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Invited Review Article

Major turnover of biotas across the Oligocene/Miocene boundary on the Tibetan Plateau

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ABSTRACT

In this paper, we review evidence for a major biotic turnover across the Oligocene/Miocene in the Tibetan Plateau region. Based on the recent study of six well-preserved fossil sites from the Cenozoic Lunpola and Nima basins in the central Tibetan Plateau, we report a regional changeover from tropical/subtropical ecosystems in the Late Oligocene ecosystem (26–24 Ma) to a cooler, alpine biota of the Early Miocene (23–18 Ma). The Late Oligocene fossil biota, comprising of fish (climbing perch), insects and plants (palms), shows that the hinterland of the Tibetan Plateau was a warm lowland influenced by tropical humidity from the Indian Ocean. In the Early Miocene, the regional biota became transformed, with the evolution and diversification of the endemic primitive snow carp. Early Miocene vegetation was dominated by temperate broad-leaved forest with abundant conifers and herbs under a cool climate, and mammals included the hornless rhinoceros, *Plesiaceratherium*, a warm temperate taxon. This dramatic ecosystem change is due to a cooling linked to the uplift of Tibetan region, from a Late Oligocene paleo-elevation of no greater than 2300 m a.s.l. in the sedimentary basin to a paleo-elevation of about 3000 m a.s.l. Another factor was the Cenozoic global climatic deterioration toward to an ice-house world.

1. Introduction

The Tibetan Plateau is the highest and largest plateau on Earth, with an average elevation over 4000 m above sea level (a.s.l.), and supports a typical alpine ecosystem (Hoffmann, 1991). But during the early Cenozoic, some parts of Tibet were warm lowlands as indicated by the vertebrate and plant fossils found in this area (Wu et al., 2017). The Cenozoic uplift of the Tibetan region was one of the most important orogenic events of the last 500 Myrs (Yin and Harrison, 2000; Ding et al., 2017a), which not only greatly changed topography and climate in Asia and more widely, but also strongly influenced the evolution of the biosphere.

Since the breakup of Gondwana in the Cretaceous, the Indian Plate drifted northwards at a rapid rate (Ding et al., 2017a; Spicer et al., 2020b). Until the mid-Cretaceous, however, there still was an ocean with a width of at least 6000 km between the Indian and Eurasian plates (Rao et al., 2019). The Indian Plate collided with the Eurasian continent in the early Cenozoic, and the Tibetan Plateau began to take form gradually (Molnar et al., 2010). Based on the stratigraphic data from the Yarlung Zangbo suture zone and its two sides, the beginning of this collisional phase was estimated as early as 65–60 Ma. The collision was considered to initiate in the middle at first and then proceeded diachronously to the eastern and western tectonic syntaxes of the two sides (Ding et al., 2017a), before which the east-west Gangdise mountains likely rose on the southern margin of Tibet with scale and height similar to today according to the analyses of isotopic paleoaltimetry (Ding et al., 2014). These proposed tectonic patterns provide new insights to reconstruct the orogenic history of the Tibetan Plateau. Moreover, these new perspectives enrich our understanding of the background of paleoecosystem turnovers in Tibet. After decades of groundbreaking field work and research, paleontological data from the Tibetan Plateau have become enriched (e.g., Chang et al., 2010; Wang et al., 2015b; Deng et al., 2019a for the Cenozoic vertebrate fossils), but the evidence available so far is unbalanced in temporal and spatial coverage.

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Previously, macrofossils were collected mainly from the middle-late Neogene deposits surrounding the plateau, and the Paleogene data were rare in the central plateau. Only a few Eocene fossil localities, such as the Gemusi mammal fauna with the present elevation of 4200 m in the eastern Tibetan Plateau (Zong et al., 1996) and the Moincer angiosperm flora presently at 5000 m a.s.l. in the western Tibetan Plateau (Geng and Tao, 1982) are known, both showing typical tropical or subtropical lowland habitats. In recent years, a series of important paleontological discoveries were achieved (Deng et al., 2015, 2019a; Wang and Wu, 2015; Wang et al., 2015a; Chang and Miao, 2016; Wu et al., 2017, 2019b; Xu et al., 2019; Ding et al., 2017b; Jia et al., 2019; Jiang et al., 2019; Yang et al., 2018; Su et al., 2019; Liu et al., 2019; Low et al., 2020; Tang et al., 2019; Huang et al., 2020; Zhou et al., 2020). A great number of well-preserved and highly diverse plant and animal fossils was discovered from the Oligocene strata in northern Tibet, elucidating the general features of the Tibetan Paleogene ecosystem before the strong uplift of the Tibetan region. Among them, paleoichthyological and paleobotanical evidence displays interregional effects in biogeography, with influences to remote Africa, Europe, and even North America (Jia et al., 2019; Jiang et al., 2019; Liu et al., 2019; Wu et al., 2019b). These research results provide direct evidence for constraining the timing of a major biotic turnover in Tibet at the critical boundary between the Oligocene and Miocene, in response to the uplift of the Tibetan region during the Cenozoic (Yin et al., 2008; Meng et al., 2017; Guo and Wilson, 2019).

The surface of the modern Tibetan Plateau is characterized by cryospheric conditions with high elevation and low temperature. From Mesozoic oceans to the completely terrestrial ecosystem of the Cenozoic, the incremental process was accompanied by tectonic movements, but also continuously remolded by the past global change. Recent research on the Cenozoic paleontology and stratigraphy of the Tibetan Plateau demonstrates an outstanding richness of sedimentary and fossil records in Tibet, which testifies to Cenozoic changes in the region (Deng et al., 2011, 2012a, 2012b, 2019a; Wu et al., 2017, 2019b; Ma et al., 2017; Mao et al., 2019), and elucidates many significant changes in the landscape and the ecosystem during the uplift of the Tibetan region. According to Deng et al. (2019b), significant terrestrial ecosystem transformations in Tibet happened at this Paleogene/Neogene boundary. Based on updated fossil materials and paleoenvironmental analyses in the central Tibetan Plateau, we hereby focus on this major Tibetan biotic turnover across the Oligocene-Miocene transition and its tectonic background, and discuss biological evolution in the region under the dual influences of the topographical uplift and climatic variation.

2. Geological setting

Due to the Cenozoic uplift of the Tibetan region, associated strata have undergone major denudation, and Cenozoic terrestrial deposits are well-developed only in a few fault-bounded tectonic basins. Some Cenozoic basins are developed along the Bangong Co-Nujiang suture zone (Luo et al., 1996) and other parts on the Tibetan Plateau (Fig. 1). Although most of these basins cover only small areas, their sedimentary sequences preserve key information on tectonic movements for surrounding regions, and thus are important targets to studying the orogenic history of the Tibetan Plateau during the Cenozoic, a special focus for multi-disciplinary Earth scientists in the past decade (Rowley and Currie, 2006; DeCelles et al., 2007; Kapp et al., 2007; Wang et al., 2008, 2012, 2014a; Clark, 2011; Ding et al., 2014; Sun et al., 2014; Ma et al., 2017; Botsyun et al., 2019; Han et al., 2019; Mao et al., 2019). In particular, a number of new paleontological discoveries from six well-preserved fossil sites of the Lunpola (Lunbori, Chebuli, Dayu, and Jianglang) and Nima (Jianglongtangga and Songwori) basins, serve as excellent direct evidence for the plateau's paleoenvironment, drawing considerable interest by many colleagues in the geosciences (Deng et al., 2012b; Wang and Wu, 2015; Wu et al., 2017, 2019b; Cai et al., 2019; Jia et al., 2019; Jiang et al., 2019; Low et al., 2020; Su et al., 2019).

The fossiliferous beds that are of main concern to the present study are typically represented by the Lunbori section (31°57′27.6″N, 89°47′55.7″E, 4624 m a.s.l.) of the Lunpola Basin. The total thickness of the Dingqing Formation at Lunbori is 989.5 m (upper part of the Lunpola section in Fig. 2). The lower layers alternated between gray thick- to huge thickly-bedded shale and thinly-bedded limestones, banded gray oily shale, brownish yellow shale, and light brown silty marlites, with a thickness of 109.4 m. The middle layers alternated between gray shale

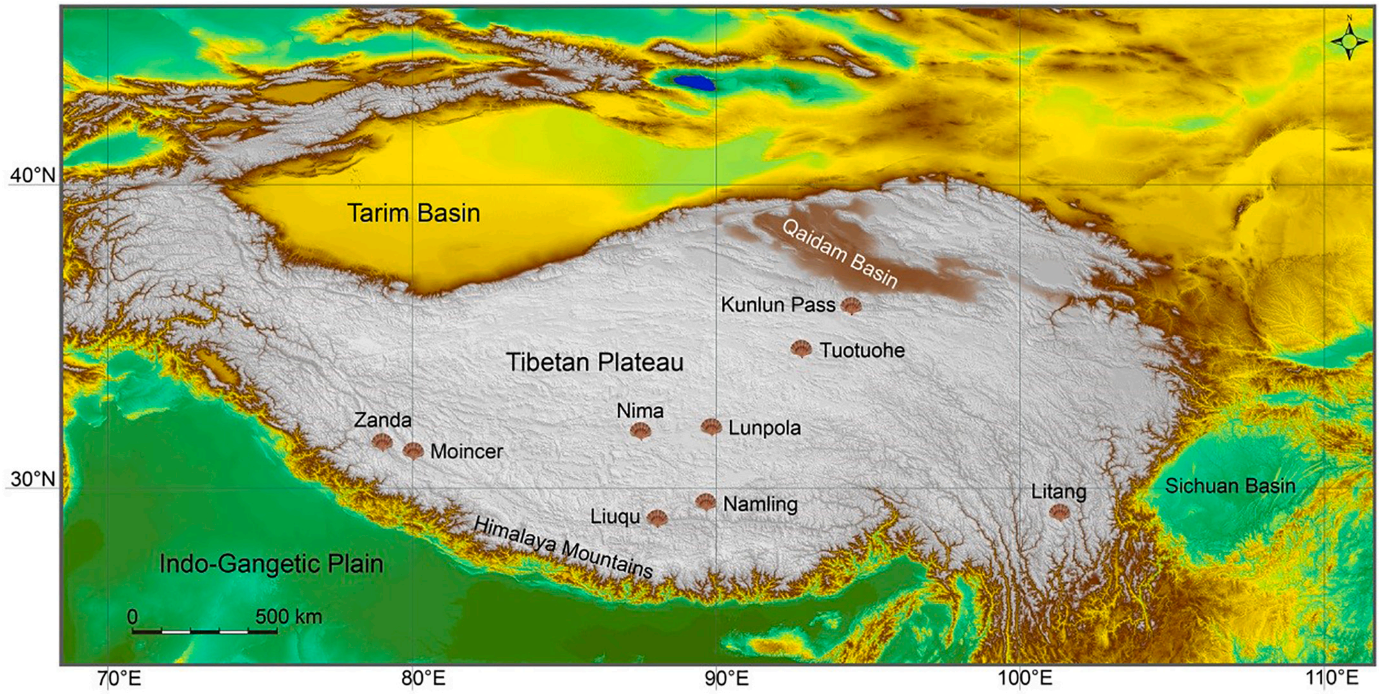

Fig. 1. Geo-topological map showing the localities of the Cenozoic stratigraphical sections containing fossils on the Tibetan Plateau. The image was generated by GEBCO (www.gebco.net) which is available to the public.

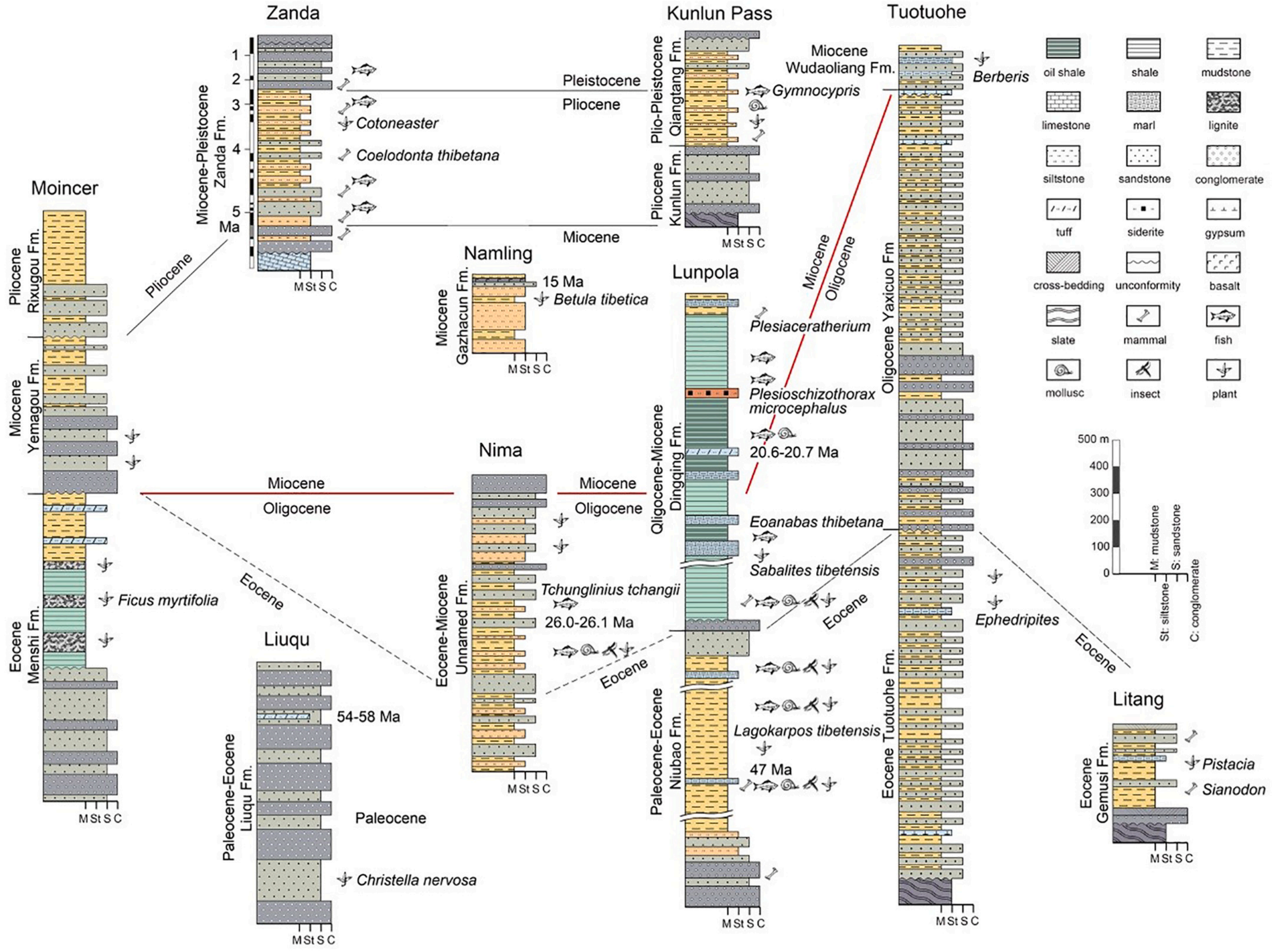

Fig. 2. Correlation of the Cenozoic stratigraphical sections on the Tibetan Plateau. Data source: Moincer, Geng and Tao (1982); Zanda, Wang et al. (2013); Liuqu, Ding et al. (2017b); Namling, Guo et al. (2019); Nima, Wu et al. (2019a); Kunlun Pass, Song et al. (2005); Lunpola, measured by the present authors; Tuotuohe, Cai et al. (2008); Litang, Zong et al. (1996).

and brownish-gray paper-thin oil shale, containing horizons of banded brownish-yellow thinly-bedded siderites, with a thickness of 583.7 m. The upper layers alternated between brownish-gray thickly-bedded paper-thin oil shale and thickly-bedded gray shale, banded reddish-brown, gray and light yellow massive mudstones, brown thinly-bedded silty mudstones, and thinly-bedded tuffaceous sandstones with a thickness of 209.3 m. The top layers constituted gray thinly-bedded mudstones, marlite, and gray thinly-bedded shale, banded brownish-gray paper-thin oil shale and light yellow thinly-bedded marlites with a thickness of 87.1 m.

Strata of other Paleogene and Neogene fossil localities on the Tibetan Plateau are correlated with the Lunpola deposits (Fig. 2). In the Dingqing Formation at Lunbori Hill, its lower layers correspond to the fossiliferous beds at Dayu (32°01′57.8″N, 89°46′08.9″E, 4683 m a.s.l.) on the north side of this hill, yield rich fossil fishes (*Eoanabas thibetana*, *Tchunglinius tchangii*, and others), mammals (Zapodidae), plants (*Sabalites tibetensis*, *Koelreuteria lunpolaensis*, *Ailanthus maximus*, *Cedrelospermum tibeticum*, *Limnobiophyllum pedunculatum*, and others), and insects (*Aquarius lunpolaensis*, and others); its middle layers contain well-preserved fish (Cyprinidae), insect, and plant fossils with a volcanic ash age of 20.7–20.6 Ma (Mao et al., 2019); and its upper layers bear bivalves, fish (*Plesioschizothorax microcephalus*), and mammals (*Plesiaceratherium* sp. and rodents, Deng et al., 2012b).

In the Lunpola Basin, the Paleocene-Eocene Niubao Formation is more than 3000 m in thickness and is dominated by red sandstones and conglomerates (Bureau of Geology and Mineral Resources of Xizang (Tibet) Autonomous Region, 1993). The Jianglang flora has been recently discovered from five layers of mudstones in the middle part of the Niubao Formation (Fig. 2). U-Pb dating of a tephra-rich horizon near one fossil-bearing layer in the section at Jianglang (31°37′30.4″N, 90°01′44.5″E, 4850 m a.s.l.) shows that the Jianglang flora is ~47 Ma (Su et al., 2020).

The Nima Basin is west of the Lunpola Basin on the opposite side of Lake Siling Co (Fig. 1). The two basins share the same tectonic history, so their Cenozoic sedimentary sequences and structures have many similarities. We found a large number of fish, plant and insect fossils at Jianglongtangga (31°47′41.6″N, 87°45′39.0″E, 4810 m a.s.l.) and Songwori (31°54′47.3″N, 88°06′48.6″E, 4794 m a.s.l.) sections of the Nima Basin (Fig. 2), and their features are very similar to the fossil assemblage from the lower Dingqing Formation in the middle part of the Dayu section of the Lunpola Basin.

3. Late Oligocene ecosystem in central Tibet

The pre-Oligocene plant and mammal records on the Tibetan Plateau were discovered from Liuqu, Jianglang, Tuotuohe, Moincer, and Gemusi

(Figs. 1-3) (Geng and Tao, 1982; Chen et al., 1983; Guo, 1986; Zong et al., 1996; Miao et al., 2016; Xu et al., 2019; Del Rio et al., 2020; Su et al., 2020), which indicates warm-adapted animals and vegetation of a subtropical to tropical lowland (about 1000 m) forest, derived from the Cretaceous plants that preferred a warm-hot climate in the Tibetan region (Li et al., 2019). As a result, the origins of the modern plant biodiversity were established in the Eocene, concurrent with the beginning of pronounced topographic relief across the Tibetan region (Spicer et al., 2020a).

Until the Oligocene, fossil remains of tropical and subtropical fish, plants and insects, which were collected from the lacustrine deposits in the Lunpola and Nima basins in central Tibet (Figs. 1, 2), suggest that the inland of the Tibetan Plateau region was still a warm and humid lowland at 26 Ma, and that warm and humid airflow from the south penetrated deeply into the central part of the Tibetan Plateau (Wang and Wu, 2015; Wu et al., 2017; Jia et al., 2019; Liu et al., 2019; Low et al., 2020; Su et al., 2019).

3.1. Plant fossils

Abundant plant fossils are preserved from lacustrine shale or thinly-bedded silty mudstones in the lower member of the Dingqing Formation in the Lunpola Basin and the southern Nima Basin as well as the Qiuwu Formation near Xigaze (Geng and Tao, 1982; Li, 2004). The Lunpola plant fossils comprise over 50 species, and represent a well-preserved and diverse Tibetan assemblage, including *Sabalites* (Palmae), *Cedrelospermum* (Ulmaceae), *Koelreuteria lunpolaensis* (Sapindaceae), *Handeliodendron* (Hippocastanaceae), *Pistacia* (Anacardiaceae), *Exbucklandia* (Hamamelidaceae), *Limnobiophyllum* (Araceae), *Typha* (Typhaceae), Araliaceae, Bignoniaceae, and Lauraceae (Wu et al., 2017). All these taxa or their relatives are now distributed in subtropical and tropical regions of Asia.

If these fossil species had similar environmental preferences to their modern relatives, this plant fossil assemblage under a uniformitarian principle of interpretation, may be deemed most likely to have thrived in a subtropical or tropical habitat at low altitude, after paleotemperature adjustment. It is noteworthy that among the 15 arboreal eudicotyledonous species of this fossil assemblage, only five possessed serrated leaves, while the other 10 species had entire leaves. Because mean annual temperature has a significant positive relationship with proportion of entire leaved species of arboreal eudicotyledonous plants in a flora (Wolfe, 1979), it shows that the Nima and Lunpola basins had warm temperature during the Late Oligocene. Taking specifically climatic factors pertaining to the newly discovered palm fossils into consideration, the mean temperature of the coldest month in this region during the Late Oligocene was not lower than 5.2 °C (Su et al., 2019).

A one-meter-long leaf fossil of *Sabalites tibetensis* collected from Late Oligocene strata in the Lunpola Basin is the youngest palm fossil recorded from the Tibetan Plateau (Fig. 3I). The Palmae group contains over 2500 living species distributed across the world, predominantly in the tropics and sparingly in the subtropics. The mean temperature of 5.2 °C for the coldest month is a key limiting factor for the growth of palms

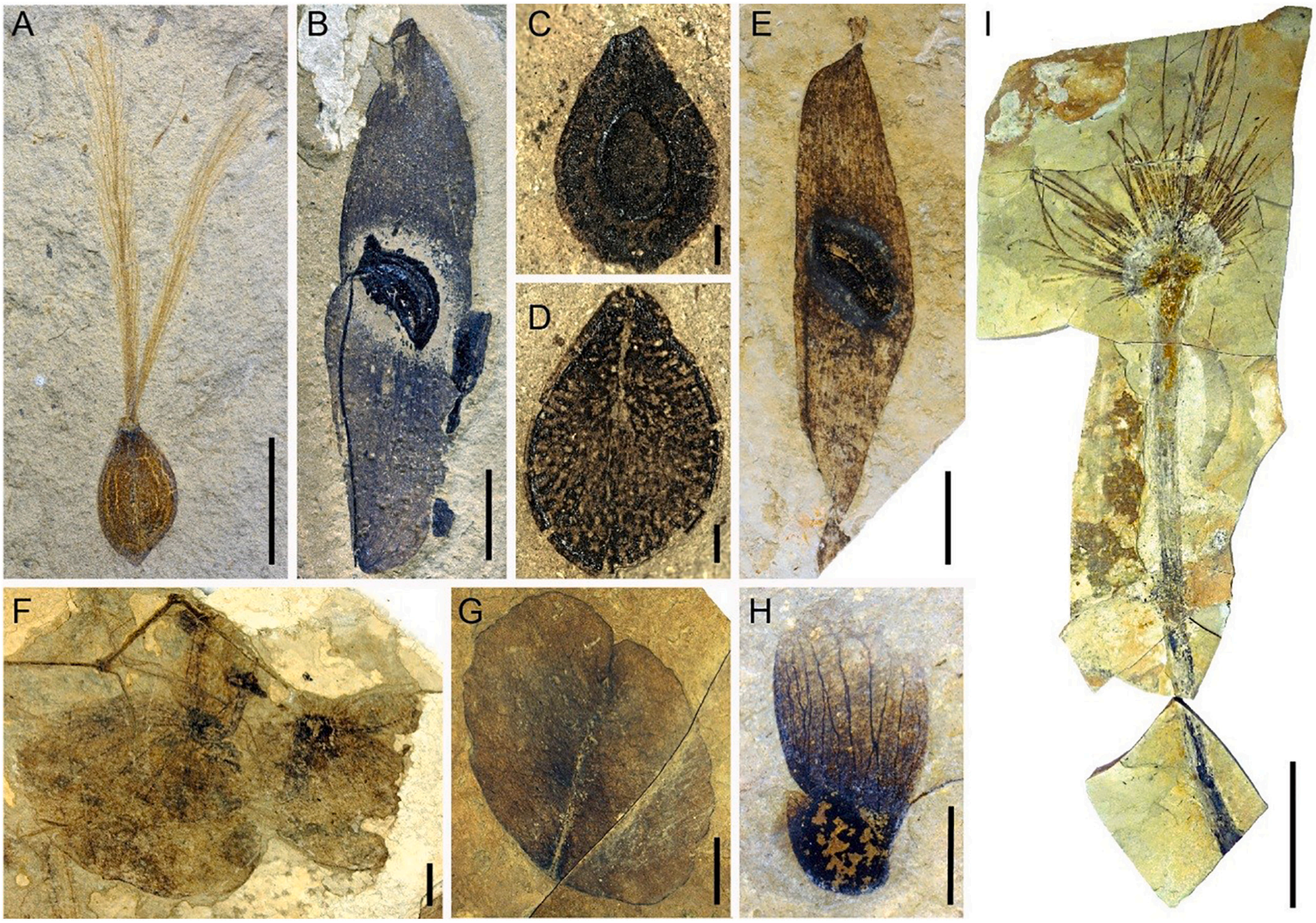

Fig. 3. Plant fossil species from the Lunpola Basin. A. *Lagokarpos tibetensis* (unknown family); B, E. *Ailanthus maximus* (Simaroubaceae); C. *Asclepiadospermum marginatum* (Apocynaceae); D. *Asclepiadospermum ellipticum* (Apocynaceae); F. *Limnobiophyllum pedunculatum* (Araceae); G. *Koelreuteria lunpolaensis* (Sapindaceae); H. *Cedrelospermum tibeticum* (Ulmaceae); I. *Sabalites tibetensis* (Arecaceae). Scale bars: A, B, E, F, G = 1 cm, C, D = 1 mm; H = 5 mm; *I* = 10 cm.

(Reichgelt et al., 2018). Su et al. (2019) employed paleoclimatic models which simulated 13 different topographic and geomorphic environments, showing that the altitudinal distribution of palms in the central Tibetan Plateau was not higher than 2300 m a.s.l. and in a valley system during the Late Oligocene. Along with environmental changes caused by the uplifts of the Tibetan region and the Himalayas, many species disappeared from this region.

The well-preserved fruit and leaf fossils of the genus *Cedrelospermum* were discovered from the Late Oligocene deposits in the Lunpola and Nima basins, representing a new species *Cedrelospermum tibeticum* (Fig. 3H, Jia et al., 2019). This first discovery of fossil *Cedrelospermum* fossil on the Tibetan Plateau perhaps indicates a warm and humid environment.

The capsular valve fossils of the genus *Koelreuteria* (the golden rain tree) discovered from the Oligocene deposits of the Lunpola Basin include *Koelreuteria lunpolaensis* (Fig. 3G) and *K. miointegrifoliola*, the latter of which is similar to living species *K. bipinnata* (Jiang et al., 2019). Trees of *K. bipinnata* can reach a height of 20 m, and they are distributed in subtropical or tropical forests with the highest elevation of 2500 m. In the central Tibetan Plateau during the Late Oligocene, *K. miointegrifoliola* may have had a similar habitat to this living relative. Other fossil floras in China containing *K. miointegrifoliola*, such as the Late Miocene Xiananshan flora in eastern China also represented warm and humid subtropical lowland vegetation (Li and Guo, 1982; Li, 1984). Based on the modern distribution of the golden rain tree, the environment in central Tibetan Plateau was warm and humid, with a low elevation (Jiang et al., 2019).

Rich aquatic plant fossils are collected from the same beds with the aforementioned macrophytes. The fossil *Limnobiophyllum pedunculatum* of the family Araceae is characterized by completely preserved infructescences and seeds, representing the first record of this genus in Tibet and even East Asia (Fig. 3F, Low et al., 2020). Although Araceae have adapted to diverse habitats, they are generally regarded as ideal floral indicators for environment (Wong, 2013), and are frequently found in humid tropical and temperate forests. They inhabit a spectrum of ecosystems from aquatic environments to arid regions, but over 95% of these species are tropical plants from humid environments. The extant relative *Lemna* grows in still or slowly flowing freshwater of tropical and temperate lowlands (Mkandawire and Dudel, 2005a, 2005b). Combined with other paleobotanical evidence, therefore, it shows that the hinterland of the Tibetan Plateau was warm and humid during the Late Oligocene as before. The genus *Limnobiophyllum* was globally extinct after the Miocene, probably due to global cooling (Zachos et al., 2008) and orogenic factors (Potter and Szatmari, 2009; Molnar et al., 2010).

The aforementioned plants altogether are typical of a tropical-subtropical forest assemblage. Supplemented by studies of other fossil species from Tibet over this period, the fossil flora from the Dingqing Formation will provide a rich volume of information on the paleoenvironment of Tibet. A palynological analysis for the same period from the Nima Basin showed possible distribution of conifer forests, shortly prior to the sharp proliferation of broad-leaved forests in the Late Oligocene (Wu et al., 2019a), indicating topographical relief surrounding the fossil locality (Su et al., 2019) or a vegetation response in hinterland of the Tibetan Plateau to the Late Oligocene warming (Wu et al., 2019a). In this period where vegetation types in the region varied, the climate was still humid, with mean annual precipitation of 400–850 mm or even up to 1000 mm (Wu et al., 2019a). It is noteworthy that angiosperm pollen grains are rarely preserved in fossiliferous beds with rich macrophyte specimens, which is perhaps related to sedimentary controls on taphonomy.

3.2. *Insect fossils*

Characteristic biological structures of aquatic insects indicate their specific environmental adaptations, so provide us with paleoenvironment indicators. In the Lunpola Basin and the adjoining Nima Basin, rich insect fossils (Fig. 4) were collected from the Late Oligocene, including the water strider *Aquarius lunpolaensis* (Hemiptera, Gerromorpha, Gerridae, Fig. 4A). Based on a detailed observation of the fossil specimens, *A. lunpolaensis* was coated by dense setae all over its body, especially on the legs as seen on its extant relatives, which may serve the function of water resistance (Cai et al., 2019). Combined with extreme similarities of size and limb morphology between *A. lunpolaensis* and its extant relatives, one may deduce that these ancient water striders lived on the water surface of paleo-lakes in the central Tibetan Plateau. These paleolakes were situated at low altitudinal elevation, and their water surface was still and not frozen, which would to hinder the water strider's movement (Hu et al., 2003), an interpretation consistent with the paleoenvironment suggested by the fossil aquatic plants, such as *Limnobiophyllum pedunculatum* (Low et al., 2020).

3.3. *Fish fossils*

The fish fossils accompanying the aforementioned plant assemblage and insect fossils from the Dingqing Formation in the Lunpola and Nima basins represent some typical or subtropical forms. The reported forms include *Tchunglinius tchangii* (Barbinae, Cyprinidae, Fig. 5B) (Wang and Wu, 2015) and *Eoanabas thibetana* (Anabantidae, Fig. 5A), the latter representing the first fossil record of the Perciformes on the Tibetan Plateau (Wu et al., 2017). Combined with fossil rodent biochronology and an ^{40}Ar/^{39}Ar age of 23.5–26 Ma (DeCelles et al., 2007) for the fossiliferous bed, these fishes are dated to the Late Oligocene.

The modern distribution of the Barbinae within the Cyprinidae is limited to Asia, central and southern Europe, and Africa (Skelton, 2001; Berra, 2007). Among them, the forms at warmer and lower altitude have fewer vertebrae - about 30 vertebrae for the tropical species in Asia. On the other hand, the fishes that live in cold areas at high elevation have more vertebrae. For example, modern schizothoracines (snow carps) of the Barbinae today endemic on the Tibetan Plateau have about 50 vertebrae (Wu and Chen, 1980). Combined with other morphological characters, the 33 vertebrae of *T. tchangii* indicate similar to the modern small barbine *Puntus* distributed in South Asia and Africa. *T. tchangii* would be a fish that lived in a warm area at low elevation, representing an evolutionary stage of the regional fish fauna before uplift of the Tibetan region (Wang and Wu, 2015).

Plenty of fossil remains of *Eoanabas thibetana* were discovered not only in the Nima Basin, but also from the Dingqing Formation of the Lunpola Basin. The modern anabantids (climbing perches) are distributed in small, shallow, and weakly flowing water bodies of South Asia, Southeast Asia, and sub-Saharan Africa, with optimal temperature of 18–30 °C (Wu et al., 2017), as in the central zones of the modern tropical monsoon region of Africa and Asia (Berra, 2007; Zhang and Wang, 2008). Based on its unique labyrinth organ, the climbing perch can draw oxygen directly from air, and then climb up banks to move to another body of water (Norris, 1994; Berra, 2007). The labyrinth organ of *E. thibetana* is similar to the modern Asian climbing perches with the strongest ability to breathe in air, indicating similar physiological characteristics and behavioral ecology, and a warm and humid climate. Fossils of *E. thibetana* preserve a spinous contact organ in the cheek area of male fish, which can stimulate female fish when they mate, showing the fossil climbing perch's similarity to its modern descendants in reproductive behavior (Wu et al., 2017). The reproductive behavior of the modern climbing perch is directly related to tropical monsoon rainfall throughout its distribution (Forselius, 1957; Skelton, 2001).

3.4. *Mammals*

A skeleton with skull, mandible, and limb bones of the family Zapodidae was discovery from the lower part of the Dingqing Formation at Dayu in the Lunpola Basin (Fig. 6B). Zapodids are small rodents whose tail and hind legs are modified for moderate saltatorial locomotion. The modern relatives of this family inhabit riparian-deciduous woodlands

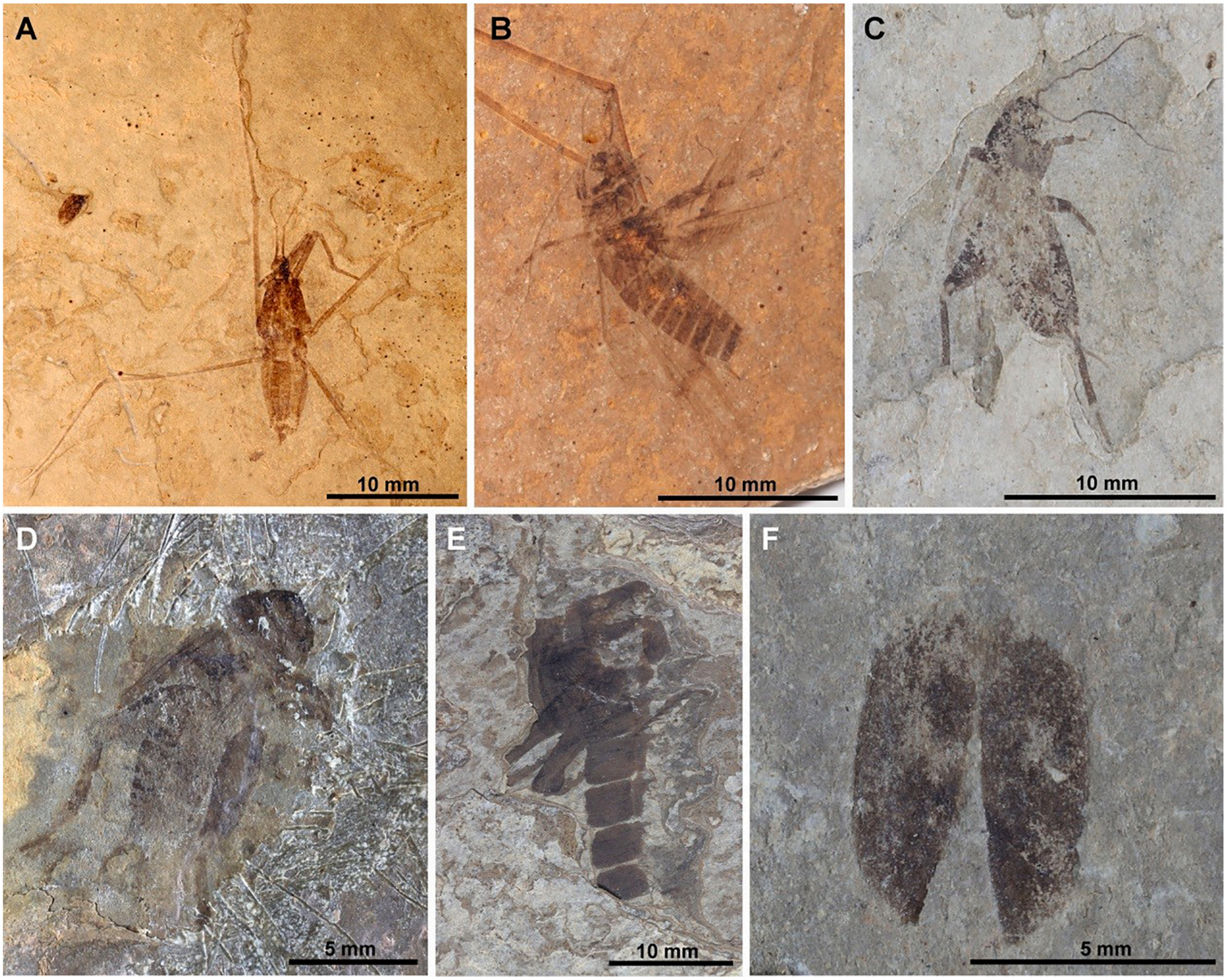

Fig. 4. Fossil insects from the Upper Oligocene of the Dayu section in the Lunpola Basin. A. *Aquarius lunpolaensis*, Hemiptera; B. An insect of Ensifera (Orthoptera); C-E. Insects of Orthoptera; F. An insect of Coleoptera.

and dense forests or wet grassy areas and meadows in mountains, but not deserts (Daxner-Höck, 1999).

During the Oligocene, giant rhinos lived in northwestern China, north of the Tibetan Plateau, while they were also distributed in the Indo-Pakistan subcontinent to the south of the Tibetan Plateau, which indicates that the elevation of the Tibetan Plateau was not too high to prevent dispersals of giant rhinos and other large mammals north and south of the Tibetan region (Deng and Ding, 2015).

4. Miocene ecosystem of the central Tibetan Plateau

The modern ecosystem of the Tibetan Plateau is composed of animals and plants adapted to cold, alpine or even cryospheric environments, and lacking tropical and subtropical relatives in the Paleogene. The fish fauna has evolved into the endemic schizothoracines on the Tibetan Plateau, and the mammals are represented by the cold-adapted snow leopard (*Panthera uncia*), lynx (*Lynx lynx*), Tibetan wild ass (*Equus kiang*), white-lipped dear (*Cervus albirostris*), yak (*Bos mutus*), Tibetan antelope (*Pantholops hodgsonii*), Tibetan gazelle (*Procapra picticaudata*), blue sheep (*Pseudois nayaur*), and wild sheep (*Ovis ammon*). When did the tropical-subtropical ecosystem transform into the high-altitude cryospheric environment of today? We found the answer in the Lunpola, Nima, Hoh-Xil, and Namling basins on the Tibetan Plateau, where the Early Miocene ecosystem had changed profoundly.

4.1. Vegetation

The Late Oligocene lower member of the Dingqing Formation contains an *Ulmus-Salix* pollen assemblage (Wang et al., 1975), which is confirmed by our new discovery including fruit and leaf fossils of *Cedrelospermum* (Ulmaceae) (Jia et al., 2019) and *Salix* (Salicaceae). In the Early Miocene middle member of the Dingqing Formation, angiosperm pollen grains are in greater quantity than gymnosperm ones, comprising 55–73% of the total pollen count, and the diverse angiosperm flora was dominated by deciduous broad-leaved trees. Among them, *Quercus*, *Salix*, and *Juglans* were the predominant forest plant species of the time, whereas gymnosperm trees were secondary and mainly composed of *Pinus*, *Picea*, and *Abies*. Herbs started to expand further, reflecting that the climate turned temperate from the tropical and subtropical Late Oligocene (Wang et al., 1975).

A palynological analysis by Sun et al. (2014) further affirmed that tree pollen grains accounted for 74.8% at 23.2–21.1 Ma of the Early Miocene, with shrub and herb pollen grains at 7.0% and 11%, respectively. The pollen samples were primarily derived from conifers,

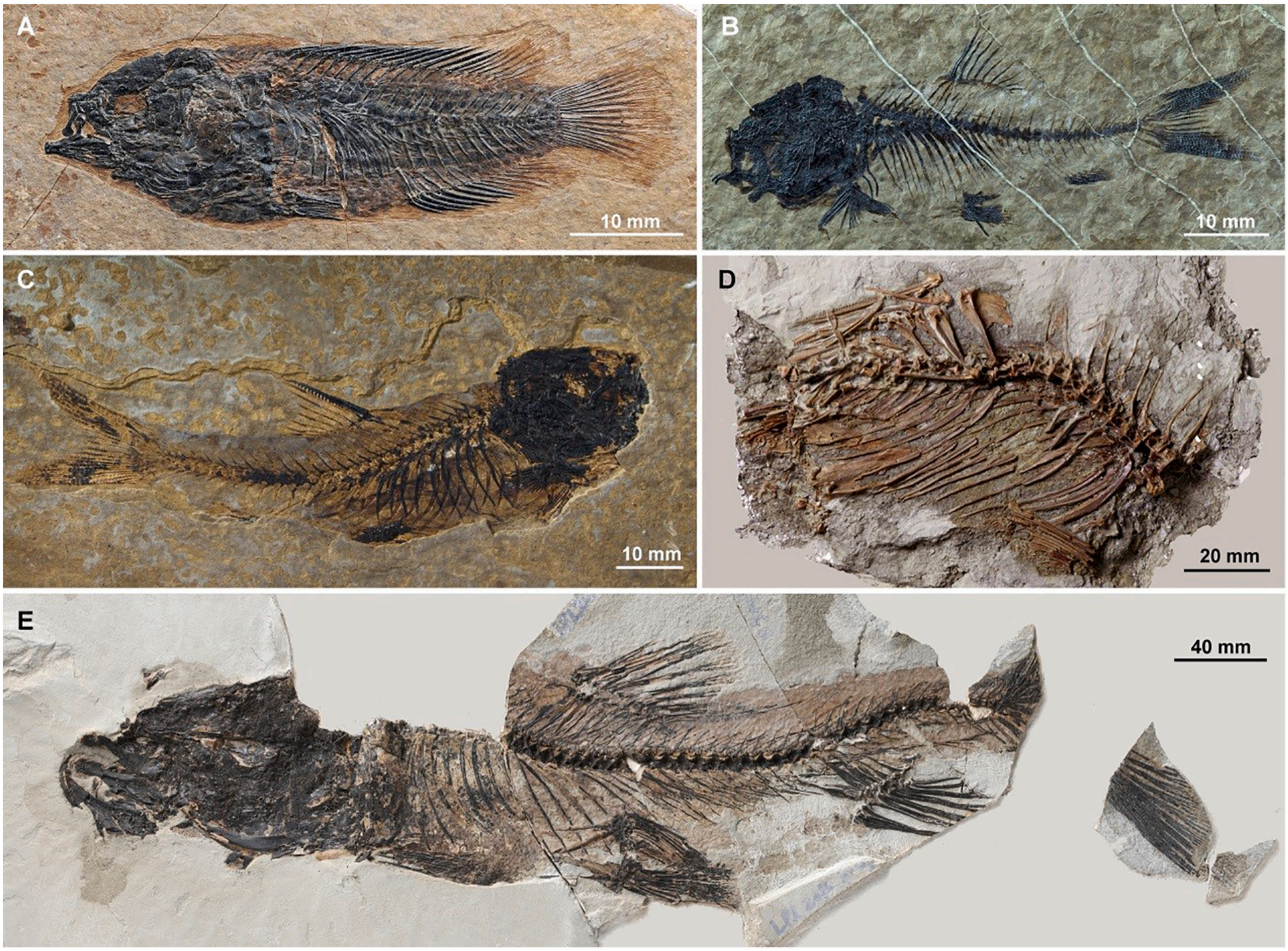

Fig. 5. Cenozoic fossil fishes from the Tibetan Plateau. A. Climbing perch, *Eoanabas thibetana* (IVPP V 22782) from the Late Oligocene of the Nima Basin; B. Cyprinid fish, *Tchunglinus tchangii* (IVPP V 18945) from the Late Oligocene of the Nima Basin; C. A cyprinid fish (IVPP V 26885) from the Late Oligocene of the Lunpola Basin; D. A highly specialized schizothoracine fish (IVPP V 26886) from the Pliocene of the Zanda Basin; E. A primitive schizothoracine fish, *Pelsioschizothoracine microcephalus* (IVPP V 26887) from the Early Miocene of the Lunpola Basin.

dominated by *Pinus* (31–69%, mean 50%) and accompanied by *Keteleeria* (0–7.1%, mean 2.1%) and *Podocarpus* (0–3.9%, mean 1.6%). Broad-leaved trees were dominated by *Quercus* (0.7–17.4%, mean 7.1%) and accompanied by *Rhoipites* (0–9%, mean 3.2%) and *Betula* (0–17.9%, mean 2.4%). In shrubs and herbs, *Ephedra* (0–12.8%, mean 4.7%) and *Chenopodium* (0–23.3%, mean 4.1%) were the most abundant.

Between 21.1 and 19.8 Ma, tree pollen grains declined to 64%, while shrubs and herbs accounted for 17% and 10.4%, respectively. The coniferous trees *Pinus* (9–66%, mean 38.7%), *Cedrus* (0–5.1%, mean 1.5%), *Picea* (0–5.5%, mean 1.1%) and *Podocarpus* (0–4.3%, mean 1.1%) were dominant. Broad-leaved trees accounted for only 18%, mainly including *Quercus* (0–21.9%, mean 8.8%), *Rhoipites* (0–9.4%, mean 3.3%) and *Betula* (0–7%, mean 2.6%). Shrubs were dominated by *Ephedra* (1–25%, mean 14%), and herbs by *Chenopodium* (0.5–12%, mean 3.9%). This floral assemblage indicates that the altitude of central Tibetan Plateau had achieved over 3000 m a.s.l, and the climate had become relatively cool (Sun et al., 2014).

Plant megafossils also indicate the vegetation turnover from a warm ecosystem to a temperate flora. For example, the fossil *Berberis* cf. *asiatica* of the Berberidaceae from the Early Miocene deposits in the Hoh-Xil Basin, northern Tibetan Plateau represented a habitat with an elevation between 1395 m and 2931 m (Sun et al., 2015). Until the Middle Miocene, the leaf fossils from Namling County, central southern Tibet include 9 families, 13 genera and 25 species, representing a typical boreal temperate mostly deciduous broad-leaved forest attesting to a cool humid climate. The Namling flora is dominated by eudicotyledonous angiosperms, and the most significant family is the Betulaceae with 4 genera and 10 species, mainly *Betula himalayensis* and *B. tibetica*. Similar living species are all distributed in the high mountains of Tibet and adjacent regions. Next in abundance are representatives of the Salicaceae with two genera and five species, followed by Sapindaceae with one genus and three species. Other commonly represented families are the Fagaceae and the Ericaceae with one genus and two species each. Four families, Schisandraceae, Grossulariaceae, Rhamnaceae and Torricelliaceae, are represented by only one genus and one species each. All taxa bear serrate margins except two species of *Rhododendron* (Guo et al., 2019).

4.2. *Fish fossils*

The modern river system of the Tibetan Plateau is complex, with rivers and lakes rich in a distinctive ichthyofauna composed mainly of cyprinid schizothoracines. Traditionally, the schizothoracines are divided into three evolutionary grades including the primitive, specialized and highly specialized ones, and morphological characters and altitudinal distributions are correlated. The primitive grade, with

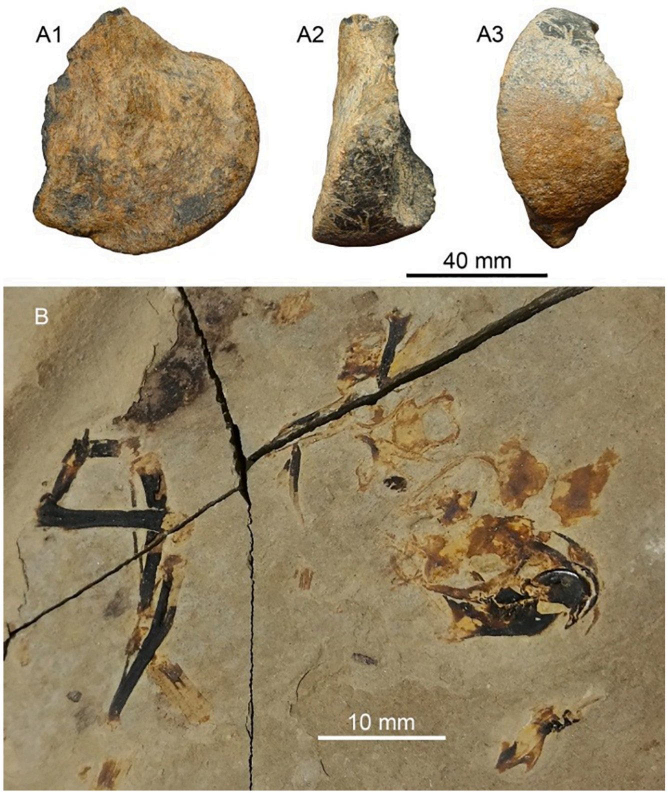

Fig. 6. Mammalian fossils from the Lunpola Basin. A. *Plesiaceratherium* sp., distal extremity of humerus (IVPP V 18082), Early Miocene, upper part of the Dingqing Formation at Lunbori, 1. Medial view, 2. Anterior view, 3. Distal view; B. A rodent of Zapodidae, skeleton, Late Oligocene, lower part of the Dingqing Formation at Dayu.

three rows of pharyngeal teeth on each hypopharyngeal bone, is generally found at an altitudinal level of 1250–2500 m. The specialized species (rows of pharyngeal teeth) are distributed at about 2500–3750 m a.s.l. Among the highly specialized fish, some have two and others have one row of pharyngeal teeth, and all occur at elevations between 3750 and 4750 m (Cao et al., 1981). This pattern has been termed "ascent with modifications" (Chang et al., 2010; Chang and Miao, 2016), epitomizing the evolutionary response of the Tibetan fish fauna to the uplift of the Tibetan region (Cao et al., 1981; Chen et al., 1996). Moreover, freshwater actinopterygians are mostly cold-blooded, so they are very sensitive to environmental changes. Fish fossils are usually preserved in situ, therefore, morphological characters of schizothoracines and assemblage features of fossil ichthyofaunas reflect paleo-altitude and paleoenvironment of their bygone habitat (Chang and Miao, 2016).

In the Early Miocene deposits of the Lunpola Basin, the tropical actinopts represented by *Tchunglinius tchangii* and *Eoanabas thibetana* had disappeared and were replaced by the primitive schizothoracine *Plesioschizothorax microcephalus* (Fig. 5E) and other cyprinid fishes (Fig. 5D). *P. microcephalus* is a primitive schizothoracine with three rows of pharyngeal teeth (Wu and Chen, 1980), slightly more derived than the extant *Schizothorax* species of the primitive grade (Chang et al., 2008). The skeleton of *Plesioschizothorax microcephalus* contains more than 46 vertebrae, more than those (about 40 vertebrae) of the Pliocene barbine fish found in Zhoukoudian, close to 40° north latitude, indicating the former had gradually adapted to cool climate along with Tibetan uplift (Wu and Chen, 1980).

4.3. Mammals

The distal extremity of a rhinocerotid humerus (Fig. 6A) discovered from the Early Miocene part of the Dingqing Formation in the Lunpola Basin is nearly completely identical in morphology with that of *Plesiaceratherium gracile* from the late Early Miocene Shanwang Fauna in Linqu, Shandong Province, eastern China. The Lunpola fossil was identified as *Plesiaceratherium* sp. (Deng et al., 2012b). Compared with the completely preserved skeletons of *P. gracile* from Shanwang, the Lunpola *Plesiaceratherium* would have had a shoulder height of about 1.3 m, a body length of about 2.5 m, and a body weight of about 2 t. Previously, fossils of the genus *Plesiaceratherium* were found only in two Chinese localities, Shanwang in Linqu, Shandong (Young, 1937), and Jiulongkou in Cixian, Hebei (Chen and Wu, 1976). Moreover, *Plesiaceratherium* fossils were also found in Western Europe (Heissig, 1999), chronologically dated to a late Early Miocene interval between two cooling events: Mi-1b at 17.8 Ma and Mi-2 at 16 Ma (Böhme, 2003). The presence of *Plesiaceratherium* in Tibet proves that the region had deviated climatically from a tropical/subtropical habitat since the Early Miocene, with a cooler temperate climate. As the Tibetan Plateau rose continuously, it reached modern elevation (over 4000 m a.s.l.) and overall size during the Pliocene (Deng et al., 2012a), at which time the vegetation in the Tibetan Plateau, as represented by the Qangze (Xiangzi) flora in the Zanda Basin (Figs.1, 2) was dominated by typical deciduous shrubs found in a plateau environment (Huang et al., 2020). The highly specialized schizothoracines with one row of pharyngeal teeth appeared in the Zanda Basin (Fig. 5D) and the Kunlun Pass Basin (Figs. 1, 2) (Chang et al., 2010; Wang and Chang, 2010; Chang and Miao, 2016).

Cold-adapted mammals originated when the Tibetan Plateau reached its modern elevation and became a cold, bleak landscape in the Pliocene. Examples are the known most primitive woolly rhino known (Deng et al., 2011) as well as the respective precursors of the snow leopard, Arctic fox, and mountain sheep (Tseng et al., 2014; Wang et al., 2014b, 2016), demonstrating that some members of the cold-adapted Quaternary mammal fauna evolved on the Tibetan Plateau during the Pliocene.

5. Dynamic mechanisms for Oligocene-Miocene ecological transition

The origin and evolution of organisms are intimately linked to their environments. For the terrestrial ecosystem of the Tibetan Plateau, in which plants are the primary producers, mammals as the representative terrestrial consumers, and fishes as the typical aquatic consumers, ecosystem evolution must be tightly related to topographic deformation caused by tectonic movements and by regional climatic transformation driven by global changes (Fig. 7).

5.1. Late Cenozoic tectonic movements on the Tibetan Plateau

The Tibetan uplift was a complex, multi-phase process with strong heterogeneities in tempo and regional impacts (Harrison et al., 1992; Zhong and Ding, 1996; Zhang et al., 2010; Wang, 2013). When the African, Indian, and Eurasian plates accelerated to converge at 34 Ma, the beginning of the Oligocene, the once vast singular expanse of the Neo-Tethys Ocean was separated into two branches, south and north. This combined with the sea level drop to cause global cooling (Sun et al., 2017). The south-north convergence of the plates within Asia since the Eocene slowed significantly at the terminal Oligocene, and central Tibetan Plateau was close to its current geographical position (paleo-latitude). The interior deformation of the plateau started to transform, from a strong compressional mode to tension from this period (Meng et al., 2017). Therefore, the transition from the Oligocene to the Miocene was regarded as an important turning point for the formation and evolution of the Tibetan Plateau, before and after which the geodynamic

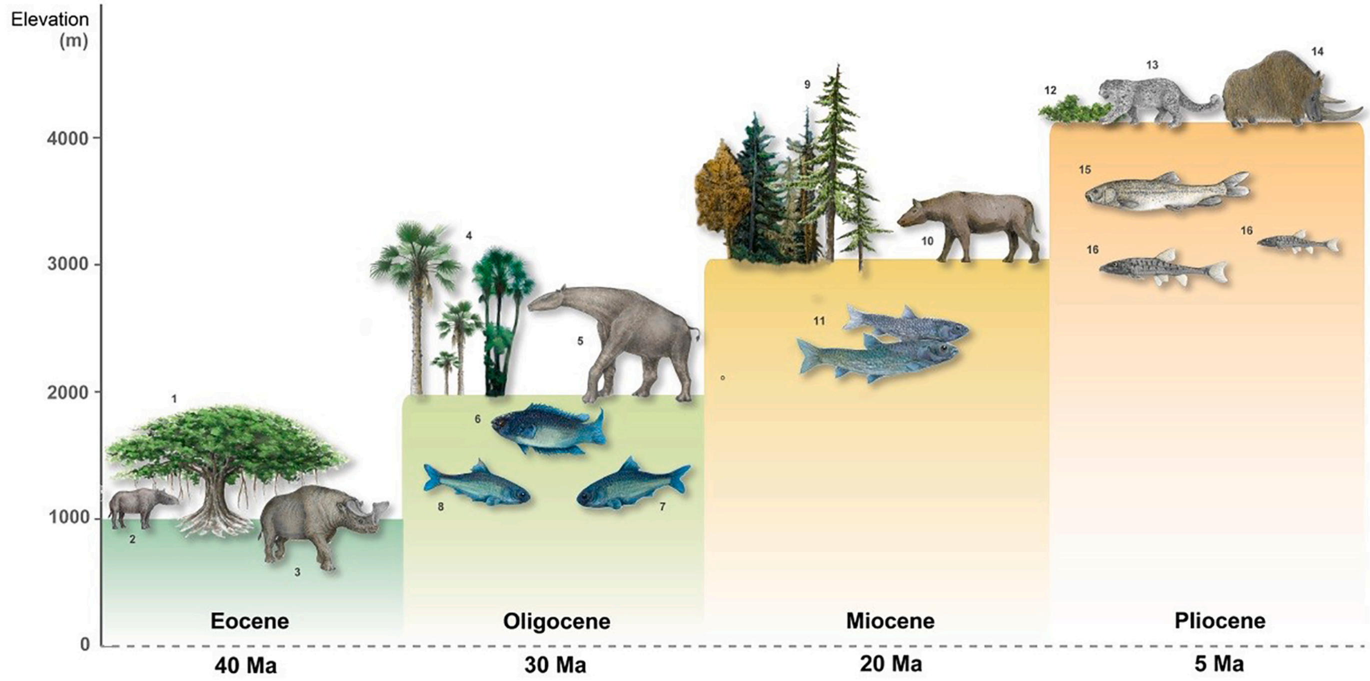

Fig. 7. Evolution and turnovers of the Cenozoic terrestrial ecosystems in the fossil-bearing basins of the Tibetan Plateau from the Eocene to the Pliocene (Art by Feixiang Wu). 1. Banyan tree (*Ficus*); 2. Amynodont; 3. Titanothere; 4. Palm (*Sabalites tibetensis*); 5. Giant rhino (*Paraceratherium*); 6. Climbing perch (*Eoanabas thibetana*); 7. Cyprinid fish (*Tchunglinus tchangii*); 8. A cyprinid fish; 9. Coniferous forest; 10. Hornless rhino (*Plesiaceratherium*); 11. Primitive schizothoracine fish (*Plesioschizothorax macrocephalus*); 12. Shrubs (*Cotoneaster*, *Spiraea*, *Caragana*); 13. Primitive snow leopard (*Panthera blytheae*); 14. Primitive wholly rhino (*Coelodonta thibetana*); 15. Highly specialized schizothoracine fish (naked carp, *Gymnocypris*); 16. Plateau loach (*Triplophysa*).

environment underwent significant shifts, and the strike-slip movements and deformational features of major faults surrounding the plateau were enhanced greatly. Thermochronological studies with apatite and zircon suggested that rapid denudation and cooling happened at about 25 Ma in the Qianlian, Laji, and Ela mountains in northern Tibetan Plateau as well as Tianshan mountains north of the Tarim Basin. A rapid left-lateral strike-slip movement occurred between 30 and 25 Ma in the Altyn Tagh Fault, and large-scale thrust uplift arose at that time in the Kunlun mountains (Pan et al., 2013; Wang, 2013). High-resolution seismic reflection data confirm that dramatic brittle deformation and thrust uplift took place at about 23 Ma in the West Kunlun mountains (Jiang et al., 2013), and significant uplift of the East Kunlun happened over 29–24 Ma (Yin et al., 2008). Guo and Wilson (2019) indicated a transformation in the distribution and nature of magmatism in Tibet at ca. 25 Ma, which reflects a significant change in the Himalayan-Tibetan orogen and associated mantle dynamic processes in the Early Miocene.

Concerning tectonic movements between 56 and 38 Ma, most researchers believe that this phase is the most intense period for the subduction and collision of the Indian Plate with the Eurasian Plate (Zhong and Ding, 1996; Zhang et al., 2010; Wang, 2013). In that time, there were remote effects of plate collision in the northern Tibetan Plateau, but elevation was not yet high overall (Tapponnier et al., 2001). Detailed studies of geotectonic evolution on the Tibetan Plateau revealed that at about 25 Ma, the effects of tectonic activities were widespread across the plateau, indicating that the present tectonic and topographic configuration of the plateau oversaw their foundations in the Oligocene, and the subsequent uplift was related with the outward expansion of the plateau (Wang, 2013). During the Late Oligocene, the central Tibetan Plateau underwent intense continental collision, so enormous south-north compressional action caused strong deformation and well-developed folds and faults of the Mesozoic strata in the Qiangtang Block (Horton et al., 2002; Kapp et al., 2005). Meanwhile, the remarkable uplift of the Lunpola area happened by 23.7 Ma (Ma et al., 2017). Reconciling a multidisciplinary range of evidence, the elevation of the central Tibetan Plateau was close to 3000 m in the terminal Oligocene (Deng et al., 2012b; Sun et al., 2014; Jia et al., 2015; Botsyun et al., 2019). The phytolith fossils of the Qiangtang-Hoh Xil area reflected a rapid cooling event between the Late Oligocene and the Early Miocene, corresponding to the uplift and northward growth of the Tibetan Plateau. The uplift was strengthened further in the earliest Miocene, and the overall topographic pattern started to change (Wang et al., 2010).

Therefore, growing geological evidence reflects that the transition from the Oligocene to the Miocene was a critical period for the tectonic evolution of the Tibetan Plateau. The cooling effect, which was produced by an elevation close to 3000 m a.s.l. in the uplift of the central Tibetan region during the Early Miocene, drove transformation of the terrestrial ecosystem of this region toward a faunal and floral community with temperate features from a tropical or subtropical environment of the Paleogene. Moreover, the early representatives of modern biological forms of the Tibetan Plateau appeared, such as the primitive schizothoracines (Wu and Chen, 1980; Chang et al., 2008).

5.2. *Background on global changes from Oligocene to Miocene*

In a global perspective, the overall trend of climate changes through the Cenozoic was that from greenhouse to an icehouse world. In the Late Oligocene, the global climate tended to be stable generally (Zachos et al., 2001). Based on studies for stable isotopes of deep-sea foraminiferal shells, we know that the Late Oligocene was in a megathermal period (Pekar and DeConto, 2006).

A series of fluctuations reflected by the δ^{18}O records indicate global warming or cooling and the growth or decay of the ice sheet since the Cenozoic. Immediately following the global cooling and the rapid expansion of the Antarctic ice sheet in the beginning of the Oligocene, deep sea δ^{18}O signatures maintained relatively high values (>2.5‰) with ice sheets reaching 50% modern size (Zachos et al., 1993). These ice sheets lasted until the Late Oligocene (27–26 Ma) when the warming reduced the size of the Antarctic ice sheet. From that time until the Middle Miocene at about 15 Ma, the global ice volume maintained a low level, and temperature of the sea bottom increased gradually although this duration included several short-term glacial stages, known as the Mi events (Zachos et al., 2001). Short intervals between glacial stages might provide conditions for some animals and plants to survive in cool habitats. For example, the rhino *Plesiaceratherium* lived in the Lunpola Basin between the two cooling events of Mi-1b and Mi-2 (Böhme, 2003).

Based on the arid or humid climatic proxies of different stages in the Cenozoic, the monsoon pattern similar to that of the present in East Asia appeared between the Late Oligocene and the Early Miocene; this was controlled by the planetary wind system previously (Wang, 1990; Guo et al., 2008; Sun and Wang, 2005). The critical turn for the Tibetan Plateau at the Oligocene/Miocene boundary coincided with appearance of the monsoon climate pattern revealed by the reconstruction of paleoenvironments; the reorganization of atmospheric circulation patterns revealed by the onset of the eolian dust of East Asia coincided with the beginning of the aridification of central Asia (Xiao et al., 2014). Meanwhile, the intensive and extensive uplift was a decisive factor promoting dry and cold climate on the Tibetan region after the Late Oligocene (Pan et al., 1995).

By understanding the uplift process of the Tibetan region and the past global change as well as their intimate relationship, it is known that the phased climatic variations within the plateau might result from superposition of both factors, further forcing the terrestrial ecosystem to turn from a warm system toward cool conditions.

6. Conclusions

The transition from the Oligocene to the Miocene was the critical period for the tectonic history of the Tibetan Plateau. The central Tibetan Plateau contains a relatively complete terrestrial sedimentary sequence from the Paleogene to the Neogene, serving as a hotspot for studying the geological history and paleoenvironment of the Plateau. A series of paleontological discoveries in this region during recent years has outlined the basic features and variations of the ecosystem in that time. The Late Oligocene fauna with the representative climbing perch and the flora with palms showed a tropical or subtropical ecosystem and indicated a warm and wet lowland. Since the beginning of the Miocene, the dominant coniferous forest, hornless rhinos, and snow carps formed a typical temperate ecosystem and indicated an appreciably cooler climate. The ecosystem of the Tibetan Plateau underwent a marked turnover from Late Oligocene tropical/subtropical habitats to Early Miocene temperate conditions, driving the emergence of early representatives of the modern faunal and floral elements typical of the region. The great turnover of the ecosystem coincided approximately with the wholesale uplift of the Tibetan region, and the major global changes during the Cenozoic.

Author contributions

T.D. designed the study; S.-Q.W. and T.D. studied the biostratigraphy; T.D., F.-X.W., T.S., and Z.-K.Z. studied the fossils; T.D. wrote the paper.

Declaration of Competing Interest

The authors declare that they have no conflict interests.

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