# Early mammals: **Teeth, jaws and finally … a skeleton!**

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**Surprising new fossils – a skeleton and a jaw – give us a much clearer picture of mammals that lived during the time of non-avian dinosaurs; the new finds illuminate the early evolution of the lineage leading to modern mammals, and challenge traditional understanding of placental mammal evolution and biogeography.**

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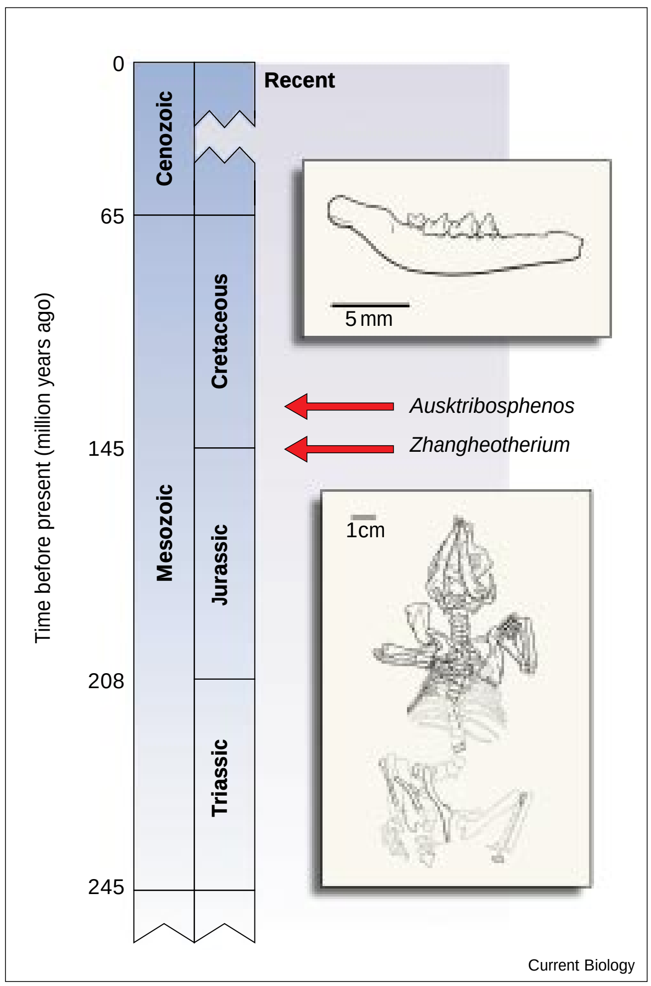
Mammals first appeared 210 million years ago, during the Late Triassic, the first interval of the Mesozoic Era (Figure 1), and at about the same time as crocodiles, turtles and dinosaurs. This was a time of dramatic transition; numerous more archaic lineages went extinct and were replaced by lineages that were to dominate the continental fauna up to the present. Geography was also dynamic [1]; before the Late Triassic, continents were sutured together into a single 'supercontinent', known as Pangea. By the end of the Triassic and the beginning of the succeeding Jurassic period, Pangea split into Laurasia in the north, including North America, Europe and Asia, and Gondwana in the south, formed by South America, Antarctica, Africa, Australia and India. During the Cretaceous, the last interval of the Mesozoic, Laurasia and Gondwana underwent further fission. Continents were flooded by shallow seaways, creating isolated landmasses. This pattern of continental fragmentation doubtless catalyzed the divergence of different lineages of mammals, birds and other land organisms.

For over a century, isolated teeth and jaws have been the primary evidence for the fascinating interplay between changing geography and environment, and the evolution of mammals that lived during the Mesozoic [2]. Although a few Mesozoic mammals are known from more complete skull and skeletal evidence, the durable, enamel-clad teeth are the most frequently recovered fossils and, for numerous groups of mammals, they are the only fossils available. Thus, the phylogeny of mammals — the understanding of the relationships among both extant and extinct groups — has been based extensively on comparisons of fossil teeth among different lineages. Mammalian teeth are indeed remarkably diverse and complex, and convey a great deal of information on phylogeny, function and feeding strategies [3]. For example, the massive tusks of elephants, the chisel-like incisors of rodents, and our own spatulate front teeth showcase the extraordinary diversity of the mammalian incisors. The cheek teeth, molars and premolars, are likewise complex and varied in size, shape and cusp arrangement.

In the shadow of the thunderous dinosaurs, Mesozoic mammals were rather unimpressive. Very few mammals were larger than a domestic mouse, and none was larger than a small cat; their isolated teeth often measure less than a millimeter in length. Finding those rare teeth requires a well-trained eye, patience and a great deal of luck. New specimens of Mesozoic mammals invariably excite the paleontological community, but a finding that

**Figure 1**




Time column showing the main divisions of the Mesozoic and the approximate age of the recent discoveries discussed in this article. (Illustration by Ed Heck.)

provides more than teeth or fragments is a real *cause célèbre*. Recently, Hu *et al.* [4] reported on an almost complete skeleton of a symmetrodont mammal, *Zhangheotherium quinquecuspidens*, from the latest Jurassic or earliest Cretaceous period — approximately 145 million years before present — of Liaoning Province, eastern China. Symmetrodonts are remote relatives of the two major groups of living mammals: marsupials, including the possums, opossums and kangaroo, and placentals, including whales, bats, horses and humans. The findings of Hu *et al.* [4] are particularly important, as symmetrodonts were previously known only from fragmentary teeth and jaws.

The name symmetrodont refers to a distinctive feature of their dentition: the major cusps of the cheek-teeth are symmetrically arranged, forming a sharp triangle. *Zhangheotherium* was a small mammal with a skull about an inch long and needle-sharp cusps on its teeth. These cusps were ideally suited for puncturing and crushing hard-bodied insects and other small prey. The precious symmetrodont skeleton from China is preserved in a slab of rock representing the bottom of a shallow fresh-water lake (Figure 2). As is common in fossils found in such environments, the specimen has been flattened by the weight of the overlying sediments. The dentition relates the Chinese symmetrodont to other specimens from Spain, England and North America. These localities represent areas that were part of Laurasia in the Late Jurassic, and were at least intermittently connected to each other.

The jaws and the skull of *Zhangheotherium* show a mixture of primitive and advanced features. This animal still possesses impressions of the extra jaw bones present in more primitive forms, but absent among modern mammals. Like other Mesozoic mammals, the living egg-laying monotremes, marsupials and some fossil placental relatives, *Zhangheotherium* has epipubics, or marsupial bones that protrude from the front of the pelvic girdle. Epipubics may have functioned in stabilizing the abdomen of a female bearing her newborns or suckling young, and may also have aided in locomotion in both males and females [5]. *Zhangheotherium* also has an ankle spur, which in the male platypus is related to a venom gland, but this function is uncertain in the fossil.

One of the most interesting aspects of the China symmetrodont concerns the bones of the ear region. This anatomical area in Mesozoic mammals shows a progressive increase in complexity that forecasts the sophisticated ears of living mammals [6]. The complexity in ear architecture is related to highly varied adaptations to hearing. For example, the high frequency echolocation of bats and whales, and the ultralow frequency hearing of elephants are two extremes of a cornucopia of acoustic specializations [7]. The Chinese symmetrodont has a finger-like petrosal — the bone encasing the inner ear — suggestive of a simple, straight cochlea. The cochlea, the organ of the inner ear designed for distinguishing different frequency sounds, is proportionally longer and spiraled among marsupials and placentals. This difference indicates that the precise frequency mapping in the hearing of modern mammals had not yet evolved in *Zhangheotherium* and other basal mammals.

**Figure 2**

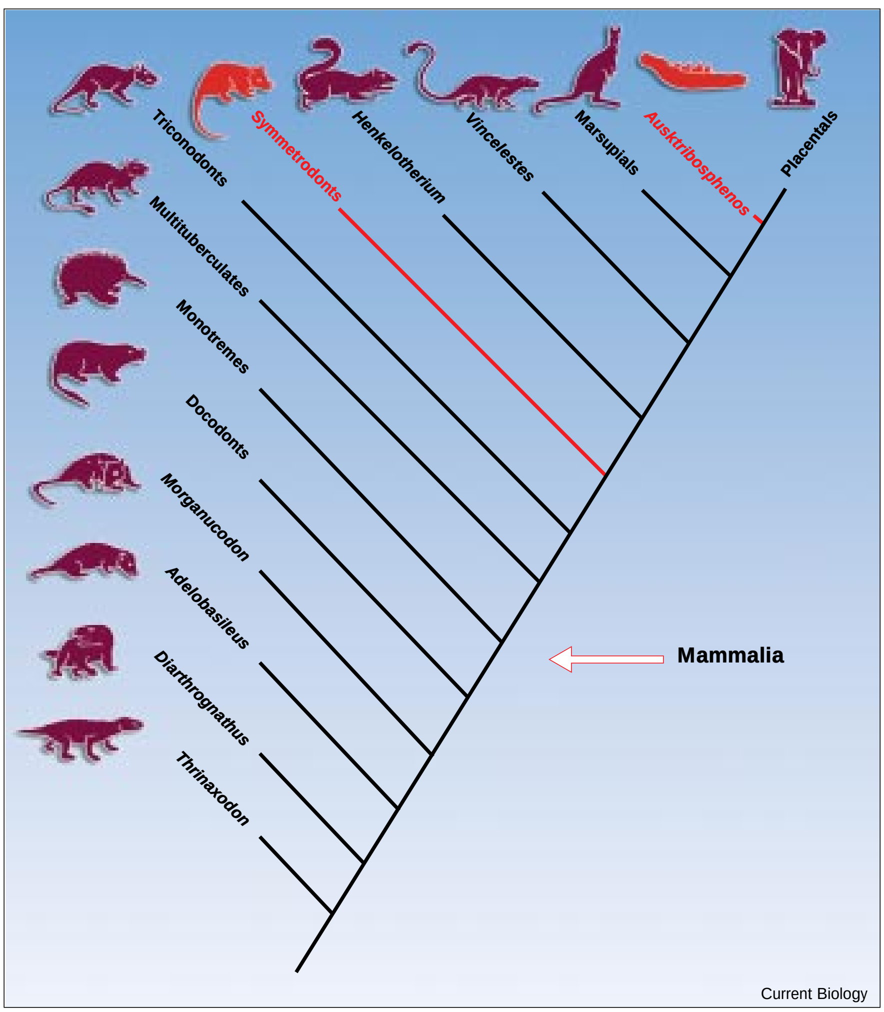
The symmetrodont *Zhangheotherium*, with a penny for scale. The anterior half of the specimen is perfectly articulated, but some of the posterior elements are lost and preserved only as molds. (Photograph courtesy Z. Luo.)

But not all the features in *Zhangheotherium* are primitive. The little mammal shows an advanced postcranial skeleton. The vertebrae are differentiated into dorsals and lumbars — elements only incipiently differentiated in living monotremes — and the sacrum is formed by three or more vertebrae. The most striking evolutionary advances in *Zhangheotherium* concern the shoulder girdle. Monotremes and most non-mammalian vertebrates adopt a sprawling posture for locomotion on land, wherein the limbs are splayed out from the body while the animal is walking. In these forms, the pectoral girdle and the collar bone are anchored to the rib cage via a series of bones that prevents the shoulder from moving. By contrast, marsupials and placentals lack the elements fastening the collar bone and have highly mobile shoulders. They also have limbs that more directly extend under the body. *Zhangheotherium* is a felicitous illustration of an intermediate stage in the origin of the modern shoulder girdle. It still retains an extra element in addition to the collar bone, but this is much reduced, allowing the shoulder girdle to be quite mobile.

A similar reduction of the intermediate elements takes place during ontogeny in marsupials [8], providing another example where neontology and paleontology mutually illuminate a complex morphological transformation. Scars and fossae in the shoulder blade indicate that the pectoral and shoulder muscles of *Zhangheotherium* were much like those in living marsupials and placentals. In *Zhangheotherium*, however, the two ends of the humerus are at an angle to each other. This twisting of the humerus indicates that, despite the modern aspect of the pectoral girdle, the 'arms' were still laterally directed as in more basal forms, though not to such an extreme degree as in monotremes.

Hu *et al.* [4] included information from the shoulder girdle, petrosal and other aspects of the skeleton of *Zhangheotherium* in a phylogenetic study of the basic mammal lineages. Their results support the traditional claim that symmetrodonts are part of the stem group leading to modern mammals, and show that Mesozoic mammals exhibited a complex mosaic of advanced and primitive features. Indeed the pivotal role of fossils in providing a clear map of mammalian phylogeny and history is especially demonstrated by this fossil. While some recent gene studies have linked the monotremes with the marsupials [9], morphological evidence strongly indicates that marsupials and placentals form a natural grouping that excludes the earlier-branching monotremes.

**Figure 3**




A diagram illustrating the position of symmetrodonts and *Ausktribosphenos*, as reported by Rich *et al.* [10], in relation to the major groups of mammals. Which groups are included in Mammalia varies according to the definition accepted by different authors. Here, 'mammals' are the common ancestor of living mammals and all its descendants, but other researchers would expand this definition to include forms such as *Morganucodon* and *Adelobasileus*. (Illustration by Ed Heck.)

Symmetrodonts like *Zhangheotherium* and other fossil mammals bolster this standard view, because they further separate the marsupial–placental clade from the monotreme clade by a number of evolutionary steps (Figure 3). Importantly, these critical taxa and their unique evidence for morphological transformations are only accessible through fossil evidence. These events cannot be traced by gene studies, where the data almost exclusively come from living taxa.

A complete symmetrodont skeleton is an unusual discovery, but similar symmetrodont teeth are known from all the major land masses of Laurasia and, logically, we expect them to be represented by more than just teeth. *Zhangheotherium* fills a gap we knew existed. The fossil record of Mesozoic mammals is, however, so poor that many times a new fossil does not fill a gap. Instead, such a fossil offers surprising insight into how far short we are of rounding out the story of Mesozoic mammal evolution. In a paper recently published in *Science*, Rich *et al.* [10] have just described such a fossil — a lower jaw with four teeth from the the Early Cretaceous of Australia, 122 million years ago, perhaps 20 million years younger than *Zhangheotherium*. Rich and coworkers baptized the new mammal *Ausktribosphenos*, meaning 'the Australian Cretaceous tribosphenic mammal'. 'Tribosphenic' refers to the kind of cheek teeth present in marsupials, placentals and very close relatives. *Zhangheotherium*, being a primitive member of this lineage, lacks a tribosphenic dentition.

The most provocative aspect of the report by Rich *et al.* [10] is that the authors present their fossil as a basal placental mammal. This would be a shocking revelation. Most paleontologists think of placental mammals as originating in Asia, some time during the Early Cretaceous, and migrating from there to North America during the Late Cretaceous. The Cretaceous mammalian faunas of Laurasian continents were formed mostly by marsupials, placentals and multituberculates, an extinct group of rodent-like mammals. In Gondwana, the Cretaceous mammalian fauna was formed by descendants of more archaic ancestry which were extinct or very rare in the northern continents. By the end of the Cretaceous, North and South America would have become faunistically connected. The marsupials and placentals would then have spread into South America from the north. From South America and Antarctica the marsupials, but not the placentals, would have reached Australia, where they would have flourished in isolation [11,12]. Terrestrial placentals would have entered Australia not earlier than five million years ago, when Australia buoyed close to Asia (bats reached Australia earlier during the Tertiary period). The Rich *et al.* [10] finding would push back the Australian record of terrestrial placentals at least 100 million years, and upset long-standing views of biogeographic history by suggesting the presence of placentals on a Gondwanan continent in the early Cretaceous.

Given our ignorance of mammalian evolution in Cretaceous Gondwana, the hypothesis put forward by Rich *et al.* [10] is possible, but it is not probable because the identity of *Ausktribosphenos* as a placental is widely questioned [13]. The specimen lacks a process in the jaw that is universally present in placentals but lacking in primitive forms such as *Zhangheotherium*. Grooves and an additional bone in the inner side of the jaw, as well as basal ridges on the teeth of *Ausktribosphenos*, are further differences with respect to later placentals, but similarities to symmetrodonts and forms that are basal to tribosphenic mammals. Whatever the affinities of *Ausktribosphenos*, the specimen raises provocative questions concerning the anatomical evidence for the major mammalian groups. Meanwhile this fossil, like *Zhangheotherium*, brings fresh news from our distant past.

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