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Evolution & Behavior

Early chewing and swallowing

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ABSTRACT

A 165 million-year-old mammalian skeleton from China with preserved tongue bones demonstrates that active muscle-powered swallowing originated much earlier in mammalian evolutionary history than anticipated. This was obviously linked to complex cheek teeth capable of efficient chewing.

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Chewing and controlled swallowing are requirements for efficient food ingestion and civilized table manners. Active muscle-powered swallowing is typical mammalian and differentiates mammals, including humans, from other vertebrates. Reptiles, such as crocodiles and birds, devour their unchewed prey in huge chunks or even entirely (e.g., fish), mainly by gravitation. They lift their heads, and the food slides down the throat. Besides making a bewildering picture in a restaurant, the swallowing of large chunks of prey is less efficient regarding energy gain because it requires much longer digestion time.

Active swallowing is correlated to a mobile hyoid apparatus (tongue bones), a system of tiny bony elements in the throat that are derived from the second and third branchial arches of ancestral fish. These structures are also present in embryo development of mammals and other vertebrates. In reptiles, the hyoid apparatus is horseshoe-shaped and rigid, whereas, in modern mammals, it is a complex saddle-shaped system of tiny bones. These bones have mobile articulations, allowing active muscle-powered swallowing for enhanced energy gain from the chewed (=predigested) food.

The tiny hyoid bones are rarely preserved as fossils, the main reason why the evolution of the mobile hyoid apparatus in mammalian history is unknown. A virtually complete skeleton of the Middle Jurassic (about 165 Million years old) early mammal *Microdocodon* from Inner Mongolia sheds light on the evolution of swallowing in mammals. *Microdocodon* belongs to docodontans, an extinct branch of early mammal relatives with complex teeth suitable for efficient chewing. The skeleton of *Microdocodon* has large parts of the hyoid apparatus

preserved. It provides the opportunity to test the hypothesis of a linked evolution of efficient chewing and mobile hyoid apparatus capable of muscle-powered swallowing.

In the articulated skeleton of *Microdocodon*, the bones are preserved as sharp impressions in the extremely fine-grained embedding sedimentary rock. We used high-resolution micro-computed tomography for 3D reconstructions of the bones from these natural molds. The hyoid bone impressions are preserved largely articulated and in the correct anatomical position. High precision molding and transparent epoxy resin casting of the skeleton and teeth supported the detailed reconstruction of the dentition and hyoid apparatus of *Microdocodon*. For comparative purposes, we used the hyoid apparatuses of extant mammals.

To our surprise, we found the hyoid apparatus of *Microdocodon* to be astonishingly modern, similar to that of extant mammals. This evidence was particularly compelling because *Microdocodon* belongs to an early diverging, long-extinct lineage of early mammal relatives. The hyoid apparatus of *Microdocodon* exhibits a saddle-shaped arrangement of the tiny tongue bones with mobile articulations. The cheek teeth of *Microdocodon* have a complex pattern of cusps and crests with a precise fit of upper and lower tooth rows, indicating the capability for efficient chewing.

The presence of a complex and mobile hyoid apparatus combined with complex cheek teeth in *Microdocodon* supports the hypothesis that the evolution of both features was closely linked. Teeth that efficiently comminute the food make only sense if the animal is capable of efficient, muscle-powered swallowing. The discovery of *Microdocodon* also demonstrates that the evolution of a complex and mobile hyoid apparatus predated the origin of the mammalian middle ear with three ear ossicles. Modern mammals have three ear ossicles (stirrup, hammer, and anvil) transmitting the eardrum's vibrations into the inner ear and acting as a sound amplifier. In reptiles and birds, only one ear bone (the stirrup) is present, whereas anvil and hammer are still attached to the skull and mandible for jaw articulation (so-called primary jaw joint). Like the hyoid bones, the middle ear bones are derivatives from a branchial arch of ancestral fish (the first of six altogether). Docodontans still possess the primary jaw joint of reptiles and birds with the mammalian ear ossicles attached to the skull and mandible. Therefore they do not belong to Mammalia sensu stricto (crown mammals) but are placed outside Mammalia on the mammalian stem lineage. *Microdocodon* is clear evidence that the active muscle-powered swallowing and efficient chewing of modern mammals evolved well before the origin of crown Mammalia, much earlier than anticipated.

The decoupled transformation of the second and third branchial arches into a mobile hyoid apparatus independently from the morphological change of the first branchial arch into the mammalian middle ear bones raises the question of what triggered the "active swallowing first“ in mammalian evolutionary history.