

# A dwarf among giants: *Titanohyrax tantulus* (Hyracoidea, Mammalia) from the Eocene of Chambi, Tunisia and Glib Zegdou, Algeria

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The Hyracoidea was a successful mammalian order in Africa from the early Eocene to the mid-Miocene. Through the Eocene/Oligocene, hyracoids represented the dominant 'ungulate' group in terrestrial ecosystems. Among them, the genus *Titanohyrax* embraces very large species as well as a small one, *T. tantulus*, only known from the ?early/middle Eocene of Chambi, Tunisia. Recently, the generic affinity of this species has been disputed, implying a latest Eocene origin for *Titanohyrax*. Testing the competing hypotheses requires new data as most species of *Titanohyrax* are documented by few specimens. Based on new fossils from Chambi and CT scan analysis of the holotype, we revised *T. tantulus*. A complete skull from the coeval locality Glib Zegdou, Algeria, is also discussed. This analysis reveals that the holotype bears a part of dP3-4 and M1-2 rather than dP2-M1 as it was proposed. More importantly, derived dental characters, including a small compressed hypocone on P2-M3 and highly molarized P3-4 with a W-shaped ectoloph, are distinctive features of Titanohyracidae. Enamel microstructure also indicates affinities with the titanohyracids *Antilohyrax* and *Afrohyrax*. *Titanohyrax tantulus* and *Antilohyrax* also share a tall, narrow and vertically oriented supraoccipital and no diastemata between the anterior teeth. Moreover, the lack of postorbital bar, a well-developed metastylid on p3-m3, and broad spatulate lower incisors, that lacked tines or serrations, are diagnostic characters of *Titanohyrax*. As a result, there is no apparent reason to question the generic affinity of *T. tantulus*. However, the latter differs substantially from the other species of the genus, in harboring a suite of primitive characters: lower crowned cheek teeth, absence of mesostyle on P1- 2, less labially expanded mesostyle and parastyle on P4-M3, more labially positioned paracone and metacone, blunt parastyle and mesostyle, longer preprotocrista and prehypocrista, and presence of a paraconular swelling on molars. *Titanohyrax tantulus* finally differs from late Eocene titanohyracids (*Antilohyrax* and *Titanohyrax* sp.) in having sharp supraorbital ridge and extensive sagittal crest, certainly also primitive cranial characters. To conclude, *T. tantulus* represents an early offshoot of the titanohyracids; this family thus testifies to the longest fossil record among hyracoids. It only disappeared during the early Miocene, likely due to competition with artiodactyls and perissodactyls.

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