The Ascent of Mammals

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June 2016

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One early winter evening in 1824, English naturalist and theologian William Buckland rose to address the Geological Society of London. Anticipation filled the room. Buckland was known for his energetic lectures at the University of Oxford, where he would buzz around in full academic regalia, passing around severed animal parts and fossils to his adoring students. For years there had been rumors that Buckland had gotten his hands on some giant fossil bones, found by workers quarrying roofing stone in the English countryside. After nearly a decade of study he was finally ready to make an announcement. He told the audience that these bones had belonged to an ancient lizardlike animal much larger than any modern lizard. He called it *Megalosaurus*. The crowd was enraptured. Buckland had just unveiled the very first dinosaur.

That evening was a seminal moment in scientific history, touching off humankind's enduring fascination with dinosaurs. But what is largely forgotten is that Buckland made another announcement that day, concerning a discovery much smaller in physical size but equally revolutionary. In reviewing the other fossils found alongside *Megalosaurus* in the stone quarries, Buckland had noted a “most remarkable” find: two tiny mammal jaws, about the size of mouse jaws. Until then, scholars thought mammals were a recent creation, appearing long after primeval geologic eras ruled by giant salamanders and lizards. The two minuscule jaws, their cusped teeth so unmistakably mammalian, were the first sign that this group had a much deeper history.

These jawbones raised a host of questions. How far back in the distant past did mammals originate? What were mammals doing during that long span of history when dinosaurs reigned? How did the classic mammal blueprint—with fur, mammary glands, big brains, complex teeth and keen senses, among other traits—originate? And why did one particular group of mammals—placentals like us (which give birth to live, well-developed young)—rise to dominance, with more than 5,000 species, running the gamut from featherweight bats to behemoth blue whales, spread across the planet today?

For nearly two centuries after Buckland's lecture these questions remained difficult to answer because so few fossils of early mammals were known. A surge of spectacular fossil discoveries over the past 15 years is at last allowing scientists to chart their evolutionary journey from the tiny critters living in the shadow of *Megalosaurus* to the astonishing array of forms that have come to rule the modern world.

Modest Beginnings

Like all eventual dynasties, mammals come from humble stock. In scientific parlance, they are defined as that group on the tree of life that contains the egg-laying monotremes, the marsupials (which raise their tiny babies in a pouch) and the placentals, as well as all the extinct descendants of their common ancestor. The first critters that started looking and behaving like today's mammals were an assortment of stem mammaliaforms, a fancy name for the very closest relatives of true mammals. They themselves evolved from cynodonts—primitive species that still retained many features of their reptilian forebears.

The earliest traces of stem mammaliaforms date to about 210 million years ago, in the Late Triassic period—a heady time in evolution. A few tens of millions of years earlier, nearly all life was extinguished in a volcano-triggered mass extinction that marked the end of the Permian period and ushered in the Triassic. After most of the giant amphibians and reptiles that ruled the Permian died out, many of today's most important animal groups rose up in the postapocalyptic vacuum. Turtles, lizards, frogs, crocodiles, dinosaurs (which eventually became birds) and the mammaliaform forerunners of mammals all got their start during this time of radical change.

Some of the best fossils of Triassic mammaliaforms come from rocks surrounding an icy arm of the Arctic Ocean called Fleming Fjord that cuts into the coast of eastern Greenland. A wealth of tiny teeth and jaws found there in the 1990s has helped paint a portrait of the immediate ancestors of mammals. These fossils were not easy to come by. Farish Jenkins of Harvard University, a legendary paleontologist who died in 2012, and his intrepid team pried them from the frozen rocks. Jenkins was just as engaging and dramatic in his lectures as Buckland. The debonair professor dressed in beautifully tailored suits and drew meticulous chalk diagrams of skeletons and organ systems in his anatomy lectures. A former U.S. Marine, Jenkins was a daring leader of fossil expeditions who always carried a rifle to protect his Arctic teams from that constant danger of high-latitude fieldwork: polar bears.

Jenkins's crews discovered fossils of three main types of stem mammaliaforms: kuehneotheriids, morganucodonts and haramiyidans. All were small, shrew- to mouse-sized animals that had already developed several important mammal hallmarks. Most notably, they were covered in fur, which provided insulation from the cold and helped to dissipate heat when temperature rose. And their skulls had a simplified hinge joint that worked with enlarged jaw-closing muscles to both strengthen and fine-tune chewing movements, compared with the haphazard bite-and-swallow technique of cynodonts. Cusps on the teeth, particularly the molars at the back of the jaws, made chewing even more efficient.

Fossils from Greenland and other continents reveal that a landmark shift in tooth development accompanied those innovations in the jaw. Whereas cynodonts had teeth that continuously grew, shed and regrew throughout life, the stem mammaliaforms exhibited our familiar pattern of baby teeth being replaced by adult teeth. Although we humans may curse our peculiar dentition when we lose teeth as adults and cannot grow new ones, our unique modes of tooth growth and replacement are intimately related to one of the signature features of mammal biology. Youngsters without teeth or with baby teeth can nurse on their mother's milk, produced by the mammary glands that give the mammal group its name. These stem mammaliaforms would thus have likely nourished their young in the same way as modern mammals, a watershed evolutionary change that allowed mammals to grow faster, allowing for better survival of their young, and to attain higher metabolisms that enabled stem mammaliaforms to be active in colder environments, especially in the darkness of night.

The stem mammaliaforms show the beginnings of other key mammal traits, too, including some that heightened intelligence and sensory perception. Advances in CT scanning over the past decade have allowed paleontologists to visualize details of the internal anatomy of fossilized bone, including brain cavities and nerve paths. This technology has revealed that these early mammals possessed huge brains compared with those of their ancestors, although they were not so enormous as modern mammal brains. They also had larger olfactory bulbs and auditory regions that imparted keen senses of smell and hearing and expanded brain regions that processed tactile input from skin and hair. They even upgraded their inner ear by surrounding it with solid bone to insulate the sensitive hearing apparatus from the loud noises caused by chewing.

Although they were starting to acquire some nifty features of modern mammals, the tiny Triassic stem mammaliaforms were hardly the dominant animals of their day. That distinction belonged to dinosaurs and crocodiles, which were beginning to reach monstrous sizes and ascend to the top of the food chain. But what these protomammals lacked in size, they made up for in variety. Recent research led by Pamela Gill of the University of Bristol in England has revealed a surprising diversity of dietary adaptations among these creatures. Using synchrotron beam lines to scan mammaliaform teeth and engineering software to model their function, Gill and her colleagues showed that morganucodonts had strong enough jaws to crush large insects with crusty exoskeletons, such as beetles, whereas kuehneotheriids had gracile jaws and delicate teeth that could probably handle little more than soft worms or moths. Additional work by one of us (Luo) illustrates that haramiyidans could slice and grind small plants with their uniquely mobile jaws.

The Jurassic Big Bang

The stereotypical view of mammal evolution holds that these protomammals stagnated for tens of millions of years during much of the Mesozoic era (the interval between 252 million and 66 million years ago that comprises the Triassic, Jurassic and Cretaceous periods). While their dinosaur overlords reigned supreme, the protomammals were relegated to an unremarkable existence as small insect eaters that lived on the ground and scurried through the undergrowth. But a flood of new fossil discoveries from locales across the globe has put the lie to this notion. The adaptability seen in the stem mammaliaforms was to become a common motif throughout the evolution of mammals, including the long period over which they overlapped with dinosaurs, and this propensity for adapting to change by diversifying appears to have been a key to their success.

In the case of the stem mammaliaforms, their sharp senses and fine-motor coordination (both enhanced by larger brain size), along with elevated metabolism, enabled them to thrive in the cold and dark of the night. These same characteristics may have helped them survive when another catastrophe struck. The geologic record shows that as the Triassic gave way to the Jurassic, about 200 million years ago, the supercontinent Pangaea tore apart. Volcanoes spewed from the widening cracks between the emerging continents, poisoning the atmosphere and causing ecosystems to collapse. The stem mammaliaforms were apparently able to make it through this hellacious event, establishing themselves in niches not accessible to many other vertebrates of the time.

Many dinosaurs managed to survive the end-Triassic mass extinction, and this group still headlined the Jurassic. But 30 million years into that interval, the mammal lineage underwent another, far larger burst of evolution. Much of the evidence for this explosion of new forms comes from the thousands of stunning fossils that have been collected over the past decade from the Tiaojishan rock formation in northeastern China. These exquisitely preserved specimens include fossils of insects, feather-clad dinosaurs and more than two dozen mammal skeletons, many surrounded by a halo of wispy hair. About 160 million years ago these animals had the misfortune of living in lakes and forests that were periodically bombarded by volcanic eruptions, which killed and entombed them before they could decay.

Studies of these Chinese fossil mammals conducted by Luo and other researchers, including a team led by Jin Meng of the American Museum of Natural History in New York City, show that these creatures possessed a remarkable variety of body types that allowed them to invade a wide array of ecological niches. *Castorocauda*, a late-surviving stem mammaliaform, was a prairie dog–sized creature with webbed hands and feet and a flattened tail like a beaver's. It is the earliest known swimming mammal. *Docofossor* burrowed underground with shovel-like clawed hands, and its wide fingers had a fused joint, bringing to mind modern African golden moles. *Agilodocodon* was an agile tree climber that fed on sap by gnawing through tree bark with its spade-shaped teeth. Perhaps the strangest of all was *Volaticotherium*, which would have looked like a flying squirrel when gliding between branches, riding air currents with a membrane stretched between its arms and legs. And these specialized mammals were not restricted to China. *Fruitafossor* from Colorado, described by Luo and John Wible of the Carnegie Museum of Natural History in Pittsburgh, was an ant-eating digger. All told, the new Jurassic mammal fossils exhibit almost every major way of life seen in today's small mammals.

During the Middle Jurassic, 174 million to 164 million years ago, the number of mammal species skyrocketed. Statistical analyses by Roger Close, now at the University of Birmingham in England, that map skeletal characteristics onto a genealogy to calculate rates of anatomical changes over time show that these Jurassic species were evolving remarkably faster than the stem mammaliaforms of the Triassic—up to twice as fast at times. This accelerated pace of change laid the foundation of the mammal family tree: through it, the lineages leading to today's monotremes (the egg layers) and therians (the broader group that comprises the marsupials and placentals) diverged from each other, like two siblings setting out to form their own broods.

Although many of the diverse Jurassic mammals described here belonged to now extinct lineages sandwiched between the monotremes and therians on the family tree, they are nonetheless vitally important to understanding the origins of extant mammals because they help to reveal the morphology of those mammals' ancestors. These long-dead genealogical branches flourished alongside the forerunners of today's mammals during the Jurassic and later in the Cretaceous before they disappeared. And they experimented with many of the same feeding and locomotion styles, converging on one another and on modern mammals' ancestors in an evolutionary frenzy. Researchers are thus keen to unravel why these early specialists failed to survived to modern times.

Flower Power

By the dawn of the Cretaceous period, about 145 million years ago, the modern mammal blueprint was established. Big brains and fast growth rates continued to be key traits of the group. And a new, seemingly minor evolutionary change had emerged as a game changer: the advent of so-called tribosphenic molars, in which a projection on the upper molar fits into a basin on the corresponding lower molar and the two work together to crush food just like a mortar and pestle. This tooth arrangement opened a whole new realm of dietary possibilities to mammals.

Armed with the functionally more versatile tribosphenic teeth, therians began to diversify. The evolutionary lines that would eventually lead to today's major mammal groups—the eutherians that evolved into placentals and the metatherians that later became marsupials—splintered off from one another and started down separate evolutionary paths. Remains of the oldest and most primitive members of these lineages come from China, where they scurried on the forest floor under the feet of feathered dinosaurs well before 125 million years ago.

Although these pioneering therians were around in the early part of the Cretaceous, it was not yet their time to shine. They were few and small, rarely much larger than a gerbil. Instead slightly more primitive mammals known as triconodonts and symmetrodonts presided over the mammal scene for the first 30 million years of the Cretaceous, continuing their earlier successes of the Jurassic. Some of these species were the largest mammals of the entire Mesozoic—such as the meter-long, 14-kilogram *Repenomamus*, a wolverine-sized creature from the Early Cretaceous of China whose fossilized stomach contents included the bones of small dinosaurs.

Then something unexpected happened, an event that would reset the course of mammal history. A totally new type of plant evolved—angiosperms, the flower- and fruit-bearing shrubs and trees that make up most of today's plant species, provide many of our dietary staples and decorate our gardens. During the middle part of the Cretaceous, angiosperms colonized landscapes across the world, providing mammals with new sources of food: the fruits and flowers themselves and the insects that fed on them. The tribosphenic molars of therians, with their dual crushing and shearing abilities, were perfect tools for processing this new fare, and the therians proliferated as a result. Meanwhile mammals with more primitive dentitions, such as the dinosaur-eating *Repenomamus*, went into decline and never made it out of the Cretaceous.

Even with this new windfall of feeding opportunities, the success of the therians was still not assured, however. Competition was brewing. While therians were feasting on bugs during the middle and later parts of the Cretaceous, some other, more primitive mammal groups evolved complex dentitions that were well suited to slicing and grinding the new angiosperms. The northern continents became overrun by multituberculates—bucktoothed vermin that looked like rats. Despite appearances, these creatures were not closely related to true rodents but rather converged on a rodentlike body plan because they were eating similar foods. Recent studies by Gregory Wilson of the University of Washington and David M. Grossnickle of the University of Chicago have applied sophisticated statistical analysis to big databases of fossil measurements to show that multituberculates were thriving in the latest part of the Cretaceous. They were evolving into many species, growing to ever larger sizes and developing more intricate molars in a coevolutionary dance with the spreading angiosperms.

The southern continents appear to have hosted competitors to therians, too. Paleontologists still know very little about those southern mammals from the latest Cretaceous, but provocative new finds suggest that a weird group was prospering: the gondwanatherians (which, despite their name, were not true therians). For many decades the only records of these mysterious mammals were isolated teeth: high-crowned molars with enamel that grows throughout life like those of horses and cows—ideal for grinding tough plant material. In 2014 a team led by David Krause of Stony Brook University unveiled the first skull of a gondwanatherian, which belonged to a new species called *Vintana* that lived in Madagascar in the very latest Cretaceous. It resembled a beaver and possibly fed on some of the first evolving Cretaceous grasses.

From Catastrophe, Opportunity

During the final stanza of the Cretaceous, some 66 million years ago, mammals were doing well on the whole. Certainly they had come a long way since their Triassic debut, with many insect-eating therians, plant-munching multituberculates and gondwanatherians woven into the food webs topped by big dinosaurs such as *Tyrannosaurus*. They were still limited to inhabiting the understory, however, unable to push out into new kinds of habitats.

But their fortunes—and indeed those of many other organisms—changed in an instant when an asteroid shot down from the sky, unleashing a cocktail of wildfires, tsunamis, earthquakes and volcanic eruptions that reshaped the earth in a matter of days and weeks. These catastrophes and longer-term climatic and environmental changes triggered by the asteroid were too much for the dinosaurs. And just like that, these majestic creatures that had prevailed for more than 150 million years were swept into the dustbin of prehistory.

Mammals also felt the pang of extinction. Evidence for their decline has come from a prominent fieldwork program originally led by William Clemens of the University of California, Berkeley, and now led by Wilson, which for five decades has meticulously collected fossils from across the extinction interval in Montana. The findings show that many larger mammals and those with more specialist diets went extinct with the dinosaurs. The metatherians that were beginning to flourish in the Late Cretaceous were nearly wiped out, and if not for a few plucky species that survived the gauntlet, their descendants, the modern kangaroos and koalas of Australia, would have never had the chance to evolve.

Among the other mammals that made it through were some of the earliest placentals—those species like us that give birth to relatively well-developed young. Molecular clock studies, which calculate when distant ancestors diverged from one another based on DNA differences in living species, indicate that the common ancestor of placentals evolved alongside the dinosaurs in the Cretaceous. But only after the end-Cretaceous extinction did these advanced mammals burgeon and split into the major modern subgroups, including rodents and primates. The reason for their sudden about-face is clear. With *Tyrannosaurus, Triceratops* and kin out of the way, these placentals now had a clear playing field to conquer, and once again they quickly evolved to fill available niches.

Although researchers have long suspected that the death of the dinosaurs was instrumental in the rise of mammals, we now have a far better understanding of the exact role it played: specifically, it was the spark that ignited a placental revolution. Like all revolutions, this one happened very quickly, on the order of thousands of years, a pittance in geologic terms. One of us (Brusatte) has been doing fieldwork in New Mexico to better understand the many facets of this critical moment in evolution, from which mammals made it through the catastrophe to how the diets and behaviors of these survivors aided them in this postapocalyptic world. There the candy-striped badlands of the Nacimiento Formation hold the world's best record of how mammals blossomed after the dinosaurs died. Brusatte's colleague Thomas Williamson of the New Mexico Museum of Natural History & Science has been scouring these rocks for more than 25 years and has collected many thousands of fossils, almost every one of which he can recall in precise detail, thanks to his photographic memory. The fossils consist of jaws and teeth belonging to a myriad of mammal species ranging from shrew-sized insectivores to saber-toothed meat eaters and herbivores the size of cows. They lived a mere 500,000 years after the asteroid hit, a testament to how rapidly placentals were taking over the planet once they got their chance.

Because of their success, we humans are here to tell the tale. Among the placentals that Williamson has unearthed in New Mexico is a skeleton of a puppy-sized creature, called *Torrejonia*, with gangly limbs and long fingers and toes. It lived about 63 million years ago, but when looking at its graceful skeleton, you can almost picture it leaping through the trees, its skinny toes gripping onto the branches. *Torrejonia* is one of the oldest known primates, a distant cousin of ours. Another 60 million years or so of evolution would eventually turn small protoprimates into bipedal-walking, philosophizing apes. Just another chapter in the mammals' evolutionary journey, now 200 million years long and counting.