This rat-sized *Liaoconodon hui* is one of many fossils from northern China that are sharpening the picture of how mammal traits evolved.

THE MAKING OF MAMMALS

An explosion of fossil finds is allowing our early mammal ancestors to leap out of the shadow of the dinosaurs. **By John Pickrell**

Night is falling in the early Jurassic 185 million years ago, and the *Kayentatherium* is tending to her newly hatched brood. Heavy rains pummel the bank above her den as she looks over her dozens of tiny young. She is about the size of a large cat and could easily pass for a mammal, but her large jawbone, characteristic teeth and lack of external ears give her away: she is a cynodont, a member of the group from which mammals evolved. At some point without warning, the sodden bank collapses, entombing the hatchlings and their mother in mud.

There they remained until the summer of 2000, when a fossil-hunting crew led by Timothy Rowe at the University of Texas at Austin chanced upon their scattered bones among rocks of the Kayenta Formation in northern Arizona.

That initial encounter with the fossils did little to impress the palaeontologists. They dug up the block and shipped it back to the laboratory for safekeeping. It wasn't until nine years later that a specialist preparing the fossil for study noticed something startling: embedded in the block were tiny teeth, and jawbones just 1 centimetre in length. "Immediately they stopped the preparation and thought about ways of non-destructively examining the babies," says Eva Hoffman, at Texas with Rowe at the time and now a palaeontologist at the American Museum of Natural History in New York City. Instead of breaking into the rock, Hoffman and Rowe digitally extracted the bones with a microcomputed tomography (microCT) scanner, which uses X-rays to create fine-grained 3D images.

What they found inside the rock were the first known babies of mammals or their relatives from the Jurassic — and not just one, but 38 of them, placing this among the most significant discoveries related to mammal origins made in the past decade[1]. *Kayentatherium* is at the cusp of mammalhood — and researchers say that it provides crucial insights into which traits define mammals and which were present in their earlier relatives.

Kayentatherium's skeleton is mammal-like in many ways, but the fossil suggested that it still reproduced very much like a reptile, giving birth to large litters of small-brained offspring. By contrast, "mammal moms invest a lot in a smaller number of babies, each of which has a better chance of surviving", says Hoffman. Mammal babies spend longer under their parents' care, developing relatively large brains, whereas these fossil hatchlings had well-developed bones and teeth, hinting that they could fend for themselves and were not nourished by milk, as all mammals are today.

The find is among a mass of discoveries in the past 10–20 years that are illuminating milestones in mammalian evolution. Although major finds are emerging all over the world, the largest number are coming out of China;

J. MENG *ET AL. NATURE* **472**, 181–185; 2011

together, they have overturned the now dated belief that dinosaur-era mammals were small, unremarkable insectivores, eking out a life in the shadows of the giant reptiles.

The fossils have revealed that early mammals were ecologically diverse and experimenting in gliding, swimming, burrowing and climbing. The discoveries are also starting to reveal the evolutionary origins of many of the key traits of mammals – such as lactation, large brains and superbly keen senses.

"The explosion of early-mammal discoveries, particularly from China, over the last two decades has been eye-opening, mind-numbing and absolutely dazzling," says David Krause, a vertebrate palaeontologist at the Denver Museum of Nature and Science in Colorado.

This avalanche of discovery is also stirring up debate: some researchers disagree over which fossil groups are true mammals and the shape of the mammal family tree. "We want to understand our early history in the language of evolutionary biology, and that's what fires me up," says Zhe-Xi Luo, a palaeontologist at the University of Chicago in Illinois. "That's why this entire field is so interesting, because the fossil record is getting better and better, and we are starting to really tackle some of these questions."

Out of the shadows

In 1824, at the Geological Society of London, naturalist William Buckland presented bones from one of the first known dinosaurs, *Megalosaurus*. At the same talk, he revealed tiny mammalian jaws that had been found in the same fossil deposit. Their presence suggested that mammals had a very deep history, but as would happen repeatedly, the dinosaur discoveries completely overshadowed the mammal ones.

The slow trickle of mammal finds from around the world continued for 150 years. Then in 1997, researchers described the first ancient mammal from the fossil-rich rocks of Liaoning in northeastern China[2], and the floodgates opened. Since then, 50 or more near-complete and "beautiful specimens" have been found there, according to Jin Meng, a palaeontologist at the American Museum of Natural History. Like the dinosaur fossils, they are dug up by local farmers and sold on to museums.

But the dinosaurs continued to get the vast majority of the attention, says palaeontologist Steve Brusatte at the University of Edinburgh, UK. "It's only that very recently, through the work of Luo, Meng and others, that the mammals are getting their due."

Most of China's mammal fossils were formed when volcanoes buried the animals in ash – and they are exquisitely detailed. Typical mammal fossils from the Mesozoic era (252 million to 66 million years ago) are little more than teeth and jaw fragments, but Chinese specimens often have entire skeletons, with fur, skin and internal organs. "We have a lot of detail to answer scientific questions," says Meng, He is interested in understanding the evolution of the mammalian ear, for instance.

The finds overturned previous dogma. "We used to say that during the time of dinosaurs, mammals were totally unspectacular. That they were just these little mousey things scampering around in the shadows," says Brusatte. But these animals "were undergoing their own evolutionary explosion", he says.

Mammals first appeared at least 178 million years ago, and scampered amid the dinosaurs until the majority of those beasts, with the exception of the birds, were wiped out 66 million years ago. But mammals didn't have to wait for that extinction to diversify into many forms and species. "These new discoveries document a huge, hitherto-undreamed-of ecological diversity," says Richard Cifelli, a palaeontologist at the University of Oklahoma in Norman.

Among the first innovations that researchers began to find in fossil form were those to do with locomotion. In 2006, Meng's team reported the first gliding mammal[3], 164-million-year-old *Volaticotherium*, which had wing membranes made of furry skin, like today's flying squirrels. In 2017, Luo's team added *Vilevolodon* and *Maiopatagaium*[4,5], which lived at around the same time and belonged to a group called the haramiyids. These animals swooped between the trees alongside some of the first flying dinosaurs, taking advantage of previously unexploitable food resources.

> "THESE NEW DISCOVERIES DOCUMENT A HUGE, HITHERTO-UNDREAMED-OF ECOLOGICAL DIVERSITY."

Researchers found other specializations that they assumed had evolved only later: *Agilodocodon* could climb trees and gnawed into bark to feast on sap[6]; the platypus-sized river-dweller *Castorocauda* had webbed feet and a beaver-like tail for swimming[7]; and *Docofossor* had paws and claws for digging, and looked like a modern mole[8].

These mammals had also adapted to a multitude of diets, much more diverse than previously assumed. In 2014, Krause described the groundhog-like *Vintana* from Madagascar[9], a herbivore that perhaps fed on roots and seeds. And the wolverine-sized carnivore *Repenomamus*, which Meng's team reported in 2005, had baby dinosaur bones in its stomach[10]. Many of these new-found fossil mammals belong to long-extinct subgroups, says Meng. In contrast to the panoply that existed in the Mesozoic, mammals today come in just three varieties: placentals, which make up the majority of species and include humans; marsupials, such as kangaroos and koalas, in which gestation in the womb is brief and development continues in a pouch; and the egg-laying monotremes, represented only by the platypus and several echidnas. "But in geological history, there were many other groups such as multituberculates, triconodonts and haramiyids," says Meng. "Mammals were actually very diverse in the Jurassic."

Some, such as the shrew-like *Juramaia* – described by Luo's team in 2011 and dated to 160 million years ago – are among the earliest placental mammals and therefore have the potential to be our ancestors[11].

And a few dinosaur-era mammals were much bigger than suspected, too. *Repenomamus* was 12–14 kilograms, and the racoon-sized *Vintana* weighed in at 9 kg. "It's exciting that we kind of busted the old myths that early mammals came from a very humble generalized ancestor," says Luo.

The finds are not solely from China. Important fossils are also coming from the United States, Spain, Brazil, Argentina, Madagascar and Mongolia. Some of the most intriguing and oldest fossils – as well as the biggest gaps in our knowledge – relate to the southern continents, where only five genera of Mesozoic mammals and their relatives are known, compared with more than 70 genera from northern latitudes. In the past two decades, Brazil has yielded several Triassic fossils that are more than 200 million years old. Guillermo Rougier, a palaeontologist at the University of Louisville in Kentucky, describes them as "incredible discoveries" that are right on the cusp between mammals and their cynodont ancestors. "These forms really show a very transitional progression from things that are typically non-mammalian, to things that pretty much have all the features of early mammals."

Mammal must-haves

The latest finds are also offering clues to the evolution of key mammal features. For instance, the keen hearing of mammals is partly down to tiny bones in the middle ear – the malleus, incus and ectotympanic. But in the reptilian ancestors of mammals, these bones were part of the jaw, and were used for chewing instead of hearing. Mammal forerunners, such as shrew-like *Morganucodon* from 205 million years ago, sported a prototype of the mammal arrangement that allowed for both functions[12].

In 2011, Meng reported an intermediary[13]: a 120-million-year-old specimen from China belonging to a group of mammals called eutriconodonts and named *Liaoconodon hui* (see 'Mammal hallmarks'). The rat-sized fossil revealed three middle-ear bones, but they were still attached to the jaw **CONTINUED ON P.472 ▸**

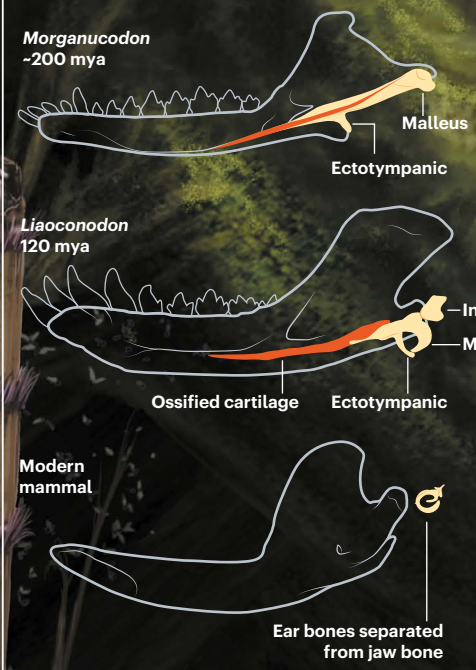
MAMMAL HALLMARKS

A raft of extraordinary fossil finds is revealing details of how mammals evolved from reptilian forebears more than 178 million years ago. Discoveries in the past two decades show that early mammals were a diverse bunch, with sophisticated skills such as gliding and burrowing that researchers thought evolved only later. Many of the features that define mammals – like suckling milk, exceptional hearing and small litter sizes – had already appeared by the time true mammals were roaming the land, rivers and skies.

By John Pickrell
Illustration by Davide Bonadonna
Design by Wes Fernandes

WALKING WITH DINOSAURS

Early mammals like this rat-sized species *Liaoconodon hui* coexisted with feathered dinosaurs like *Sinotyrannus* in the temperate ecosystems of the Cretaceous in what is now Liaoning in northern China.

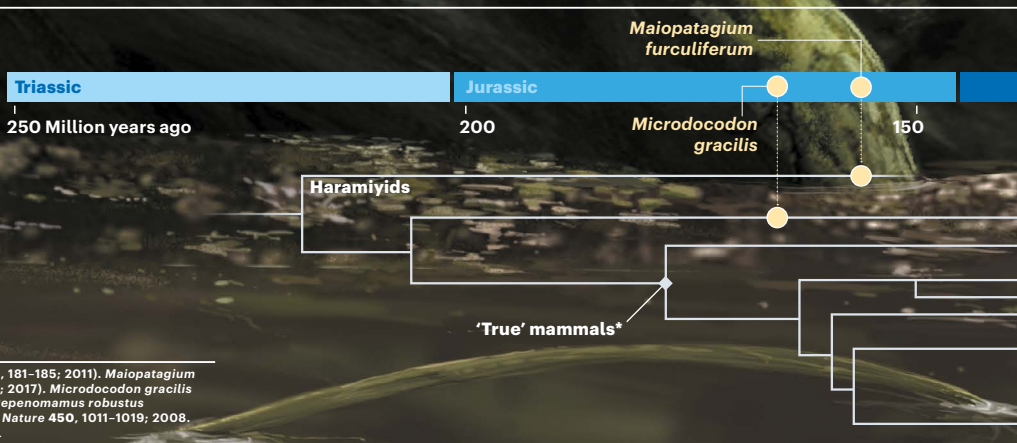


JAW BECOMES EAR

Mammals have three middle ear bones – the malleus, incus and ectotympanic bone (yellow) – responsible for their fine hearing. In reptiles and the ancestors of mammals, these bones formed part of the jaw and helped to process food. When researchers reported *Liaoconodon hui* in 2011 (main picture), they realized it represented a transitional state: a piece of hardened cartilage in the jaw (orange) supported some of the bones and the eardrum.

DEBATABLE DYNASTY

Researchers disagree about the shape of the mammal family tree, which species fall in or out of it, and even where the tree begins. One view suggests that the earliest true mammals are 178 million years old; another argues that the oldest mammal dates from 208 million years ago. Many recent fossil finds represent long-extinct groups that branched off before the tree gave rise to the three groups of modern mammals.



Liaoconodon hui and evolution of the ear bones (J. Meng *et al. Nature* **472**, 181–185; 2011). *Maiopatagium furculiferum* and gliding mammals (Q.-J. Meng *et al. Nature* **548**, 291–296; 2017). *Microdocodon gracilis* hyoid bone and suckling (C. F. Zhou *et al. Science* **365**, 276–279; 2005). *Repenomamus robustus* (Y. Hu *et al. Nature* **433**, 149–152; 2005). Timeline adapted from Z.-X. Luo *Nature* **450**, 1011–1019; 2008.

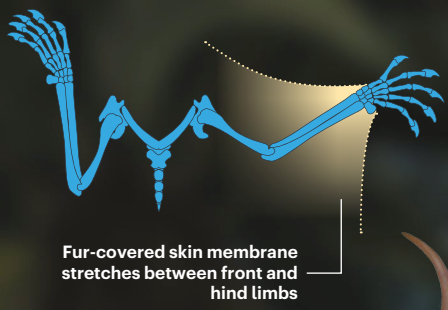
*Researchers do not know the exact timing of when lineages split from each other

GALLERY OF TALENTS

Many archetypal mammalian features evolved in a short burst early in mammal evolution, including innovations in movement, development and diet.

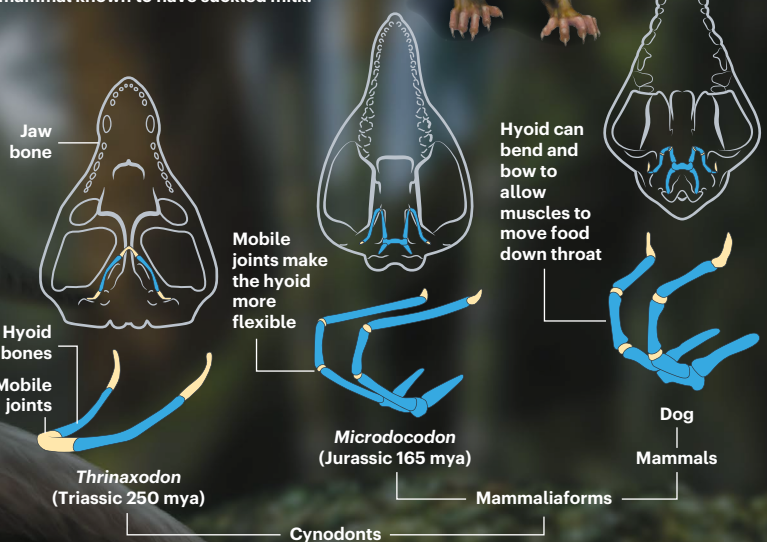
SKY GLIDERS

Several modern mammals glide on wings of stretched skin, but the exquisitely preserved furry membranes of Jurassic-era *Maiopatagium furculiferum* revealed that this ability evolved early, by 160 million years ago. Squirrel-sized *Maiopatagium* probably feasted on fruit, but other gliders from the same period had teeth more suited to seeds.



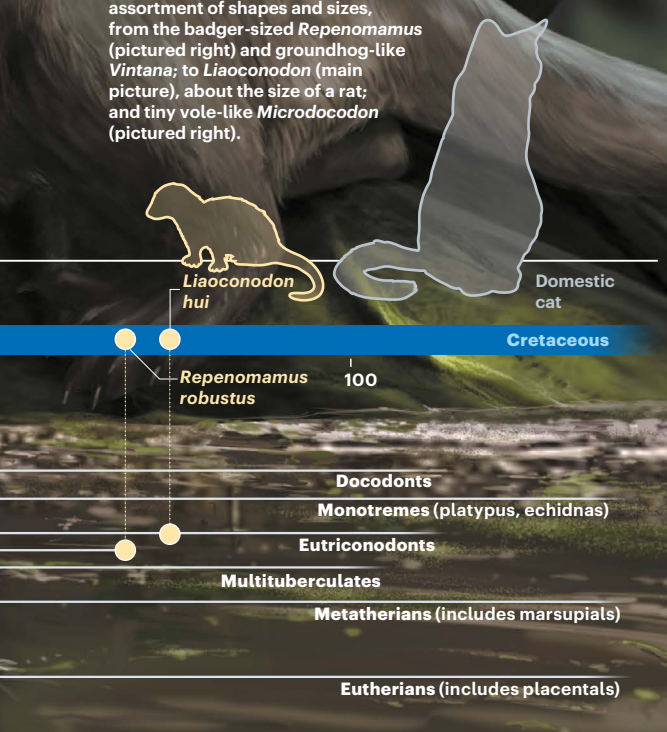
SUCKLING AND SWALLOWING

All mammals nourish their young with milk, and to do this, the juveniles require a special bone in their throats to suckle and swallow. *Microdocodon gracilis* from the Jurassic has a form of this hyoid bone that resembles that of modern mammals and is the earliest mammal known to have suckled milk.



GREAT AND SMALL

Early mammals came in a wide assortment of shapes and sizes, from the badger-sized *Repenomamus* (pictured right) and groundhog-like *Vintana*; to *Liaoconodon* (main picture), about the size of a rat; and tiny vole-like *Microdocodon* (pictured right).



DINOSAUR DINNER

Species like *Repenomamus robustus* from the Early Cretaceous challenge the typical stereotype of early mammals as diminutive insect-eating fluffballs. This creature was the size of a badger and a specimen found in 2005 had the bones of a baby dinosaur – a beaked, bipedal *Psittacosaurus* – in its stomach.

ZHE-XI LUO/UNIV. CHICAGO

This exquisitely preserved 160-million-year-old specimen of *Maiopatagium furculiferum* shows how early gliding evolved.

▸ by cartilage. "The hearing function and the chewing function were still not completely separated," he explains. This was hard evidence of the evolutionary transition from jaw to ear.

Another unique trait of mammals is the sophisticated way they chew and ingest food in small parcels, rather than swallowing things whole as snakes and alligators do. To make that possible, mammals evolved a wide variety of complex teeth for biting and grinding food.

But as babies, mammals are nourished another way – by suckling from their mother's mammary glands. "Our whole group is named after this incredible biological innovation," says Luo. Drinking milk is made possible by the ability to suck and swallow, aided by the hyoid bones in the throat and muscles that support them. This apparatus also forms the voice box.

In July, Luo published a paper revealing a 165-million-year-old vole-sized docodont – a close relative of true mammals – that had the hyoid bones of its throat preserved[14]. *Microdocodon gracilis* is the earliest animal known to have been able to suckle like a modern mammal.

This level of detail is rare, and – similar to the study of the *Kayentatherium* hatchlings – the work on both the ear and throat bones has been made possible only through advances in microCT scanning techniques, says Krause. The technique has also revealed details about the olfactory abilities and brains of early mammals. These revelations are "breathing life into these early mammals in ways that were previously impossible and almost inconceivable", he says.

Much of the constellation of features we think of as defining mammals – complex teeth, excellent senses, lactation, small litter size – might actually have evolved before true mammals, and quite quickly. "More and more it looks like it all came out in a very short burst of evolutionary experimentation," Luo says. By the time mammal-like creatures were roaming around in the Mesozoic, he says, "the lineage has already acquired its modern look and modern biological adaptations".

Family drama

Although the experts concur on many points, there is still much debate about how early mammal groups are related, and which groups are true mammals. That leads to uncertainty about how key traits evolved, says Hoffman.

One sticking point between Meng and Luo, who have each developed their own evolutionary trees, is the haramiyids. Meng thinks this early group belongs with true mammals, whereas Luo is convinced it's a side branch. The oldest known haramiyids are from 208 million years ago in the Triassic. If they are true mammals, then mammal origins date back at least that far – if not, then the oldest known mammal is 178 million years old, well into the Jurassic.

More fossils will help to resolve such questions, and bring more surprises. Krause and Meng say they are both studying exciting fossils, but are yet to publish their findings on them, and tens of unstudied specimens lie piled in the offices of their Chinese colleagues.

Palaeontologists have many items on their wish lists. One characteristic that Luo wants to understand is growth rates. Reptiles grow slowly throughout their lives, whereas mammals grow in bursts in youth and then plateau. He'd love to find a series of fossils from babies to adults to watch this happening. "That is one of the most critical features in mammals that help to define our biology," he says.

Both Hoffman and Meng agree that embryos and more babies would be significant finds – and, like the *Kayentatherium* discovery with its dozens of hatchlings, they would help us to pinpoint the date that mammal-style small litter sizes appeared. Meng's dream is to find a pregnant mammal. "This is always in my mind that I will find a mammal that inside the skeleton you can see some very delicate skeleton, which is either an egg that hasn't hatched, or it's a more interesting fetus," he says.

If the flurry of discoveries has taught researchers anything, it's that every fossil find has the potential to add a chapter to evolutionary history or even flip the prevailing narrative on its head. "We're really in this exciting, almost manic phase of lots of new evidence coming in, and it's going to take time to synthesize," says Brusatte.

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