A New Haramiyid Indicating a Complex Pattern of Evolution in Mesozoic Mammals

major unsolved problem in mammalian evolution is the origin of Allotheria, including Multituberculata and Haramiyida. Multituberculates are the most diverse and best known Mesozoic era mammals and ecologically resemble rodents, but haramiyids are known mainly from isolated teeth, hampering our search for their phylogenetic relationships. Researchers from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), CAS, the Shandong Tianyu Museum of Nature and the Linyi

University reported a new haramiyid from the Jurassic period of China, *Arboroharamiya jenkinsi*, a partial skeleton with both mandibles associated with teeth and isolated upper teeth. This largest known haramiyid reveals additional mammalian features of this group, and helps to identify other haramiyids represented by isolated teeth, indicating a complex pattern of evolution involving many convergences and/or reversals existed in Mesozoic mammals, as reported August 8 in *Nature*.

Reconstruction of Arboroharamiya jenkinsi. (Image by BI Shundong)





The new specimen was unearthed from the Middle–Late Jurassic Tiaojishan Formation in the town of Mutoudeng, Qinglong County, Hebei Province, China, dated about 160 million years. Researchers said it is the largest known haramiyid with a body mass estimated at 354 grams.

Arboroharamiya, as with other mammals, has body hair (preserved as impressions), a single-boned (dentary) mandible that implies a three-boned middle ear. The dentition is differentiated into incisors and multi-rooted premolars and molars, with the canine presumably lost. It differs from other mammals but is similar to allotherians in having two mesiodistally aligned rows of cusps that allow orthal (vertical) and palinal (backward), but not proal (forward) or transverse jaw movement in mastication.

Arboroharamiya is also similar to other haramiyids in having basined molars with cusps of uneven heights, but differs from them in being larger and having a more inflated a1 and elongate central basin surrounded by more cusps in lower molars. Arboroharamiya further resembles multituberculates in having one pair of enlarged lower incisors, a multi-cuspate upper incisor, loss of the canine, two upper and lower molars, and the mandibular with a mesially extended masseteric fossa and a condyle positioned low and oriented more vertically than transversely. It differs from the Jurassic multituberculates in having a small angular process and a highly specialized dentition with one lower premolar and two upper premolars and with an occlusal pattern in which the enlarged a1 bites into the basin of the upper molar.

"Arboroharamiya demonstrates convincingly that haramivids had become highly specialized in the Jurassic. It displays several mammalian features and fills some morphological gaps between Haramiyavia and multituberculates", said corresponding author Dr. BI Shundong of the IVPP, "Although morphological characteristics support allotherians as a clade, Arboroharamiya shows again that homoplasy is a common phenomenon within Mesozoicmammals. Some features of Arboroharamiya, such as the reduced dentition shared with advanced multituberculates and elongated digits shared with more advanced arboreal mammals, must be convergences. On the other hand, the dentition with multiple premolars in Jurassic multituberculates has to be considered as reversed from the condition of Haramiyavia. Regardless of various phylogenetic scenarios involving allotherians, morphological convergences and/or reversals were common in the early stage of mammalian evolution".

"It has a novel dentition, a mandible resembling advanced multituberculates and postcranial features adapted for arboreal life. Our phylogenetic analysis places Haramiyida within crown Mammalia, suggesting the origin of crown



The holotype specimen and line drawing of *Arboroharamiya jenkinsi* (STM33-9). (Image by BI Shundong)



Teeth, mandibles and tooth occlusal relationships of *Arboroharamiya jenkinsi*. (Image by BI Shundong)

Mammalia in the Late Triassic period and diversification in the Jurassic, which contrasts other estimated divergence times of crown Mammalia", said first author ZHENG Xiaoting, curator of Shandong Tianyu Museum of Nature.

This work was supported by the National Basic Research Program of China (also dubbed as "973" Program), the National Natural Science Foundation of China, and the Hundred-Talent Programof the Chinese Academy of Sciences.