Global and Planetary Change 174 (2019) 58–69

Contents lists available at ScienceDirect

Global and Planetary Change

journal homepage: www.elsevier.com/locate/gloplacha

Invited review article

Review: Implications of vertebrate fossils for paleo-elevations of the Tibetan Plateau

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ARTICLE INFO

Keywords:
Tibetan Plateau
Paleo-elevation
Vertebrate fossil
Fish
Mammal
Plant

ABSTRACT

The uplift of the Tibetan Plateau is an important geological event, but there is considerable controversy about its growth history. Different geological observations contribute to this controversial issue, while data from geochemistry, tectonics, and paleontology further fuel the debate. Vertebrate fossils have provided significant evidence for documenting the uplift of the Tibetan Plateau in the geologic past. The earliest fossil evidence recently collected from the Oligocene Dingqing Formation in central Tibet includes the climbing perch and cyprinine fish fossils whose modern close relatives are distributed in the tropical zone of Asia and Africa. These discoveries not only are significant for the phylogeny and zoogeography of fishes, but also imply that the hinterland of the Tibetan Plateau was a warm and humid lowland at ~26 Ma. The co-existing plant assemblage, which includes palms and golden rain trees among others, indicates that the warm and humid airs from the Indian Ocean could flow deeply into central Tibet, consistent with the inference from the fish fossils. Since that time, the geographical features and natural environments within the Tibetan Plateau have greatly changed. The Tibetan Plateau was consistently uplifted in the Early Miocene and reached an elevation of ~3000 m, which was demonstrated by fish, mammal, and plant fossils. The endemic schizothoracines (snow carps) originated from the Miocene when the Tibetan Plateau turned into a barrier for mammalian migrations between north and south sides. A series of fish and mammal fossils provided unequivocal evidence that the Tibetan Plateau uplifted close to its modern elevation in the Pliocene and developed a cryospheric environment. As a result, the plateau region became the origination center for the cold-adapted Quaternary Ice Age fauna.

1. Introduction

The Tibetan Plateau, between the Kunlun Mountains and the Himalayas, consists of terranes accreted successively to Eurasia (Dewey et al., 1988). The Tibetan Plateau was developed by the closure of the Tethys oceans between two great land masses since the Paleozoic: Laurasia in the north and Gondwana in the south (Hsü et al., 1995; Sengör and Natal'in, 1996).

The Triassic marine limestones are distributed in the Himalayas where the ichthyosaur *Himalayasaurus tibetensis* was discovered by paleontologists in 1970s, including a fragmentary skull with upper and lower jaws, vertebrate, pectoral girdle and fore-limbs. It is a large shastasaurid, probably exceeding 15 m in total length. The material was collected from the Norian Qulonggongba Formation of the Upper Triassic at Tulong in Nyalam, Tibet, China (Dong, 1972; Fig. 1).

Two specimens of a helicoprionid shark were found near Qubu in Tingri County at an elevation of about 4880 m (Fig. 1). The fossil-bearing dolomitic limestone beds are dated on the base of ammonites and other invertebrates as of the Early Triassic. The two specimens, a tooth-row fragment (Fig. 2) and a preorbital part of skull evidently belong to the same species. The material represented a unique species and was named *Sinohelicoprion qomolangma* (Zhang, 1976).

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https://doi.org/10.1016/j.gloplacha.2019.01.005
Received 28 June 2018; Received in revised form 6 January 2019; Accepted 7 January 2019

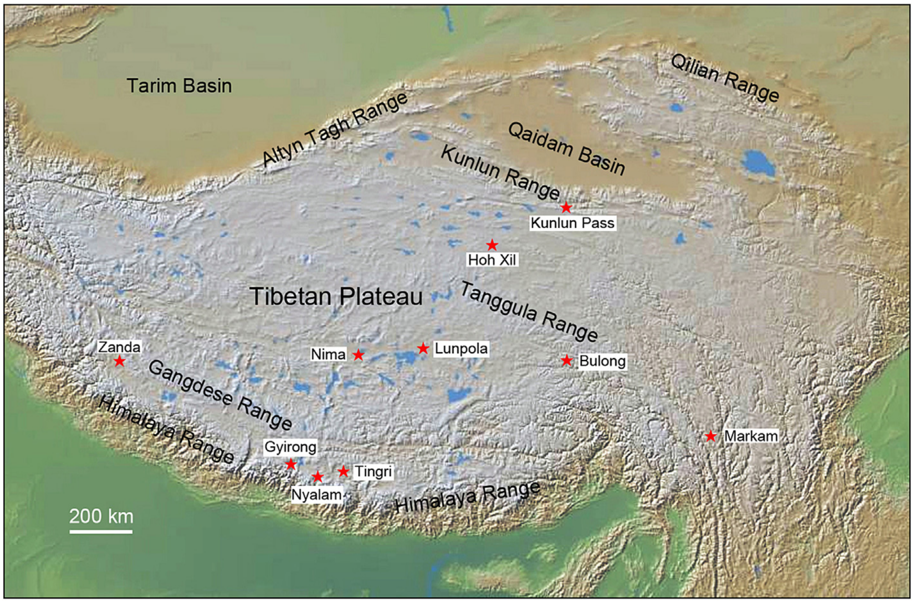

Fig. 1. Geographic map of main vertebrate fossil localities (stars) in the Tibetan Plateau.

Fig. 2. A tooth-row fragment (V 4752.2) of the helicoprionid shark *Sinohelicoprion qomolangma* from Tibet.

Gondwana began breaking up between the Jurassic and the Late Cretaceous, pushing Africa and India north across the Tethys. During the same time, some part of eastern Tibet emerged from ocean gradually. Between 180 and 135 Ma, during the Middle and Late Jurassic time, the Qamdo region of Tibet was covered by an ancient lake where dinosaurs and other reptiles lived on shores. The lake was drained to the east by a river that flowed into another lake in the Sichuan Basin. As a result, both the sediments and the faunal remains preserved within them are similar in the Qamdo and Sichuan basins (Dong and Milner, 1988).

The teeth of a primitive sauropod from the Middle Jurassic Chaya Group closely resemble those of *Datousaurus* from the Sichuan Basin. *Datousaurus* is a large primitive sauropod with a deepened, heavily built skull. The sacrum and pelvis of *Monkonosaurus lawulacus* from the Loe-ein Formation of the Early Cretaceous at Lawula Mountain in Markam, Tibet, China proved the occurrence of stegosaurs in the Tibetan Plateau (Fig. 1). *M. lawulacus* is a medium-sized stegosaur (Dong and Milner, 1988; Li et al., 2008).

After breaking apart from the supercontinent of Pangea in the Mesozoic, the separated Indian plate moved northward at a fast speed, and finally collided with Eurasia in the beginning of the Cenozoic (Ding et al., 2017), which was arguably the most important orogenic event in the earth's history of the last 500 Ma. Since then, the Tibetan Plateau has begun to take shape gradually. The uplift of the Tibetan Plateau was not at a constant speed or a one-time rapid movement, and it underwent different phases (Deng and Ding, 2015). Each phase of the uplift modified the topography of the Tibetan Plateau, and the great influence of the uplift on climate and environment was surely reflected in the biotic turnover because animals and plants were sensitive to climatic and environmental changes. In recent years, a series of important discoveries of vertebrate and other fossils were made during many expeditions to the Tibetan Plateau, which have provided significant insights into the uplift process of the Tibetan Plateau and its influence on biological evolution.

2. Tropical or subtropical ecosystem in the Oligocene

Related to the history and process of the Tibetan Plateau uplift there have been heated debates, especially over paleoelevations at different geological times (Garzione et al., 2000; Rowley et al., 2001; Spicer et al., 2003; Currie et al., 2005; Cyr et al., 2005; Rowley and Currie, 2006; Wang et al., 2006; DeCelles et al., 2007b; Sun et al., 2007; Wang et al., 2008a, 2008b; Saylor et al., 2009; Quade et al., 2011; Deng et al., 2012b; Wang et al., 2012, 2013; Xu et al., 2013; Ding et al., 2014). Some researchers considered that the Tibetan Plateau did not strongly rise to its modern elevation until the Late Miocene (Xu et al., 1973; Harrison et al., 1992; Molnar et al., 1993; Coleman and Hodges, 1995; Qiu et al., 2001; Wang et al., 2006; Zhou et al., 2007; Chang et al., 2010; Sun et al., 2014; Deng et al., 2015b; Sun et al., 2015; Jia et al., 2015). On the other hand, several authors argued that the Tibetan Plateau was formed at an early stage of the Indo-Asian collision and reached its modern elevation in the Paleogene or Middle Miocene, or by mid-Eocene mainly based on stable isotope evidence (i.e., $\delta^{18}O$ values of carbonates or δD values of plant lipids) and plant fossils (Rowley et al., 2001; Spicer et al., 2003; Cyr et al., 2005; Mulch and Chamberlain, 2006; Rowley and Currie, 2006; DeCelles et al., 2007b; Polissar et al., 2009; Quade et al., 2011; Xu et al., 2013; Ding et al., 2014).

The Lunpola Basin in central Tibet is at the center of the controversy (Fig. 1). This basin has well-developed Cenozoic strata and an average elevation of about 4700 m a.s.l. (above sea level). The total thickness of

Cenozoic deposits in the Lunpola Basin is over 4000 m, and consists of the Niubao Formation in the lower part and the Dingqing Formation in the upper part. Estimations of the paleo-elevation of the Lunpola Basin have been very different. During the deposition of the Dingqing Formation, the lowest estimate has been reported to be about 1000 m (Ma, 2003), but the highest published estimate is 4500 m inferred from the $\delta^{18}O$ values of lacustrine carbonates (Rowley and Currie, 2006). Quade et al. (2011) also reconstructed the paleoelevation of the Lunpola Basin using the $\delta^{18}O$ values of paleosol carbonates in the Niubao Formation and concluded that the area had reached its modern elevation by 35–40 Ma.

The use of $\delta^{18}O$ values of terrestrial carbonates (or δD values of plant lipids) to reconstruct the paleoelevation, which is often referred to as the “stable isotope paleoaltimetry”, is based on the observation that the stable isotope ratios in meteoric water and stream water generally decrease with elevation in a given area. The method uses the $\delta^{18}O$ values of carbonates (or δD values of plant lipids) to reconstruct the $\delta^{18}O$ (or δD) values of ancient meteoric waters and the latter are then employed to calculate the paleoelevations by using the modern meteoric water isotopic lapse rate in the study area (e.g., Rowley et al., 2001; Currie et al., 2005; Cyr et al., 2005; Rowley and Currie, 2006; DeCelles et al., 2007; Saylor et al., 2009; Quade et al., 2011). As stated in Quade et al. (2011), using oxygen isotopes in carbonates to reconstruct paleo-elevation requires many assumptions including: (1) paleo-temperature of carbonate formation can be reliably constrained (e.g., for Lunpola Basin, the formation temperature of lacustrine and soil carbonates was assumed to be 10 ± 10 °C by Rowley and Currie (2006) in order to calculate the $\delta^{18}O$ value of ancient meteoric water from the $\delta^{18}O$ of carbonate); (2) lacustrine and soil carbonate samples selected for paleoelevation reconstruction were formed in isotopic equilibrium with meteoric water; (3) isotopic composition of the carbonate has not been altered by diagenesis; (4) the modern precipitation $\delta^{18}O$ lapse rate in the study area has not changed over time and thus can be applied to the distant past; (5) climate change did not occur or is minimal over the geologic time period of interest; and (6) $\delta^{18}O$ of paleo-meteoric water at a low elevation site along the storm track can be reliably constrained. The assumption of unchanging precipitation $\delta^{18}O$ lapse rate over the geological time also implies little or no change in the moisture sources, monsoon strength, wind pattern, precipitation amount, and temperature in the study region since the Indo-Asian collision in the early Cenozoic, as all these factors can exert significant influences on the isotopic composition of local precipitation (e.g., Araguas-Araguas et al., 1998; Tian et al., 2001; Johnson and Ingram, 2004; Vuille et al., 2005; Wang et al., 2008b).

Unfortunately, these assumptions, which are the foundation that the stable isotope paleoaltimetry is built on, may not be valid, leading to erroneous interpretations of paleoelevation. For example, studies have shown that meteoric water $\delta^{18}O$ lapse rate varies spatially and temporally likely due to variations in wind and precipitation patterns and other local/regional weather processes (see review by Blisniuk and Stern, 2005). Climate model simulations have also demonstrated that the mountain building affects not only the precipitation $\delta^{18}O$ but also the $\delta^{18}O$ lapse rate (Ehlers and Poulsen, 2009; Poulsen et al., 2010). In addition, studies have shown that climatic variation, in particular variation in monsoon strength, significantly influences the $\delta^{18}O$ of precipitation in the Asian monsoon region including the Tibetan region (e.g., Thompson et al., 1989, 2000; Cheng et al., 2016). The effects of climate change (e.g., strengthening or weakening of the monsoon) on precipitation $\delta^{18}O$ are as large as or larger than the elevation effect. Given the above considerations and our knowledge of Cenozoic climate changes (e.g., Zachos et al., 2001), assumptions (4) and (5) are unlikely to be valid and thus the uncertainties in the paleoelevation estimates based on the $\delta^{18}O$ values of terrestrial carbonates are likely much greater than reported.

Our initial evidence with important information of the Tibetan Plateau uplift came from the Nima Basin in central Tibet, 200 km to the west of Lunpola Basin (Fig. 1). In 2010, rich fish fossils were discovered from the gray to grayish-red lacustrine shales and mudstones in southern Nima Basin, among them *Tchunglinius tchangii* (Fig. 3), a new cyprinid genus and species was named by Wang and Wu (2015). Given the age of 23.5–26 Ma for the strata dated by $^{40}Ar/^{39}Ar$ method (DeCelles et al., 2007a), *T. tchangii* was implied to live in the Late Oligocene. The subfamily Cyprininae of the Cyprinidae are wide-spread in Asia, central and southern Europe, and Africa in the Eastern Hemisphere. Species in regions with low elevation and warm climate have fewer vertebrae, such as modern tropical genera and species of Asia with about 30 vertebrae (Wu and Chen, 1980). On the other hand, the species in regions with high elevation and cold climate have more vertebrae, such as modern schizothoracines (snow carps) of the Cyprininae endemic in the Tibetan Plateau with almost 50 vertebrae. *T. tchangii* has 33 vertebrae, much less than the modern snow carps of the Tibetan Plateau and close to the tropical cyprinines of Asia, such as the recent small-bodied *Puntius*; therefore, *T. tchangii* should be a fish in an environment of low elevation and warm condition. As a result, the *T. tchangii* fossils suggest a Paleogene tropical-subtropical lowland fish fauna before the uplift of the Tibetan Plateau (Wang and Wu, 2015).

Fig. 3. Holotype (IVPP V 18945) of the cyprinine *Tchunglinius tchangii* from Tibet.
(Modified from Wang and Wu, 2015)

This initial finding led to more field work in the Tibetan Plateau, resulting in the discoveries of richer and more diversified fossils from the Nima and the Lunpola basins. Among these fossils, the climbing perch (Fig. 4A) and accompanying plant fossils as indicators of low elevation and warm, humid habitat provide stronger evidence to reconstruct the uplift history of the Tibetan Plateau.

The climbing perch belongs to the family Anabantidae, suborder Anabantoidei (Percormorphaceae sensu Hughes et al., 2018), and is distributed mainly in South Asia, Southeast Asia, and central and western Africa in the modern world (Tim, 2007). The habitat of modern climbing perches is usually below 500 m a.s.l., and no > 1200 m a.s.l., with an air temperature of 18–30 °C (www.fishbase.org and Skelton, 2001). Climbing perches live in environments of lakes and rivers or swamps and pools, preferring shallow, stable, and oxygen-deficient water bodies with dissolved oxygen even below 1 mg/L (Randle and Chapman, 2004). In contrast, most fishes need the dissolved oxygen above 4 mg/L for their normal activities. The climbing perch is characterized by a labyrinth organ in its gill cavity, which is specialized in its gill bones and has a shape like a flower (Fig. 4B). With this organ, the climbing perch can breathe oxygen directly from air because the surface of the labyrinth organ is covered by respiratory epithelia with rich capillary vessels, which is different from other normal gills. Blood through the labyrinth organ flows back to the heart from the vein. Due to the complicated structure of the labyrinth organ, it occupies a large space in the gill region, such that breathing within water is greatly diminished (Liem, 1987). As a result, sufficient oxygen for the survival of this fish cannot be obtained through breathing in water, and the climbing perch thus has to lift its head into the air to breathe, even crawling out of the water to “walk” on the shore.

The climbing perch fossils discovered in central Tibet are the earliest and the most primitive fossil representative of the family

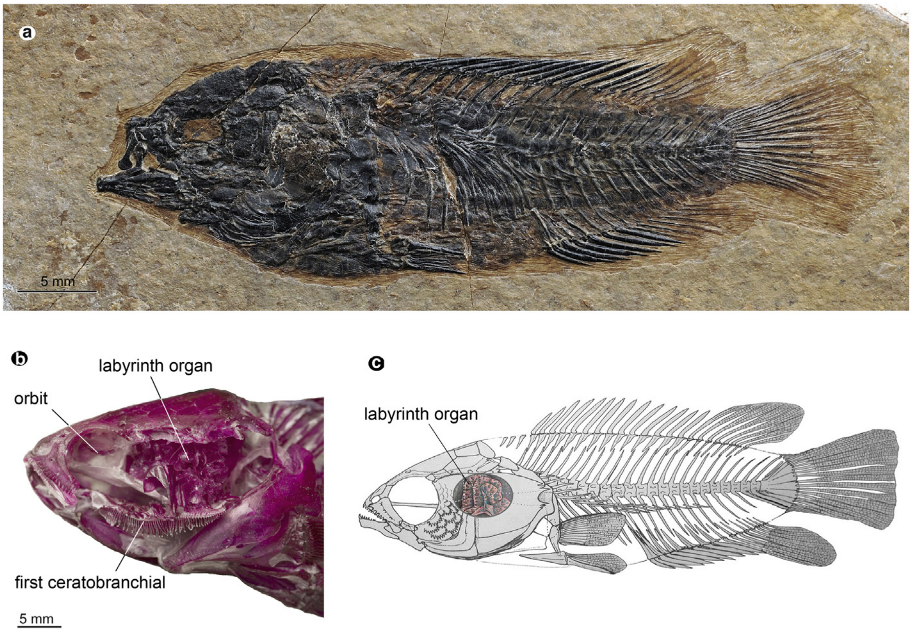

Fig. 4. Anatomy of the earliest climbing perch *Eoanabas thibetana* from Tibet.
A. holotype of *Eoanabas* (IVPP V 22782a); B. labyrinth organ of extant climbing perch, *Anabas testudineus* (collection no. OP 432). C. osteological restoration of *Eoanabas*, not to scale.
(Modified from Wu et al., 2017)

Anabantidae (Fig. 4A). These fossils were established as a new genus and species *Eoanabas thibetana*, which traces the fossil record of the Anabantidae about 20 million years earlier than previously known (Wu et al., 2017). The labyrinth organ was observed in the specimens of *E. thibetana* based on a scanning electron microscope (Fig. 4C), and the cancellous structure on bones shows that the development of its labyrinth organ is very close to the modern Asian climbing perch with the strongest breathing capacity in air. The studied result indicated that the Tibetan climbing perch has similar physiological characteristics and ecological behaviors to those of the modern climbing perch, so it implied a warm and humid environment, and its habitat should be a limited water body. Physiological features of the climbing perch show that this fish cannot live in lakes with a high elevation because frozen lake surface in the winter makes it impossible for the fish to breathe in air. However, the fossil locality is presently situated in an area with an elevation of about 5000 m, strong ultraviolet radiations, a low annual average temperature of the water body about −1.0 °C, strong water mobility, and relatively high level of dissolved oxygen (Chen et al., 2001), which is much different from the habitat of the fossil climbing perch at 26 Ma. Thus, it can be seen that the geographical features and natural environment have gone through extreme changes since the time of *Eoanabas thibetana*.

The plant assemblage associated with *Eoanabas thibetana* in the same lacustrine deposits includes several aquatic herbs such as duckweed (*Limnobiophyllum*) and bulrush (*Typha*) as well as a diverse lowland vegetation such as palms, golden rain trees (*Koelreuteria*), *Pistacia*, Ulmaceae, Araliaceae, *Handeliodendron*, *Exbucklandia* and aspens (*Populus*) (Wu et al., 2017; Jiang et al., 2018). The relatively high percentage (> 60%) of the entire-margined types among the woody dicot leaves also suggests a warm and humid climate, and the plant fossils indicate their environment at a paleo-elevation lower than 2000 m. Some fossil insects found from the same strata also indicate a similar paleo-elevation (e.g., Cai et al., 2018) (Fig. 5).

Fig. 5. Ecological reconstruction of the Lunpola biota in central Tibet during the Late Oligocene.
(Art by Feixiang Wu)

Jiang et al. (2018) described two species of *Koelreuteria*, namely *K. lunpolaensis* and *K. miointegrifoliola*, based on exquisitely preserved capsular valves from the Late Oligocene of the Lunpola Basin. The diverse *Koelreuteria* confirms a warm and humid environment with a low elevation in central Tibet during the Late Oligocene based on their modern distributions, because the extant species of *Koelreuteria bipinnata*-type (*K. bipinnata*, *K. henryi*, and *K. elegans*), which are the living relatives of *K. miointegrifoliola*, inhabit subtropical to tropical forests at elevations of up to 2500 m (Xia and Luo, 1995; Xia and Gadek, 2007). Other fossil plant assemblages containing *K. miointegrifoliola* in China, e.g. the late Early Miocene Shanwang flora (Hu and Chaney, 1938) and the Late Miocene Xiananshan flora (Li and Guo, 1982; Li, 1984) in East China, also represent a subtropical lowland vegetation in a warm and humid climate. Fossil evidence indicates that the Tibetan Plateau was a center for diversity and diversification of *Koelreuteria* in the Oligocene/Miocene.

The occurrence of the water skater *Aquarius lunpolaensis* supports the hypothesis that the elevation of central Tibet was comparatively low at about 25 Ma. The present altitudinal distribution of *A. najas*, the extant species closely related to *A. lunpolaensis*, provides new clues about the paleo-elevation of the central Tibet in the Late Oligocene. Although there is uncertainty about the exact distribution of *A. najas*, the species appears to be currently almost confined to the lowlands of the British Isles, Denmark, southern Norway, Sweden, Finland, Greece, Morocco, Algeria, and Tunisia (Damgaard, 2005). Therefore, it is likely that the fossil species *A. lunpolaensis* lived in a similar lowland habitat in the Late Oligocene of central Tibet (Cai et al., 2018).

This Late Oligocene biota in central Tibet indirectly shows that the warm and humid airflow from the Indian Ocean could penetrate into central Tibet. In other words, the huge range of mountains which stretches from east to west along the south margin of the Tibetan Plateau had not been uplifted to its modern elevation at that time, so that it could not block the warm and humid airflow from the south.

In summary, the uplift history of the Tibetan Plateau reconstructed by the analysis of fossil assemblages is much different from the popular viewpoint that the Tibetan Plateau reached its modern elevation in the Oligocene and even the Eocene, which was based on inferences from some geological, geophysical, and geochemical data. Hence, the multiple lines of evidence will enable a more nuanced view and modify the previously proposed uplift models of the Tibetan Plateau.

3. Gradual uplift in the Miocene

Entering the Miocene, the Tibetan Plateau uplifted steadily. In central Tibet, the tropical fishes represented by *Tchunglinius tchangii* and *Eoanabas thibetana* have disappeared, and the endemic schizothoracines in the modern Tibetan Plateau have appeared. The snow carps were subdivided into three grades of primitive, specialized, and highly specialized evolutionary levels according to different anatomical characters and elevation distribution: the primitive forms have three rows of pharyngeal teeth on each hypopharyngeal, and they are distributed usually in an elevation range of 1250–2500 m; the specialized fishes have two rows of pharyngeal teeth, and they are distributed in about 2500–3750 m; the highly specialized snow carps have two rows and even one row of pharyngeal teeth, and they are distributed in about 3750 m and 4750 m (Cao et al., 1981). The fossil snow carp *Plesioschizothorax microcephalus* was found from the Early Miocene member of the Dingqing Formation with a modern elevation of 4540–4550 m in the Lunpola Basin, which belongs to the primitive grade with three rows of pharyngeal teeth. This evidence indicates that the paleo-elevation of this basin should have been uplifted to near 3000 m adjusted by the paleo-temperature during that time (Chang and Miao, 2016).

A rhinocerotid fossil was discovered also from the Early Miocene member of the Dingqing Formation with a modern elevation of 4624 m in the Lunpola Basin. The specimen is the distal extremity of a humerus, and its features are almost identical with those of *Plesiaceratherium gracile* from the late Early Miocene Shanwang fauna in Linqu, Shandong, China. The mammalian fossils from Shanwang are mainly forms living on forest edges and in swampy areas, especially *Palaeomeryx*, *Lagomeryx*, and various squirrels (Qiu and Yan, 2005). However, forms that lived in grasslands are rare, which indicates that the ecosystem was a subtropical or warm temperate forest during that time. Judging from the flora in the Shanwang Basin, many species are subtropical evergreen or deciduous broadleaf plants, which also indicate a warm and humid climate (Yan, 1983; Tao et al., 1999). The sporopollen assemblage of the Dingqing Formation is similar to that of the Shanwang Formation, reflecting the warm and humid climate at that time (Wang et al., 1975), so that the rhino *Plesiaceratherium* of the Lunpola Basin should also live in an evergreen broadleaf forest during the Early Miocene. In the global climatic background, the rhino *Plesiaceratherium* lived between the two cooling events of Mi-1b at 17.8 Ma and Mi-2 at 16 Ma (Wang et al., 2003), but the temperature during that time was higher than that of the modern levels (Zachos et al., 2001). In fact, the historic temperature was 4 °C higher than modern temperatures, as calculated from oxygen isotopes (Pekar and DeConto, 2006). The distribution of vertical vegetation zones is directly related to atmospheric temperature. A temperature increase of 4 °C between the Early Miocene and the present would drive the boundaries of the vertical vegetation zones about 670 m higher, caused by a temperature lapse rate of 0.6 °C/100 m (Wang et al., 2004). As a result, the highest elevation of the *Plesiaceratherium* habitat in the Lunpola Basin is close to 3000 m (Deng et al., 2012b).

Fossil broadleaf plants were discovered from the lacustrine marl of the Miocene Wudaoliang Formation in the Hoh Xil Basin (Fig. 1), including a *Berberis* leaf, and the fossil locality is situated at the modern elevation of 4600 m. The Wudaoliang *Berberis* leaf is similar to that of the modern *B. asiatica* whose vertical distribution is limited to a range of 914–2286 m a.s.l. According to the paleoclimatic cycle recorded by carbon and oxygen isotopes in the lacustrine deposits of the Wudaoliang Formation, the age of the strata is within 24.1–14.5 Ma based on the correlation with the oxygen isotopic curve of deep sea using a climatostratigraphic method, and the horizon of the *Berberis* corresponds to the age of 17 Ma approximately. Because a fossil species and its nearest living relatives may occupy a similar or same ecological niche, the paleoelevation of the *Berberis* fossil locality at Wudaoliang should be within 1395–2931 m adjusted by the Miocene global temperature, which shows that the paleoelevation of the Hoh Xil Basin as well as northern Tibetan Plateau was lower than 3000 m in the late Early Miocene (Sun et al., 2015).

The modern elevation of the fossil locality at Woma of the Gyirong Basin in Himalayas is 4384 m (Fig.1), and the age of the *Hipparion* fauna at this locality is the late Late Miocene with a paleomagnetic dating of 7 Ma (Yue et al., 2004). The ecological features of the Woma *Hipparion* fauna show mixed forest and grassland mammals, and it has differentiated from the Siwalik *Hipparion* fauna in South Asia (Flynn et al., 2013), which indicates that the Himalayas have been a significant barrier to mammalian migrations during this period. Based on a stable carbon isotopic analysis, the δ^{13}C values of *Hipparion* tooth enamel samples from the Gyirong Basin range from −2.4‰ to −8.0‰, with an average of −6.0‰ ± 1.1‰, indicating a mixed C$_3$ and C$_4$ diet. The food of the *Hipparion* horse includes 30%–70% C$_4$ plants, showing an ecological environment characterized by woodland (Fig. 6). C$_4$ plants

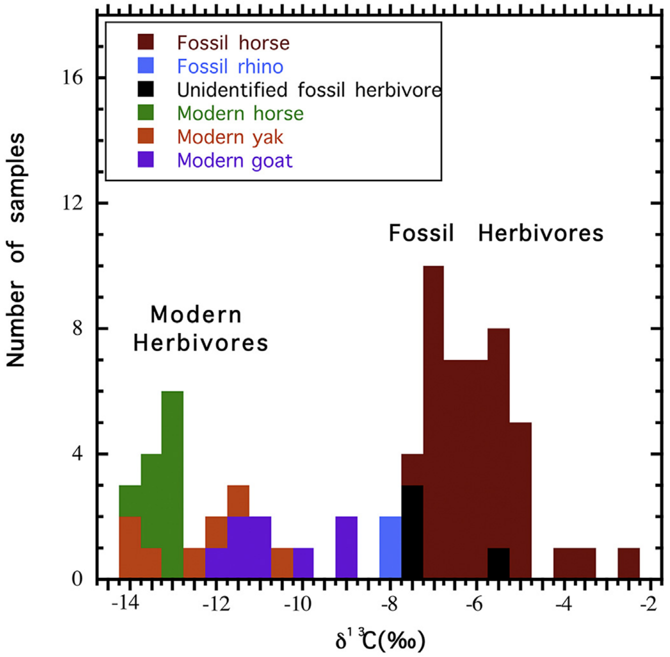

Fig. 6. Stable carbon isotopic composition of tooth enamel from both modern and ancient herbivores in the Gyirong Basin in the high Himalayas.
(From Wang et al., 2006)

are more prevalent than C_3 plants in higher temperature, more sunlight, and enough water vapor, but C_4 plants are rare or absent in high latitudes or high elevations above 3000 m and in regions characterized by winter rainfall (Deng and Li, 2005). Adjusted by paleotemperature, carbon isotopic data indicate that the paleoelevation of the Gyirong Basin was most likely 2400–2900 m at the age of about 7 Ma of the Late Miocene (Wang et al., 2006).

The discovery of *Hipparion* fossils in the Gyirong and other basins was important evidence for the time and height of the Tibetan Plateau uplift (Huang and Ji, 1979), but the research result had a great misunderstanding in detail. These *Hipparion* fossils were collected from three localities over 4000 m a.s.l., such as Woma in Gyirong County (4300 m), Dati in Nyalam County (4950 m), and Bulong in Biru County (4500 m) (Fig. 1). However, the three localities were initially determined as the Pliocene in age, which came from a wrong understanding of the equid evolution. In the beginning of the 20th century, the American paleontologists considered that the Miocene was the age of *Anchitherium*, the Pliocene represented the *Hipparion* time, and the Quaternary was characterized by the genus *Equus* (Qiu et al., 1987). In fact, the first appearance of the genus *Hipparion* in Eurasia is at the lower boundary of the Late Miocene (Deng et al., 2015a; Fang et al., 2016). As a result, the three *Hipparion* localities in Tibet were demonstrated to belong to the Late Miocene in age (Qiu and Qiu, 1995; Yue et al., 2004; Deng et al., 2015b).

In the ecological and environmental comparison of these equid fossils, *Hipparion* was regarded as one form of animal (Huang and Ji, 1979). On the other hand, *Hipparion* is a genus with over 200 nominal species (Woodburne and Bernor, 1980). Different species of the same genus may have much diversified ecological habitats and behaviors. All modern equids, for example, belong to different species of the genus *Equus*, but there are great ecological differences between zebras (*Equus burchelli*, *E. grevyi*, and *E. zebra*) in Africa and the wild horse (*E. przewalskii*) in Asia. Although *E. hemionus* and *E. kiang* have the closest relationship, they have much different elevations for their habitats. Huang and Ji (1979) considered that the *Hipparion* horses in North China lived within the elevation of 500–1000 m, and the *Hipparion* horses in South Asia at the elevation of about 500 m. So they concluded that the *Hipparion* horses in the Tibetan Plateau lived below 1000 m a.s.l., and the Tibetan Plateau uplifted by 3000–4000 m from the Pliocene. However, both these previous age judgement and elevation estimation are wrong.

In fact, mammalian fossils have been used to study the uplift of the Tibetan Plateau since the 19th century. In 1839, Scottish geologist, paleontologist, and botanist Hugh Falconer discussed the uplift of the Tibetan Plateau. He reported some rhinocerotid fossils collected from the Zanda Basin north of the Niti Pass in Nagri, Tibet, China from the Tibetan merchants across the pass (Falconer, 1868; Fig. 1). Modern rhinos still live in the Indian plains, so Falconer naturally considered that the rhinos from the Zanda Basin should also indicate low elevation as for living animals. The age of these rhinocerotid fossils meant that since several million years ago, the Himalayas have uplifted by $>$ 2000 m.

A skeleton of *Hipparion zandaense* was discovered from the Pliocene deposits in the Zanda Basin with a modern elevation of about 4000 m, and the reconstructed locomotive functions depending on its reduced side toes, strong V-scar of first phalanx III, and greatly hypertrophied medial trochlear ridge of the femur indicated that this horse had a fast running ability and a long-period standing (Fig. 7), both of which are advanced features in open environments. The Himalayas have appeared as a mountain range since the Miocene, with the appearance of vegetation vertical zones following thereafter (Wu, 1987), so the open landscape must be above the timberline in the vegetation vertical zones. In the Zanda area, the modern timberline is at an elevation of 3600 m between the closed forest and the open steppe (Wang et al., 2004). The mid-Pliocene when *H. zandanense* lived was in a global climate with a temperature of ~ 2.5 °C warmer than today (Zachos et al., 2001). Based on a temperature lapse rate of 0.6 °C/100 m, the elevation of the timberland line in the Zanda Basin during the time of *H. zandaense* should be situated at 4000 m. As a result, the Zanda Basin reached its modern elevation at least by the mid-Pliocene (Deng et al., 2012a).

Tseng et al. (2013) described a new species of the cursorial hyaenid *Chasmaporthetes*, *C. gangsriensis* from the Zanda Basin, which is smaller than other Plio-Pleistocene Eurasian records of the genus. Metatarsal and phalangeal elements referred to *C. gangsriensis* are long and gracile, indicating cursorial abilities typical of *Chasmaporthetes*. With an age of Early Pliocene (4.89–4.08 Ma), *C. gangsriensis* is morphologically the most basal Pliocene *Chasmaporthetes* in China. The discovery of this cursorial hyaenid species provides additional evidence for open environments in the western Himalayan foothills no later than the Pliocene, as consistent with previous evidence from Zanda Basin's fossil horses and herbivore enamel isotope analyses (Deng et al., 2012a).

A highly specialized snow carp with one row of pharyngeal teeth was produced from the Pliocene deposits of the Zanda Basin in southern Tibetan Plateau, and the highly specialized genus *Gymnocypris* was collected also from the Pliocene of the Kunlun Pass Basin in northern Tibetan Plateau (Wang and Chang, 2010; Fig. 1). These two localities have modern elevations of 3900–4400 m and 4769 m, respectively. In other words, highly specialized snow carps have lived in the two basins during the Pliocene, which also prove that the Tibetan Plateau was close to its modern elevation from its south and north parts in that time based on fish fossils (Chang and Miao, 2016).

4. Cradle of the Ice Age fauna

When the Tibetan Plateau reached its modern elevation, the climate in this region was characterized by the cryosphere, which must have caused the biota to make corresponding changes to adapt to the cold conditions or become extinct. For a long time, the Quaternary Ice Age fauna was recognized to be tightly related to the Pleistocene global cooling, and the large body size and long hair, especially snow-sweeping structures of these mammals were adaptive characters for cold environments, among which the woolly mammoths and woolly rhinos were the most representative. These very interesting extinct mammals have been popular among ordinary people and scientists for many years, and the above-mentioned characters of them have been assumed to evolve along with the expansion of the Quaternary ice sheet. In other words, these mammals were implied to originate in the Arctic Circle of high latitudes (Darwin, 1859), but this hypothesis had no credible evidence for a long time.

The most primitive woolly rhino found from the Pliocene mammalian assemblage of the Zanda Basin proves that some members of the Ice Age fauna originated and evolved in the Tibetan Plateau before the Quaternary when the vast region including the Arctic Circle was in a warmer environment than the present climate. The ancestors of the Ice Age mammals were “trained” by the cold winter in the high elevation environment of the Tibetan Plateau, and formed preadaptation to the coming Quaternary Ice Age climate. Finally, they expanded to the dry and cold steppe in northern Eurasia successfully. This new discovery overturned the hypothesis of origin of the Ice Age mammals from the Arctic Circle (Darwin, 1859), and demonstrated that the Tibetan Plateau was their initial evolutionary center, and the Out of Tibet hypothesis was proposed (Deng et al., 2011).

Coelodonta thibetana lived in the mid-Pliocene at about 3.7 Ma, and its phylogenetic position was at the most basal position of the woolly rhino linage, which was the known earliest record of the woolly rhino. Along with the appearance of the Quaternary Ice Age at about 2.6 Ma, *C. thibetana* departed from the plateau zone. Via some transitional forms, it finally reached to the low elevations and high latitudes in northern Eurasia, and became an important member of the flourishing *Mammuthus-Coelodonta* fauna in the Middle and Late Pleistocene (Fig. 8). The strongly roughened and relatively large nasal horn boss, occupying the entire dorsal surface of the nasal, indicates a large and

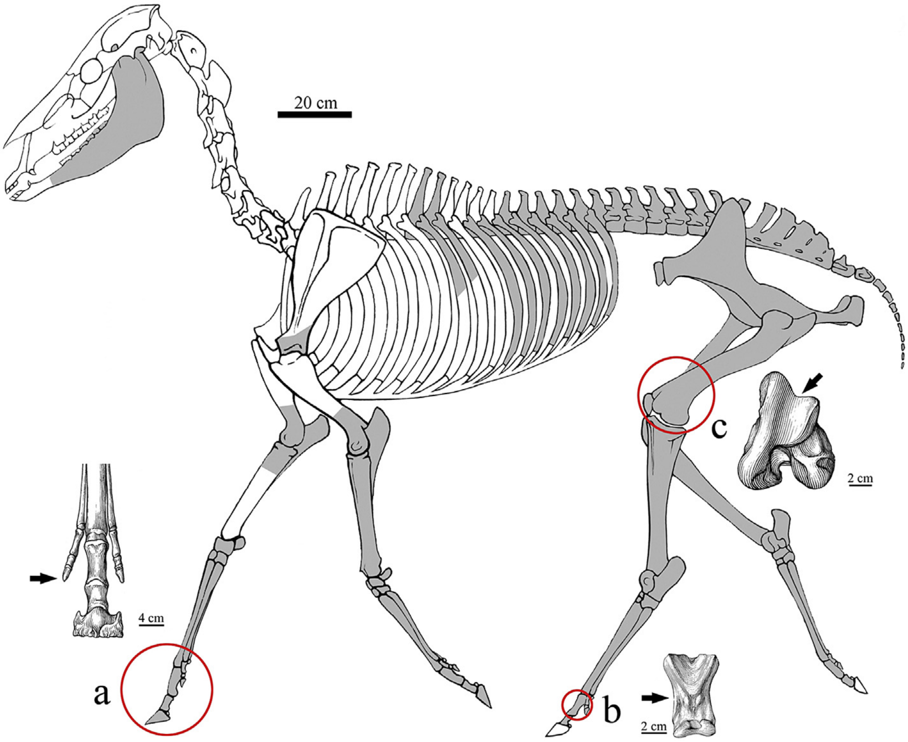

Fig. 7. *Hipparion zandaense* skeleton (IVPP V 18189) and its forefeet (a), hind first Ph III (b), and femora (c). Reconstruction of skeleton showing preserved bones in dark gray.
(Modified from Deng et al., 2012a)

Fig. 8. Origin of the woolly rhino in the Tibetan Plateau during the Pliocene and its expansion in Eurasia during the Quaternary.
(from Wang et al., 2015b)

bilaterally flattened nasal horn. A smaller frontal horn is implied by a wide and low dome on the frontals. The forwardly inclined nasal horn can sweep snow to find dry grass for diet. The wide nasal bones and an ossified nasal septum indicate that its two nasal cavities are very large and more important to increase heat exchange in cold air.

Combining DNA data of living big cats (the subfamily Pantherinae), the morphological study for the felid fossils discovered from the Zanda Basin with the phylogenetic analysis method of all evidence reveals that these fossils represent an independent species of the genus *Panthera*, *P. blytheae*, which is the sister group of the living snow leopard. *P. blytheae* is the known oldest pantherine in the world, and its distribution in the strata of the Zanda Basin has a paleomagnetic dating range of 5.95–4.10 Ma, which represents the earliest appearance of the felid pantherines in the world, showing that pantherines existed in Central Asia from the Late Miocene to the Pliocene. Previous molecular study suggested that taxa of the pantherine linage had the earliest divergent

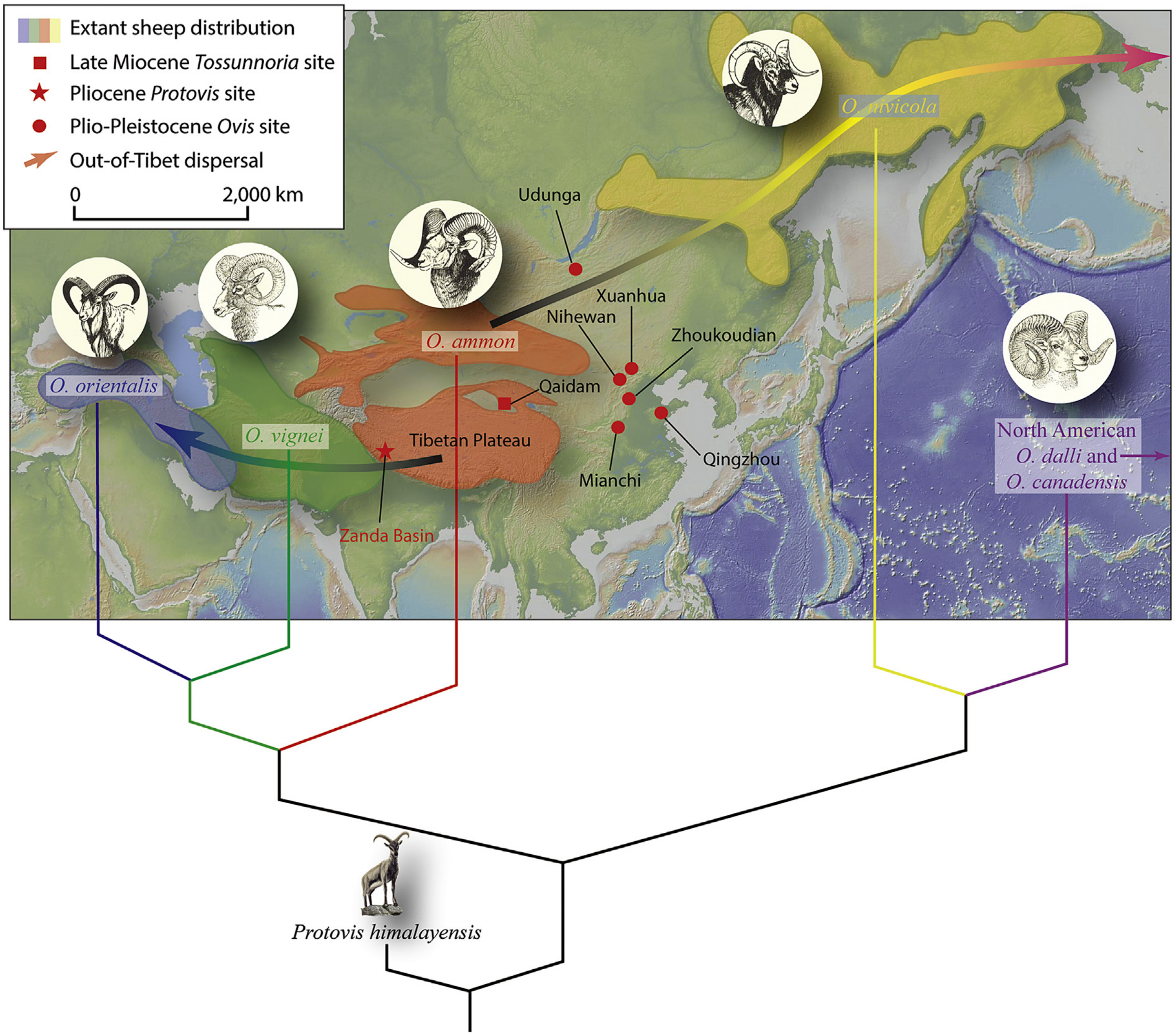

Fig. 9. Map of extinct and extant species of *Ovis* in Eurasia and their evolutionary relationships.
(From Wang et al., 2016)

time of the Late Pliocene (Johnson et al., 2006; Davis et al., 2010), but this viewpoint has been revised by the new result that pantherines appeared in the Miocene which is the earliest divergent time of the living felids. As a result, pantherines should originate in the Tibetan Plateau and its adjacent region. A paleogeographical analysis indicated that the diversified evolution of this linage must have a close relationship to the uplift of the Tibetan Plateau and its environmental effect in the late Cenozoic (Tseng et al., 2014).

Because the Tibetan Plateau has the vastest frozen terrain and glaciers except the Arctic and Antarctic, it is not only called the ‘roof of the world’, but also the ‘third pole’ of the Earth. Like the Arctic and Antarctic mammals, mammals living in high and cold areas of the Tibetan Plateau have long and thick winter fur for protection against freezing temperatures, among which carnivores have a more predatory niche than those in other regions. A fossil canid from the Pliocene deposits of 5–3 Ma in the Zanda Basin was established as *Vulpes qiuzhudingi* whose lower carnassial tooth bears a striking resemblance to highly hypercarnivorous function of the living arctic fox and different from that of other living foxes with more omnivorous diet (Wang et al., 2014). The body size of *V. qiuzhudingi* is even larger than that of the arctic fox, which is a survival strategy to reduce heat loss based on Bergmann's Rule, indicating that *V. qiuzhudingi* is more adaptable to cold climate (Szuma, 2008). The fossils of *V. qiuzhudingi* shows that this species in the mammalian fauna of the Tibetan Plateau is the early ancestor of the arctic fox, and its habitat in Himalayas is separated from the nearest living arctic fox geographical range in the Arctic Circle by at least 2000 km. This discovery not only makes us recognize the features of the Pliocene Ice Age fauna in the Tibetan Plateau, but also reveals the relationship between the two faunas in the Pliocene Tibetan Plateau and the modern Arctic Circle, demonstrating that the uplift of the Tibetan Plateau had significant influence on the global climate, and the old fauna of the Tibetan Plateau was also the basis of modern faunal diversity and zoogeographical distribution (Wang et al., 2014).

Wang et al. (2015a) reported an early record of a hypercarnivorous canid, *Sinicuon* cf. *dubius*, from the Zanda Basin. They constrained the fossil to within a narrow age range of 3.8–3.4 Ma in the mid-Pliocene. Presence of this hypercarnivorous canid in the Pliocene of Tibet, along with the pantherine cat *Panthera blytheae* and the fox *Vulpes qiuzhudingi*, suggests a predator guild with predominately carnivorous diet characteristic of modern arctic carnivores such as the arctic fox and polar bear. Wintering in extremely cold climates may have been the cause of such adaptations. *Sinicuon* shows transitional morphology to modern hypercarnivorous hunting dogs in southern Asia (*Cuon*), suggesting a linkage of the high Tibetan Plateau to the southern continents.

Modern wild sheep, *Ovis*, is widespread in the mountain ranges of the Caucasus through Himalaya, Tibetan Plateau, Tianshan-Altai,

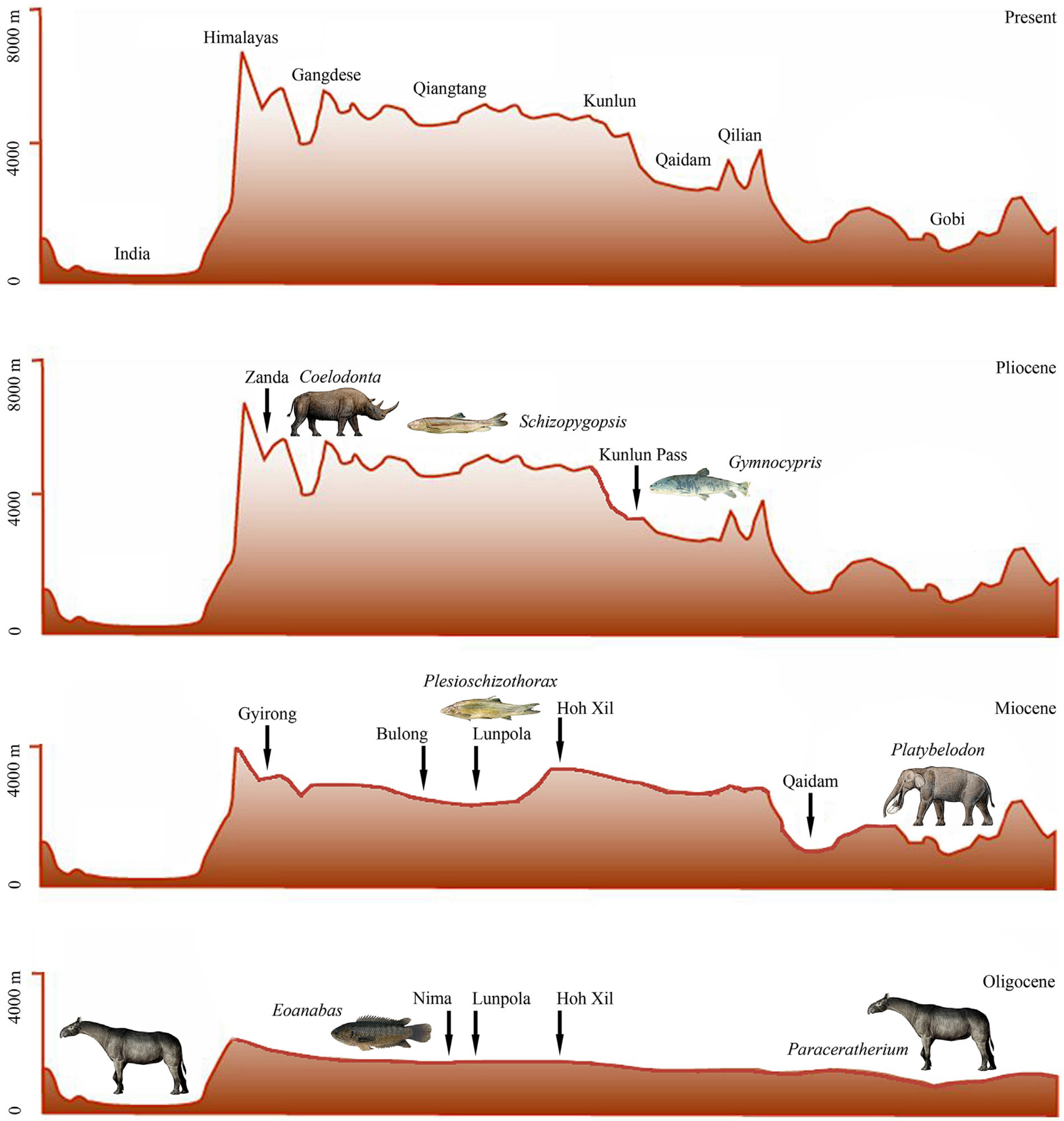

Fig. 10. South-north elevation profiles of the Tibetan Plateau from the Oligocene to the Present based on paleontological evidence, showing distribution of the Oligocene giant rhino (*Paraceratherium*) and climbing perch (*Eoanabas*), the Miocene shovel-tusked elephant (*Platybelodon*) and primitive snow carp (*Plesioschizothorax*), and the Pliocene woolly rhino (*Coelodonta*) and highly specialized snow carps (*Schizopygopsis* and *Gymnocypris*).
(Modified from Deng and Ding, 2015)

eastern Siberia, and the Rocky Mountains in North America (Rezaei et al., 2010). In Eurasia, fossil sheep are known at a few Pleistocene sites in North China, eastern Siberia, and Western Europe, but are so far absent from the Tibetan Plateau. An extinct sheep, *Protovis himalayensis* from the Pliocene of the Zanda Basin not only expands fossil sheep records to the Pliocene Tibetan Plateau, but also suggests that the Tibetan Plateau, possibly including Tianshan-Altai, represents the ancestral home ranges of mountain sheep and that these basal stocks were the ultimate source of all extant species (Fig. 9), consistent with the previous Out of Tibet hypothesis (Deng et al., 2011). *P. himalayensis* is smaller than the living argali (*Ovis ammon*), and it shares with *Ovis* posterolaterally arched horncores and partially developed sinuses and possesses several transitional characters leading to *Ovis*. The fossil locality of *P. himalayensis* is not far from one of the paleo-islands formed by metamorphic basement rock, and these cliffs probably provided protection from predators in times of danger (Wang et al., 2016).

An analysis of stable carbon isotopes in herbivores' tooth enamel from the Zanda Basin indicate that C_3 plants were the dominant vegetation in the Zanda area during the Pliocene (Wang et al., 2013), suggesting that *Protovis* likely subsisted on C_3 plants like modern bovids on the Tibetan Plateau. Ancestral sheep in the Tibetan Plateau occupied the same range of distribution as the modern argali so that it adapted to high altitude and cold environments in the Pliocene, when conditions elsewhere (including the high Arctic regions) were much warmer (Ballantyne et al., 2010). These ancestral stocks evolved rapidly to morphological conditions similar to that of living *Ovis*. By the time the Ice Age arrived around 2.6 Ma, *Ovis* possessed a competitive advantage for surviving in freezing environments and spread rapidly to regions surrounding the Plateau and beyond, reaching North America during the Late Pleistocene (Wang, 1988; Wang et al., 2016).

5. Conclusions

The Tibetan Plateau is the youngest and highest plateau on Earth, and its elevation reaches one-third of the height of the troposphere, with profound dynamic and thermal effects on atmospheric circulation and climate. The uplift of the Tibetan Plateau was an important factor of global climate change during the late Cenozoic and strongly influenced the development of the Asian monsoon system. However, there have been heated debates about the history and process of Tibetan Plateau uplift, especially the paleo-elevations in different geological times (Deng et al., 2012a).

Our research shows that the paleo-elevations of the Nima and Lunpola basins were lower than 2000 m during the Oligocene, and the general topography of the Tibetan Plateau at that time had not enough height to hinder the migration of large-sized mammals. For example, the giant rhino *Paraceratherium* and others still passed through the Tibetan Plateau from north to south. Until the Miocene, data of the Gyirong, Lunpola, and Hoh Xil basins reflect the uplift of the plateau to reach about 3000 m, which became an obstacle for the exchange of the shovel-tusked elephant *Platybelodon* and other mammals. Up to the Pliocene, the Zanda Basin in southern Tibetan Plateau and the Kunlun Pass Basin in northern Tibetan Plateau reached the modern elevations of > 4000 m, causing the formation of the cryospheric environment and the appearance of the Ice Age fauna (Fig. 10).

Paleontologists have long been searching but unsuccessfully for the ancestors of the Quaternary Ice Age fauna that adapted to cold climate in the Pliocene and Early Pleistocene Arctic tundra and steppe. The research on the mammalian fossils found from the late Cenozoic deposits in the representative Zanda Basin of the Tibetan Plateau has now led to the realization that the cold climate of the Tibetan Plateau, which reached the modern or near modern elevation during the Pliocene, forced the ancestors of the Quaternary Ice Age fauna to spend their early evolutionary time in cold environments.

Acknowledgements

We gratefully acknowledge the enthusiastic participation of our field work in the Tibetan Plateau, including Zhijie Jack Tseng, Liu Juan, Gary Takeuchi, Xie Guangpu, Ni Xijun, Zhang Chunfu, Zhao Min, Wang Ning, Shi Qinqin, Li Yangfan, Li Yu, Li Yikun, Sun Boyang, Lu Xiaokang, Dong Liping, Rong Yufen, Sun Danhui, Xiong Wuyang, Li Chunxiao, Bi Dairan, Fang Gengyu, Su Tao and other colleagues in Xishuangbanna Tropical Garden, CAS. We thank Prof. Chang Mee-mann for her valuable discussion. The reviewers and editors are kindly acknowledged for their comments on the manuscript. Special thanks to Prof. Guo Zhengtang for his invitation to write this review paper. This work was supported by the Chinese Academy of Science (XDA20070203, XDB26000000, QYZDY-SSW-DQC022, GJHZ1885) and the National Natural Science Foundation of China (41430102).

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