

Review

Phylogeography of regional fauna on the Tibetan Plateau: A review

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Received 4 July 2008; received in revised form 24 September 2008; accepted 10 October 2008

Abstract

The studies of uplift and glaciations of the Tibetan Plateau are summarized, and a series of recent case studies of the endemic species based on DNA sequences are detailed. In general, these molecular data show that all the organisms originated from Early Pliocene to Late Miocene, and then multi-stages of divergence/speciation occurred within each taxa following their original occupation on the plateau, mainly as a result of periodic glacial cycles and geographic isolation. The regional fauna may have undergone several range contractions and expansions during the Pleistocene glaciations. However, the population expansion and refugia may vary in space, time, and extent. The regional fauna of the Tibetan Plateau may be combinations of ancient movement from adjacent zoogeographical regions, speciation *in situ*, and postglacial colonization from adjacent areas. Geomorphic and climatic changes on the plateau definitely have a remarkable influence on the regional and adjacent biogeographic patterns, and the mechanism is very complex.

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Keywords: Divergence; Refugia; Postglacial colonization; Phylogeography; Regional fauna; Tibetan Plateau

1. Introduction

The Tibetan Plateau is the largest, highest and also one of the youngest plateaus on the Earth, usually referred to as the “World’s Roof”. Its geomorphologic formation and environmental changes during the Cenozoic have considerably influenced the structure and evolution of the component fauna of the plateau as well as the adjacent areas. In this review article we attempt to outline the main progress made on the studies of uplift and glaciations of the Tibetan Plateau so far, and to highlight some currently interesting phylogeographic studies of the regional fauna of the plateau.

2. Uplift of the Tibetan Plateau

Models of the Tibetan Plateau growth vary much in time and space. It has been proposed that significant surface uplift in the Qiangtang terrane occurred in the Early Cretaceous (145 Myr), followed by major surface uplift within the Lhasa terrane between 100 and 50 Myr ago [1]. This hypothesis remains disputed by other models of plateau growth ranging from Oligocene (e.g., 30 Myr ago) gradual surface uplift [2] to more recent (<7 Myr ago) and abrupt surface uplift [3]. Some scientists believe that the plateau was uplifted to its highest average elevation 14 Myr ago, and decreased in height afterwards [4–6] or the elevation has remained constant during the recent 15 Myr [7]. Other scientists concluded that the plateau reached the present elevation around 8 Myr ago [8–12]. The third idea, believed mainly by Chinese scientists, is that

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the most recent and abrupt uplift of the Plateau took place 3.4 Myr ago, and the plateau with 4500 m elevation was formed in the Quaternary [13–16]. Despite the tempo-spatial variation of the models of the plateau growth, many of these studies suggest oblique stepwise growth of elevation northward and eastward after the India–Eurasia collision [2,17–20].

A very recent study by Wang et al. [21] based on geological and geophysical evidence supports the idea that the central plateau (the Lhasa and southern Qiangtang Terranes, namely, the proto-Tibetan Plateau) was elevated 40 Myr ago, and the south and north of the proto-plateau gained the present elevation significantly later. During the Eocene time, the northern boundary of the proto-plateau was in the region of the Tanggula Shan. The plateau subsequently expanded as a result of the continued northward collision of India with Asia. To the south, the Himalaya rose during the Neogene; to the north, the Qilian Shan rapidly uplifted in the Late Cenozoic (Fig. 1).

3. Glaciations

The Tibetan Plateau not only has the largest modern middle-low latitude glaciations, but also experienced extensive Quaternary glaciations. Uplift of the Tibetan Plateau since the development of the Asian continent during the Late Cenozoic is the key factor initiating environmental changes in East Asia. The development of the Pleistocene glaciers of the Tibetan Plateau is closely related to the progressive uplift of the plateau and the surrounding mountains.

Many studies [22–29] have indicated that up to four Pleistocene glaciations can be recognized in the Tibetan

Plateau and the adjacent Himalaya Mountains. From the oldest to the youngest, these are designated as the Xixabangma (Early Pleistocene), Nyanyaxungla (Middle Pleistocene, about 0.7 Myr ago), Guxiang (late Middle Pleistocene), and Baiyu (late Pleistocene) events, among which Nyanyaxungla Glaciation was the largest in the extent. The histories of Pleistocene glacial evolution differ in various areas throughout the plateau, and the pattern is also very complex.

According to the “*Quaternary Glacial Distribution Map of Qinghai–Xizang (Tibet) Plateau*” edited by Li et al. [30], the area of the ancient ice cap during the last glacial maximum (LGM) exceeded 500,000 km² in high Asia, and 350,000 km² in the Tibetan Plateau, marked by piedmont glaciers, ice caps and trellis valley glaciers in many high peak regions (Fig. 2). But there is no evidence of a unified ice sheet covering the whole plateau throughout the Quaternary glaciations [29–31], possibly as a result of the declined precipitation and aridity following the uplift of the plateau.

4. Regional fauna

Mountain ranges are seen as important for divergence and speciation both in the tropics [32] and in more temperate regions [33–35], and the Tibetan Plateau is also a major feature in modeling the biogeographic pattern in China [36–38].

The fauna components of the plateau are mainly Palaeartic and Oriental, the remaining being endemic species, widely distributed species, and a few others of uncertain affinity [39,40]. The percentages of endemic species are

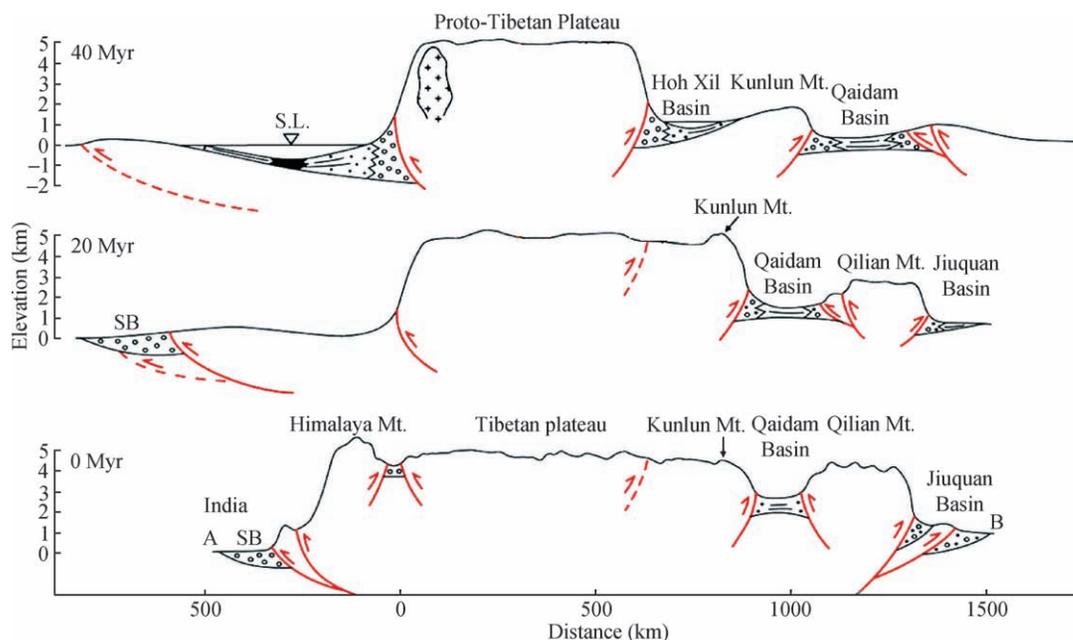


Fig. 1. Schematic paleogeographic cross-sections of the Himalaya and Tibetan Plateau, showing the surface-uplift history for the Tibetan Plateau, in which the plateau grows northward and southward from an elevated proto-Tibetan Plateau (Lhasa and Qiangtang terranes) beginning in the Late Paleogene. SB, Siwalik foreland basin. The Yaluzangbu River has been fixed as a reference point. Red lines and arrows represent faults. The position of the 0 Myr cross-section line runs about from point 89°20'E, 25°N to point 100°20'E, 40°N (cited and modified from Ref. [21]).

quite low, with only 23.6% among mammals and 4.3% among breeding birds [39]. There is only one endemic genus of mammals, i.e. *Pantholops*, and a few in birds, i.e. *Pseudopodoces*, *Kozlowia*, and *Urocynchramus*. The estimates of endemics partly supported the hypothesis that the Quaternary ice sheet had not wiped out the fauna of the plateau. However, the scarcity of peculiar genera indicates that the plateau fauna is rather recent.

Zhang and Zheng proposed that the present distribution of animals on the plateau is mainly consequent to historical migrations [40]. Many species existed on the plateau for a long period of time and have spread to other regions, hence for these species, such as the snow finch complex (*Montifringilla*, *Pyrgilauda*, *Onychostruthus*) and pikas (*Ochotona* sp.), the plateau serves as a distribution center. Belik [41] considered that the Himalayas and their surrounding ridges, but not the desert upland of the Tibetan Plateau, are the centers of origin and contemporary variety of alpine fauna. The climatic deterioration occurring during the uplift and the ice ages has induced the immigration of animals from central and northern Asia; while the forest-living or thermophilic animals retreated to the southeastern margin in the Hengduan mountains, which were formed in conjunction with the uplift of the Tibetan Plateau. The diverse habitats and lack of glaciations make the Hengduan mountains serve as a refuge, as well as a diversification center for many animals [39,40,42]. During Pleistocene glaciations, this area formed a shelter not only for some relics, such as *Ailuropoda melanoleuca*, *Ailurus fulgens* among mammals, and *Picoides tridactylus*, *Perisoreus internigrans*, *Tetrastes sewerzowi* among birds [39], but also for many species now distributed on the platform of the plateau. Lei et al. [43] found that the species richness is the highest in this area, where 67 species account for 54.4% of all 104 endemic birds in China. Parsimony analysis of endemism (PAE) for aphids identifies four major centers of endemism in the south-western mountains and Himalayas areas, and that the biodiversity patterns of endemism and species richness are geographically and quantitatively congruent in the Tibetan Plateau region [44]. These studies reflect the regional ecological, historical and environmental complexity.

5. Phylogeographic studies

Phylogeography is a field of study concerned with the principles and processes governing the geographic distributions of genealogical lineages, especially within closely related taxa [45,46]. The genealogical lineages can be reflected by DNA haplotype sequences, which are joined by mutational steps into a network, and then can be placed in a geographical context. A combination of such techniques is being sought to extract the data's full information, and so seek patterns and test geographical evolutionary models. According to Ref. [45], phylogeographic patterns can be divided into five major categories, which reflect different temporal scales and spatial aspects of population genealogical structure and can be explained by

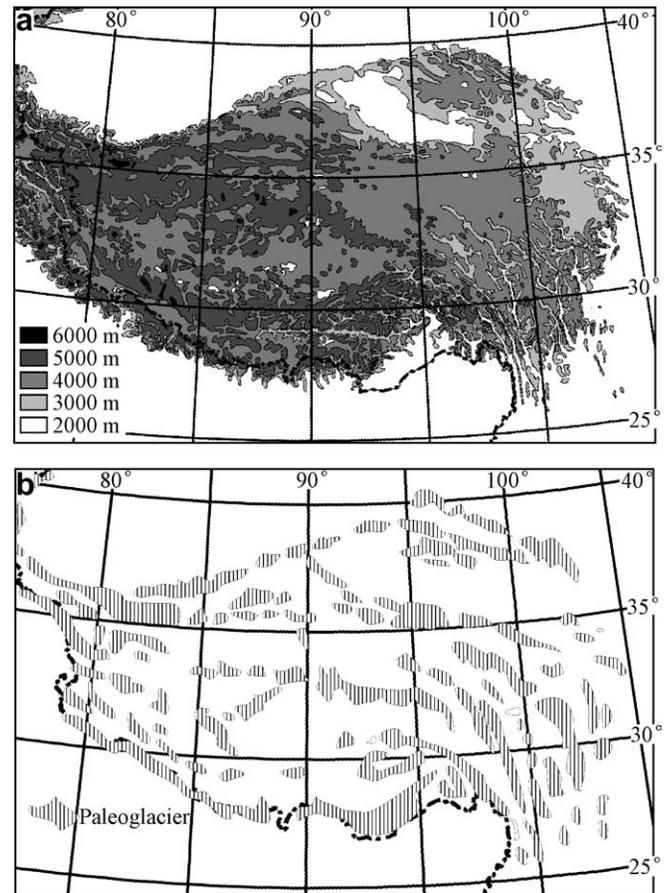


Fig. 2. Physical geography of the Tibetan Plateau (a), showing the mountains running east-west. (b) Ice cover during the LGM on the Tibetan Plateau (after Ref. [29]).

ecological and historical factors (see explanations of these categories in detail in Ref. [46]).

Many phylogeographic studies within the endemic species to the Tibetan Plateau using molecular markers appeared recently, allowing us to seek the common evolutionary patterns of the regional fauna and to understand the influence of the topographic and environmental changes on the speciation process. Here, a few detailed case studies on endemic species or some alpine species on the Tibetan Plateau are summarized.

5.1. Ground tit

The ground tit (*Pseudopodoces humilis*), an endemic bird to the Tibetan Plateau, dwells above the tree line (3300 to perhaps 5480 m) on rocky steppes and grasslands of the Tibetan Plateau. Previously known as Hume's ground jay, it had long been misclassified as a member of the crow and jay family (Corvidae) and was considered to be close to the genus *Podoces* until 1978 because of several traits shared in common with it. A recent study [47] removed it from the Corvidae and suggested that it should be the most aberrant member of the tits and chickadees (family Paridae) based on three independent datasets drawn from com-

parative osteology, the nuclear *c-myc* gene, and the mitochondrial cytochrome *b* gene, although *Pseudopodoces* shows little superficial resemblance to tits and chickadees [48]. *Pseudopodoces* is considered as the only species of parid with a distribution limited to the Tibetan Plateau. The cytochrome *b* divergence between *Pseudopodoces* and other species of titmice and chickadees is $\sim 9.4\%$ (uncorrected), roughly the level of divergence among parid subgenera [49], which translates a divergence time of about 5 Myr ago by applying the estimated rate of 2% sequence divergence per million years in the cytochrome *b* gene in many passerine birds [50–55]. This is consistent with an hypothesis that the uplift of the Tibetan Plateau provided a tectonically active geomorphological region, and a species of parid invaded the emergent high steppes and became the ancestor of *Pseudopodoces*; finally, morphological evolution in a novel adaptive zone altered its appearance [47].

Yang et al. [56] studied the phylogeographic structure of the species by using the mitochondrial control region and found two major clades (the plateau platform clade and the Qilian Mountains clade), which are separated geographically by the Qaidam Basin about 0.85 Myr ago. The authors postulated that the Qaidam Basin Desert and Quaternary glaciations might have jointly led to the differentiation between the two clades. Population expansion inferred for the two separated populations occurred about 0.17 Myr and 0.014 Myr ago, respectively, and restricted gene flow with isolation by distance was detected within the platform region, congruent with the expansion occurring after the extensive glacial period.

5.2. Snow finch complex

All species except one in the snow finch complex (Passeridae: *Montifringilla*, *Pyrgilauda*, and *Onychostruthus*, see Ref. [57]) occur sympatrically on the Tibetan Plateau and surrounding areas. Hence, the Tibetan Plateau is considered as the distribution center of the snow finch [39]. The monophyly of the snow finch complex group was well supported in Qu et al.'s study [58] and three major evolutionary lineages were recognized. The first clade *Pyrgilauda* consists of *ruficollis*, *blanfordi*, and *davidiana*; the second clade *Montifringilla* consists of *nivalis*, *henrici*, and *adamsi*; and the third distinct lineage within the snow finch complex consists of *taczanowskii*, which has been placed into its own genus, *Onychostruthus*. By applying the 2% rate rule, the authors estimate that the ancestor of the snow finch complex clades might have been split from their close sister group *Petronia* between 2.5 and 3 Myr ago. In fact, the uncorrected distances of the cytochrome *b* gene between the snow finch complex and the *Petronia* range from 8.56% to 9.68% in the study, which indicates that the divergence between them may be a little earlier, around 5 Myr ago. The subsequent splits of the snow finch complex into three clades occurred around 2–2.5 Myr ago.

Phylogeographical studies of the two snow finch species *O. taczanowskii* and *P. ruficollis* clearly show that there is

no distinct intraspecific phylogeographic structure across their ranges [59,60], although the average nucleotide diversity of the 41 individuals of *P. ruficollis* was 0.262%, which is much higher than that of *O. taczanowskii* (0.117%). There may be three main reasons behind the feature of no distinct phylogeographic structure: (1) high gene flow resulting from high mobility and lack of geographical barriers; (2) a relatively homogeneous habitat through the distribution range; and (3) a relatively fast and recent population expansion. The phylogeographic pattern of the snow finch is rather different from that of the ground tit, and the authors consider that snow finches may have a stronger ability of flight and a tendency to seasonal locomotion. The time estimates derived from the mismatch distributions suggest that the present postglacial colonization of the two snow finches occurred between 0.07 and 0.19 Myr ago [59,60].

5.3. Snowcock

Snowcock (*Tetraogallus*) is a unique group in the Galliformes, evolving in high mountains and being distributed at the highest altitude of all the Galliformes [61]. The group includes five species, Caspian (*T. caspius*), Caucasian (*T. caucasicus*), Tibetan (*T. tibetanus*), Altai (*T. altaicus*), and Himalayan snowcocks (*T. himalayensis*) (Fig. 3).

Molecular phylogenetic study of *T. tibetanus*, *T. altaicus*, and *T. himalayensis* based on 535 nucleotides in the mtDNA Cyt *b* found that *T. tibetanus* has approximately equal genetic distance to *T. himalayensis* and *T. altaicus* (6.5% and 6.7%, respectively), which translates a divergence age of about 4 Myr ago, and the divergence between the latter two species occurred 0.69 Myr ago [62]. The ancestor of current snowcocks could have inhabited Himalayanshan, Tangulashan, Hengduanshan, and the northern mountains of Kalakunlunshan, Kunlunshan, Arjinshan, Qilianshan, and Tianshan, of which Koslova [63] and Potapov [64] are believed to be the region of origin of *Tetraogallus*. The snowcock ancestor may have been distributed in the vast region of the present Qinghai–Tibetan Plateau platform before 4.0 Myr ago, and have fluctuated repeatedly during Pleistocene glaciers and interglaciers. The uplift of the Tibetan Plateau and peripheral mountains led to the divergence between *T. tibetanus* and the ancestor of *T. himalayensis* and *T. altaicus*. Then the ancestor of *T. himalayensis* and *T. altaicus* began to diffuse, primarily throughout the margins of the Qinghai–Tibetan Plateau, including Kalakunlunshan, Kunlunshan, Arjinshan, Qilianshan, and Tianshan during the largest Nyanyaxungla glacier in the middle of the Pleistocene. The following interglacial period made the habitats of snowcock fragmented, and then *T. himalayensis* and *T. altaicus* occurred as a result of vicariance events. On the other hand, the *T. tibetanus* ancestor inhabited a widespread area of the Tibetan Plateau and diffused during the glaciations (Fig. 3).

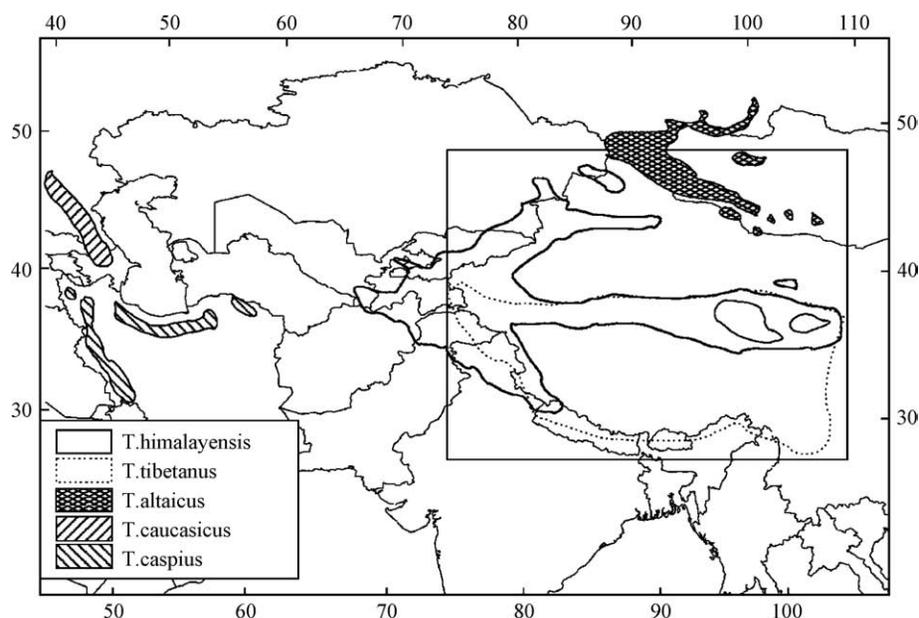


Fig. 3. Recent distribution of five *Tetraogallus* species (cited from Ref. [62]).

5.4. Eared pheasant

Eared pheasant, *Crossoptilon*, is an endemic genus to China, of which four species are recognized: *C. crossoptilon*, *C. harmani*, *C. auritum* and *C. mantchuricum*. All the species considered as threatened are listed in the Red Data Book of China and of Asia [65,66]. The distribution of the *Crossoptilon* genus is highly isolated. The distribution range can be divided into two main areas. One is in southwestern China, the Hengduanshan Mts. region, which is distributed by the white-eared pheasant (*C. crossoptilon*), blue-eared pheasant (*C. auritum*) and Tibetan-eared pheasant (*C. harmani*), among which, *C. harmani* is restricted to the Tibetan Plateau. The other is in central China, the Shanxi–Hebei–Shaanxi Mountains belt regions, which is distributed by the brown-eared pheasant (*C. mantchuricum*) [67,68].

Based on the mitochondrial *Cyt b* and control region sequences, Wu et al. [69] analyzed the phylogeny within the genus *Crossoptilon*, and found two major groups, one group including *C. crossoptilon* and *C. harmani*, and the other including *C. auritum* and *C. mantchuricum*. Based on the genetic divergence (2.42–3.16%), these two groups are estimated to have diverged 1.5 Myr ago, followed by differentiations occurring within each group. Based on the divergence between the *Crossoptilon* sp. and its sister species *Lophura swinhoii* and *Lophophorus impejanus* (6.3% and 8.0%, respectively), as well as the 2%/Myr rate rule, the ancestors of *Crossoptilon* might have occurred 5 Myr ago [69]. The genus *Crossoptilon* is usually considered to have originated in the region of the Hengduan Mountains following the uplift of the Tibetan Plateau. One branch stayed nearby the original center and diverged into *C. crossoptilon* and *C. harmani*; the other branch

spread towards north China and diverged into *C. auritum* and *C. mantchuricum* [67,69].

5.5. Pikas

Pikas seem to have a close association with some bird species, such as Hume's ground tit (*P. humilis*) and six species of snow finches, and appear to be both an allogenic engineer and a keystone species in the fauna of the Tibetan Plateau [70]. Most pikas are restricted to the Tibetan Plateau and adjacent areas, thus, the Tibetan Plateau is often considered to be the origin and distribution center of pikas [39,40].

Five major splits were found in the *Ochotona* genus based on 402 bp mitochondrial *Cyt b* sequences, according to the estimate of the divergence rate of 3%/Myr for mammalian species [71]. It was proposed that the uplift of the Tibetan Plateau and the radiation prompted by environmental changes could play a major role in the differentiation of the five groups, especially the surrounding Tibetan Plateau group, Tibetan Plateau group and the Huanghe group.

In a previous study of Yu et al. [72], the pikas distributed on the Tibetan Plateau were clustered into two groups, the mountain group and the shrub–steppe group, and the divergence was estimated to occur about 2.4 Myr ago. The divergence between the *cansus/annectens* clade and the *nubricalcurzoniae* clade occurred about 1.2 Myr ago.

5.6. Tibetan gazelle

The Tibetan gazelle (*Procapra picticaudata*) is a threatened species and is mainly distributed on the Qinghai–

Tibet Plateau and adjacent areas of China. To describe the evolutionary history and to assess the genetic diversity within this monotypic species and population structure among different geographic locations in China, Zhang and Jiang [73] sequenced the mitochondrial control region (CR) and Cyt *b* gene for 46 individuals from 12 geographic localities in Qinghai, Tibet, Xinjiang, Gansu, and Sichuan. A total of 25 CR haplotypes and 16 Cyt *b* haplotypes were identified from these gazelle samples. CR haplotype diversity (0.98) and nucleotide diversity (0.08) were both high. Phylogenetic trees indicate that the Tibetan gazelle in China can be divided into three main geographic clades: Tibet, Sichuan and Qinghai–Arjin Shan–Kekexili. Based on the estimated divergence rate of the CR, a recent coalescence time of approximately 2.2–4.4 million years was predicted among the Tibetan gazelle samples. Such a differentiation may reflect a geographic separation resulting from the environmental shifts and geographic isolation during the Late Pliocene to the Early Pleistocene.

All statistical analyses indicate that there was no single expansion or contraction in all populations of the Tibetan gazelle, but suggest that the Sichuan and Tibet populations were once fragmented in history but have merged again. The results suggest that the present population structure has resulted from the habitat fragmentation during the recent glacial period on the Qinghai–Tibet Plateau and then population expansion from glacial refugia after the glacial period. It is likely that the present populations of Tibetan gazelle exhibit a pattern reminiscent of several bottlenecks and expansions in the recent past.

5.7. Tibetan chiru

The Tibetan antelope or chiru (*Pantholops hodgsonii*) is endemic to the Tibetan Plateau of China and is considered a keystone species for the plateau ecosystem. Ruan et al. [74] studied the population genetic structure based on the complete mitochondrial control region sequences. The results showed relatively high nucleotide diversity (1.87–2.47%) for the Tibetan antelope, with no geographic partitioning. Statistical analysis indicated a postglacial range expansion from large ancestral populations, with no correspondence with the recent drastic decline in population size.

Ruan et al. [74] proposed that the limited geographic structure and correspondingly high estimates of gene flow among areas, coupled with the incongruence of genetic and geographic distances, may indicate strong historical connections between populations. The populations might have been anciently separated, with many intermediate haplotypes being lost over time by gradual lineages sorting, and then range/population expansion and genetic admixture lead to the specific phylogeographic structure. The distribution of suitable calving grounds is regarded as the most significant factor influencing the migration patterns to result in discriminated degrees of genetic exchange among populations.

5.8. Fish

Biogeographic analyses of freshwater fishes can provide a link between the geological and biotic evolution of the Tibetan Plateau, because their dispersal and distribution depends strictly on the formation and direct connections between drainages [75–79]. The alpine fish fauna of the Tibetan Plateau includes two major groups. One group is the subfamily Schizothoracinae, which has been a model group for testing hypotheses of speciation that explain these high levels of species richness, especially a possible correlation between diversification and geological uplift of the Tibetan Plateau [80–85]. This subfamily consists of 15 genera, including about 100 species [86]. More than 70 species of 12 of these genera are limited to the Tibetan Plateau [81,82]. Another is the family Sisoridae, one of the largest and most diverse Asiatic catfish families, with most species occurring in the water systems of the Tibetan Plateau and East Himalayas, presenting another ideal group for investigating the history of the plateau [37,87].

Chen et al. [37] proposed that the ichthyo-fauna differentiation due to the uplift of the Tibetan Plateau might have been reflected in the zoogeographic division, by analyzing the process and the uniqueness of the ichthyo-fauna from a historically temporal and spatial point of view. According to their study, the ichthyo-fauna occurred following the uplift of the plateau, and diversified as a result of long-term adaptation to geomorphic and environmental changes, which led to the division among the Holarctic Region, the Oriental Region and the Tibetan Plateau Region. They came up with the view that these three regions must have equal positions in zoogeographic divisions, and considered that the natural distribution boundary of plateau fishes (i.e. the subfamily Schizothoracinae and the genus *Triplophysa*) formed the demarcation line of the Tibetan Plateau Region.

He and Chen [88] recovered the phylogenetic relationships among 23 species and subspecies of the highly specialized grade schizothoracine fishes distributed at 36 geographical sites in the Tibetan Plateau and its surrounding regions by analyzing Cyt *b* gene sequences. The molecular estimates of divergence times revealed that the highly specialized grade schizothoracine fishes may have originated in the early Pliocene, and the major cladogenetic events of the highly specialized schizothoracine fishes occurred at these phases: 5 Myr, 4 Myr, 3.6–3.5 Myr, 3.0–2.9 Myr, 2.7–2.4 Myr, 1.7–1.6 Myr and 1.3–0.9 Myr ago. The results provided support for the assumption that the origin and evolution of schizothoracine were in close correlation with marked environmental changes caused by violent upheaval of the plateau.

Genetic diversity and population histories of *Schizopygopsis pylzovi* were studied by analyzing the complete sequences of 1140 base pairs of the Cyt *b* gene from 133 specimens on the Qinghai–Tibetan Plateau by Qi et al. [84]. The lowest genetic diversity (0.0018–0.0021) of *S. pylzovi* occurred in the Qaidam Basin, which experienced extre-

mely harsh and dry events during the late Pleistocene, indicating that the populations have experienced the severe bottleneck in history. The statistical data show that the species *S. pylzovi* underwent a sudden population expansion around 0.11 Myr ago, after the historical tectonic event of the Gonghe Movement (0.15 Myr ago) [89]. Fluctuations of the ecogeographical environment and major hydrographic formation may have promoted contiguous range expansion of freshwater fish populations, whereas the geological barriers among drainages have resulted in the fragmentation of population and restricted the gene flow among populations.

Peng et al. [79] analyzed the phylogeny of extant glyptosternoid catfishes within the Tibetan Plateau area, based on nucleotide sequences of one nuclear and two mitochondrial genes. The age of the most recent common ancestor of the glyptosternoid catfishes was estimated at about 6–8 Myr ago, with the second phase of speciation occurring between 3.5 and 1.5 Myr ago. Therefore, the authors support the view that the Tibetan Plateau reached its maximum height 8 Myr ago but was then lowered by extensional faulting, with a recent rapid uplift of the plateau occurring about 3.6 Myr ago accompanied by the largest glacier in the Northern Hemisphere.

5.9. Lizard

Phrynocephalus vlangalii, a small toad-headed viviparous sand lizard, is restricted to dry sand or Gobi desert highlands between major mountain ranges in the Tibetan Plateau. Jin et al. [90] obtained mtDNA sequences (partial ND2, tRNATrp and partial tRNAAla) from 293 *Phrynocephalus* individuals sampled from 34 sites across the plateau. The results show that *P. vlangalii* comprises seven well-supported lineages that correspond to distinct geographical areas with little or no overlap, and shares a most recent common ancestor at 5.06 ± 0.68 Myr ago. This is much older than intraspecific lineages in other Tibetan animal groups. Many small terrestrial animals have limited vagility, so it is not surprising that these species often display strong mtDNA phylogeographic structures.

Analysis based on tests of population expansion, estimation of node dates, and significance tests on clade areas indicated that phylogeographical structuring in *P. vlangalii* has been primarily shaped in three main stages, which occurred during the Pliocene and Pleistocene, specifically 3.2 Myr, 2.5 Myr and 1.9 Myr ago. In addition, the geographic partitions correspond to the appearance of major mountain ranges that formed physical barriers, such as the Qaidam Basin, Tanggula Mountains, Nanshan Mountains and Anyemanqen Mountains. Populations from the Qaidam Basin are shown to have undergone major demographic and range expansions in the early Pleistocene (1.6 Myr ago), consistent with the colonization of areas previously covered by the huge Qaidam palaeolake, which desiccated at the onset of the Pleistocene [91,92].

6. General features and discussion

These phylogenetic and phylogeographic studies reflect some general features in the following aspects.

6.1. Age of origination/divergence

The genetic differences among species or separated populations reflect an accumulation of *de novo* mutations post-dating population separation, and/or effects of lineage sorting (extinction) from a highly polymorphic ancestral gene pool, and may allow us to estimate their ages of origination or divergence based on certain molecular evolutionary rates. Studies of molecular phylogeny and phylogeography of organisms endemic to the plateau can present a tentative alternative approach for investigating the historical processes of the geological events and evolution of the regional fauna.

All the case studies show that nearly all of the studied taxa in this review diverged from their close relatives from Early Pliocene to Late Miocene (from 4 to 8 Myr ago). The data are also consistent with the lineages divergence of some alpine plants endemic to the Tibetan Plateau, such as the divergence between the “alpine shrub” vs. “coniferous forest” within *Nannoglottis* [93]. The coincidence of divergence times estimated from different taxa indicates that there may be a shared response to a common geological event. The origination age of these endemic taxa may reflect extensive geomorphologic and climate changes coupling with the phased uplift of the plateau. The ancestors invaded the emergent high plateau and evolved into peculiar groups with good adaptations to high altitudes.

In general, multi-stages of divergence/speciation from the Late Pliocene to Middle Pleistocene occurred within each taxa following their original occupation on the plateau. For example, the divergences within the sand lizard (*Phrynocephalus vlangalii*) occurred 5.1 Myr, 3.2 Myr, 2.5 Myr, 1.9 Myr ago, and are considered to have close associations with the phased orogenic movements, because the uplift of ranges on the Tibetan Plateau offered geophysical barriers (Fig. 4(a)). Deep divergence and phylogeographic structuring were also found in the ground tit, the Tibetan gazelle, the pikas, the snow finch complex, the fish snowcocks, and the ancient population subdivision in the Tibetan chiru. The divergence/speciation may also rely on the fragmentation of habitats due to geographic isolation and environmental shifts, such as repeated glaciations, shrinkage and expansion of lakes (especially for fishes), desertification of the Qaidam Basin (e.g. for ground tit, Fig. 4(b)). Climatic changes might have caused the migration of the organism, for example, organisms retreated to their refugia during the glaciations, and expanded during the interglacial, thus populations were geographically isolated as a result of vicariance or dispersal, and diverged due to chance sorting and accumulation of *de novo* mutations.

Although there is no extensive geomorphic tectonics in North America during the Pleistocene, the climate cycles of the past two million years also repeatedly transformed the North American landscape as the continent oscillated in time between cold glacial and warmer interglacial periods [94]. There are several studies concerning whether Pleistocene glaciations caused substantial avian diversification in North America [95–99]. Their major conclusion is that speciation events in the avian fauna of America were driven by climatic oscillations of the Pliocene and Pleistocene more or less. According to Ref. [100], speciation durations normally entail at least two million years on average, and it was also documented that the Pleistocene had considerable impact on phylogeographic patterns within and among closely related species of many vertebrates.

Therefore, the phased diversification of the fauna on the Tibetan Plateau does not necessarily reflect the stages of abrupt uplift of the Plateau since 3.4 Myr. In this review, we agree with the view that the plateau may have been uplifted to a significant level before Pleistocene, and suggest that the multi-phased divergence within the endemic species may be a result of periodic glacial cycles and geographic isolation, rather than abrupt and extensive Pleistocene uplift.

6.2. Refugia and population expansion

All the analyses indicate that the species of the plateau experienced extensive population oscillations during the Pleistocene glaciations. Viewed in the light of repeated ice ages in the Pleistocene throughout the Tibetan Plateau, the regional fauna may have undergone several range contractions and expansions. However, the population expansion and refugia may vary in space, time, and extent, among the species. We consider that there may be some reasons behind the phylogeographic inconsistency among sympatrically distributed species. The main reason may be different population history, population size and dispersion ability, because species may have taken different refugia and expansion routes, and differs in “response” times to isolating events due to different population sizes. Besides, there are some minor factors such as molecular evolution rates, life cycle, and breeding behavior. All these factors may vary among species.

The lack of phylogeographic structuring in *O. taczanowskii* and *P. ruficollis* indicates that both of them experienced a long-term bottleneck or repeated bottlenecks with associated loss of genetic materials as new areas were colonized during the episodic glaciations [101,102]. Higher genetic diversity was found in the eastern margin of the plateau for both snow finches, indicating that this area might provide refugia for them during the glaciations. Sino-Himalayan and southeastern regions are usually considered to serve as a refuge for Asian birds and mammals as well as a center of their evolution [39,40,103,104]. Theoretically and practically, the mountains running east–west and ice cover could possibly provide corridor for eastward retreat during glaciations (Fig. 2). The population expansion times of both snow finches, and ground tit varies from 0.014, 0.07 Myr to 0.19 Myr, being largely consistent with the last two interglacials on the Tibetan Plateau. We can conclude that the current distribution range through the plateau of snow finch birds possibly is the result of postglacial colonization from a very small effective population size and from one single source. Evidence from the Qinghai–Tibetan Plateau endemic plant *Juniperus przewalskii* (Cupressaceae) also supports postglacial recolonization of the plateau platform by contrasting phylogeographic structures of the haplotype-rich plateau edge area and the almost haplotype-uniform plateau platform region [105]. The expansion time of *S. pylzovi* was estimated to have taken place 0.11 Myr ago, consistent with the Gonghe Movement estimated to have occurred around 0.15 Myr ago, which had a significant impact on the evolution and development of the contemporary drainage systems [106,107]. This movement promoted range expansion and population dispersion of *S. pylzovi*. Differently, for sand lizard (*Phrynocephalus vlangalii*), populations expanded to the Qaidam Basin around 1.6 Myr ago, when the huge Qaidam palaeolake began to desiccate in the early Pleistocene. The high genetic diversity and deep phylogeographic structure indicate that this species may have found more than one single refugia

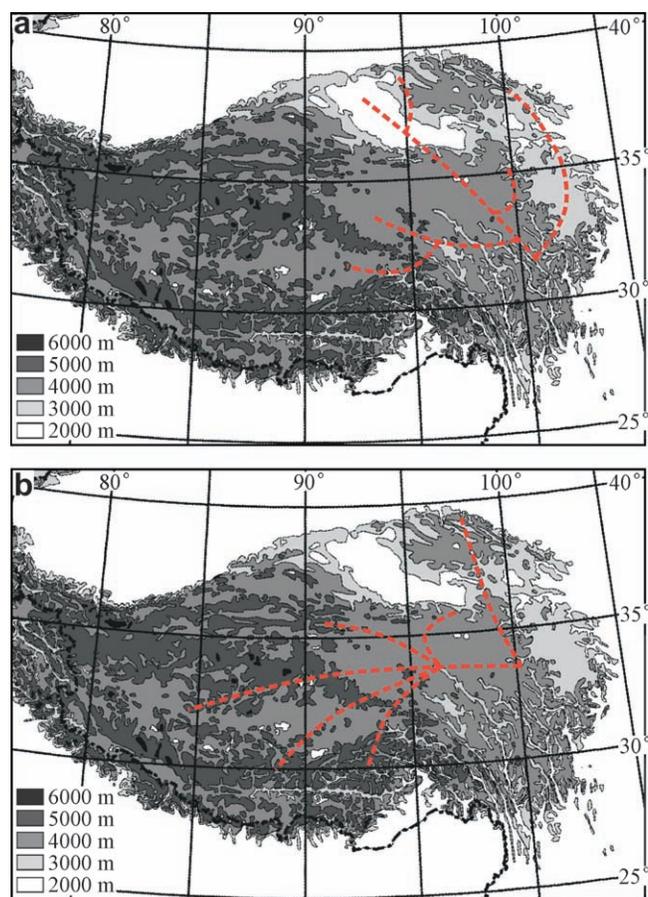


Fig. 4. Simplified schematic of geographic partition in mtDNA haplotypes for *Phrynocephalus vlangalii* (a) and *Pseudopodoces humilis* (b) based on phylogenetic analysis.

during the Pleistocene glaciations and experienced complex interglacial expansion. Similarly, the Tibetan gazelle and the Tibetan chiru might have also retreated to different refugia during the prevailing glaciations, and experienced severe genetic drift, but it is likely that the obvious admixture between separated populations following the postglacial expansion only happened to the latter. The influence of Pleistocene glaciations on snowcocks may be the reverse, because of their special habitats beyond the snowline. From the distribution areas of snowcocks (Fig. 3), it is obvious that their distributions are restricted to only mountains or the high platform of the plateau mosaically, possibly as a result of habitat fragmentation and range shrinkage due to the retreat of glaciations during the last interglacial period.

6.3. Origin and history of regional fauna

Most of the organisms reviewed here have their closely related sister groups sympatrically or around the plateau, and most of these divergence events appear to be pre-Pleistocene, suggesting that the plateau endemic be closely related to and have originated from local or adjacently distributed fauna. Johansson et al. [108] compared the relative importance of immigration versus *in situ* speciation to the build-up of the Himalayan avifauna, by evaluating the biogeographic history of the *Phylloscopus/Seicercus* warblers, which is well represented in Himalayan forests. The results indicate that virtually no speciation has occurred within the Himalayas. Instead, several speciation events are attributed to dispersal into the Himalayas followed by vicariance between the Himalayas and China/Southeast Asia before Pleistocene, this is consistent with orogenic uplift of the Himalayas 10 Myr ago [109]. These results prove that the uplift of the Tibetan Plateau provides an important obstacle for the spread of many species and consequently accelerates vicariance speciation, not only of the plateau fauna, but also of those distributed around the plateau. During the Pleistocene glaciations, some species went extinct over large parts of their range, some dispersed to new locations, some survived in refugia and then expanded again, and this must have occurred repeatedly and made the regional fauna more complex.

To sum up, the regional fauna of the Tibetan Plateau may be combinations of antique movement from both Palearctic and Indomalayan zoogeographical regions, speciation *in situ*, and postglacial recolonization from adjacent areas. Geomorphic and climatic changes on the plateau definitely have remarkable influences on the regional and adjacent biogeographic patterns, and the mechanism is very complex.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (Grant No. 30670276) and Chi-

na Postdoctoral Science Foundation (Grant No. 20070420416).

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