

THE SYSTEMATIC POSITION OF THE SABER-TOOTHED AND HORNED GIANTS OF THE EOCENE: THE UINTATHERES (ORDER DINOCERATA)

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Abstract

Ever since their discovery in the American West in 1871, the saber-toothed horned uintatheres, belonging to the order Dinocerata have defied placement on the mammalian tree. Previous researchers have suggested a wide range of relationships to insectivores, rodents, condylarths, proboscideans, pantodonts, and South American xenungulates.

Utilizing a large dataset of characters downloaded from Morphobank, the two best known Middle Eocene uintatheres species *Uintatherium anceps* and *Eobasileus cornutus* were added to a large character matrix of **4,541 morphological characters** sampled across **86 other mammalian taxa**. Parsimony analysis was performed using nearest-neighbor interchange in Mesquite, as well as search algorithms using TNT to find the most parsimonious placement of Dinocerata among other mammals. **Uintatheres were found to be most closely related to the xenungulate *Carodnia vieirai*** (together as *Uintatheriamorpha*).

If the molecular supported Afrotheria clade is held together, **Uintatheriamorpha is positioned within Laurasiatheria** (Liptyphla, Pholidota, Carnivora, Perissodactyla and Cetartiodactyla) excluding Chiroptera. The most parsimonious tree using TNT search algorithms split the Afrotheria clade across Mammalia, and resulted in the placement of rodents, proboscideans, hyraxes and sirenians among a polyphyletic ungulate clade including uintatheres. In light of molecular data for living mammals, uintatheres were found within a monophyletic ungulate clade and not closely related to Afrotheria. The early Paleocene North American *Protungulatum donnae* is considered the most primitive member of a monophyletic clade that includes Condylarthra, Meridiungulata, Dinocerata + Xenungulata, Perissodactyla, and Cetartiodactyla. Morphological similarities between proboscideans, sirenians and uintatheres are likely convergent adaptations.

Uintatheres group within other mesoaxial-grade ungulates, including perissodactyls, phenacodont condylarths, and South American ungulates, suggesting an interchange between North and South America during the early Paleocene, and isolation of Africa.

Uintatheres share the following synapomorphies with other mesoaxial ungulates:

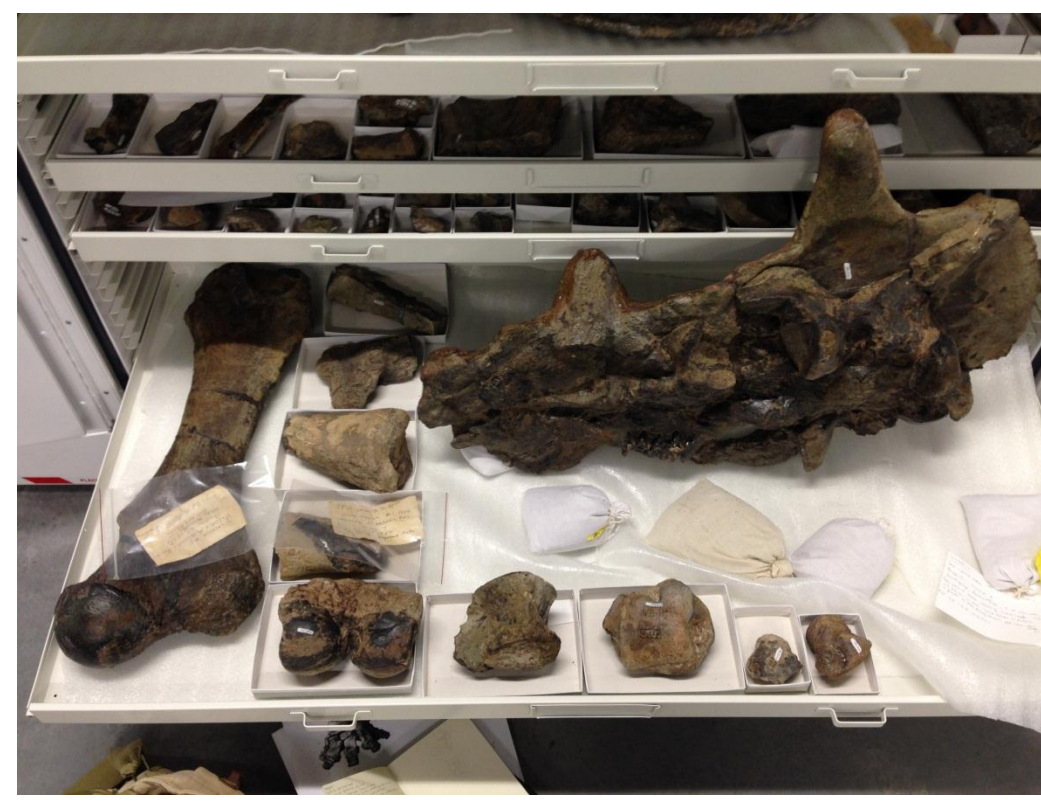
- 1) presence of hooved distal phalanges, 2) weight bore principally by third metacarpal as central axis of the fore and hind foot, 3) loss of the centrale bone (with no indication of fusion with scaphoid), 4) lack of a deep cotylar fossa on the astragalus.

The nearest living relatives of uintatheres are rhinos, horses and tapirs.

Methods

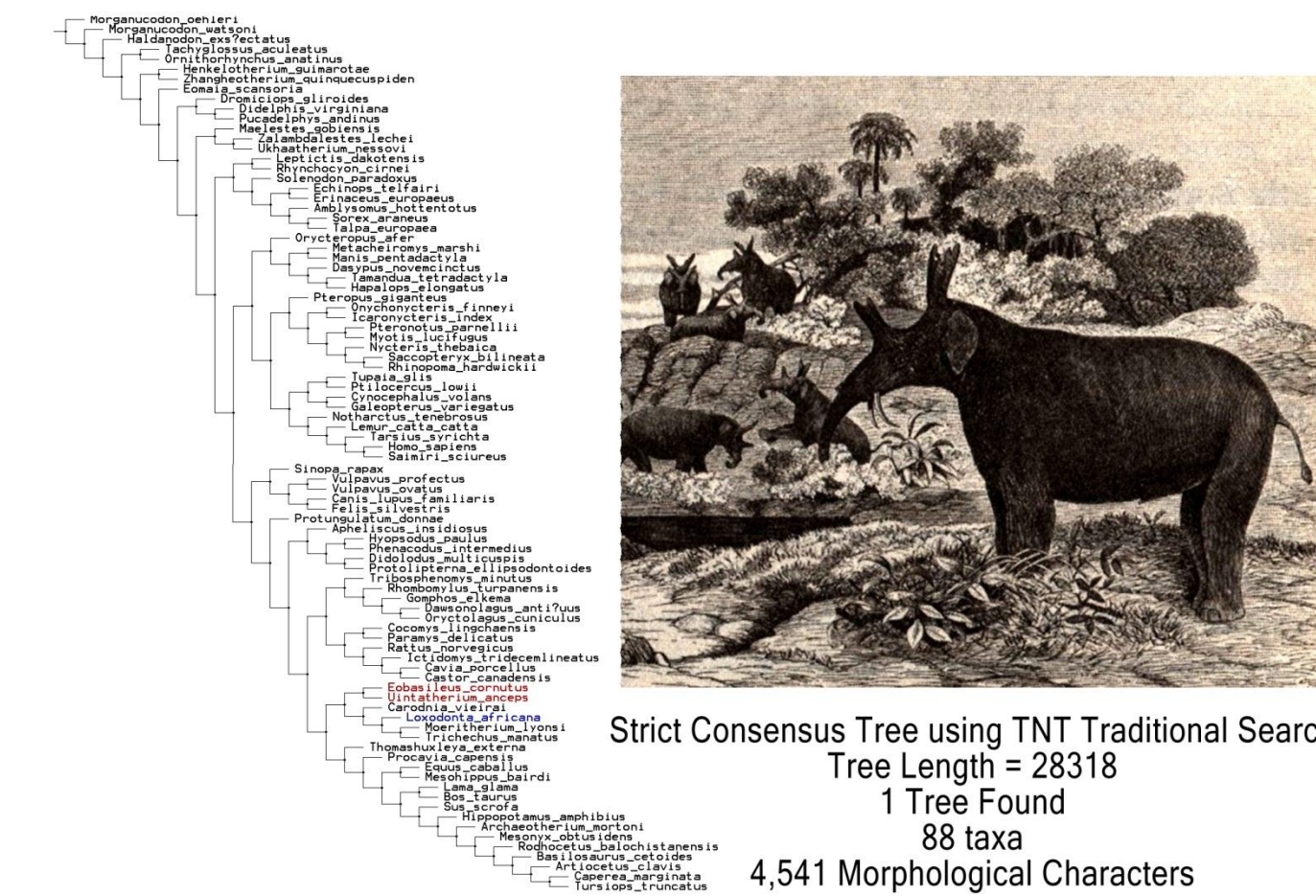
To investigate the systematic relationship of uintatheres with other mammals both living and extinct I utilized the O'Leary et al. (2013) MorphoBank character matrix which contains 4,541 morphological characters coded for 86 mammalian species.

Using publications and fossil specimens housed at the Field House Museum in Vernal, Utah, two of the most well known uintatheres were added to the character matrix: *Eobasileus cornutus* known from the Uintah North American Land Mammal Age in the Uinta Formation of Utah and Washakie Formation of Wyoming and *Uintatherium anceps* known from the Bridgerian North American Land Mammal Age of the Bridger Formation of Wyoming. The resulting character matrix was analyzed with the computer program TNT to retrieve the most parsimonious tree (Goloboff et al 2000). As well as using the computer program Mesquite (Maddison & Maddison, 2011) to analyze resulting trees and map morphological characters across various clades.

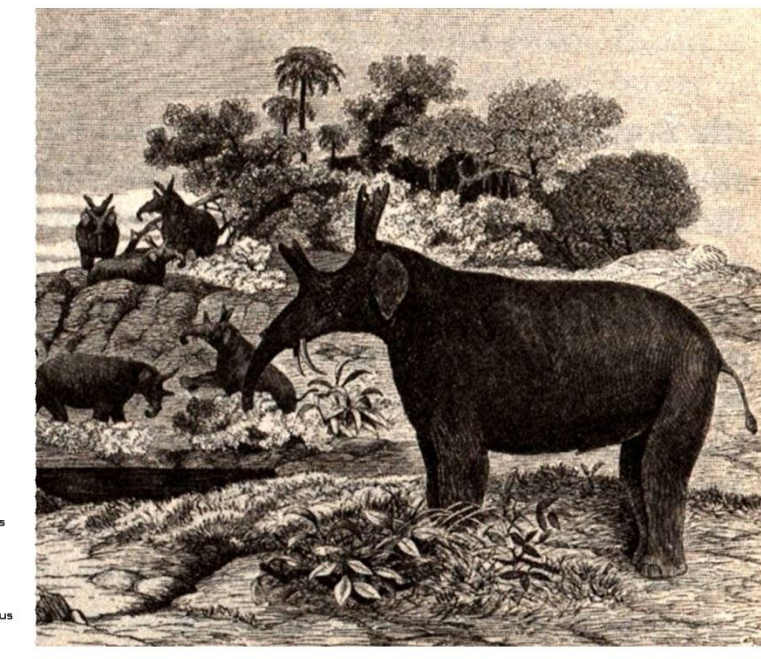


FHPR 1151 *Eobasileus cornutus* from the Washakie Formation of Wyoming

The Elephant in the Tree (effect of Afrotheria)

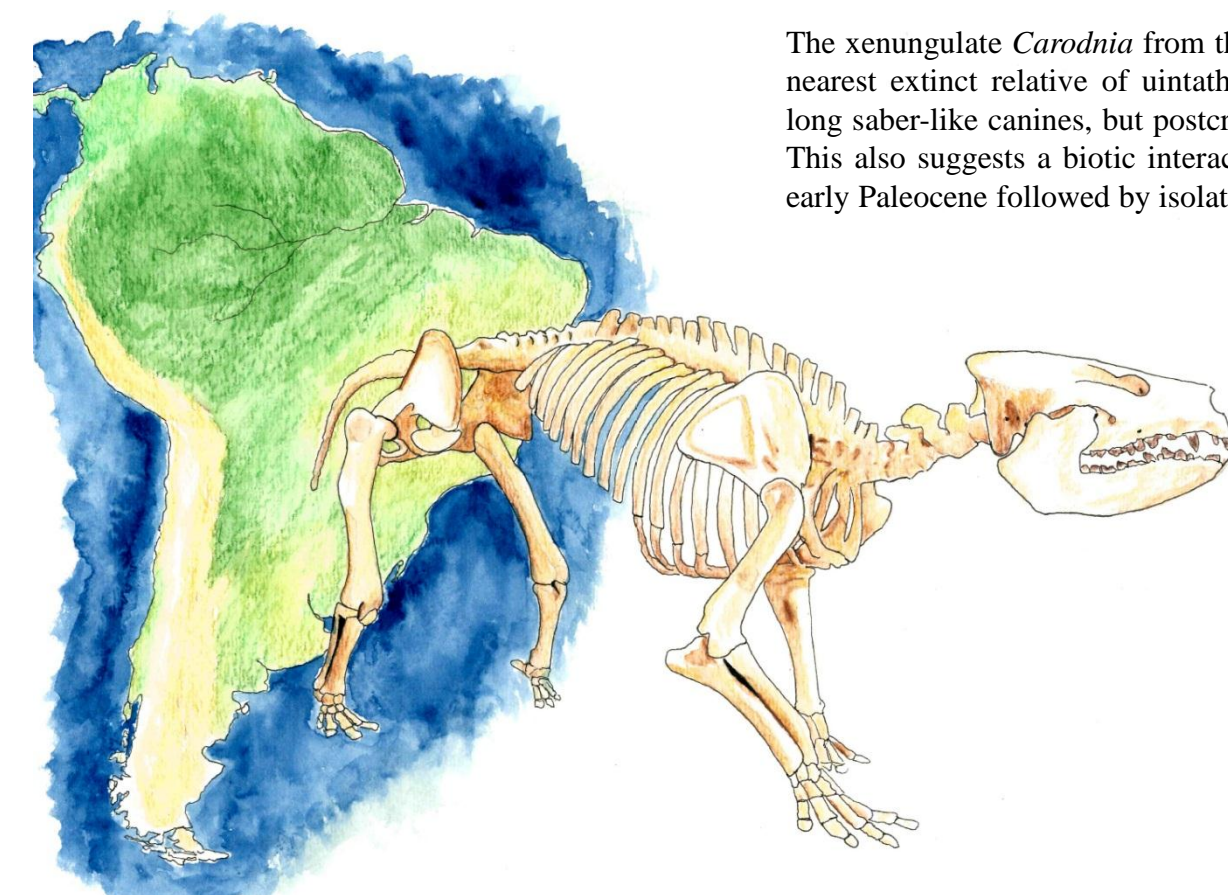


A single most parsimonious tree was found using a traditional search algorithm in TNT the results show a close relationship of uintatheres with the African Elephant *Loxodonta africana*. Such a relationship harks back to early notions of Cope (1872), that uintatheres were an extinct member of the proboscideans (Wheeler, 1960). However, recent molecular phylogenies strongly support the Afrotheria clade, which was not resolved using morphological evidence, and members are widely distributed in the tree. The close relationship between uintatheres and proboscideans is likely due to homoplastic characters associated with large graviportal adaption found in both elephants and uintatheres. Using molecular support, the Afrotheria clade was held as a true monophyletic grouping, and a new search algorithm was performed on morphological characters.



Strict Consensus Tree using TNT Traditional Search
Tree Length = 28318
1 Tree Found
88 taxa
4,541 Morphological Characters

The South America Connection

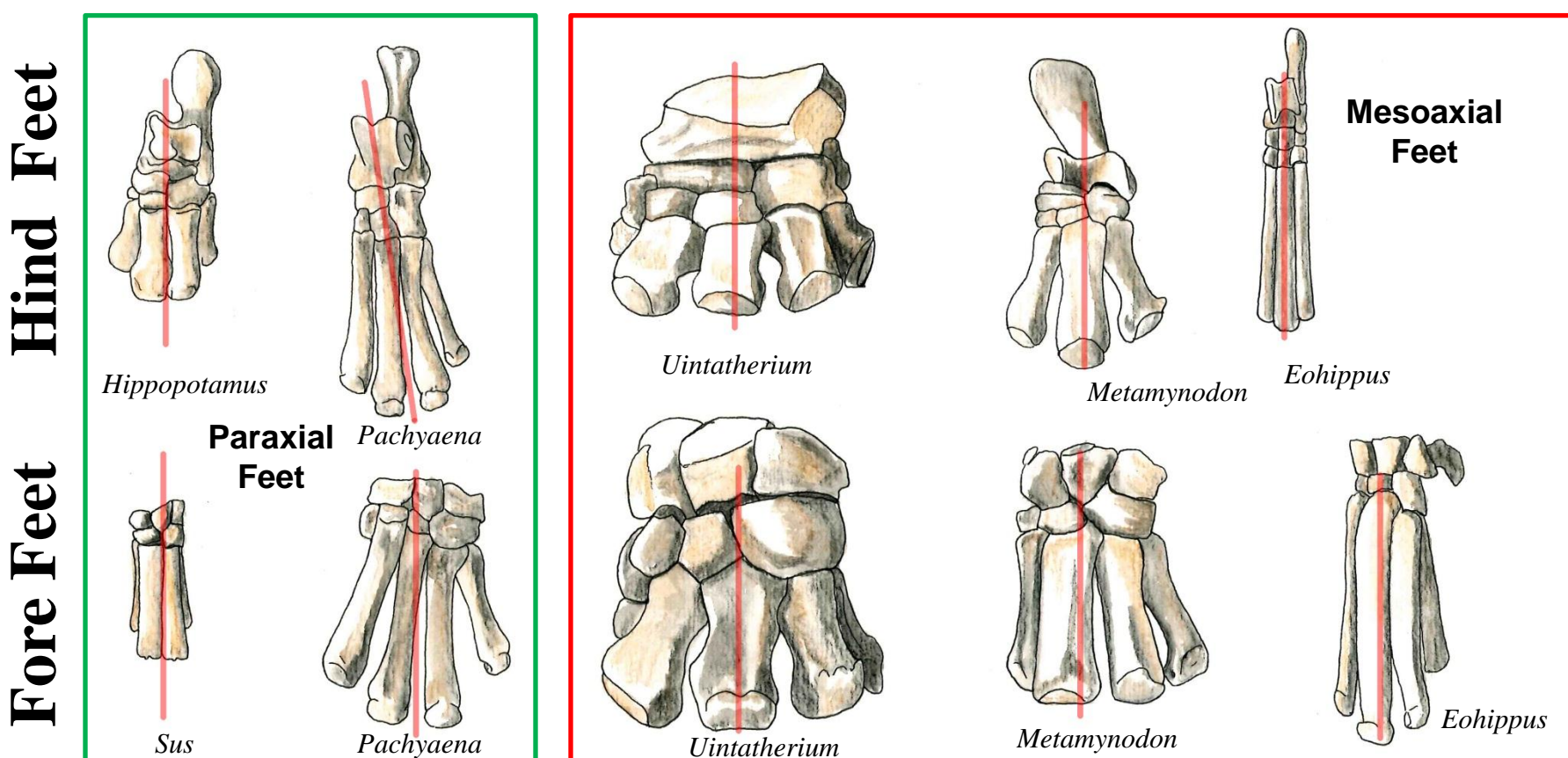


The xenungulate *Carodnia* from the Paleocene of South America was found to be the nearest extinct relative of uintatheres. *Carodnia* lacks the characteristic horns and long saber-like canines, but postcranial features in the limbs support this relationship. This also suggests a biotic interaction between North and South America during the early Paleocene followed by isolation during the late Paleocene and Eocene.

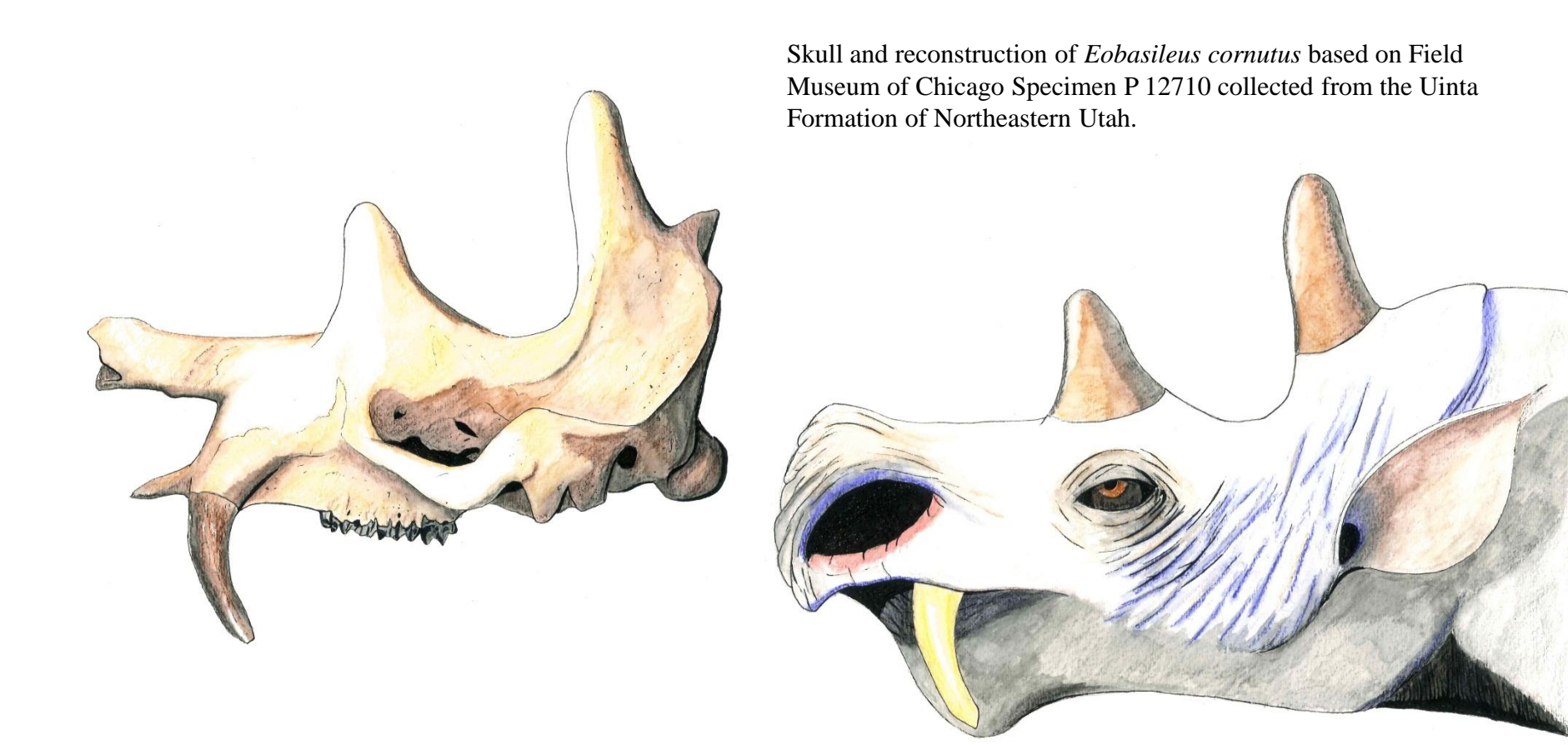
A clade composed of Xenungulata and Dinocerata (Uintatheriamorpha) is supported by a number of synapomorphies, including traits of the nasal bone, maxilla-frontal contact, zygomatic arch, and a number of characters of the posterior premaxils, as well as a number of postcranial features in the feet. This relationship has been supported by various authors (Wheeler, 1961; McKenna, 1980; Gingerich, 1985; Schoch and Lucas, 1985; Lucas, 1993) as well as criticized (Rose, 2006). Fossil pantodonts, once thought close relatives to uintatheres (Osborn, 1898) have long been argued unrelated based on major differences in the dentition (Simpson, 1929). By including more early fossil ungulate mammals, such as pantodonts in future studies, the strength of a monophyletic Uintatheriamorpha clade can be further tested.

The Importance of Ungulate Feet

The position of the central axis in the feet is an important character that divides the major groups of early ungulate mammals. Uintatheres exhibit a mesoaxial condition similar to phenacodont condylarths, South American ungulates, and perissodactyls.

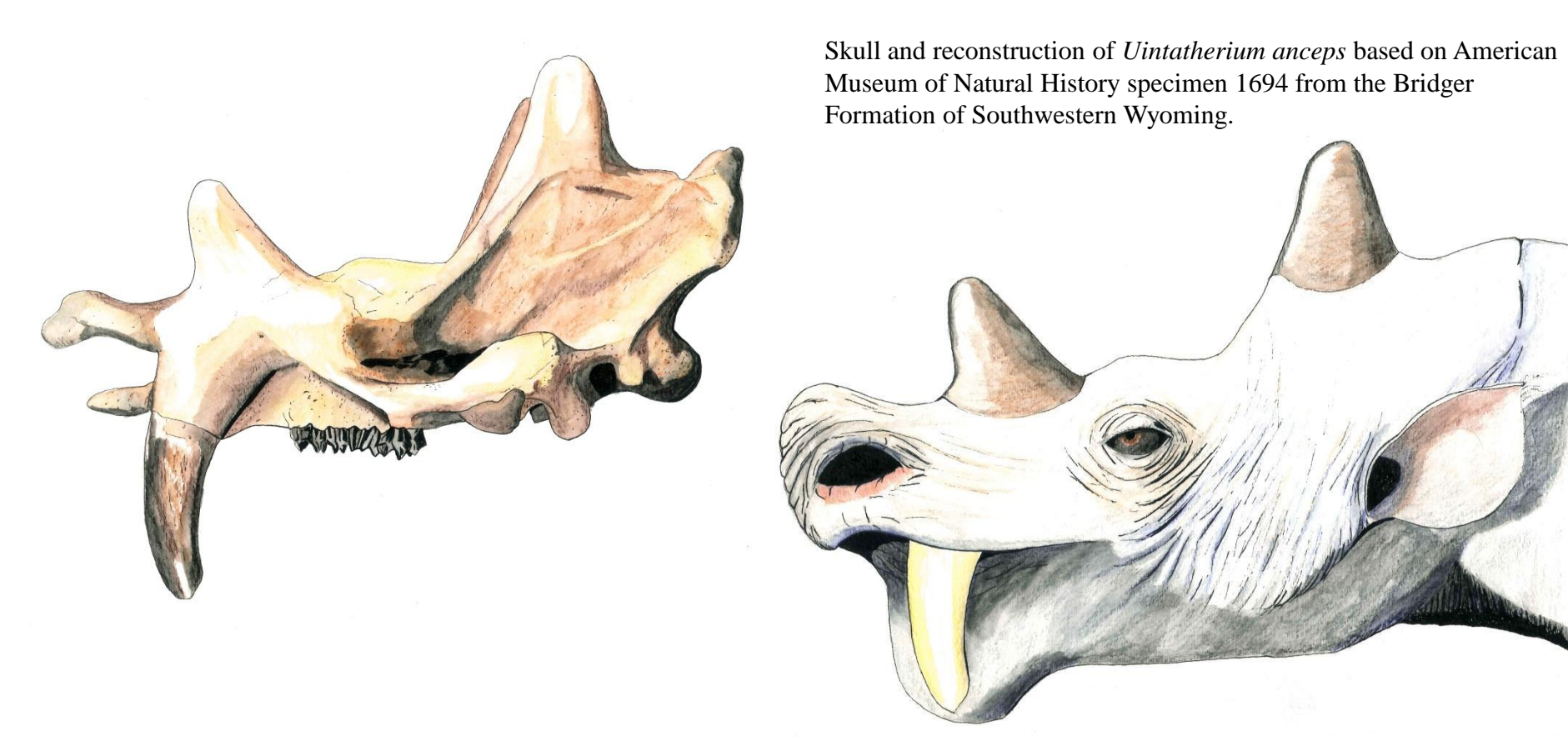


Eobasileus cornutus



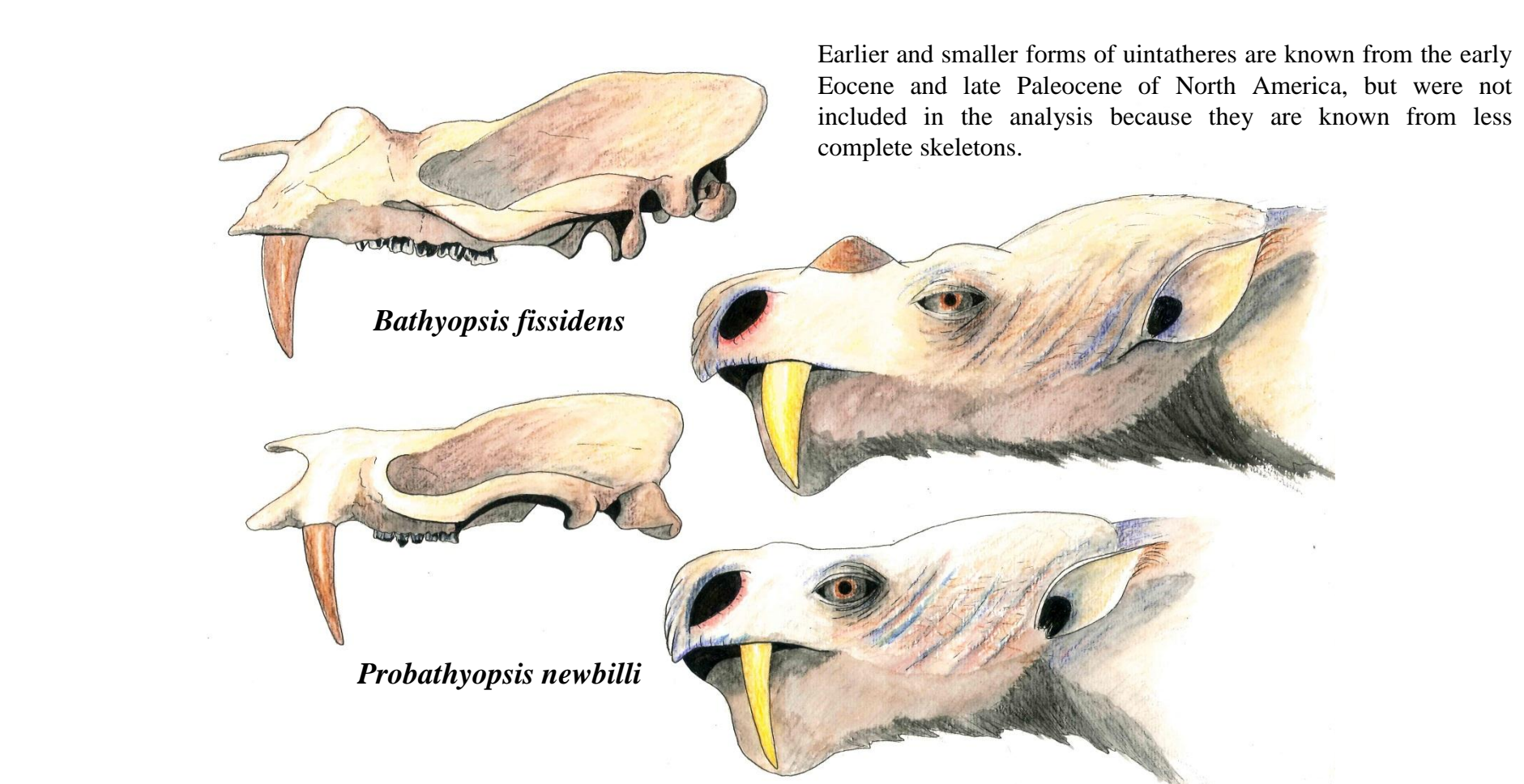
Skull and reconstruction of *Eobasileus cornutus* based on Field Museum of Chicago Specimen P 12710 collected from the Uinta Formation of Northeastern Utah.

Uintatherium anceps



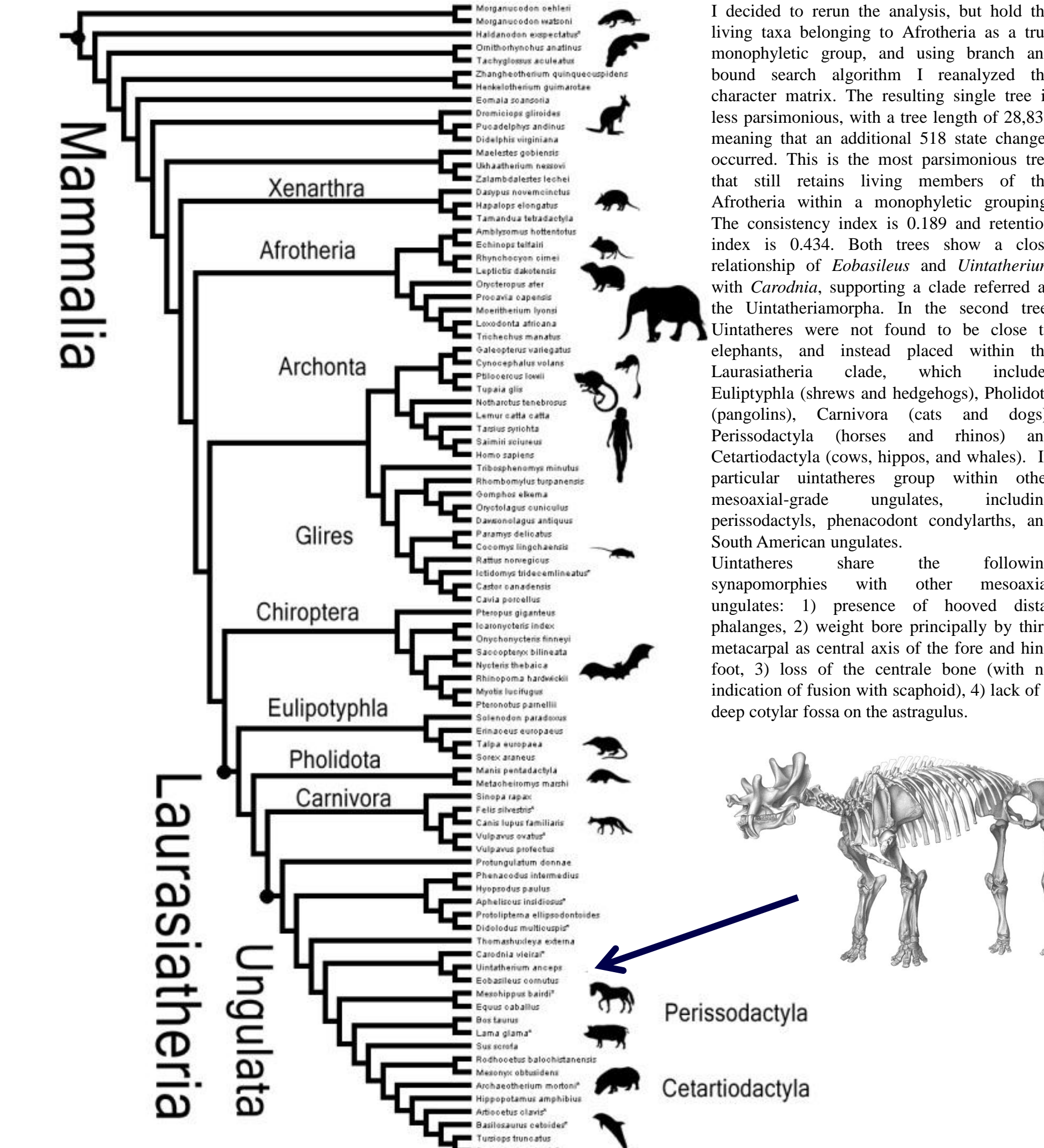
Skull and reconstruction of *Uintatherium anceps* based on American Museum of Natural History specimen 1694 from the Bridger Formation of Southwestern Wyoming.

Early Uintatheres from North America

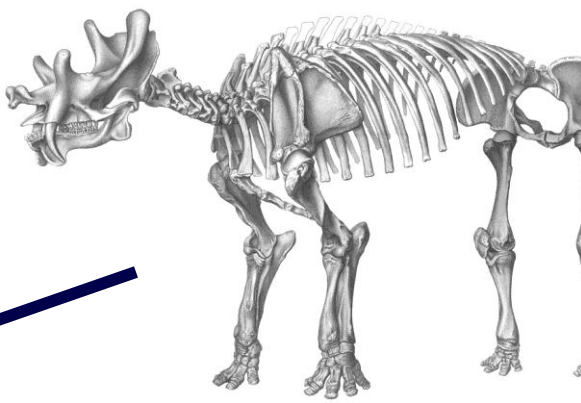


Earlier and smaller forms of uintatheres are known from the early Eocene and late Paleocene of North America, but were not included in the analysis because they are known from less complete skeletons.

The Accepted Phylogenetic Tree



I decided to rerun the analysis, but hold the living taxa belonging to Afrotheria as a true monophyletic group, and using branch and bound search algorithm I reanalyzed the character matrix. The resulting single tree is less parsimonious, with a tree length of 28,836 meaning that an additional 518 state changes occurred. This is the most parsimonious tree that still retains living members of the Afrotheria within a monophyletic grouping. The consistency index is 0.189 and retention index is 0.434. Both trees show a close relationship of *Eobasileus* and *Uintatherium* with *Carodnia*, supporting a clade referred as the Uintatheriamorpha. In the second tree, Uintatheres were not found to be close to elephants, and instead placed within the Laurasiatheria clade, which includes Eulipotyphla (shrews and hedgehogs), Pholidota (pangolins), Carnivora (cats and dogs), Perissodactyla (horses and rhinos) and Cetartiodactyla (cows, hippos, and whales). In particular uintatheres group within other mesoaxial-grade ungulates, including perissodactyls, phenacodont condylarths, and South American ungulates. Uintatheres share the following synapomorphies with other mesoaxial ungulates: 1) presence of hooved distal phalanges, 2) weight bore principally by third metacarpal as central axis of the fore and hind foot, 3) loss of the centrale bone (with no indication of fusion with scaphoid), 4) lack of a deep cotylar fossa on the astragalus.



Perissodactyla
Cetartiodactyla