Tibetan Plateau: From a Tropical Haven for Flora and Fauna to a Cradle of Ice Age Fauna Postprint

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Abstract

New genera and species of climbing perches and barbs discovered in the Oligocene strata of northern Tibet, China, have their extant close relatives living in tropical regions of Asia and Africa. This is not only of great significance for fish phylogeny and zoogeography, but also indicates that the interior of the Tibetan Plateau was still a warm and humid lowland 26 Ma ago. Associated plant fossils such as palms and calamus also indicate the same environment, suggesting that warm and humid air currents from the Indian Ocean could penetrate at least into northern Tibet at that time. Since then, the geographical features and natural environment of the plateau interior have undergone tremendous changes. The Tibetan Plateau continued to uplift during the Miocene, reaching its modern height by the Pliocene and forming a cryospheric environment. Ancestor types of woolly rhinoceros, snow leopard, arctic fox, and argali discovered in the Pliocene deposits of the Zanda Basin show that Quaternary glacial fauna adapted to cold environments originated on the Tibetan Plateau, thus proposing and further refining the "Out of Tibet" theory for the origin and dispersal of cold-adapted animals.

Full Text

Preamble

Topic: Progress of Comprehensive Scientific Research on the Tibetan Plateau

New genera and species of climbing perch and cyprinine fish have been discovered in the Oligocene strata of northern Tibet, whose extant close relatives all inhabit tropical regions of Asia and Africa. These findings are significant not only for fish phylogeny and zoogeography but also indicate that the hinterland of the Tibetan Plateau was a warm and humid lowland approximately 26 million years ago, as evidenced by associated plant fossils such as palms and golden rain trees. This suggests that warm and humid air currents from the Indian Ocean could penetrate at least as far as northern Tibet during that time. Since then, the geographical features and natural environment of the Tibetan Plateau interior have undergone tremendous changes. The plateau experienced continuous uplift throughout the Miocene, reaching its modern elevation by the Pliocene and forming a cryosphere environment. Ancestors of the woolly rhinoceros, snow leopard, arctic fox, and argali sheep discovered in the Pliocene deposits of the Zanda Basin demonstrate that the Quaternary Ice Age fauna adapted to frigid environments originated on the Tibetan Plateau, leading to the proposal and further refinement of the "Out of Tibet" theory for the origin and dispersal of cold-adapted mammals.

Keywords: Tibetan Plateau, paleo-elevation, tropical, Ice Age, fauna

Introduction

During the Triassic period over 200 million years ago, the region now occupied by the Tibetan Plateau was a vast ocean. Marine limestone of Triassic age is distributed throughout the Himalayas, where paleontologists discovered fossils of *Himalayasaurus tibetensis* [1] and *Sinohelicoprion qomolangma* [2] during the first comprehensive scientific expedition to the Tibetan Plateau in the 1970s. By the Jurassic-Cretaceous period, parts of southeastern Tibet had gradually emerged from the marine environment, forming freshwater lakes in the Qamdo Basin similar to those in the Sichuan Basin at that time. Dinosaurs and other animals lived along the lake shores, such as *Monkangosaurus lawulacus* and *Datousaurus* sp. found in Markam [3].

After the breakup of Pangaea in the Mesozoic, the Indian plate drifted northward at a relatively rapid rate and eventually collided with the Eurasian continent in the early Cenozoic, representing the most important mountain-building event in Earth' s history over the past 500 million years and marking the beginning of Tibetan Plateau formation. The uplift process was not uniform or a single sudden event but occurred in different stages [4]. Each uplift episode transformed the plateau' s topography, while organisms, being extremely sensitive to climatic and environmental changes, recorded these profound impacts in their succession. Recent investigations and research on the Tibetan Plateau have yielded a series of important discoveries that clearly depict the plateau' s uplift process and its effects from the perspective of biological evolution.

Paradise of Tropical Fauna and Flora

The initial evidence comes from the Nima Basin on the northern Tibetan Plateau. In 2010, we discovered abundant fish fossils in the gray siltstone and mudstone deposits on its southern margin, establishing a new genus and species of cyprinine fish, *Tchunglinius tchangii* [5]. Based on 40Ar/39Ar dating of this stratigraphic section yielding ages of 23.5-26 Ma [6], *Tchunglinius tchangii* is inferred to have lived during the Late Oligocene. Cyprinine fish are distributed across Asia, southern Europe, and Africa in the Eastern Hemisphere. Species living in low-altitude warm regions have fewer vertebrae—modern Asian tropical taxa have only about 30—whereas those inhabiting cold, high-altitude regions have more vertebrae, with modern Tibetan Plateau endemic schizothoracine fish having nearly 50. *Tchunglinius tchangii* possesses 33 vertebrae, far fewer than modern schizothoracines but similar to tropical Asian cyprinines, indicating it inhabited low-altitude, warm regions. This suggests that the Nima Basin area remained in a low-elevation, warm environment during the Late Oligocene.

Further investigations in the Nima Basin and the Lunpola Basin to its east revealed even richer and more diverse fossils. Among these, climbing perch and associated plants indicating warm, lowland environments provide powerful evidence for reconstructing the plateau' s uplift history. Climbing perch belong to the family Anabantidae within the suborder Anabantoidei. Their modern distribution is primarily in tropical South and Southeast Asia and central-western Africa, mostly below 500 m elevation and never exceeding 1,200 m, with temperatures between 18-30°C. They inhabit shallow, quiet, oxygen-poor waters at lake-river margins or swampy pools, where dissolved oxygen can be as low as 1 mg/L, whereas most fish require over 4 mg/L for normal life activities.

The unique feature of climbing perch is the labyrinth organ in their gill chambers, a specialized structure derived from gill bones with a flower-like morphology. This organ enables direct air breathing, as its surface is covered with respiratory epithelium rich in capillaries, with blood returning to the heart via veins unlike normal gills. Due to the labyrinth organ' s complex structure occupying substantial space in the gill chamber, the aquatic respiratory gills are significantly reduced, preventing adequate oxygen uptake for survival. Consequently, climbing perch must frequently extend their heads above water to breathe air, even crawling onto land after rains.

The climbing perch fossil discovered in northern Tibet represents the earliest and most primitive fossil record of the family, named as a new genus and species, *Eoanabas thibetana* [7], pushing the family's fossil record back by approximately 20 million years. Scanning electron microscopy of *Eoanabas* specimens reveals the labyrinth organ, with perforations on the bone plates indicating a development level closest to modern Asian climbing perch with the strongest air-breathing capacity. These findings demonstrate that *Eoanabas thibetana* possessed physiological characteristics and ecological habits similar to modern climbing perch, indicating a warm and humid environment with likely restricted water bodies (Fig. 1 [Figure 1: see original paper]).

However, the fossil locality today sits at nearly 5,000 m elevation with intense UV radiation, water temperatures averaging approximately -1.0°C annually, and high flow rates with elevated dissolved oxygen—markedly different from the environment 26 million years ago when climbing perch lived there. This demonstrates that the geographical features and natural environment of the Tibetan Plateau interior have undergone tremendous changes since the time of *Eoanabas thibetana*.

The associated plant community from the same strata includes palms and calamus with typically large leaves favoring warm, humid conditions, as well as aquatic arum plants closely related to duckweed, further supporting the inference of a low-altitude, warm environment. These fossils prove that the paleoelevation of the growth locality did not exceed 2,000 m, with some insects from the same horizon indicating similar paleoaltitudes. This Late Oligocene biota in northern Tibet indirectly demonstrates that warm and humid air currents from the Indian Ocean could penetrate deep into northern Tibet, meaning the massive east-west mountain ranges along the southern margin of the modern Tibetan Plateau had not yet uplifted to their present height and thus could not block southern moisture flow.

The Gradual Uplift History of the Tibetan Plateau

Entering the Miocene, the Tibetan Plateau experienced continuous uplift. Tropical fish represented by *Tchunglinius* and *Eoanabas* disappeared from northern Tibet, replaced by modern Tibetan endemic schizothoracine fish. Schizothoracines are classified into three grades based on different characteristics and distribution altitudes: primitive grade with three rows of pharyngeal teeth on each inferior pharyngeal bone, generally distributed between 1,250–2,500 m; specialized grade with two rows of pharyngeal teeth, distributed between approximately 2,500–3,750 m; and highly specialized grade with two rows or even a single row of pharyngeal teeth, distributed between approximately 3,750–4,750 m [8].

The *Plesioschizothorax macrocephalus* discovered in the Early Miocene Dinqing Formation of the Lunpola Basin at its present altitude of 4,540–4,550 m belongs to the primitive grade with three rows of pharyngeal teeth, indicating that the paleoelevation at that time did not exceed 3,000 m [9]. In the Lunpola Basin at 4,624 m elevation, rhinoceros fossils were also found in the Early Miocene Dinqing Formation, specifically a distal humerus nearly identical to *Plesiaceratherium gracile* from the Late Early Miocene Shanwang fauna in Linqu, Shandong. The Shanwang mammalian fauna primarily comprises forest-margin and swamp-dwelling types, especially primitive deer, cupped deer, and diverse squirrels, with grassland types being scarce, indicating a subtropical or warm temperate forest environment. The Shanwang flora contains many subtropical evergreen or deciduous broadleaf plants, reflecting a warm and humid climate. The sporopollen assemblage characteristics of the Dinqing Formation are similar to those of the Shanwang Group, reflecting a warm and humid temperate climate, with the Lunpola *Plesiaceratherium* inhabiting an evergreen broadleaf forest zone. In the global climatic context, *Plesiaceratherium* lived between the Mi-1b cooling event at 17.8 Ma and the Mi-2 event at 16 Ma, though temperatures remained higher than today, with oxygen isotope calculations indicating temperatures approximately 4°C higher than modern values [10].

Plant vertical zonation is directly related to temperature. Based on the 4°C higher temperatures of the Early Miocene compared to present, a 670 m elevation difference is generated by the temperature lapse rate. After correction, the living environment of *Plesiaceratherium* in the Lunpola Basin is estimated to have been near 3,000 m elevation [11].

Broadleaf plant fossils, including *Berberis*, were discovered in the Miocene Wudaoliang Formation lacustrine marl of the Hoh Xil Basin, with the fossil locality at 4,600 m modern elevation. The Wudaoliang *Berberis* fossil resembles modern *B. asiatica*, whose vertical distribution is limited to 914–2,286 m elevation. Based on carbon and oxygen isotope paleoclimatic cycle records from the Wudaoliang Formation lacustrine deposits, correlation with deep-sea oxygen isotope curves via climatostratigraphic methods yields ages within 24.1–14.5 Ma, with the *Berberis* fossil corresponding to approximately 17 Ma. Since fossils and their extant closest relatives likely occupy similar or identical niches, the paleoelevation of the Wudaoliang *Berberis* fossil locality, after correction for Miocene global temperatures, should be at 1,395–2,931 m, indicating that the Hoh Xil Basin and northern Tibetan Plateau did not exceed 3,000 m elevation by the end of the Early Miocene [12].

The modern elevation of the Gyirong Basin in the Himalayan region is 4,384 m, with its Hipparion fauna dated to the Late Late Miocene at 7 Ma by paleomagnetic analysis [13]. The ecological characteristics of the Gyirong Hipparion fauna show roughly equal proportions of forest and grassland animals, diverging from the Siwalik Hipparion fauna of South Asia, indicating that the Himalayas had become a significant barrier to faunal migration by this time. Stable carbon isotope analysis of Gyirong Basin Hipparion fossil enamel yields 13C values of -2.4‰ to -8.0‰, averaging -6.0‰±1.1‰, indicating a mixed C3 and C4 diet with 30%–70% C4 plants in their food, showing an open forest ecosystem. C4 plants have advantages over C3 plants under conditions of higher temperature, better light, and sufficient moisture, but are scarce or absent in high-latitude regions, areas above 3,000 m elevation, and regions with winter precipitation [14]. After paleotemperature correction, carbon isotope data suggest the Gyirong Basin elevation was most likely 2,400–2,900 m at approximately 7 Ma in the Late Miocene [15].

In the Pliocene strata of the Zanda Basin in Ngari region, *Hipparion zandaense* skeleton fossils were discovered. Reconstructed locomotor function shows rapid running capability and prolonged standing time, advantages only in open terrain. The Himalayas had formed and created vertical vegetation zonation since at least the Miocene, with open grassland existing only above the timberline in this vertical spectrum. The modern timberline in the Zanda region is at 3,600 m elevation, while during the Mid-Pliocene warm period 4.6 Ma ago when *Hipparion zandaense* lived, global temperatures were about 2.5°C higher than today [16]. According to the temperature lapse rate, the timberline in Zanda during that period should have been at 4,000 m elevation. The *Hipparion zandaense* skeleton was found near 4,000 m elevation, indicating that the Zanda Basin had already reached its current elevation by at least the Mid-Pliocene [17] (Fig. 2 [Figure 2: see original paper]).

Highly specialized schizothoracine fish fossils with only one row of pharyngeal teeth were also found in the Pliocene strata of the Zanda Basin in southern Tibet, while *Gymnocypris* from the Pliocene of the Kunlun Pass Basin in northern Tibet also belongs to the highly specialized grade. The modern elevations of these two localities are 3,900–4,400 m and 4,769 m respectively. In other words, highly specialized schizothoracine fish existed in both basins during the Pliocene, demonstrating from both southern and northern sides that the Tibetan Plateau had approached its modern elevation by that time [10].

Cradle of Ice Age Fauna

After reaching modern elevation in the Pliocene, the Tibetan Plateau' s climate and environment acquired cryosphere characteristics, inevitably causing corresponding changes in biota. The Quaternary Ice Age fauna has long been recognized as closely related to global cooling events of the Pleistocene. Their large body size and long hair represent adaptations to cold environments, particularly body structures capable of sweeping snow, with mammoths and woolly rhinoceroses being most representative. These fascinating extinct animals have received widespread attention, with their characteristics once assumed to have evolved with the expansion of Quaternary ice sheets—that is, these animals were hypothesized to have originated in high-latitude Arctic regions [18]—but this hypothesis has lacked credible evidence.

The discovery of the most primitive known woolly rhinoceros in the Pliocene mammalian fauna of the Zanda Basin proves that some members of the Ice Age fauna had already evolved on the Tibetan Plateau before the Quaternary, while vast regions including the Arctic were in warmer-than-present conditions. Ancestors of Ice Age animals were "trained" by harsh winters in the high-altitude environment of the Tibetan Plateau, enabling pre-adaptation to later Quaternary glacial climates and ultimately successful expansion to the dry, cold steppe regions of northern Eurasia. This discovery overturns the Arctic origin hypothesis for Ice Age animals, proving that the Tibetan Plateau was their original evolutionary center and leading to the "Out of Tibet" hypothesis for Ice Age fauna [19].

Tibetoceras thibetana (*Coelodonta thibetana*) from the Mid-Pliocene approximately 3.7 Ma occupies the most basal position in the woolly rhinoceros phylogenetic tree, representing the earliest known record of woolly rhinoceros. As Quaternary glaciation became evident at 2.6 Ma, *Coelodonta thibetana* left the plateau, passing through intermediate stages to eventually reach low-elevation, high-latitude regions of northern Eurasia, becoming important members of the flourishing mammoth-woolly rhinoceros fauna of the Middle and Late Pleistocene (Fig. 3 [Figure 3: see original paper]). A rough surface covering the entire dorsal nasal bone indicates that *Coelodonta thibetana* possessed a large, laterally flattened nasal horn in life, with a smaller frontal horn inferred from a broad, low ridge on the frontal bone. The forward-leaning nasal horn was used to scrape away ice and snow in winter to find dry grass for feeding. The very broad nasal bones and ossified nasal septum indicate not only large nasal cavities but, more importantly, enhanced heat exchange in cold air.

Canid fossils from the Pliocene deposits (5-3 Ma) of the Zanda Basin were named as a new species, *Vulpes qiuzhudingi*, whose lower carnassial has well-developed cutting functions similar to the modern arctic fox, unlike other extant fox species with more omnivorous diets [20]. *Vulpes qiuzhudingi* was even larger than the arctic fox, representing a heat-loss reduction strategy according to Bergmann' s rule and indicating greater adaptation to cold climate. This discovery shows that the Tibetan Plateau fossil fauna contains an early form of arctic fox, whose modern representative lives over 2,000 km from the Himalayas. This finding not only illuminates the Pliocene Ice Age fauna of the Tibetan Plateau but also reveals their relationship with modern Arctic fauna, proving that the plateau' s uplift had major impacts on global climate while its ancient fauna contributed to modern biodiversity and zoogeographic distribution.

Morphological studies of felid fossils from the Zanda Basin, combined with DNA data from extant large cats of the subfamily Pantherinae, using total evidence phylogenetic analysis, demonstrate they represent a new pantherine species, *Panthera blytheae*, sister to the living snow leopard. *Panthera blytheae* is the oldest known pantherine globally [21]. The paleomagnetic age range of Zanda Basin strata is 5.95–4.10 Ma, representing the earliest worldwide appearance of pantherine cats, indicating they existed on the Tibetan Plateau from Late Miocene to Pliocene. Previous molecular biology studies suggesting the earliest divergence of pantherine lineages occurred in the Late Pliocene are refuted; this research demonstrates pantherines had already originated during the Miocene when extant felid lineages first diverged. Pantherines should therefore have originated on the Tibetan Plateau and adjacent regions, with paleogeographic analysis indicating their diversification was necessarily linked to plateau uplift and its environmental effects during the Late Cenozoic [22].

Modern argali sheep (*Ovis*) are widely distributed across the Caucasus, Himalayas, Tibetan Plateau, Tien Shan-Altai Mountains, eastern Siberia, and the Rocky Mountains of North America. In Eurasia, argali fossils were previously known only from a few Pleistocene localities in North China, eastern Siberia, and western Europe, with no records from the Tibetan Plateau. The new genus and species *Protovis himalayensis* discovered in the Pliocene of the Zanda Basin not only extends the sheep fossil record to the Pliocene of the Tibetan Plateau but also shows that the plateau (and possibly the Tien Shan-Altai region) represents the ancestral area for argali sheep. This basal group is the most recent common ancestor of all extant argali species, consistent with the "Out of Tibet" origin theory for Ice Age fauna. *Protovis* is smaller than modern Asian argali but shares characteristics such as posterolaterally curved horn cores, partially developed frontal sinuses, and transitional features toward modern argali. The fossil locality is near a paleoisland formed by metamorphic basement, with cliffs providing protection from predators [23].

Carbon isotope analysis of herbivorous mammal fossils from the Zanda Basin indicates C3 plants dominated the vegetation during the Pliocene [24], showing that ancestral Tibetan sheep, like modern Tibetan bovids, fed on C3 plants. Ancestral argali on the Tibetan Plateau had adapted to high-altitude cold environments by the Pliocene, while other regions including the high-latitude Arctic were in warmer conditions. This ancestral group rapidly evolved toward the modern argali morphology, and when the Quaternary glaciation began at approximately 2.6 Ma, they possessed competitive advantages for survival in frozen environments, enabling rapid dispersal to surrounding regions of the Tibetan Plateau and more distant areas.

Our research results indicate that during the Oligocene, basins such as Nima and Lunpola did not exceed 2,000 m elevation, and the overall topography of the Tibetan Plateau was insufficient to hinder large animal dispersal, allowing mammals like *Paraceratherium* to traverse between northern and southern plateau regions. By the Miocene, data from Gyirong, Lunpola, and Hoh Xil basins reflect plateau uplift to approximately 3,000 m elevation, becoming a barrier for mammal dispersal for taxa such as *Platybelodon*. By the Pliocene, basins including Zanda and Kunlun Pass had reached modern elevations above 4,000 m, forming a cryosphere environment that gave rise to Ice Age fauna (Fig. 2). For a long time, scientists have searched for ancestors of the cold-adapted Quaternary Ice Age fauna in Pliocene and Early Pleistocene Arctic tundra and dry cold steppes without success. Now, through research on mammalian fossils from Late Cenozoic deposits on the Tibetan Plateau, particularly those from the Zanda Basin, we recognize that the plateau, having reached modern elevation in the Pliocene, provided the cold, high-altitude environment where ancestors of Ice Age fauna underwent their initial stages of cold adaptation evolution.

References

1. Dong Z M. Ichthyosaur fossils from the Mount Everest region. *Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Monograph Series A*, 1972, 9: 7-10.

2. Zhang M M. A new species of helicoprion from Tibet. *Geological Science*, 1976, (4): 332-336.

3. Dong Z M, Milner A C. *Dinosaurs from China*. London: British Museum (Natural History), 1988.

4. Deng T, Ding L. Paleo-altimetry reconstructions of the Tibetan Plateau: progress and contradictions. *National Science Review*, 2015, 2(4): 417-437.

5. Wang N, Wu F X. New Oligocene cyprinid in the central Tibetan Plateau documents the pre-uplift tropical lowlands. *Ichthyological Research*, 2015, 62: 274-285.
6. DeCelles G P, Kapp P, Ding L, et al. Late Cretaceous to middle Tertiary basin evolution in the central Tibetan Plateau: changing environments in response to tectonic partitioning, aridification, and regional elevation gain. *Geological Society of America Bulletin*, 2007, 119: 654-680.
7. Wu F X, Miao D S, Chang M M, et al. Fossil climbing perch and associated plant megafossils indicate a warm and wet central Tibet during the Late Oligocene. *Scientific Reports*, 2017, 7: 878.
8. Cao W X, Chen Y Y, Wu Y F, et al. Origin and evolution of schizothoracine fish and their relationship to Tibetan Plateau uplift. In: *Timing, Magnitude and Form of Tibetan Plateau Uplift*. Beijing: Science Press, 1981. 118-130.
9. Wu Y F, Chen Y Y. Neogene cyprinid fish fossils from northern Tibet. *Vertebrata PalAsiatica*, 1980, 18: 15-22.
10. Zhang M M, Miao D S. Cenozoic fish fossils from the Tibetan Plateau and their paleoenvironmental significance. *Chinese Science Bulletin*, 2016, 61(9): 981-995.
11. Pekar S F, DeConto R M. High-resolution ice-volume estimates for the Early Miocene: evidence for a dynamic ice sheet in Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2006, 231: 101-109.
12. Sun B, Wang Y F, Li C S, et al. Early Miocene elevation in northern Tibet estimated by palaeobotanical evidence. *Scientific Reports*, 2015, 5: 10379.
13. Yue L P, Deng T, Zhang R, et al. Paleomagnetic chronology and record of Himalayan movements in the Longgugou section of the Gyirong-Oma Basin in Xizang (Tibet). *Chinese Journal of Geophysics*, 2004, 47(6): 1135-1142.
14. Deng T, Li Y M. Vegetational ecotype of the Gyirong Basin in Tibet, China and its response in stable carbon isotopes of mammal tooth enamel. *Chinese Science Bulletin*, 2005, 50(12): 1225-1229.
15. Wang Y, Deng T, Biasatti D. Ancient diets indicate significant uplift of southern Tibet after ca. 7 Ma. *Geology*, 2006, 34(4): 309-312.
16. Zachos J, Pagani M, Sloan L, et al. Trends, rhythms, and aberrations in global climate 65 Ma to Present. *Science*, 2001, 292: 686-693.
17. Deng T, Li Q, Tseng Z J, et al. Locomotive implication of a Pliocene three-toed horse skeleton from Tibet and its paleo-altimetry significance. *PNAS*, 2012, 109(19): 7374-7378.

18. Darwin C. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life*. London: John Murray, 1859.
19. Deng T, Wang X M, Wu F X, et al. A primitive Late Pliocene woolly rhino suggests high-plateau origin of Ice Age megaherbivores. *Science*, 2011, 333: 1285-1288.
20. Wang X M, Li Q, Takeuchi G T. Out of Tibet: an early sheep from the Pliocene of Tibet, *Protovis himalayensis*, gen. et sp. nov. (Bovidae, Caprini), and origin of Ice Age mountain sheep. *Journal of Vertebrate Paleontology*, 2016, 36: e1169190.
21. Tseng Z J, Wang X M, Slater G J, et al. Himalayan fossils of the oldest known pantherine establish ancient origin of big cats. *Proceedings of the Royal Society B*, 2014, 281: 20132686.
22. Wang X M, Tseng Z J, Li Q, et al. From "Third Pole" to North Pole: a Himalayan origin for the arctic fox. *Proceedings of the Royal Society B*, 2014, 281: 20140893.
23. Wang Y, Deng T, Biasatti D, et al. Paleoaltimetry of the Late Miocene Gyirong Basin, southern Tibet. *Acta Geologica Sinica*, 2015, 89(S1): 284-285.
24. Deng T, Wu F X, Wang N. Terrestrial paleoenvironment and paleoecology in Tibetan Plateau: progress and prospects. *Gondwana Research*, 2015, 27(4): 1335-1354.
25. Li Q, Wang X M, Li Z, et al. A new species of woolly rhinoceros from the Pliocene of the Zanda Basin, Tibet. *Vertebrata PalAsiatica*, 2015, 53(4): 281-294.

Note: Figure translations are in progress. See original paper for figures.