Mammalian evolution: **An early record bristling with evidence**

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Some shocking revelations in the fossil record – including fossilized hair as well as teeth and skeletons – both illuminate and complicate views on the biology and evolution of ancient mammals that lived during, and just after, the age of the dinosaurs.

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Early mammals were inauspicious creatures. The first mammal-like forms appear in the fossil record during the late Triassic period, about 225 million years ago (Figure 1). They were small, superficially shrew-like forms, some no longer than a few centimeters. In the shadow of the dinosaurs — a group that coincidentally also made its first appearance in the late Triassic — the early mammals were certainly less than imposing. Throughout the Mesozoic period — for over 160 million years — the largest mammal was no bigger than a ground hog. Moreover, the many wondrous and sometimes bizarre mammals we know today — such as the whales, bats, elephants, and scaly pangolins — were not part of the Mesozoic and early Cenozoic scene. Such elaborations were to mark the later phase of mammalian history, after the non-avian dinosaurs were decimated at the end of the Cretaceous period [1,2].

So was this earlier interval of mammalian history devoid of intriguing evolutionary stories? Not by any means. A number of important, albeit smallish, ancient mammalian lineages diversified. Many of these were sharp-toothed, meat, insect or egg eaters, in form and presumed habits not unlike living shrews and their relatives, the spiny hedgehogs and tenrecs. But another important component of these early mammal communities was the herbivorous forms. Notable among these were the multituberculates (Figure 2), forms with enlarged chisel-like incisors and, as the name suggests, complex molars and premolars appointed with many small cusps.

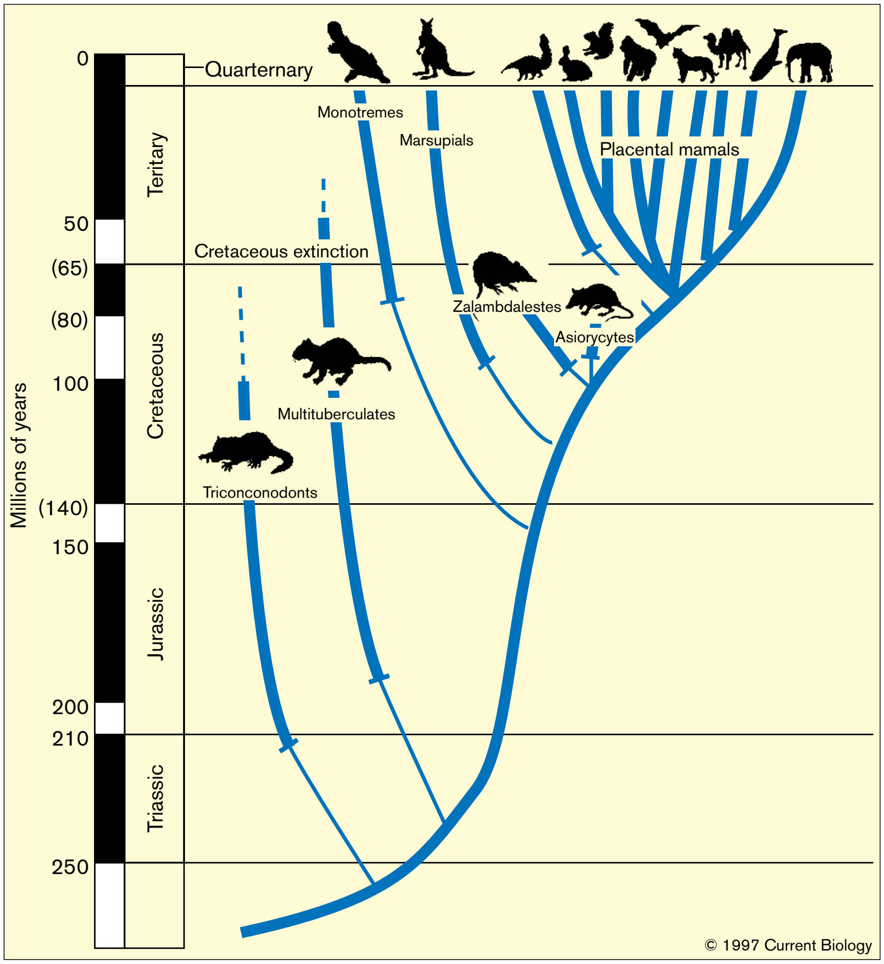
Multituberculates have a dentition designed for chopping seeds and plants with the front incisors, and mashing the cellulose material between their multicuspate cheek teeth. Indeed, multituberculates serve as remarkable ancient versions of modern rodents [3], that most speciose order of living mammals which includes squirrels, rats, mice, the beaver and many more gnawing forms. It is, however, important to note that multituberculates are not close relatives of rodents — they are in fact a basal branch of the Mammalia that appeared long before the vast radiation of placental, or eutherian, mammals that includes the rodents, primates, carnivores and many other orders (Figure 1).

Despite the fact that multituberculates are no longer with us — the last multituberculate disappeared from the fossil record in the late Eocene, about 35 million years ago [4,5] — much about their anatomy and function can be inferred from their hard, skeletal evidence. For example, recent research substantiates earlier conclusions that these animals had powerful jaw muscles, extending from the cheek bone (the zygomatic arch) to the lower jaw, which allowed a powerful back-and-forth movement of the jaws that enhanced the grinding of grainy and fibrous food [6].

Further insights into the lives of the multituberculates have recently come with some remarkable discoveries of fossils from northern China. Two paleontologists, Jin Meng and André Wyss [7], recently reported evidence of hair from fossil excrement, or coprolites, as well as fossilized regurgitated bird pellets, from a locality called Bayan Ulan in Inner Mongolia, China (Ulan is the Mongolian word for red, referring to the red-colored clays that produced the fossils). As the fossil assemblage from these beds is of Late Paleocene age — roughly 55 million years ago and a mere 10 million years after the Cretaceous (non-avian dinosaur) extinction event — this disclosure is arresting in its antiquity. Meng and Wyss were able to identify hair types for at least four different taxa of mammals, including, notably, a multituberculate known as *Lambdopsalis*.

The match between a hair type and its extinct bearer is more straightforward that it might seem. Meng and Wyss [6] restricted their analysis to coprolites containing skeletal remains of a single species, generally a single individual, allowing for secure identification of the hair. Reliable information on detailed hair structure was obtained by examination of the hair cuticle under a scanning electron microscope (SEM); hairs from a ‘hoofed’ ungulate mammal and two ancient rodent relatives were examined as well as that from *Lambdopsalis*. The result is a world record — the earliest evidence of hair in mammals. The details of scale structure on the hair shafts under SEM depend on the preservation. The smaller the grain size of the surrounding matrix and the less the bacterial decomposition, the more pristine the structure. In the case of *Lambdopsalis*, the hair shafts were seen to have a series of diamond-shaped cuticular scales.

Figure 1



The evolutionary branching events for some major mammalian groups. The thick lines above the horizontal dashes indicate the age range of the group, inferred from the fossil record. Other thick and thin black lines are only hypothesized branching times. The position of multituberculates in this scheme is a matter of controversy; this group could also be connected at the node leading to the monotremes, marsupials and placentals. (Based on a diagram by Ed Heck.)

Hair is recognized as a unique mammalian feature related to insulation, which helps to control the internal body temperature and so contributes to the mammalian property of endothermy, or 'warm-bloodedness'. All living mammals, including the very ancient group the monotremes (the duck-billed platypus and echidna), have hair, although hair may be drastically reduced in some mammals, such as whales and hippopotomuses. It may not seem surprising that multituberculates share this hirsuteness, but as the record of early mammalian evolution is restricted virtually to skeletons it has been difficult to know when hair emerged as a mammalian character, and the new fossil evidence does bear on our views of mammalian evolution.

Currently there is debate concerning the relationships of multituberculates. Some argue that multituberculates are actually an earlier, or more basal, branch than that leading to monotremes and therians (marsupials and placentals) [8]. Others argue that multituberculates are closely related to either monotremes or therians [9]. If multituberculates are more basal in position, we can say that hair evolved as a very early step in the branch leading to living mammals. Even if multituberculates are nested more intimately within the mammal tree, we can now infer that hair was a very ancient feature of the mammalian lineage. *Bona fide* multituberculates go back at least to the Jurassic Period at about 155 million years. They thus have a record that predates the first appearance of the precursors of the living mammalian groups by about 35 million years.

This estimate for the age of multituberculates, and their hair, may actually be rather conservative. For more than a century and a half, paleontologists have pondered over some isolated teeth of an enigmatic group, the haramiyids, presumed to be possible close relatives of multituberculates [10]. Fossil evidence of the haramiyids is frustratingly fragmentary, but they have attracted unusual attention because they are spectacularly old. Teeth of these animals are known from the late Triassic at an impressive 210 million years before present. A new and exciting discovery from the upper Triassic of East Greenland [11] has now provided the first evidence of associated upper and lower teeth and jaws, as well as parts of the skeleton, in haramiyids. The discovery also plays havoc with the venerable association between haramiyids and multituberculates.

The research team that described the new haramiyid specimens found these precious fossils during a rigorous field season in Greenland. Jenkins *et al.* [11] conducted painstaking analysis of the complex cusp structure on the molars in their new haramiyid, a form named *Haramiyavia clemmenseni*. From this analysis they reconstructed the pattern of occlusion during chewing between the upper and lower teeth. They found that, despite the general multicuspate resemblance in the molars of multituberculates and haramiyids, their occlusion patterns were not at all alike. Instead of the back-and-forth, or palinal, occlusion

Figure 2

The skull, shoulder girdle, and forelimb of the late Cretaceous multituberculate *Kryptobaatar*. The skull is about 3 centimeters long. (Photograph courtesy Ed Heck.)

necessary for grinding that typifies multituberculates, haramiyids brought their teeth together in a straight up-and-down, or orthal, movement that meant puncturing rather than grinding.

This is a striking departure from what might be imagined as the occlusion pattern in a multituberculate precursor. Moreover, the authors noted that, in many features, *Haramiyavia* showed a primitive combination of characters more like other Triassic mammal-like forms, the morganucodontids, than the later multituberculates. This mosaic of primitive features and a highly distinctive and specialized dentition for orthal chewing persuaded Jenkins *et al.* [11] that haramiyids are a divergent branch unrelated to multituberculates, suggesting that a diversification of mammalian-like lineages must have predated their first appearance in the late Triassic.

Greenland haramiyids will assuredly be scrutinized by other research teams. Debate will likely ensue as to whether haramiyids, their distinctive occlusion notwithstanding, still maintain some, albeit more distant, affinity to multituberculates, based on long cited similarities in some wear facets, parallel alignment of cusps on the cheek teeth, the forward leaning incisors and gaps, or diastema, between anterior teeth. Whatever the resolution on the matter, one can only be impressed by the fresh evidence from Mesozoic and early Cenozoic sites that underscores such issues.

In the last few years, the fossil record has been generous in providing not only evidence of hair in multituberculates and jaws with teeth in haramiyids, but teeth of possible 'hoofed' mammals from the early Cretaceous [12] and remarkably complete skeletons of both multituberculates and placentals from the late Cretaceous [13]. If the dramatic inflow of information on these ancient creatures is sustained, we might someday discover whether, like the multituberculates, the haramiyids were hairy.

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