are inset a little closer to the tongue rather than out near the edges of the jawbone. We also have cheeks that help hold food within our mouths while we chew.

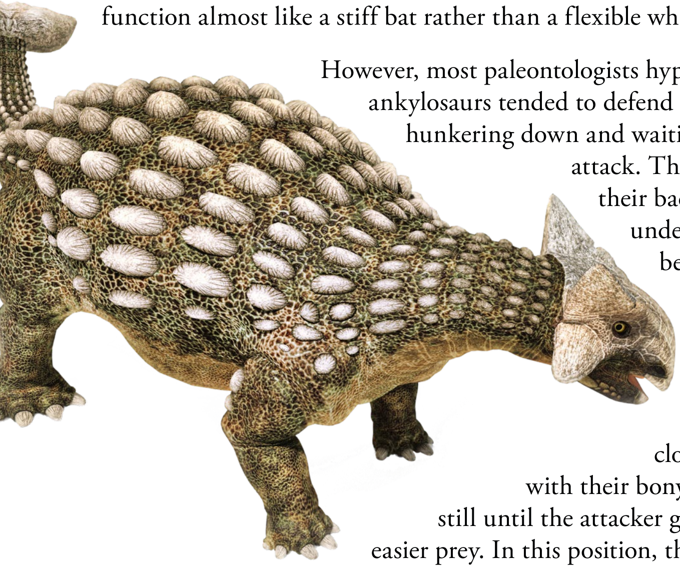
Though they didn't have molars, many ornithischians did some in-mouth processing of their food—chewing or grinding or slicing—before swallowing. Having that inset row of teeth allows space for skin or a muscular cheek to help them keep food in their mouths in the same way. This is another significant ornithischian innovation. It helps paleontologists distinguish their jaws and teeth from the more basic organization seen in the saurischian herbivores—the prosauropods and sauropods, which swallowed their vegetation down with little to no in-mouth processing. Instead, they relied on downstream specializations of the intestine to help digest all that tough plant matter. Many of the ornithischian groups also exhibit a bony beak at the front of the lower jaw that is overlain by a keratinous covering, similar to the beaks of living birds. This feature helped them selectively snip vegetation.

There are many ornithischian groups. They comprise a wild menagerie sporting plates, spikes, horns, frills, bills, bony domes, tusks, and armor. Paleontologists think that many of these features are related to the social lifestyles of these groups. Many of them spent time with other members of their species. This meant building elaborate structures to help attract mates, repel rivals, and protect one another. Paleontologists think that many of these features are secondary sexual characteristics that show up only at puberty and identify males and females. Their features reflect these ideas about sexual selection, female choice, and sociality among these beautiful dinosaurs.

There are five large groups of Ornithischia. Ankylosauria is known for armor and tail clubs. Stegosauria is known for plates and spikes. Since these groups share the elaboration of bones that grow in the skin, paleontologists know that they are close relatives. Ceratopsia includes all the animals with nose and eye horns and frills made up of the bones on their forehead and on top of the skull. Pachycephalosauria is the bone-headed dinosaur group. The bony domes of pachycephalosaurs are made up of the same bones that ceratopsian frills are. Thus, paleontologists usually lump these two groups together as close relatives among Ornithischia. Finally, there are the Ornithopoda dinosaurs. This group includes the duckbilled dinosaurs and their relatives.

ANKYLOSAURIA

Some ankylosaurs had a fearsome tip-of-the-tail club that they could swing around with great force to fend off potential predators—and maybe rivals of their own species. These tail clubs came in different shapes and sizes. The tail vertebrae in front of the club were often fused together. This made the tail function almost like a stiff bat rather than a flexible whip.



However, most paleontologists hypothesize that ankylosaurs tended to defend themselves more by hunkering down and waiting out an incoming attack. Their armor is only on their backs, meaning their underside still would have been quite vulnerable. Instead of fighting, ankylosaurs may have simply laid down, pulled their arms and legs in close, closed their eyes with their bony eyelids, and kept still until the attacker got bored and found easier prey. In this position, they'd be a nearly impenetrable mass of bone.

STEGOSAURIA

Like ankylosaurs, members of Stegosauria also have elaborate osteoderms that decorate their bodies in the form of thin, flat bony plates sticking up from the back, along with spikes, usually on the tail. *Stegosauria* is derived from the Greek words for "roofed" and "lizard." This group includes *Stegosaurus*.

Since each genus of stegosaur had a different array of plates and spikes on its body, it's easy to tell one stegosaur from another. In early members of the group, the plates were pretty small and often paired. In later members of the group, the plates were tall and alternated their position from left to right down the spine. Some stegosaurs even had vicious-looking spikes sticking out from their shoulders or following the plates along the back.

Unlike the plates, the tail spikes of stegosaurs are always pointy. All stegosaurs share at least one pair of spikes sticking out sideways at the end of their tails. And in stegosaurs, the tail was mobile, allowing a wide range of motion for swinging that spiked tail back and forth as an impressive weapon.

PACHYCEPHALOSAURIA

Pachycephalosaurs are the awesome, bipedal, bone-headed dinosaurs. Their name derives from the Greek for "thick-headed lizards" and pays homage to their skulls, which can be more than six inches thick. These bony domes are built from an elaboration of two bones of the skull: the frontal, equivalent to our forehead, and the parietal, equivalent to the bone at the top of our skulls. Unlike human skulls, though, pachycephalosaur skulls are mostly bone. Their modest little brains were buried deep inside that thick covering.

Many pachycephalosaur species further elaborate their heads with a ring of little bumps and spikes. Explanations for the functions of these bumps have included that they were the result of disease or that they were employed as battering rams. More recent work has pointed to the relative fragility of these bony bumps. This may suggest that they are all about attracting the ladies.

CERATOPSIA

Closely related to the pachycephalosaurs are ceratopsians. The Ceratopsia group is named from the Greek for one of these dinos' most recognizable features—they are, collectively, the "horned faces." With the bony frill sweeping up behind their skulls and sharp, pointy horns poking up from the nose and above the eyes, the *Triceratops* "three-horned" beast is easy to recognize.

Ceratopsians also take the specializations for herbivory to new extremes. Like all other ornithischians, they have a bony beak on their bottom jaws. However, all ceratopsians have an extra bone at the front end of their upper jaw. This extra bone is in front of the bone called the premaxilla. Like in humans, in most dinosaurs, this is the only bone at the front of the mouth. It is the bone that holds our front teeth, the incisors. In all other backboned animals, the right and left premaxillae meet each other in the middle. But in ceratopsians, they connect instead to a single, midline bone shaped like a little triangle. This bone is called the rostral bone. In ceratopsians, it builds a true beak that makes these dinosaurs look like they have a parrotlike mouth.

Ceratopsians also innovate a new way of organizing the teeth farther back in the jaws. They have a literal conveyor belt of teeth that are packed closely together so their tops form a continuous surface. Therefore, when the ceratopsians close their jaws, the teeth act like giant grinding scissors.

The Ceratopsia evolved toward the end of the Mesozoic and were around for only about 15 million years before the great extinction. Even so, they diversified into a wide array of forms, most easily identified by the variety that their horns and frills take—built from the bones of the forehead, top of the skull, and cheek.

The horns of ceratopsians vary from species to species. Some are simple lumps on the scale of inches while others can be longer than five feet. In life, these horns and the frill would have been covered by a layer of keratin. Ceratopsian horns likely had multiple purposes, including species identification, battling with other members of their own species, and fending off predators. Modern horned animals use these structures for the same diverse behaviors.

ORNITHOPODA

The Ornithopoda dinosaurs are the duckbilled dinosaurs and their close relatives. Ornithopoda includes a wide range of differently sized herbivores. This group was originally named for the dinosaurs' three-toed, birdlike feet. However, a more appropriate name would probably have referenced their mouths instead.

Like most ornithischians, all ornithopods have a beak in the front of their jaws, but it's different from the beaks of ceratopsians. Instead of an extra bone at the front of the upper jaw, in ornithopods, the front of the upper jaw dips forward to stick out a little—kind of like a duck's bill. The changing arrangement of the jaws imparts a powerful bite in this group of dinosaurs. Ornithopoda includes little, bipedal, tusked, beaked herbivores as well as large animals that needed to drop down to all fours to support their massive bodies.

Hypsilophodon, a kid-sized dinosaur, was a speedy little runner. It used chisel-like back teeth to help grind food in its mouth. The first discoveries of *Hypsilophodon* occurred in England in 1849, making it one of the first dinosaurs ever found. Since then, it has become incredibly well known, with skeletons representing all ages.

Iguanodon is also an ornithopod. Fossils of *Iguanodon* were a critical piece of Sir Richard Owen's argument that paleontologists needed to coin a new term for this group of strange, giant reptiles in 1842.

It's from these groups of ornithopods that the last and most renowned group of ornithopods stem—the iconic duckbilled dinosaurs known as hadrosaurs. Like other ornithopods, these dinosaurs are well known for their plant-eating prowess. And similar to ceratopsians, hadrosaurs evolved a dental battery of cheek teeth and became experts at chewing their food. Many members of the group exhibit elaborate crests atop their skulls. The crests of hadrosaurs are built from their nose bones. These elaborate crests help paleontologists identify different hadrosaur species and likely were not only for show. Since they were filled with convoluted air-filled labyrinths, they would have served as perfect resonators for making sounds.

TOOLS IN YOUR TOOL KIT

Note that there are many animals that lived alongside dinosaurs that people lump in with the group—even though many of these creatures don't belong there. For example, take certain swimming reptiles. Even though all these animals inhabited the marine waters of dinosaur worlds, they are not even remotely related to dinosaurs. Instead, mosasaurs, plesiosaurs, and ichthyosaurs represent three different instances of terrestrial vertebrates returning to the sea and adapting to a fully aquatic lifestyle. These animals are marine reptiles. All three of these animals are far more closely related to lizards and snakes than they are to dinosaurs.

Now consider the pterosaurs—the flying reptiles. These animals are definitely not dinosaurs either, although they are much more closely related. They walk with their legs a little more under their bodies, kind of like dinosaurs. But these flying reptiles are the first group of backboned animals to evolve flight. They are super weird, with a wing that is built from a membrane that hangs from their ring finger down to their hip or ankle. They also have strange adaptations of their tails and skulls for flying.

And finally, mammal-like reptiles were not dinosaurs either. This type of animal was extinct long before dinosaurs showed up. Some of its relatives live on Earth today. Mammal-like reptiles have a specialization of their skulls that makes them closer to humans than to dinosaurs. Even though they are scaly and look fierce like theropods, the sprawling posture of their hind limbs shows that they stand like lizards and not at all like dinosaurs.

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HOW ROCKS REVEAL DINOSAUR SECRETS

Changing geography drives environmental change, and environmental change drives evolution. When paleontologists find dinosaur fossils, they can get clues to the dinosaurs' evolution by also examining their environment as it was preserved in rocks. Part of being a dinosaur paleontologist is thinking about things that happened a long time ago, in environments that looked very different from the way they do today. This requires thinking in terms of geological time. To this end, this lecture compares *T. rex*, *Stegosaurus*, and humans.

GEOLOGY AND DINOSAURS

T. rex and *Stegosaurus* lived farther apart in geological time than the length of time between *T. rex* and humans. *Stegosaurus* was running around in the Jurassic period, about 150 million years ago, while *T. rex* was on the prowl in the Cretaceous period, about 66 million years ago. That's a difference of roughly 85 million years. Since we live now and *T. rex* lived 66 million years ago, that means *T. rex* lived about 20 million years closer to us than it lived to *Stegosaurus*.

During its 4.6-billion-year history, Earth has undergone some dramatic changes that both created environments hospitable to life and destroyed them. Occasionally, life gets knocked down via geologically induced environmental changes that force mass extinctions. At the same time in human history that the field of paleontology was beginning to stand on its new, shaky legs, another discipline, geology, was also being born. It is no surprise that these fields grew together.

A significant and relatively recent discovery in geology was that the continents have moved around over the course of Earth's history. This is all because of what lies beneath our feet, deep under Earth's crust, where internal heat and convection drive the formation of new oceanic crust and the subduction of old crusts at the margins of continents. This is the study of plate tectonics. Plate tectonics is the ongoing process that has resulted in the dramatic movement of continents—sometimes crashing into one another, sometimes pulling apart.

Earth's internal heat engine results in a sequence of rock formation and destruction called the rock cycle. Three different types of rocks result from this cycle. Igneous rocks are formed from the cooling and crystallization of liquid magma as it comes close to the surface. Sedimentary rocks are formed from the breakdown of other types of rocks into tiny particles, or sediments. And metamorphic rocks are heated and pressurized igneous or sedimentary rocks that recrystallize at high temperatures. Only two of these are relevant in the context of studying dinosaurs: Sedimentary rocks are the archive of the dinosaur fossil record, and igneous rocks allow paleontologists to precisely date how long ago dinosaurs lived.

DEPOSITIONAL ENVIRONMENTS

Igneous rocks don't usually yield fossils—any dead stuff would burn up in the molten lava. The fossil record is built only in specific sedimentary environments. As a result, when you consider the record of life on Earth, the reality is that it is limited in scope, forming only where sediments are accumulating and burying dead things on the surface. Fortunately, sedimentary environments are highly varied, from deserts—where wind is blowing sand around—to alluvial fans, lakes, rivers and their floodplains, and the marine environments out in the oceans, where water is carrying sediment and depositing it in low spots called basins. Together, all these places are called depositional environments.

Desert or windblown sand environments are called eolian depositional environments. These are excellent places to preserve amazingly detailed skeletal fossils. Modern examples of these environments are the Sahara, the Mojave, and even the Sand Hills in Nebraska. In the rock record, an eolian environment preserves evidence of cross-bedded sand layers—crisscrossing patterns that indicate where a giant sand dune was migrating millions of years ago. During the Mesozoic, eolian environments in Mongolia have yielded many spectacular dinosaur fossils. One such discovery was of two dinosaurs locked together in three dimensions. One of the dinosaurs was a species of ceratopsian called *Protoceratops*. The other was the small-bodied theropod *Velociraptor*. These two dinosaurs dueled to the death and were buried under a collapsing sand dune.

The next depositional setting is a lake-based, or lacustrine, environment. In these depositional settings, it is common for fine-grained sediments to gently filter to the bottom. In the rock record, lacustrine environments yield finely striated, stripy rocks. Lakes can also be anoxic at the bottom, meaning that there is an absence of oxygen. This can prevent the degradation of dead stuff that happens to land on the bottom. Thus, it has a better chance to get slowly and gently covered by sediment. When this happens, paleontologists can find amazingly well-preserved soft-tissue details, including eye spots, coloration patterns, and stomach contents. Fossils excavated in Liaoning province in China include dinosaurs so well preserved that paleontologists can still find the cells that impart coloration to their feathers, enabling them to determine that some of these animals were white and black with rusty red heads.

By far, the most common kinds of depositional settings to preserve dinosaur fossils are rivers and their floodplains—called fluvial environments. These were great places for dinosaurs and other animals to live, with abundant freshwater and ample food. It turns out that they were excellent locations to get fossilized, too, since the sand migrates on the river bottom. And when a river breaks its levees and water spreads out onto the surrounding floodplain, the muddy sediment carried in suspension will eventually settle as the water recedes, potentially burying things on the surface. Since floodplains can act like a lacustrine environment, they are also ideal settings for preserving fossils.

In the modern world, sedimentary units of ancient rivers and their floodplains can be identified by looking at cliffs that include sandstones, which are the preserved river channels, and mudstones, which are the preserved floodplain sediments. In these kinds of depositional settings, paleontologists find most of the dinosaur fossil record, including bone beds, nesting grounds, and even footprints.

Finally, there are marine depositional environments. Deepwater locations are similar to lacustrine environments in terms of their fine-grained, sedimentary record. Because deepwater marine settings also contain anoxic zones that decrease the chance of scavenging, they lead to the amazing preservation of complete specimens. Marine deposits are often made up of finely bedded, black, organic-rich shale. Of course, since dinosaurs were terrestrial creatures, paleontologists rarely find them in these sedimentary rocks.

Occasionally, a random chunk of a dinosaur tail has been known to float out to sea and be discovered in marine rocks. But far more common are the preserved remains of marine reptiles. Some of the most famous discoveries of marine reptiles were made by Mary Anning in the early 1800s, in the shales that line the southern coast of England. These fossils are so well preserved that they contain all the bones of the skeleton, still in their anatomical positions—or articulated. They have even recorded the moment of live birth (and unfortunately, subsequent death) of an ichthyosaur baby.

ORDERING TIME AND INDEX FOSSILS

Now consider how researchers use rocks to reveal the history of life. To do this, they need to put these rocks in order—from oldest to youngest. There are two main ways that they measure time. The first is measuring time in a numerical, or absolute way, by expressing it in numbers. These might be with hours and minutes or with dates.

When talking about dinosaurs, paleontologists use geological time, which is a coarser measure of events—like saying that *T. rex* went extinct 66 million years ago. The general date can be marked with a high degree of accuracy. With dinosaurs, paleontologists also measure time in terms of durations. For example, they say that the Jurassic period lasted from 201 to 145 million years ago—a duration of about 55 million years.

However, the initial understanding that time was vast and that things had changed during the enormity of time was more of a relative process. The first key to unlocking Earth's history was having the basic understanding of how rocks form. But researchers also needed to understand a little more about how they form strata—or layers—and what those strata say about the order of events in deep time.

Putting strata in order begins by recognizing that the rocks on the bottom of a geological unit are the oldest. As new depositional events occur, they happen on top of the older, underlying rocks. This sequence allows researchers to say, relatively speaking, whether something happened more recently or longer ago. This is how they begin to understand relative time.

The next step is to remember that sedimentary rocks contain fossils. And if a fossil is found embedded in a unit of rock, then that fossilized organism lived, died, and was buried while that layer of strata was forming. If paleontologists find one fossil in one layer and another fossil in a different layer higher up, it makes sense to say that the fossil higher up lived more recently than the deeper fossil. Researchers might not yet know how much more recently, but they know the relative order.

However, since plate tectonics causes rocks to twist, turn, uplift, subduct, and bend, sometimes layers that are originally on the bottom end up on top. Thus, researchers need to make sure that they find structures in the sedimentary rocks, such as mud cracks, ripple marks, or other indicators, to ensure that they know which direction was up. Otherwise, they might be putting the rocks and the embedded fossils in the reverse relative order.

Then, they can begin to use the principles of biostratigraphy to link rocks that are far apart from one another because of the fossils that they contain. These important fossils are called index fossils. Usually, they are small-bodied, have hard parts (like a shell), are geographically widespread, and were present on Earth for a relatively short period of geological time. Generally, two rock units containing these index fossils can be correlated. In other words, they were deposited at about the same relative time.

ORGANIZING TIME

Early geologists created the first relative geological time scale using these basic principles of how rocks are organized. They put rocks around the world—along with the fossils that they contained—into a relative order, from oldest to youngest. The boundaries between these large chunks of time are based on major changes in Earth's environment. These changes often reflect periodic mass extinctions and therefore changes in the index fossils within rocks.

Early geoscientists gave names to each different chunk of geological time—organizing them into larger chunks and smaller sub-chunks. In geological time, the largest units are called eons. Pretty much every living thing evolved during the Phanerozoic—a word that means "visible life." The Phanerozoic eon gets broken up into smaller eras. From oldest to youngest, they are the Paleozoic, Mesozoic, and Cenozoic. These eras get divided into smaller periods, such as the Triassic, Jurassic, and Cretaceous.

However, for a complete geological time scale including absolute numeric dates for major events, radioactivity is required. Igneous rocks include unstable radioactive elements, the parent isotopes. These eventually break down to more stable configurations, the daughter isotopes, at regular, predictable rates. The amount of time it takes for half the parent isotope to degrade to the more stable daughter isotope is called the half-life. For these radioactive elements, researchers can use the ratios of parent-daughter isotopes to determine how much time has transpired since an igneous rock crystallized. Igneous rock units often bracket sedimentary rocks containing fossils. Thus, by accurately dating both igneous units, researchers can limit the time window for the deposition of a fossil-bearing sedimentary unit.

For example, the Judith River Formation in central Montana represents an ancient river system and its accompanying floodplains. It is relatively close to the shoreline of what was once the Western Interior Sea. This geological unit is well known for its spectacular dinosaur fossils as well as for the remarkable preservation of tiny fossils that record the diversity of organisms present in these dinosaur worlds.

In the Cretaceous, volcanoes to the west were pumping ash into the atmosphere. This ash rained down from the sky and was incorporated into the sedimentary rock record. The layered record of ash from these periodic volcanic eruptions allows for radiometric dating. It provides "bookmarks" in the geological record to pinpoint different events in time with absolute dates. For rocks more than 78 million years old, researchers can narrow down the temporal interval for some localities to within a 10,000-year window of time. The result is an incredibly powerful tool for reconstructing ancient ecosystems, understanding the rates of evolutionary change over time, and considering how long it takes a fossil record to form.

These methods make it possible for paleontologists to know that dinosaurs originated 230 million years ago and that all the dinosaurs—except for birds—were wiped out by an asteroid impacting the earth 66 million years ago. For about 165 million years, dinosaurs ruled their terrestrial worlds.

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HOW BONES BECOME FOSSILS

The best way to become immortal is to become a fossil. This lecture digs into the nature of the fossil record. The study of dinosaur origins, evolution, lifestyles, and extinction all comes down to fossils. Here, you will find out how fossils get preserved. You will also discover the ways paleontologists use some serious detective work to reveal so much about these "terrible lizards."

FOSSIL CATEGORIES

A fossil can be technically described or defined as any evidence of past life. Importantly, a fossil can be as vague as a chemical difference in ancient rocks that allows researchers to pinpoint the presence of some microscopic organism that subtly modified an atmosphere billions of years ago.

There are basically two large categories of fossils. The first is body fossils, which include the actual preserved parts of ancient living things. These are things like bones, teeth, shells, eggs, wood, pollen, feathers, leaves, and seeds. Trace fossils are the second large category. These are literally the preserved hints of an organism's activity or interaction with an environment. Great examples of trace fossils include things like fossilized footprints, fossilized nests or burrows, and feces—or coprolites.

These two distinct categories of fossils reveal different aspects of dinosaur lives. For example, because body fossils preserve the actual skeletal remains of dinosaurs, they are the key to unlocking the details of how dinosaurs looked. These anatomical remains are also the data that paleontologists employ when they study how different dinosaurs are related to one another. The structural features in their bones serve as important anatomical data that paleontologists analyze in studies of evolutionary history. Even cooler, bones preserve evidence of breakage, damage, and disease. Studying bones and teeth together allows researchers to develop hypotheses about how strong a dinosaur's bite might have been. And since bones also preserve the bumps, grooves, ridges, and rough spots that are related to muscle articulation, they are key to understanding how dinosaurs moved, grew, lived, and even died.

Trace fossils are often harder to assign to a specific dinosaur species. However, these kinds of fossils provide a different suite of valuable data. They give paleontologists unique insight into the behavioral characteristics of dinosaurs. Researchers might find the scratches of tooth marks from a sharp-toothed carnivorous dinosaur scoring the bones of another animal and use these to gather a hint at what dinosaur feeding ecology was like.

Want to know whether dinosaurs may have taken care of their nests? It might be revealed through a study of nesting structure and egg orientations. How fast were dinosaurs? Measuring the stride length between individual footprints can give you a clue. What about the external appearance of dinosaurs? Occasionally, paleontologists find preserved impressions of the skin of dinosaurs that allow them to reconstruct a dinosaur's soft external anatomy.

HOW FOSSILS GET PRESERVED

There are a handful of different modes of preservation that make it possible for the fossil record to exist. The first and most important step is to get buried. The first two modes of fossilization that commonly preserve dinosaur bones and teeth are called permineralization and replacement.

As the sediments burying a dinosaur transition to sedimentary rock, the soft, squishy parts of the carcass decay away relatively quickly, leaving behind the skeleton's hard, mineralized components of bones and teeth. As water moves through the sediment, cementing grains together to form sedimentary rocks, it carries along dissolved minerals. As this watery, mineral-rich solution permeates buried skeletal remains, minerals precipitate within the bones. This specific mode of fossilization is called permineralization. This is why many of the open spaces in fossils that would have held blood vessels and cells are infilled with rock.

Replacement occurs when the leftover bone mineral that originally formed the skeleton essentially gets traded out or replaced with new minerals coming in from outside or gets recrystallized with water from the atmosphere. Permineralization and replacement act in concert to result in dinosaur body fossils that are often heavy, dark in color, and brittle.

Carbonization often occurs in fine-grained depositional settings, such as lake bottoms or deepwater marine environments. Carbonization results from high pressure on sedimentary rocks that essentially compresses all the organic materials out of a biological structure, except for the carbon. The original organic remains are preserved as a thin film of carbon on the bedding planes of fine-grained sedimentary rocks. Carbonization can yield remarkably detailed fossils and frequently preserves soft tissue. Some of the best evidence for the connections between birds and dinosaurs comes from carbonized fossils found in localities with exceptional soft-bodied preservation. Paleontologists call fossil sites like these Lagerstätte—a German word that translates to "storage place." The first evidence of the close

relationship between dinosaurs and birds came from a Jurassic Lagerstätte called Solnhofen in Germany. Here, a well-preserved *Archaeopteryx* was found with an articulated skeleton and carbonized feathers.

Molds and casts preserve a three-dimensional impression of remains that are buried in sediment. The mold is the mineralized impression that the organism left in the sediment. Sometimes sediment fills this space and becomes mineralized, recreating the original shape of the remains. Essentially, a mold is an impression, and a cast is a copy of the original. Molds and casts are great ways to preserve footprints, nesting structures, skin impressions, and burrows.

A final way that dinosaur fossils are occasionally preserved is in amber. Amber begins as a sticky resin that organisms can become trapped in, which is why it is best at preserving relatively small creatures. Once an organism is trapped, the resin undergoes molecular changes that result in hardening over time.

Most of the time, preservation in amber results in the outside of an organism being exquisitely preserved in three dimensions. Typically, the inside of organisms are usually not quite as well conserved, probably due to the organism's own internal microbiota degrading the internal anatomy after death.

Though entire dinosaurs could never be preserved in amber, little bits and pieces sometimes are. Recently, the feathery tail of a dinosaur was discovered in a chunk of 99-million-year-old amber from Myanmar. Other pieces of amber preserved dinosaur feathers that were damaged by the presence of preserved parasitic insects that resemble the nymph states of modern-day lice.

TAPHONOMY

It's important to understand how tough it is to become a fossil. This is studied by paleontologists who specialize in the science of taphonomy. *Taphonomy* literally means "the science of burial." Taphonomic research helps paleontologists understand how accurately the fossils they're studying represent the true living assemblage of dinosaurs and their ecosystem partners tens or hundreds of millions of years ago. Taphonomists are concerned with the rules of death and burial that dictate an organism's chance of making it into the fossil record. They ask questions about when, where, and how death occurred.

Think about all the things that might happen to a recently dead animal before its journey to becoming a fossil begins. It's hard once you die not to be scavenged, not to have your body ripped apart and torn to shreds, not to have your own microbiome feed on your own carcass from the inside out as you lie dead on the surface. And don't forget about physical disintegration and chemical weathering.

HOW TO BECOME A FOSSIL

The best way to ensure a good start to your taphonomic journey is to get off the surface as soon as possible. From there, the varied modes of fossilization may kick in to help preserve remains into the future. The following are some rules that any organism on Earth should follow if they'd like to up their chances at immortal fossilization.

1. Don't be soft. Organisms that are made only of soft parts have a much harder chance of fossilizing. Soft, squishy stuff is the first thing to degrade away once an organism dies. But even though these creatures rarely make it into the fossil record, when they do, they can be spectacularly preserved. Luckily, dinosaurs all have some hard parts in the form of their bones and teeth.

2 Don't be too tiny or too large. Organisms that are tiny are often quite fragile. If not snapped up, swallowed in a single quick bite, and completely digested, these tiny organisms may also be more easily destroyed by the processes of weathering on the surface. Likewise, if you're a giant animal, like an adult sauropod, the chance that your entire body can get under the surface in one go is hard to imagine. This rule might also help to explain why fossils of Mesozoic mammals, birds, and baby dinosaurs are all pretty rare. The same goes for the rarity of discovering a completely articulated adult dinosaur.

3 It might be a great idea to go ahead and bury yourself alive. Paleontologists have found excellent examples of lungfish burrows in drought-stressed Cretaceous rocks and Triassic mammal-like reptiles curled up in their burrows while volcanic eruptions are wreaking havoc on land. There is even good evidence of at least one dinosaur that took this approach. In 2007, the bones of an adult and two juveniles called *Oryctodromeus* were discovered in the chamber of a burrow filled by a flooding river up on the surface. Similarly, dinosaur eggs are occasionally partially buried upon laying, making their transition into the fossil record one step simpler.

4 Consider dying with a bunch of your friends. Think about the effects that mass death accumulations have on scavenging. Take an example from the modern world. One wildebeest crossing a river full of crocodiles is almost surely going to be killed, eaten, and scavenged until little of it remains to get buried by sediments moving in the channel. Now, what if you add a few hundred or thousand more wildebeests moving and dying en masse? The predators and scavengers in the system will not be able to eat everything available. This means that a few lucky carcasses will slip through this important filter. These might get lucky enough to be buried before their scavengers get hungry again.

Food overload creates a great opportunity for entry into the fossil record—particularly when mass mortality occurs in a place like a river during the flood stage, with sediment moving downstream to capture carcasses. Paleontologists find dinosaur sites like this fairly often, and they call them bone beds. Bone beds are especially common in species that exhibit some gregarious behavior.

5 You must die in the right place at the right time. This essentially means that you must die in a sedimentary basin. Sedimentary basins are low spots on Earth's surface where deposition is actively occurring and sedimentary rocks that can bury fossils are accumulating.

SEDIMENTARY BASINS

Dying in swampy places isn't ideal for the natural processes of fossilization. Swamp chemistry is often too acidic (or too basic) to promote preservation. Your bones will literally dissolve before you can ever enter the subsurface. Fossils form in places where there is water or wind moving sediment on the surface. These kinds of environments are also the sorts of places where plant and animal life thrive. Luckily, dinosaurs lived in a tectonically active world, and sedimentary basins were abundant.

Consider all the places on Earth that lack a great fossil record. Paleontologists are fairly certain that dinosaurs lived in places where their fossils can't be found. Take, for example, the contrasts in the dinosaur fossil records in the states of Minnesota and Montana. In the Cretaceous, a shallow continental seaway basically divided North America into eastern and western halves. Minnesota had plenty of beautiful shorelines on the eastern side of that seaway, and Montana had them on the western side.

Out in Montana, westward mountain-building helped to create a sedimentary basin in which the extraordinarily fossiliferous Judith River Formation was deposited 76 million years ago. This formation includes rocks that record the migrating coastline regressing when the sea was shallower and transgressing as the seaway became more extensive. Paleontologists find tons of fossils of all kinds of animals here.

But in Minnesota, there was no sedimentary basin. The same kinds of environments existed there, and the same kinds of animals populated those ecosystems—but their fossils are absent. It's all about that larger geological context when it comes to getting lucky enough to reappear millions of years after death.

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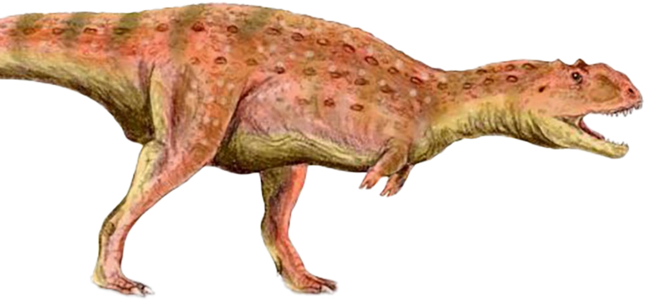

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A DINOSAUR MYSTERY IN MADAGASCAR

This lecture ties together how the principles of geological time, biostratigraphy, plate tectonics, and taphonomy all work together in the real world. You will journey across the globe to the Great Red Island of Madagascar. Today, Madagascar lies several hundred miles off the east coast of Africa, across the Mozambique Channel, in the Indian Ocean. Its geographic isolation has resulted in an extraordinary pattern of endemism—meaning that it has plants and animals that are both native to and restricted to a particular area. Madagascar is home to some of the world's most unique flora and fauna.

MADAGASCAR'S PLATE TECTONICS

Although in some places the African mainland is a mere 260 miles away, many groups of plants and animals don't exist on the island of Madagascar. Mammal paleontologist David Krause originally hypothesized that many of the ancestors of Malagasy mammals would be present in more ancient rocks preserved on the island. He set out on a series of expeditions to search the fossil record for the mysterious origins of Madagascar's modern mammals. The story was intriguing, in part because of Madagascar's complicated plate tectonic history.

At the beginning of the Mesozoic era, around 250 million years ago, Madagascar was positioned in the heart of the southern-hemisphere supercontinent Gondwana. For a long time, it was nestled in between what would become Africa to the west, India to the east, and a combination of Australia, Antarctica, and New Zealand to the south. A series of dramatic rifting events began around 160 million years ago. These progressively disaggregated the supercontinent into a series of smaller, separate landmasses.

The first rifting event dragged Antarctica and Australia away from the Africa-Madagascar-Indian landmass. By the Late Jurassic, about 160 million years ago, the Indo-Madagascar subcontinent rifted away from the east coast of Africa and began a southerly drift. In the Late Cretaceous, around 88 million years ago, an initial rift formed between Madagascar and the Indian subcontinent that left Madagascar stranded in the Indian Ocean. By the end of the Mesozoic era 66 million years ago, Madagascar had been completely isolated from all other landmasses for more than 20 million years. Significant questions—how, when, and exactly where all these weird living animals' ancestors came from—could only be answered by going back in time, closer to the moment of geographic isolation.

When paleontologists dive into a new research area, the first and most important step is to begin to develop a picture of all the work that has come before. In the case of Madagascar's animals, Krause began poring over the literature in search of any record of fossils found in older-than-modern rocks. There were plenty of archival papers that documented the discoveries of fossilized giant lemurs; pygmy hippos; the eggs and skeletons of giant, flightless

Aepyornis; and even giant tortoises. Most of these discoveries were made in cave and stream deposits. But, in Krause's quest to push back in time, he kept coming up empty-handed.

Radiocarbon dating indicates that, at most, these subfossil finds were between 12,000 and 26,000 years old. The youngest dates indicated ages of only 500 to 1,000 years old. All these findings were simply way too young to shed any light on the origin of these crazy creatures. To answer his questions, Krause would have to go as far back as the timing of the rift itself, around 88 million years ago.

Krause finally struck pay dirt when he unearthed a series of papers written in the late 19th and early 20th centuries. These reported a handful of fragmentary dinosaur bones uncovered in northwestern Madagascar, from hilly outcrops exposed on the right bank of the Betsiboka River. In 1896, French naturalist Charles Depéret described fragments of both sauropod and theropod dinosaurs from rocks that he guessed were Cretaceous in age based on the presence of nearby invertebrates and the dinosaur bones and teeth. Krause dove headlong into exploring this region, which Depéret called the "Meravana."

Krause wrote an exploratory grant to the National Geographic Society. Then, he mounted an expedition to the northwestern corner of the island aimed at searching for these sedimentary rocks. He thought that perhaps going back in time to after the separation of the island from the other Gondwanan landmasses would provide the necessary clues to decipher these evolutionary mysteries.

THE MAEVARANO FORMATION

An area called the Maevarano Formation yielded many dinosaurs in the quarry called MAD 93-18. The numbers indicate that this was the 18th locality discovered in the first year of fieldwork, 1993. Over a few seasons, the site yielded tons of long-necked dinosaur fossils, including nearly complete skeletons of juveniles and adults, and the skeletal material that came from MAD 93-18 was super important.

The tailbones that were found pointed toward a close relationship between a newly discovered animal and a specific, late-surviving group of titanosaurs. This group of sauropods includes the largest dinosaurs of all time and some interesting island dwarf species. Some titanosaurs are armored, with bony plates called osteoderms that lie within their skin. The group evolved in the southern supercontinent of Gondwana, at the end of the Jurassic period. Then, as the continents drifted, so did the dinosaurs, diversifying as they evolved with their changing ecosystems.

Unfortunately, most titanosaur fossils were known from only a few fragmentary bones. The new skeletal material at MAD 93-18 blew the lid off of paleontologists' understanding of titanosaurs. For the first time, they discovered and described the entire skeleton and skull of one of these enigmatic giants. Even better, MAD 93-18 included three different geological horizons showing distinct time periods, each containing abundant and well-preserved titanosaur fossils at a variety of different ages.

This work found a new genus and species of titanosaur, *Rapetosaurus krausei*, that helped clarify Charles Depéret's original discoveries from the 1800s. *Rapeto* comes from the Malagasy legend of a giant, mischievous beast that wandered the hills, accidentally causing trouble. The species name was given in honor of Krause.

MAJUNGASAURUS

A number of years later, geologist Ray Rogers was checking out the end of a four-foot-long hip bone of *Rapetosaurus*. At the thin end of the element, he pointed out deep gouges—hundreds of parallel scrapes—that striated the bone. He and a colleague eventually realized that these marks were accompanied by punctures and tiny scrapes. They were looking at the marks of a carnivore's teeth scraping the meat from the end of this dead sauropod hip bone. These were the signature tooth marks of an ancient seven-meter-long, sharp-toothed, two-legged theropod, *Majungasaurus*—the top carnivore in the ecosystem.

As the search through the fossils continued, an interesting and unexpected pattern began to emerge. They found many *Majungasaurus* tooth marks on the bones of *Rapetosaurus*. But just as common were tooth marks upon the ribs and vertebrae of *Majungasaurus* itself. What other carnivore was out there?

To figure this out, the researchers carefully compared the shape and size of all the tooth marks they spotted with the jaws and teeth of all the potential culprits in the Maevarano ecosystem. The candidates included another small, bucktoothed carnivorous dinosaur called *Masiakasaurus* as well as a whole array of diverse crocodilians. The researchers were able to rule out all the other potential suspects. The sharp-toothed transgressor feeding upon *Majungasaurus* carrion was none other than *Majungasaurus*. Cannibalism as an ecological strategy is not uncommon in living animals. But harder to definitively determine was whether *Majungasaurus* killed the individuals it dined on or if it was an opportunistic scavenger taking advantage of the dead.

MAD 05-42

One of Rogers's favorite localities in the Maevarano ecosystem is called MAD 05-42. At this locality, the dead are pouring from the rocks. Rogers has spent years dissecting this locality to help answer questions about the pattern of mortality that has created such a remarkable fossil record in the Maevarano Formation. His work ties together evidence from rocks and evidence from bones to paint a picture of multiple seasons of dinosaur death.

At MAD 05-42, one nearly complete *Majungasaurus* skeleton rested on its left side, head and neck pulled backward toward the hips in a death pose. Only the tip of the tail was missing. Nearby, other carcasses in different states of preservation and disarray were present. Some were still largely intact, while others had only an element or two. Small baby sauropod bones were mixed in and scattered. The partial delicate skeletons of birds lay alongside the giant femora of a sauropod or the shoulder blade of another *Majungasaurus*. What caused the deaths of all these unfortunate creatures? Did they all die here, or were they brought together only after death, by some sedimentological process? And how did they die?

Dinosaur burial grounds like this one are common in the Maevarano Formation. The rocks that make up this sedimentary unit alternate between layers of beautiful white sandstones that preserve tiny, dark brown, shiny fossils. These white sandstones represent times when rivers were flowing with shallow water and life thrived in the ancient Maevarano ecosystem. Interbedded between these “good-times” rocks are massive, thick, greenish-gray, clay-rich sandstones preserving multiple layers of mass death. The Maevarano Formation was deposited well before the mass extinction horizon that marks the last moments of dinosaurs’ rule on Earth. All the evidence found indicates that these rocks were laid down sometime between about 70 and 68 million years ago. This means that the high rate of death in the ecosystem wasn’t tied to the great global mass extinction that marked the end of the Cretaceous period.

Rogers and his students focused on the taphonomic data to gauge the story of mortality preserved in MAD 05-42. They looked for clues of bone modification. Were the bones bitten? Burned? Trampled or broken? Were the carcasses intact, or were they disturbed so that they became disarticulated, possibly by scavengers or predators dismembering carrion? What types of rocks were the skeletons buried in? And what did the various kinds of animals and their different types of preservation potentially reveal about how the bodies were buried and what might have happened to preserve them after burial?

Rogers noticed that different skeletons exhibited distinctive postmortem histories. Some skeletons were mostly intact, while others were scattered about and disarticulated. Some bones were perfectly preserved. Others exhibited cracks, splintering, and breakage that indicated prolonged exposure to the elements. If all these animals dropped at once, they would most likely exhibit the same postmortem details. Instead, their bones indicate that the animals in this fossil assemblage died over a period of time.

Rogers then looked to the rocks to help him understand the environmental conditions that may have prevailed. In the Cretaceous, Madagascar exhibited a highly seasonal, semiarid climate. Data in support of this reconstruction includes evidence from ancient soils, which preserve the traces of plants with long vertical roots. Vertical roots allow plants adapted to dry environmental conditions to seek deep underground sources of water and nutrients. The white and greenish alternating sediments of the Maevarano Formation also provide evidence that water flow fluctuated dramatically at different times of the year. In the rainy season, broad, shallow rivers brought life to the ecosystem. But in the dry season, all kinds of animals gathered around shriveled pools in search of sustenance. Sometimes these ancient rivers went dry.

The culprit of this mass death event indiscriminately selected victims. The bone beds include a diverse array of animals. Size didn't matter. Neither did lifestyle. Since the evidence suggests that the bone beds formed over a period of time, a dramatic instantaneous event can be ruled out. The repeat occurrences of bone beds, layer upon layer, also mean that the culprit struck repeatedly and often.

The taphonomic, geologic, and anatomical evidence points to a single killer: drought. The Maevarano ecosystem was arid and highly seasonal. Animals who congregated around dwindling water supplies were primed to make it into the fossil record. They concentrated their own corpses in low spots that would eventually contain waterborne sediment perfect for burying the dead. These drought-stricken creatures would have crept to the ever-smaller pools in the drying riverbeds and then perished as water and food supplies disappeared.

Lucky for the paleontologists who work on the Maevarano ecosystem, many of these dead got preserved. How? It comes back to those green-gray rocks that yield the repeat bone beds. When the droughts came to an end, the rains returned. These torrential downpours would mobilize sediment in a milkshake-like slurry of clay, sand, and water called debris flows. These flows would roll down the dry riverbeds, surging over the landscape and roiling over the unlucky dead, entombing them.

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TRACING THE DINOSAUR EVOLUTIONARY TREE

In the 1700s, a Swedish botanist named Carolus Linnaeus came up with a standard way to categorize known life on Earth. His method was called the *Systema Naturae*. It lists the categories of living things—kingdom, phylum, class, order, family, genus—all the way down to the smallest unit of biodiversity: the species. This gave scientists a common language for talking about all life on Earth. Still, no one had yet figured out why organisms shared characteristics. The key to unlocking this mystery wouldn't be discovered until a century later. This lecture is about the important contributions of Charles Darwin and Alfred Russel Wallace, who both independently came up with the theory of evolution by natural selection.

THE THEORY OF NATURAL SELECTION

Charles Darwin's contributions to the theory of evolution by natural selection were by far the most extensive. He originally consolidated his thoughts in the 1820s while sailing the globe on the HMS *Beagle*. His visits to South America and the Galapagos Islands provided the raw materials for the theory, which he built upon over the next decades with copious evidentiary support. In the Indonesia archipelago, Alfred Russel Wallace hit upon the same core ideas and shared his thoughts with Darwin. Together, they shared their ideas on the origin of species to the prestigious Linnean Society of London in 1858. A year later, Darwin published *On the Origin of Species*.

The theory of natural selection provided a simple way for new species to form according to nature. Every organism within a population varies in its ability to acquire resources. Because these resources are limited, organisms must compete for them. Those best suited to gathering resources are more likely to survive, reproduce, and potentially pass their special traits on to their offspring. Over time, these traits may become more prevalent in some but not in others. These differences in traits allow us to identify a new species.

This view highlights that all life on Earth shares a common ancestry. The treelike, branching patterns of shared and divergent evolutionary histories result in the hierarchical groups first scientifically recognized by Linnaeus. Organisms that share a more recent common ancestry fit into smaller groups. Larger groups share a more distant common ancestry.

For example, consider all land animals, or tetrapods. All these organisms share the presence of four legs because they inherited them from an ancient common ancestor. Their front legs may have evolved into arms (e.g., humans) or wings (e.g., birds), but the core components—bones, muscles, nerves, and blood vessels—all point to a long history of evolutionary sameness.

When you line up the hierarchical categories established by Linnaeus for *Triceratops* and for humans, you can see the parts of our history that are shared (Chordata, Vertebrata, Tetrapoda, and Amniota). You can also note the point of divergence from our shared ancestor to head down on our own evolutionary paths. Dinosaurs come from one group of reptiles, while humans come from another. This view of life allows researchers to trace shared ancestry among all life on Earth.

Before Darwin and Wallace's idea, scientists viewed the origin and evolution of species through a lens of getting better over time in a directed and intentional way. Now, researchers realize that change, success, and survival are all about the ways that species adapt to their environments. In reality, fitness is always relative. It must be viewed in the context of a constantly changing environment. Instead of a ladder of improvement, species exist in a vacillating landscape of change. Sometimes you're on top of the roller coaster, but often you're slowly sliding away from a fitness peak or hanging out in the "survival of the good-enough" zone. Often, environments change quickly enough that species evolution simply can't keep pace—and when this happens, it can result in extinction. It's not that extinct animals are better, worse, or even poorly adapted. It only means that environmental shifts outpaced evolution's ability to modify their genomes quickly enough to keep up.

As researchers' understanding of evolution has developed over time, the fundamentals have been supported by data from sources as diverse as comparative anatomy, developmental biology, studies of the genomes of living organisms—and yes, the fossil record.

SIMILARITIES AND DIFFERENCES

With the development of these sciences, paleontologists have come to realize that some of Linnaeus's original groups mistakenly lumped together creatures that were distantly related because they shared some superficial similarities. As it turns out, there are different ways of being the same. Sir Richard Owen was responsible for one of the key unifying principles that helps researchers understand one type of similarity: the principle of homology. Homologies are traits that are shared because they are derived from a common ancestor. They help researchers identify true evolutionary groups called monophyletic groups.

Now, researchers always want their classifications to reflect this evolutionary history. Homologous traits may have undergone evolution that makes them look or work distinctively in each descendant group. Thus, even though these traits have a common origin, they can have different functions. Still, researchers can trace their shared history through evolutionary trees. For example, when considering the tetrapods, you can see that their arms and legs are built from the same basic building blocks: one large bone at the top, two smaller bones down below, and a whole bunch of little bones at the ends. Evolution has worked with the raw material of this limb anatomy to mold fins, wings, and even the loss of limbs in animals like snakes.

In contrast, sometimes the shared similarities you spot are the result of convergent evolution. Think of this process as evolution hitting upon—or converging upon—the same anatomical solution to a common functional problem. Since these traits share specific functions, they often look alike. However, they are built from different underlying structures.

This type of similarity is distinct from homology. It essentially results from evolution repeating itself. These types of characteristics can easily mislead researchers when it comes to building evolutionary trees. They might group together creatures that are quite distantly related. In actuality, though, these analogous traits highlight evolution's remarkable way of finding solutions that work well in an environment.

In the age of Linnaeus, sometimes organismal groups were mistakenly diagnosed by the presence of such analogous features. For example, Linnaeus originally grouped birds and mammals together into Homeothermia because they were the only known warm-blooded animals on Earth. Now researchers know that they evolved their unique types of warm-bloodedness independently. Once you strip the features down and dissect the data, the differences in the ways that these groups thermoregulate highlight their distant ancestry.

If you evaluate all marine animals that began life on land, they share some features with sharks, which have always lived in the ocean. The similarities of torpedo-shaped bodies, tail flukes, fins, and even countershading are all indications of superficial similarities. A casual observer might imagine that they were all close relatives because of these superficial features. Another great example is the evolution of wings in birds, bats, and pterosaurs. At first glance, you might imagine that wing-bearing animals might be each other's closest relatives. But their differences make it easier to see how each of these animals evolved their wings independently from different common ancestors.

CLADISTICS

To test different competing hypotheses of evolution, paleontologists now use a method called cladistics, first developed in the 1950s. In cladistics, they enter data into a computer program on different features in a group of interest as well as a comparative "outgroup." They then ask the program to organize the data using parsimony to determine which organisms are more closely related to others by distributing the various features in the simplest way possible. This method results in a branching, treelike diagram. Close relatives are nearer to one another on the tree. They share some group of diagnostic features that would allow paleontologists to place a newly discovered animal within the group down the road.

Cladistics builds testable hypotheses of how different organisms are related and which characteristics they share. And, because it works from general principles, another scientist could take the same data and find the same answer. Or they could add in a newly discovered fossil species and revise the tree to incorporate this new data. Now, paleontologists have realized that some of the earlier groups created by the Linnaean taxonomic system hide important parts of the evolutionary story.

Take, for example, birds. In the Linnaean system, birds belong in their own special group—Aves—because they seem so different from other living creatures. They are warm-blooded, have feathers, and have beaks instead of teeth. Animals like turtles, snakes, lizards, and crocodiles belonged to a different group—Reptilia—because of their cold-blooded, scaly-skinned biology. But being scaly and cold-blooded is a primitive feature for land-living animals, not a specialization. There aren't any features that are uniquely shared by these reptiles that aren't also shared by birds.

When researchers employ cladistic methods for grouping organisms based on their homologous features, they realize that birds are a part of Reptilia. And birds and crocodiles are more closely related to each other than to lizards. Dinosaurs also fit within this group—but they are even more closely related to birds than they are to crocodiles.

Evolution holds Dinosauria together. Evolution is the reason researchers can say confidently that birds are dinosaurs. With evolution in mind, paleontologists can connect the dots between these different groups—and between other dinosaur groups—and move even farther out to a broader array of backboned animals with distinctive trails of homologous anatomical breadcrumbs.

SAURISCHIA AND ORNITHISCHIA IN LIGHT OF EVOLUTION

Remember that Ornithischia included a bunch of different creatures known for their backward-facing pubis, their wild ornamentation, and their specializations for eating plants. These same general features help paleontologists determine which ornithischian groups are most closely related to one another. The tanklike ankylosaurs and plated and spiked stegosaurs are each other's closest relatives. They are grouped together in a special ornithischian subgroup called Thyreophora. This name translates to "shield bearers." Most members of the group are well known for the bony osteoderms that grow in their skin.

The large group of ornithischians called Ornithopoda is full of disparate body plans. It includes little herbivores like *Hypsilophodon*, *Iguanodon*, and the hadrosaurs. The head crests of hadrosaurs are built of an elaboration of a couple of skull bones—the bones of the nose, called the nasal bones, and the bones of the forehead, called the frontals. These bones were stretched out and coiled around to create fancy crests that may have played a role in vocalization.

The final subgroup of ornithischians is also all about the headgear. The Pachycephalosauria, those dome-headed bipeds, and the horned and frilled Ceratopsia are more closely related to one another than they are to any other dinosaur group. The reason is reflected in their special conjoined group name: Marginocephalia. Marginocephalians elaborate the back part of their skulls by building a shelflike projection. The name *Marginocephalia* translates to "ridge-headed."

The other major tribe of dinosaurs is the Saurischia. This group includes both herbivores and carnivores. Saurischia can be divided into two groups: Sauropodomorpha and Theropoda. Sauropodomorpha includes the animals paleontologists used to think of as prosauropods as well as the giant sauropods. When paleontologists first discovered prosauropods and sauropods, it was tough to imagine a connection between them. But nowadays, they realize that a specific group of larger-bodied prosauropods likely diversified into the ancestral sauropods. Sauropods inherited their small heads, long necks, and large guts from their prosauropod ancestors. However, in other ways, they are completely distinctive.

A specific subgroup of sauropods called Titanosauria includes dinosaurs that lived up to the end of the Cretaceous period. Their fossil record yielded the first occurrence of an osteoderm with a sauropod skeleton. Early in the days of exploring Madagascar's ancient fossil record, this discovery prompted some paleontologists in the 1800s and early 1900s to hypothesize that there must be an ankylosaur yet to be discovered in the rocks there. This was only because of the osteoderm. The scientist proposing the new species did so a bit cautiously. It took 100 years, and many additional discoveries, for that association to be confirmed.

Now paleontologists know that some titanosaurs had osteoderms, which they convergently evolved with their thyreophoran cousins. However, they likely used them in a completely different manner. These osteoderms might have been a useful store for mineral resources that would allow these giant dinosaurs to steal minerals from their own bodies to shell eggs without compromising the integrity of their limbs.

Finally, Theropoda includes all the meat-eating dinosaurs. Along one branch of this theropod family tree is a special group known as the Maniraptora. It is from this group that birds originate.

THE SYNAPSIDA AND SAUROPSIDA

Remember that swimming, non-bird flying, and sail-backed creatures are not dinosaurs. To understand why, consider a large group of hard-shelled, egg-laying terrestrial vertebrates called amniotes. Their unique eggs distinguish them from amphibians, which have to lay their eggs in a watery world. Amniotes fully venture out for a life lived on dry land. Amniota includes a few important groups. One, the Synapsida, leads to mammals—though the group starts out scaly and cold-blooded like other reptiles. It is here that the sail-backed reptiles like *Dimetrodon* fit into this story. *Dimetrodon* shares special features of its skull with other synapsids—including us. *Dimetrodon* is more closely related to us than it is to any dinosaur.

The other group, called Sauropsida, is where to look for the other swimming and flying beasts of the Mesozoic. Sauropsida contains many creatures typically thought of as reptiles. Sauropsids are divided into two large tribes: the lepidosauromorphs, where lizards and snakes fit in, and the archosauromorphs, where crocodiles, dinosaurs, and birds belong. The Mesozoic swimming reptiles are more closely related to lizards and snakes. Each of the three most common marine reptile groups evolved their own specializations separately. They aren't each other's closest relatives. And the flying reptiles called pterosaurs are a bit more closely related to dinosaurs than to crocodiles.

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WHAT DID *T. REX* TASTE LIKE?

This lecture examines the evolutionary link between dinosaurs and modern birds. Modern birds are an insanely diverse group. They have a global distribution, live in the coldest and hottest places on Earth, migrate incredible distances, and even fly higher than the peak of Mount Everest. They were such a special group that in the 1700s, Carolus Linnaeus assigned them to their own group: Aves. The fact that birds are dinosaurs makes them key to developing a deep understanding of pretty much everything about dinosaurs.

WHAT MAKES BIRDS DINOSAURS?

Birds are dinosaurs. When researchers plug them into cladistic analyses of vertebrate evolution, the most parsimonious position for them is deep within Dinosauria. Dinosauria comprises any animal that is a descendant of the most recent common ancestor of the theropod *Megalosaurus* and the ornithopod *Iguanodon*.

When Linnaeus originally defined Aves, there was a suite of characteristics that distinguished flying birds from all other known animals. Birds have beaks instead of teeth. They have feathers. They have wings made of specialized feathers hanging from their arm bones. And they have feet that are often good for perching.

Moreover, their bones are thin, with hollow spaces on the insides—this makes them quite lightweight. A critical bone in the wrists of birds is a little half-moon-shaped bone called the semilunate carpal that allows them to fold their wings and helps power the flight stroke. At least for the flying birds, their bony sternum is broad and keeled forward to accommodate powerful flight muscles. Birds have a short little stubby tail made of fused tail vertebrae. Bones are fused in other parts of their skeleton too. Birds have fewer individual skull bones than most other reptiles, and their hip elements get fused together seamlessly into the synsacrum. One of the most important bone fusions, found in the clavicle, is the furcula—or wishbone.

Birds also have a unique anatomy that supports their special way of breathing. They have rigid lungs that are connected to a series of air sacs. Some of these air sacs lie within the cavities of their bodies, and some of them perforate their vertebrae and bones to invest these hollow elements with air. They help circulate air and also contribute to a reduced body mass for flight.

Birds breathe using a circular pattern. Their initial breath bypasses the lungs and fills air sacs, where some oxygen is extracted. The next breath pushes that air into a different set of air sacs, where more oxygen is extracted. The next breath pushes that same air into the lungs, where even more oxygen is drawn out. As a result, birds are far more efficient extractors of oxygen than mammals are. This might help fuel their high metabolism, rapid growth rates, and warm-blooded bodies.

Charles Darwin predicted that, if his theory was correct, researchers should find "transitional forms" in the fossil record. These are creatures that could not easily fit into existing taxonomic categories because they exhibited characteristics of more than one group. Two years after Darwin's publication of *On the Origin of Species*, such a specimen was uncovered at the Jurassic-aged Solnhofen limestone Lagerstätte. The first hint was a single fossil feather, preserved as a carbonized impression among amazingly preserved fish, invertebrates, and plants. Soon afterward, an entire skeleton emerged from the rocks. It had the toothed skull and long bony tail of a reptile but feathers and wings akin to those in living birds. This remarkable new animal was called *Archaeopteryx*, which translates to "ancient wing."

Over the next 100 years, many more specimens of the mysterious *Archaeopteryx* would be uncovered at Solnhofen. So many features pointed to a link between dinosaurs and birds, but for years, one critical element appeared to be missing: Where was the *Archaeopteryx* wishbone? This tiny, fragile element appeared absent in the assembled *Archaeopteryx* specimens. For many scientists at the time, the perceived lack of a furcula in both *Archaeopteryx* and theropod dinosaurs eliminated the possibility that these two groups of animals could be related. And it changed the way people viewed dinosaurs for years to come—as overgrown, slow-moving, cold-blooded beasts.

THE DINOSAUR RENAISSANCE

One afternoon in late August 1964, Yale paleontologist John Ostrom was prospecting for fossils in the Cloverly Formation, an outcrop of Early Cretaceous sedimentary rocks in southern Montana. Suddenly, Ostrom and his assistant, Grant E. Meyer, noticed a black, shiny bone sticking out from the rocky slope a few feet below them. They realized that they were seeing a large, sharp-clawed dinosaur hand. As the specimen was exposed, they started to spot the sharp, serrated teeth of a theropod dinosaur. Continued digging exposed a foot that would change the study of dinosaurs forever. This three-toed foot had two toes with ordinary claws. However, the innermost toe was tipped by a large, sickle-shaped, deadly claw. Ostrom eventually called this new theropod *Deinonychus*, which means "terrible claw."

Ostrom and his team studied and reconstructed the detailed anatomy of at least four *Deinonychus* individuals recovered from the same area. In 1969, Ostrom published his work. He described a "fleet-footed, highly predaceous, extremely agile, and active animal, sensitive to many stimuli and quick in its responses." One of the undergraduate student members of the 1964 expedition, Robert Bakker, contributed a drawing to accompany Ostrom's paper. The illustration depicted *Deinonychus* in full sprint. The discovery, the paper, and the imagery would launch a revolution in dinosaur biology that paleontologists call the dinosaur renaissance.

Ostrom continued his research. During museum visits in Europe in the 1970s, he realized the similarities in the detailed articulations and anatomy of the skeletons of *Deinonychus* and *Archaeopteryx*. This prompted him to revive the old hypothesis championed by Thomas Huxley that birds were descended from theropod dinosaurs like *Deinonychus*. He laid out more than 20 different anatomical similarities between *Archaeopteryx* and theropod dinosaurs. For the next 30 years of his career, he published papers detailing the connections between dinosaurs, birds, and the evolution of flight.

Other major contributors to the dinosaur renaissance include Robert Bakker, who published *The Dinosaur Heresies* in 1986. This book pushed the ideas of the active, agile dinosaur. At the same time, Jack Horner was busy finding the first North American baby dinosaurs and nests. Suddenly, not only were dinosaurs more active, like birds, but they were also good parents. Jack published his book *Digging Dinosaurs*, a pop science summary of his work, in 1988. As the 1990s got rolling, Canadian paleontologist Philip Currie began working with scientists in China who revealed the first discoveries of feathered dinosaurs.

DINOSAUR SKIN ADAPTATIONS

Feathers are complicated biological structures. They are built of a central rachis with projecting barbs linked together by barbules and hooklets. The connections between the barbs are partly what dictates the shape of the feather.

The fossil record indicates that the first feathers evolved in a specific group of theropod dinosaurs called coelurosaurs. This group includes tyrannosaurs, ornithomimids, therizinosaurs, and compsognathids. Dinosaur feathers are often fuzzy and downy, and were likely used to keep warm or for display. In a few dinosaurs, like the tiny *Microraptor*, primary feathers are present on the arms and legs. In other dinosaurs, like *Velociraptor*, direct evidence of feathers comes from the presence of little bumps on the ulna called quill knobs, where feathers articulated with the arm bones.

Deeper in the dinosaur family tree, the evidence for feathers is less common. However, there is evidence for a wider array of special skin adaptations. Animals like sauropods, hadrosaurs, ceratopsians, ankylosaurs, and stegosaurs likely didn't have feathers. Paleontologists have many skin impressions of these animals, and all exhibit scaly skin. In a few rare instances, other kinds of skin adaptations have been recovered in dinosaurs, such as the specialized quills on the tail of a little ceratopsian. However, these unique cases are another example of convergent evolution. The data supports the idea that feathers first evolved in a subgroup of theropods.

BONY SIMILARITIES

Many of the features of bones in birds can be found deep down in the dinosaur family tree—some so far back that they branch into a much broader group of dinosaurs. For instance, the semilunate carpal is also present in the Maniraptora subgroup. This bone changes the ways that these theropods can move their hands. It allows side-to-side and rotational movements.

And although wishbones seemed to be absent in theropod dinosaurs for many years, they'd only been misidentified in many of the theropods that have them. Now paleontologists have identified furculae from Early Jurassic theropod dinosaurs, indicating that this feature is a pretty ancient part of the theropod body plan.

What about those short little tails of birds? Some theropod dinosaurs that are more closely related to birds also have them. A recently discovered species of oviraptorosaur is the first theropod to exhibit a short little bony tail made up of fused tailbones.

Even further back evolutionarily, the vertebrae of both theropod and sauropod dinosaurs exhibit perforations on their surfaces and internal hollows that correspond to the pneumatic vertebrae of birds today. This also points to the presence of air sacs similar to those connected to the lungs in modern birds. In sauropods, the presence of such air sacs lightens their estimated body mass by as much as 10%.

SOFTER STUFF

If hollow vertebrae are consistent with the presence of air sacs, this is a good indication that avian-style air flow may have been present in both theropods and sauropods. This would push the origin of this innovation back to the base of the saurischian family tree.

As mentioned previously, this novel way of extracting oxygen is linked to high rates of metabolism in living birds, which correspond to a warm-blooded lifestyle and super-fast growth rates. Analysis of the microscopic structure of both saurischian and ornithischian dinosaurs indicates high vascularity and cell densities, disorganized bone mineral, and abundant bone remodeling. All of this is consistent with a more mammalian or avian growth strategy. This may indicate baseline metabolic rates that were elevated in all dinosaurs. It also points to birds inheriting at least a boost in growth and metabolic strategies from their ancient dinosaur precursors.

The preservation of soft tissues in some fossils also supports the connection between dinosaurs and birds. Beta keratin—the unique protein that builds feathers, beaks, and claw sheaths in modern birds—has been preserved on the sickle-shaped toe claw sheath of a 66-million-year-old theropod from Madagascar. And work on *Tyrannosaurus rex* fossils has revealed the presence of amino acids that are consistent with those of modern chickens.

Modern evolutionary development biologists have also found evidence of extinct genes in living chickens that, in earlier evolutionary history, would have built teeth and long bony tails. In this way, the genome of living birds preserves a “molecular fossil record.” This allows researchers to test hypotheses about the ways that mutations changed gene expression millions of years ago to result in novel morphologies.

Finally, there is also great evidence for birdlike behavior from dinosaurs, such as the discovery of an oviraptorid sitting atop a nest of eggs. The original discoveries in Mongolia of these dinosaurs associated with nests prompted early workers to name the first such theropods *Oviraptor*. This was a nod to the idea that these big, bad meat-eaters were stealing eggs from the nests of unassuming herbivorous dinosaurs. Imagine the surprise of the scientists who finally popped open one of the well-preserved fossil eggs to find a baby *Oviraptor* inside.

And don't forget about the duck-sized juvenile troodontid theropod discovered in Liaoning province, China. The hind legs are folded beneath the body, much like the roosting posture for modern birds. The head is tucked under one of the forelimbs. The tail wraps forward, circling the body. Scientists proposed that this dinosaur was preserved while it was asleep. The pose prompted the name *Mei long*, which translates to "soundly sleeping dragon."

SOME FUN FACTS

Here are some of the most common questions paleontologists get asked about dinosaurs.

What's the largest dinosaur? It is likely to be a sauropod—probably something like *Argentinosaurus*. And technically, the smallest dinosaur so far known is the bee hummingbird, weighing only about two grams.

Could scientists splice dinosaur and frog DNA to make a dinosaur, as they did in *Jurassic Park*? Frog genomes would never do the trick. All they would need to do to make a dinosaur is manipulate the DNA of living dinosaurs—the birds.

What's the fastest dinosaur? That depends on whether you are considering the fastest terrestrial runner or the fastest flier. For a terrestrial runner, you can quickly rule out large extinct theropods like *T. rex*. Researchers estimate that, like ostriches, a few of the smaller therapods probably topped out at around 45 or 50 mph. However, if considering any type of movement, then the winner is the peregrine falcon, which can dive at speeds of more than 200 mph.

What's the smartest dinosaur? Among living birds, it would probably be those problem-solving, tool-using crows; the language-learning parrots; or the vocalization imitators like the superb lyrebird.

Did *T. rex* taste like chicken? No—chicken tastes like *T. rex*!

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DINOSAURS IN YOUR BACKYARD

The split between birds and their theropod ancestors occurred between 165 and 150 million years ago, back in the Jurassic period. By the Cretaceous period, birds thrived, diversifying in shape and size. At the end of the Cretaceous, birds were decimated alongside their dinosaurian compatriots. The ancestors of modern birds quickly radiated into empty niches, eventually differentiating into the more than 10,000 species of birds present today. This lecture is all about the path of this remarkable evolutionary story. *Birds* here refers to the group that includes all modern birds as well as extinct creatures like *Archaeopteryx*, but excludes the extinct birdlike dinosaurs like *Troodon*.

DINOSAURS AND BIRDS

The earliest hints of the similarities between dinosaurs and birds were noted by Sir Richard Owen in his paper naming the first fossil bird, *Archaeopteryx*. After the publication of Charles Darwin's theory of evolution, Thomas Huxley argued for the close relationships between *Archaeopteryx* and small theropod dinosaurs like *Compsognathus*. After a half-century-long hiatus, driven in part by the perceived lack of a wishbone in these animals, John Ostrom and the other dinosaur renaissance men announced abundant new data and rigorous cladistic analyses that pushed birds deep into the dinosaur family tree. With the discovery of fluffy dinosaurs in China in the 1990s, the case was made. From there, the evidence has only grown. There's no denying that birds are glorified dinosaurs.

By the earliest days of the Cretaceous period, birds had diversified into myriad forms. Many of these ancient bird fossils have come from Lagerstätte in northeastern China. There, thousands of birds with varied ecology and anatomy existed around 130 to 120 million years ago. In that relatively short interval, evolution had already produced little aerial avian acrobats, semiaquatic forms, and larger-bodied ecological generalists. By the Late Cretaceous, the new group gained specific skeletal adaptations that made them skilled, powerful fliers.

Researchers in the Upper Cretaceous Maevarano Formation have recovered some amazing ancient birds that fit right into this critical period in bird evolution. The first avialan from the formation is *Vorona*. This is a crow-sized animal known from only a few skeletal elements. The second avian is *Rahonavis*, which exhibits skeletal features that can be interpreted as either a non-avian theropod or one of the earliest birds, most closely related to *Archaeopteryx*. It is now known as an early-diverging, non-avian theropod. It exhibits quill knobs that record the presence of feathers on its arms but has a mouth full of sharp little teeth.

Only a couple of years ago, a brand-new specimen named *Falcatakely* was recovered that can confidently be placed, along with *Vorona*, into the group of early birds called the enantiornithines. This group represents the first great diversification of birds. This little bird had a sickle-shaped beak, like that of a toucan. But instead of building that toucan-shaped beak from the premaxillae, *Falcatakely* built its giant beak in the style of more primitive birds, like *Archaeopteryx*, with a small premaxilla and a large maxilla. These discoveries were made through virtual dissection and preparation. In these newer techniques, fossils are scanned using a high-resolution micro-CT scanner and then digitally modeled.

In a single ecosystem in Madagascar, there are full-on birds with derived, fancy beaks; primitive birds that clearly had flight feathers attached to their arms; and animals that are so squarely on the dino-bird border that they keep bouncing back and forth as new fossils are discovered. The growing fossil record allows paleontologists to decipher the critical steps required for birds to gain their signature body plans and behaviors. These steps didn't happen all at once. They were gradually assembled in different, relatively distantly related avian groups.

LEARNING TO FLY

What were the key steps on the way to the sky? Shrink, lighten up, use those feathers in a new way, get smart, stroke, radiate, and survive.

SHRINK

The first step on the way up is to shrink. The oldest birds and their closest non-bird theropod relatives—including dromaeosaurs and troodontids—were already headed that way. These animals were only about as large as a modern chicken. They also had lightweight, air-filled bones, long arms, feathers, and sometimes even wings. This small body trend is the culmination of a 50-million-year history of evolutionary miniaturization in this line of animals, which began in the Maniraptora group. Once this push toward smaller size got going, and especially once birds evolved powered flight, their body sizes shrunk at a rate of about 160 times faster compared to the rest of their evolutionary history.

LIGHTEN UP

The origin of the efficient flow-through lung and air sac system in birds today can be traced deep into the reptile family tree. Both living crocodiles and monitor lizards exhibit circular breathing like birds, but they lack the air sac system. Air sacs came next, evolving as a specialization in early saurischian dinosaurs. Most saurischian dinosaurs—including birds—have distinctive holes in their vertebrae and other bones where these air sacs infiltrated these elements.

Another key step toward a lighter body? Ditch those heavy enameled teeth in favor of something a little lighter and a little more manipulative. Most Jurassic-period birds, including *Archaeopteryx*, still have tiny teeth in their rapidly shrinking skulls. Some Cretaceous birds, especially those adapted for diving, hang on to their teeth as well. But although some birds flew with teeth in their jaws, getting airborne is easier without them.

All modern birds have a gene that can be traced back about 100 million years that deactivates the formation of teeth. The loss of teeth and the development of a beak happened at about the same time in what seems to be a two-stage process. The first phase of change focused on the front of the jaws, with tooth loss and partial beak development. In the second phase, tooth loss and beak development continued from the front of the jaws to the back. This explains why there are some early birds—like *Ichthyornis*—that have a beak up front and teeth in the back.

USE THOSE FEATHERS IN A NEW WAY

The evolution of feathers has been confirmed by their presence in a diverse array of theropods. Some paleontologists speculate that the simple, filamentous, hairlike structures observed in a few plant-eating ornithischian dinosaurs might even hint at a deeper origin for feathers among dinosaurs. That said, the best fossil record of feathers is among the theropods. The initial down-like structures were elaborated into more complex, vaned feathers akin to those in modern birds and maniraptoran theropods.

Some theropods exhibit feathers almost indistinguishable from those of today's birds. In *Microraptor*, these vaned feathers extend from both the arms and legs. Biomechanical models indicate that *Microraptor* could have employed its four wings to glide. For most theropods, feathers may have been used for functions such as display, egg brooding, ornamentation, and thermoregulation. Flight was merely a happy accidental evolutionary development that built upon raw materials that were already present.

GET SMART

Bird brains are special and evolved along with small size and light body mass prior to the evolution of flight. Modern birds exhibit incredible senses. They process three-dimensional data in flight and practice vocal learning. In different taxa, they have highly developed senses of hearing, vision, and smell for finding mates and food. These adaptations for intelligence are mediated, at least in part, by an expansion of the forebrain relative to body size. Forebrain expansion begins early in the evolutionary history of theropod dinosaurs.

STROKE

The undercover anatomy that supports the unique mechanism for flight in modern birds wasn't easy to evolve. The critical change in bone and muscle anatomy mostly focused on the upper arms and shoulders. The theropods most closely related to birds lacked most of the key features needed for powered flight. Maniraptoran theropods first evolved the half-moon-shaped wrist bone that allows a bird to fold its wings.

But even with wishbones and semilunate carpals, the earliest birds still lacked most of the bony features related to powered flight. The mishmash of their anatomy suggests that the first fliers probably had primitive and variable flight capacities. Some may have used fan-shaped feathered tails to increase lift. Others had long tails to stabilize in-air movements. And others, like *Archaeopteryx*, may not have been fliers at all given their lack of most powered flight anatomical signatures—including a broadened sternum for the attachment of strong musculature. These key features appear only in birds that evolved later on.

The final puzzle piece when it comes to the evolution of flight is how it began. All modern birds employ their wings as an airfoil. This provides lift and reduces turbulence and friction. Most of the power of flight comes from the downstroke, fueled by powerful pectoral muscles that attach from the keeled sternum to the arm bones. During the upstroke, birds partially bend their wings using their semilunate carpals, which helps minimize drag. This stroke involves a deeper muscle that slides through an opening between the humerus and furcula, helping to stabilize flight.

If gliding was the starting point for development of the flight stroke, these alternatives are often positioned as a “trees-down” or “arboreal” origin of flight. However, if flapping was the starting point, other scientists contend that the “ground-up” or “cursorial” approach to the origin of flight makes more sense. These two alternatives are based on the idea that gliding requires smaller muscle mass to support the same body weight, whereas flapping requires large muscle masses and enormous work.

Scientists in support of the traditional trees-down hypothesis cite the easier biomechanical sequence for the eventual evolution of flapping flight in birds. It theorizes a progression from being up in the trees and jumping out of those trees with a gliding, controlled fall that employed the arms and legs to direct the aerial descent.

There are more than 30 independently evolved lineages of tree-dwelling vertebrates that employ gliding to descend to the ground. And there is evidence that some non-avian dinosaurs may have evolved side-body skin flaps that would have served as parachutes if these behaviors occurred. Taxa like the four-winged *Microraptor* may have also employed a similar leap-and-glide strategy. That said, there are few, if any, anatomical indications that the ancestors of modern birds spent any time up in the trees.

What about the ground-up hypothesis? In recent years, experimental work in fluffy baby birds has prompted a new idea based on a running and flapping model. Ken Dial, a scientist at the University of Montana, has conducted experiments with juvenile birds to develop a model of wing-assisted incline running. In this model, a bird uses the flapping motions of its wings while running up inclines to develop enough force to propel itself. It does so to gain access to protection, escape from predators, or acquire food. The key argument for this model is that flapping is ancestral for birds. The developing wing can provide useful force for locomotion, even before a baby bird is capable of powered flight.

By the Early Cretaceous period, bird diversity included seedeaters, long-tailed birds, stump-tailed birds, and even diving birds—with sizes ranging from sparrows to turkey vultures. By the end of the Cretaceous, birds were diverse. They included old-school birds living right alongside members of the Neornithes, or the “new birds.”

RADIATE

The dramatic mass extinction event that marked the end of the Cretaceous period triggered a cataclysm that devastated terrestrial ecosystems. The data suggests that birds suffered high rates of mortality and extinction. This curtailed a great deal of early bird diversity. It remains unclear exactly why the group was so heavily affected. Researchers know that multiple lineages of Cretaceous neornithine birds passed through the extinction event. These animals indicate that the ancestors of shorebird-like species were the only dinosaurian survivors. Within 15 million years after the Cretaceous mass extinction, nearly every group of modern birds had originated and diversified.

SURVIVE

Modern birds are the descendants of a long history, one that extends back hundreds of millions of years and has undergone unpredictable twists and turns from four-winged fliers to fuzzy carnivores.

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MARINE MONSTERS OF THE MESOZOIC

This lecture covers the Mesozoic marine monsters. The seagoing vertebrates, such as dolphins, whales, penguins, walruses, and sea turtles, descended from those that first evolved in marine environments but then innovated a new lifestyle on land. The group of terrestrial vertebrates is called tetrapods. Amphibians are included in this group, as are reptiles, mammals, dinosaurs, and birds. Some tetrapods even developed a suite of features that allowed them to break away from their tie to water. These tetrapods are called the Amniota. These animals lay hard-shelled eggs or give live birth on land.

BACK TO THE SEA

From the group of fully terrestrial animals, some lineages went back to the sea, evolving unique new specializations for life in marine systems. Perhaps this was driven by resource availability or exploiting a new environmental niche. This were probably triggered by an accidental error in the genome—or a mutation—resulting in a new feature that could be tried out in different environments. This well-worn evolutionary pattern has been repeated over many instances of convergent evolution.

Take the example of two marine animals—a shark and a dolphin. Aside from the basic shapes of their external bodies, they are different in almost every other way. Consider how each animal breathes. Sharks breathe by swimming, mouths partially open, to move water across gills. Those gills have many tiny capillaries that allow them to extract oxygen from the water and exchange that oxygen with carbon dioxide coming back from their body's circulatory system. Dolphins have to swim up to the surface and take in a deep breath of air. Oxygen flows from the surface air into their lungs, where gas exchange happens via alveoli. Then, they must hold their breath when they dive back underwater.

Moreover, the bodies of sharks are made of cartilage, while dolphins have skeletons made of bone. In sharks, the front fin is made of thin, cartilaginous rays. In dolphins, the front fin is a modified hand, made up of the same bones that are found in human hands (but with more phalanges). Sharks don't have hair, but baby dolphins do. And finally, dolphins have horizontal tails, while sharks have vertically oriented tails. All these differences highlight the pattern of convergent evolution that you can observe in many amniote groups over the history of life on Earth.

For those amniote lineages that returned to the sea, the environment helps push the evolution of form toward the same basic tricks that are well suited to water. One of the best examples of this is found in the fossil record of whales. It preserves an awesome story of gradual transitions from fully terrestrial wolflike creatures, with four legs and sharp, carnivorous teeth, to animals with shorter forelimbs, paddle-like hands, and a longer, more muscular tail. The pelvis gets smaller and separates from the backbone. This allows whales to use their whole vertebral column for swimming. Why? Because marine mammals like dolphins and whales evolved from land mammals whose backbones don't bend from side to side when they walk, but rather undulate in a wave, up and down.

CLEARING THE PLAYING FIELD

Consider some of the first groups of organisms that capitalized on this return-to-the-sea strategy in the Mesozoic. There are two things to remember about this period of time. First, the beginning of the Mesozoic era was marked by a significant mass extinction event. The Permian-Triassic extinction wiped out an estimated 95% of all life on Earth. The marine world was decimated, just like the terrestrial world was. For any organism lucky enough to pass through that massive extinction filter, the other side was a world full of open niches where evolution could do its work.

The second thing to remember is what the globe looked like. The planet at the beginning of the Mesozoic was a world with great expanses of land and water. There were no polar ice caps. Ocean environments persisted throughout the whole Mesozoic. They sometimes even included giant continental seaways, like the Western Interior Sea, that divided the North American continent in the Cretaceous period into eastern and western halves.

The most straightforward way to tackle the diverse array of Mesozoic marine monsters is to start with their evolutionary tree. Considering the amniotes, you can follow their branches to our own lineage (the synapsids) and to the group typically thought of as reptiles, or the diapsids. This group gets split into two large tribes: the lepidosaurs, including living lizards and snakes and all their close relatives, along with many extinct animals; and the archosaurs, including crocodiles, pterosaurs, dinosaurs, and birds. The swimming reptiles aren't dinosaurs or archosaurs. In an evolutionary sense, they are nested within the lepidosaurs but clumped together with lizards and snakes.

THE MARINE MONSTERS

The beginning of the Triassic witnessed an adaptive radiation. The survivors of the Permian-Triassic extinction event diversified in a geologically short period of time. It was in these early days that the first land-based Triassic reptiles began to colonize the seas.

The earliest seaward forays resulted in a bunch of cool-looking, weird early experiments with marine life. Animals like *Tanystropheus*—from the Greek words for "long" and "hinged" to describe its neck—showed up with its needlelike, fish-eating teeth. Or consider the placodonts—Greek for "tablet teeth." These marine reptiles had a mouth full of crushing plates.

These first marine reptiles still had fingers and toes—though they may have had webbing between them—and likely still spent time on shore. A key adaptation among these earlier experimenters was the innovation of retaining and hatching eggs within the mother's body until the babies were able to swim and fend for themselves. These marine reptiles could stay in the water, retaining their eggs internally, and eventually give live birth to well-developed young. This key amniote adaptation allowed marine reptiles to diversify even more. By the Middle Triassic, the three major groups that would rule the oceans until the Cretaceous-Paleogene extinction 66 million years ago were already present. They are the plesiosaurs, the mosasaurs, and the ichthyosaurs.

The marine reptiles were discovered before the first dinosaurs were. In the early 1800s, fossils were beginning to be seen as the remains of animals that lived in ancient worlds. There was significant amateur and scientific interest in the new field of undergroundology. On the British coast, a sequence of marine shale was the collecting ground for Mary Anning. Around 1810, when Mary was only 12 years old, she and her brother spotted the strange smiling mouth of the first-ever-found marine reptile poking out of the Jurassic-aged marine shales near her home in Lyme Regis. They dug into the hill, exposing a five-meter-long skeleton that was eventually named *Ichthyosaurus*, from the Greek for "fish lizard." Moreover, in 1823, Mary discovered a complete specimen of *Plesiosaurus*, meaning "near to lizard." Remember, the first known dinosaurs weren't consolidated into a group by Sir Richard Owen until 1841.

Marine reptiles are often found in beautiful condition, preserved in three dimensions, with all their bones still intact and articulated perfectly. Since they lived and died in marine ecosystems, their dead bodies would often drift down to the seafloor. In certain conditions, they'd be spared from harmful processes like scavenging, bacterial decay, weathering, or disarticulation. Sometimes, if they were covered over by sediment quickly enough, bacteria wouldn't even have time to degrade all their soft parts.

PLESIOSAURS AND MOSASAURS

The plesiosaurs have four fins, built by elongating the phalanges. This is called hyperphalangy. Plesiosaurs take this basic body plan and evolve into two main groups. The elasmosaurs are known for their long necks and small skulls. The pliosaurs are known for having short necks and humongous skulls. This type of variation points to some niche partitioning in this group of marine reptiles. Some plesiosaurs, like living whales, may have been up to 45 feet long. Plesiosaurs also have little conical teeth perfect for stabbing fish. They were fearsome predators in Jurassic and Cretaceous oceans.

The next group of marine reptiles is comprised of the mosasaurs. These beasts were prowling around in ocean ecosystems when the last dinosaurs were ruling the Late Cretaceous world on land. Mosasaurs are closely related to modern-day lizards like Gila monsters or monitor lizards. Mosasaur limbs have transitioned into webbed hands and feet. They have real separation between their fingers and toes. And the tails of mosasaurs are broad and flattened from top to bottom, giving them a great propulsive tool in their underwater world. In terms of moving through water, some mosasaurs may have exhibited more sinuous, snakelike swimming. Others exhibit the streamlined, sleek bodies indicative of tuna-like swimming and a highly agile, predatory lifestyle.

Some mosasaurs exhibit cranial kinesis, in which there is significant movement between skull bones, and movement at the joint between the upper and lower jaws. Some of this movement is sliding, and some is rotational. This gives mosasaurs a fearsome bite and an ability to open their jaws much wider. There is great evidence of mosasaur diets preserved in shale sedimentary rocks from the Western Interior Sea—many ammonites and sea turtle shells punctured by the sharp teeth and powerful jaws of these terrifying predators.

ICHTHYOSAURS

The ichthyosaurs were some of the largest and most specialized of the marine reptiles. They were among the first to diversify in Triassic oceans and among the first to go extinct. By the time the last dinosaurs had evolved, the ichthyosaurs had disappeared. These dolphin-like swimmers were top predators in marine ecosystems for more than 150 million years.

The group is far more diverse than you might expect, ranging from nearshore, eellike, undulating swimmers to giants that cruised the ocean. Massive anatomical changes occurred in the Ichthyosauria group to transform ancient land reptiles into this fully aquatic species. Every part of their bodies was impacted—from their pointed faces to their dorsal fins and their exaggerated front flippers with intense hyperphalangy, accompanied by the disappearance of their hind legs.

And then there are the hockey-puck-like stacks of vertebrae that promoted side-to-side locomotion. Some even evolved humongous eyes that indicate they were able to capture the little bit of light present at great depths. The eyes of some ichthyosaurs were so large that they exhibited special bones, called sclerotic rings, that helped support their mass. Modern animals that have big eyes, like owls, have the same kinds of rings in their eyes too.

Some ichthyosaurs have been preserved with remarkably detailed skin impressions outlining their bodies in a halo that highlights their torpedolike shapes. From such impressions, you can see that their tails included small bones supporting the bottom part of the vertical fin, but not the top.

However, recent data indicates that ichthyosaurs fell victim to two climatic hits. The first came about 100 million years ago, in the middle of the Cretaceous period, when marine waters were deepest and oxygen concentration in those waters was relatively low. Then, a few million years later, came another, similar hit. Perturbation in ocean and atmospheric temperature may have been serious enough to push ichthyosaurs to the end of the road.

When paleontologists find the articulated skeletons of plesiosaurs and ichthyosaurs with babies, they can recognize that—in all cases—the babies are being born tailfirst. Only animals that stay put in the water would have such an adaptation. Compare this with modern whales and dolphins, which also give birth tailfirst. If marine mammal babies were born headfirst like in other mammals, they would risk drowning while being born because birth may be a long ordeal. Thus, by giving birth tailfirst, ichthyosaurs and plesiosaurs converged upon the solution to this problem.

SPINOSAURUS

Were there any swimming dinosaurs? The jury is still out on that one. However, some recent discoveries in the deserts of North Africa have rekindled a long-standing debate that a large-bodied theropod called *Spinosaurus* may have patrolled the waterways in its ecosystem in search of its next fishy meal. *Spinosaurus*, which means "spine lizard," was discovered in the desert of the Bahariya Oasis in Egypt in the early 1900s. Its large size, sharp teeth, and distinctive vertebral spines made it an instantly recognizable superstar dinosaur. The bones from the original find were

destroyed during the bombing of Munich in World War II. New finds of *Spinosaurus* have prompted some researchers to investigate its biomechanical capacity for swimming, with differing conclusions.

Some researchers point to the fish-eating, conical, simple dentition of *Spinosaurus*, combined with its unusual tall and flat tail. They say that this tail could have propelled *Spinosaurus* through an underwater world efficiently. This would make it the only known aquatic predatory dinosaur. Other researchers note that the tall spinous processes and resulting bony fan on the animal's back would cause too much drag for it to be an efficient swimmer.

Isotopes preserved in the teeth provide hints at this dinosaur's diet. Although there is a signature of fishy feasting, there is also strong evidence that *Spinosaurus* regularly dined on other dinosaurs and terrestrial vertebrates. Moreover, these researchers point to the details preserved in the geological record that indicate estuary-like, swampy environments. With that giant sail on the back, these scientists argue that the only way for *Spinosaurus* to be an energy-efficient swimmer would be to swim at depth. However, this doesn't seem plausible given the geology of the surrounding rocks.

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WEIRDEST WONDERS ON WINGS

Not all creatures living in the age of dinosaurs were dinosaurs. Just as there were non-dinosaur monsters in the ocean's depths, there were also great beasts that weren't dinosaurs in the skies. In this lecture, you will learn about the phenomenal pterosaurs. (The *p* is silent.) *Ptero* comes from the Greek for "wing," which means that pterosaurs are known as the "winged lizards." These guys are one of the wildest inventions of evolution ever.

VERTEBRATE WINGS

Pterosaurs are pretty remarkable because they are the first group of backboned animals to take to the sky. Recall that the animals living in the age of dinosaurs were extremely diverse. Although at first glance they might all look basically the same, pterosaurs are incredibly different. They have specializations for life in all sorts of different skyward ecosystems.

In terms of their evolutionary history, pterosaurs are most closely related to crocodiles, dinosaurs, and birds. Thus, they are in that group of ruling reptiles, the archosaurs. Pterosaurs are a bit more closely related to the dinosaur-bird part of this family tree. They share a handful of features with dinosaurs and their living descendants—namely, the way that their legs and ankles are built.

All pterosaurs are characterized by their unusual wings. Based on the evidence, pterosaurs were the first among the vertebrates to lift off from the ground into the air. They did this in a completely unique way. Consider the comparative anatomy of the way wings are built in three different types of creatures: pterosaurs, birds, and bats. Flight requires the addition of some kind of supported airfoil, or wing, that is attached to the arms.

Consider the bones that make up the wing supports for pterosaurs, birds, and bats. Starting at the shoulder, there is the humerus—this is the upper arm, the place where the bicep muscle is. The radius and ulna are the bones of the forearm. These are connected to a bunch of tiny wrist bones called the carpals. The bones inside the hand, in the area of the palms, are called the metacarpals. Humans have five of these, which is the ancestral number for tetrapods. Finally, the fingers are made up of phalanges. For fliers, the phalanges are pretty important. But each of the vertebrate fliers modified these arm elements in distinctive ways that highlight their convergent evolution.

Bats have a familiar handlike structure inside their wings. Bats still have a humerus, radius, and ulna, like humans. They have carpals, five metacarpals, and a bunch of phalanges, also like humans. To turn that typical mammalian hand into a bat wing, evolution elongated both the metacarpal and the phalanges and stretched a thin, flexible membrane in between them. For good measure, that membrane was extended from the pinky finger to the ankle and all the way up to the arm bones.

Birds also hang onto their humerus, radius, and ulna. At the wrist, they have carpals, but most importantly, they have the semilunate carpal. Birds have lost two fingers over the course of their evolutionary history. They are left with only three remaining fingers, which get fused together into a stiff little nub. The flight feathers of birds are suspended from their humerus, ulna, and fused-together fingers.

Pterosaurs, too, have the humerus, radius, and ulna. They have carpals but evolved a new bone unique to them. They also have most of their metacarpals. However, at the ring finger, not only does the metacarpal get super long but also each of the distal phalanges stretches out and elongates. Pterosaurs hang their entire wings from their ring finger and from their arms. This thin wing membrane made of skin stretches from the tip of this insanely long ring finger and along the sides of the body.

Still, despite the differences between these three kinds of wings, there are some similarities. All these wings are built from arms, wrists, and fingers. However, each wing emphasizes different components of these body parts. They even use different materials—skin or feathers—for the flying surface. The important takeaway from these wings of vertebrate fliers is convergent evolution.

THE PTEROSAURS

In many ways, you can think of all other vertebrate fliers as copycats of these awesome pterosaur pioneers. There are great fossils of pterosaurs from places like Solnhofen. These sites preserve exquisite soft-tissue details in pterosaur fossils that give paleontologists a great look at how their wings are attached to the sides of the body.

Pterosaurs can be divided into two distinctive groups. The first evolved pterosaurs are called the rhamphorhynchids. These pterosaurs are relatively small-bodied, with a long bony tail, and heads that lack fancy head ornamentation. This group includes many diverse genera and species. The other major group of pterosaurs is the pterodactyls. These pterosaurs evolved a bit later—likely from a rhamphorhynchid ancestor—and include large-bodied species. Pterodactyls have short, stubby tails and elaborate cranial crests. Many pterosaurs had heads that were larger than their bodies. These creatures evolved along with dinosaur ancestors in the Triassic—and also gained a global distribution.

All pterosaurs have a handful of diagnostic features in common. Imagine a pterosaur body plan from the inside out. The wing finger and bones of the arm are both strong and lightweight, their interiors filled with air. The bones themselves are crisscrossed by thin struts or lined with helices that reinforce the strength of these thin-walled tubes. At the wrist, pterosaurs evolved a special bone called the pteroid that is found in no other animal. It was likely connected by a ligament to the shoulder and supported the leading edge of a wing membrane that ran from the bend of the elbow to the shoulder. The phalanges of that long wing finger were moved around by long tendons that were connected to muscles in the forearm. It's an effective way to distribute muscular force over long distances. Tendons stretched to the tip of the wing finger, transmitting force and stabilizing the wing during flight. The powerful muscles needed to flap its wings attached to a broad, flat sternum, with plenty of expanded surface area for the origin of these large muscles.

Pterosaur wings were made of tissue layers that included thin, delicate muscles, loops of blood vessels, and connective tissue invested with actinofibrils that helped to stiffen the wings and reduce vibration. The presence of that pervasive blood supply to the wings is similar to what researchers observe in bats. Bats also have delicate, thin, skin-based flight membranes.

When bats tear their wings, they need to heal them quickly. Wings are the bat's key form of locomotion, which means they're also the key means for catching food. Therefore, if a wing is injured, the bat has a high risk of dying. To help them heal quickly, bat wings, like those of pterosaurs, are invested with blood that supplies both energy and healing white blood cells if the wings become damaged. A bat with a hole in a wing membrane can completely repair the wing in a couple days, allowing it to fly again. It's likely that the looping vasculature network in pterosaur wings served a similar function.

Pterosaurs also exhibited hairlike or feather-like integumentary fibers, called pycnofibers, that come from the skin. These fibers take on a variety of different morphologies—from fluffy hairs to downy feathers—and are distributed all over the body in pterosaurs. The presence of pycnofibers on the wings and bodies of some pterosaurs have hinted at the possibility that they may have had warm body temperatures. These insulating structures prevent the rapid exchange of heat.

Pterosaur embryos have been discovered inside eggs, which turn out to be a little softer-shelled than in most other reptiles. Pterosaur nests discovered with the fossilized remains of adult pterosaurs also point to the possibility that pterosaurs were good parents. Perhaps they took care of their eggs and nests at least until the babies hatched. Details of development were revealed by taking a close look at the bones and muscle scars of the embryos. Though their leg bones look ready to go, key features of the muscle attachments to the upper arm are still poorly formed. This points to baby pterosaurs that probably popped out of their eggs ready to walk but needed a little more time before they were ready to fly.

Pterosaur diets are super diverse, as recorded by the many different head shapes, tooth morphologies, and teeth arrangements within the jaws. For example, *Pterodaustro* has a crazy-looking lower jaw full of thin, delicate teeth and no teeth on its top jaw at all. Paleontologists think *Pterodaustro* would scoop up water filled with tiny invertebrates, close its mouth, and strain out the food by letting the water flow between its teeth. Other pterosaurs have short, sharp teeth that may have been great for catching fish. Still others have teeth located only at the front of their unusual jaws. Often, teeth isolated at the front part of the face point to a selective and particular diet. And of course, there's reason to imagine that pterosaurs—especially the large species—fed on small dinosaurs.

PTEROSAUR MOVEMENT

Early scientists imagined that pterosaurs were probably fairly competent land locomotors. However, debates raged about the way they might have walked. Other scientists imagined that pterosaurs would have been incapable of effective terrestrial locomotion and might have been capable only of climbing. In this scenario, grounded pterosaurs would have had to push themselves around with their bellies dragging across the ground.

Luckily, for paleontologists, pterosaur footprints hold the answer. There are many footprints of pterosaurs walking on the ground. This record extends back in time to some of the oldest, smallest pterosaurs known: the long-tailed rhamphorhynchids. A bird-sized rhamphorhynchid trackway was discovered in France, alternating front and back footprints, each only a few centimeters long. These tracks show that early pterosaurs walked using both their arms and legs. Their fingers in their forelimb traces point forward, indicating that they were good walkers. Later pterosaurs were also capable of walking on land using all four limbs.

Pterodactyls were supported on land by their phalanges in the forelimbs and by the entire bottom of their hind feet. Only the first three fingers regularly touched the ground. The elongated fourth finger was probably folded and stored up close to the body when not in flight. Thus, both the arms and legs were held near the body in a more upright position most of the time. The exception comes only when running or walking quickly, which pushes the forelimbs into a slightly more sprawled position to gain a greater reach with each forward step.

PTEROSAUR FLIGHT

Michael Habib spent years working out the mathematical possibilities for exactly how pterosaurs got airborne. According to Habib's work, there are three prerequisites for flight in giant vertebrates. First, they must have skeletons that are both strong and light. Pterosaurs meet this requirement easily. Second, they must have a mechanism for producing serious lift. The membrane-based wings of pterosaurs and bats produce more lift per unit speed and area than the feathery wings of birds. And finally, they have to have a mechanism for a powerful launch.

The four-limbed ground locomotion of pterosaurs may have been a critical piece of their launch mechanism. Habib used mathematical modeling to develop a well-supported hypothesis for pterosaur takeoff. The key to pterosaur launch may have been a two-stroke leap. Following an initial push-off driven by the hind limbs, they could have employed a catapult-like movement with their forelimbs. This would have allowed them to integrate the stored elastic energy of the long tendons in their hands with their powerful forelimb flight muscles to get airborne.

Different pterosaur species flew in different ways. This can be recognized in part by the shapes of their wings. Even early pterosaur wing morphologies indicate relatively slow and highly efficient flight, with excellent potential for maneuverability. The largest pterosaurs, such as *Quetzalcoatlus*, probably wouldn't have had to flap their wings continuously to stay aloft. In fact, for these largest pterodactyls, continuous flapping over long periods of time may have been biomechanically impossible. Paleontologists think that these largest pterosaurs were capable of rapid cruising, with an ability to powerfully flap their wings in short bursts.

Pterosaurs with especially long and narrow wings might have flown continuously for long periods of time. Perhaps they touched down only to mate or lay eggs. *Nyctosaurus*, from the Greek for "night lizard," is thought to have had the best capacity for continuous soaring flight among vertebrates. The wing shapes of pterosaurs across their family tree, combined with their cranial feeding adaptations, all point to adaptation as aerial predators. Thus, nyctosaurs wouldn't have needed to land to eat.

Another cool aspect of pterosaur paleobiology is the analysis of the cranial anatomy of pterosaurs from both groups. Comparisons of CT scans from the skulls of pterosaurs indicate that both the large pterodactyls and the smaller rhamphorhynchids had the brainpower to process detailed three-dimensional data.

Pterosaurs ruled the skies for more than 80 million years. The end of their reign came with that cataclysmic asteroid impact 66 million years ago. It's unclear why some birds might have survived while the pterosaurs were wiped out. Some researchers suggest it is about being too large during the apocalypse. Others point to the environmental conditions after the event, in which atmospheric conditions may have discouraged soaring around the world for months on end. This would have forced the starvation-based extinctions of anything that had to fly to survive.

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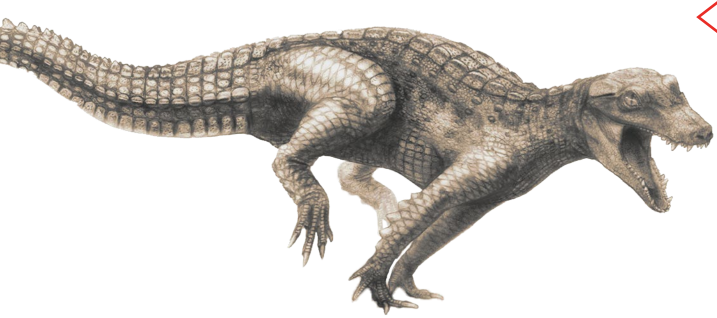


THE NON-DINOSAURS IN THE AGE OF DINOSAURS

This lecture will consider all the other creatures that tend to go missing in popular artwork and media treatments of dinosaur worlds. These include turtles, crocodiles, snakes, scorpions, birds, and mammals. These are the smaller, inconspicuous creatures that ran beneath the feet of dinosaurs, buzzed annoyingly in their ears, and occasionally may have even preyed upon them. These creatures fill out dinosaurian ecosystems. When they are put into the mix, the entire world springs to life.

CREATURES OF THE MAEVARANO FORMATION

Recall that in Madagascar, paleontologists are working in sedimentary rocks that make up the Maevarano Formation. The sandstones and ancient soils in the formation record a paleoenvironment that alternated between intense, prolonged droughts and periods of abundant rain, making it a perfect place to get fossilized.

Death came frequently during the dry seasons in ancient Madagascar. For those that fed upon the dead, widespread mortality created an environment of plenty. There is an entire ecosystem created in and around the carcasses in the fossil record. Necrophagy—the act of consuming decaying flesh—is a critical niche within ecosystems if biological recycling is to occur.

Using a scanning electron microscope and thin sections of bones viewed at high magnification, paleontologists have found the fossilized signatures of the teeniest scavengers preserved as microscopic pits and tunnels through the deepest interiors of *Rapetosaurus* bones. And in many dinosaur bones in the Maevarano Formation, researchers have located the traces of pupae and the specific feeding characteristics of carrion beetles. Centimeter-long oval pits scored by little cross-hatched scrapes tell the tale. These little pits are commonly found in the spongy bone of dead dinosaurs, where adult beetles laid their eggs. After hatching, larval beetles continued to feed on the rotting meat but also used their strong mandibles to excavate these pits in the bones. The larvae then crawled into the pits and pupated there before undergoing metamorphosis and continuing the cycle of necrophagy.

What kinds of fish swam through the wide, shallow waterways that were common in the Mahajanga Basin 70 million years ago? Paleontologists have found tons of little fish vertebrae and teeth. However, most of the fragmentary body fossils aren't detailed enough to allow them to identify these fish too specifically quite yet. As it turns out, though, one kind of fish leaves behind a specific sort of trace fossil that allows for a precise identification.

MAEVARANO LUNGFISH

Ray Rogers is great at reading the rocks that entomb fossils for clues about ancient ecosystems. Rogers recognized an unusual sandstone outcrop in the field area that exhibited a bunch of circular and dumbbell-shaped features. He excavated down and essentially created a cross section through the surface circles and dumbbells. The unusual features extended down into the Cretaceous subsurface, cutting across layers of rock and deforming the linear bands of sediment as they went. He mapped more than 70 of these structures in approximately 100 square meters of outcrop, which indicated that they weren't random. The only thing that made sense was that these features were left behind by animals burrowing into the soft sediment.

But what kind of animal? All evidence pointed to lungfish. The features were the right size and especially the right shape, starting off as lengthy circular or oval tubes. But eventually, underground, the tubes changed into a dumbbell shape where the animal would have folded itself in half near the bottom of the burrow.

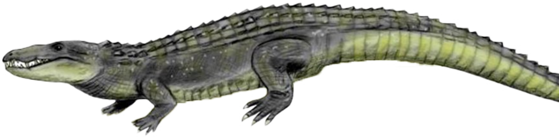
You see, when times get tough, lungfish have a trick up their sleeves: They squirm down into muddy sand at the bottom of their rivers and surround themselves with a mesh of sticky, hydrating mucus that keeps them from drying out. Then they slow down their heart rate and essentially go to sleep, estivating underground. Even if the rivers that they swim in during better times dry up completely, the lungfish can wait in their burrows until the rains return water to the system. As those first drops of rain soak the riverbed above, the lungfish sense the change, wake up, and wiggle back out. This process of burrowing in and out created the distinctive trace fossils that Rogers discovered in the Maevarano Formation.

MAEVARANO CROCS

A diverse clan of crocodiles hunted the land and rivers of Madagascar throughout the Cretaceous. So far, paleontologists have uncovered more than seven different types of crocs in the formation. These range in size from the 3-foot-long *Araripesuchus* to the 10-foot-long *Mahajangasuchus*. Some of these crocodiles would have looked familiar—their body plans were pretty similar to those of modern crocs, alligators, and gharials. For instance, the large-bodied crocodile *Mahajangasuchus* had a semiaquatic lifestyle, like crocodiles and alligators today. But in the past, there were many that adapted to a terrestrial lifestyle, making them look quite different. In Madagascar, *Araripesuchus* pursued small prey on long legs that were suited for running, not swimming.

During a field season in Madagascar, croc specialist Greg Buckley and a paleontologist came across a slope in the Maevarano Formation that was littered with bones called osteoderms or scutes. They make up the armor plates that give crocodiles their distinctive scaly-looking exteriors but are bony plates that grow within the skin. The duo tracked the bones back up the hill to the area where they seemed to be pouring from the rocks. Over the next week or two, they carefully excavated this specimen and could see all the armor plates, arms, and legs. The hope was that this new specimen would be an elusive long-snouted crocodile. They decided to stop the excavation and project forward a few feet so that they wouldn't disturb the delicate skull—if there was one—as they extracted the specimen from the hill. This meant that they applied plaster and burlap to a large rectangular block of sand and bone. Then, they carried this giant block for miles back to camp.

The specimen was placed into a crate, loaded onto a ship, and transported to their museum. Buckley excitedly cracked open the plaster surrounding the bones and was met with one of the most bizarre and unexpected things ever found in Madagascar. The specimen lacked the elongated skull and conical teeth typical for most crocodiles. Instead, the skull sported a snout that was perfectly preserved but looked as though it had run into a wall. The teeth were shaped like little mittens, flattened front to back, with little bumps that looked more like the dentition of a plant-eating lizard than any known crocodile. Buckley named the new crocodile *Simosuchus*, which literally translates to "pug-nosed crocodile." It was an armadillo-like, heavily armored, squat, dog-sized, plant-eating crocodile.



MAEVARANO TURTLES

Maevarano baby dinosaurs and small crocs like *Simosuchus* would have had good reasons to be crafty, armored, camouflaged, and quick. A giant frog hopped through the ecosystem. *Beelzebufo* means "devil toad." Like modern frogs, *Beelzebufo* was carnivorous and probably ate pretty much anything it could wrap its mouth around, including prey close to its own size. This was a frog that was larger than a basketball, horned, and hungry.

The discovery of new bone beds usually happens the way that it happened for *Simosuchus*: Someone will spot a little trail of broken fragments of bone, which have weathered out of somewhere upslope. Then, they'll track those bits and pieces back to the source. Often enough, though, important discoveries occur completely by accident. This can happen when paleontologists' sights have been set on digging up something else that they've found. Along the way to exposing the layer of interest, they have to remove plenty of rock. They call the sediments that lie on top of the target fossils overburden. One of the first tasks in opening a new fossil quarry is to remove all the overburden.

Once in a while, while removing that overburden, someone's shovel or pick comes down upon another bone-bearing horizon—often one that they couldn't see from the surface. Such is the story of a recently described new species of turtle from the Maevarano Formation.

Only one meter above a layer containing a promising bone-bearing horizon filled with croc and dinosaur fossils, a lucky paleontologist struck pay dirt with their pick—it was a complete skeleton of a well-preserved turtle. The new species was named *Sahonachelys mailakavava*, which combines the Malagasy words *sahona* for "frog," *mailaka* for "quick," and *vava* for "mouth" with the Greek word *chelys* for "turtle." The name thus means "quick-mouthed frog turtle." Details of its anatomy indicate that, along with its turtle features, it had a slightly frog-shaped, flattened skull with a broad mouth. Strong throat muscles allowed *Sahonachelys* to suction feed. By widening the space inside the mouth and throat, negative pressure literally allowed prey to be sucked down *Sahonachelys*'s gullet in the blink of eye.

In the Maevarano rivers, *Sahonachelys* joins another genus of turtle called *Sokatra*. Both are members of a group called the side-necked turtles, which have to pull their necks into their shells in a sideways loop. These turtles spent most of their time in muddy river bottoms and shallow pools. There, they fed on invertebrates, including mollusks, worms, and insects. These two turtles may have estivated through the dry season by burying themselves in the mud.

MAEVARANO SNAKES

The Maevarano snake assemblage is more diverse than any other Cretaceous snake fauna anywhere on Earth. It also exhibits a size range that is equivalent to that observed in modern tropical faunas. So far, more than six species of snakes have been recovered, none of which are closely related to snakes that inhabit modern Madagascar. The largest (and scariest) snake is an eight-meter-long, heavy-bodied ambush predator that researchers hypothesize subdued its prey via constriction. At around 26 feet long, it is the largest snake ever discovered in Mesozoic rocks anywhere on Earth. Another closely related snake was only about three meters long. However, it has anatomical features that suggest it was a powerful headfirst burrower. The smallest snake in the assemblage so far is most closely related to a group of snakes that typically specialize in aquatic environments. But *Kelyophis*—“little snake”—lacks most of these key specializations for swimming, perhaps due to the arid and relatively dry Maevarano ecosystem.

ANCIENT MALAGASY MAMMALS

Recall that the paleontology project on the Great Red Island began in search of ancient mammals that might shed light on the origin of the modern-day Malagasy endemic fauna, including lemurs. To date, paleontologists have recovered two exceptional mammal fossils from the Mahajanga Basin. It took a hospital CT scanner to see through sediment and reveal these important and exciting new creatures.

The first mammal came out of a discovery of fish bones. A paleontology team located a great sedimentary layer that contained tons of fish parts. The team decided to encase the entire layer in a large plaster jacket so that the work of exposing each tiny, fragile fragment could be done in a more controlled setting.

Everything in paleontology takes patience. From the long ship ride from Madagascar to New York Harbor and then the truck ride to Denver to the uncrating and curating of the field jackets, the researchers had to wait a few years to study this block. At long last, the plaster jacket ended up on a hospital CT scanner. There, in the corner of the plaster jacket, was the unmistakable skull of a mammal. Mammals have a different organization of the bones in their skulls, which makes it easy to identify them, even in a low-resolution CT scan. The new animal was named *Vintana*, a Malagasy word that means "lucky."

The skull was nearly five inches long—twice the size of the previous Southern Hemisphere record holder and much larger than the skulls of most other Mesozoic mammals, which were closer to the size of shrews or mice. Based on this large skull, *Vintana* is estimated to have weighed about 20 pounds. The skull preserves wide, enlarged eye sockets that would have held substantial eyes, perhaps for night vision. Its teeth are made for nipping and grinding plants, with molar-like back teeth. And the shape and size of the inner ear and nasal passages indicate that *Vintana* was great at hearing and sniffing.

The second mammal was also collected by happenstance, in association with a small crocodile. The team used plaster and burlap to protect rock surrounding a hatchling-size crocodile specimen they spotted. When the large block was CT scanned, tucked within was the most complete mammal skeleton ever discovered in any Mesozoic rocks in the Southern Hemisphere. It's the only known skeleton of a poorly known group of early mammals called the gondwanatherians. When preparators popped open that plaster jacket, they realized that every bone was preserved and still in anatomical position.

The new mammal was named *Adalatherium*, which means "crazy beast." *Adalatherium* was about as long as an average house cat and weighed in at only about seven pounds. It had tons of holes in the bones of its face that served as passageways for nerves and blood vessels. This indicates that *Adalatherium* had a sensitive snout covered in whiskers.

Its front teeth were rabbitlike, and its back teeth were made for breaking down a diet of tough plants. *Adalatherium*'s front legs were stacked under the torso, like most living mammals organize their limbs. These front legs exhibit broad paws and claws that point to a burrowing or digging lifestyle. But the hind legs were sprawled out to the sides, held in a position more like that seen in lizards than in mammals. Researchers used to imagine that the gondwanatherian mammals were closely related to modern-day sloths, anteaters, and armadillos. Instead, *Adalatherium* helps demonstrate that gondwanatherians were merely an early, interesting evolutionary experiment for mammals. Eventually, the entire group would go extinct, but not until after the end-Cretaceous extinction event 66 million years ago.

Regarding the exceptional preservation of this articulated specimen of *Adalatherium*, it may have been buried quickly after death before scavengers could tear the carcass apart. Alternatively, perhaps it was buried alive in the fine-grained debris flows that churned down the riverbed at the end of the dry season when the rains returned.

MAEVARANO BIRDS

Overhead, the Maevarano skies were alive with a diverse array of birds. The two best-preserved birds are crow-sized. *Vorona* is a flying bird that retained teeth and clawed fingers on the wings, like other members of the enantiornithines. A second, recent discovery of the unusual skull of *Falcatakely* throws another largish bird into the mix. *Falcatakely* has a scythe-shaped beak, similar to the humped beaks of hornbills and toucans. This unusual beak evolved independently in these different avian lineages, with connections between individual skull bones that are still dinosaur in nature.

A final feathered dinosaur named *Rahonavis* has stumped paleontologists since it was first discovered. With clear evidence of flight feathers on the arms and a toe perfectly suited for perching, it was initially interpreted as a true bird. More recent work has pushed this winged creature back down into the theropod family tree.

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DISSECTING A *T. REX*

This lecture covers some of the new methods used to look at fossils through the exciting insights they've given researchers into *Tyrannosaurus rex*. Estimated to have been about 40 feet long, with a mass similar to that of a modern African elephant, *T. rex* had two powerful legs directly under its body and a tail that extended straight out. Its arms were so short that they couldn't even reach its mouth. Its jaws were giant and sported six-inch-long serrated, conical teeth. The teeth also have little bumpy serrations that make them perfect for slicing through flesh.

THE EXTANT PHYLOGENETIC BRACKET

One of the most powerful methodological tools that has evolved since 1995 is the extant phylogenetic bracket (EPB). This is a method for inferring whether an extinct species had a certain feature by examining the traits that researchers can directly observe in its nearest living—or extant—relatives.

The EPB is a powerful method for interpreting dinosaur features, especially those not easily preserved in the fossil record. Reconstructions of the soft-tissue structures, sensory capacities, and behaviors of dinosaurs are regularly grounded in comparative approaches like this that draw extensively on observations made in living animals. The firsthand knowledge of the soft-tissue systems in today's animals provides critical information on how these soft parts interact with bones to produce osteological correlates. These are little traces on bones that reveal the presence of particular structures.

The EPB works by looking at two living organisms that "bracket" the fossil creature of interest. Since dinosaurs and pterosaurs both fit within Archosauria, paleontologists can use the two groups of living archosaurs—crocodilians and birds—to "bracket" their interpretations. If the two living relatives share a particular feature in common, paleontologists can use the principle of parsimony to reasonably hypothesize that the extinct dinosaur or pterosaur also had this feature. Essentially, they are hypothesizing that the shared feature must have evolved before the diversification of the group. Thus, all members of the group inherited a particular feature from their common ancestor.

If you want to try to determine whether *T. rex* might have had color vision, it would be pretty tough based only on the study of bones. But with the EPB, you can ask, "Do *T. rex*'s living relatives see in color?" It turns out that both crocodilians and birds do see in color. Thus, you can reasonably hypothesize that *T. rex* did as well.

However, if only one member of the EPB has a particular feature, then you can't be as confident in your assessment of *T. rex*. With color vision, birds can rely on ultraviolet (UV) wavelengths, but most crocodilians cannot see in the UV spectrum. *T. rex* may have been able to see in the UV spectrum, indicating that this feature evolved in the common ancestor of *T. rex* and birds. Or it may not have been able to see in the UV spectrum, which would mean that this feature evolved independently in birds. Either answer is equally likely. Researchers often frame their hypotheses of such soft parts within the EPB to add a bit of testability and rigor to their considerations.

Here's another great example: Did dinosaurs like *T. rex* have fleshy lips that could fully cover their teeth? Employing the EPB gives you a likely "no" answer. *T. rex* was probably more like the Komodo dragon, which has skin made up of specialized scales that covers most of the teeth. But the tips of the teeth probably would have been visible at all times in *T. rex*, like in crocs and Komodos.

T. REX'S BRAIN

The braincase region of the skull houses the brain and cranial nerves. It also partially or completely encloses some of the most important sense organs—including the inner ear, the eye, and the structures associated with smell.

In fossils, braincases are deep within the skull and often get filled by sediment, making them difficult to study. Back in 1912, Henry Fairfield Osborn attempted to describe *T. rex*'s brain structure by pouring plaster into a cut-open skull specimen to reveal the rough shape of the brain via a cranial endocast. However, while this method provided an important first glimpse of the brain of dinosaurs, it was destructive to the fossil.

Fortunately, paleontologists now have access to CT scanning. This method has revolutionized the study of dinosaur braincases. It allows researchers to peer inside and visualize three-dimensional structures without harming the skulls. They can even digitally remove bone to reveal the detailed shape of the brain space within.

Researchers at Ohio University employed these methods with several braincases of *T. rex* to reveal new information on its sensory biology and behavior. They were interested in collecting data that might help resolve a long-standing debate on whether these dinosaurs were scavengers or active predators. The early debate was sparked by an endocast that seemed to indicate that the most significantly developed region of the brain was the region involved in smelling. Some paleontologists reasoned that a great sense of smell was a prerequisite for finding and feeding on carrion. They argued that this was *T. rex*'s primary feeding strategy.

The Ohio scientists CT scanned several different *T. rex* skulls and performed digital dissections that allowed them to study general brain anatomy and other tiny structures that were preserved. Their overall findings indicated that the brain and sensory structures of *T. rex* were consistent with an active, predatory way of life. For instance, the bony labyrinth—a structure that includes the semicircular canals and the cochlea and is key for the coordination of movement and hearing—indicates that *T. rex* was capable of rapid tracking movements of the eyes, head, and neck. In addition, the anatomy of the cochlea suggests that hearing was important to tyrannosaurs and that these dinosaurs had a particular sensitivity to low-frequency sounds. Low frequencies are transmitted easily over long distances and through closed habitats. Hearing low frequencies may have been important for *T. rex* in tracking prey or in intraspecies communication.

The scans also showed an expansion of the structures used for smell, including an increased size of the olfactory nerve. A good sense of smell is important for all kinds of behaviors—including tracking potential prey, finding mates, and understanding territorial boundaries. The totality of cranial and anatomical data points to an active, agile, and terrifying predator.

THE BITE OF THE TYRANT LIZARD KING

Now, consider the anatomy of *T. rex*'s skull. The skull bones are not completely fused together. Do these loosely connected bones indicate that *T. rex* skulls were mobile and flexible? Do they mean that *T. rex*'s skull risked distortion and breakage if it bit down too hard?

One way to test the physical properties of *T. rex*'s skull is borrowed from engineering. In the 1940s, a method was created that allowed for the quantitative analysis of the physical properties of man-made structures. The method—called finite element analysis (FEA)—has now been applied to dinosaur fossils.

Emily Rayfield, a scientist in the UK, constructed a computerized mesh that defines the three-dimensional shape of a typical *T. rex* skull. Then, she used actual tooth puncture marks in pieces of bone bitten by a *T. rex* to model what would occur when bite forces were strong enough to do this kind of damage. Using FEA to measure the distortion of her model, Emily found that the skull of *T. rex* was adapted to resist biting and tearing forces. This indicated that *T. rex* likely fed by biting into flesh and pulling back. Her analysis revealed that the major stress of biting was transmitted throughout the bones of the face. The loose connections served as little shock absorbers that protected the skull and the organs it contained.

HOW FAST WAS *T. REX*?

Clocking *T. rex*'s top speed requires researchers to integrate data from footprints, the skeleton, modern comparative biology, and mathematical modeling. Some paleontologists imagined that *T. rex* may have been capable of running at speeds ranging from 25 to 45 miles per hour. But compare *T. rex* and modern elephants, which have similar adult body masses. Elephants can't do much more than amble without risking the integrity of their skeletons. Paleontologist John Hutchinson's research set out to test the possibility of a speedy *T. rex* using the methods of biomechanics. Hutchinson asked, "If *T. rex* could run at high speed, how large would its leg muscles need to be?" He created a computer model that explored this at a variety of predicted speeds. The model indicated something impossible: If *T. rex* were to run fast, it would have required more than 85% of its total body mass to be locked up in only its leg muscles. Hutchinson's analysis means that *T. rex* would have been constrained to lower speeds.

He also used his model on smaller dinosaurs and found that they needed much less muscle mass to run as fast as an adult *T. rex*. Thus, *T. rex* probably ran at speeds between 10 and 20 miles per hour; it probably walked at around 3 miles per hour.

MORE DETAILS ABOUT *T. REX*

Geochemical analysis of teeth, bones, and eggshells allows paleontologists to discern more specific paleobiological details in extinct animals—including diets, migration patterns, and body temperatures. These methods have all been tested in detail in living animals.

For instance, paleontologists use calcium isotopes to investigate the diets of carnivores. Ratios of calcium isotopes preserved in bones and teeth help reveal things like how often bones were consumed. In *Tyrannosaurus*, researchers recognized a pattern of calcium isotope variation consistent with it being an active eater with a high rate of eating bones. This data confirms the basic notion that *T. rex* was a Late Cretaceous apex predator.

Other isotopes in bones and teeth are powerful proxies for reconstructing migration patterns in dinosaurs. Since strontium isotopes vary with various types of surface rocks, dinosaurs would have incorporated different isotopes of strontium from ingested food and water into their bones and teeth. This provides a geographic fingerprint of where dinosaurs were feeding. Changes in strontium isotopes indicate that *T. rex* and its prey may have migrated throughout the year.

Carbon and oxygen form the main chemical ingredients in bones, eggs, and teeth. These elements preferentially bond. Clumped isotope analysis allows researchers to examine these bonded elements and predict the body temperature at which these chemical bonds formed. For example, studying the clumped isotope details of theropod eggshells reveals the body temperature of the animal that laid the eggs.

DATA EVERYWHERE

Some of the most important new data sources that paleobiologists have at their disposal are online databases, such as the Paleobiology Database. Databases like this allow paleontologists to ask significant questions about evolution for every dinosaur living anywhere on the globe.

In a 2021 study, Katlin Schroeder and her colleagues employed the database to test whether low dinosaur species diversity and their unusual body size distribution could be explained by the large disparity between baby and adult dinosaur body sizes. They queried the database to collect data for 43 dinosaur communities across 136 million years and 7 different continents.

They found that megatheropods like *T. rex*, which weigh more than 2,200 pounds as adults, had specific effects on dinosaur community structures. Communities with megatheropods lacked carnivores weighing between 220 and 2,200 pounds because juvenile megatheropods took up the possible niches that otherwise would have been available to mid-sized carnivores. This resulted in low species diversity among these dinosaur communities. This pattern is consistent among all the sampled communities, time periods, and continents. This suggests that these theropods shifted their primary ecological niche as they grew up. These changing roles in ecosystems were important factors in creating the structure and diversity in dinosaur communities overall.

T. REX'S NUMBERS

Did you ever wonder how many *T. rexes* ever lived? Or how many *T. rexes* might have lived at a single time? Or, on average, how large the range of an adult *T. rex* might have been?

Charles Marshall, a paleontologist at the University of California, Berkeley, and his students decided to tackle these questions using some pretty simple mathematical principles combined with current knowledge of living populations and the *T. rex* fossil record. They mined the published scientific literature for information to plug into their mathematical model. They estimated things like the age of sexual maturity for *T. rex* at about 15 years, a body mass at sexual maturity around 13,000 pounds, and a species longevity of about 2.5 million years. Then, the team estimated that at any one moment, there were around 20,000 *T. rexes* alive on Earth. If they persisted for 2.5 million years, then the total number that ever lived was around 2.5 billion.

They were also able to tie in the existing fossil record known for *T. rex* to estimate how likely it might have been for them to get preserved in the fossil record. Only about 1 in 80 million individuals might have been lucky enough to be preserved. That's only 1 in 16,000 individuals where their fossils are most abundant. Part of this study was the determination of population size in areas that we're familiar with. For example, about 3,800 *T. rex* lived at a single time in an area the size of California. On average, only 2 *T. rexes* would have lived within an area the size of Washington DC.

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HOW DID DINOSAURS GET SO BIG?

Dinosaurs are a remarkable group of animals for many reasons, one of which is the giant range of body sizes and shapes that their adult forms take. This lecture will take you deep inside dinosaur bones and share the tools that paleontologists use to investigate the growth rates of dinosaurs. It starts with the sauropod giants and touches on a few other dinosaurs to fully flesh out the story of growing dinosaurs.

GETTING BIG

Consider the size differential between the tiniest known adult dinosaur—about the size of a chicken—and the largest extinct dinosaur, a sauropod like *Patagotitan*. Even more interesting is that all dinosaurs, including the giant sauropods, started out small. They hatched from eggs that were no larger than soccer balls.

When the first sauropod bone, a single tail vertebra, was found in the mid-1800s, Sir Richard Owen named it *Cetiosaurus*, or "whale lizard." In a few years' time, Owen would coin the term Dinosauria for three other giant reptiles. However, he famously left *Cetiosaurus* out—assuming that at such a large body size, this creature could never have walked upright on land like the other three dinosaurs. Instead, he imagined that that tailbone belonged to a giant marine crocodile, which would need its massive body to be supported by water. Unfortunately for sauropods, the "overgrown lizard" image would continue to haunt them for more than a century.

Some paleontologists took sauropods out of the water but positioned them with limbs sprawled out to the side, like those of a lizard or crocodile. However, the anatomy of sauropods pointed to an elephant-like body with pillar-shaped limbs. They thought this posture would have only been possible if sauropods spent their entire lives walking with their giant rib cages and internal organs hanging down into trenches. Other paleontologists kept sauropods up to their armpits or necks in water. They even suggested in some cases that their nostrils would have been perfect snorkels for underwater walking and that their strange teeth might have been best suited for nibbling on clams.

All sauropods hatch from eggs that are no larger than large grapefruits. Somehow, nearly all of them grow to enormous proportions as adults. They hit upon their weird body plan early in their evolutionary history and stick to it, with only relatively small variations in neck length, skull and tooth shape, tail anatomy, and body size, giving rise to the more than 200 species discovered so far.

Though the 1980s and ’90s saw the height of the dinosaur renaissance, sauropods were still kind of stuck in the Dark Ages. Paleontologists were still publishing papers suggesting that sauropods, growing at similar rates to living cold-blooded lizards and crocodiles, would have taken more than 100 years to reach sexual maturity—and even longer to reach their giant adult body sizes.

Now, think about it: Would it make any good biological sense to grow extremely slowly for a century before you could reproduce? Chances are you’d be eaten by the ferocious theropods long before you ever got a chance to mate. But if this hypothesis doesn’t make great logical sense, then how did sauropods do it?

ONTOGENETIC SERIES

To study dinosaur growth, researchers need to have skeletons that span many growth stages—from tiny babies to large adults and all sizes of juveniles and subadults in between. This is what researchers call an ontogenetic series. It is the starting point for figuring out how fast any kind of extinct dinosaur may have grown.

Once researchers have an ontogenetic series, it is time to focus on the bones. Luckily, vertebrate bones serve as an archive for all kinds of data about their lives. On the outside, bones show bumps and grooves that indicate the presence of tendons and muscle insertions, which provide the key data researchers need to answer questions about movement. Their shapes reveal the anatomical details that allow for the determination of how different animals are related.

Bone shapes can even give hints about how an animal’s skeleton functions—the limbs of diggers look different than those of runners, swimmers, and fliers. And the insides of bones tell researchers even more. Whether in living animals or fossil species, bones preserve microscopic details within that provide clues to their growth history, age, gender, body temperature, and even specific intervals of stress, disease, or injury they may have experienced during life.

A PRIMER ON BONE HISTOLOGY

When an animal's overall body is growing quickly or slowly, its bones do the same thing. When researchers crack open a bone and take a look at it under a microscope, they see complex and beautiful patterns that can be used as proxies for overall body growth patterns. The study of the microscopic structure of bones is called bone histology.

Bones are growing, changing, dynamic tissues. However, in addition to cells and blood vessels, bones also include a microscopic mineral component. Long bones start out in embryos as little cartilage models. Once they are vascularized by an artery that supplies nutrients, a group of these calcified cartilage cells dies. They are replaced by new cells called osteoblasts. Osteoblasts begin forming bone matrix, which consists of an interweaving network of the elastic protein collagen. This makes bones a little flexible. As bones are forming, osteoblasts also concentrate the mineralized, crystalline component that gives bones their rigidity and hardness. These crystals are made of calcium phosphate hydroxide, or hydroxyapatite. Collagen molecules and hydroxyapatite crystals line up in parallel as bones grow.

As bone growth continues, the osteoblasts become trapped along with blood vessels that are helping to supply that developing bone with nutrients and remove waste. Once trapped, these osteoblasts change their role to become bone-maintaining cells rather than bone-building cells. They are now called osteocytes. This type of bone is called primary bone. Its organization documents the relative speed of bone deposition.

There are several signs that researchers look for to assess how an animal is growing. The faster an organism is growing, the more disorganized its primary bone matrix will be. The more abundant the osteocytes, the faster bone is being deposited. The higher the blood supply, the faster a bone is growing. This means that more blood vessels are traveling in more diverse directions within a bone. Some go around in circles along the circumference of the bone, some radiate out from the center of the bone like the spokes of a wheel, and some travel up and down the long axis of the bone, intersecting with one another in an interweaving network. In slower-growing bones, minerals and proteins have time to align themselves in tiny, thin parallel layers. There are fewer osteocytes and less blood supply.

Luckily for paleontologists, the accompanying spaces within the crystalline matrix where soft parts sat when the dinosaurs were alive are preserved. This means that they can directly compare the primary bone structures of living and fossil animals and extract similar data from each. Sometimes, in slow-growing animals, researchers observe highly mineralized rings within the bones that point to complete cessation of bone growth for a period of time. These rings are called lines of arrested growth (LAGs). They are most common within the bones of slow-growing, cold-blooded animals, which must pause their growth seasonally during the cold times of the year. These LAGs also occur in fast-growing organisms, sometimes because of some external stress (like drought), and then once the animal reaches adult size.

Researchers have put all these different things about bone growth to the test in living vertebrates. Specifically, they've investigated whether bone growth rates accurately reflect overall body growth rates and if particular microscopic patterns in bones could be linked to a specific growth rate in living animals.

It turns out that researchers can do both. Thus, they are able to pinpoint a range of possible rates for different patterns of primary bone growth. Generally speaking, among living animals, reptiles grow slowly, and mammals and some birds have growth rates that overlap. Other kinds of birds grow faster than any other living creature. This means that researchers can measure the amount of primary bone in a dinosaur fossil, compare its microscopic organization to living animals, and determine precisely how long that dinosaur bone took to form.

Consider a thin fossil section with many little squiggles all over the place, with different orientations. These are the spaces where a rich network of blood vessels supplied this fast-growing bone with nutrients. Tiny little black specks are the spaces where bone cells would have been when the animal was alive. If you could zoom in even closer, you would see that the preserved microscopic minerals are also crazily organized. All these features point to a relatively speedy growth rate. Now, consider a thin fossil slice with hardly any of those blood vessel squiggles; sparse, tiny spaces for bone cells; and many LAGs. Even at the tiniest microscopic level, the minerals that made up this bone are super organized, creating lines that you can easily see. All these features indicate that this bone was growing much more slowly than the previous one.

SECONDARY BONE

Faster-growing animals need to continually remodel their primary bone tissue. Thus, they use their own bone minerals to do so. Sometimes they'll need to repair a microfracture or grow some bone more rapidly to accommodate changing body mass or behaviors. Other times, they'll need to use their own bone minerals when shelling eggs or growing skeletons for their own offspring.

Here's how it works: Cells called osteoclasts travel around the blood supply and begin to dissolve the bone around the blood vessel they're traveling in. This causes all those minerals and protein components to enter the bloodstream so that they can be moved to places where they are more needed in the body. Nearby osteoblasts move into the newly open spaces left behind and begin to redeposit new bone. This process results in a characteristic lifesaver shape called secondary bone. In older animals, many intervals of remodeling have occurred, erasing the original bone and leaving behind many overlapping generations of secondary bone "lifesavers."

Remodeling is exactly why paleontologists need to look at the ontogenetic series of dinosaurs when trying to understand how quickly or slowly they grew throughout life. Usually, large adult dinosaur bones have almost all their primary bone tissue completely remodeled by secondary bone. If that's the case, all researchers can say is that the bone has been remodeled. As they sample smaller and younger individuals of a single species, they are essentially looking back in time to reconstruct what the primary bone looked like before it was remodeled.

When paleontologists study bone histology in dinosaurs, it's kind of dramatic. The first step is identifying the ontogenetic series. Ideally, in the series, several different bones will be studied that represent different "functional environments" because bone microstructure is driven by a multitude of things. For example, in the study of the *Apatosaurus*, several different arm and shoulder bones were sampled. In the forearm, the radius is a non-weight-bearing element, while the ulna is the weight-bearing element. The scapula forms in a slightly different way than these two forearm bones and gives you another point of comparison. Researchers expect that each of these bones will show some differences. However, they are looking to see if there are consistent patterns within each that will allow them to make an assessment of growth.

Then, they must cut the bones open to look inside. They usually use the midshafts of long bones to take samples because these preserve the longest records of growth. Sometimes they'll take only a wedge out of the bone using small handsaws with blades lined with diamond dust. At other times, they purposefully—and carefully—break the bone at an existing midshaft crack so that they can take a chunk out and have rough edges to glue back together. This allows for the preservation of total bone length. Occasionally they get lucky, and a curator will allow them to cut the bone completely in half, usually using a high-speed diamond-edged saw. They then embed this chunk of bone in plastic, vacuum out all the bubbles, and make thin sections using a slow-speed, diamond-edged, water-cooled saw. The wafers get glued onto glass slides and are then ground down by hand on a lapidary wheel lined with diamond grit paper. The goal is to grind the layers down, carefully, until light passes through the bone when it is placed underneath a transmitted light microscope.

FROM *APATOSAURUS* ONWARD

Remember that paleontologists once assumed that sauropods were like overgrown reptiles, growing slowly and steadily for 100-plus years—and maybe even until they died. Paleontologists have sampled a whole bunch of bones, spanning juvenile to adult *Apatosaurus* ontogenetic stages. Unlike the bones of reptiles, these bones were highly disorganized, densely vascularized, and without any LAGs until they were humongous. Throughout their growth, remodeling was pervasive. A paleontologist was able to use the comparative, quantitative data from living animals to determine that *Apatosaurus* would have grown from juvenile to adult size (that's about 75 feet long, about 60 to 70 tons) in about 20 years.

These shocking results turned the old idea of reptilelike sauropods completely on its head. To dig deeper, a team compiled data from the published literature on other dinosaurs to see if they could determine whether dinosaurs had their own unique standard growth rate. Or did some dinosaurs grow like reptiles, some grow like birds, and some grow like mammals? They generated growth curves for dinosaurs small and large. They included dinosaurs that were closely related to birds and ancient dinosaurs at the base of the family tree. They included herbivores and carnivores. This work resulted in identification of the maximum growth rate that these diverse dinosaur species could achieve. The growth curves allowed them to determine how long dinosaur growth spurts might have been and how many pounds they were packing on during these intervals.

What they found was that all dinosaurs grew faster than reptiles. As a whole group, dinosaurs grow most like slower-growing birds and mammals. Additionally, not every dinosaur grows the same way. Tiny theropods closely related to birds grow the slowest among dinosaurs—only two times faster than reptiles. This means that birds innovated their speedy growth rates independently. Large sauropods like *Apatosaurus* grew about 50 times faster than living reptiles and put on about 50 pounds per day when they were growing at their peak. These numbers are right in alignment with the other largest vertebrates of all time—the whales.

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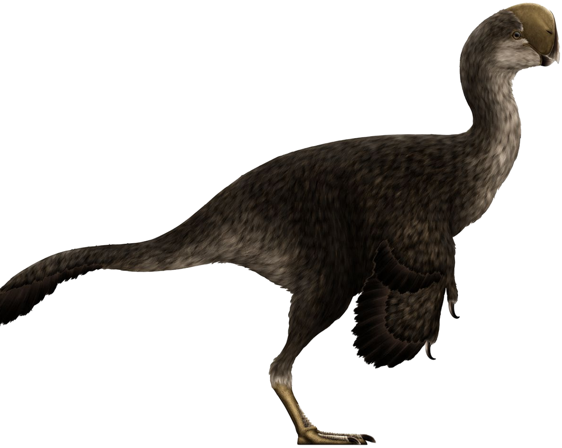

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WERE DINOSAURS WARM-BLOODED?

Now that researchers know that birds are dinosaurs, they're presented with a bit of a conundrum. Birds are warm-blooded creatures, capable of maintaining a pretty constant body temperature by generating their own heat. In contrast, the other group of modern animals closely related to dinosaurs—the crocodilians—are cold-blooded. Since the two living relatives of dinosaurs exhibit different strategies, multiple answers are plausible for dinosaurs. Did dinosaurs run warm like birds or cold like crocs? Or did they do neither? This lecture considers the evidence.

PHYSIOLOGY AND METABOLISM

When talking about warm-blooded and cold-blooded animals, these terms don't have anything to do with the actual temperature of an organism's blood. Instead, these two phrases are related to how an organism gets most of its energy.

Physiology is simply the science of how organisms and their constituent parts function. There are many branches of physiology. Thermal physiology, or thermophysiology, is all about the study of how animals regulate their body temperatures. These types of regulatory responses may include involuntary reactions to getting too cold or too hot, like shivering or panting. They also include voluntary responses, like standing in the sun to warm up on a cold day.

Now consider metabolism. Metabolism can be defined as the sum of all the chemical equations that convert food to energy and waste. It is a biological process that helps build, grow, or maintain the body's structures. The heat produced by metabolism helps to fuel the chemical reactions that break down the inputs efficiently into outputs. An organism's body temperature is intimately linked to metabolism.

THERMOREGULATION CATEGORIES

Often when talking about the distinctions between warm-blooded and cold-blooded animals, what researchers are noticing are the underlying differences in thermoregulation and metabolism. When you picture a modern-day warm-blooded animal, you think of mammals and birds, which have a body temperature higher than the ambient temperature. In contrast, when you picture a living cold-blooded animal, you probably imagine reptiles, amphibians, and fish, whose body temperature is closely linked to their surroundings. But the discussion of simply "warm-blooded" and "cold-blooded" is a bit more complicated. Instead of this stark distinction, it's useful to think a little more specifically about the links between thermoregulation and metabolism as researchers develop categorizations for modern organisms and hypotheses about dinosaurs. There are two kinds of classification that are important.

Classification 1 is focused on thermoregulation and relates to the constancy of body temperature. There are two options: You might be an organism that maintains a relatively constant body temperature, called a homeotherm;

or you might be an organism whose body temperature is more variable, called a poikilotherm. Homeothermic animals are able to maintain a body temperature within a few optimal degrees. They do this through involuntary mechanisms related to their thermal physiology. For example, shivering generates heat energy, and sweating or panting helps with cooling an organism. Most mammals and birds are homeotherms.

Poikilothermic animals have an internal body temperature that fluctuates more dramatically and is dependent to a greater extent on environmental conditions. Poikilotherms don't have as many involuntary mechanisms for maintaining their body temperature. Instead, they must change their position to regulate their temperature. Most reptiles, amphibians, and fish are poikilotherms.

Classification 2 is focused on metabolism and relates to the source of body heat. Once again, there are two options: You might be an organism whose metabolic processes produce enough heat energy to optimize your internal chemical reactions during metabolism. If so, you are an endotherm. Most mammals and birds are endotherms. If, however, your metabolism doesn't generate enough heat to optimize internal chemical reactions, you might need a little extra hit of energy from the sun to raise your body temperature. If you rely on these extrinsic sources of heat energy, then you are an ectotherm. Most reptiles, amphibians, and fish are ectotherms.

Most mammals and birds are homeothermic endotherms. This means that they maintain a constant body temperature that is generated mostly by their own metabolism and regulate that temperature by involuntary mechanisms. Homeothermic endotherms require large amounts of food and must breathe quickly to maintain the heat generated by their bodies. Because their body temperature is constant, they can be active for more of the day. They can survive in all kinds of environments.

In contrast, most fish, amphibians, and reptiles are poikilothermic ectotherms. Their body temperature fluctuates based on external conditions. Although their metabolism does produce heat as a by-product, it isn't enough to optimize chemical reactions in the body. Thus, they rely on the sun to help warm them up to a higher temperature. Poikilothermic ectotherms don't need as much food or oxygen and can go longer between periods of eating. They can't live in cold environments, and when the sun sets, they slow down as well.

Interestingly, there are animals that cross the boundaries of these categories. For example, large sea turtles and some deep-sea fish can be categorized as poikilothermic endotherms. Their large body mass and constant movement generates a body temperature that is warmer than ambient temperatures. These animals may still experience some fluctuation in body temperature as a function of the outside environment and might require additional input from the sun for full optimization of their body's metabolism.

Some scientists have argued that dinosaurs may have been similar, using terms like mesothermy, gigantothermy, or mass homeothermy to describe the possible process for dinosaurs. This is an interesting idea but one that is hard to apply to dinosaurs as a group. Keep in mind that many dinosaurs were small, even as adults. And all dinosaurs started off tiny. Therefore, the argument that dinosaurs were simply too big to cool down seems implausible.

DINOSAUR BRAINS

Were dinosaurs homeothermic endotherms, poikilothermic ectotherms, or homeothermic ectotherms? Perhaps the best place to start is with the generalized dinosaur body plan, especially as it relates to how they moved.

The first person to suggest that dinosaurs may have been different from regular reptiles was Sir Richard Owen. He wondered whether the long, upright legs of dinosaurs might have been an indication that they were warm-blooded like living birds and mammals, which have a similar, non-sprawling stance. Trackway fossils tell paleontologists that dinosaurs were able to keep a pace that is well aligned with running and walking speeds for large modern mammals. Not so for modern reptiles, which cannot generate and sustain fast running and walking speeds.

Next, consider the relationship between brain and body size. This ratio is the encephalization quotient (EQ). Generally speaking, the larger the EQ, the larger the brain. When compared across species, organisms with larger relative brains are often considered more intelligent. In addition, intelligent, large brains require more metabolic energy to keep going. Thus, usually, animals with the highest EQs are also homeothermic endotherms.

Dinosaurs are famous for their tiny brains, especially when compared to the giant body sizes that many species reached as adults. But not all dinosaurs had small brains. Theropods had especially large brain-body sizes, particularly in those small theropods that are closely related to birds. Some of these dinosaurs have EQs that are higher than those of typical mammals. Because dinosaurs exhibit such a large range of body sizes, other dinosaur EQs are similarly broad, ranging from 0.2 for sauropods up to about 2.0 for ornithopods and some theropods. Brain-to-body size ratios don't give researchers much resolution when it comes to determining whether the relationship between brain size and body temperature holds true for dinosaurs.

DINOSAUR CIRCULATION

Were the hearts and circulatory systems of dinosaurs up to the task of pumping blood effectively enough to fuel high rates of metabolism? Researchers can employ the EPB to answer this question. Both birds and crocodiles exhibit advanced, four-chambered hearts capable of generating high blood pressure. Four-chambered hearts allow a complete separation of blood flowing to the body and to the lungs.

To pump blood all the way out to the skulls of sauropods, a four-chambered heart would be needed. The same four chambers would be important to fuel running in theropods and ornithopods, which is consistent with the tracks found. Mammals also exhibit a four-chambered heart. Thus, two groups of homeothermic endotherms share this feature with one group of poikilothermic ectotherms: the crocs. Therefore, paleontologists can't be sure if dinosaurs would have employed their hearts more like birds and mammals or more like crocodiles.

In the Mesozoic, climates at both the North and South Poles weren't as harsh as they are today. However, they were still pretty cold and experienced extremes in seasonal daylight. Nevertheless, a diverse array of dinosaurs lived in these regions, including representatives for many of the major dinosaur groups. Their presence in polar environments strongly suggests they were metabolically different from living reptiles. The only animals that thrive in polar environments today are homeothermic endotherms, such as mammals and birds. Reptiles are excluded, in part due to the seasonal absence of sun. Paleontologists don't find reptiles in the polar fossil beds either—only dinosaurs.

DINOSAUR BONE HISTOLOGY

Bone histology was hinted at early on as solid evidence for warm-bloodedness in dinosaurs. Beginning with the work of French paleontologist Armand de Ricqlès in the late 1960s, right at the start of the dinosaur renaissance, scientists began noticing that the microstructural anatomy of dinosaurs looked pretty weird. Instead of an orderly, organized, poorly vascularized structure and LAGs, as in the bone tissue of reptiles, dinosaur bones were different. No matter which dinosaur was studied, the bones were more disorganized and exhibited much higher vascularity. Occasional LAGs were present but most commonly at the outsides of bones, indicating the attainment of adult size, and secondary bone, indicating remodeling was pervasive. These patterns of reworking hinted that dinosaurs might be more like mammals and birds, with a higher need for mineral metabolism as they grew.

For a number of years, the presence of LAG growth within dinosaur bones led some paleontologists to argue that these signatures were more indicative of the cold-blooded reptilian lifestyle, in which dinosaurs would be forced to stop growing for the cold season every year. More recent work has disputed the annual nature of these LAGs in dinosaurs. Now researchers see that even warm-blooded mammals living in drought-stressed or nutrient-poor environments may put their growth on pause to stay alive.

One of the best indicators of metabolic status is drawn from bone histological data. Paleontologists have calculated maximal growth rates in dinosaurs and found that all dinosaurs grew faster than reptiles. Maintenance of these high rates of growth for years of life history points toward homeothermic endothermy, in the style of birds and mammals.

Though this next characteristic isn't true for all dinosaurs, it definitely points toward homeothermic endothermy: Some dinosaurs had insulation. Feathers first evolved in dinosaurs, and at the start, they were more akin to downy insulator feathers. The only modern animals that have insulation are warm-blooded. Cold-blooded organisms don't want to prevent the rapid transfer of heat energy from the sun to their internal bodies if they are cold. And if they are too warm, they want to be able to dissipate that heat quickly. Insulation is a great indication that at least some dinosaurs were potentially warm-blooded. Similarly, some of the unusual skeletal features in other dinosaurs may have played an involuntary role in thermoregulation. Perhaps the plates of stegosaurs, osteoderms of titanosaurs, and frills of ceratopsians helped cool the blood via heat exchange.

ISOTOPES

Isotopes have proven incredibly important for providing information on body temperature in dinosaurs. In one method, the focus is on two isotopes of oxygen: ^{16}O and ^{18}O . These isotopes are found in precipitation and freshwater. They vary with latitude based on average yearly temperatures. Since parts of bones and teeth are made of oxygen, this ambient oxygen gets brought into the lattice of skeletal and dental tissues during life and can persist through the long process of fossilization. Oxygen isotope values vary with latitude in crocodile teeth but stay consistent with latitudinal differences for both sauropods and theropods. This finding points to a more constant body temperature for dinosaurs in comparison with crocodiles from the same paleoenvironments.

Another tool uses isotopes of carbon and oxygen to investigate body temperature directly. These methods indicate that bird body temperatures range from 64°F to 111°F. Meanwhile, crocodilians have an average high temperature between 68°F and 84°F, with a variable low that depends upon ambient temperature. Sauropods such as *Camarasaurus* and *Brachiosaurus* had average body temperatures of around 96°F to 101°F. *Oviraptor*, a small theropod, had an average body temperature around 89°F. This data also points to body temperatures consistently higher than those for cold-blooded poikilothermic ectotherms.

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THE EATERS AND THE EATEN IN THE DINOSAUR AGE

When it comes to dinosaur diets, they run the gamut—from the herbivores that crunched, sliced, diced, raked, and chewed land plants to the carnivores, which were all about the bite. This lecture will explore the menu for dinosaurs. You will also learn about their specialized feeding strategies—from the business end up front to the tail end of the digestive process. And don't forget that as integral components of their ecosystems, dinosaurs sometimes served as food for others.

WHAT DINOSAURS ATE

Although most theropods were ferocious carnivores, a handful of them lost their sharp teeth in favor of a different food source. For instance, *Oviraptor*, a maniraptoran theropod closely related to birds, lost its teeth in favor of a powerful beak it may have used for crushing hard nuts, seeds, eggs, and possibly even shellfish or insects.

For herbivorous dinosaurs, there were more options as plant diversity increased over time. You can think of plant evolution transpiring in three large waves. The first wave resulted in the diversification of seedless vascular plants like ferns that reproduce using spores. At the beginning of the age of dinosaurs, about 230 million years ago, vascular plants were already common on land. There was a diverse array of ferns, with some as large as trees. There were also unusual trees called lycopods and sphenopsids—like the water-loving plant genus *Equisetum*, or horsetails.

The second wave of plants to evolve comprised the gymnosperms—the first seed-bearing plants. They include evergreens, cypress, cycads, and ginkgos. They're much taller and woodier than the first-wave plants. Their unique innovation of seeds meant that they spread rapidly during the Late Triassic, when those first-wave ferns and others were on the decline.

The gymnosperms dominated dinosaur ecosystems until the Cretaceous, when the third wave of plants, known as angiosperms, evolved. By the Early Cretaceous period, they had developed a variety of strategies to attract herbivores and pollinators. They had bright, tasty flowers and fruit along with tough seeds that could withstand animal digestive tracts.

There has been some evidence of herbivorous dinosaurs and plants coevolving, particularly in Cretaceous ecosystems. One study compiled a database of Cretaceous dinosaur and plant distributions to begin to test out coevolutionary interactions over time. They looked into a variety of different dinosaur groups, including sauropods, stegosaurs, ankylosaurs, ornithopods, ceratopsians, pachycephalosaurs, and herbivorous theropods. They also examined major groups of plants, including ginkgos, angiosperms, cycads, and conifers.

For the most part, there was no positive correlation between diversity patterns in major groups of herbivorous dinosaurs and flowering plants. That said, one group—the dome-headed pachycephalosaurs—did exhibit a positive correlation with angiosperms. Perhaps this hinted at a coordinated evolutionary history between the two groups. In contrast, stegosaurs showed a significant negative correlation with flowering plants and a significant positive correlation with nonflowering cycads. Both stegosaurs and cycads appear to decline in concert during the Early Cretaceous period.

For a long time, paleontologists had no fossil record of grass that extended back into the age of dinosaurs. However, it turns out that diverse grasses were present but not widespread. At least for the late-surviving dinosaurs in the Southern Hemisphere, grass may have also been an enticing food source.

THE EATERS

Dinosaurs replaced their teeth throughout their lives via a conveyor-belt-like system below the gums. As soon as a tooth was lost or wore down, a new one would take its place. This means that the fossil record of shed dinosaur teeth is rich. Since teeth were always being lost and were particularly tough skeletal elements, they had a pretty good chance of being fossilized.

The shape of teeth is often the first clue to diet and taxonomic identity. Think back to the first finds of dinosaur fossils. *Megalosaurus* and *Iguanodon* included different types of teeth—one with teeth for chomping and slicing meat and the other with teeth ready to process plants. There is a great deal of variation in the shapes of teeth, even in animals that ate the same kinds of things. For example, *Camarasaurus* and *Brachiosaurus* are two closely related sauropods that share spoon-shaped teeth. *Diplodocus* and *Apatosaurus* are two other closely related sauropods that share pencil-shaped teeth. These simple differences in teeth point to different feeding strategies among these contemporary sauropods. Unlike camarasaur-style teeth, which were specialized for biting leaves off branches, diplodocid teeth were built for stripping leaves.

Microwear analysis is used to explore the relationship between dinosaur diets and dentition. Paleontologists use scanning electron microscopes to zoom in on the tiniest details of teeth and begin to resolve microscopic scratches, grooves, and pits that can be linked to different types of vegetation. A diet of mostly soft ferns and fruits, for example, wouldn't leave deep scratches in tooth enamel. However, a diet that included leaves with an occasional stiff branch mixed in would. A diet rich in grass would also include many scratches since grass cells contain tough, glass-like silica.

The relatively delicate teeth of many herbivorous dinosaurs indicate that most didn't spend much time processing their food by chewing. Instead, they may have relied on other digestive processes, such as fermentation in the gut, to break down the tough vegetation in their diets. Several scientists have suggested that some dinosaurs may have needed to grind up their veggies in a gizzard. In a few living archosaurs, gizzards hold small stones known as gastroliths, or "gizzard stones," that help with the mechanical breakdown of plant material. Though sauropods are commonly assumed to have used gastroliths to aid in digestion, the fossil evidence in support of this hypothesis is scant at best. Polished gastroliths have been found in association with a couple of species of small, primitive ceratopsians from Mongolia.

Regarding theropods, their teeth are wildly variable, particularly with respect to shape, compression, bluntness, and serration patterns. Some theropod teeth were more useful for slicing, as in *Deinonychus*. The blunter teeth of *Tyrannosaurus*, however, seem to have been capable of crunching through bone.

Going beyond teeth to the fossils of jaws and skulls, things get even more interesting. Ankylosaurs, stegosaurs, and pachycephalosaurs all share relatively delicate, mitten-shaped teeth that weren't great for in-mouth processing. They also exhibit a sharp front edge of their jaws that would have been covered by a keratinous beak, called a rhamphotheca. These dinosaurs would nip vegetation with their beaks and pulp their food slightly in the mouth. Then, they would rely on the rest of their digestive systems to break down those energy resources.

Moreover, ceratopsians, hadrosaurs, and one group of sauropods all evolved dental batteries. A dental battery occurs when all the teeth in each jaw are tightly packed together so that the tops of the teeth form a continuous flat surface. In ceratopsians, these dental batteries acted like a giant pair of scissors, shearing food to bits whenever the dinosaur closed its jaws. In hadrosaurs, the dental battery ground food to a pulp. Both ceratopsians and hadrosaurs combined these dental batteries with toothless beaks up front, perfect for selecting the right bite. The sauropod dinosaur *Nigersaurus* independently evolved its own unique version of a dental battery. More than 500 tiny peg-shaped teeth were aligned in a straight row right at the front of a squared-off muzzle. This indicates that *Nigersaurus* was grazing near the ground.

DISPELLING A FEW MYTHS

In ceratopsians, the teeth on both the upper and lower jaws are inset toward the tongue. This leaves slight excavations on the edges of the jaw bones that need to be explained. Traditionally, the explanation has been that ceratopsians must have had muscular cheeks like mammals. But Larry Witmer, who has pioneered the rigorous application of the EPB to tons of questions about dinosaur soft parts, noted some key anatomical differences in mammals and dinosaurs. Using the EPB, Witmer has argued that crocodiles or eagles might be better analogues. Instead of muscular cheeks, he maintained that these areas of dinosaur mouths supported an extension of the keratinous covering of the beak. There is no evidence for cheeks so far in any dinosaur.

Details pave the way for the fall of another popular dinosaur myth: that of pack hunting. The evidence for pack hunting is pretty sparse. The most famous support for pack hunting comes from Early Cretaceous sites in Montana, where the skeleton of a plant-eating dinosaur called *Tenontosaurus* was found with many *Deinonychus* teeth. The original research suggested that this was evidence of social groups in the form of pack hunting. But the site was a bone bed that included an assemblage of an Early Cretaceous community. More recent work on the fossils from this locality included detailed taphonomic work, which revealed another plausible story. The *Deinonychus* that shed their teeth may have done so feeding on the dead *Tenontosaurus*. Alternatively, the teeth may have accumulated over time alongside the bones of turtles, fish, crocodiles, and other reptiles.

One of the most spectacular fossils ever found comes from the Late Cretaceous of Mongolia and lends credence to the idea that at least some small theropods were likely solitary hunters. The fossil preserves a single *Velociraptor* locked in a battle to the death with a small *Protoceratops*.

Though pack hunting is unlikely for these small raptors, for large tyrannosaurs, it has become increasingly clear that they spent time together—at least sometimes. A few field localities in Canada have yielded Cretaceous bone beds of *Albertosaurus*—a close relative of *T. rex*—showing that these animals had all died together at the same time. The group includes young dinosaurs, juveniles, and larger adults. Similar sites have been uncovered in Mongolia and the United States and suggest that these guys may have been more social than other, smaller theropods. This contention gets additional support from the signatures of partially healed bite marks that reveal a pattern of nasty interactions among tyrannosaurs. It may be the case that tyrannosaurs interacted with each other using their teeth to communicate and compete. Then, they may have put their differences aside to feed together.

Recall that FEA has allowed paleontologist Emily Rayfield to investigate the distribution of stress throughout the skull of some theropods when biting. For instance, she determined that *Allosaurus* was specialized for rapid chopping bites rather than strong, forceful biting. Using FEA, Rayfield was also able to estimate that the bite force of *T. rex* was three to four times stronger than the bite force of *Allosaurus*.

Differences in the teeth of these two carnivores also point to variations in feeding behavior. *Allosaurus* has bladelike teeth with serrations on the front and back edges that would have ripped through flesh with ease. The serrations twisted around the teeth to make slicing even more efficient. This is in stark contrast to the blunter, fatter, banana-shaped teeth of *Tyrannosaurus*, whose forceful bite would first deeply puncture and then pull through the penetrated flesh using the energy from its powerful neck muscles. *T. rex* was a bone biter, wearing down its teeth rapidly with repeated impacts.

THE TAIL END

Evidence for dinosaur diets also comes from dinosaur droppings, or coprolites. Karen Chin is the world's foremost expert on coprolites. Chin and her team found the largest dinosaur coprolite known, at about 17 inches long and with a volume of more than 2 liters. Karen used a microscope to peer inside and was quickly able to rule out herbivorous dinosaurs as the source. This giant coprolite preserved the remains of a juvenile duckbilled dinosaur, which was a tasty, one-bite snack for a giant theropod.

Other coprolites have yielded important insights into the diets of herbivorous dinosaurs. A hadrosaur coprolite preserved evidence of little bits of shelled invertebrates—crustaceans—preserved amid fragments of rotting wood, fungal hyphae, and the burrows of ancient dung beetles. A sauropod coprolite from the Late Cretaceous recovered in India preserved unique, silica-rich phytoliths—special cells that help build grasses. This coprolite pushed the fossil evidence for the first grass back in time by millions of years. It also revealed that the titanosaur that pooped it out had been busy eating from nearly every part of the ecosystem—treetops, shrubs, and grasses at foot level. This helped revise the idea that the long necks of sauropods were all about stretching tall. They were just as useful for expanding the feeding envelope.

THE EATEN

The Early Cretaceous mammal *Repenomamus* weighed around 25 pounds. One specimen of *Repenomamus* was found preserved with the remains of a juvenile ceratopsian named *Psittacosaurus* in its gut cavity. *Sanajeh*, an egg-eating Indian snake, was discovered coiled within a nest of titanosaur eggs. Its skeleton was wrapped around eggs in the nest, with a baby titanosaur alongside, about to become a hapless victim.

Dinosaurs were also hosts to parasites, including fleas, ticks, and lice. Fleas were long thought to have evolved alongside us mammals and modern birds. But new discoveries in China from Jurassic and Cretaceous rocks have turned that idea on its head. Fleas back then were more than double the size of their modern counterparts—sometimes up to 20 millimeters long. They had siphoning mouthparts that were like armored sawlike projections. Thus, it's clear that these fleas had to have been feeding on something with a hide much tougher than that of early mammals or birds. In addition, the mammals at the time were mostly quite small—meaning these fleas would have sucked them dry. These giant Jurassic fleas likely sliced through tough dinosaur skin in search of a blood meal. As for ticks, 99-million-year-old Cretaceous amber fossils discovered in Myanmar preserve ticks hanging onto a dinosaur feather.

Another chunk of amber from Myanmar also yielded fluffy dinosaur feathers. A closer look revealed a bunch of lice. They are tiny, only about 2.5 times as wide as a human hair, and with mouthparts made for chewing. One of the preserved feathers was damaged by chewing, similar to what occurs in modern birds infested with lice.

Of course, dinosaurs also carried diseases and endoparasites—and they may have even picked up some of these problems through the bites of fleas, ticks, and lice. Another dinosaur coprolite preserves traces of a protozoan and three different types of parasitic worms. These ancient microorganisms resemble endoparasites that commonly infest modern animals. The protozoan cysts were most similar to a type of modern amoeba. And the evidence of wormy parasites included the eggs of both trematodes, or flukes, and nematodes, or roundworms.

Modern-day trematode infections include things like schistosomiasis, which can result in all kinds of terrible symptoms—from intense abdominal pain to paralysis. Trematodes typically have a two-host life cycle. They have a vertebrate primary host, like a dinosaur, where reproduction occurs, and then an intermediate host, usually an aquatic snail. Nematodes, like hookworms, typically infect the digestive system in modern animals, sometimes causing severe iron deficiency in their vertebrate hosts. Infections are usually acquired from the environment—often through contaminated food or water—but can also be acquired through insects.

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THE TOUGH LIVES OF *ALLOSAURUS* AND *T. REX*

The study of dinosaur disease and injury is called paleopathology. Things that might have been horrible for dinosaurs are a boon to science, opening new doors to understanding dinosaurs in their world. This lecture focuses on two of the most injured dinosaurs of them all: the Jurassic theropod *Allosaurus* and the Cretaceous theropod *Tyrannosaurus rex*. Large-bodied dinosaurs like these, with their active, predatory lifestyle, are frequently found with numerous fractures, bite marks, and other damage. Even these top predators sometimes fell to the tiniest of all organisms—bacteria.

DINOSAUR DEATHS

Sometimes a dinosaur bone is unearthed that preserves unusual features that can be linked to diseases or injuries equivalent to those experienced by animals and humans today. However, there are many things that can happen to bones right after death. Insect borings of carrion beetles pupating within dinosaur bones leave unusual features on the surfaces, but they don't represent diseases or injuries that impacted the dinosaur while it lived. Similarly, modern plant roots, erosion, breakage, and other types of chemical weathering all leave distinctive marks on fossil bones. And don't forget about the long, arduous history of fossilization. Pathologies must be distinguished from postmortem changes that can occur during fossilization and exhumation.

Once these other markings are accounted for, ancient bones can tell stories of the tough lives of dinosaurs. They have a special role to play in providing insights into behavior, physiology, and life history. Pathologies have been recorded in pretty much every kind of dinosaur. The bony evidence has documented injuries and diseases, including fractured and stress-fractured bones, amputations, bite marks and scratches, cancer and tumor growth, respiratory infections, developmental anomalies, and many distinctive types of bacterial and fungal infections. Of these, the nonlethal pathologies are among the most interesting. They can tell us something about the behaviors that animals exhibited in life and especially how their bodies responded to all these stressors.

ALLOSAURUS

In the Late Jurassic period, the plains and lowlands of the North American West were stalked by *Allosaurus*. In the Cleveland-Lloyd Quarry, about 46 different *Allosaurus* individuals are preserved. Adult *Allosaurus* weighed between 1.5 and 2 tons and reached a size of up to 35 feet long. It had two powerful hind legs and employed its sharp-clawed, three-fingered hands and daggerlike, recurved, and serrated teeth to subdue prey. Its skull provides clues to how it may have captured and dined on its prey. *Allosaurus*'s jaw-closing muscles attached to the lower jaw close to the joint, imparting a relatively weak bite force. Its bite was only about as strong as that of a modern lion or leopard. But *Allosaurus* was still fierce. Its teeth were serrated on both front and back surfaces. The serrated edges twisted along each tooth, making them perfect for gripping, ripping, and spiraling through muscle.

The sinuous S-shaped neck of *Allosaurus* was supported by strong muscles used to thrust its head forward and drive its open upper jaw down into the bodies of its victims. The flexible bony skull absorbed the jarring impact of this action, distributing force effectively throughout the head. Anatomical reconstructions have allowed paleontologists to get to the bottom of how *Allosaurus* fed. It would have stripped meat from carcasses by swiftly retracting its head straight up and back.

In the 1990s, a nearly complete skeleton of an *Allosaurus* was recovered from the Morrison Formation in Big Horn County, Wyoming. This subadult specimen gained the nickname Big Al. All told, the exceptionally preserved skeleton recorded 19 osteological pathologies on the vertebrae, ribs, bones of the tail, hips, hands, and feet. These pathologies fit into two large categories: first, those resulting from traumatic injury, and second, those resulting from an infection. Sometimes, of course, secondary infections follow a primary injury. Lucky for Big Al, all the fossilized pathologies occurred some significant amount of time before death because all show signs of healing.

Among the most significant of these traumatic injuries were bone fractures. If these don't rapidly kill the animal that experiences them, a healing response begins. Typically, this is through the formation of a bony callus. This is essentially an irregular lump of newly formed bone that rapidly grows in the normally soft and flexible connective tissue close to the break. This helps to stabilize the injury by surrounding the immediate area of the broken bone. If the healing process commences and is undisturbed by infection or displacement, the callus will eventually be remodeled and smoothed over. Once in a while, especially with fractures, intense mechanical loading can rupture the bony callus and its blood vessels. This eventually results in the formation of a false joint. The broken ends of the bone might smooth over and never fully stitch themselves back together, leaving a movable joint between them. This usually causes chronic pain. Big Al exhibits bony calluses on a number of its ribs and vertebrae and on one of its fingers.

How would a viral, bacterial, or protozoan infection appear in the fossil record? A bony abnormality caused by these sorts of infections is called osteitis. If an infection becomes chronic and impacts the bone marrow, it is called osteomyelitis. Dinosaurs were probably more like living birds, which don't produce pus. Instead, they produce a protein called fibrin that helps wall off the infected area to prevent spread into the bloodstream. These types of bony infections also result in superficial bony outgrowths, called exostoses, that are usually connected to the interior of bones via lesions. Big Al exhibits a couple of abnormal toe bones. Both are characterized by rough and expanded surface textures with lesions that penetrate deep into the bones' interiors.

Most pathologies in all sampled *Allosaurus* seem to be traumatic in origin. There are only a few recorded examples of a secondary infection following an injury. Some paleontologists suggest that this might mean that inflamed wounds would quickly lead to death. Others suggest that this might mean that the *Allosaurus* immune system was great at prohibiting infection. The abundant record of healed injuries points more to the latter. Signatures of infection tend to be localized to single bony elements. This hints at an immune system that is effective at isolating infection, preventing spread, and minimizing the risk of lethality.

The severity of pathology in *Allosaurus* points to a lifestyle with frequent exposure to hazards. Epic battles between *Allosaurus* and its potential prey almost certainly resulted in injuries or death for one or the other animal. Take, for example, the recent find of an *Allosaurus* tail vertebra with a puncture wound that precisely matches the shape of a *Stegosaurus* tail spike. Paleontologists have also found a *Stegosaurus* neck bone with a U-shaped bite mark that looks like it came from the jaws of an *Allosaurus*.

TYRANNOSAURUS REX

Fast-forward 80 million years, into the Late Cretaceous. The nearshore ecosystems of the Hell Creek Formation in western North America were ruled by *T. rex*. *T. rex* had one of the most powerful bites among land-living animals and exhibited a forceful, bone-crushing hard chomp. An adult *T. rex* topped the scales at around seven tons. It stood nearly 13 feet tall at the hips and was 40 feet long. Although shed teeth are scattered throughout the Hell Creek Formation exposures, the record of complete skeletons is quite elusive.

To date, fewer than 50 skeletons have been recovered, most preserving less than 15% of the skeleton. By far one of the most complete *T. rex* skeletons out there is a specimen nicknamed Sue that now resides at the Field Museum of Natural History in Chicago.

Sue's skeleton is riddled with problems. Three of Sue's right-side ribs exhibit the signatures of healing breaks. The injuries to these three ribs lie along the same horizontal axis and exhibit a similar relative degree of healing. These similarities probably indicate that all three ribs were fractured at the same time. One of the ribs shows a false joint formed at the intersection of the two broken rib halves. This demonstrates that the rib was likely mobile during the formation of the soft callus and that healing would have been repeatedly disrupted. The proximity of these broken ribs to several other pathologies on Sue's right shoulder and upper arm indicates that they may also be linked to a single traumatic event, like a fall or a blow to the right side. These shoulder and arm pathologies include pits and spurs that have been linked to the shoulder musculature and tendons pulling away from the bone and prompting extraneous bone growth.

Sue's injuries extend to the left side of the body as well. The left fibula in the lower leg exhibits an extensive irregular bone growth that extends the entire circumference and nearly two-thirds the length of the bone shaft. When paleontologists utilized CT scanning to look at this pathology from the inside out, they found that the bony callus is characterized by pores and channels that open externally. Perhaps these served as a drainage point for an infection within the bone. Infections of this sort, without a bony fracture, are common in elements that lack protection from robust musculature. Luckily for Sue, since paleontologists think dinosaurs exhibited a more birdlike immune response, infections of this sort were quickly isolated and contained.

Sue's lower jaw bones are pitted with smooth-edged holes. When these were first discovered, paleontologists imagined that the holes were the result of a bite by another *T. rex*. Later hypotheses suggested that the holes may have formed as the result of a bacterial infection drawn from common bacteria like *Actinomyces*, which causes painful lesions in the mouths and skull bones of today's mammals. But now, additional study has called both hypotheses into question.

The holes weren't evenly spaced enough to have resulted from a bite and were all at different stages of healing. The lower jaw is one of the least accessible sites on the skull to bite. Moreover, the holes are circular rather than teardrop-shaped, which is the predicted morphology of a puncture-and-pull style of bite. Instead, the shape of the holes points to a much smaller culprit: a tiny, single-celled, parasitic eukaryote similar to modern-day *Trichomonas*, which can be transmitted through drinking water. Once it has colonized the mouth, it attacks soft tissue, essentially eroding away chunks of the jaw bones. The parasite infects the throat, esophagus, and mouth, causing painful lesions and making eating and drinking difficult. Some scientists believe that this tiny organism may have been the killer of the mighty Sue through starvation and dehydration.

Interestingly, Sue's bones also show signs of gout. Gout is a metabolic disorder that is caused by the excessive accumulation of uric acid in the body. This can create lesions within the joints and arthritis. Gout is hypothesized to result from a diet high in meat protein—which, of course, was all that *T. rex* ate.

When considering the age-specific mortality for the North American tyrannosaur species, researchers can see that there is high juvenile survivorship and increasing mortality later in life. This pattern of survival favors the accumulation of many pathological traces. The vast majority of dinosaurs that exhibit bony pathologies are those in midlife. They have had a long time to collect wounds, injuries, and infections, yet go on to survive and heal.

On the flip side, most diseases that cause death do not leave traces within bones. This means that they are osteologically invisible. Many individuals in a population would likely die before showing any bony manifestations of illness. Acute illnesses are often so fast-moving that they kill the sick in only a few days or hours. It's only in those special cases, where a dinosaur is healthy enough to mount an intense immune response but ill enough to manifest it in their bones, that paleontologists have the clues left behind.

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REIMAGINING EVERYTHING ABOUT DINOSAURS

This lecture tackles the body language of dinosaurs. It tells the story of what they were doing with all the crazy anatomical features on their bodies. You'll learn how paleontologists begin to answer that question, employing methods from comparative biology to nail down the relationship between form and function in these beautiful dinosaur bodies. You'll also learn a little more about how paleontologists test ideas about these features and what they think dinosaurs were doing with them.

THE TOOLS IN OUR TOOLBOX

When trying to investigate the ways in which dinosaurs may have utilized their bizarre features, paleontologists have a few tools in their arsenal—namely, modern analogues and comparative biology. First, researchers can look at living animals in modern ecosystems that have similarly bizarre structures to see what they do with them. What do modern creatures do with their anatomical features? Perhaps paleontologists can extrapolate back in time to dinosaurs if the features are built similarly, which allows them to come up with some potential ideas for function.

Of course, researchers also have the EPB in their toolbox. They can ask what animals from the crocodile-line or bird-line archosaur groups do with their strange ornaments, then push that function backward in time into the dinosaur world as well. Looking at bracketing animals can give researchers some important insights into the ways dinosaurs may have looked that would be hard to discern otherwise.

Finally, researchers can investigate the feasibility of potential functions through biomechanical testing. Essentially, this allows paleontologists to examine whether the anatomical feature of interest could stand up to the particular function they think it might have had. A structure can only do what researchers say it does if it holds up to the proposed function without breaking—or even killing the organism.

Take an example from modern-day bighorn sheep. These animals have fierce battles during mating season in which they literally slam their skulls together. They have a number of specific safety features built into their bodies that make this behavior possible without much risk of serious injury or death. First, they have tons of air spaces in their horns and skulls that help distribute the force of impact, thereby protecting their brain. Second, the foreheads of bighorn sheep and other types of headbutting mammals also tend to be relatively flat. This ensures a specific contact interaction with another skull. Third, the shape of the horns helps to result in more precise contact, which distributes the force throughout the skull in precisely the right way. And bighorn sheep also have adaptations for headbutting behavior in the musculature of their necks and shoulders that provide further protection. If researchers think that a dinosaur might have exhibited headbutting behavior, they could look to see if the dinosaur had similar types of biomechanical protections.

For example, consider pachycephalosaurs. These popular dinosaurs have historically been depicted ramming their skulls together in epic intraspecific battles. But how accurate might this vision be? In the early 2000s, a team of researchers argued that since headbutting in living animals requires built-in safety mechanisms, without them, pachycephalosaurs—whose name means “thick skull”—might have been down for the count after a bout. The jury is still out on whether pachycephalosaurs had head-to-head battles. There might be another good explanation for their bony domes.

When combining modern analogues, comparative biology, and biomechanical testing, researchers learn that sometimes dinosaurs’ bizarre features have a specific, helpful role to play when it comes to defense. This is particularly true when considering features that might impart some protection for potential prey.

DISPLAYS

Much of the time, structures that are energetically expensive to build and maintain have something to do with sex. Structures built for battling may not exist only for defense against potential predators. They might also allow dinosaurs to engage in battle with other members of their own species for mates or territory.

Another significant function of ornamental features is for display. Display includes having characteristics that help identify a member of a particular species—they could be bony features, colors, plumage, or even behaviors like singing and dancing. Sometimes males of the same species will employ postural display to highlight their dominance. This allows them to fend off rivals without engaging in a physical battle.

And of course, displays can be used to attract mates. Researchers typically think of this in the realm of sexual selection. Here, females are choosy, picking among males that exhibit fancy features. These features surreptitiously signal the fitness of the male, who is exhibiting the genetic robustness to build such resource-heavy features. Because females often invest more in offspring, they must ensure that they are choosing to mate with males who are genetically fit and whose offspring may have a better chance of survival. Therefore, female choice is often the driving force behind the evolution of these bizarre structures.

MULTIPURPOSE FUNCTIONS

The lines between different functions in living animals can be blurred a bit. Some features may serve as multipurpose tools to be utilized in both defense and protection, or double as a means for mate acquisition.

Consider ankylosaurs, which are covered in bony armor. Bone plates called osteoderms grow within the skin of ankylosaurs and are so pervasive that they essentially cover the entire back of the animal. Even the eyelids of ankylosaurs have a thin bony protective layer within. These bony plates would certainly have helped to protect ankylosaurs from carnivorous predators in their world. In addition, they have swingable clubs at the tips of their tails that might have been great for bludgeoning an attacker. Of course, these same features could have been used in more intraspecific competition with other ankylosaurs. However, based on comparisons with living animals, it seems pretty clear that such body armor is for protection and defense. When researchers look to living organisms with similar features, they can see that lizards and armadillos often use their bony osteoderms as a protective armor in the face of predation.

One genus of ankylosaur called *Borealopelta* also had an extra predator evasion method at its disposal: color. The skeleton of *Borealopelta* was discovered in Cretaceous rocks in Alberta, Canada, and was so well preserved that even the keratin sheaths that would have overlain the osteoderms in the skin were still intact, and scientists were able to detect some evidence of organelles called melanosomes that dictate skin color. The preserved melanosomes indicate that *Borealopelta* would have been reddish-brown on top and lighter on the belly. This type of coloration is called countershading. It's a great way to camouflage in terrestrial and marine environments.

What about stegosaurs? These herbivorous dinosaurs exhibited varied ornamentation in the form of plates and spikes, covered in keratinous sheaths. But once in a while, these features may have also played a role in fending off a hungry theropod. An interesting injury preserved in the pelvis of a carnivorous

Allosaurus has been hypothesized to come from the swing of a *Stegosaurus*'s tail. A tail-spike-shaped hole in the *Allosaurus* pelvic bone is surrounded by a baseball-sized callus that may indicate a healing, infected wound.

Recall that the ceratopsians had frills and sharp bony horns that ornamented their faces. Could these features have had anything to do with defense? Of course! Don't forget that animals like *Tyrannosaurus rex* lived in the same environments as *Triceratops* and its relatives. There is amazing fossil evidence of a *T. rex* tooth that was embedded in the face of a *Triceratops* while it was still alive. The healing around this puncture indicates that the *Triceratops* survived the attack. Paleontologists also have good evidence that *Triceratops* engaged in battles with other *Triceratops*. Healed puncture wounds discovered near the eyes, ears, and base of the frills are precisely placed signatures of the impact of a head-to-head *Triceratops* battle.

SEXUAL DIMORPHISM

In addition to protection and defense, anatomical features might have been used for other purposes as well, including sexual dimorphism. For example, in birds, the males tend to be colorful and flashy, while the females are duller and more apt to be camouflaged. These differences come about from selection pressures for more elaborate features over time. This pushes dimorphism in anatomy, form, and behavior to maximize mating success.

Among ceratopsians, the most obvious differences are the variety of shapes that their horns and frills exhibit. Their head ornamentations are the most identifiable features of their bodies for paleontologists—and probably for them. Those horns and frills are clearly a signature of species membership. Often, that is tied to sexual dimorphism. Paleontologists know that the horns and frills of ceratopsians don't get elaborated until pretty late in life. It's only when they reach sexual maturity and are ready to mate that researchers begin to see real distinctions and growth of these decorations. This is another sign that these features might be sexually dimorphic.

That said, *Triceratops* didn't use its fancy headgear only for looks. Battle scars on the skulls of *Triceratops* preserve evidence of Cretaceous combat at rates that are much higher than you would expect if these fancy features were only for showing off. When compared to the skulls of another species of ceratopsian called *Centrosaurus*, *Triceratops* skulls are 10 times more likely to record evidence of injury. Interestingly, the most likely culprit for all these *Triceratops* face and frill wounds are the horns of other *Triceratops*. Paleontologists hypothesize that this means that *Triceratops* locked horns and wrestled like modern-day deer and antelope since the injuries share similarities with those from the horned animals of today. They likely resulted from misplaced horns or a thrust from a competitor. Like these modern analogues, ceratopsians probably also evolved different types of horns that helped to minimize the risk of traumatic injury.

Recall that for decades, the question loomed as to whether pachycephalosaurs were headbutters like bighorn sheep. Perhaps there's a better explanation for their skulls. Testing the idea required an analysis of the biomechanical properties of those bony domes. The first study that took the question to task focused on the microscopic organization of their skulls. Porous areas of the dome are full of blood supply and radiating bone mineral. Some researchers have argued that these would have been great at absorbing the shock of impact. Instead, a new study recognized that these radiating structures were only present in younger animals, filling in and smoothing out into adulthood. Thus, it appeared that this unique internal anatomy was there to help the dome rapidly expand in conjunction with the onset of sexual maturity. The fancy features of pachycephalosaurs change significantly through life, getting more elaborate and specific as they become adults.

An alternative view questioned whether the dome functioned purely in sexual display or species recognition. It pointed to the intense resource investment that would have been required to build such a structure. If pachycephalosaurs used their domes in intraspecific fights, then butting two bony skulls together would have certainly resulted in occasional injuries that may have been recorded as pathologies in the fossil record. To test this hypothesis, this research group investigated the frequency of pathologies in the skulls of pachycephalosaurs. They found that about 20% of domes exhibit signs of osteomyelitis. This study didn't control for the age of the dinosaurs as in the original headbutting analysis. However, it did provide some interesting new insights that warrant further investigation. Perhaps instead of headbutting, pachycephalosaurs flank-butted. Perhaps their special skulls were simply all about saying hello to the opposite sex. Or maybe they were clumsy and bumped their heads all the time.

Did you ever wonder if sauropods had any anatomical weaponry or sexual display features? No one knows. But consider why sauropods might have such long necks. Think about living animals that exhibit lengthy necks and what they do with them. Giraffes battle for mates and territory with their necks. They literally slam their necks into each other. Perhaps the sauropods used their long necks for more than stretching out to eat.

ATTRACTING MATES

Some theropod dinosaurs may have been extremely fancifully equipped for display. Given the presence of feathers in a number of theropod lineages, it makes great sense that they could have shaken a tail feather or two in the spirit of modern bird mating dances.

What about singing? Serenades are among the most common forms of display exhibited by animals across the tree of life. It's almost certain that dinosaurs were singers too. One of the most interesting hypotheses for dinosaur vocalization has centered on the outrageous noses of hadrosaurs like *Parasaurolophus*. For years, the bizarre, species-specific cranial crests sported by members of this duckbilled dinosaur group prompted an array of potential functions. Some scientists suggested they might have been a type of weapon. Others suggested that they were cranial air tanks or would have been great at bumping tree branches out of the way. One scientist even went as far to suggest that perhaps they were snorkels that would have allowed these dinosaurs to submerge.

But in the 1970s, science finally turned to modern analogues to help solve the mystery. Researchers suggested a dual function in visual display and sound resonation during vocal communication. Like most secondary sexual characteristics, the nasal crests of duckbilled dinosaurs are only elaborated at sexual maturity. Thus, they would have been perfect for singing to a mate. The internal anatomy of the crest is a long, bent tube that would have allowed low-frequency vibrations produced in the throat to amplify effectively.

Additional studies included other crested duckbilled dinosaurs and supported the idea that nasal crests were great vocal resonators. And by studying the anatomy of the ear still preserved inside the skulls of these diverse dinosaurs, researchers have learned that they were well suited to detect low-frequency rumbles.

Finally, colorful bodies are shared by all reptiles. It is a "primitive characteristic" that they inherited from a common ancestor. This means that when you see birds or lizards or crocodiles that aren't colorful, it's likely because they evolved body colorations away. Many of these animals see in the UV spectrum, making them look even more colorful to each other than they do to us. Luckily, in a few cases, there is evidence of actual color preserved in some dinosaur skin and feather impressions that show that dinosaurs were stripy rust and white or iridescent black.

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DINOSAUR EGGS AND BABIES

This lecture explores one of the most adorable things on planet Earth—ever. It's time to talk about dinosaur babies. Here, you will learn about all things related to dinosaur eggs and discover whether dinosaurs cared for their young. Later on, the lecture highlights some of the sauropod work done in Madagascar. You will also learn about a fun detective story that highlights what the earliest months of life were like for soon-to-be giant dinosaurs.

AMNIOTE EGGS

To begin, dinosaurs—and all terrestrial vertebrates that are not amphibians—belong to a group of animals called amniotes. Amniotes lay shelled eggs that can allow them to reproduce away from the water. All dinosaurs laid eggs like almost every other amniote. Amniote eggs have different shell types. Sometimes they can be softer and less mineralized, like the eggs of a sea turtle. Lizards and crocodiles lay leathery eggs that are a bit more flexible. Birds lay hard, crunchy-shelled eggs. And ancient dinosaurs laid their own hard-shelled eggs.

CROCODILIAN AND BIRD EGGS

The archosaurs living today give paleontologists the best hints at what might have been going on in the world of dinosaurs. Crocodiles have two functional oviducts, where they shell their eggs. Since all the eggs are formed at once, they take the shape of equidimensional ovals. When crocodiles are ready to deposit these eggs, they scoop out a sandy hollow for a nest and lay all of them in rapid succession. Hatching occurs in a narrow little window of time, en masse. For anywhere from six to nine months, the baby crocodiles hang out close to the parent. In fact, when the initial move from nest to water occurs, the parent helps the babies by scooping them up with their jaws and gently carrying them.

Birds typically have one functional oviduct and shell their eggs one at a time. This imparts a slightly irregular shape to the egg, with one skinnier end and one fatter end. They lay their eggs one by one. Birds have a wide variety of nesting and parental care techniques. Some birds, like ostriches, lay their eggs in an open ground nest and then lie down beside them to allow the radiating heat from their bodies to warm the eggs. In contrast, other birds sit on top of their eggs to keep them warm.

Once baby birds hatch, they exhibit two options for post-hatching behavior. The first is precocity—this means that the baby birds, such as ostriches, are pretty self-sufficient once they hatch. They can walk around on their own legs and eat by themselves. Most other birds, such as robins, are altricial. Their limbs exhibit large cartilage caps that make them too soft to walk on right away. Thus, these birds are nest-bound and completely dependent on their parents to deliver food back to the nest.

Eggs are remarkable little "independent oceans" that allow amniotes to move away from laying squishy eggs in watery environments. If you count birds as dinosaurs, the largest egg award goes to a more recently extinct dinosaur: the elephant bird, or *Aepyornis*. This bird went extinct on Madagascar when humans arrived there around 30,000 years ago. Modern-day dinosaurs also lay the smallest known amniote eggs—those of hummingbirds are about the size of a jellybean. Mesozoic dinosaurs mostly had pretty small eggs. Even the largest dinosaur eggs were no bigger than a soccer ball. Most dinosaurs laid eggs about the size of a softball or large grapefruit.

Another fun fact about eggs? They can be colorful. All egg coloration is the result of two major pigments in different combinations. One of these is a pigment that results in blue-green hues, and the other pigment imparts brownish-red hues.

The color of eggs has functional significance. It can be used for camouflage and also help form a protective sunscreen layer that deflects UV rays from the egg, preventing them from mutating the baby's genetic code. Also, pigments sometimes impart antibacterial properties that help keep bacteria out of the eggs. Color can also be useful for animals to identify eggs that belong to their own species.

The microscopic pores in eggshells allow the embryonic animal inside an egg to exchange oxygen and carbon dioxide with the outside world. The pores flow through a crystalline structure that allows eggshells of different animal groups to be relatively precisely identified. The density of pore spaces has something to tell researchers about whether the eggs may have been buried or laid on the surface. Eggs that are buried, like crocodile eggs, have more pores per egg because they need more conduits to exchange oxygen and carbon dioxide in a buried nest. In contrast, eggs in open nests require fewer pores. Researchers can use the relationship between egg porosity and open or closed nests in living animals to predict whether fossil animals with similar porosities were laying their eggs out in the open, burying them under vegetation or sediment, or even sitting on them to brood.

DINOSAUR GENDER AND EGGS

What do paleontologists know about dinosaur soft parts, like oviducts or external genitalia, like penises? Is there any way to tell a male from a female dinosaur? For the most part, researchers aren't sure because the soft stuff of dinosaurs doesn't usually get preserved in the fossil record. Like their living archosaur relatives, dinosaurs had cloacae. A cloaca is like a one-stop shop for the exit of both the urogenital system and the digestive system. In some living crocodilians and birds—and many other living reptiles—the cloaca houses a protrusible penis that is exposed only during mating. Because only 3% of living birds have true penises, researchers can't say much that is definitive about the presence of such a feature in dinosaurs. That said, these diverse organs are common among land-living animals, especially in those with unusual body shapes, such as turtles. Having a penis can sometimes ensure more precision when it comes to mating, making it more likely that a male is able to inseminate a female.

It has been a little bit easier to make determinations about sex in female dinosaurs. Paleontologists use two clues to help: medullary bone and the anatomical signatures of oviducts. Medullary bone is an interesting type of highly vascularized bone tissue that forms on the interior marrow spaces in bird bones when they are getting ready to shell their eggs. It essentially allows birds to mobilize bone mineral from their own bodies for use in the bones and eggs of their offspring. Medullary bone has been discovered in a variety of dinosaurs, indicating that these specimens are ovulating females.

What about the hallmarks of oviducts? In a few cases, paleontologists find oblong eggs that appear to have been laid in pairs. Perhaps this means that the egg layer had two functional oviducts, like crocodiles, but shelled only one egg at a time in each, more like birds. An exceptionally preserved partial oviraptor skeleton found in China gave paleontologists a little confirmation of this idea. This fossil preserved two shelled eggs within the pelvis, side by side. The paired eggs indicate two functional oviducts, with one egg produced at a time.

Paleontologists have found many dinosaur eggs worldwide. Dinosaur eggs come in all shapes and sizes. When researchers combine what they can learn from eggs' shape, microstructure, porosity, and where they occur in time and space, they can characterize eggs into different oospecies. This is a kind of taxonomy that allows researchers to group similar eggshell styles together, even when they're not positive which dinosaur laid the eggs. Unless paleontologists discover eggshells in association with identifiable embryos or associated adults, it can be hard to link eggs to particular dinosaurs. Thus, occasionally, they use ootaxonomy to develop a naming protocol for eggshells.

Only when paleontologists find embryonic dinosaurs preserved inside specific types of eggs can they tie a particular oospecies to broad groups of dinosaurs. In other words, researchers can sometimes say that they know sauropods laid eggs with an egg microstructure characterized by a particular suite of features and a certain egg morphology. Then, the next time they find an egg without an embryo but with these eggshell characteristics, they can reasonably hypothesize that that egg might have also been laid by a sauropod.

DINOSAUR NESTS AND PARENTING

There are many ways that dinosaurs built their nests, and there are many different ways that paleontologists think dinosaurs might have brooded or cared for their nests. Some theropod nests take on a general morphology where the eggs are all arranged in a spiral shape. This means that the eggs were manipulated within the nest once they were laid. Perhaps these theropods were organizing their eggs to optimize incubation temperatures within their nests. The same thing occurs in the nests of *Protoceratops*, a little herbivorous ceratopsian from Mongolia. This means that some dinosaurs were definitely involved in tending nests of unhatched eggs.

Rarely, paleontologists have even found dinosaurs sitting atop their eggs. Recall the case of the early discoveries and subsequent misinterpretations of *Oviraptor*. The name *Oviraptor* translates to "egg thief" because the first finds included these theropods near eggs that researchers assumed to be from an herbivorous dinosaur. This prompted the idea that *Oviraptor* was stealing the eggs from the nest. However, it was eventually discovered that *Oviraptor* parents were protecting their nests through brooding.

However, it seems that other dinosaurs might not have been such great parents. One great example? The sauropods. There are several localities on Earth with identifiable sauropod nests. Generally, sauropod eggs are round and seem to be laid, but they're not organized. Instead, paleontologists see a large dump of disorganized eggs—essentially a pile of eggs. Paleontologists imagine that sauropods would have used their legs to kick out a low, hollow space, laid their eggs—sometimes as many as 50 per nest—and then wandered away. This makes pretty good sense when you consider the scale of sauropods. Their eggs would have been easily crushed by a simple misstep.

In a few cases, there is evidence that some dinosaurs returned to nesting localities year after year and that sometimes many different individuals may have laid their eggs in the same place at the same time. There is an amazing fossil locality nicknamed Auca Mahuevo where many sauropod nests were discovered that contained embryonic titanosaurs within eggs. The number of nests and their distribution in space point toward some colonial nesting and a return to this nesting ground over time, or site fidelity. Multiple sedimentary layers preserve nests containing eggs. The proximity of nests within a single horizon at Auca Mahuevo seems to leave little space for one adult sauropod—let alone several adults—to move among them. This may point to more limited nest tending in this group of dinosaurs. Instead, sauropods seem to have laid many eggs, hatched many babies, and bet on the loss of many juveniles along the way.

The fossil record for eggs and nests for duckbilled hadrosaurs is well known from North America. The famous dinosaur nesting site in Montana, Egg Mountain, documents three notable finds: a colonial nesting strategy, site fidelity for the hadrosaur *Maiasaura*, and a nesting site for a small theropod called *Troodon*.

These sites provided some interesting data on the potential for post-hatching care in *Maiasaura*. There are many nests that preserve broken-up eggshells and partial baby skeletons—ranging in size from small hatchlings to toddler-sized animals. To determine whether these small hadrosaurs were nest-bound, paleontologist Jack Horner thin-sectioned their long bones and studied the preserved cartilaginous ends. He hypothesized that the large cartilage plugs at the ends of baby hadrosaur bones would have made it impossible for them to run around on their own. Horner suggested that this bone structure would have required a baby *Maiasaura* to hang out within the nest, relying on its parents to bring food back until it was large enough to leave the nest and be independently mobile.

Eggshell porosity in dinosaur eggs can tell paleontologists about whether their eggs were exposed or buried. Researchers can see the preserved porosity in dinosaur fossils, like those channels that exist in the eggs of living animals. This information reveals that while some dinosaurs left their eggs exposed on the surface, others buried their eggs.

An interesting discovery is that some dinosaur eggshells preserve the two pigments seen in all modern bird eggshells. Thus, for a few rare dinosaur eggs, paleontologists can make pretty good guesses about the colors they might have been. The most exciting one belongs to an oviraptorid dinosaur. The eggs looked bluish when they were discovered. It turns out that the primary pigment preserved in the microscopic structures of these eggshells is the same one that makes modern eggs blue. From this information, paleontologists can hypothesize that these dinosaurs laid blue-green eggs, like modern emus.

The fact that these eggs are pigmented might have implications for the mode of incubation as well. If they were exposed to the surface most of the time, perhaps that blue-green color served as sunscreen, as it does in emus.

BABY SAUROPODS

One of the missing parts of the sauropod fossil record has been their babies. This led some scientists to propose that perhaps sauropods gave live birth to 500-pound newborns. That would certainly help explain why paleontologists don't usually find small sauropods.

The discoveries of sauropod embryos at places like Auca Mahuevo put to rest the idea that live birth was a specialization of sauropods. However, it only made the question about their babies more pressing. If sauropods were laying nests with 50 softball-sized eggs, researchers would expect high rates of mortality in those babies—that means many dead little things that might get swept into the fossil record. But there was no record of baby sauropods to build from. Thus, researchers couldn't answer any questions about the earliest life history for the largest of all dinosaurs.

It turns out that a paleontologist's casual search through a cabinet of unknown fossils found over 11 different field seasons in Madagascar led to the discovery of the tiniest hatched baby sauropod ever discovered. Based on comparison with other fossils in the collection, this baby was less than 10% the size of the biggest known *Rapetosaurus*. Even more interesting, each of these little bones looked pretty much the same as the adult bones in the collection. The proportions of the femur were retained from infant through to juvenile, subadult, and adult sizes. Given these proportional similarities, paleontologists were able to calculate the scaling relationships between elements to estimate body size, including mass, in this tiny titanosaur. It would have stood knee-high—about 35 centimeters at the hip or shoulder—and weighed less than 50 pounds when it died.

BABY *RAPETOSAURUS*

Baby *Rapetosaurus*'s bone tissue records fast growth. These baby bones were once packed with blood vessels and cells that helped fuel its rapid growth right out of the egg. All the bones document that the baby was less than three months of age at the time of death. This means that it had gone from hatching to 50 pounds in a pretty short interval of time. This makes good sense when considering the similar pattern of fast growth in much larger sauropods, which were collectively among the fastest-growing dinosaurs ever.

Paleontologists also spotted a strange pattern in each of the bones. Deep inside the bone cortex, there seemed to be a little ring around the circumference of each bone. When the researchers zoomed in, they realized that this was a zone of relatively low vascularity that indicated a pause or serious slowdown in growth. They turned to the published literature from living animals to help them determine what this growth slowdown so early in life meant.

They discovered that in pretty much every animal, the moment of birth or hatching is traumatic and super tiring. Thus, it is normal for newborn or newly hatched babies to pause their growth to recuperate from that stress for a short interval before turning on their regular growth rate. During that interval, babies that have powered their way out of an egg lie around absorbing their yolk sac and recovering from the hard work of being born. The signals that these pauses create within bones are called hatching lines, birth lines, or neonatal lines. The researchers had identified hatching lines within these baby sauropod bones. This means that they could predict hatchling size using pretty simple math. At hatching, *Rapetosaurus* would have been about six inches tall and weighed five pounds. *Rapetosaurus* was about the size of a chihuahua at hatching, and a couple months later, it was the size of a golden retriever.

What about parental care? When the paleontologists took a close look at the preserved cartilage at the ends of the baby bones, they noticed thin cartilage layers that were more like those of precocial birds than the thick, squishy cartilaginous ends of bones in altricial birds. They also looked for signatures of bone remodeling, which begins once baby animals start loading their bones to walk around. The researchers found the characteristic lifesaver-shaped structures that indicated *Rapetosaurus* babies were already using their bones enough to have prompted some serious remodeling. Together, these two signatures seemed to indicate a fairly precocial lifestyle. It seems that a baby *Rapetosaurus* hatched out of the egg and was pretty much ready to go, foraging on its own and evading predators from the start.

This research helped paleontologists realize how different newborn sauropods were from adults. Baby bodies were already built for the future loads they'd have to carry as adults. This is why the limbs were proportionally identical. Being overbuilt for a small body size has many implications for movement and locomotion. Like small elephants, baby sauropods would have been capable of running, jumping, rolling around, and standing on their hind legs. They were likely camouflaged like modern baby animals are, with muted colors, stripes, and spots that helped them blend into the world around them. They ate different food than their adult counterparts—and in some ways were like totally different animals.

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HOW DINOSAURS CONQUERED THE COLD

From what paleontologists know, dinosaurs did live in places like the ones that most people imagine when they try to situate them all those millions of years ago. But dinosaurs were found everywhere. No corner of the globe was free of the reign of Dinosauria—from equatorial islands to the highest latitudes on Earth. They even lived at the North and South Poles. This lecture shares the story of the dinosaurs that conquered the cold: the polar dinosaurs.

MESOZOIC POLAR ENVIRONMENTS

In the modern world, there are two poles. Technically speaking, the north polar region is that area north of 60° latitude, and the south polar region is that area south of the 60° mark. The modern-day north polar region is the Arctic. It's basically a frozen ocean, surrounded by land. The south polar region is the Antarctic, and it's a giant landmass surrounded by oceans. The Antarctic is generally colder than the Arctic.

Both poles experience less intense solar radiation than the rest of the globe. They are heavily glaciated with year-round, permanent ice, and they exhibit extreme variations in seasonal daylight. During the wintertime, each pole experiences 24 hours of darkness. In the summer, each pole has 24 hours of daylight. Today, the largest land vertebrates in the Arctic are polar bears, and those in the Antarctic are penguins. Both are endothermic or warm-blooded animals. It seems that being warm-blooded might be a prerequisite for survival at the polar regions of the earth—at least in Earth's current configuration.

But what about polar environments back in the Mesozoic era? Before the continents began to rift, both polar regions included significant landmasses. However, since the Mesozoic was warmer overall than our modern world, the poles lacked permanent ice caps. This is why there were much higher sea levels and shallow continental oceans during the Mesozoic. But these polar regions still experienced less solar radiation overall and were relatively cool. As in the modern world, there would have been extreme variations in seasonal light: 24 hours of darkness in winter and 24 hours of sunlight in the summer.

How do researchers determine what the air temperature was more than 66 million years ago? Scientists have taken a look at modern ecosystems and realized that the shapes of leaves provide clues to ambient temperature. In places where temperatures are pretty warm, leaves tend to have smooth margins because they don't need as much surface area to have efficient photosynthesis. In cooler climates, leaf margins become serrated and rough, increasing the area for photosynthesis. This relationship is well established in modern ecosystems. Thus, researchers can study the margins of preserved leaves in different places and estimate temperatures from there.

These types of studies have revealed that mean annual temperatures at the Cretaceous North Pole ranged from 2°C to 13°C (36°F to 55°F). At the Cretaceous South Pole, the temperatures ranged from −6°C to 5°C (28°F to 41°F).

DINOSAURS AT THE POLES

Consider the north polar dinosaurs, known from the North Slope of Alaska. So far, paleontologists have been able to identify a diversity of these dinosaurs on the basis of partial skeletons, isolated bones and teeth, and even footprint fossils. At least 12 different types of dinosaurs have already been discovered, all living in the Late Cretaceous between about 75 and 70 million years ago. All these dinosaur species have also been discovered at lower latitudes in western North America.

The most common north polar dinosaur is the duckbilled hadrosaur, *Edmontosaurus*. It weighed between four and five tons and is one of the largest known hadrosaurs from North America. A ceratopsian called *Pachyrhinosaurus* is also well known from the North Slope. *Pachyrhinosaurus* didn't have the nose horns typical of other kinds of ceratopsians. Instead, it sported massive, flattened, rugose bosses—a large one over the nose and a smaller pair over each eye. Its frills were decorated with unusual little flattened horns that pointed forward and down from the top edge of the frill. These dinosaurs also exhibited both a sharp, pointed beak and a thick row of cheek teeth great for grinding down tough plant material. A smaller-bodied herbivorous ornithopod called *Thescelosaurus* also lived at the top of the world. This little dinosaur was bipedal and probably only a few meters long from head to tail. It would have grazed on vegetation low to the ground and used its little beak to selectively choose its food.

Theropods include the large-bodied *T. rex* and *Albertosaurus* and a few smaller species that may have been feathered, such as *Troodon*, *Dromaeosaurus*, and *Sauronitholestes*. Though pretty rare in the lower latitudes, *Troodon* is much more common up north. Data suggests that the *Troodon* species found in Alaska are larger than the species known from places like Montana and Alberta. This is perhaps the result of Bergmann's rule, which states that larger species are found in colder environments. There is even evidence of a diving bird called *Hesperornis* known from the North Slope fossil sites.

In the south polar regions, you can see a pattern. Way back then, there were two modern landmasses that were tucked below the 60° south latitudinal barrier: Antarctica and the southern part of Australia. Australia is known for small-bodied ornithischian dinosaurs and fleet-footed, turkey-sized herbivores like *Leaellynasaura* and *Qantassaurus*. Sauropods and ankylosaurs also lived in polar Australia, as did a diverse array of theropods.

Farther south, in the Transantarctic Mountains, records of dinosaurs include even older fossil records, with prosauropods and theropods, like *Cryolophosaurus*, known from the Jurassic period. *Cryolophosaurus* would have been about 20 feet long and weighed about 1,000 pounds. This ranks it as one of the largest theropods known from this Early Jurassic time period. *Cryolophosaurus*, whose name means "frozen crested lizard," sported a distinctive head crest made of an upward curve of its forehead bones. The crest is relatively thin and delicate, prompting the hypothesis that it may have been used in intraspecies recognition and sexual display.

Overall, in the polar environments, dinosaurs seemed to survive with no problem. Although their diversity might seem pretty high, it is relatively small compared to that of contemporary dinosaur ecosystems known from lower latitudes. The pattern of reduced biodiversity with increasing latitude is a trend that is also observed in modern ecosystems.

COPING WITH THE COLD

What was there for polar dinosaurs to eat? The most abundant record on this question comes from the North Pole. There, climatological data from fossil pollen, leaves, and preserved wood points to Cretaceous forests with a mixed canopy. Deciduous conifers and regular conifers dominated the tree line. The understory vegetation included a diversity of flowering plants, ferns, and cycads. When winter came, these plants would have gone dormant. This means that they wouldn't have been replenishing the necessary food resources for herbivorous dinosaurs during that cold, dark winter. If dinosaurs stuck around, they would have had to significantly reduce their intake of plant material during the winter months.

Thus, perhaps dinosaurs migrated to warmer climates when the cold and dark set in. Some scientists have suggested migration as the only plausible explanation for the presence of dinosaurs at the poles. For north polar dinosaurs, this seems to be a realistic possibility because they lived in the contiguous North American landmass and could easily have headed south. Interestingly, scientists have a modern analogue to frame this hypothesis.

Juvenile caribou must reach at least 80% of adult length and close to 75% adult mass before they can undertake a migration from their northern home. Considering the bones of preserved *Edmontosaurus* from the North Slope, a number of small juveniles have been recovered at only about 35% adult size and about 10% adult body mass. These juveniles were proportionally much smaller than juvenile caribou. Thus, it seems unlikely that they would be able to undertake similar long-distance migrations at such small sizes. More recently, the discovery of just-hatched baby dinosaurs in the Arctic suggests that these dinosaurs could have stayed put as well.

At the South Pole, a northward migration would have been prohibited by significant marine barriers. If dinosaurs stayed put, then they may have evolved specializations that supported this year-round lifestyle and equipped them to deal with the lengthy, dark winter. Investigations of bone histology have provided possible evidence that some small-bodied Australian ornithomimosaurs may have hibernated during the winter. Regularly spaced growth rings point to annual or seasonal temporary pauses in active growth. They are similar to structures that occur in living mammals and reptiles that hibernate. Other sampled ornithopods don't preserve such growth rings, pointing to a different growth strategy in the two groups. It's important to note that growth rings do not necessarily indicate hibernation. They form in many living vertebrates due to other factors, including low food and resource availability, and simply as a result of evolution holding onto more ancestral types of growth patterns.

Living in dens and hibernating would have only been options for the relatively small dinosaurs in these polar environments. So far, there is no evidence of burrowing or denning in any polar dinosaur. The histological evidence is pretty inconclusive, but it does indicate that different polar dinosaurs grew differently. Some paused throughout their life history, and others grew continuously and rapidly.

POLAR ADAPTATIONS

In both the north and south, researchers find evidence of specialization for seeing in the dark in two distantly related dinosaur groups. In the north, *Troodon* appears to have been well suited for life at high latitudes. At any latitude, *Troodon* is known for its relatively large eyes. Perhaps these eyes proved adaptive for seeing in the low-light conditions of wintertime north polar settings. A similar pattern occurs in the small ornithopod called *Leaellynasaura* found in Australia. It has increased orbital diameters compared to closely related, lower-latitude dinosaurs.

Recently, a selection of fossilized feathers discovered in Australia indicates that some unknown species of dinosaurs inhabiting the ancient polar environments had feathery body coverings. The feathers weren't associated directly with bones, making a precise association impossible. But they included large feathers about a half an inch long that resemble flight feathers, alongside small, fluffy feathers more similar to the downy feathers of living birds. They are hypothesized to belong to small, flightless theropods. Remember that the first feathers to evolve were fuzzy, downy feathers. These feathers would have been great at holding heat close to the body.

One of the most significant drivers of the end of the dinosaurs was a post-impact interval of darkness. Clouds of dust and ash in the atmosphere blocked sunlight for a lengthy period of time. This resulted in a shutdown of photosynthesis and an eventual breakdown of the primary food chain. Though many of the localities that yield polar dinosaurs occur long before the extinction event, North Slope dinosaurs occur closer in time to it. These types of polar dinosaurs would have already been adapted for scrounging around for food in the winter and surviving in dark environments for months out of every year. But eventually, even these cold-adapted creatures would have succumbed to the lengthy, severe conditions that characterized the extinction event.

Finally, remember that endothermic animals can keep their own bodies warm when it's cold out through the energy generated by their metabolism. Ectotherms, however, have to use the sun to keep them warm. The presence of dinosaurs at both ends of the earth is among the coolest evidence out there for higher metabolic rates in dinosaurs.

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THE EXTINCTION THAT ENDED THE DINOSAURS

Extinction provides an important mechanism for making room for surviving species to diversify. Often, the pop cultural perspective on extinction is filled with visions of failure. The extinction of the dinosaurs is frequently viewed through this lens. But consider the lengthy reign of dinosaurs on Earth. Dinosaurs spent more than 160 million years ruling Earth's terrestrial ecosystems. And technically, when you consider those modern dinosaurs flying around today, it means that dinosaurs have been around for more than 230 million years. Most species in the fossil record have a longevity of only a few million years; therefore, it can be argued that the longevity of dinosaurs on Earth indicates great success. This is why the extinction of the dinosaurs at the end of the Cretaceous is so interesting. How and why did such a widespread, diverse, and long-lived group of creatures perish? This lecture will explore the devastating end of the age of dinosaurs.

TWO TYPES OF EXTINCTION

Researchers divide extinction into two categories. The first and most common is background extinction. This is usually related to a mismatch between a species and its environment. When an environment changes more quickly than genetic evolution can keep up, species are pushed into extinction over multiple generations.

Background extinctions tend to impact species with specific lifestyle requirements. Think of these groups as being intolerant of much variation in their ecosystems. Once dinosaur evolution got going in the Late Triassic, dinosaurs diversified into a wild array of forms, with lifestyles to match. But the specializations that led to their success during the age of dinosaurs were the same features that placed them at a higher risk for background extinction.

For a long time, scientists hypothesized that perhaps background extinction drove dinosaurs to the bitter end at the close of the Cretaceous period. In fact, this is unquestionably how many dinosaur species did go extinct. Remember that by the end of the Cretaceous, many thousands of dinosaur species had already vanished. For example, *Stegosaurus* lived during the Jurassic period and went extinct more than 80 million years before *T. rex*'s lineage came on the scene in the Cretaceous.

Researchers often think of the smaller, more geographically widespread, and more ecologically tolerant creatures on Earth as having a little more resistance to background extinction events. If the range of a species encompasses the entire globe, it can tolerate many climates and eat many different kinds of food. That means it might be lucky enough to survive somewhere, even during the worst of times.

The second type of extinction is called mass extinction. Mass extinctions decimate an unusually large amount of diverse animal and plant life in a relatively short period of geological time. During mass extinction events, the percentage of organisms that go extinct is elevated well beyond the average background rate. There have been five mass extinctions recorded in the fossil record over the last 550 million years. These are nicknamed the big five.

THE BIG FIVE

The two oldest of the big five mass extinctions happened about 440 and 365 million years ago. These events—the Ordovician and Devonian extinctions—decimated biodiversity on a global scale when Earth's climate dramatically cooled. Since most of the planet's creatures thrived in vast oceans, the warm-water-loving marine creatures were driven to extinction.

By far the worst mass extinction in Earth's history took place about 250 million years ago, several million years before dinosaurs evolved. The Permian extinction was caused by intense global warming as huge volumes of lava poured over what is today Siberia. This changed the chemistry of Earth's atmosphere and warmed oceans to a nice Jacuzzi-like temperature. This acidified the oceans, and Earth turned into a runaway hothouse. The fossil record shows that nearly 95% of all life on Earth was wiped out in this event.

The fourth of the big five occurred at the end of the Triassic period. This extinction was prompted by another bout of volcanism-induced global temperature rise as the supercontinent Pangaea broke apart. Small early dinosaurs were the lucky survivors of this event. Other vertebrate species died off.

At the end of the Cretaceous period, the fifth of the big five extinctions wiped out all the non-bird dinosaurs. This extinction is referred to as the Cretaceous–Paleogene, or K–Pg, event. Geologists use the term *Paleogene*, abbreviated as Pg, for the time interval immediately following the extinction.

Long before people even knew what dinosaurs were, the K–Pg extinction event was noted because of the disappearance of a bunch of easily fossilized marine invertebrates in rocks that were correlated around the world. In fact, the divide between the Mesozoic era and Cenozoic era is demarcated by the K–Pg extinction. It was easy for early geologists building the first geological time scales to spot this extinction because of the dramatic faunal transition that occurred across this temporal boundary.

WHAT CAUSED THE K–PG EVENT?

One of the best clues about the nature of extinction involves the organisms that were wiped out. Regarding the K–Pg mass extinction event, researchers need a culprit that can decimate a wide range of diverse species. In the sea, the mass extinction of tiny marine algae, plankton, and marine invertebrates occurred. All the Cretaceous plesiosaurs and mosasaurs were killed off. On land and in freshwater ecosystems, a wide array of diverse crocodiles, turtles, and freshwater sharks were also hard-hit. More than half the known diversity of terrestrial plants was also lost during the K–Pg extinction. As for terrestrial animals, a whole host of mammals, most tree-dwelling birds, and all Late Cretaceous non-avian dinosaurs were culled. The same is true for flying pterosaurs and some species of diving birds too.

It's also important to consider the survivors—of which there were many. Remember, any groups that were present in the Cretaceous that have living relatives had to come through the K–Pg mass extinction event. This includes a wide array of plants, insects, amphibians, turtles, crocodiles, ground-dwelling birds, snakes, and the ancestors of all the major groups of living mammals. In the search for the cause of the K–Pg extinction, researchers have to look for evidence apart from the details of who died and who survived. This independent data is found in rocks.

Sixty-six million years ago, there were two planetary-scale disturbances that both affected the biosphere. However, disentangling the contributions of each to the K–Pg extinction continues to be the subject of intense scientific scrutiny. The first disturbance was a swell of volcanic activity from an igneous province known as the Deccan Traps, located in present-day India. This event resulted in more than 1 million cubic kilometers of lava flooding Earth's surface and the deep sea. The Deccan Traps erupted over a period of about 1 million years. There were several critical pulses just before and after the main K–Pg event. Two other mass extinction events—the Permian and end-Triassic—as well as other major ecological crises in Earth's history have been temporally correlated to flood basalt eruptions like this. These events modify Earth's atmosphere by releasing carbon dioxide and sulfur dioxide. This can promote rapid and intense global climate change. Such prolonged volcanic outgassing was sufficient to wipe out enormous numbers of species in the third and fourth extinction events. Perhaps the Deccan Traps increased environmental instability and warming or sufficiently stressed global ecosystems so that they became vulnerable, leading to the fifth catastrophic extinction event.

The second disturbance was identified in the 1980s. An approximately six-mile-diameter meteorite struck the earth precisely 66.6 million years ago. This kicked off an undeniable cascade of global calamity. The impact is recorded by the 200-kilometer-wide Chicxulub crater off the coast of the Yucatán Peninsula in the Gulf of Mexico, along with a signature of a global ejecta that includes a spike in metallic elements including iridium, osmium, and nickel. Other signatures were sedimentological features like tektites—little blobs of melted rock—and shocked quartz, in which the mineralogical microstructure of quartz gets reorganized because of high heat and pressure. Such deformation of the crystalline structure of quartz is only known to occur from nuclear weapons, meteorites, and some instances of lightning.

The role of the impact in the K–Pg extinction is no longer debated. However, some scientists have questioned whether the Chicxulub meteorite was the sole or main driver of the event. Recent work focused on detailing the timing and environmental effects of the Late Cretaceous volcanism in India indicates that at least half of the outgassing occurred tens of thousands of years before the impact. This outgassing appears to be comparable to other, more recent warming events that didn't result in mass extinctions or major biotic turnover. Conditions likely returned to normal, allowing for the return of "pre-outgassing communities" before the impact. These new analyses have considered climatic, biotic, and carbon cycling data. Thus, they effectively rule out the Deccan volcanism as the sole driver of the K–Pg mass extinction.

That leaves only one smoking gun: a huge hunk of rock from outer space. The horror began upon impact, in a single, precise location, that released thousands of times more energy than detonating all the nuclear weapons on Earth at once. The initial impact would have heated, vaporized, and ejected into the atmosphere the surrounding rock and water. This sent black carbon dust, ash, and sulfate aerosols into the atmosphere. These particles would have circled the globe within a few hours.

In the minutes and days after the impact, the global reentry of molten, ejected rock as small particles called spherules is thought to have temporarily raised atmospheric temperatures to the point of spontaneous combustion near the impact site. Pizza-oven-hot temperatures are likely to have been felt even hundreds of kilometers away. A thin layer of spherules that mark the broiling of Earth's surface can be found worldwide in the geological record of the K–Pg interval. Many organisms living in terrestrial ecosystems may have been incinerated within minutes by this impact fireball and the rain of molten hot rock from the sky. Even thousands of kilometers away, organisms would likely have experienced severe heat stress leading to death over a period of a few days after the impact. Wildfires would have raged as these molten particles returned to Earth, burning vegetation over wide swaths of land.

Minutes after the asteroid landed in the shallow water in the Gulf of Mexico, a 1.5-kilometer-high wave moving at a rate of more than 140 kilometers per hour would have decimated surrounding shallow water and coastal environments. Within the first 24 hours, the resulting tsunami propagated around the world's oceans. It devastated nearshore ecosystems on a global scale. After the initial wave, subsequent massive waves continued to pummel coastlines all over the world.

In the days and years that followed, vaporized sulfur and nitrogen reacted to form acids. Along with CO_2, these compounds acidified the rain—which in turn acidified the oceans. The lofted black carbon soot and ash circling the globe would have effectively blocked sunlight, plunging the earth into darkness and dramatically cooling global temperatures. Data indicates that this smokelike debris was retained in the upper atmosphere. This led to an inhibition of photosynthesis and a global temperature drop of anywhere between 9°C and 70°C on land. The resulting shutdown of photosynthesis would have disrupted food webs from photosynthesizers to herbivores to carnivores. The darkness may have lasted for decades after the impact. Dinosaurs thus perished, along with many other members of end-Cretaceous ecosystems.

THE SURVIVORS

Remarkably, there were creatures that survived the K–Pg event. Some became the ancestors of our modern flora and fauna. Researchers are not yet sure how they survived. The patterns of survivorship are somewhat mysterious.

Sometimes they're at odds with what researchers observe in the modern world. Take, for example, amphibians. A whole host of amphibians came through the K–Pg event relatively unscathed. But in the modern era, amphibians are super sensitive to environmental perturbations. In fact, changes in their diversity have prompted some scientists to suggest that we are at the beginning of a sixth great mass extinction—this one mediated by human-induced rapid climate change. How did such sensitive creatures make it through the K–Pg extinction filter?

There seem to be several key traits that gave organisms a slight advantage when it came to surviving the apocalypse. First, widespread ecological generalists were more likely to survive. If organisms could tolerate a wide range of temperatures, eat many different kinds of food, or have a population with a global range, they would have been more likely to endure. This might be the case for many tiny marine organisms that survived.

Second, animals able to shelter underwater or in burrows may have had a better shot at survival. Because the immediate effects of the impact included intense heat, fire, and acid rain, getting off the surface was probably key. For example, only a tiny fraction of ground-dwelling and aquatic birds present in the Late Cretaceous survived the K–Pg extinction. Their ability to swim, dive, and/or burrow may have been critical to survival. Moreover, all mammalian survivors were small-bodied animals that may have inhabited burrows.

Third, organisms able to hibernate, estivate, or reduce metabolic requirements through torpor also had increased chances of survival. Some fish (for example, lungfish); amphibians; small reptiles, including turtles, snakes, and lizards; and mammals may have benefited from these strategies.

Fourth, species that dined on the dead were more likely to survive. Organisms that were adept at feeding on the dead would have experienced a windfall of food resources. When scavenging is combined with other traits—like living in a sheltered freshwater ecosystem and having a flexible metabolism that can allow long periods of starvation—organisms survived across the K–Pg boundary.

Fifth, being small was probably a key characteristic of survivors. Larger and more specialized animals are vulnerable to extinction. They evolve more slowly because it takes longer to reproduce. They also need plenty of resources to sustain those large, calorie-expensive bodies. There is no fossil record of survivors with body masses of more than about 25 kilograms. Finally, never underestimate the power of luck when it comes to surviving mass extinction. Sometimes organisms find themselves in a protected little pocket of Earth that is a safer haven from the fallout of an event.

A BRAVE NEW WORLD

The K–Pg extinction annihilated all dominant species on the land, in the water, and in the sky. The remaining Earth ecosystems were barren, lonely, and devoid of any large or diverse living things for a long while. But in time, survivors adapted and radiated into the vacant niches left behind by the extinction's victims. Thus, the impact-generated extinction created the opportunity for a suite of diversifications that led to today's global biodiversity. The recovery to pre-extinction levels of diversity may have only taken a few thousand years.

The first post-extinction survivors to explode in diversity were fungi and microbes with a primary feeding strategy focused on detritus. Plants recovered rapidly thanks to their resilient seeds and spores and the potential for asexual reproduction. The plant recovery succession begins with ferns, then gymnosperms, then angiosperms. Estimates are that the development of this full "pioneer succession" on the road to recovery took less than 1,000 years.

The recovery of primary productivity in ocean ecosystems took a little longer, probably on the order of tens of thousands of years. This was likely due to ocean chemistry mediated by the K–Pg acidification side effects combined with the secondary Paleogene pulses of Deccan volcanism.

An awesome story of post-K–Pg adaptive radiation occurs in our own lineage—the mammals. After the extinction, surviving mammalian lineages evolved quickly to fill the niches that were left empty. The mammal radiation transpired in concert with plant adaptation. The diversification of plants triggered the diversification of mammals. The mammal radiation likely mirrored the plant story, with a recovery in diversity in only a few thousand years. A few hundred thousand years after the K–Pg extinction, some mammals were 100 times bigger than the tiny species that squeaked through the extinction.

And finally, what about the dinosaurs that survived—the birds? The ground-dwelling, toothless birds that survived would have had to eke out a living on seeds, holding on until the forests returned. Somehow they did, and the regenerated forests yielded a diversity of new habitats ripe with environmental variation that prompted a major adaptive radiation in these dinosaur survivors. Within a few million years, bird evolution was clicking right along, even producing large, flightless, predatory birds. The result is more than 10,000 species of birds living today.

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DINOSAUR RESURRECTION

This final lecture takes a look at whether humans could somehow bring dinosaurs back to life. The story begins in 1990 with the publication of Michael Crichton's novel *Jurassic Park*. The book and film were built around the notion that a wealthy entrepreneur had discovered a way to tap into damaged dinosaur DNA they found preserved in ancient mosquitos trapped in amber. With the tools of genetic engineering, they splice the dinosaur DNA together with that of living reptiles, birds, or amphibians to fill in the gaps of the genomes that were lost to time. As a result, they bring various dinosaurs back from the dead and create a dinosaur theme park on an island. Since the 1990s, paleontologists have been hard at work to try to do some of what Michael Crichton's creative mind inspired. Could researchers someday resurrect dinosaurs? And even if they could, should they?

PART 1: DO DINOSAUR FOSSILS PRESERVE SOFT TISSUES?

In the last 20 years or so, there have been news reports touting the discovery of dinosaur soft tissues—including preserved blood vessels, little bits of organic bone material, bone-building cells, and even possible red blood cells. Paleontologists have been on the hunt for the preserved soft parts of dinosaurs since at least 2003. This is when the first blood vessels and cells were thought to be recovered in demineralized bone fragments from a 68-million-year-old *T. rex*. Chemical analysis of these unexpected squishy parts revealed the presence of collagen. This protein helps build bones at the microscopic level and imparts a little elasticity to the skeleton. This finding stirred a vigorous debate among paleontologists. How could proteins survive the vagaries of the fossil record, sticking around for tens of millions of years?

Since the first paper appeared in 2005, follow-up studies have come out at a rate of about one every couple of years. Each asks a different question. In the first follow-up paper, researchers ran an evolutionary analysis that included the protein sequence data—basically, the pattern of amino acids that fold and twist to make the specific collagen molecule—and compared it to the protein sequences of living chickens. They also sampled the preserved collagen sequences of a fossilized mastodon and living mammals. The results supported the hypothesis that the collagen recovered belonged to a *T. rex* and the mastodon. And it correctly placed the *T. rex* within Archosauria. Meanwhile, it grouped the mastodon with living elephants.

The next paper took a closer look at the tiny, soft, transparent structures recovered from the *T. rex* and from a hadrosaur, *Brachylophosaurus*. These structures resembled modern osteocytes, which are the cells that maintain bone in living animals. To test the hypothesis that these cell-like structures were original, the team borrowed techniques from modern immunology and chemistry. They confirmed the presence of small amounts of DNA and ruled out that the DNA they found belonged to bacteria.

If DNA, cells, and proteins are potentially preserved in these ancient fossil bones, how could they have made it through the long and arduous process of fossilization? It turns out it might be all about chemistry. Moreover, those proteins may not be quite what they seem.

The traditional story of fossilization is that within a few million years (or maybe even less), all proteins in animals' soft parts should be completely degraded. A team from Yale University studied the chemistry of bones, teeth, and eggshells from animals ranging from the Late Triassic to the modern era. All the modern specimens contained soft tissue—but so did many of the fossil samples. The scientists used a method called Raman microspectroscopy, which bounces a laser off fossils to reveal their molecular makeup (a non-destructive analysis). They found that these strange soft structures were not made up of original dinosaur proteins. Instead, the structures were made of new, chemically transformed compounds that replaced the original protein molecules while preserving the overall shapes of the original soft parts. The shapes remained because these newly formed chemical compounds resist degradation and dissolution. Bottom line? Although actual dinosaur DNA might be hard to come by, other detailed data on soft parts is available in the fossil record of dinosaurs.

PART 2: THE GENES OF LIVING DINOSAURS

What might the DNA of living dinosaurs have to say about the unfolding evolutionary story that led to all the adaptations exhibited by modern birds? This idea is built upon researchers' rapidly expanding understanding of the genome, especially the genetic wilderness of the in-between regions of protein-coding genes. Some of these stretches of DNA include so-called pseudogenes—or "fossil genes." These are the ancient genes passed on from ancestors to descendants.

Over time, these fossil genes are modified by mutations that have changed their function—sometimes by so much that these once-useful genes are no longer needed. They continue to come along for the ride in modern creatures because it is too difficult for evolution to throw them away. Evolutionary developmental biology—or "evo-devo"—combines the fields of evolution, genetics, developmental biology, and paleontology to investigate how changes in deep time may have occurred on a molecular level.

Through a series of experiments in the 1970s, people working in evo-devo started looking at model organisms—especially fruit flies—to try and understand how DNA works in building new structures. Sometimes a mutation would occur that might result in a fruit fly hatching with legs where its antennae should be, for example. These discoveries led to the detailed study of gene expression. This is how the genome directs the building of animal bodies.

One of the key discoveries of molecular biology since the early 2000s is the realization that all animal life is genetically quite similar. In reality, humans share most of our genetic code with penguins or dinosaurs. By expressing some genes but not others, different animals can come to evolve over vast amounts of time. This means that the genome is like a fossil record of molecular evolution that can be mined for the discovery of fossil genes. By exploring this genetic fossil record preserved in living animals during embryonic development, evo-devo scientists can answer specific questions about the genetic underpinnings of major evolutionary transitions.

Their goal is to understand how small genetic changes can result in the development of innovative new structures and morphologies. So long as these genetic mutations aren't fatal, they can be tried by natural selection. Eventually, they can lead to the evolution of new, fantastic groups of life on Earth.

THOSE CRAZY WRISTS

Recall the semilunate carpal, which arose in theropods that are closely related to modern birds. It turns out that later birds went even wilder with their wrist remodeling, shifting from as many as nine individual wrist bones in early dinosaurs to only four bones in living birds. One of the challenges has been telling which dinosaur wrist bones are the ancestral bones for the simplified wrists of birds. An embryological study has helped solve this mystery.

In some cases, a single bird wrist bone results from the embryonic fusion of one or more dinosaur elements. In other cases, birds have reacquired bones that were lost in their dinosaur precursors. With only the fossil record at hand, researchers might misidentify bird wrist bones. With only the developmental data, researchers might underappreciate the evolutionary history of these innovative features. It is the combination of data from evolution and development that makes this approach so powerful.

BABY FACES (WITH FINGERS)

Embryonic alligator skulls look similar to the skulls of adult chickens. And fossilized baby dinosaur skulls look like the skulls of adult birds. This interesting morphological similarity prompted Arkhat Abzhanov, then a biologist at Harvard, to propose an interesting hypothesis: Could dinosaurs have shortened their skull development early on in life to result in a more birdlike skull anatomy? This idea is about heterochrony, which concerns how the timing or rate of development can result in dramatically different morphologies. Researchers think these small developmental shifts can help drive evolutionary history in many major vertebrate groups.

Abzhanov and his team collected data on ancient embryonic dinosaurs and early birds, tracking the morphological changes across the dinosaur-bird transition. He identified a few different examples of growth truncation called paedomorphosis. This is the retention of juvenile characteristics into adulthood. The team saw this in the shortening of the snout and the enlargement of the part of the brain associated with vision.

Abzhanov also identified an example of an elongated period of development that results in morphological change, called peramorphosis. The bones that build the beaks of birds represent peramorphosis since their development is stretched out in birds. These findings indicate that over evolutionary time scales, modern birds became more and more baby-like in appearance. Essentially, a modern bird looks like a baby dinosaur—one that is able to reproduce.

Next, Abzhanov's team turned their attention to the genetic mechanisms that build bird beaks. It turns out that a few minor genetic changes can morph a beaked chicken embryo into a dinosaur-style beakless face. The beaks of birds are made of the premaxillae. These are the same bones that you have located where your front teeth are in the upper jaw. However, our own premaxillae are unfused.

To determine how the fusion in the bird premaxillae happens genetically, Abzhanov's team mapped out the activity of two different genes that are expressed in the separate premaxillae of most living animals. Reptiles and mammals have two patches of gene expression, one for each side of the nose. Birds have only one for in front of the nose. Since dinosaurs also have separated premaxillae, paleontologists can assume an alligator pattern of gene expression in dinosaurs. The researchers then turned off the expression of the genes in chick embryos, but only in the middle part of the face. The result? They created a chick embryo with a skull that resembled that of a dinosaur or an alligator.

THE MUTANT PYGOSTYLE

One of the most recognizable differences between the skeletons of birds and those of most dinosaurs is the short little tail of birds known as the pygostyle. The transition to this new tail anatomy seems to have occurred over a relatively short evolutionary interval. These tails are critical components of the powered flight strategies of birds. They are also connected to feathers employed in mating displays and are used to communicate, wiggling and flashing to warn other birds when danger is nearby.

The pygostyle is present in the entire diversity of living birds. There is a great fossil record that documents the anatomical transition from the long and flexible dinosaur tail to this newer, shorter form in birds. The external, phenotypic changes seen in the anatomy of birds relative to that of their dinosaur precursors result from changes that occur during embryonic development. Thus, researchers can investigate an array of potential genetic mutations in embryonic model organisms that may have been responsible for the evolution of stubby tails.

Research has focused on two kinds of model organisms: mice and chicks. Research can't pinpoint exactly what mutations occurred early in bird evolution—or even which dinosaur was the true ancestor that exhibited the original mutation. However, paleontologists have learned enough to get closer to understanding how chickens might have lost their long tails. Genetic and fossil evidence indicate that it's possible that a single mutation could have occurred in a feathered maniraptoran dinosaur. A current working hypothesis is that the genetic change (or changes) occurred in genes that are involved in lengthening the vertebral column.

All this amazing genetic work is providing incredible insights into the tool kit that builds bodies and showing how small genetic changes can have a big impact.

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QUIZ

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1 Which of the following anatomical features is not present in (most) theropod dinosaurs?

a. air sacs
b. recurved claws
c. a furcula
d. a backward-facing pubis

2 Which of the following geological time periods is not characterized by a major mass extinction?

a. the Jurassic
b. the Cretaceous
c. the Permian
d. the Triassic

3 Which of these dinosaur groups exhibits tanklike armor and (at least sometimes) ferocious tail clubs?

a. Stegosauria
b. Theropoda
c. Pachycephalosauria
d. Ankylosauria

4 Which of the following does not help researchers put rocks into a relative geological order?

a. biostratigraphy
b. lateral continuity
c. phylogeny
d. superposition

5 Which of the following is a good rule to follow if you hope to make it into the fossil record?

a. Have a small, soft body.
b. Be sure to die in a swampy area.
c. Make sure to have some hard body parts.
d. Live and die alone.

6 Which anatomical structure is most important for determining whether a dinosaur is a saurischian or an ornithischian?

a. the teeth
b. the hips
c. the tail
d. the ankles

7 Which of the following is the best environment for preserving fossils?

a. a deciduous forest
b. a coniferous forest
c. the Alaskan tundra
d. a river and its floodplain

8 Which organism is the best example of an index fossil that could be useful in monitoring extinction, or in biostratigraphy?

a. *T. rex*
b. algae
c. ginkgo leaves
d. foraminifera

9 Which of the following can be aged with radiometric dating?

a. fossils
b. sedimentary rock
c. igneous rock
d. metamorphic rock

10 This theory helps explain why background extinctions happen.

a. the principle of original horizontality
b. the red queen hypothesis
c. the Central Atlantic Magmatic Province
d. uniformitarianism

11 Which is an example of evolutionary homology?

a. the wings of birds and pterosaurs
b. the wishbones of dinosaurs and birds
c. the backward-facing pubis in ornithischian dinosaurs and birds
d. the torpedo-shaped bodies of ichthyosaurs and dolphins

12 What does the word *dinosaur* mean?

a. “angry reptile”
b. “fearfully great reptile”
c. “ferocious animal”
d. “two-legged lizard”

13 Which geological time period did dinosaurs first appear in?

a. the Paleocene
b. the Cretaceous
c. the Permian
d. the Triassic

14 Which one of these other animals hadn't evolved during the age of dinosaurs?

a. penguins
b. fleas
c. crocodiles
d. snakes

15 One of the first discoveries of dinosaurs was made by Gideon Mantell and his wife, Mary Ann. What did they find?

a. giant herbivorous teeth
b. leg bones
c. giant carnivorous teeth
d. hip bones

16 Which of these dinosaurs was not included in Sir Richard Owen's original designation in 1842?

a. *Megalosaurus*
b. *Brontosaurus*
c. *Hylaeosaurus*
d. *Iguanodon*

17 How are rhamphorynchids different than pterodactyls?

a. Only pterodactyls have actinofibrils.
b. Only rhamphorynchids have pteroid bones.
c. Only rhamphorynchids have long bony tails.
d. Only pterodactyls have wings extending from their fourth finger.

18 Which of the following does not provide supporting evidence for the hypothesized asteroid impact at the end of the Cretaceous period?

a. microtektites and spherules
b. a crater in the Yucatán Peninsula
c. a global iridium spike
d. long-term global warming throughout the Cretaceous

19 The extant phylogenetic bracket does which of the following?

a. relies on living mammals to help explain dinosaur biology
b. employs living archosaurs (crocodiles and birds) to frame hypotheses on dinosaur biology
c. explains how evolutionary trees are built
d. documents anatomical similarities between marine reptiles and dinosaurs

20 Which of the following anatomical structures does not support the evolutionary relationships between maniraptoran theropod dinosaurs and living birds?

a. feathers
b. the semilunate carpal
c. the pygostyle
d. osteoderms

21 What data cannot help reveal the diets of dinosaurs?

a. their fossilized feces (coprolites)
b. their teeth
c. biomechanical modeling of their skulls
d. analysis of the bacteria preserved within their guts

22 Almost all of the following data support the idea that some, if not all, dinosaurs were colorful. Which data do not support this hypothesis?

a. their extant phylogenetic bracket
b. the color of skin and feathers occasionally preserved in the dinosaur fossil record
c. the anatomy of their eyes
d. their evolutionary relationships with living lizards

23 Scientists are using embryonic living dinosaurs (e.g., chickens) to learn the genetic underpinnings of major morphological changes during the course of dinosaur evolution. What is this field of study called?

a. finite element analysis
b. evolutionary developmental biology
c. melanosome preservation
d. bone histology

24 Which descriptor does not apply to all dinosaurs?

a. extinct
b. diverse and geographically widespread
c. extremely variable in body size
d. behaviorally complex

25 It is clear from the dinosaur fossil record that at least some of them may have been gregarious (they lived in groups and were social). Which piece of evidence provides the least conclusive evidence in support of this hypothesis?

a. the ratio of prey to predatory dinosaur species
b. the fact that dinosaurs have lots of display structures
c. multiple trackways of the same species at the same locality
d. single-species mass-death assemblages

26 The extinction of all non-avian dinosaurs coincides with all of the following except which?

a. the extinction of plesiosaurs
b. the first appearance of mammals
c. the impact of a large meteorite
d. the end of the Mesozoic era

27 Evidence for parental care in the large-bodied hadrosaur *Maiasaura* might be based on all of the following except which?

a *Maiasaura* adults have been found sitting on nests of eggs.
b. Ends of juvenile *Maiasaura* bones are poorly ossified.
c. Baby *Maiasaura* look very different than their adult counterparts (also known as “the cute factor”).
d. Bones of hatchlings are found in nesting structures.

28 Which of the following is not evidence that at least some dinosaurs were homeothermic endotherms?

a. rapid growth rates recorded by bone histology
b. downy feather-like structures
c. oxygen isotope ratios of teeth
d. skin impressions that preserve sweat glands

29 Dinosaur growth patterns vary widely, depending on the type of dinosaur under study. Which feature is not used by paleontologists to help determine dinosaur growth?

a. the size of their hearts and lungs
b. the patterns of blood supply inside their bones
c. the density of cells within their bones
d. the intensity of bone remodeling

30 Which dinosaur has been found sitting atop nests of eggs, brooding its young in a manner similar to that of living birds?

a. the titanosaur *Rapetosaurus*
b. the theropod *Tyrannosaurus*
c. the theropod *Oviraptor*
d. the stegosaur *Stegosaurus*

ANSWERS

1: d, **2:** a, **3:** d, **4:** c, **5:** c, **6:** b, **7:** d; **8:** d, **9:** c, **10:** b, **11:** b, **12:** b, **13:** d, **14:** a, **15:** a, **16:** b, **17:** c, **18:** d, **19:** b, **20:** d, **21:** d, **22:** c, **23:** b, **24:** a, **25:** a, **26:** b, **27:** a, **28:** d, **29:** a, **30:** c

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WONDRIUM

Printed in the United States of America

4840 Westfields Boulevard, Suite 400
Chantilly, VA 20151-2299
USA
1-800-832-2412