What a multituberculate might have looked like.

The Lost Tribe of the Mammals

Deep in our history, an enigma defies all categories

By RICHARD MONASTERSKY

Anyone who believes that the reign of the dinosaurs ended long ago has not visited the gift shops at the American Museum of Natural History in New York. Walk into the "Dinostore" and it becomes clear that *Tyrannosaurus rex* and its kin still rule, at least over the world of consumer merchandise. The extinct reptiles stare back from racks of T-shirts, ties, hats, necklaces, earrings, and bracelets. Their images adorn stickers, shoelaces, and stuffed animals. You can even buy trays that produce dino-shaped ice cubes.

Completely missing from this blitz of products is any hint of the museumgoers' early relatives—the mammals that lived alongside the dinosaurs during Earth's Mesozoic era. The reason seems obvious: Mammals from that span were little, shrewlike creatures, not the sort of animal that prompts children to call instinctively, "Mommy, I want that."

Yet in evolutionary terms, Mesozoic mammals underwent remarkable adaptations that in some ways dwarf those of their larger, reptilian neighbors. Though mammals of this time remained small, they developed the specialized teeth, highly sensitive hearing, and enlarged brains that would later drive their rise to power. Chief among these early mammals was an order called the multituberculates, a tongue-twisting name that paleontologists often shorten to multis.

"Multituberculates are probably the most interesting group of mammals that ever lived," says Guillermo W. Rougier, a paleontologist at the American Museum. "They appeared in the upper Triassic period, 210 million years ago, and they became extinct in the Eocene epoch, a little more than 30 million years ago. So they survived for a huge span of time."

Despite their evolutionary endurance record and their wide diversity of species, multituberculates have remained an enigma, even after a century of study. So little is known about these creatures that paleontologists are still debating what multituberculates looked like, how they originated, and, most important, how they relate to the mammals living today.

"One potential reason for their obscurity is that no one has been able to figure them out," says David W. Krause of the State University of New York at Stony Brook.

A bevy of new fossil discoveries from Mongolia, Madagascar, and Greenland is now helping paleontologists draw a more complete picture of this pivotal group of early mammals. Researchers unveiled some of their most recent finds at a symposium on multituberculates held at the American Museum in October as part of the annual meeting of the Society of Vertebrate Paleontology.

The history of mammalian evolution is a tale told largely by teeth, and the story of multituberculates provides no exception. The unwieldy name of this group refers to a dental detail: the uncommon number of tubercles, or cusps, on their molars. Their grins also revealed large front incisors, which would have made multis look vaguely like rodents, a group that appeared only within the last 50 million years or so. This distinctive dental equipment is the primary feature that sets multituberculates apart from other mammals.

Teeth play an important role in mammalian paleontology, in large part because ancient mammals had tiny, fragile skeletons that rarely left any other enduring remains. Fortunately, teeth can provide a wealth of information because each line of mammals developed extremely specialized batteries of incisors, premolars, and molars. Even a single tooth can reveal the identity of an ancient mammal.

During an expedition to Madagascar in 1995, Krause and his colleagues discovered three teeth from two types of Cretaceous multituberculates that lived roughly 75 million years ago. Although one tooth is badly worn and another consists of a broken fragment, the find is significant because it shows that multituberculates colonized a much wider part of the globe than previously imagined.

Paleontologists have long known that multis thrived on the continents of the Northern Hemisphere, where their fossils often make up more than 75 percent of mammal remains at Mesozoic sites. Their record in the Southern Hemisphere is extremely spotty: The Madagascar find is only the third reported discovery of multis there. Paleontologists had previously unearthed multituberculates in Argentina and found equivocal hints of them in Morocco.

The Madagascar teeth show clearly that, in the Southern Hemisphere, these mammals reached beyond South America. In addition, says Krause, the discovery will help in reconstructing the geography of the time. The giant landmass called Pangaea, which contained all the continents, had splintered apart by the time of the Madagascar multis. Yet one of the newfound teeth from Madagascar shows a close relationship to teeth of species from Argentina, so a path linking the two regions must have existed earlier in the Cretaceous.

Through comparisons of multis, dinosaurs, and other animals, paleontologists hope to resolve whether that route ran through Africa or cut across the combined continent of Antarctica and India.

While Krause and his colleagues must content themselves with a fistful of teeth from Madagascar, the Gobi Desert in Mongolia has provided scientists with a veritable treasure trove of multituberculate specimens. Expeditions by the American Museum staff since 1991 have yielded a collection of 400 multituberculate skulls, many of them belonging to complete skeletons from the late Cretaceous period. Previously, the tally of all known multituberculate skulls numbered less than 50, with even fewer complete skeletons.

"I think there's going to be a lot of shocking information coming out in the next several years. It will completely revise a lot of thoughts we have about multis," says paleontologist Michael J. Novacek, the leader of the Mongolian expeditions.

As Novacek, Rougier, and their colleagues sift through the catch from Mongolia, one of the foremost questions they will ponder is where multituberculates belong in the mammalian family tree. Paleontologists divide today's mammals into two major groupings: monotremes and therians. Monotremes, the primitive, egg-laying mammals, include only the duck-billed platypus, a creature called the echidna, and a few extinct forms. Their fossil record goes back to at least the Cretaceous. Therians comprise both the marsupials, such as the kangaroo, and the placental mammals, to which humans and most other living mammals belong. The lineage leading to therians had appeared by the Jurassic.

Multis have yet to find a permanent home within this phylogenetic classification system. Until the last few years, most paleontologists regarded multis as a primitive offshoot from the line that later led to monotremes and therians. Recently, however, other evolutionary trees have sprouted in the scientific literature. Some researchers now believe that multis are closely related to the monotremes, whereas others see them as close relatives of the therians.

To crack this problem, paleontologists are turning to a technique known as cladistic analysis. The process starts with researchers studying many skeletal features on multituberculate fossils and other mammals, both living and extinct. They consider which features are primitive and which represent advanced specializations. Then, a computer program analyzes the database and constructs an evolutionary tree by grouping animals that share the greatest number of advanced features.

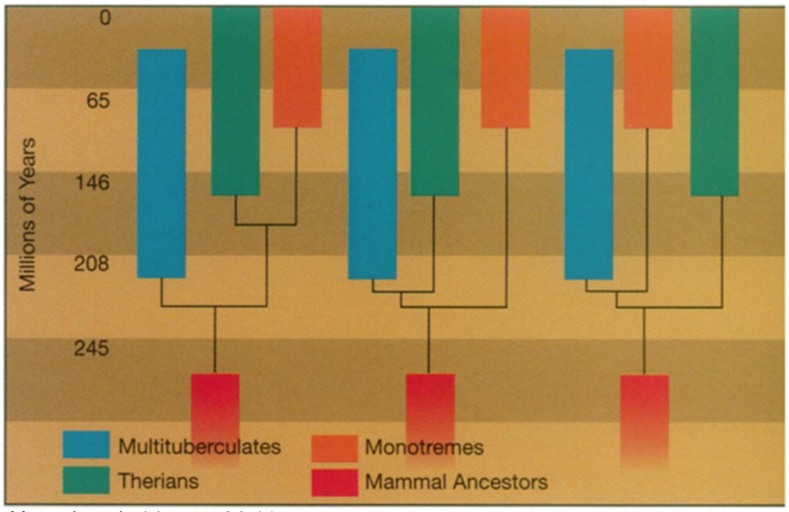
So far, cladistic analyses of multituberculates have yielded equivocal conclusions. Last year, Jin Meng of the University of Massachusetts at Amherst and André R. Wyss of the University of California, Santa Barbara studied the ear bones of a Chinese multi called *Lambdopsalis* and placed multis closest to the monotremes. They published their results in the Sept. 14, 1995 NATURE. In the same issue, though, Paul C. Sereno of the University of Chicago and Malcolm C. McKenna of the American Museum came to the opposite conclusion. Their cladistic analysis of the shoulder of a Mongolian fossil called *Bulganbaatar* led them to place multis closer to therians.

Both studies suffered, says Rougier, because they included relatively few characteristics from a limited number of animals. The paucity of information weakened the cladistic tests. With the new Mongolian fossils, paleontologists expect to be able to beef up their analysis by gleaning much more detailed information about the multituberculate skeleton.

The answer to the phylogenetic debate has important implications for understanding the evolution of modern mammals, says Rougier. If multis were closely related to either therians or to monotremes, then the two lineages leading to modern mammals must have appeared back in the Triassic period, extremely early in mammalian history. Such a conclusion would deliver a blow to paleontologists, who have few mammal fossils from the Triassic and subsequent early Jurassic. Says Rougier, "It would mean that we don't have much information about most of the evolution of mammals."

If the early record of mammals in general is poor, the record for multis is dismal. All of the fossil evidence from the first 55 million years of multituberculate history could be balanced on one finger. The only specimen from this vast slice of time is a broken tooth from the late Triassic, roughly 210 million years ago. The next oldest multituberculate fossil comes from the late Jurassic, about 155 million years ago.

Instead of filling out as new fossils emerge, the early history of multituberculates has just taken a turn for the worse with a fossil find from the late Triassic of Greenland. While prospecting in 212-million-year-old rocks, Farish A. Jenkins Jr. of Harvard University and his colleagues discovered several specimens of haramiyids, an early type of mammal. Many researchers consider haramiyids to be early relatives, or perhaps even ancestors, of multituberculates. Yet until the Greenland find, the entire fossil record of haramiyids had consisted of isolated teeth. Paleontologists could not tell how the teeth were arranged in the jaw or even which way they were oriented.



Homeless in history: Multituberculates could reside on any of three positions in the mammalian tree. On the left, multis split off early from modern mammals. In the center, multis are more closely related to therians. At right, multis are closer to monotremes.

Jenkins' group identified haramiyid jaws with the teeth in place, as well as additional parts of the skeleton. Among other revelations from the fossils, the teeth in the upper jaw do not fit the classic multituberculate arrangement, with the second molar offset toward the center of the mouth.

"That shows rather well that haramiyids are not closely related to multituberculates," says William A. Clemens of the University of California, Berkeley, one of the leaders of the multituberculate symposium.

This discovery makes the origin of multis even murkier than it had been, because paleontologists can no longer use haramyids to gain clues about early multituberculate evolution.

According to Krause, "This is one of the most significant and remarkable discoveries with reference to determining the early phase of multituberculate evolution."

While the early history of multis remains hidden in the rocks, it is clear that this group began to thrive by the late Jurassic and diversified into a vast array of different species during the Cretaceous period. Although unrelated to modern rodents, multis apparently achieved their success by occupying the same ecological niches that rodents hold today.

Some multis scampered along the ground, whereas others lived in trees, using their reversible hind feet to climb down headfirst, much like modern squirrels. Many multis had an herbivorous diet, while some apparently consumed insects. It is even possible, says Clemens, that they dined on dinosaur eggs: One multituberculate species turned up in a Montana fossil site that also held dinosaur eggs and nests.

Multituberculates were among the survivors of the giant asteroid impact 65 million years ago that dropped the curtain on the age of the dinosaurs. Even so, these resilient mammals went extinct about 35 million years ago, at the end of the Eocene epoch.

The rise of true rodents may have triggered the downfall of the multis, at least in North America. Krause has correlated the arrival of rodent immigrants from Asia with the disappearance of North American multituberculates during the Eocene. As for other continents, the sparse record of multis has less to say. "We don't have a clue of what caused their extinction on other continents," concludes Krause.

Despite all the outstanding questions, the rash of new discoveries has given paleontologists grand hopes for understanding the tiny creatures that lived in the shadow of the dinosaurs. "These are really exciting times for those of us who work on this enigmatic group of early mammals," says Krause. □