PERSPECTIVE

Outstanding Discoveries in Paleomammalogy in the Last One and a Half Decade

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Abstract: Since the last comprehensive review of the then state-of-the-art progress in paleomammalogy in 2010, there has been substantial further advances in understanding the middle ear development and phylogeny of Mesozoic mammals, evolution of early primates, and so on. The post-dentary bone morphologies of two Jurassic mammaliaforms, *Dianoconodon youngi* and *Feredocodon chowi*, demonstrate the detachment mechanism of post-dentary bones from the dentary and the eventual breakdown of the Meckel's cartilage during the evolution of mammaliaforms. The middle ear of the Early Cretaceous *Liaoconodon hui* defines the transitional mammalian middle ear. The Createaceous stem therian *Origolestes lii* displays the decoupling of hearing and chewing apparatuses and functions. In addition, the discovery of *Ambolestes zhoui*, an Early Cretaceous eutherian, demonstrates that *Sinodelphys*, the oldest purported marsupial, is actually a eutherian. The early Eocene haplorrhine primate, *Archicebus achilles*, resurrects the possibility that Asia was an important stage for early primate evolution. Not only has knowledge concerning these topics been further deepened, but new knowledge has also been acquired concerning Late Cenozoic herbivores and primates in paleomammalogy on the basis of these new discoveries.

Keywords: middle ear, Mesozoic mammals, early primates, hominoid extinction, Neogene mammals

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Introduction

Wang and Ni (2010) reviewed the then state-of-the-art advances in several aspects of paleomammalogy, such as the discovery of ossified Meckel's cartilage in several critical Mesozoic mammals and its relation to the mammalian middle ear development, the pseudotribosphenic pattern in the molars of *Shuotherium*, the earliest and most primitive primate *Teilhardina asiatica,* and so forth. Since then in the last one and a half decade, not only has knowledge concerning these topics been further deepened, but also new knowledge has been acquired concerning Late Cenozoic herbivores and primates in paleomammalogy on the basis of new discoveries. Here we present scientific works represented by thirteen more *Nature* or *Science* papers by the IVPP colleagues that have brought this remarkable progress into reality. Of course, these research outcomes are only the pyramidion of the

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paleomammalogy pyramid. Without the basic accumulation of exhaustive explorations and description of vast amounts of mammalian fossils acting as the base, they would not be able to shine up there.

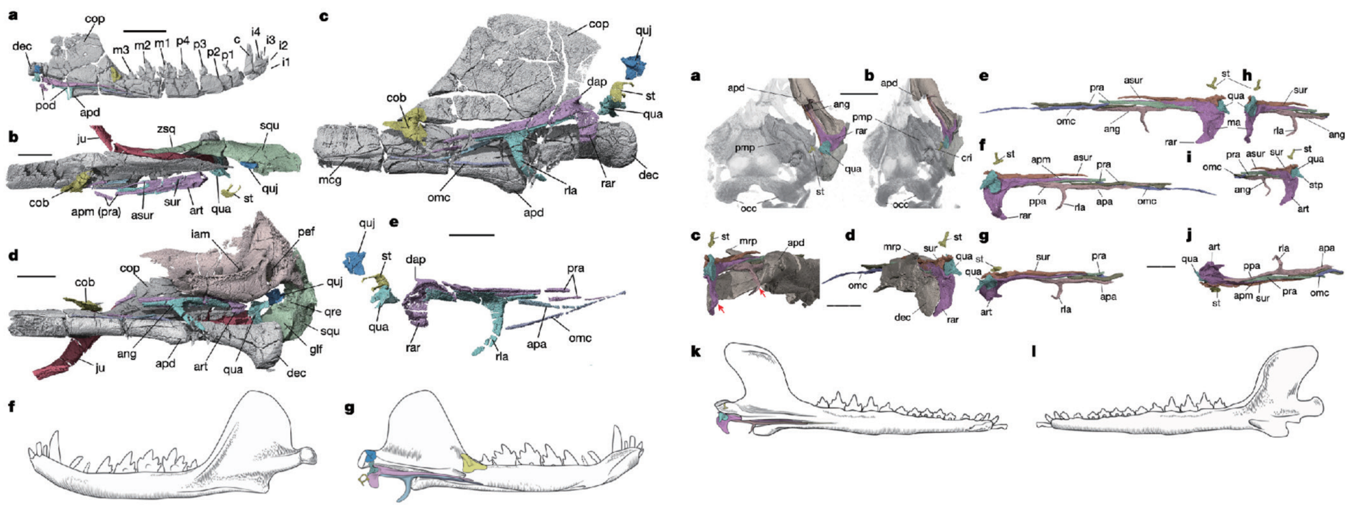
Middle Ear Evolution of Mesozoic Mammals

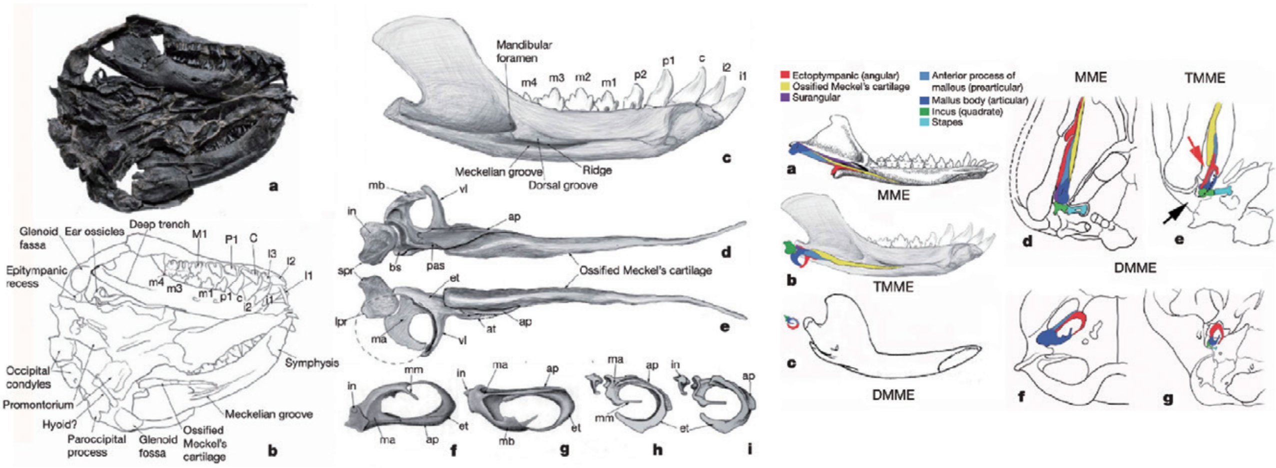
The lower jaw of non-mammalian amniotes is composed of the tooth-bearing dentary and several post-dentary bones; that of mammals is formed by the dentary alone. In contrast, there is only one ossicle in the middle ear of non-mammalian amniotes, but there are multiple ossicles in mammals. Fossils have shown a series of reduction of the post-dentary bones during synapsid evolution towards mammals, and developmental studies have demonstrated homologies of mammalian middle ear ossicles with their reptilian precursors, including the malleus (=articular + prearticular), incus (quadrate) and ectotympanic (=angular). In basal mammaliaforms, such as *Morganucodon*, the post-dentary bones have greatly reduced but still attached to the dentary, serving a dual function for hearing and feeding. The mandibular middle ear (MdME) of *Morganucodon* is regarded as the prototype that gives rise to the definitive mammalian middle ear (DMME) in which the angular, articular plus prearticular, and quadrate are strictly auditory structures and fully divorced from the feeding apparatus.

Incorporation of the lower jaw elements and quadrate into the middle ear on the cranium represents an innovative feature of mammals and has been regarded as a classic example of gradual evolution in vertebrates, a subject that has attracted enormous attention. Conventional research on the evolution of the mammalian middle ear has focused primarily on detachment of the post-dentary bones, in which transitional changes are often inferred from grooves on the mesial surface of the dentary or from fragmentary specimens.

The dual jaw joint of *Morganucodon* consists of the dentary-squamosal joint laterally and the articular-quadrate one medially. The articular-quadrate joint and its associated post-dentary bones constitute MdME, the precursor of the mammalian middle ear. Mao *et al*. (2024) reported MdME from jwo Jurassic mammaliaforms: *Dianoconodon youngi*, a morganucodontan-like species from Yunnan and *Feredocodon chowi*, a pseudotribosphenic shuotheriid species from Inner Mongolia. *Dianoconodon youngi* shows many previously unknown post-dentary bone morphologies and exhibits features that suggest a loss of load-bearing function in its articular-quadrate joint. The middle ear of the shuotheriid approaches DMME condition in

Lower jaw and mandibular middle ear of *Dianoconodon youngi* (left) and the shuotheriid docodontiform *Feredocodon chowi* (right)





Skull and ear ossicles of ***Liaoconodon hui*** **(left) and morphological transference of mammalian middle ear (right)**

that it has features that are suitable for an exclusively auditory function, although the post-dentary bones are still attached to the dentary. With size reduction of the jaw-joint bones, the quadrate shifts medially at different degrees in relation to the articular in the two mammaliaforms. These changes provided evidence of a gradual loss of load-bearing function in the articular-quadrate jaw joint – a prerequisite for the detachment of the post-dentary bones from the dentary and the eventual breakdown of the Meckel's cartilage during the evolution of mammaliaforms.

Meng *et al*. (2011) reported the first unambiguous ectotympanic (angular), malleus (articular and prearticular) and incus (quadrate) of an Early Cretaceous (120 Myr) eutriconodont, *Liaoconodon hui*, from the Jehol Biota, Liaoning. Interestingly, the ectotympanic and malleus have lost their direct contact with the dentary bone but still connect the ossified Meckel's cartilage (OMC). This morphology defined a distinct stage in the evolution of the mammalian middle ear, which has been named as the transitional mammalian middle ear (TMME). TMME narrowed the morphological gap between MdME in basal mammaliaforms and DMME of extant mammals. OMC served for a stabilizing mechanism bridging the dentary and the detached ossicles during the mammalian evolution.

Based on multiple skeletal specimens from the Cretaceous of Liaoning, Mao *et al*. (2020) described a new stem therian mammal *Origolestes lii* that displays decoupling of hearing and chewing apparatuses and functions. Its auditory bones, including the surangular, have no bone contact with the ossified Meckel's cartilage; the latter is loosely lodged on the medial rear of the dentary. This configuration probably represents the initial morphological stage of DMME. It has become clear that hearing and chewing apparatuses have evolved in a modular fashion. Starting as an integrated complex in non-mammaliaform cynodonts, the two modules, regulated by similar developmental and genetic mechanisms, eventually decoupled during the evolution of mammals, allowing further improvement for more efficient hearing and mastication.

Han *et al*. (2017) described a new Jurassic gliding euharamiyidan mammal, *Arboroharamiya allinhopsoni* that possesses a five-boned auditory apparatus consisting of the stapes, incus, malleus, ectotympanic and surangular, representing the earliest known DMME. The acquisition of the auditory bones in euharamiyidans was related to the formation of the dentary-squamosal jaw joint, which allows a posterior chewing movement, and had evolved independently from the middle ear structures of monotremes and therian mammals. The phylogenetic analyses of *Arboroharamiya allinhopsoni*, *Arboroharamiya jenkinsi* reported by Zheng *et al*. (2013), and *Sheshou lui*, *Xianshou linglong*, and *Xianshou songae* reported by Bi *et al*. (2014) collectively placed these euharamiyidan species within Crown Mammalia together with multituberculatans, indicating the origin of mammals in the Late Triassic. Wang *et al*. (2019) report-

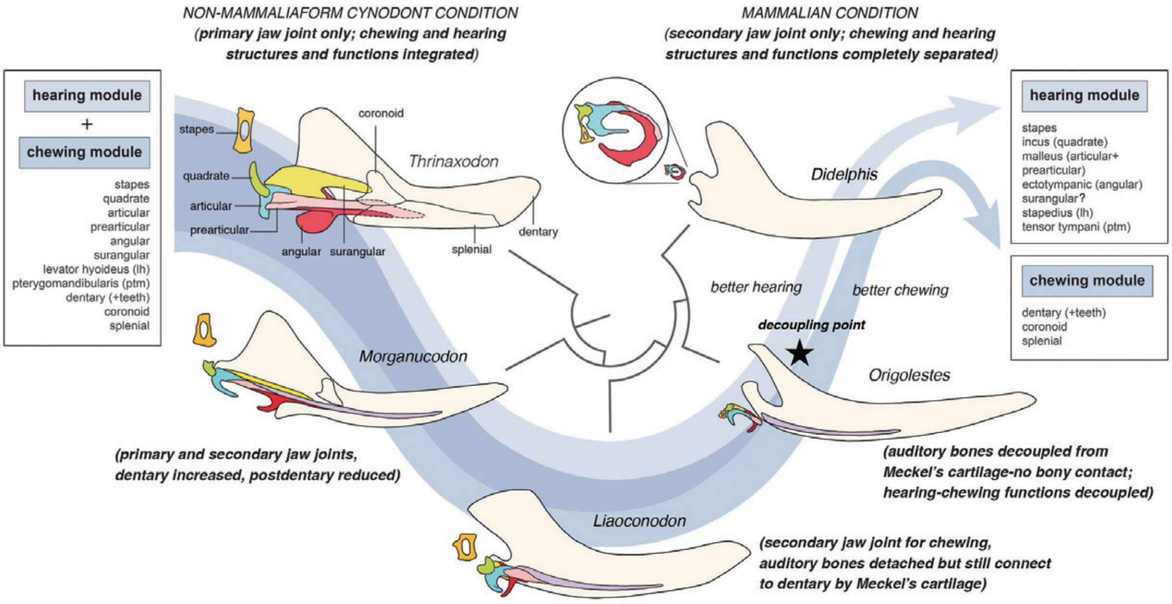
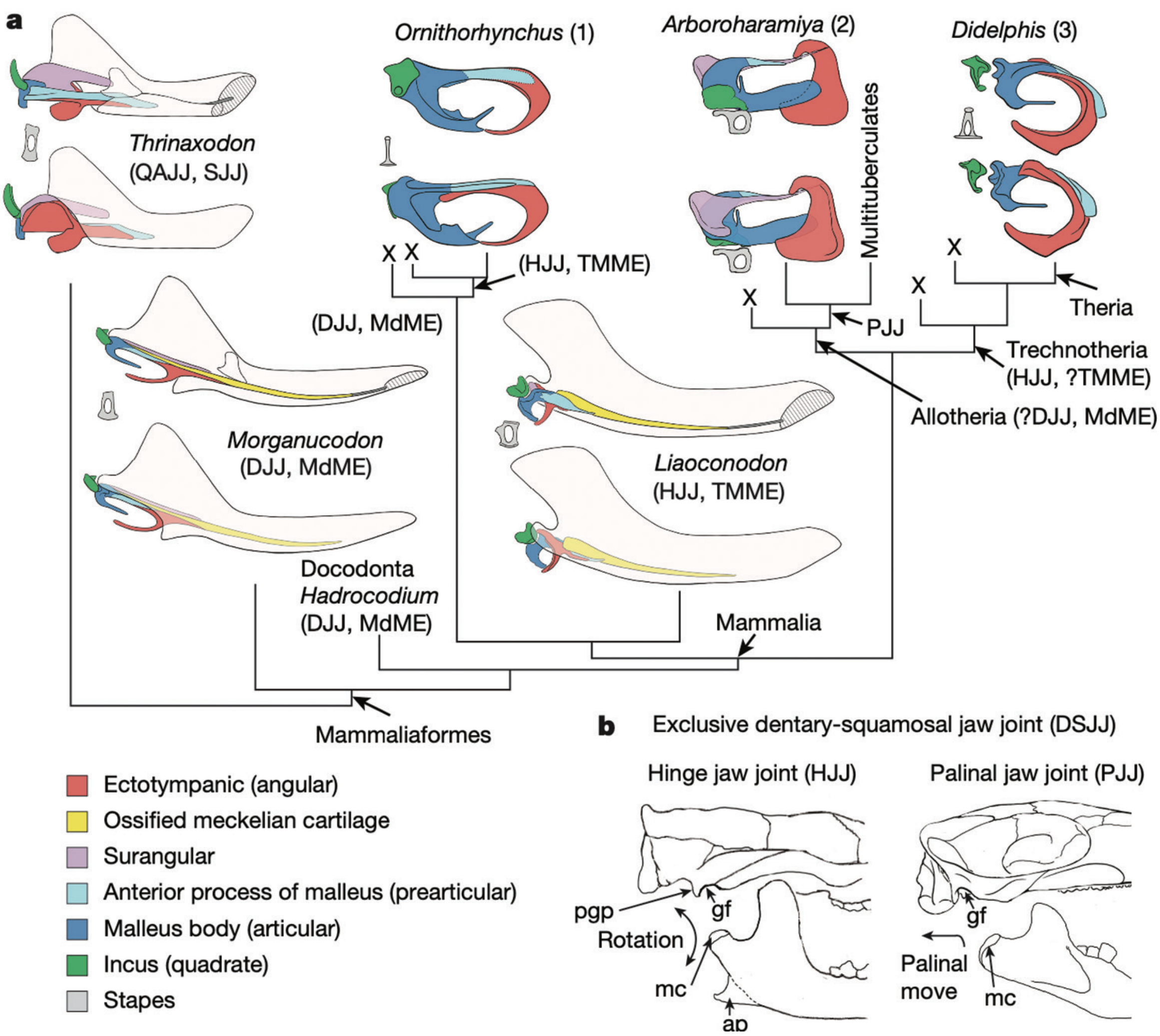


Diagram illustrating evolutionary stages from the condition in non-mammaliaform cynodonts to that in mammals.



Comparison of mammaliaform middle ears and jaw joints.

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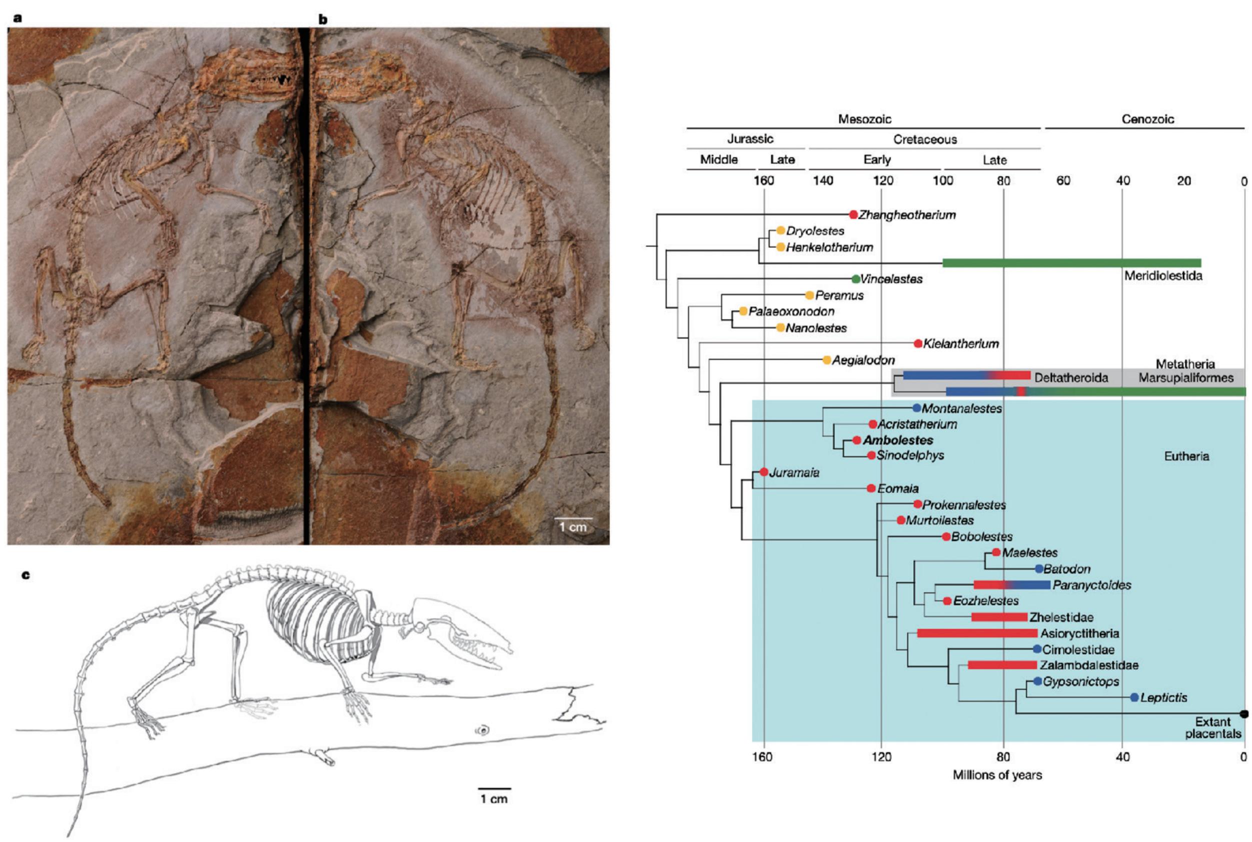
ed a new eobaatarid multituberculate, *Jeholbaatar kielanae* from the Cretaceous of Liaoning. It has complete post-dentary elements that are well-preserved and detached from the dentary bones. *Jeholbaatar kielanae* revealed the transformation of the surangular jaw bone from an independent element into part of the malleus of the middle ear, and presence of a restricted contact between the columelliform stapes and the flat incus. Based on this, the authors proposed a dichotomic evolutionary pattern for the malleus-incus joint in mammaliaforms, with the two bones connecting in either an abutting or an interlocking arrangement, reflecting the evolutionary divergence of the dentary-squamosal joint. The phylogenetic analysis also indicated the acquisition DMME in allotherians, including *Jeholbaatar kielanae* was independent of that in monotremes and therians. It was also suggested that the co-evolution of the primary and secondary jaw joints in allotherians was an evolutionary adaptation allowing feeding with unique palinal (longitudinal and backwards) chewing.

Early Mammalian Evolution Unveiled by Amazingly Preserved Fossils

In addition to the extensive attention received by the middle ear evolution of Mesozoic mammals, some amazingly preserved fossils have revealed other aspects that would change conventional views on the evolution of early mammals.

Molecular estimates of the divergence of placental and marsupial mammals and their broader clades (Eutheria and Metatheria, respectively) fall primarily in the Jurassic period. Supporting these estimates, *Juramaia* – the oldest purported eutherian – is from the early Late Jurassic (160 million years ago) of northeastern China. *Sinodelphys* – the oldest purported metatherian – is from the same geographic area but is 35 million years younger, from the Jehol biota. Bi *et al.* (2018) reported a new Jehol eutherian, *Ambolestes zhoui*, with a nearly complete skeleton that preserves anatomical details that are un-



Holotype specimen of *Ambolestes zhoui* (left) and its relationships to other mammals (right)

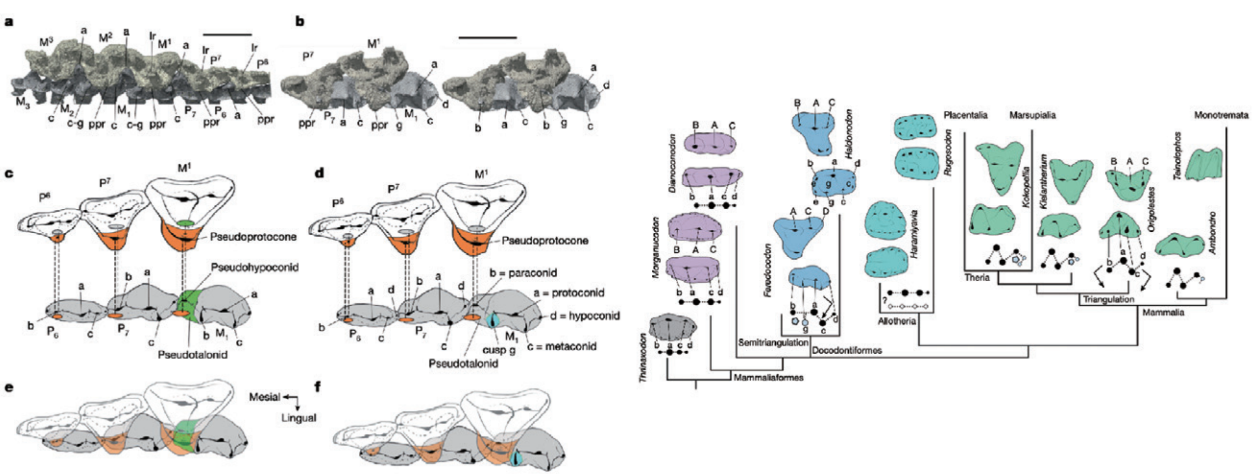
known from contemporaneous mammals, including the ectympanic and hyoid apparatus. The new fossil demonstrates that *Sinodelphys* is a eutherian, and that postcranial differences between *Sinodelphys* and the Jehol eutherian *Eomaia* – previously thought to indicate separate invasions of a scansorial niche by eutherians and metatherians – are instead variations among the early members of the placental lineage. The oldest known metatherians are now not from eastern Asia but are 110 million years old from western North America, which produces a 50-million-year ghost lineage for Metatheria.

Shuotheriids are Jurassic mammaliaforms that possess pseudotribosphenic teeth in which a pseudotalonid is anterior to the trigonid in the lower molar, constrasting with the tribosphenic pattern of therian mammals (placentals, marsupials and kin) in which the talonid is posterior to the trigonid. Mao *et al*. (2024b) reported a new Jurassic shuotheriid, *Feredocodon chowi*, represented by two skeletal specimens from Inner Mongolia. Their complete pseudotribosphenic dentitions allow reidentification of dental structures using serial homology and the tooth occlusal relationship. Contrary to the conventional view, *Feredocodon chowi* shows that dental structures of shuotheriids can be homologized to those of docodontans and partly support homologous statements for some dental structures between docodontans and other mammaliaforms. The phylogenetic analysis based on new evidence removes shuotheriids from the tribosphenic ausktribosphenids (including monotremes) and clusters them with docodotans to form a new clade, Docodontiformes, that is characterized by pseudotribosphenic features.

Early Evolution, Critical Turnover and Extinction Events of Primates in Asia

In paleomammalogy, not only are Mesozoic mammals always under the spotlight, origins, evolution and extinctions of primates are also intriguing topics. Three stories were told by Chinese primate fossils spanning a vast range of geological time from Eocene to Pleistocene. Ni *et al.* (2013) reported a nearly complete and partly articulated skeleton of a primate haplorrhine, *Archicebus achilles*, from the early Eocene of Hubei (ca. 55 million years ago), which is also the oldest fossil primate of this quality ever recovered. Its

Tooth occlusion and competing hypotheses for tooth cusp homology of *Feredocodon* (left) and primiary tooth patterns of mammaliaforms in the phylogenetic frame (right)

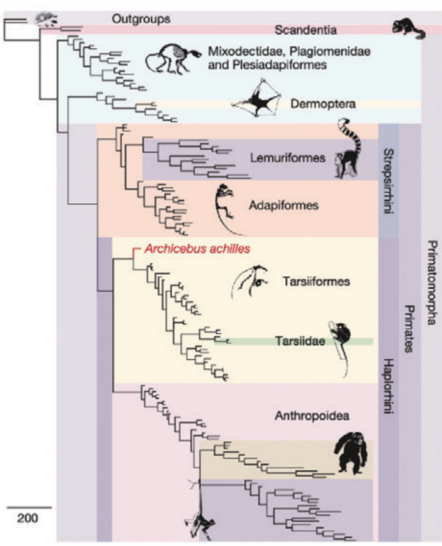


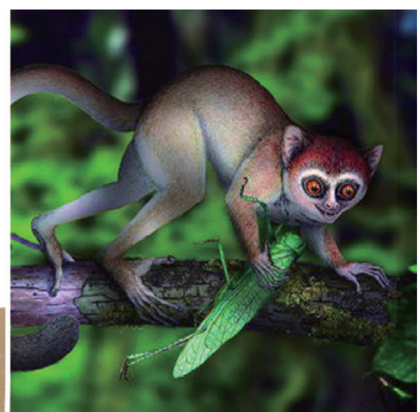
hind legs and nearly all the vertebrae in its long tail are strikingly well-preserved, giving us a clear picture of the animal's lower half. By comparing *Archicebus achilles*'s anatomy with the bodies of all living and fossil primates, as well as closely related mammals, the authors determined that it is most likely a very early ancestor of modern tarsiers, small nocturnal primates that today are found on only a handful of islands in Southeast Asia. Although the existing evidence places the creature just slightly toward the tarsier branch of the primate family tree, *Archicebus achilles* has some strikingly anthropoid-like features. With relatively short toes and a short heel bone, they look almost exactly like the feet of small South American monkeys such as marmosets but almost nothing like modern tarsier feet. What's more, its eye sockets were relatively small, suggesting that it hadn't yet evolved the gigantic eyeballs that allow modern tarsiers to see in the dark. *Archicebus achilles* told us that the common ancestor of tarsiers and anthropoids was a hybrid. It wasn't completely monkey-like, but it certainly wasn't completely tarsier-like, either. It had certain features of both lineages.

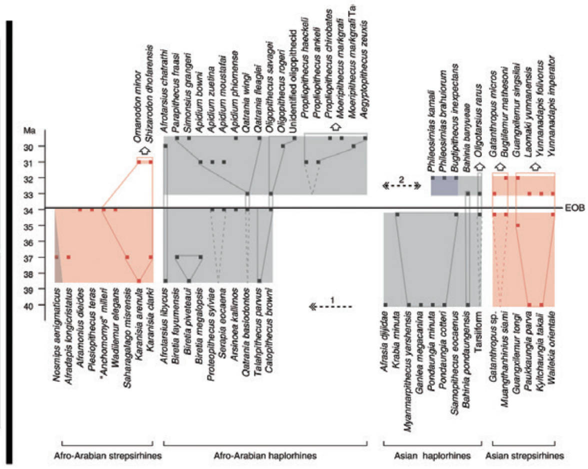
Profound environmental and faunal changes are associated with climatic deterioration during the Eocene-Oligocene transition (EOT) roughly 34 million years ago. Ni *et al.* (2016) reported a diverse primate fauna that weathered the EOT from the early Oligocene of Yunnan. In marked contrast to Afro-Arabian Oligocene primate faunas dominated by anthropoids, this Asian fauna is dominated by strepsirhines. The divergent responses shown by Afro-Arabian and Asian primates across the EOT set the stage for subsequent macroevolutionary patterns within this group. Africa became the geographic nexus of anthropoid evolution, whereas Asia continued to harbor sivaladapid strepsirhines and tarsiid haplorhines.

The largest ever primate and one of the largest of the southeast Asian megafauna, *Gigantopithecus blacki*, persisted in China from about 2.0 million years ago until the late Middle Pleistocene when it became extinct. Its demise is enigmatic considering that it was one of the few Asian great apes to go extinct in the last 2.6 million years, whereas others, including orangutans, survived until the present. The cause of the disappearance of *Gigantopithecus blacki* remains unresolved but could shed light on primate resilience and the fate of megafauna in this region. Zhang *et al.* (2024) applied three multidisciplinary analyses – timing, past environments and

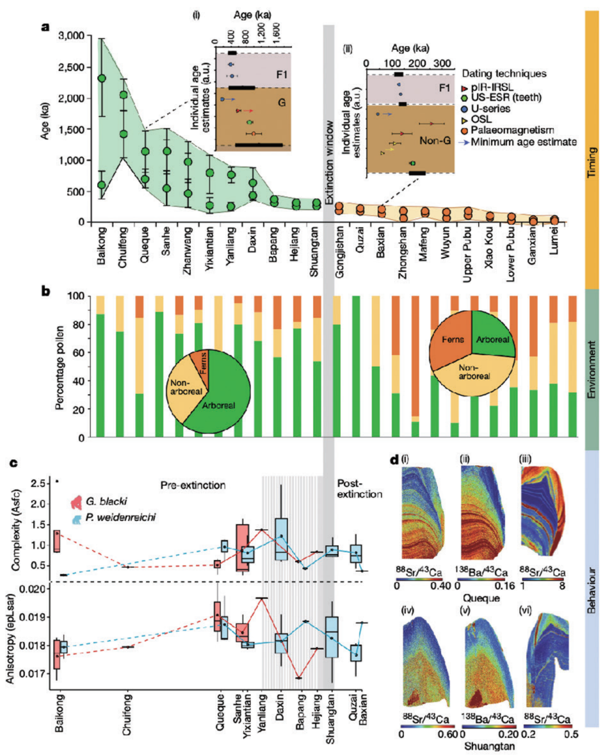
Phylogeny, fossil skeleton and reconstruction of *Archicebus achilles*







Diverse primates from the early Oligocene of Yunnan and Divergent taxonomic composition of fossil primates across the Eocene-Oligocene boundary (EOB) in Afro-Arabia and southern Asia.



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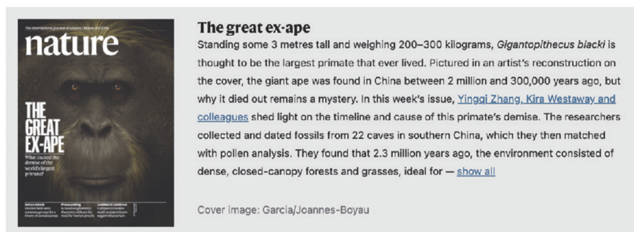
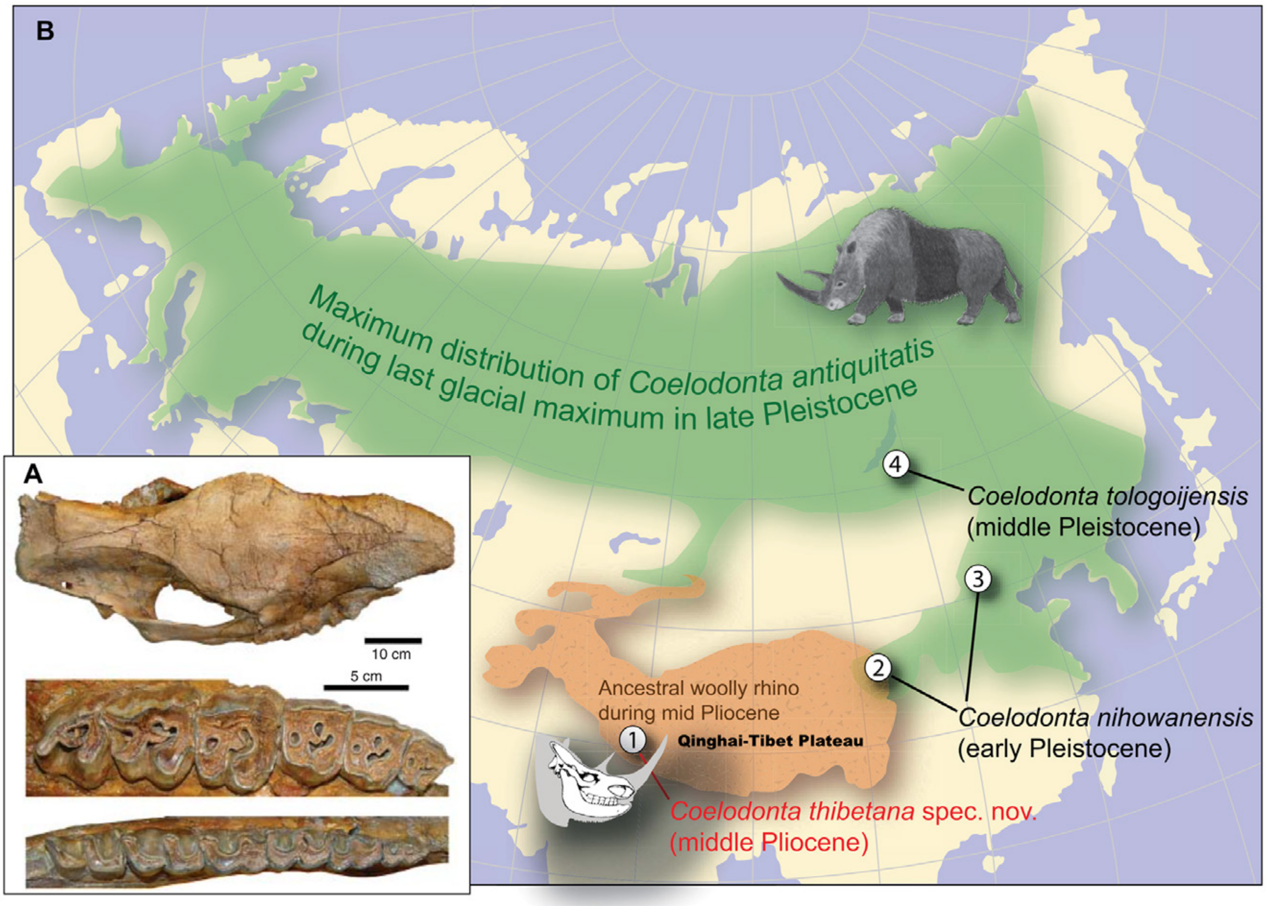


Example datasets to support the extinction event of *Gigantopithecus blacki* and the cover image.



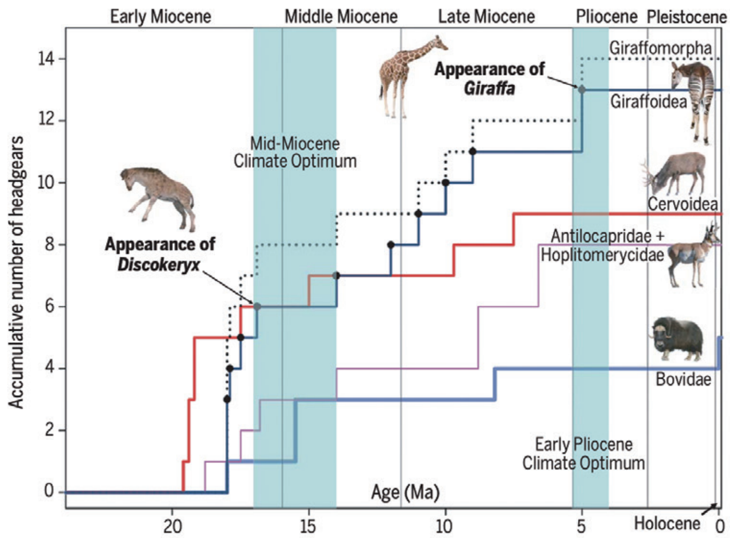
Fossils of *Coelodonta thibetana* (A) and Origin, distribution, and dispersals of woolly rhinos in Eurasia (B)

behavior – to 22 caves in southern China, and used 157 radiometric ages from six dating techniques to establish a timeline for the demise of *Gigantopithecus blacki*. Their results showed that from 2.3 million years ago the environment was a mosaic of forests and grasses, providing ideal conditions for thriving *Gigantopithecus blacki* populations. However, just before and during the extinction window between 295,000 and 215,000 years ago there was enhanced environmental variability from increased seasonality, which caused changes in plant communities and an increase in open forest environments. Although its close relative *Pongo weidenreichi* managed to adapt its dietary preference and behavior to this variability, *Gigantopithecus blacki* showed signs of chronic stress and dwindling populations. Ultimately its struggle to adapt led to the extinction of the greatest primate ever inhabiting the earth.

Intriguing Stories about Late Cenozoic Mammals

Although Late Cenozoic herbivores are less attractive than primates and Mesozoic mammals, there is still outstanding work that has been done to answer scientific questions in similar aspects of Paleomammalogy.

Ice Age megafauna have long been known to be associated with global cooling during the Pleistocene, and their adaptations to cold environments, such as large body size, long hair, and snow-sweeping structures, are best exemplified by woolly mammoths and wooly rhinos. These traits were assumed to have evolved as a response to the ice sheet expansion. Deng *et al.* (2011) reported a new Pliocene mammal assemblage from a high-altitude basin in the western Himalayas, including a primitive wooly rhino, *Coelodonta thibetana*. These fossils, unearthed from the Qinghai-Tibet Plateau, suggest that some megaherbivores, which became preadapted for the Ice



Male combat in the representative giraffoids.

Age, successfully expanding to the Eurasian mammoth steppe.

The long neck of the giraffe has been held as a classic example of adaptive evolution since Darwin's time. Wang *et al.* (2022) reported an unusual fossil giraffoid, *Discokeryx xiezhi*, from the early Miocene of Xinjiang, which has an unusual disk-shaped headgear and the most complicated head-neck joints in known mammals. The distinctive morphology and finite element analyses indicate an adaptation for fierce head-butting behavior. Tooth enamel isotope data suggest that *Discokeryx xiezhi* occupied a niche different from that of other herbivores, comparable to the characteristic high-level browsing niche of modern giraffes. This study shows that giraffoids exhibit a higher headgear diversity than other ruminants and that living in specific ecological niches may have fostered various intraspecific combat behaviors that resulted in extreme head-neck morphologies in different giraffoid lineages.

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