

The rise of the Age of Mammals and the role of early Paleocene 'condylarth' *Tetraclaenodon* (Mammalia, Phenacodontidae) from the San Juan Basin of New Mexico

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With the dawn of the Paleogene, the mammalian survivors of the Cretaceous–Paleogene mass extinction, 66 million years ago, found themselves in an emptied landscape. Within a million years of the bolide impact, placental mammals reached a diversity and abundance never seen during the Age of Dinosaurs. The North American 'condylarths' were amongst the first mammals to diversify during the early Paleogene and are often considered the ancestral 'stock' from which other euungulate groups evolved. Amongst these, Phenacodontidae are often regarded to lie at the base of the perissodactyl family tree, but their phylogenetic position, and that of other 'condylarths', remain contentious. *Tetraclaenodon*, a medium-sized herbivorous phenacodontid from the Torrejonian (~64 to ~62 Ma) of North America is generally recognized as the oldest member of Phenacodontidae, and thus is instrumental for untangling the evolutionary relationships of 'condylarths' and perissodactyls. Here we present new information on *Tetraclaenodon* based on a description of new and previously known fossil material from the San Juan Basin of New Mexico, U.S.A., which we studied using high-resolution computed tomography (CT) scanning. From CT scans of the cranium, we segmented the brain endocast, which is relatively small and smooth (lissencephalic), similar to that of other Paleocene mammals. The petrosal lobules, which are involved in eye movement coordination, are small. The semi-circular canals associated with balance, provide an agility score of 3 indicating that *Tetraclaenodon* was probably moderately agile, similar to the extant raccoon dog or the armadillo. A multivariate analysis of tarsal measurements for a sample of Paleocene and extant mammals, which informs locomotor style, indicates that *Tetraclaenodon* was most suited to terrestrial locomotion. This is in line with anatomical and myological features of the limbs of *Tetraclaenodon* and other phenacodontids, early perissodactyls and extant mammals. These findings contradict previous studies that designated *Tetraclaenodon* as a scansorial mammal, capable of habitually climbing trees. Our results shed light on the locomotory adaptations of *Tetraclaenodon* in comparison to more cursorial phenacodontids and perissodactyls, such as *Phenacodus* and *Hyrachyus*. The earliest member of the perissodactyl stem lineage apparently lacked the more cursorial adaptations of their relatives in the late Paleocene and onwards.