

The impact of Xizang (Tibet) uplift on Cenozoic mammals in eastern Asia: A review of paleontological evidence and interpretations

1. Introduction

The uplift of the Qinghai-Xizang (Tibet) Plateau constitutes one of the most dramatic and significant geological events of the Cenozoic Era. This monumental orogenic process has not only sculpted the distinct high-altitude ecosystems of the plateau itself and its surrounding regions but has also acted as a pivotal force in shaping the climatic and environmental trajectory of the vast Eurasian continent. The cascading effects of this tectonic upheaval — primarily through the intensification and reorganization of atmospheric circulation patterns, notably the Asian monsoon systems, and the creation of formidable topographic barriers — have profoundly influenced the evolutionary pathways, diversification, migration, and extinction of mammalian faunas across eastern Asia (Fig. 1). This special issue synthesizes recent paleontological findings to elucidate the complex and dynamic relationship between the Xizang uplift and mammalian evolution from the Oligocene to the Late Pleistocene. It draws upon specific case studies ranging from the emergence of giant herbivores in the Eocene to the radiation and extinction of Pleistocene megafauna, highlighting the interplay between tectonic forcing, climatic change, and biotic response. The central theme underscores that the plateau's rise was not merely a backdrop but a dynamic engine driving faunal turnover, biogeographic patterning, and ecological specialization throughout the Cenozoic.

2. Tectonic, climatic, and biotic frameworks: The Xizang engine

Before delving into specific faunal examples, it is essential to establish the mechanistic links between the Xizang uplift and mammalian evolution. The provided documents outline a clear chronological and causal chain:

Topographic and climatic reconfiguration: The attainment of substantial elevation by the Miocene established the plateau as a formidable barrier to faunal exchange. This barrier curtailed the exchange of mammals between eastern and southern Asia, effectively partitioning biogeographic realms and fostering endemic evolution in isolated regions (Deng et al., 2021). Concurrently, the rise of the plateau dramatically altered atmospheric dynamics. The initiation and intensification of the Asian monsoon system, a direct consequence of this uplift, became a significant force, strongly influencing both climate and mammalian distributions from the Miocene onwards (Deng and Ding, 2015). This created a stark precipitation gradient, leading to distinct differences in the faunal assemblages observed between northern and southern China during the Miocene.

Timeline of environmental change: The climatic impacts were phased. In Central Asia (including northwestern China), significant aridification began in the Eocene, progressed through the Oligocene, and culminated in major environmental shifts at the Eocene-Oligocene boundary: an event linked to the Mongolian Remodelling (Meng and MacKenna, 1998). Later, during the Pliocene, a strengthened monsoon enhanced humidity in northern China, facilitating the northward migration of southern Chinese faunal elements, best recorded in sites like the Yushe Basin in Shanxi Province (Tedford et al., 2013). Finally, by the Quaternary, a modern-like configuration of mammalian components and their distribution patterns solidified (Qiu, 2006).

The interplay of forces: These processes — barrier formation, aridification of the continental interior, and the creation of monsoonal humid corridors — acted in concert and opposition over time, creating a complex, shifting mosaic of habitats. Mammalian evolution in eastern Asia during the Cenozoic must be viewed through the lens of organisms navigating and adapting to this constantly

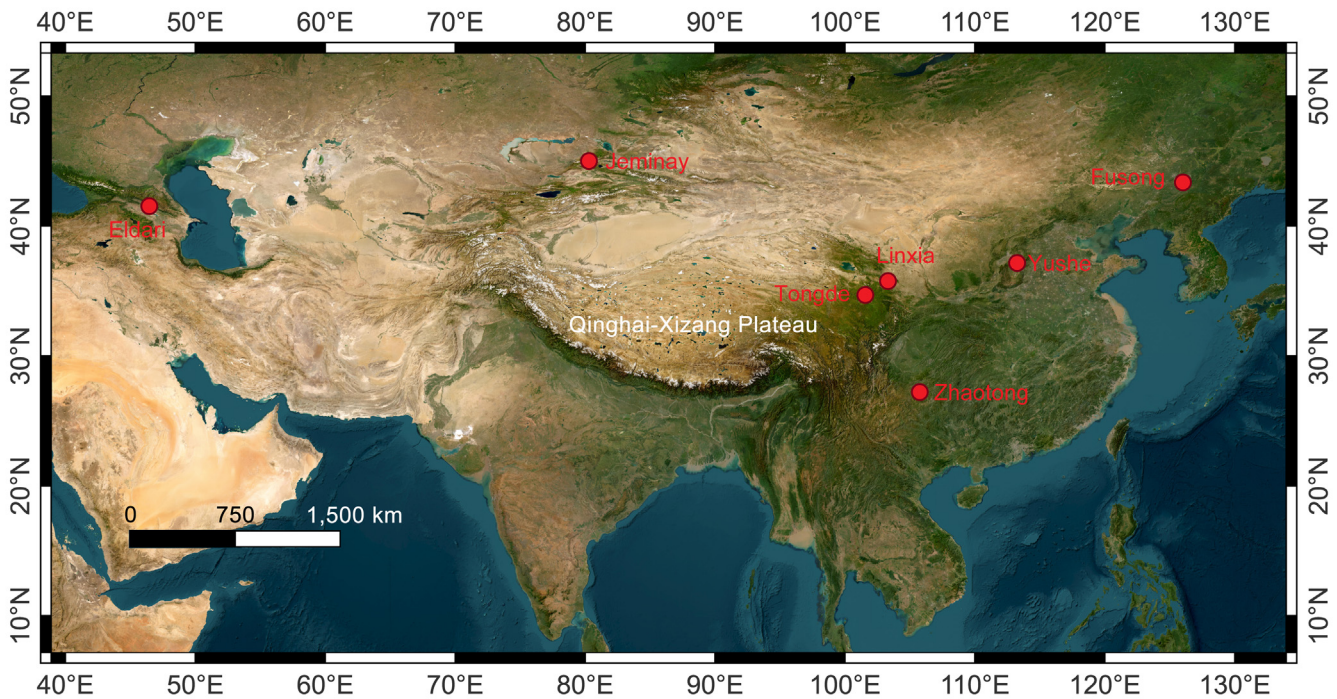


Fig. 1. The location of the Qinghai-Xizang Plateau and the sites of Cenozoic mammal fossils from Eurasia studied in this special issue.

changing environmental stage, set in motion by the rise of Qinghai-Xizang Plateau.

3. Case studies in mammalian response: From Eocene ungulates herbivores to Pleistocene faunas

The impact of these large-scale changes is vividly documented in the fossil record. The following sections examine specific clades and time periods that illustrate key evolutionary and biogeographic responses.

3.1. Eocene: Biogeographic barrier and mammal exchange

The rising Qinghai-Xizang Plateau and associated Himalayan orogeny created formidable north-south biogeographic barriers, while also opening and closing east-west dispersal routes.

Entelodonts, like *Brachyhyops*, were large, bunodont omnivores/predators that thrived in the Late Eocene. Their presence in the aridifying environments of Xinjiang (Jeminyay) and Inner Mongolia, China suggests they were ecological generalists capable of exploiting the changing ecosystems of Central Asia before their eventual extinction. The Bering Land Bridge remained a critical conduit for large mammal exchange. *Brachyhyops*, the oldest member of Entelodontidae, appears in the late Middle Eocene of

both Asia (*B. yunnanensis*) and North America (*B. wyomingensis*), suggesting an earlier Asian origin and rapid dispersal into North America (Yu et al., 2026).

3.2. Oligocene: Faunal remodeling and endemic evolution

The Tala Formation of the Linxia Basin in Gansu Province, China represents the basal Cenozoic strata of the region and provides a critical window into the early stages of post-uplift environments. For a long time, the age of this formation was poorly constrained due to a lack of mammalian fossils. The recent discovery of a fragmentary mandible of the chalicothere *Schizotherium ordosium* provides the first biostratigraphic anchor (Quan et al., 2026). This discovery confirms a late Early Oligocene age (ca. 30–28.5 Ma) for the upper Tala Formation.

The presence of *S. ordosium*, a large, clawed perissodactyl browser, in these strata is significant. Its confirmed age helps calibrate paleomagnetic data from the Linxia Basin sequence. More broadly, this period corresponds with the onset of significant aridification in Central Asia (Qiu and Li, 2005). *Schizotherium*, as part of the wider “*Paraceratherium* fauna” that succeeds the Tala Formation in the overlying Jiaozigou Formation (Deng et al., 2013), represents a component of the Early Oligocene mammalian communities that were beginning to experience the envi-

ronmental consequences of the Xizang uplift and global cooling. The establishment of such endemic Asian faunas, distinct from their European counterparts, marks the beginning of a long-term biogeographic separation influenced by the evolving Qinghai-Xizang region. At the same time, the significant aridification that occurred in Central/Eastern Asia led to the dispersal of faunal elements of the *Paraceratherium* fauna westward to the Balkans (Spassov, 1989; Spassov and Popov, 2007).

3.3. Miocene: Isolation and diversification

The Late Miocene (11.6–5.3 Ma) was a period of major faunal turnover globally, closely tied to climatic cooling and increased aridity. In Asia, the role of the Xizang topography and the monsoon in modulating these changes is paramount, as evidenced by research on bovids and carnivores.

The discovery of *Pachyportax zhaotongensis* n. sp. from the Shuitangba locality (~6.2 Ma) in Yunnan Province, China offers a compelling narrative of isolation and adaptation in the southern refugia (Guo et al., 2026). *Pachyportax*, a small-sized bovine, originated in the Late Miocene Siwaliks (southern Asia) and subsequently dispersed to Southeast Asia and the Arabian Peninsula. Its arrival in Yunnan represents a key biogeographic event.

The combined effects of the Xizang uplift and the East Asian monsoon maintained a humid, forested climate in regions like the Zhaotong Basin in southern China, even as much of Eurasia and Africa underwent late Cenozoic aridification. This area became a refuge for animals in the Late Miocene, hosting a highly diverse fauna adapted to warm, humid conditions, including the hominoid *Lufengpithecus*.

Stable isotope analysis ($\delta^{13}\text{C}$) of *P. zhaotongensis* enamel reveals it was an obligate C_3 feeder (consuming plants like trees and shrubs from closed-canopy forests), unlike its relatives (*Selenoportax* and *Pachyportax* from the Siwaliks and Arabia) which showed transitions to or reliance on C_4 grasses (open habitat plants). This indicates that the Zhaotong environment provided abundant forest food sources, allowing this lineage to survive as a specialized browser to a very late age, isolated from the dietary shifts of its relatives elsewhere.

A sea-level drop at ~11 Ma facilitated the dispersal of Siwalik faunas, including bovids like *Selenoportax* and *Pachyportax*, into Southeast Asia and southern China. Thus, while the Qinghai-Xizang Plateau acted as a barrier to north-south exchange, the southeastern corridor allowed faunal movement, with southern China becoming a terminus and refuge for these lineages.

The redescription of hyaenid remains from the Late Miocene (Vallesian, MN 10) site of Eldari, Azerbaijan, as *Dinocrocota gigantea* expands the known range of this giant, hypercarnivorous hyena (Khantemirov et al., 2026). *D. gigantea*, previously well-known from China

and scattered European localities, is now confirmed in the Caucasus.

This discovery highlights the Caucasus as a crucial region situated among potential migration routes for large mammals between Asia, Europe, and Africa during the Late Miocene. The “explosive” radiation of *Dinocrocota* during the early Vallesian is noted to coincide with the spread of *Hipparion* across Eurasia, marking a major faunal turnover event often linked to environmental changes.

The presence of *D. gigantea*, an active hunter akin to the extant spotted hyena (*Crocota crocuta*), in diverse environments from China to Azerbaijan speaks to the wide adaptability of some mammalian carnivores during this dynamic period. It also underscores that while regional endemism was increasing for some groups (like bovids in southern refugia), other large, mobile predators maintained vast distributions, their movements potentially facilitated by shifting biome boundaries driven by the evolving Xizang-induced climate patterns.

3.4. Pliocene: Modernization and dispersal

The description of a new cranium of “*Gazella*” *nihensis* from the Pliocene of the Qinghai-Xizang Plateau offers insights into the complex evolution of antelopes (Antilopina) in Asia (Wang et al., 2025). The taxonomic history of fossil “*Gazella*” in Eurasia is extremely complex, with many species now likely belonging to distinct lineages.

The Tongde specimen of “*G.*” *nihensis* exhibits a combination of specialized features: an elongated braincase, occipital condyles protruding caudally beyond the paroccipital process, a weakly curved cranio-facial axis, and strongly caudally inclined horn cores. This morphology is distinct from most Antilopina but shares certain traits with living taxa: the elongated, less-bent braincase resembles the gerenuk (*Litocranius walleri*), while the strongly backward-inclined horns resemble those of the dibatag (*Ammodorcas clarkei*) and springbok (*Antidorcas marsupialis*).

Critically, it is tested the hypothesis that “*G.*” *nihensis* is related to the living Xizang antelope (*Pantholops hodgsonii*) and gazelles of the genus *Procapra* (Xizang gazelle, Przewalski’s gazelle, and Mongolian gazelle). The cladistic analysis suggests “*G.*” *nihensis* might indeed be closer to the *Procapra* clade than to the true *Gazella* (e.g., *G. subgutturosa*) clade. This supports the view that the differentiation between the *Gazella* and *Procapra* lineages was already underway in the Pliocene, likely driven by adaptations to the increasingly arid and high-altitude environments on and around the rising Qinghai-Xizang Plateau. The evolution of *Procapra*, a genus endemic to the high steppes and deserts of Central and East Asia, can thus be seen as a direct evolutionary response to the new habitats created by Xizang uplift.

While the Eurasian lineage *Mammut borsoni* and the North American *M. americanum* were long considered separate, phylogenetic analysis suggests a close relationship

between North American forms and the Eurasian *M. shansiense* from the Pliocene of the Yushe Basin in Shanxi Province, China (Zhang et al., 2026). This supports hypotheses of multiple dispersal waves of Mammutidae from Eurasia to North America, though recent ancient DNA data revealing deep Pliocene splits within North American mastodons indicates a more complex history than morphology alone can reveal. *M. shansiense* displays the classic “Λ-shaped” loph(id)s and open interloph(id)s typical of later mammutids, adapted for shearing tough vegetation. Its morphology is more derived than *M. borsoni* and aligns closely with *M. americanum*, suggesting convergent or related adaptations to similar open or mosaic habitats.

3.5. Pleistocene: Adaptation and extinction

The Villafranchian stage in the mammal fauna evolution in Eurasia (between ca. 3.6/3.4 Ma and ca. 1.2 Ma) is associated with the beginning of the formation of the modern appearance of the mammalian fauna of today’s Paleoafrican. This is a time of particularly intense dispersal of species from Central Asia to Western Eurasia (Spassov, 2024). At the same time, the fauna south of the Qinghai-Xizang Plateau (the region of the Indian subcontinent and Southeast Asia) continues, for climatic reasons, to become increasingly isolated from the fauna of Central Asia and Western Eurasia.

Conversely, the altered climate and newly formed habitats in Central and Eastern Asia facilitated dispersal events. The opening of arid corridors in Central Asia, driven by plateau-induced rain shadows, likely enabled the spread of open-habitat specialists. The dispersal history of the bovid genus *Soergelia* illustrates complex patterns. Originating from a *Kabulicornis*-like form in Central or East Asia during the Late Pliocene, *Soergelia* species show dispersals linked to environmental change. *S. longdanensis* n. sp., the earliest definitive species (2.595–2.137 Ma) from the Longdan locality of the Linxia Basin, dispersed northward into Siberia, evolving into *S. elisabethae*. This species later dispersed westward into Europe and eastward into North America around 0.8 Ma, giving rise to *S. mayfieldi* (Bai and Wang, 2026).

This pattern suggests northward and intercontinental dispersals were facilitated by the development of steppe/tundra-steppe environments during the Pleistocene, potentially linked to increased glaciation (Middle Pleistocene Transition). *Soergelia*, a Pleistocene caprine, exhibits morphological variations suggesting dietary niche partitioning: *S. minor* in Europe was a browser in woodland/forest-steppe, while *S. longdanensis* in the arid, cold grassland environment of the Linxia Basin was likely a grazer.

The specialized pliohyracid *Postschizotherium*, found in the Early Pleistocene of the Linxia Basin, exhibits high, unilaterally hypsodont (curved) teeth with cementum, adaptations suggestive of a gritty, grassy diet (Xing et al., 2026). Its cranium, with high, laterally projecting orbits

and an enlarged maxillary sinus, is interpreted as an adaptation for a semi-aquatic, hippo-like lifestyle in riverine environments within a drying landscape.

Environmental pressures also drove changes in body size and cranial morphology. *Postschizotherium* represents a gigantism trend within hyracoids, evolving large body size possibly as an adaptation for competing in new herbivore guilds or for thermoregulation in cooler climates. Its unique cranial features (extreme lateral orbit projection and complex pre-orbital fossa) are convergently seen in other semi-aquatic mammals like oreodonts and hippos, indicating niche specialization in response to landscape changes.

The Early Pleistocene (~2.6–2.0 Ma) Longdan locality reveals a mosaic environment. While traditionally thought to represent open, arid conditions, the presence of *Postschizotherium*, *Ursus*, *Prionailurus*, and *Manis* indicates pockets of relatively humid, forested habitats persisted alongside grasslands. This mosaic is attributed to the complex effects of the Xizang uplift, which simultaneously intensified aridity in the basin’s interior while possibly enhancing orographic precipitation on its margins. The fauna shows mixed signals: *Soergelia longdanensis* was a grazer adapted to dry, cold grassland, while other taxa indicate woodland/forest refugia.

The mammalian assemblage from the Fusong Xianren Cave in Jilin, northeast China (~80–49.9 ka), provides a snapshot of a typical Late Pleistocene “Mammoth Steppe” fauna on the eastern edge of Eurasia (Liu et al., 2026). This fauna includes *Ursus arctos* (brown bear), *Crocota ultima* (the last Eurasian giant hyena), *Panthera tigris* (tiger), *Equus caballus* (horse), *Stephanorhinus kirchbergensis* (Merck’s rhinoceros), *Sus scrofa* (wild boar), *Cervus elaphus* (red deer), and *C. grayi* (Gray’s deer, a form of sika deer).

The species composition, dominated by forest-adapted browsers like *S. kirchbergensis* and *C. grayi* but also including open-ground grazers/mixed feeders like *Equus* and the likely open-ground scavenger/hunter *C. ultima*, suggests a mosaic environment. This is interpreted as “extensive, patchy forests” with shrublands and grasslands at the edges, under a generally temperate but fluctuating climate. This habitat mosaic is consistent with the complex, seasonally variable environments shaped by the East Asian monsoon, whose intensity and reach were themselves influenced by the Xizang topography.

The presence of trampling and weak weathering marks on bones indicates the fossils were exposed on the surface briefly and trampled (possibly by humans or other large mammals) before deposition in the cave. While not directly demonstrating hunting, it places these mammals in a landscape frequented by humans and other large fauna. The site adds to the record of the *Mammuthus-Coelodonta* fauna, which eventually succumbed to a combination of climatic upheavals during the Pleistocene-Holocene transition and potential human pressure. The uplift of Qinghai-Xizang Plateau, by creating the severe climatic oscillations of the

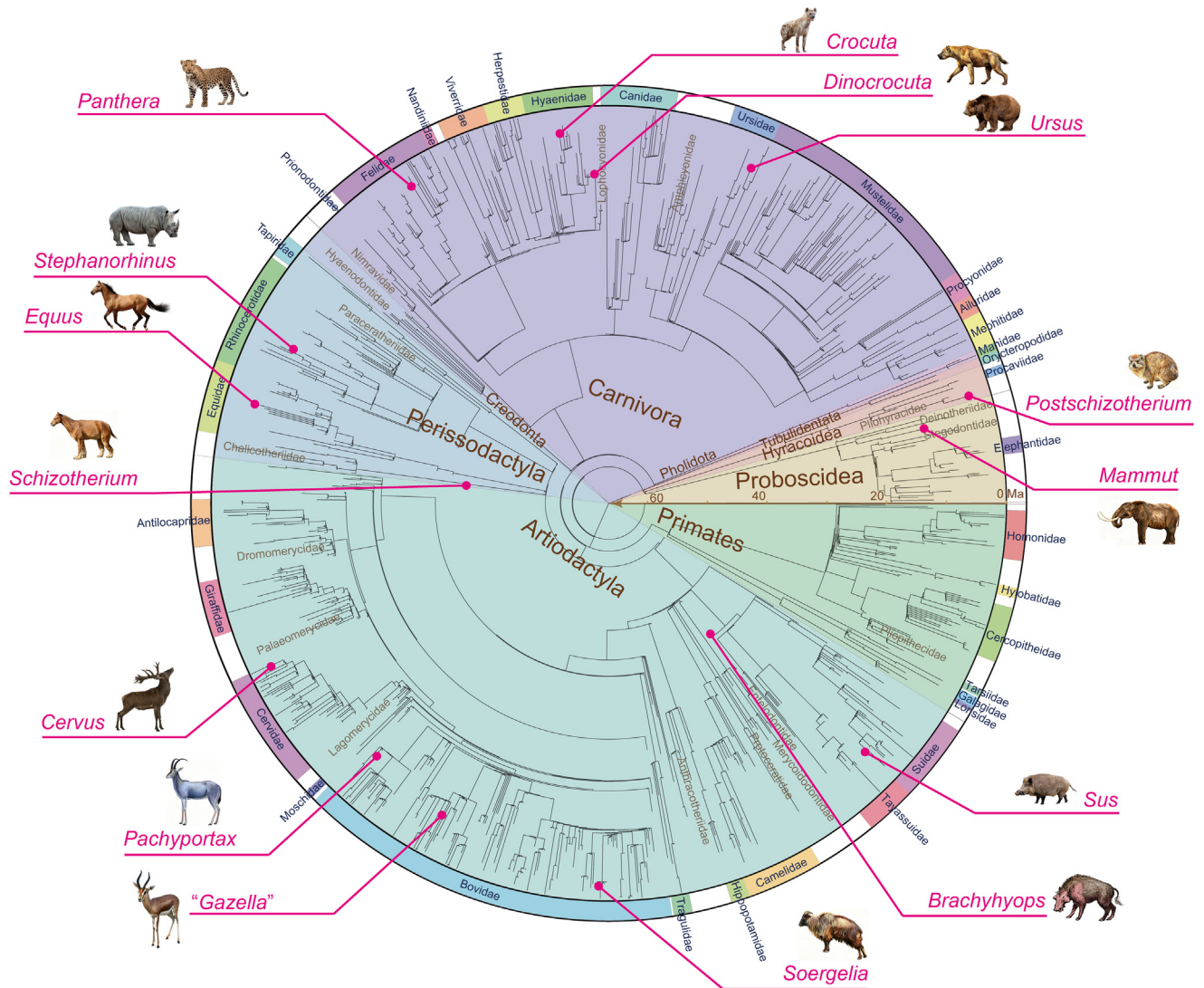


Fig. 2. The positions of various mammalian fossils on the phylogenetic tree and the Cenozoic geological time scale.

Quaternary ice ages, set the stage for these final acts of megafaunal evolution and extinction.

4. Synthesis and key themes

Integrating the evidence from these disparate studies (Fig. 2), several overarching themes emerge regarding the impact of Xizang uplift on Cenozoic mammals in eastern Asia:

Dual role as barrier and corridor: The Qinghai-Xizang Plateau primarily acted as a major topographic barrier, segregating the Palearctic (northern) and Oriental (southern) zoogeographic realms from the Late Miocene onward. This is explicitly stated in the review and supported by the distinct faunas north and south of the plateau. However, it also created conditions for new dispersal routes, such as the

Southeast Asian pathway used by *Pachyportax* and others, facilitated by sea-level changes and monsoonal climates.

Driver of endemism and refugia: The creation of unique high-altitude habitats and the maintenance of humid forest refugia in the southeastern foothills (like Yunnan) directly promoted endemic evolution. Lineages like *Pachyportax zhaotongensis* and the ancestors of *Procapra* evolved distinct adaptations (e.g., persistent C₃ browsing, specialized cranial morphology) in these isolated or novel environments. The differentiation of the *Procapra* lineage from other antilopines is a prime example of *in-situ* evolution on the plateau's margins.

Climate modulator and faunal turnover catalyst: The uplift's most pervasive influence was through climate. The onset of Central Asian aridification (leading to Mongolian Remodelling and giant rhino evolution in the Oligo-

cene), the intensification of the Asian monsoon (driving Pliocene northward migrations and supporting humid refugia), and the amplification of Quaternary glacial-interglacial cycles all trace back to the Xizang tectonics. Each climatic shift precipitated faunal turnover, extinction of less-adapted forms, and radiation of new, adapted ones (e.g., the Vallesian turnover with *Dinocrocuta* and *Hipparion*, the Quaternary *Mammuthus-Coelodonta* fauna).

The impact was not a single event but a protracted, staged process: in the Eocene and Oligocene, initial aridification begins, shaping early faunas; in the Miocene, the Qinghai-Xizang Plateau reaches significant elevation, becoming a barrier; monsoon system initiates, creating strong N-S faunal provincialism, and southern refugia become important; in the Pliocene, monsoon intensifies, facilitating latitudinal range shifts, and modern groups differentiate; in the Pleistocene, modern biogeographic patterns solidify, and strong glacial-interglacial oscillations impact steppe and forest faunas, culminating in megafaunal extinctions.

Understanding this impact requires synthesizing data from disparate fields: precise geochronology (paleomagnetism, isotopic dating), stable isotope ecology (dietary reconstruction), functional morphology (cranial and dental adaptations), and detailed taxonomic/systematic work to unravel phylogenetic relationships. The studies reviewed here exemplify this integrative approach.

5. Conclusion

The uplift of the Qinghai-Xizang Plateau stands as the dominant geological narrative of Cenozoic Asian environmental history. Its fingerprints are indelibly stamped on the evolutionary history of the region's mammals. From the Eocene entelodonts of the nascent basin sediments to the Pleistocene megafauna of the eastern forests and steppes, mammalian evolution has been a story of adaptation to a world physically and climatically transformed by this colossal geological event. The fossil record reveals a dynamic interplay: the plateau acted as a diversifying force, fostering endemism in its shadow; as a climatic pump, driving aridification and monsoon that selected for new adaptations; and as a biogeographic switchboard, alternately isolating and connecting populations. The case studies all tell different chapters of the same overarching story. As paleontological exploration and analytical techniques continue to advance, our understanding of this profound tectonic-biotic relationship will further deepen, illuminating how the Earth's most spectacular plateau shaped the destiny of its mammalian inhabitants.

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