

Tibetan Plateau: An evolutionary junction for the history of modern biodiversity

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Abstract Holding particular biological resources, the Tibetan Plateau is a unique geologic-geographic-biotic interactively unite and hence play an important role in the global biodiversity domain. The Tibetan Plateau has undergone vigorous environmental changes since the Cenozoic, and played roles switching from “a paradise of tropical animals and plants” to “the cradle of Ice Age mammalian fauna”. Recent significant paleontological discoveries have refined a big picture of the evolutionary history of biodiversity on that plateau against the backdrop of major environmental changes, and paved the way for the assessment of its far-reaching impact upon the biota around the plateau and even in more remote regions. Here, based on the newly reported fossils from the Tibetan Plateau which include diverse animals and plants, we present a general review of the changing biodiversity on the Tibetan Plateau and its influence in a global scale. We define the Tibetan Plateau as a junction station of the history of modern biodiversity, whose performance can be categorized in the following three patterns: (1) Local origination of endemism; (2) Local origination and “Out of Tibet”; (3) Intercontinental dispersal via Tibet. The first pattern is exemplified by the snow carps, the major component of the freshwater fish fauna on the plateau, whose temporal distribution pattern of the fossil schizothoracines approximately mirrors the spatial distribution pattern of their living counterparts. Through ascent with modification, their history reflects the biological responses to the stepwise uplift of the Tibetan Plateau. The second pattern is represented by the dispersal history of some mammals since the Pliocene and some plants. The ancestors of some Ice Age mammals, e.g., the wholly rhino, Arctic fox, and argali sheep first originated and evolved in the uplifted and frozen Tibet during the Pliocene, and then migrated toward the Arctic regions or even the North American continent at beginning of the Ice Age; the ancestor of pantherines (big cats) first rose in Tibetan Plateau during the Pliocene, followed by the disperse of its descendants to other parts of Asia, Africa, North and South America to play as top predators of the local ecosystems. The early members of some plants, e.g., Elaeagnaceae appeared in Tibet during the Late Eocene and then dispersed and were widely distributed to other regions. The last pattern is typified by the history of the tree of heaven (*Ailanthus*) and climbing perch. *Ailanthus* originated in the Indian subcontinent, then colonized into Tibet after the Indian-Asian plate collision, and dispersed therefrom to East Asia, Europe and even North America. The climbing perches among freshwater fishes probably rose in Southeast Asia during the Middle Eocene, dispersed to Tibet and then migrated into Africa via the docked India. These cases highlight the role of Tibet, which was involved in the continental collision, in the intercontinental biotic interchanges. The three evolutionary patterns above reflect both the history of biodiversity on the plateau and the biological and environmental effects of tectonic uplift.

Keywords Tibetan Plateau, Cenozoic, Biodiversity, Evolution, Plants, Fish, Mammals

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1. Introduction

Tibetan Plateau, the highest and youngest plateau all over the world, with the unique geologic-geographic-ecologic interactions, has long been considered as the “natural laboratory” for the research on the environmental changes and life’s evolutionary history (Zheng and Yao, 2006; Chang and Miao, 2016; Yao et al., 2017). Part of Tibetan Plateau has been taken on the mantle of “forbidden zones” for its severe coldness, lack of oxygen, scarce precipitation and strong ultraviolet radiation. Having said that, the Tibetan Plateau and its adjacent areas in the southwestern mountains of China, the eastern Himalayas, and the Central Asian mountains are among the 36 biodiversity hotspots identified by Conservation International (Myers et al., 2000), indicating that its biodiversity is at a fairly high level. The Tibetan Plateau has undergone complex and large-scale environmental changes during geological history (An et al., 2001; Zheng and Yao, 2006; Royden et al., 2008; Wang et al., 2008; Zhu et al., 2013; Spicer, 2017; Su et al., 2019a, 2019b). Such geological movements and geomorphological evolution triggered and formed the climate pattern in the Tibetan Plateau and its surrounding areas, such as the monsoon climate in southwestern China, characterized by seasonal rainfall (Jacques et al., 2011; Xing et al., 2012; Su et al., 2013). These changes in landforms and climate undoubtedly affect the distribution and evolution of organisms, which may have promoted the development of the biodiversity in the region and also led to the extinction of some organisms (Huang et al., 2016). Therefore, the formation of the Tibetan Plateau not only has a tremendous impact on shaping the modern biodiversity of the region, but also plays an important role in promoting the intercontinental dispersal of many species originating from the plateau and even the ancestors of many modern widespread groups (Tseng et al., 2014; Wang et al., 2014, 2016; Favre et al., 2016; Fuentes-Hurtado et al., 2016; Deng et al., 2019).

Taking mammals as an example, the mammalian fauna in modern Tibetan Plateau is characterized by high-altitude habitat, low diversity, and strong adaptability to cold and hypoxic environment. Half of the mammalian fauna are endemic to the region, which is mainly due to the strong barriers formed by the surrounding mountains (such as the Himalayas) and the harsh environment of the plateau (Hoffmann, 1991). Jiang et al. (2018) found that the total number of ungulates in the Tibetan Plateau accounts for 42% of the total in China, and the proportion of endemic species is as high as 32%. In recent years, more and more fossil records have provided important evidence for understanding the

history of mammal diversity in the Tibetan Plateau (Wang et al., 2015b; Li Q et al., 2017; Wang et al., 2019). Most of the modern mammals in the Tibetan Plateau have a long history on the plateau, at least dating back to the Pliocene, which proves that they have a long-term adaptation process in the high-altitude plateau areas. Some of them expanded their distribution in the Pleistocene and became an important member of the Holarctic realm fauna at high latitudes (Deng et al., 2012; Wang et al., 2015b). In extreme cold climates and rarefied air, the Tibetan Plateau may have become an adaptation base for these animals during the Pliocene. When the Ice Age came, the ecological environment of the Arctic and the north regions began to expand, and the fauna of the Tibetan Plateau occupied a dominant position in the competition with other fauna in northern Eurasia and even North America (Wang et al., 2015b; Deng et al., 2019).

As plants are concerned, the Tibetan Plateau and its adjacent regions bear rich plant diversity (Wu, 1987; Wu, 2008; Zhang et al., 2016), and are the centers of distribution and diversification for many taxa (Gao et al., 2015; Yu et al., 2015). The complex topography caused by rapid uplift of the plateau during the Neogene, together with the regular fluctuation of climate during the Quaternary, further accelerated the radial differentiation and diversification of plants (Qiu et al., 2011; Wen et al., 2014). The diversification at both genus and species levels related to not only the adaptable radiation of local species stimulated by the rapid uplift of the plateau, but also the species vicariance caused by the complexity of topography (Yu et al., 2018). During the late Quaternary, some species extensively migrated and spread (Cun and Wang, 2010), and some other cold-tolerant species migrated in long distance from the Tibetan Plateau into East Asia, North America, Europe, and even alpine or cold regions of Arctic (Matuszak et al., 2016). Therefore, the Tibetan Plateau is often considered as the radiation region of plants in the North Temperate Zone (Wu, 1987).

The formation of biodiversity patterns is usually considered to be related to geological activities and past climate changes, and is a moment in the long history of geological and biological evolution (Wiens and Donoghue, 2004; Sandel et al., 2011; Spicer, 2017). Not only the organisms originating in the Tibetan Plateau affect the Neogene biogeographical pattern through dispersal, but the evolution of biodiversity in China and its neighboring areas is also strongly influenced by the uplift of the Tibetan Plateau (Deng et al., 2015). The Tibetan Plateau has created conditions for the origin, differentiation and global dispersal of species, and influenced the formation and succession of modern flora and fauna, making it one of the important

centers of global species formation, differentiation and dispersal (Jiang et al., 2018). In recent years, a series of new discoveries of plateau paleontology have greatly enriched the knowledge of the life history of the Tibetan Plateau. Compared with the past, we can have a more comprehensive look at the significant role that the plateau has played in the evolution of biodiversity of the Cenozoic world from the perspective of a longer history and greater space (from the Neogene to the Paleogene). This paper systematically reviews the latest research results of plateau paleontology and summarizes the status of the Tibetan Plateau as an evolutionary junction of the development of biodiversity, which is embodied in three forms: (1) Local origination of endemism; (2) Local origination and “Out of Tibet”; (3) Intercontinental dispersal via Tibet.

2. Local origination of endemism

Due to its unique physical conditions, the Tibetan Plateau has become an “ecological island” that is isolated from the surrounding lower areas, thus forming a unique high-altitude biogeographical biota containing many endemic animal and plant species. The biodiversity of the modern Tibetan Plateau is represented by fish and mammals, which have left fossil records during the uplift of the plateau, clearly depicting the evolutionary history of their respective groups (Figure 1).

2.1 Schizothoracine fishes (snow carps)

Living schizothoracine fishes are a special group of cyprinid species that adapt to the high-altitude environment in Asia. It lives in water systems of the Tibetan Plateau and its surrounding areas and consists of 11 to 12 genera, more than 100 species and subspecies (Berg, 1912; Hora, 1953; Wu and Wu, 1992; Chen and Cao, 2000). They are considered to be a group that evolved with the uplift of the Tibetan Plateau (“Ascent with Modifications”, refer to Chang et al., 2010; Chang and Miao, 2016) as the staged differentiation of their morphological characteristics and the step-wise distribution of the elevation of the gathering place are consistent with the history of plateau uplift (Chen et al., 1996). Morphologically, they form a monophyletic group (Chen, 1998; Kullander et al., 1999; Chen and Cao, 2000), and are divided into three levels: primitive, specialized and highly specialized levels. The classification is based on the morphology of scales, the number of tentacles, the rows of pharyngeal teeth, and their distribution in three consecutive altitude ranges with decreasing water temperature (Cao et al., 1981; Chang et al., 2010; Chang and Miao, 2016). The species of the primitive level are covered with fine scales and provided with 3 rows of pharyngeal teeth and 2 pairs of tentacles, living in the water system with an altitude of 1250–2500 m; the specia-

lized species are degraded in the chest and abdomen scales, reduced to 2 rows of pharyngeal teeth and 1 pair of tentacles, living in the water system with altitude of 2750–3750 m; the highly specialized species are completely bare and scale-free, with 2 or even 1 row of pharyngeal teeth, distributed in the water system of 3750–4750 m above sea level (Cao et al., 1981) (Figure 1). Although molecular analysis suggests that the Schizothoracinae does not constitute a natural taxon, the primitive class and the specialized and highly specialized classes belong to two different clades, and each group also contains several barbinae species (Yang et al., 2015). However, the classification of Schizothoracinae has not been finalized at the current research level. Following the viewpoint of morphology, the subfamily Schizophrenidae in this paper is considered as a monophyletic group for the time being.

Based on the morphological characteristics, it is believed that the Schizothoracinae evolved from some primitive barbinae species of the family Cyprinidae during the uplift of the Neogene Tibetan Plateau (Cao et al., 1981; Wu, 1984; Chen et al., 1996). The Paleogene fish fauna in Tibet are significantly different from today's, including members of Perciformes and Cyprinidae. The main components of Cyprinidae are widely distributed barbinae-like species. During a certain period from Paleogene to Neogene, there should be a remarkable change from barbinae-like species to Schizothoracinae. Wang and Wu (2015) discovered *Tchunglinius tchangii* in the Late Oligocene strata of the Nima Basin, northern Tibet. It is small and closely related to living small fishes of the subfamily Barbinae in South Asia and Africa, such as *Puntius*. During the Oligocene, the uplift of the Tibetan Plateau was not significant, so the tropical-subtropical lowland fish such as *T. tchangii* lived in this area.

An important shift occurred at the turn from the Oligocene to the Miocene. *Plesioschizothorax macrocephalus*, an early schizothoracine fish, was discovered in the Dingqing Formation of the Lunpola Basin, central Tibetan Plateau. It is a primitive schizothoracine fish with 3 rows of pharyngeal teeth (Wu and Chen, 1980; Chang et al., 2008), living in the Early Miocene (Deng et al., 2012a). The present altitude of the fossil site is 4540–4550 m, which belongs to the distribution range of present highly specialized schizothoracines, which indicates the strong uplift of the Tibetan Plateau since the Miocene. After the Pliocene when the plateau reached its modern height and overall scale (Deng et al., 2012b), highly specialized schizothoracines with 2 or even 1 row of pharyngeal teeth appeared in the Zanda Basin in the southwestern part of the Tibetan Plateau and the Pliocene Qiangtang Formation in the Kunlun Pass in the northeastern part of the Tibetan Plateau (Chang et al., 2010; Wang and Chang, 2010; Chang and Miao, 2016). Recently, a fossil cyprinid was reported in the Qaidam Basin, and it was classified in the Schizothoracinae (Yang et al., 2018). However, the ichthyologists have some reservations about

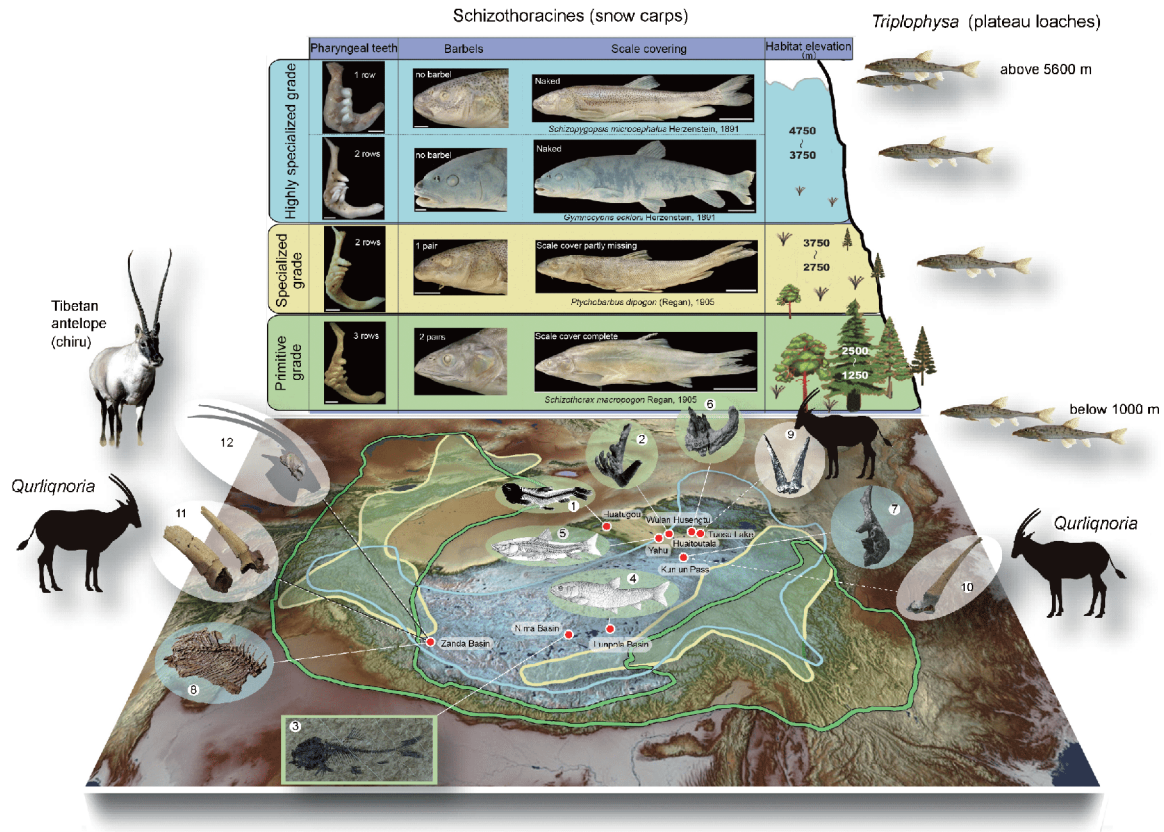


Figure 1 Local origination of endemism of fishes and mammals in the Tibetan Plateau. The morphological variations and spatial distribution (vertical plane) of living schizothoracine fishes (snow carps) in the Tibetan Plateau and the fossil records of cyprinids and bovines (horizontal plane), the altitudes on the right side represents the distribution range of *Triplophysa* (plateau loaches) in the plateau and its surrounding areas. Fossil sites and fossil taxa: 1. Oligocene cyprinid with 3 rows of pharyngeal teeth in Huatugou, Qaidam Basin; 2. Oligocene cyprinid with 3 rows of pharyngeal teeth in Wulan Husentu, Qaidam Basin; 3. Late Oligocene *Tchunglinius tchangii* with 3 rows of pharyngeal teeth in Nima Basin; 4. Early Miocene *Plesioschizothorax macrocephalus* with 3 rows of pharyngeal teeth in Lunpola Basin; 5. Pliocene *Hsianwenia wui*, with 3 rows of pharyngeal teeth in Qaidam Basin; 6. Late Miocene cyprinid with 3 rows of pharyngeal teeth in Huaitoutala, Qaidam Basin; 7. Pliocene highly specialized *Gymnocypris* with 2 rows of pharyngeal teeth in Kunlun Pass; 8. Pliocene highly specialized schizothoracine in Zanda Basin; 9. Late Miocene *Qurliqnorina* in Qaidam Basin; 10. Pliocene transitional *Qurliqnorina* in Kunlun Pass; 11. Pliocene transitional *Qurliqnorina* in Zanda Basin; 12. Pleistocene *Pantholops hundsensis* in Zanda Basin (Neurocranium fossils).

the details of the interpretations of the anatomy and the result of the phylogenetic analysis.

Gymnocypris is a major member of the highly specialized schizothoracines, composed of 10 living species and subspecies, occupying most of major water systems on the Tibetan Plateau (Wu and Wu, 1992; Chen and Cao, 2000). The Pliocene highly specialized schizothoracine fossils found in the Kunlun Pass Basin are the genus *Gymnocypris*, which were collected at the present altitude of 4769 m and originated near today's Golmud River (Figure 1). Nowadays, *Gymnocypris* still exists in the north and south of the East Kunlun Mountains. A large number of fish fossils in the Kunlun Pass Basin suggest that there was still a relatively wide distribution of water in this area during the Pliocene, and the water bodies on the north and south sides of the East Kunlun Mountains may be connected, which provides living conditions for highly specialized schizothoracines. The uplift of the Eastern Kunlun Mountains after the Late Pliocene separated water bodies in this area and promoted the dif-

ferentiation of *Gymnocypris* (Wang and Chang, 2010).

2.2 *Triplophysa* (plateau loaches)

There are about 140 valid species of *Triplophysa* (Li J X et al., 2017), mainly distributed in the Tibetan Plateau and its adjacent areas (Chen and Yang, 2005). Morphological studies suggest that the Noemacheilidae is a family within Cobitoidea (Nalbant and Bianco, 1998), and recent molecular biological studies support similar conclusions (Tang et al., 2006; Slechtova et al., 2007).

Triplophysa is the most diverse group of the Noemacheilidae, and it is also a special group of the Noemacheilidae adapted to the alpine environment of the Tibetan Plateau. Together with the cyprinid schizothoracines, it constitutes the main fish fauna of the Tibetan Plateau. Some species of the *Triplophysa* are even said to adapt to the higher altitude and harsher living environment (such as some small shallow saltwater bodies) that the schizothoracine fishes cannot sur-

vive (above 5600 m, Zhang and He, 1997), thereby becoming the fish species distributed highest in the world (Wu and Wu, 1992; He et al., 2006) (Figure 1). In some specific small waters of the Tibetan Plateau, the number of individuals of *Triplophysa* exceeds that of the schizothoracines. However, although *Triplophysa* is the only representative of the living noemacheilids in the Tibetan Plateau, their distribution is not limited to the plateau and surrounding areas like the schizothoracines. Some species are distributed eastward in waters below 1000 m in central China (Zhu, 1989).

Based on morphological characteristics and geographical distribution, many scholars believe that the origination and evolution of *Triplophysa* are related to the uplift of the Tibetan Plateau (Zhu, 1986, 1989; Wu and Wu, 1992). Molecular biological analysis also yields the same judgment (He et al., 2006; Wang Y et al., 2016), but there is no fossil evidence in the past. Wang and Chang (2012) discovered the *Triplophysa* fossils in the lower part of the Pliocene Qiangtang Formation in the Kunlun Pass Basin at an altitude of 4769 m. The number of *Triplophysa* fossils was significantly higher than that of schizothoracines in the same layer at the fossil location. This not only supports the hypothesis that *Triplophysa* originated in the Tibetan Plateau, but also shows that the composition of the fish fauna in this area was very close to today's.

The isolated water systems around the Kunlun Pass Basin, namely the Qaidam inner stream system, and the upper reaches of the Yellow River and the Yangtze River, share several species of the genus *Triplophysa*, suggesting that they may originate before these water systems were separated (Wang and Chang, 2012). On the other hand, these water systems have their own unique *Triplophysa* species, indicating that these fishes continued to differentiate after the water systems were separated from each other (Zhu, 1989; Wu and Wu, 1992; Wu et al., 1994). The discovery of the Pliocene *Triplophysa* fossils in the Kunlun Pass Basin provides preliminary evidence for the traceability of the distribution pattern of modern *Triplophysa*. According to the latest research of molecular biology (Wang Y et al., 2016), the evolutionary history of *Triplophysa* may be much earlier than the current fossil record. Collecting more and better fossil materials to carry out more in-depth systematic studies, combined with molecular analysis, is the exploration direction for the evolution history of *Triplophysa*.

2.3 *Pantholops hodgsonii* (chiru)

The origin of the chiru *Pantholops hodgsonii* provides another representative example of the local evolution of indigenous species on the Tibetan Plateau, whose ancestors can be traced back to the Late Miocene. In the Qaidam Basin in the northern part of the Tibetan Plateau, *Qurlignoria* is an extinct bovid with the straight and upward horns (Bohlin,

1937; Wang et al., 2007, 2011), which has been considered as the ancestor of the chiru (Gentry, 1968). In the Kunlun Pass Basin, 4400–5000 m above sea level on the southern side of the Qaidam Basin, the horn core fossils of *Qurlignoria* were found in the beds from Pliocene to Pleistocene (Li et al., 2014; Wang et al., 2015b). In the Zanda Basin on the southwestern margin of the Tibetan Plateau, the *Qurlignoria* horns were discovered from the Early Pliocene strata (Deng et al., 2011). In the Pleistocene, *Pantholops hundsensis*, an extinct species of the chiru, was discovered at high altitudes near the Zanda Basin (Lydekker, 1901) (Figure 1). The Late Miocene mammals in the Qaidam Basin have begun to show a certain level of localization (Wang et al., 2007). The discovery of the above-mentioned *Qurlignoria* and the chiru on the Tibetan Plateau indicates that both have a long evolutionary history in the region. Assuming that *Qurlignoria* and the chiru are closely related as indicated by the horn shape, the origin of the chiru on the Tibetan Plateau (Fernández and Vrba, 2005) is quite credible. Even if *Qurlignoria* has no close relationship with the chiru, the latter is highly likely to originate from the Tibetan Plateau. Because the chiru is completely confined to the Tibetan Plateau, it is a unique species of the plateau, whether it is walking into or out of the Tibetan Plateau.

3. Local origination and “Out of Tibet”

As an evolutionary center of biodiversity, the Tibetan Plateau has bred a unique ecological environment at different stages of its uplift; also, many species originated here spread to other parts of the world in a suitable climate. Depending on the connection of the land bridge, some groups even crossed the ocean and spread to other continents (Figure 2).

3.1 *Elaeagnus*

Elaeagnus belongs to the family Elaeagnaceae in the order Rosales, which includes three genera, namely *Hippophae*, *Elaeagnus*, and *Shepherdia*. There are more than 80 species in Elaeagnaceae with modern distribution mainly in South-east Asia. Two genera with about 60 species are distributed in China. The southeastern margin of the Tibetan Plateau is the diversification center of many plant taxa such as Elaeagnaceae, which related to the dramatic tectonic activities of the plateau (Su et al., 2019b). These tectonic activities shaped the complex topography and diverse climate types, and created conditions for speciation (Favre et al., 2015). Besides, *Elaeagnus* and *Hippophae* are distributed in different environmental conditions. As their distribution ranges on the Tibetan Plateau are concerned, the elevation ranges of most *Hippophae* species are 3000–5000 m, whereas the elevation ranges of most *Elaeagnus* species are lower than

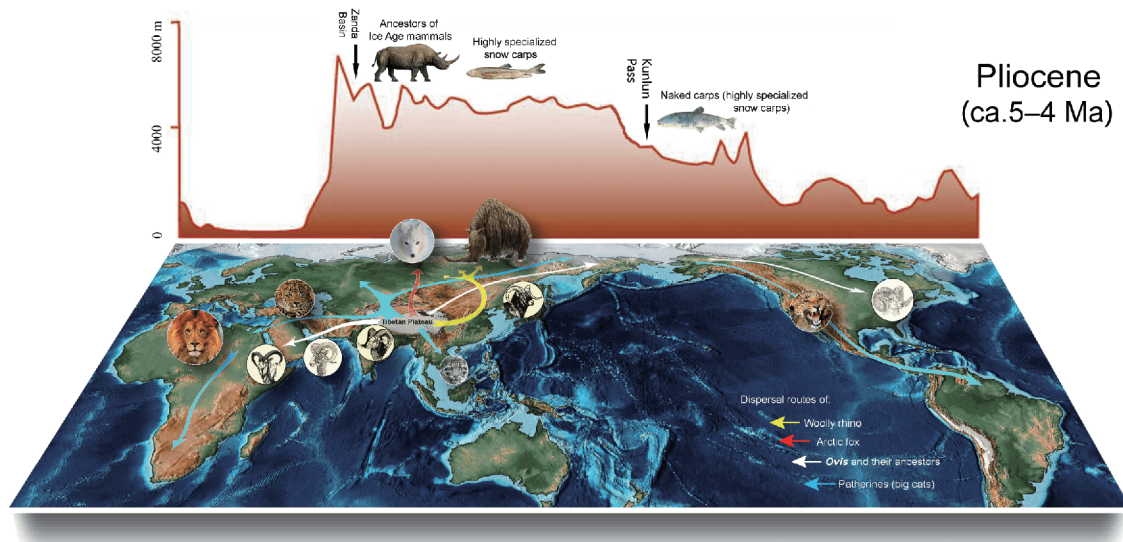


Figure 2 Local origination and “Out of Tibet” of mammals in the Tibetan Plateau.

3200 m (Qin and Michael, 2007). Therefore, these two genera have different ecological niches, which might have further promoted the speciation.

Macrofossil records of Elaeagnaceae are rare. As leaf fossil records are concerned, only one fossil species, *Shepherdia weaveri*, was reported from the Lower Oligocene of Montana (Becker, 1960) and the Miocene of Alaska, USA (Hollick, 1936). Until now, *Elaeagnus tibetensis* from the Upper Eocene of the Mangkang Basin is the earliest macrofossil record in Elaeagnaceae, and the southeastern margin of the Tibetan Plateau is also the modern diversification center of Elaeagnaceae (Su et al., 2014).

We can briefly conclude the history of distribution in Elaeagnaceae based on limited fossil records. Rosales is considered to originate during the Late Cretaceous (Friis et al., 2011; Soltis et al., 2011). The discovery of *E. tibetensis* suggests that Elaeagnaceae originated in Laurasia by the Late Eocene, much earlier than the origin during 30–10 Ma estimated by molecular data (Bell et al., 2010). Because fruits of Elaeagnaceae are colorful and eatable, birds might play important roles for the dispersal (Shafroth et al., 1995). Nowadays, only one species, *E. commutata*, is naturally distributed in North America. According to fossil records and modern distribution ranges, Elaeagnaceae might have migrated between Asia and North America via the Bering Land Bridge.

3.2 Gerridae (water strider)

The family Gerridae is a kind of common semi-aquatic insects that lives mainly in ponds, lakes, rivers and other waters in terrestrial ecosystems, and a few species of this group can also live in seawater (Andersen, 1982). According to the

taxonomy, Gerridae belongs to the order Hemiptera, infra-order Gerromorpha. The Gerromorpha is widely distributed around the world, and about 2000 species have been described and distributed in temperate, subtropical and tropical regions up to now (Polhemus and Polhemus, 2008).

The genus *Aquarius* is one of the three most common and widespread genera in the living Gerrinae (Gerridae), which is of great significance to the study of biogeography, evolutionary trend and ecological adaptability of gerrids. There are few reports on the gerrid fossils, so little is known about the early evolution and biogeography of the living gerrids. One fossil gerrid species, *Aquarius lunpolaensis* (Lin, 1981) found in the upper and middle Dingqing Formation of the Lunpola and Nima basins in northern Tibet is very close to the representative of present *A. najas* species group in external morphological characteristics. Combining the similar body shape and leg characteristics of *A. lunpolaensis* and its living relatives, it is proved that this kind of extinct gerrine once lived on the surface of ancient lakes in central Tibetan Plateau, and may also be the prey of some fish in these lakes (Wu et al., 2017). Because of its primitive ancestral characteristics, *A. lunpolaensis* may be a basal taxon of *A. najas* group, which is the sister species of three living species (Cai et al., 2019).

The living *A. najas*-group is currently distributed in the western part of the Palearctic only (Damgaard, 2005). Among them, *A. najas* is a common Palearctic gerrine in the west of the Ural Mountains (Andersen, 1990); *A. ventralis* is distributed in the Balkans and Levant regions, such as Bulgaria, Greece, Turkey, Cyprus, Lebanon, and Israel; while *A. ventralis* is distributed in the west of the Mediterranean region, such as France, Italy, Portugal, Spain, and Morocco (Andersen, 1990; Damgaard, 2005). The discovery of fossils

has proved that this group is more widely distributed (Cai et al., 2019) in the Late Oligocene (23.5–26 Ma, DeCelles et al., 2007; Sun et al., 2014). The primitive features displayed by the *A. lunpolaensis* also indicate that the un-uplifted Tibet region is an important area for the early evolution of the genus.

3.3 Arctic fox

Many morphological and physiological characteristics enable the Arctic fox *Vulpes lagopus* to adapt to cold environments: long and thick hair, 70% villus underneath, strong body, short ears and legs, thermal circulation system of feet, and slower metabolic rate in cold environments (Audet et al., 2002; Prestrud, 1991), while the Tibetan fox *V. ferrilata* also boasts (such as thick hair) (Clark et al., 2008). The most obvious feature of the living Tibetan fox is its long mouth and short limbs (Clark et al., 2008; Pocock, 1937). The total-evidence phylogenetic tree of the genus *Vulpes* shows that *V. lagopus* and *V. ferrilata* form a branch with the kit fox *V. macrotis* and the swift fox *V. velox* (Fuentes-González and Muñoz-Durán, 2012).

The geological age of *Vulpes qiuzhudingi* found in Zanda Basin is 4.42–5.08 Ma, corresponding to the Early Pliocene (Wang X M et al., 2013). The size of *V. qiuzhudingi* is similar to that of the living male *V. vulpes*, about 20% larger than that of the living and Late Pleistocene *V. lagopus*. The difference between *V. qiuzhudingi* and all other foxes is that it has more carnivorous teeth. The sharp talonid of m1-2 is mainly composed of hypoconid, the entoconid degenerates or disappears, the talonid is shorter, and the m3 is missing. *V. qiuzhudingi* was also found in the Pliocene strata of Kunlun Pass Basin in the northern Tibetan Plateau. Its dental characteristics indicate a higher altitude (4726 m), a younger geological age, and a higher carnivorous stage (Wang et al., 2014).

The characteristics of m1-2 of *Vulpes qiuzhudingi*, which point to highly carnivorous habit, are different from those of *V. ferrilata*. This feature is rarely reversed to a moderate carnivorous form during the evolution (Tedford et al., 2009; Wang et al., 1999; Wang, 1994), and high carnivory is often accompanied by an increase in body size (Van Valkenburgh et al., 2004), so *V. qiuzhudingi* and *V. ferrilata* are of different evolutionary branches. Studies have shown that *V. qiuzhudingi* and *V. lagopus* form a branch that evolved in the cold environment of the Tibetan Plateau with the *V. ferrilata* branch: the former marched to be highly carnivorous and eventually evolved into *V. lagopus*, while the latter retained the primitive characteristics of the teeth and evolved into *V. corsac* and *V. ferrilata*. Isotope analysis indicates that the Zanda Basin approached the modern average temperature of 0°C in the Pliocene (Saylor et al., 2009) or the annual average temperature was slightly higher than now (Wang Y

et al., 2013). The Zanda region in the Pliocene had a very low temperature in winter, while the polar regions of that time were much warmer than today, with an average annual temperature of 8°C (Brigham-Grette et al., 2013; Ballantyne et al., 2010; Csank et al., 2011). This shows that during the Pliocene, the environment of the Tibetan Plateau was worse than the Arctic, thus the foxes might face greater challenges for survival on the plateau.

The discovery of the *V. qiuzhudingi* traces the history of the Arctic fox's ancestor to the Tibetan Plateau (Figure 2). Its era is much earlier than previously thought, and it has very special adaptations to extensive carnivory. The real Arctic fox *V. lagopus* fossils did not appear in Europe until the Late Pleistocene (Croitor and Brugal, 2010), when they were widely spread in most parts of Europe, from Kiev in the east and Ireland in the west (Kurtén, 1968). The *V. lagopus* fossils from Siberia and North America were only found in the Late Pleistocene (Youngman, 1993; Fortelius, 2018). Similar types of cold-adapted carnivores that originated in the Pliocene Tibetan Plateau migrated to other areas during the Quaternary Ice Age, include *Chasmaporthetes gangsiensis* (Tseng et al., 2013) and *Sinicuon* cf. *dubius* (Wang et al., 2015a) etc. The close relatives of *V. lagopus* found on the Tibetan Plateau and other highly carnivorous species show that the carnivorous fauna was dominated by the hunting components, similar to those of the modern Arctic region (Arctic fox, grey wolf, and polar bear) (Wang et al., 2014). The extremely cold climate in winter may be an important selective factor for such an adaptation.

3.4 Snow leopard

The snow leopard *Panthera uncia* is a typical alpine cat, distributed in the Tibetan Plateau and its surrounding areas. It inhabits the bare rock areas of high mountains where are snow-covered for most of the year. *P. uncia* is active in the altitudes from 4000 m to near the snow line. As large living cats, Pantherinae (including *Neofelis nebulosa*, *N. diardi*, snow leopards, tigers, jaguars, leopards and lions) are among the top predators in their environment. They play an important role in today's ecosystems, but unfortunately, several of them are much endangered. Little is known about their evolutionary history before, for which only phylogenetic analysis of molecular biology can be relied on. According to the analysis of mitochondrial genome of the genus *Panthera* by the scholars including Wei et al. (2011), lions are the closest related species of *P. uncia*, while *Panthera* is composed of tigers, leopards, snow leopards, jaguars and lions. They also propose that *Neofelis nebulosa* should be classified in the genus *Panthera*.

New pantherine fossil materials are scarce and often conflict with the time estimates of molecular phylogenetic analysis (Davis et al., 2010; Werdelin et al., 2010; Werdelin

and Peigne, 2010). Molecular studies have shown that the subfamily Pantherinae has undergone a long evolutionary history, and explosive radiation has only emerged recently (Johnson et al., 2006; Davis et al., 2010). According to molecular biological information, subfamily Pantherinae should have appeared in the Miocene, while the fossils had not been clearly recorded until the Pleistocene, hence leaving a gap of 4 Myr between them. Previously, most of fossil materials of Pantherinae were poorly preserved and their systematic positions were unknown, which poses many uncertainties on the speculations of their origin centers and intercontinental dispersal routes.

Tseng et al. (2014) reported the Pliocene fossil of *Panthera blytheae* found in the Zanda Basin, Tibet. The material includes a nearly complete skull and some other specimens with a geological age of 5.95–4.42 Ma., i.e., from Late Miocene to Early Pliocene (Wang X M et al., 2013). The fossil record of the subfamily Pantherinae was consequently advanced by 2 Myr, which bridged the gap of molecular and morphological speculations on the origin time of Pantherinae. Integrating morphological and molecular biological data, including feline DNA sequences (Johnson et al., 2006; Davis et al., 2010) and mitochondrial DNA sequences of the extinct *Panthera leo spelaea* and *P. leo atrox* (Barnett et al., 2009), phylogenetic analysis incorporating six living species and four fossil species of Pantherinae, including *P. blytheae*, was carried out, and the historical biogeographical analyses based on multiple data showed that the subfamily Pantherinae originated in Asia (Tseng et al., 2014) (Figure 2). The close relationship between *P. blytheae* and *P. uncia* indicates that the clades of Pantherinae existing in Central Asia might be distributed initially in the Himalayas and Central Asian Mountains. According to the composition of the Zanda fauna, the ecological pattern between the existing snow leopard and its prey was established in the Tibetan Plateau several million years ago.

3.5 *Ovis* (argali sheep)

The living argali sheep (*Ovis*) is widely distributed in the mountains and plateaus of the Caucasus, Himalayas, Tibetan Plateau, Tianshan-Altai, Eastern Siberia, and Rocky Mountains of North America. The domestic sheep *Ovis aries* is actually domesticated from the wild argali sheep (Zeuner, 1963). Rezaei et al. (2010) identified six species within *Ovis* and divided them into two major branches: one is the Central-West Asian branch including the argali *O. ammon*, urial *O. vignei*, and mouflon *O. orientalis*, and the other is the East Asian-North American branch including the snow sheep *O. nivicola*, Dall sheep *O. dalli*, and bighorn *O. canadensis*. The divergence time of these two branches is ca. 2.42 Ma. Bibi et al. (2012) draw a similar conclusion after combining the mitochondrial DNA and morphological characteristics in

their analyses.

The fossil records of argali sheep have been found in a few Quaternary fossil sites in northern China, eastern Siberia, and Western Europe; however, they have not been found in the Tibetan Plateau before. *Protovis himalayensis* discovered by Wang X M et al. (2016) in the Zanda Basin of the western Tibetan Plateau is the latest common ancestor of argali sheep. Its geological age ranges from 5.46 to 3.10 Ma (Saylor et al., 2010a, 2010b), i.e., from the terminal of the Miocene to the Pliocene (Wang X M et al., 2013). *Protovis himalayensis* is smaller than the living argali sheep. It shares the dorsal and lateral curved horn core and the initially developed sinus of horn cores with *Ovis* in morphology. At the same time, it has several transitional characteristics that had evolved towards the analogues in *Ovis*. According to the updated cladistic analysis, *Protovis* fell in the *Ovis* lineages, and the resultant interrelationships are consistent with the dispersal routes of argali sheep's ancestors from the Tibetan Plateau or Central Asia to the east and west sides (Wang X M et al., 2016).

Being the direct ancestor of argali sheep in modern Tibetan Plateau, *Protovis himalayensis* also occupied geographic areas similar to those of the living argali sheep and were gradually adapted to the high altitude and cold environment of Pliocene, when other parts of Eurasia (including the high latitude Arctic) were warmer than the plateau areas (Balanityne et al., 2010). Their ancestral group evolved rapidly into forms similar to modern *Ovis*. By the beginning of the glacial period at 2.6 Ma, they had already some advantages in surviving and competing in cold environments, and then spread rapidly to the periphery of the plateau and beyond, and finally reached North America in the Late Pleistocene (Wang, 1988) (Figure 2). As Rezaei et al. (2010) stated, the systematic relationship and distribution of argali sheep clearly reflect their migration history: They spread successfully to new areas where the speciation occurred. Even in extremely harsh environments such as the Eastern Siberian and Alaska Mountains, *O. nivicola* and *O. dalli* survived steadily.

The living argali sheep prefers to move in steep or near high mountain ranges, and can quickly escape from predators on relatively flat slopes with the advantages of their slender legs (Schaller, 1998). During the development of the Zanda Basin, the paleotopography of the basement rocks emerged in large quantities in the basin, forming rugged landforms along the shores of the ancient Zanda lake. These steep cliffs are likely to provide protection for *Protovis himalayensis* from attacks of large predators (Wang X M et al., 2016).

3.6 *Coelodonta* (woolly rhino)

The last woolly rhino *Coelodonta antiquitatis* of the Late Pleistocene is one of the most famous extinct Ice Age ani-

mals. Having a very strong skeleton, thick fur and huge nasal horns, the woolly rhino is undoubtedly one of the most famed rhinos and one of the best-known Pleistocene animals. However, the lack of fossil records obscures their early history. Before that, only a small amount of the *Coelodonta* materials came from several Chinese sites of ca. 2 Ma (Teilhard de Chardin and Piveteau, 1930; Chow and Chow, 1965; Kahlke, 1969; Zheng et al., 1985).

Coelodonta thibetana named by Deng et al. (2011) is from the strata of the Zanda Formation in the Zanda Basin. The geological age of its fossils is 5.08–3.23 Ma, which is equivalent to the early and middle Pliocene (Wang X M et al., 2013). *C. thibetana* is different from other advanced woolly rhinos (Kahlke, 1999) in a series of features, e.g., the weak ossification of its nasal septum, accounting for only one third of the length of nasal notch (Borsuk-Bialynicka, 1973; Qiu et al., 2004; Kahlke and Lacombat, 2008). Phylogenetic analysis shows that *C. thibetana* is an advanced dicerorhine. Within the branch of *Coelodonta*, the members are positioned following the evolution of derived traits, passing from *C. thibetana*, and then *C. nihowanensis* and *C. tologojensis*, and terminating as *C. antiquitatis* of the Late Pleistocene.

The snow-scraping ability of the giant and anteriorly-inclined nasal horn may be the most critical adaptation for *Coelodonta thibetana* to live in the harsh winter on the Tibetan Plateau, which represents the unique evolutionary advantage of the *Coelodonta* lineage. Such a simple but significant “innovation” was formed before the beginning of the permanent Arctic ice sheet and laid an important pre-adaptive foundation for the successful flourishing of the woolly rhino in the Late Pleistocene Ice Age glacial fauna. Like the long-haired mammoth and the modern yak, the woolly rhino also has thick hair, which can keep itself warm. This strongly indicates that it is adapted to the life in the cold tundra and dry steppe. The broad nasal bones and ossified nasal septum suggest that *Coelodonta thibetana* has two fairly large nasal cavities, which would increase the efficiency of the heat exchange in cold air. In addition to preserving heat with their thick hair and large body, the combination of skull and nasal horn of the woolly rhino is also adapted to cold conditions (Deng et al., 2011).

The final representative of the woolly disappeared in the terminal of the Pleistocene at 10 ka (Kahlke, 1999). In addition to *Coelodonta thibetana*, the geological ages and distribution ranges of other three species of the woolly rhino are as follows: *C. nihowanensis* unearthed in northern China during the Early Pleistocene (ca. 2.5–1.8 Ma) (Qiu et al., 2004), *C. tologojensis* found in the Siberian Baikal region and Western Europe during the Middle Pleistocene (ca. 0.75 Ma) (Vangengeim et al., 1966; Kahlke and Lacombat, 2008), and *C. antiquitatis* in northern Eurasia during the Late Pleistocene (Borsuk-Bialynicka, 1973; Kahlke and La-

combat, 2008). Such notable zoogeographical patterns display a dispersal route from the Tibetan Plateau, which matches perfectly the phylogenetic interrelationships and geological chronological sequence. This supports the hypothesis that as the global climate became cool and the cold environment spread, the ancestors of the woolly rhino migrated from the high-altitude Tibetan Plateau to the high latitude Siberia (Figure 2) and eventually evolved into one of the most successful Ice Age animals in the Late Pleistocene (Kahlke and Lacombat, 2008).

4. Intercontinental dispersal via Tibet

The formation and disappearance of barriers to biotic exchanges are the significant factor to determine the modern global biodiversity (Vermeij, 1991; Klaus et al., 2016). The collision between the Indian and Eurasian plates changed the ocean-land spatial distribution pattern, and provided new conditions for the dispersal of animals and plants. As a result, substantive biotic exchanges arose between the Indian subcontinent, which was separated from the Gondwana, and the Laurasia, and deeply influenced the evolutionary history of land mammals and plants, especially some forms distributed in the Indian Ocean Rim.

4.1 *Ailanthus* (tree of heaven)

There are six woody deciduous or evergreen species in *Ailanthus* (family Simaroubaceae), which are distributed naturally in China to the north, northern Australia to the south, eastern India to the west, and New Guinea to the east (Nootboom, 1960; Van Sam and Nootboom, 2007; Su et al., 2013; Song and Xu, 2014), with the diversity center located in Southeast Asia. According to the molecular-based phylogenetic analyses, *Ailanthus* might have diverged in the family Simaroubaceae by the Late Cretaceous (Clayton et al., 2009). In China, *A. altissima* is distributed in temperate and sub-tropical regions, and some species of *Ailanthus* are distributed in the ranges of South Asia to northern Australia as well as eastern India to New Guinea (Nootboom, 1960; Song et al., 2014).

Samara fossils of *Ailanthus* have been discovered from the Cenozoic sedimentary strata, and were classified to two or three fossil species (Corbett and Manchester, 2004; Su et al., 2013; Song et al., 2014). Recently, well-preserved samara fossils of *Ailanthus* were found from three sites in Lunpola and Nima basins, central Tibetan Plateau, which was named as a new species, i.e., *A. maximus*. The geological age of these fossils from Niubao Formation in Jianglang of Lunpola Basin is the Late Paleocene to the Early Eocene, whereas the age of fossils from Dingqing Formation in Dayu of Lunpola Basin, and Nima Basin is the Late Oligocene (Liu et al.,

2019). The discovery of *A. maximus* not only expands the spatial distribution of *Ailanthus* during the Paleogene, but also suggests that the Tibetan Plateau might have played an important role in the floristic exchange between Gondwanan India and North Hemisphere. Therefore, the evolutionary history of *Ailanthus* needs to be reconsidered.

According to the fossil records, *Ailanthus* was previously considered to originate from western North America or eastern Asia in Early Eocene, and radiate to Europe and South Asia during the Oligocene (Corbett and Manchester, 2004; Song et al., 2014). Recently, wood fossils of *Ailanthoxylon* from the Deccan Plateau in India were checked again and identified as *Ailanthus* based on detailed morphological investigation, and they are usually found from the latest Cretaceous to the earliest Paleocene of that plateau, comprising the earliest fossil record of Simaroubaceae (Wheeler et al., 2017). These fossil records from the Deccan Plateau are much older than any other known *Ailanthus* fossils, which indicates that *Ailanthus* might originate from India.

Based on fossil records from northern Tibet, we note that *Ailanthus* spread from India into central Tibetan Plateau after the collision between Indian and Eurasian plates. For some taxa, the Gangdese Mountains at the south side of the Tibetan Plateau did not hamper the biotic exchanges, this condition existed in some other taxa (Shukla et al., 2016; Chen et al., 2017), frogs (Bossuyt and Milinkovitch, 2001; Li et al., 2013), and mammals (Clyde et al., 2003; Rose et al., 2014; Bai et al., 2018). During the Early Eocene, *Ailanthus* spread into northern Asia from central Tibetan Plateau, then into North America via the Bering land bridge. During the Middle Eocene, *Ailanthus* spread into Kazakhstan and other parts of Central Asia, and eventually arrived in Europe (Figure 3). The Middle Eocene fossil record from Kazakhstan might not be the earliest record of *Ailanthus* in this region, because the climate conditions in the Junggar Basin of Xinjiang Autonomous Region, and Kazakhstan during the Late Paleocene to Early Eocene were quite similar to these in eastern China at the same period according to mammal fossil records (Ni et al., 2016). After the Eocene, fossil records of *Ailanthus* had been widely reported in the North Hemisphere. Two samara fossil species of *Ailanthus*, namely *A. confucii* and *A. tardensis* from Europe and South China respectively, suggest that this genus had diversified rapidly in Europe and East Asia during the Oligocene.

The occurrence of *Ailanthus* and palms during the latest Paleocene and Late Oligocene in the central Tibetan Plateau (Wu et al., 2017; Liu et al., 2019; Su et al., 2019a) suggests that tropical to subtropical lowlands existed in Bangong-Nujiang suture zone during the Paleogene, which had provided suitable environments for the floristic exchange and dispersal during Indian and Eurasian plates. These lowlands were distributed along major sutures of the Tibetan Plateau,

and did not rapidly uplift even during the Early Eocene to the latest Oligocene, when large mammals could migrate between the south and north sides of the plateau (Deng and Ding, 2015; Deng et al., 2019) (Figure 3).

4.2 Anabantidae (climbing perches)

Anabantidae belongs to Anabantoidei (Perciformes in the traditional sense), which also includes the Helostomatidae (kissing gouramies) and Osphronemidae (giant gouramies). There are nearly 30 species of freshwater anabantids in South Asia and sub-Saharan Africa (Berra, 2007). The genus *Anabas* is distributed in Asia and the remaining species in Africa (Norris, 1994). The disjunctive distribution pattern of anabantids between Asia and Africa is a long-standing zoogeographic puzzle (Rüber et al., 2006). Previous conjectures include “vicariance caused by Gondwanan continental drift”, that is, anabantids might have originated in Gondwanan continent, hitchhike on the drifting Indian subcontinent which split from the Gondwana in the Early Cretaceous (ca. 165–121 Ma) and eventually arrived in Asia (Skelton, 1980). It is also believed that anabantids might have originated in Asia followed by their invasion into Africa in the Late Eocene. But these inferences are lack of solid evidence and historical details (Darlington, 1957; Liem, 1963; Bowmaker et al., 1978), especially fossil evidence (Rüber et al., 2006).

The drift of the Indian plate after its separation from the Gondwana is often thought to have imported many Gondwanan species into Asia (Chatterjee et al., 2017) and that can be used to explain the distribution history of certain organisms around the Indian Ocean (Rosen, 1978; Stiassny, 1991). Freshwater fishes are ideal candidates for zoogeographic research because of their lack of ability to cross water systems and large marine barriers (Rüber et al., 2006; Capobianco and Friedman, 2019).

Recently, anabantid fossils have been discovered in the Late Oligocene strata in the central part of the Tibetan Plateau. As the most complete and primitive anabantid known to date, it has mosaic features of Asian and African anabantids, which provides the possibility to solve problem concerning the evolutionary history of this group (Wu et al., 2017). Based on molecular-based phylogeny, Wu et al. (2019) analyzed a series of related fossil species such as *Eoanabas thibetana* into the phylogeny of the Anabantoidei, and constrained the anabantoid molecular clock with the above fossils. Results of the analysis show that the anabantids may have originated in Southeast Asia in the Middle Eocene and then spread to Tibet due to the existence of the interconnected water systems (Wu et al., 2017). With the completion of the India-Asia collision (Ding et al., 2017) and the closure of the Tethys Ocean (i.e., the end of the highest marine horizon), anabantids spread to the Indian sub-

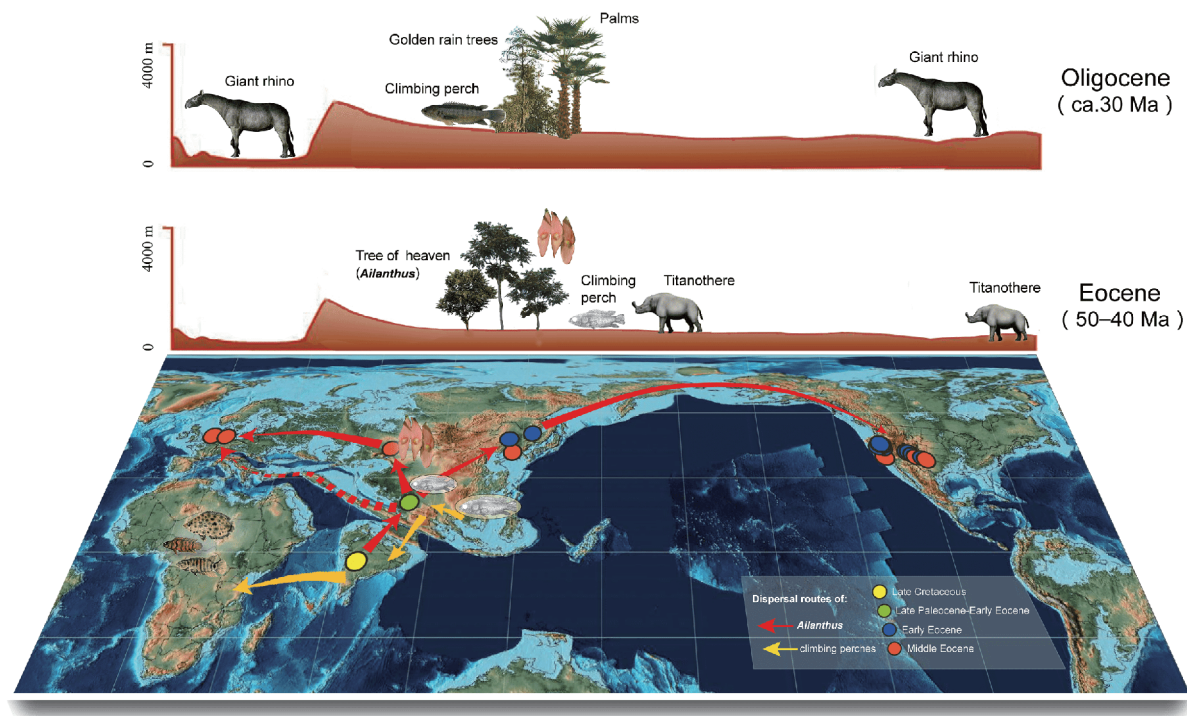


Figure 3 Intercontinental dispersals via Tibet, taking *Ailanthus* and climbing perches as examples.

continent and to African continent around 40 Ma through some biological communication channels between Indian subcontinent and African continent (Wu et al., 2019). The anabantid lineage represented by *Eoanabas thibetana* in Tibet lived there at least until the Late Oligocene, and disappeared with the cool environment brought about by the uplift of the Tibetan Plateau in the Neogene (Deng et al., 2019).

Biological exchanges between the Indian plate and the Afro-Arabian plate persist after their collision with Eurasia (Chatterjee et al., 2017). In freshwater fishes, the fossil record of channids indicates a close relationship between ancient fish in the northeastern Africa and the Indian subcontinent (Murray and Thewissen, 2008). During this period, anabantid precursors might also spread along this path, and their ability to breathe the air and crawl on land contributes to this dispersal (Norris, 1994; Berra, 2007), and ultimately achieved a high diversity in African continent where there might be little competition for survival (Gheerbrant and Rage, 2006; Norris, 1994).

5. Discussion and conclusion

The above-mentioned three patterns are the current centralized expressions on the evolutionary history of the Cenozoic biodiversity of the Tibetan Plateau, covering a variety of animal and plant categories which corresponds to the

major trophic levels of the ecosystem. Admittedly, we also recognize that the evolutionary history of some groups may be more complicated, and more evidence is needed for deeper analysis, e.g., the aquatic lytrraceae *Hemitrappa alpina*, their early fossil records have been found in Tibet, but there is a lack of fossil records in adjacent areas and of different geological ages (Su et al., 2019b). Thus, it is too early to describe their biogeographical history and its relationship with the Tibetan Plateau. In the end of Paleogene, there was differentiation of *Koelreuteria* (Sapindaceae) in northern Tibet, and the earlier fossil records of this group were recorded in the Russian Far East, Northeast China, and North America in mid-latitudes, and also in Europe (Jiang et al., 2018). Therefore, the addition of fossil materials will help to interpret the history of the whole *Koelreuteria* group in more details. With the start of the Second Comprehensive Scientific Expedition on the Tibetan Plateau, the fossil records of the plateau are accumulating rapidly, including some fossil groups recorded for the first time in the plateau area or even in Eurasia, which will greatly expand the spatial and temporal distribution of the relevant groups and enrich the knowledge on biogeographic history on the plateau under the background of environmental changes during the geological period.

The huge environmental changes since the Cenozoic in the Tibetan Plateau have posed a profound impact on the ecosystem. From a large temporal and spatial perspective, the Tibetan Plateau is an “Evolutionary Junction” for the evo-

lution of modern biodiversity. The changes in land-sea distribution caused by the plate collisions, the uplift promoted by tectonic activities and the cooling of the climate have shaped the evolution of various organisms in this region. This historical process is manifested in promoting the local origin of endemism (e.g., Schizothoracinae) featuring “Ascent with Modifications”; promoting the local origin of cold adaptation (ancestors of Ice Age fauna) or specialized species (subfamily Pantherinae) and then spreading to the surrounding areas; or bridging for those species that originated outside the plateau but once stationed in Tibet (e.g., *Ailanthus* and anabantids) for their intercontinental dispersal. The complexity of the environmental change process on the Tibetan Plateau is also reflected in its impact on the biotic world. The above-mentioned three patterns can only partially reflect the evolutionary history of the plateau biodiversity. The increasing discoveries and in-depth study of a large number of fossil materials will greatly contribute to improving the research on the life history of the plateau region, and will provide more detailed evidence for the deep analysis of the coupling relationship between life and environment in the context of plateau uplift.

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