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NEW FOSSIL FINDS REWRITE MAMMALIAN HISTORY

TWICE UPON A TIME

Jaw fossils point to multiple origins of the most mammalian of features

BY AMY MAXMEN

Tom Rich has an eye for finding bits of skulls in unlikely places. In January, he and his team reported finding a slight groove in a half inch–long jaw. Using a modified CT scanner, the researchers scrutinized the fossil they had unearthed in Australia a few years earlier. Reviewing the images of the jaw's structure, Rich and collaborators saw the groove and realized they held what remained of a duck-billed platypus out of place in the age of dinosaurs.

The jawbone's groove gave away its owner's identity because living platypus bills bear notoriously wide grooves equipped with nerves to sense their prey in fresh water. But this grooved jaw belonged to a platypus from a time when mammals supposedly were all simple, shrewlike creatures that scurried around the shadows of *T. rex*. Platypuses, however—mammals with rubbery duckbills, water-repellent fur, beaver-like tails, and webbed feet—certainly aren't plain.

In the past decade, new fossil finds have contradicted long-held views of the simplicity of primitive mammals. They seem to have been just as motley and specialized for life on the land or in water as today's mammals are. This emerging view of mammal history suggests not only that complex features evolved millions of years earlier than previously thought, but also that they might have evolved independently in different groups.

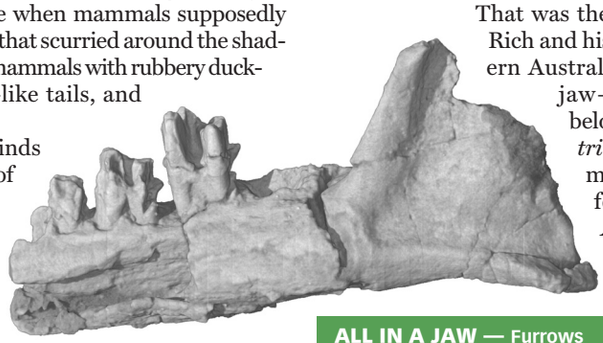
For centuries, related animals have been defined by "key innovations" that presumably allowed lineages thereafter to diversify. But some researchers now believe that these defining characteristics might actually have been commonplace and thus relatively easy to achieve—challenging the long-held notion that, as Yale paleontologist Jacques Gauthier asserts, "Complicated systems do not evolve willy-nilly."

Reports of advanced early mammals, such as Rich's platypus, suggest otherwise. The most contentious recent findings even downgrade the refined mammalian middle ear and ridged molars to less than novel. Though no reptile or other vertebrate has ever evolved these intricate hearing and chewing apparatuses, some rabble-rousing paleontologists allege that they popped up multiple times within the mammals.

It's a controversial idea: Evolutionary biologists invoke parsimony when they assume the fewest number of changes occurred during animal history, unless fossil evidence indicates otherwise. Kangaroos, wallabies, and wombats—all marsupials—bear a pouch, and so do their fossil relatives. So biologists infer that a marsupial ancestor acquired the pouch once, not three separate times. Since the fossil record is incomplete, there has been every reason to think for nearly a century that complicated structures, like the molar and middle ear, evolved one time. Not many.

Tremors shaking the old consensus began ten years ago with digs in the Southern Hemisphere, in hard-to-mine, remote lands in Antarctica and Australia. Before then, fossils of the earliest ancestors of two of the three surviving mammalian lineages had been found in Northern Hemisphere fossil beds. Dating to 144 to 119 million years ago (early in the Cretaceous period) these two lineages include the placental group, who nourish their young in a uterus through a placenta (dogs, whales, and humans are examples), and the pouch-bearing marsupials. Since members of both groups birth live young, paleontologists inferred that the groups descended from a common ancestor on the northern supercontinent Laurasia, which broke apart to form Asia, Europe, North America, and Greenland. And, millions of years later, some individuals from either line made their way south.

That was the accepted story until 1997, when Rich and his colleagues, working in southeastern Australia, dug up their first contentious jaw—a 120 million-year-old fossil belonging to a mammal named *Ausktribosphenos nyktos*. Though the jaw measured barely over half an inch, its features led the team to describe *Ausktribosphenos* as an early placental mammal. Finding a fossil of a placental mammal in the Southern Hemisphere dating back to the early Cretaceous, cast doubt on the Laurasian northern-origin hypothesis, Rich, of the Museum Victoria in Australia, and his colleagues reported in a 1997 *Science* paper.



ALL IN A JAW — Furrows in this jaw of an extinct platypus, *Teinolophos trusleri*, stir debate over how many times the same complex innovations evolved during mammalian history.

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BIG BITE What really challenged existing thinking, however, was a hefty molar embedded in the lower jaw of *Ausktribosphenos*. It was the type of tooth that distinguishes modern marsupials and placental mammals from other mammals. Yet 120 million years ago, most mammals didn't have molars. The teeth on most fossil jaws from this time were pointed. Crocodilelike, the teeth swiped past one another like blades on a pair of scissors, slicing crunchy bugs.

But *Ausktribosphenos*' tooth was clearly—and problematically—the modern crushing molar, Rich reported. Until this find, it was thought that molars developed later. Over time, the pointy back teeth would fuse in a triangular pattern, forming thicker teeth with raised projections where the apex of points used to be. The projections in upper teeth interlocked with the lower teeth, like pestles into mortars. Once formed, the elaborate teeth, called tribosphenic molars, could crush, pulverize, and grind. Mammals with this molar could munch on plants or animals.

Yet, here was *Ausktribosphenos*' advanced molar, a defining trait

in modern placental and marsupial lineages. Could it have developed an advanced feature, and then millions of years later, given rise to mammals in the north with less-pronounced molars?

Suspicious of the ramifications of Rich's claim, Zhe-Xi Luo, a paleontologist at the Carnegie Museum of Natural History in Pittsburgh, questioned whether the fossil truly belonged in the placental group. After all, Rich's identification was based on jaw details alone. To reinvestigate where *Ausktribosphenos* fits in the mammalian family tree, Luo and others analyzed the relationships among living and extinct mammals having the mortar-and-pestle-type molars. The scientists constructed a new tree by measuring similarities in 55 features preserved in the teeth and jaws of 21 modern and fossil specimens. Two distinct clans of mammals bearing the crushing molars emerged from the analysis, published in *Science* in 2001. One clan included *Ausktribosphenos* and two other molar-bearing fossils from the Southern Hemisphere, along with the monotremes—furry Australian egg-laying mammals that include the platypus and spiny anteater.

The second clan comprised fossils from the Northern Hemisphere and the placental mammals and marsupials. Thus, according to Luo's analysis, *Ausktribosphenos* wasn't in the same group as placental mammals after all.

The finding cleared up one problem, but introduced another. If the tree was correct, the molar thought to belong exclusively to live-bearing mammals had evolved separately in the egg-laying monotremes. Perhaps the crushing molar appeared to have only evolved once because of evidence.

Luo's team then suggested the unthinkable: Egg-layers had independently evolved a molar that was similar to that of other mammals. By the time modern platypuses and spiny anteaters arose without adult teeth, the biting evidence was buried in the past.

Not everyone is convinced. Regarding Luo's finding of repeated origins of the molar, Tim Rowe of the University of Texas at Austin says, "I find that there's room for a different interpretation." Disagreements often ensue when whole animals are defined by a handful of eroded bones or cracks in jaws. Paleontologists determine age by signs such as cracks in the skull. If bones are missing, incompletely formed features like molars could come from either an evolutionarily primitive adult mammal or from a juvenile, Rowe says.

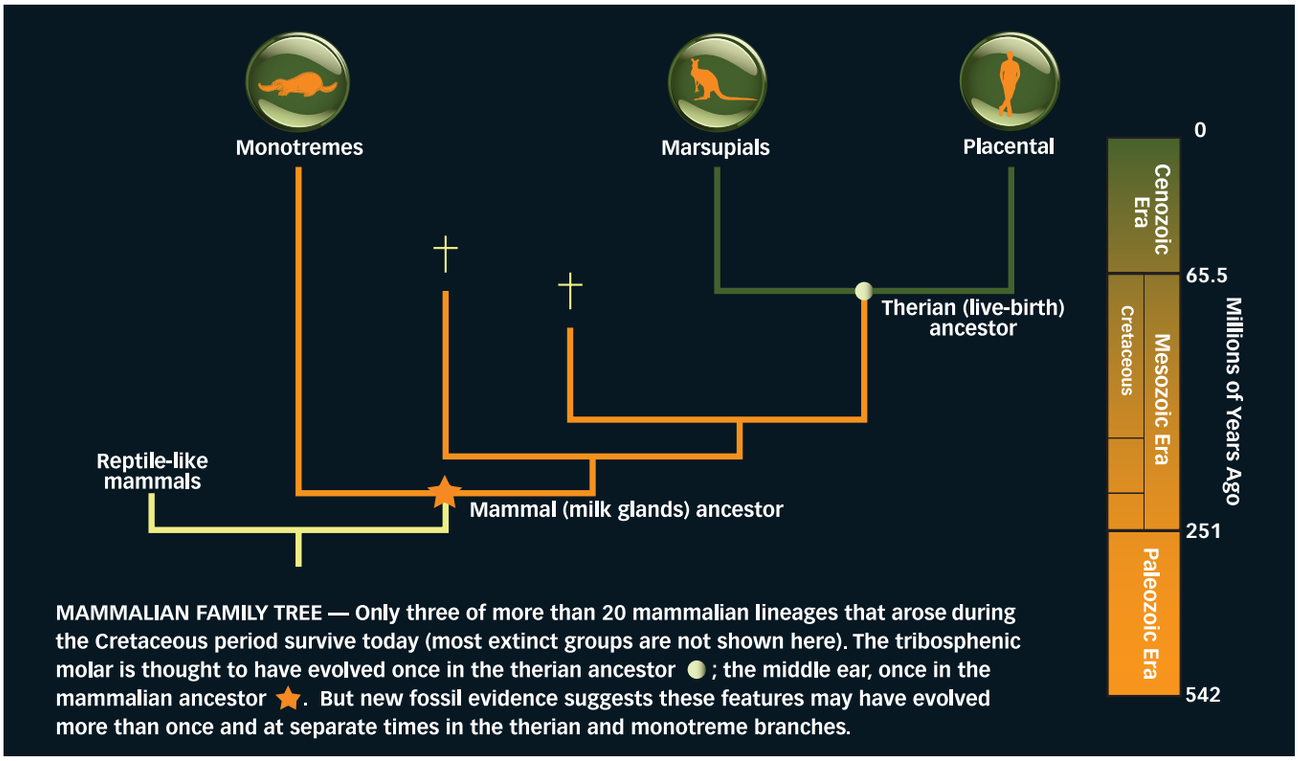
MORE THAN ONCE Despite such objections, recent reports by Rich, Luo, and a handful of paleontologists have gone further, saying that the middle ear, the very hallmark of all true mammals, was obtained by different groups, rather than by one common ancestor.

Only mammals have evolved the finely tuned architecture that characterizes the middle ear, composed of three tiny bones embedded in the skull by the eardrum. Scientists think the structure evolved from the jaw. An exquisite series of fossils along the path from reptiles toward mammals shows step-by-step changes in reptilian jaw bones. Less refined bones at the rear of the reptilian jaw can transmit sound. And in mammal-like reptiles, those bones became smaller and progressively moved back toward the skull. Next, they became loosely attached to the remaining, and enlarged, major jaw bone. In true mammals, middle ear bones are free from the jaw, allowing for acutely sensitive hearing. Paleontologists debate not whether the bones originated from the reptilian jaw, but rather how many times the bones separated from it.

> "A minor alteration during embryonic development could have led to a major innovation."
>
> — ZHE-XI LUO
> CARNEGIE MUSEUM OF NATURAL HISTORY

Enter again: Rich's team's jaw, *Teinolophos trusleri*, the Australian platypus. Years before the researchers had scanned for the jaw's finer characteristics, they reported finding a trough by the jaw joint in a 2005 *Science*. Cynodonts, extinct mammal-like reptiles that gave rise to true mammals, bore just such a trough. In it, their incompletely formed middle ear bones sat attached to the jaw bone. Seeing the same thing in a sophisticated mammal meant that the ear bones of the true mammalian ancestor must not have been fully disconnected from the jaw. The group concluded that the middle ear must have broken off from the jaw twice—after egg-laying and live-bearing mammals split off from a common ancestor.

"We suddenly had a clear indication that the middle ear didn't evolve once in this perfect stage where everything separated from the jaw in one clean sweep. In fact, there were earlier, cruder



MAMMALIAN FAMILY TREE — Only three of more than 20 mammalian lineages that arose during the Cretaceous period survive today (most extinct groups are not shown here). The tribosphenic molar is thought to have evolved once in the therian ancestor ●; the middle ear, once in the mammalian ancestor ★. But new fossil evidence suggests these features may have evolved more than once and at separate times in the therian and monotreme branches.

A. MAXMEN AND E. ROELL; INTERNATIONAL COMMITTEE ON STRATIGRAPHY (2005)

stages, in which the middle ear functioned but it wasn't a perfected system," says James Hopson, of the University of Chicago and one of Rich's co-authors.

In response, Guillermo Rougier and two other paleontologists issued a swift criticism in a following issue of *Science* in 2005 in which Rich's team published the finding. Rougier, at the University of Louisville in Kentucky, has since seen high-resolution CT scans of the *Teinolophos* jaws and says the supposed trough does not exist. "Read it and weep," he says. "I'm relieved to see that such an intricate system didn't evolve multiple times."

Rowe, who scanned *Teinolophos*, agrees with Rougier. He says, "The pieces [of the jaw] are broken, they're stained, they're small and mounted on a pin. It's easy to overinterpret."

GROWING THE TREE Yet evidence for the multiple origins hypothesis continues to grow. In a report in *Nature* last March, Luo and three colleagues described a slim bit of hardened cartilage connecting the middle ear bones to the jaw in a 125 million to 122 million-year-old primitive mammal from China. The team noted that the middle ear bones of some embryos of living mammals are transiently attached to the jaw in a similar way. The bridge in both the adult fossil and in embryos indicates one mechanism that might account for how the separation could have occurred multiple times. A minor alteration during embryonic development could have led to a major innovation, Luo says, and it could have predictably happened in multiple unrelated groups.

"This is a mechanism by which evolution operates," Luo says. "By a change in developmental timing in some lineages, you end up with different structures."

Back in the lab, scientists have found that minor genetic tweaks during embryonic development can indeed lead to major alterations in adult appearance. In turn, those changes can be amplified by natural selection over time. "In studying development, we get better appraisals on why some features appear quite fast in the fossil record," says developmental biologist Jukka Jernvall. At the University of Helsinki, Jernvall's experiments have shown how tooth shape can be predicted in mice. He anticipates a finite number of outcomes based on the behavior of a set of molecules that control tooth formation. One small change in the amount of an inhibitory molecule at an embryonic stage can snowball into a major change in adult appearance and function. Jernvall has made mouse teeth tinier than usual by slightly increasing an inhibitor at a crucial moment. And he has made mice toothier with lower levels of the inhibitor. Developmental biologists haven't yet uncovered an analogous process in the middle ear, Jernvall says.

STATS

200

Number of new Mesozoic mammals discovered since 1979

Meanwhile, paleontologists continue to scour unexcavated lands. Rich, for example, has journeyed to the northwestern block of Saudi Arabia where four-legged fossils from the age of the dinosaurs remain hidden in sand.

It's little wonder the textbooks can't keep up as fossil oddities continue pushing the origins of supposedly advanced features back in time. Since 1979, more than 200 new mammals have been discovered from fossil finds in rocks dating back to the Mesozoic Era (248 to 65 million years ago), Luo reports in the Dec. 13, 2007 *Nature*.

While all the new fossils have led to some disagreements, they also bring paleontologists closer to elucidating the true tree of mammalian ancestry. If paleontologists knew this, deciding whether the ear or molar evolved more than once would be a trivial matter of seeing who had the feature and whether or not they had a recent ancestor in common.

Astonished with new finds, Rowe says, "It's been a wealth of riches we never expected." ■