

Mammalian evolution in the Mesozoic – recent advances and perspectives.

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A long time, Mesozoic mammals were regarded as small insectivorous animals without any particular specializations. Recent discoveries have changed our picture of the mammalian evolution during Mesozoic times dramatically. The Jurassic is a period that is particularly important for mammalian evolution, because during that time important key characters of modern mammals evolved.

In the modern terrestrial biosphere mammals are the predominant vertebrates that have colonized almost all kinds of environments. Nowadays, mammals are represented by three major clades that are the egg-laying monotremes, marsupials, and placentals. Placentals and marsupials are sister-groups, combined into Theria, of which the monotremes are a more distant sister-group. The great mammalian radiation began after the extinction of the dinosaurs about 65 Million years ago, and subsequently the modern lineages arose. However, the history of mammals started much earlier, some 200 Million years ago in the Late Triassic. Two thirds of mammalian evolutionary history occurred in the Mesozoic.

Modern mammals are characterized by two highly derived character complexes that can be studied in Recent and fossil taxa as well. These are the tribosphenic molars with a grinding function in addition to the primitive piercing and cutting, and the bony inner ear with a coiled cochlea and three ear ossicles. These key-characters of modern mammals evolved during the Jurassic on the stem-lineage of modern mammals. During Jurassic times, stem therians (*sensu lato*) as well as more basal stem mammals existed that became completely extinct later in the Mesozoic. Typical representatives of Jurassic stem mammals are the docodonts, that until recently were known only by fragmentary dental remains from Europe and North America. The discovery of almost complete docodontan skeletons in the Late Jurassic of Portugal and the Middle Jurassic of China revealed unexpected fossorial and semiaquatic adaptations. Recently described *Castorocauda lutrasimilis* possesses a beaver-like, dorsoventrally flattened tail covered by small horn scales and webbing of the hind feet, perfectly adapted for swimming. The anterior cheek dentition which closely resembles that of fish-eating seals provides additional support for an aquatic lifestyle (Ji et al. 2006).

The Late Jurassic docodont *Haldanodon exspectatus* from the Guimarota coal mine in Portugal has humeri with very large, wing-like deltopectoral crests and strikingly broad shoulder and elbow joints that indicate a fossorial and possibly semiaquatic adaptation as in modern desmans (*Desmana*). Despite these specializations in the postcranial skeleton, no epiphyses were detectable in the bones of *Haldanodon* that apparently had a reptile-like lifelong growth (Martin 2005). The mandible and jaw articulation of *Haldanodon* is very primitive. A large postdentary trough housed additional lower jaw bones including the articular and tympanic bone. Accordingly, *Haldanodon* still had the primary quadrato-articular jaw joint besides the secondary (modern) squamoso-dental jaw joint, and possessed only one ear ossicle – the stapes – in the middle ear. A micro-CT study of the inner ear of *Haldanodon* revealed a short

and straight cochlear duct that represents the situation observed in cynodonts (“mammal-like reptiles”).

In contrast to *Haldanodon*, the stem therian *Henkelotherium* possesses a generalized postcranial skeleton that resembles that of small modern scansorial mammals such as *Monodelphis* and in this regard more closely corresponds to the common picture of Mesozoic mammals. Despite its locomotorial generalization, the postcranium of *Henkelotherium* is much more modern than that of *Haldanodon*, e.g. in the architecture of the shoulder girdle and the presence of epiphyses. The mandible resembles the therian condition with a reduced postdentary trough and only the secondary jaw joint present. A micro-CT of the basicranium revealed a cochlea that is coiled by 270°, which is the first direct evidence for cochlea evolution in a Jurassic stem therian.

For more than 150 years it was generally accepted that the tribosphenic molar evolved on the therian stem-lineage in the Early Cretaceous of Laurasia. Accordingly, it has been considered one of the most important synapomorphic characters of modern mammals. This palaeomammalogical view of life was shaken in 1997, when tribosphenic mammals were discovered in the Lower Cretaceous of Australia (Rich et al. 1997). It collapsed, when a mandible with tribosphenic molars was announced from the Middle Jurassic of Madagascar that is 25 Million years older than the oldest tribosphenic molar from the Northern Hemisphere (Flynn et al. 1999). Subsequently, Luo et al. (2001) coined the provocative hypothesis of an independent origin of tribosphenic molars in Southern Hemisphere Australosphenida that later gave rise to the monotremes. The discovery of Middle Jurassic *Asfaltomylos patagonicus* in Patagonia strongly supported that hypothesis (Rauhut et al. 2002). The only known mandible of *Asfaltomylos* combines a dentition of tribosphenic molars with a very primitive dental bone with a large postdentary trough that housed accessorial bones (Martin & Rauhut 2005). A striking feature on the molars of *Asfaltomylos* are the wear facets that occur on the talonid rim (apical wear) and not within the talonid basin. This indicates that probably no protocone was present in the (unknown) upper molars. Apical wear is a typical character of toothed monotremes and therefore supports a close relationship of Australosphenida to that group. Recently, Rich et al. (2005) announced a mandible of a Lower Cretaceous monotreme, *Teinolophos*, from Australia with a large postdentary trough. This is strong evidence, that in *Teinolophos* quadrate and articular were still attached to the skull and mandible and only the stapes was present in the middle ear. If this is the case, monotremes must have acquired three ear ossicles independently from the therian mammals, which means that the ear of modern mammals is not homologous. Apparently, homoplasy is much more common than so far conceived even in structurally complex organs. These exciting new fossils may just be a glimpse of what is to come and they demonstrate that we stand at the threshold of a dramatic change in the picture of mammalian evolutionary history.

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