

# Human sedentism and use of animal resources on the prehistoric Tibetan Plateau

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**Abstract:** The transition of human societies from high mobility to sedentary lifestyles had a profound impact on subsistence, technology, and the origin of civilization. Sedentism was influenced by various factors such as climate change, population growth, resource pressure, and technological innovation. The Tibetan Plateau, due to its alpine and hypoxic conditions, is an ideal region to study human adaptation to extreme environments. However, the prehistoric process of sedentism on the Tibetan Plateau is unclear and the chronological sequence and driving mechanism of sedentism on the Tibetan Plateau are still controversial. Previous studies have focused on the diffusion of agriculture from low to high elevation areas, with little attention given to the role of animal resources in sedentism. Seasonality analysis using animal remains is crucial in determining whether a site was occupied year-round. To establish the seasonal calendar of animal resource utilization, it is recommended to create a database of skeletal morphology, whole genome, and proteome of contemporary Tibetan Plateau fauna to aid in the identification of animal remains from archaeological sites. Thus, intricate web of human-animal-environment relationship and the role of animal resources in human sedentism on the Tibetan Plateau can then be evaluated.

**Keywords:** zooarchaeology; human adaptation; subsistence economy; seasonality analysis; bulk-bone metabarcoding

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## 1 Introduction

“Sedentism” refers to the gradual process whereby a community reduces its mobility and ultimately establishes a permanent settlement in a specific location year-round (Marshall, 2006). It is not a singular phenomenon, but rather encompasses various forms of habitation that arise as mobility decreases, such as “a population residing in a fixed location year-round” or “at least a portion of the population residing in the same place throughout the year” (Keeley, 1988). These forms collectively exemplify sedentism as a unique socio-geographical form, the socio-cultural patterns of which are fixed and sustained within a given region and period (Kelly, 1992). In contrast to the social attributes of random or nomadic movement, sedentism represents a significant departure from the long-standing tradition of population mobility.

The transition of human populations from highly mobile to sedentary lifestyle has yielded a profound impact on human society. The adoption of a sedentary lifestyle resulted in increased fertility rates, shorter birth intervals, reduced mortality rates, and consequently, exponential population growth. Moreover, the concentrated exploitation of resources within a fixed geographic area has the potential to amplify production rate, increase the environmental carrying capacity to sustain larger populations, and even generate food surpluses. These food surpluses have ensured sustenance for specialized artisans and acted as a catalyst for technological innovation. The distribution of elites, full-time bureaucrats, soldiers, and religious officials through the surplus food production has resulted in social stratification and political centralization, giving rise to significant changes in social organization (Diamond, 2002, 2005).

The adoption of sedentism among non-agricultural groups is widely acknowledged, although when it emerged and its relationship with agriculture vary across regions and cultures (Belfer-Cohen and Bar-Yosef, 2000; Marshall, 2006). The earliest known instances of sedentism in southwestern Asia are from the southern part of the Levant during the Natufian Culture period (13–10 ka BP) (Henry, 1985; Kuijt and Goring-Morris, 2002), at least 3000 years prior to the emergence of agricultural societies in the region (Boyd, 2006; Watkins, 2017). Agricultural villages did not appear in Mesoamerica until roughly 4.5 ka BP, although plant domestication began between 10 and 8 ka BP (Smith, 2001). Turning to East Asia, sedentary villages sustained by a fishing-hunting-gathering economy emerged in Japan during the Jomon period (~9.8 ka BP) (Habu, 2004, 2008; Pearson, 2006), while in China sedentary villages first appeared at the Shangshan site (10–8 ka BP) during the early Holocene, closely linked to the beginning of rice domestication (Jiang and Liu, 2006; Xu and Chen, 2019). Sedentary communities that rely on fishing-hunting-gathering in the Arctic and sub-Arctic regions appear frequently, such as the Chukchi, Inuit, and Aleutian people (Kelly, 1992; Fitzhugh, 2003; Vaté, 2005). Likewise, in southern Africa and the Amazon basin indigenous people persisted in both hunting-gathering and agricultural production to today (Lee, 1972; Raffles, 2004). The archaeological and ethnographic evidence above underscores the variation in the emergence timeline of sedentism across regions and cultures, as well as the different subsistence economies of these sedentary groups (Brown and Vierra, 1983).

The origin of sedentism can be attributed to a combination of natural ecological and socio-economic factors. These include climate change, population growth, resource constraints,

and technological advancements (Bowles and Choi, 2013; Dow and Reed, 2015). The “push and pull” hypothesis highlights how abundant natural resources or environmental pressures, such as drought, can “attract” or “force” people to migrate and settle in regions with favorable environmental conditions (Price and Brown, 1985). The “pull” part suggests that plentiful resources can lead to a reduction in mobility and ultimately to sedentism. For example, during the early Neolithic period in northern Africa, abundant fish and animal resources from perennial or seasonal rivers attracted hunter-gatherers to settle down and eventually to the emergence of sedentary villages. Similarly, during the Natufian culture, the use of seasonal plant resources and the exploitation of short-distance migratory animals such as *Gazella gazella* resulted in reduced mobility in non-agricultural hunter-gatherer societies (Baharav, 1983; Garcea, 2006; Rindos, 2013).

The “push” part suggests that environmental changes or livelihood pressures can compel hunter-gatherers to adopt a sedentary lifestyle. Climate change, such as resource depletion caused by drought, can force people to move and settle in regions with better environmental conditions (Bar-Yosef and Belfer-Cohen, 1989; Sobolik, 2008). Population growth also contributes to an increase in resource constraints, which can drive populations to seek settlements elsewhere (Rafferty, 1985; Keeley, 1988; Ames, 1991). Regional population growth, however, can lead to tighter internal connections within groups, making it harder to migrate even when local resources become depleted, and thus promote a shift towards a settled life. Sedentism subsequently spreads among groups, further promoting population growth through increased fertility rates, and reinforcing the “sedentary-population growth-sedentary” process, deepening the degree of sedentism (Pearson, 2006; Kelly, 2013).

The “maritime hypothesis” suggests that some societies that rely on marine resources for subsistence may develop economic intensification like agriculture societies, leading to development of sedentary lifestyles and heightened social complexity (Marshall, 2006). Additionally, uneven distribution of resources caused by geographic environmental differences can prompt hunter-gatherer populations to reduce mobility and move towards a sedentary life. Key resource areas such as ecotones play a crucial role in this process (Watanabe, 1968; Binford, 1980; Belfer-Cohen and Bar-Yosef, 2000).

From the socio-economic and political perspective, population growth, the development of food storage technology, the emergence of territorial awareness, and the establishment of individual property rights contribute to increasing connections between societies. People voluntarily or involuntarily adopt a sedentary way of life to share risks, increase cooperation, enhance resource acquisition efficiency, promote technological development, and to cope with environmental change (Wright, 1971; Green, 1978; Binford, 1980; Binford, 1982; Hitchcock, 1982; Wiessner, 1982; Brown and Vierra, 1983; Henry, 1985; Binford, 2002; Baker, 2003; Eerkens, 2003; Pearson, 2006; Bowles and Choi, 2013). The sedentary way of life subsequently spreads among groups, continuously deepening the degree of sedentism through positive feedback (Pearson, 2006; Kelly, 2013).

Multiple criteria are assessed to ascertain the presence of sedentism at a particular site. These include enduring structures constructed with significant manual labor and material resources the presence of robust material culture such as extensive grinding tools, storage facilities, and cemeteries, as well as high frequency of human commensals, specifically house mice (*Mus musculus*) and house sparrows (*Passer domesticus*). Additional indicators

of sedentism may consist of proof of seasonal habitation demonstrated by animal and plant remains, pottery, and the thickness and density of archaeological sediments (Henry, 1985; Levy, 1995; Belfer-Cohen and Bar-Yosef, 2000; Boyd, 2006; Marshall, 2006; Edwards and Wadi, 2012). As a single site may not satisfy all these criteria, it is recommended to consider multiple lines of evidence when ascertaining whether sedentism has occurred at a site.

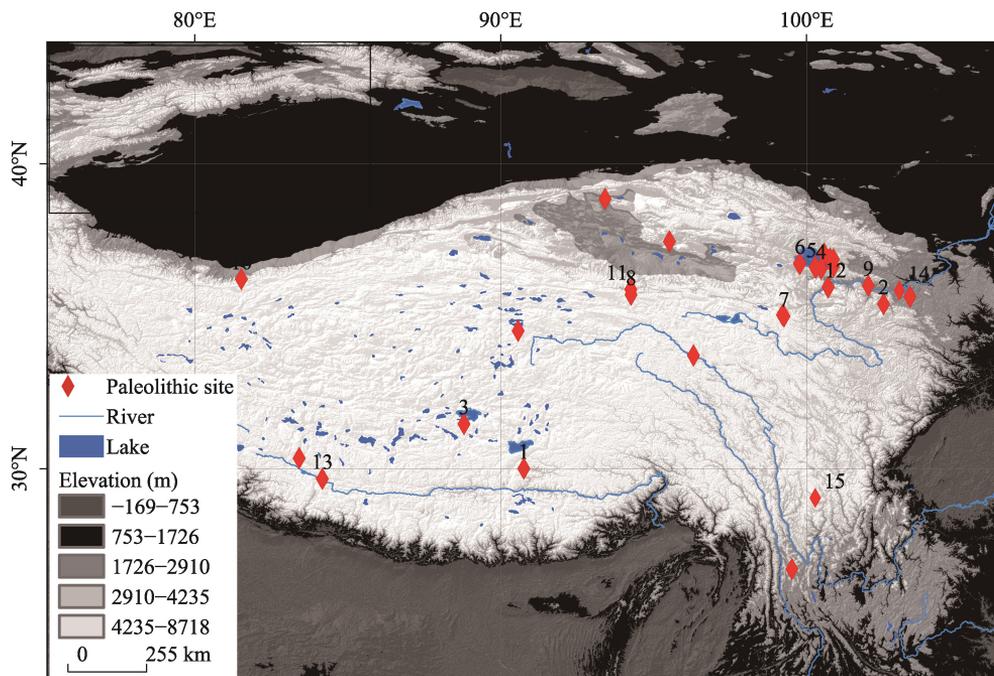
Known as the “Roof of the World”, the Tibetan Plateau has an average elevation of approximately 4320 m and a total area of  $3.0834 \times 10^6$  km<sup>2</sup> (Zhang *et al.*, 2021). The Plateau’s unique geographical and environmental features are mainly characterized by high elevation, low temperature, strong solar radiation, numerous rivers and lakes, widespread glaciers and frozen soil, high biodiversity, and significant internal environmental diversity (Zheng and Zhao, 2017). The low biological productivity caused by hypoxia and high elevation increases the cost of hunting and cannot fulfill human nutritional demands. Human physiological limitations, such as low fertility rates and high mortality rates, severely restricted early humans from changing from nomadic hunting to sedentism (Zhang *et al.*, 2018). The study of prehistoric human sedentism on the Tibetan Plateau is an important component of exploring human physiological and behavioral adaptations to high-elevation regions (Zhang *et al.*, 2016). Animals are high-protein and high-fat meat resources and provide secondary products such as wool, milk, and animal power. Therefore, they provide the material basis for human adaptation to a high-energy consumption life in cold and hypoxic environments. Understanding the animal utilization strategies of early humans holds the key to revealing the driving mechanisms of human expansion and sedentism on the Tibetan Plateau. This article systematically summarizes the research progress on the sedentism of prehistoric humans and their use of animal resources. Furthermore, it proposes tailored methods for using animal remains to investigate when and how sedentism occurred on the Tibetan Plateau.

## 2 The history of prehistoric human activities on the Tibetan Plateau

### 2.1 Archaeological evidence

Recent archaeological findings indicate that the ancient hominin Denisovans had already occupied the Tibetan Plateau as early as 200 ka BP, leaving rock art in the Plateau hinterland (Chen *et al.*, 2019; Zhang *et al.*, 2020; Zhang *et al.*, 2021; Chen *et al.*, 2022). The Piluo site in western Sichuan, dating back to earlier than 130 ka BP and located at 3750 m above sea level (a.s.l.), has yielded Acheulian hand-axes (Zhang *et al.*, 2022). *Homo sapiens* arrived in the Plateau hinterland at the Nwya Devu site (4480 m a.s.l.) around 40–30 ka BP (Zhang *et al.*, 2018), and continued to roam the Plateau until the middle and late Holocene. This is seen in sites 151 (15.4–13.1 ka BP; 3397 m a.s.l.; Wang *et al.*, 2020), Jiangxigou #1 (14.6 ka BP; 3200 m a.s.l.), and Xidatan #2 (9.2–6.4 ka BP; 4569 m a.s.l.) (Brantingham *et al.*, 2013), which provide evidence of prehistoric humans’ long-term adaptation to the high-elevation environment of the Tibetan Plateau (Figure 1).

At approximately 5.5 ka BP, human lifestyles on the Tibetan Plateau began to shift from hunting to sedentary. The earliest sedentary sites are found along the eastern edge of the Plateau, ranging from northeastern areas to western Sichuan. These sites include Zongri (5.6–4.0 ka BP, 2820 m a.s.l.) in Tongde County, Qinghai Province; Haxiu (5.5–4.7 ka BP, 2840 m a.s.l.) in Barkam County (Chen *et al.*, 2010); Yingpanshan (5.3–4.6 ka BP, 1710 m



**Figure 1** The distribution of Paleolithic sites on the Tibetan Plateau (1. Chusang (226–169 ka BP, 4369 m a.s.l.; Zhang *et al.*, 2021); 2. Baishiya Karst Cave (190–5 ka BP, 3200 m a.s.l.; Chen *et al.*, 2019; Zhang *et al.*, 2020); 3. Nwya Devu (Zhang *et al.*, 2018); 4. 151 (Wang *et al.*, 2020); 5. Jiangxigou#1; 6. Heimahe#1 (13.1 ka BP, 3200 m a.s.l.; Brantingham, 2006); 7. Xiadawu (~11 ka BP, 3988 m a.s.l.; Hou *et al.*, 2016); 8. Xidatan#2 (Brantingham *et al.*, 2013); 9. Shalongka (8.3–8 ka BP, 2046 m a.s.l.; Dong *et al.*, 2013); 10. Yangchang (7.6–7 ka BP, 2440 m a.s.l.; Han *et al.*, 2014); 11. Yeniugou (7.5 ka BP, 3800 m a.s.l.; Tang *et al.*, 2013); 12. Layihai (~7.6 ka BP, 3125 m a.s.l.; Gai and Wang, 1983); 13. Zhongba 10-1 (6.6–2.6 ka BP, 4570 m a.s.l.; Hudson *et al.*, 2014); 14. Jiangjunfu 01 (120–90 ka BP, 2673 m a.s.l.; Chen *et al.*, 2021); 15. Piluo (~130 ka BP, 3750 m a.s.l.; Zheng *et al.*, 2022)

a.s.l.) in Maoxian County (CMICRA *et al.*, 2018); Liujiashai (5.3–4.7 ka BP, 2650 m a.s.l.) in Jinchuan County, Sichuan Province (Sichuan Provincial Cultural Relics and Archaeology Research Institute *et al.*, 2021), as well as the Karuo (4.8–4.0 ka BP, 3233 m a.s.l.) and Xiaoenda sites (4.8–4.2 ka BP, 3200 m a.s.l.) in Chamdo, Tibet Autonomous Region (ACCRTAR, 1985; HSTACCRTAR, 1990). The sedentary lifestyle spread from the periphery to the interior, and by the middle of the second millennium BCE, sedentary settlements, represented by the Qugong site (3.75–3.0 ka BP, 3686 m a.s.l.) to the north of Lhasa, had emerged (IACASS, 1999). The artifacts and features discovered at these sites, particularly the houses, provide evidence of the spatio-temporal characteristics of the spread of sedentism from the periphery to the interior of the Tibetan Plateau.

## 2.2 Genetic evidence

Genetic analysis reveals a trace of archaic genetic ancestry from the Paleolithic population (62–38 ka BP) in present-day Tibetan populations, including the EPAS1 gene derived from ancient Denisovan hominins (Zhao *et al.*, 2009; Qi *et al.*, 2013; Lu *et al.*, 2016). By simulating the introgression of the EPAS1 gene into modern humans and the period of intense natural selection, Huerta-Sánchez *et al.* (2014) suggest that a population expansion event to

the Tibetan Plateau may have taken place at roughly 9 ka BP. Furthermore, studies on the whole genome indicate that a considerable proportion of genetic ancestry in present-day Tibetan populations can be traced back to the extensive expansion of ancient low-elevation populations in northern East Asia between 15 and 9 ka BP (Lu *et al.*, 2016; Hu *et al.*, 2017). Moreover, there are complex population diffusion events in the late Holocene. According to previous genetic and archaeological studies, there may have been two expansions of agricultural populations from the Yellow River basin to the northeastern margin of the Tibetan Plateau as well as to southwest China during 6.5–2.5 ka BP, and millet farming from northern China expanded to the Plateau along with wheat at about 3.6 ka BP (Wang *et al.*, 2018; Li *et al.*, 2019). Whether these were population migrations or cultural communication is still being debated. Ancient mitochondrial DNA (mtDNA) analysis has shown that prehistoric populations on the Tibetan Plateau only made a partial genetic contribution to modern Tibetan populations. Some of the ancestors of modern Tibetans may have dwelled in low-elevation regions between 4.75 and 2.775 ka BP, with a population exchange occurring between high and low elevation regions from 2.125–1.1 ka BP (Ding *et al.*, 2020). Additionally, modern Tibetan populations exhibit a small amount of genetic exchange with populations from Central Asia, the Eurasian steppe, and South Asia (Lu *et al.*, 2016). It is still challenging to determine how and when the internal differences within the Plateau populations emerged and their impact on each other. In summary, while the genetic composition of high-elevation populations already existed since the Late Pleistocene and had been inherited by later plateau populations, sedentism on the Plateau since the Holocene might have played an essential role in the formation of the genetic composition of plateau populations. It is plausible that the unique genetic characterizations of the high-elevation population had already formed in hunters-fishers-gatherers before the arrival of agriculture. Subsequently, along with the dissemination of agriculture and, perhaps, yak domestication, diverse subsistence economies in different regions gradually led to genetic differentiation within the Tibetan Plateau population. However, the limited availability of samples means that further genetic research alongside archaeology is necessary to reveal the detailed migration of Tibetan Plateau populations.

### **2.3 When did prehistoric people occupy the Tibetan Plateau all year round?**

The notion of year-round habitation on the Tibetan Plateau encompasses two distinct yet connected aspects: one pertains to continuous wandering on the Plateau without descending to low-elevation regions, while the other pertains to permanent residence in a single location, namely sedentism. The term “year-round/permanent occupation” in earlier studies emphasizes the importance of nomadism in high-elevation regions throughout the year (Chen *et al.*, 2016; Meyer *et al.*, 2017), and does not necessarily imply the concept of “sedentism” as discussed in this article. These two concepts are, however, inherently linked. While permanent habitation on the Tibetan Plateau may not necessarily entail sedentism, sedentism is undoubtedly a constituent part of permanent habitation. It is therefore imperative to undertake further exploration and analysis of year-round habitation sites, with a particular focus on seasonal patterns. Only sites that have been continuously occupied throughout the year can be deemed as sedentism in archaeology.

Some scholars suggest that humans began inhabiting areas above 3300 m on the Tibetan

Plateau year-round no earlier than 7.0 ka BP, and this was closely linked to the expansion of low-elevation agricultural populations. Meanwhile, the year-round habitation of areas above 4000 m by humans was no earlier than 4.0 ka BP and was closely associated with the domestication of yaks (*Bos grunniens*) (Brantingham *et al.*, 2010). Evidence from animal and plant remains in the northeastern Tibetan Plateau indicates that the introduction of wheat agriculture at approximately 3.6 ka BP promoted the large-scale occupation of regions above 2500 m on the Tibetan Plateau (Chen *et al.*, 2015). Additionally, the introduction of domesticated animals, such as sheep (*Ovis aries*), which can convert non-edible high-elevation plants into energy, is also believed to have played a significant role in the process of humans inhabiting the Tibetan Plateau year-round, beginning at approximately 3.6 ka BP (Madsen *et al.*, 2006; Brantingham *et al.*, 2007; Barton, 2016).

There exist divergent perspectives concerning the timing, location, and driving forces behind the early human sedentism on the Tibetan Plateau. Notably, archaeologists posit that as early as 5.0 ka BP, sedentism had emerged along the eastern edge of the Tibetan Plateau at an elevation exceeding 3000 m, based on the evidence of houses, tombs, agricultural tools, and animal and plant remains at Zongri and Karuo (ACCRTAR, 1985; Chen *et al.*, 1998). According to Zhang *et al.* (2016), the spread of millet farming played a pivotal role in the prehistoric humans' ability to enter and settle in the lower elevation river valleys of the northeastern and southeastern regions of the Plateau between 6.0 and 4.0 ka BP. Later, the introduction of wheat farming from the west fostered sedentism at higher elevations around 3.6 ka BP. Besides, scholars posit that the nomadic herding of yaks and sheep, along with the cultivation of barley, facilitated a mixed agricultural and pastoral economy and gave rise to sedentary communities of the Nomuhong culture above 2800 m in the northeastern Plateau between 3.6 and 2.3 ka BP (Zhang and Dong, 2017). Recently, Chen *et al.* (2022) established three stages in the progression of human sedentism on the Plateau: millet farming communities settled in the lower elevation river valleys of the eastern Plateau by at least 5.2 ka BP, and after 4.8 ka BP, sedentary communities at elevations exceeding 3000 m in the east of the Plateau gradually formed. Lastly, the expansion of wheat farming and animal husbandry since 3.5 ka BP fueled widespread sedentism in high-elevation areas (Zhang and Dong, 2017). Nevertheless, except for the Zongri, Karuo, and Xiaoneda sites, which have undergone archaeological excavation, other archaeological sites at elevations above 3000 m frequently lack direct evidence of sedentism.

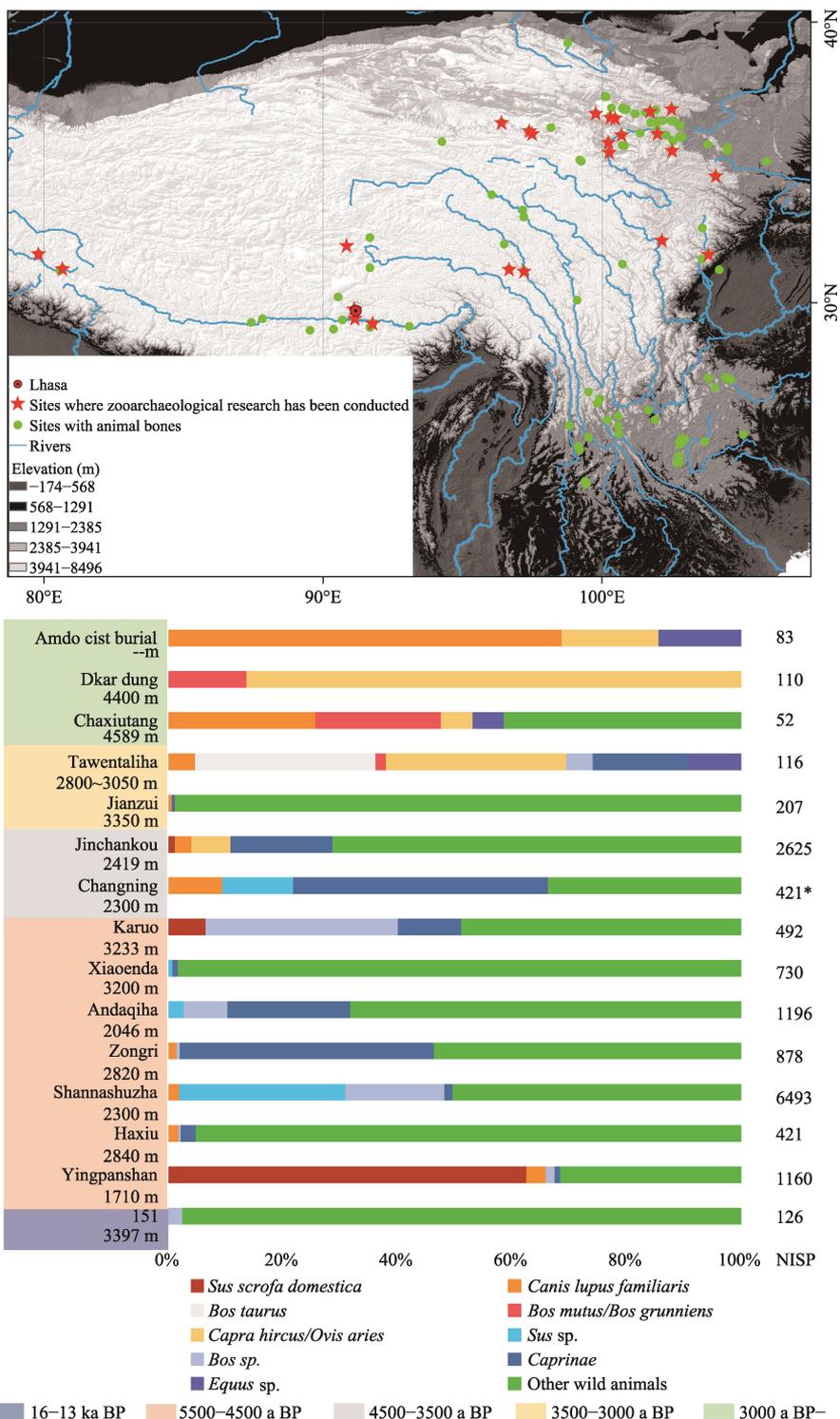
Most of the hypotheses regarding the prehistoric year-round hunting and sedentism on the Tibetan Plateau are based on the supposition that lowland agricultural populations migrated to highland regions and that the introduction of agriculture was a precondition for humans to reside in high-elevation areas throughout the year. Whether the questions of “when did humans start a sedentary lifestyle on the Plateau” and “when did the earliest agriculture on the Tibetan Plateau begin” should be regarded as identical is a matter of debate (Lu, 2017). This brings to the fore intriguing query: Could non-agricultural societies settle permanently on the Tibetan Plateau? What roles did the highland hunter-gatherers play in the early processes of sedentism and crop dissemination (Zhang *et al.*, 2016)? Scholars have argued that when discussing the issue of when humans settled on the Plateau, the significance of the use of wildlife resources is underestimated and the relationship between lowland agricultural populations and plateau hunter-gatherers is often overlooked (Lu, 2017).

### 3 Animal resource use on the Tibetan Plateau

The Paleolithic sites on the Tibetan Plateau, except the Baishiya Cave site (225–45 ka BP, 3200 m a.s.l.), are mainly open-air sites with thin cultural layers, small features such as ash pits and fire pits, and a dearth of artifacts. It is generally believed that during this period, humans only occasionally visited the high-elevation regions of the Tibetan Plateau and subsisted solely on hunting. In the middle to late stages of the Paleolithic (225–13.1 ka BP), the primary prey consisted of large and medium-sized mammals, such as rhinos (*Dicerorhinus*), Equidae, Cervidae, and Bovidae (Fan *et al.*, 2009; Gao *et al.*, 2020; Hou *et al.*, 2020). However, in the early to middle Holocene (10.4–5 ka BP), hunting focused on smaller and medium-sized mammals, including Caprinae, Antilopinae, Rodentia, and foxes (*Vulpes* spp.) (Gai, 1983; Brantingham, 2006; Wang *et al.*, 2020; Zhang *et al.*, 2020).

Around 5.5 ka BP, sedentary sites emerged in high-elevation regions, including the northeastern Tibetan Plateau and western Sichuan. During this period, there were variations in animal procurement practices among different sites. The Shannashuzha site (2312 m a.s.l.) and the Xiaoenda site only yielded remains of wild animals (Zhang *et al.*, 2019; Chen *et al.*, 2020). In contrast, sites such as Zongri and Karuo began to display evidence of animal husbandry, including domestic pigs (*Sus scrofa domestica*) and dogs (*Canis lupus familiaris*) (Huang, 1980; An and Chen, 2010; Ren, 2017). In the Hengduan Mountains, although the Haxiu site and the Yingpanshan site belong to the same archaeological culture, there are marked differences in the animal remains excavated. The Haxiu site (2800 m a.s.l.) mainly yielded wild animal remains, with only dog remains indicating animal domestication (He and Chen, 2006; He, 2015). Conversely, the lower-elevation Yingpanshan site (1710 m a.s.l.) provided mainly domesticated animal remains, including domestic pigs and cattle (*Bos taurus*) (He *et al.*, 2009). This reveals a diverse economy combining settled agriculture, animal husbandry, fishing, hunting, and gathering. The diptych of these two sites illuminates exhibit a vertical stratification in animal resource use (Figure 2).

During the period of 4.5–3.0 ka BP, the prehistoric cultural exchange between the East and West intensified, and domesticated cattle, goats (*Capra hircus*), and sheep from South-west Asia spread to the northeast of Qinghai Province and Yunnan region. The use of animal resources by ancient Tibetans diversified spatially, with cattle and sheep surpassing pigs and becoming the mainstay of livestock farming (Figure 2). Domesticated sheep and goats were first found on the Tibetan Plateau at the Jinchankou site (4.5–3.6 ka BP, 2419 m a.s.l.; Ren, 2017). At the Changning site (4.3–3.6 ka BP, 2300 m a.s.l.), the animal remains were dominated by domesticated cattle, goats, and sheep, with cattle and sheep accounting for a higher proportion than pigs and playing a significant role in the ancient people's subsistence economy (Li, 2016). The ancient people of the Qugong site in the southern Tibetan Plateau subsisted upon a combination of crop cultivation and pasturing yaks and sheep, supplemented by hunting white-lipped deer (*Przewalskium albirostris*), roe deer (*Capreolus capreolus*), musk deer (*Moschus* sp.), wild boar (*Sus scrofa*), kiang (*Equus kiang*), and various birds (IACASS, 1999). In the western part of the plateau, at the Gebusailu site, Ngari Prefecture of the Tibetan Autonomous Region, the early-phase burials (3.56–3 ka BP, 3800 m a.s.l.) contained domesticated animals such as goats, sheep, and cattle, as well as wild animals such as argali (*Ovis ammon*) and deer. In the subsequent late-phase burials (2.31–2.127 ka BP), sheep, goats, cattle, horses, kiang, and fish were discovered (TICRCR, 2017). After



**Figure 2** The archaeological sites with animal remains unearthed on the Tibetan Plateau and their proportions of animals (annotation: left column gives the names and elevations of the sites in chronological order, horizontal bars show the percentage of animal types recorded for each site, and the right column gives the Number of Identified Specimens (NISP) at the sites; \* is MNI the Minimum Number of Individuals at Changning site.)

3.0 ka BP, sheep, goats, cattle, horses, dogs, and yaks were widely raised on the Tibetan Plateau and played vital roles in people's daily lives and social rituals (Zhang *et al.*, 2015; Zhang and Lu, 2017; Lu *et al.*, 2021) (Figure 2).

In general, the sedentary processes and economic forms of prehistoric humans on the Plateau were diverse. However, it is noteworthy that systematic zooarchaeological research has mostly been conducted at low elevations, pre-dating 6.0 ka BP, where there is tangible archaeological evidence of long-term use of houses, agriculture, and livestock. Unfortunately, there is a lack of relevant information and seasonality analysis for other sites. Moreover, the spread of domesticated dogs, pigs, cattle, sheep, goats, and horses to the Tibetan Plateau, as well as their significance and influence on human behavior during different stages of economic activity, remain unclear. The domestication origin and development process of yaks, as well as their role in the prehistoric human sedentary process on the Plateau, are still unknown. In-depth zooarchaeological research, combined with a comprehensive analysis of the seasonal and economic characteristics of the sites is required to provide better answers to the above questions.

## 4 Animal resource use and seasonality analysis of archaeological sites

### 4.1 Animal resource use analysis

Animal remains retrieved from archaeological sites are a primary source of information about human exploitation of animal resources. Techniques employed in zooarchaeological research include but not limited to species identification, age and sex determination, cull pattern analysis, morphometric analysis, taphonomic analysis, quantification, and pathological analysis. On this basis, the ancient ancestors' ability to develop and use animal resources, the strategies and modes of obtaining, slaughtering, transporting, processing, and consuming animal resources, and the restoration of ancient human living environment are discussed. Furthermore, research into the patterns of site use (such as seasonal use and duration of occupation), the formation processes of a site, the post-depositional events, as well as the domestication and dissemination of ancient domesticated animals, the evolution of secondary products, and the societal development process has been rigorously conducted (Lyman, 1994; O'Connor, 2008; Reitz and Wing, 2008; Davis, 2012; Gifford-Gonzalez, 2018).

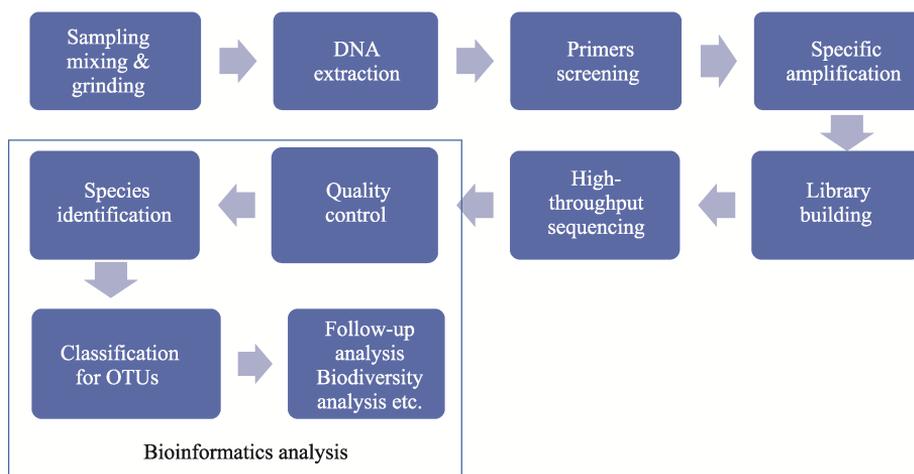
Identification of animal remains is fundamental in the field of zooarchaeology and a large number of modern animal bones are required for comparison as reference specimens. The Tibetan Plateau is home to a diverse array of wildlife, including over 1,100 different species comprising 190 mammals, 817 avian species, 55 reptiles, 45 amphibians, and 159 fish, of which many are indigenous to the Tibetan Plateau's unique ecosystem (Wu and Wu, 1992; Ma, 2004; TZCLG, 2005; Liu *et al.*, 2013; Lu, 2018). For instance, among the 29 mammalian species found in Qiangtang Plateau, 11 ungulates are endemic to the Plateau, such as *Bos mutus*, *Pantholops hodgsonii*, and *Equus kiang* (Lu, 2018). Although Tibetan Plateau animal specimens are chiefly held in museums and research institutions, only skulls are typically preserved due to storage constraints, causing issues with animal taxonomy and rendering postcranial bones unsuitable for zooarchaeological research. In addition, current bone atlases offer scant descriptions of indigenous animals from the Tibetan Plateau, such as the wild yak, white-lipped deer, and kiang, with morphological investigations of these species remaining

rare (Wang *et al.*, 2020). Therefore, it is indispensable to establish a repository of bone morphology data pertaining to the living animals populating the Tibetan Plateau.

Even with a firmly established corpus of animal morphology, identifying substantial amounts of fragmented animal bones unearthed from archaeological sites, particularly remains of fish and avian species, is still a daunting task. Therefore, the incorporation of advanced techniques such as ancient DNA analysis and Zooarchaeology by Mass Spectrometry (ZooMS) can significantly enhance the effectiveness of research and the precision of species identification.

#### 4.1.1 Bulk bone metabarcoding in species identification

Bulk bone metabarcoding (BBM) is a sophisticated methodology that employs high-throughput sequencing and metabarcoding analysis to ascertain the species composition of bulk bone samples at one time (Murray *et al.*, 2013). BBM involves DNA extraction from bulk bone samples, amplification using specific PCR primers, and sequencing the amplified products to identify the constituent species present within the fragmental bone samples. This technique can be used to analyze animal assemblages in archaeological sites (Figure 3).



**Figure 3** Experimental workflow of bulk-bone metabarcoding (OTU = operational taxonomic unit)

In 2013, the first application of BBM was undertaken on bone fragment powder samples excavated from the Devil's Lair and Tunnel cave sites in southwestern Australia, which revealed valuable information about the species composition of mammals, birds, and reptiles (Murray *et al.*, 2013). Since then, BBM has been used in tropical regions such as Madagascar, Australia, and New Zealand, as well as in the small Caucasus Mountains and Brazil, to analyze bone fragments spanning from 42 to 0.1 ka BP. These analyses have been employed to discuss the species and subsistence strategies of ancient human populations in exploiting animal resources, biodiversity changes, environmental transformations, and the impact of human activities on the ecological environment (Douglass *et al.*, 2018; Seersholm *et al.*, 2018, 2021a, 2021b; Antonosyan *et al.*, 2019). BBM requires only a small sample size to identify morphologically indistinguishable animal bone fragments, and can recognize abundant species in fossil records, as well as a wide range of extinct species. Hence, BBM is deemed an innovative and effective method for identifying animal communities in archaeo-

logical sites, characterized by its precision, sensitivity, and feasibility (Greally *et al.*, 2015, 2016).

#### 4.1.2 The feasibility of using BBM for species identification in zooarchaeology on the Tibetan Plateau

The implementation of BBM for species identification in ancient animal bone samples requires careful consideration of several factors. First, successful implementation depends on the identification of appropriate barcode pairs with short, variable DNA regions suitable for amplifying specific taxonomic groups. It is crucial that the amplified gene fragment has sufficient differences in base pairs between different species while maintaining small differences within the same taxa. Currently, for mammalian samples, 16S rRNA gene barcodes are commonly used, while 12S rRNA primers are used for avian and fish species-specific amplification (Table 1).

**Table 1** Primers for specific amplification in bulk-bone metabarcoding

Name		Primer (5'–3')	Target taxa	Target gene	Reference	Amplicon length (BP)	Annealing temperature (°C)
12SAH	Forward	CTGGGATTAGATACCCCACTAT	Bird	12S rRNA	Cooper, 1994	229–235	57
	Reverse	CCTTGACCTGTCTTGTAGC	Bird	12S rRNA	Cooper, 1994	229–235	57
Mam16S	Forward	CGGTTGGGGTGACCTCGGA	Mammal	16S rRNA	Taylor, 1996	89–115	57
	Reverse	GCTGTTATCCCTAGGGTAACT	Mammal	16S rRNA	Taylor, 1996	89–115	57
12S-V5	Forward	ACTGGGATTAGATACCCC	Fish	12S rRNA	Riaz <i>et al.</i> , 2011	106	58
	Reverse	TAGAACAGGCTCCTCTAG	Fish	12S rRNA	Riaz <i>et al.</i> , 2011	106	58

Second, the precision of BBM identification outcomes hinges on the caliber of the reference database. Establishing a standardized DNA barcode reference database, a species information database, as well as an information sharing and application platform would be advantageous for enhancing the accuracy of BBM identification (Chen *et al.*, 2016). According to statistics, the Tibetan Plateau is home to over 190 mammal species, 817 bird species, and 159 recorded documented fish species (Wu and Wu, 1992; Ma, 2004; TZCLG, 2005; Liu *et al.*, 2013). Using the National Center for Biotechnology Information (NCBI) data sharing platform, this study statistically queried the mtDNA database of 149 mammal species, 152 fish species, and 234 bird species (mainly waders and waterfowl) on the Tibetan Plateau (Table 2). The results indicate that 119 mammal species, 112 fish species, and 152 bird species possess complete mtDNA reference sequences, accounting for 78.87%, 73.68%, and 64.96% of the total number of species in each category, respectively. The animal species that lack mtDNA data are primarily Vespertilionidae, Muridae, Columbidae, and Caprimulgidae, which are also relatively scarce in archaeological sites on the Tibetan Plateau. Therefore, we believe that the current Tibetan Plateau animal mtDNA database platform can, in essence, support the analysis of BBM data, but further supplementation and enhancement are still needed.

Finally, in comparison to metabarcoding research on contemporary samples, BBM is frequently employed to examine ancient samples, which harbor highly degraded and fragmented ancient DNA, and the length restrictions curtail the resolution of BBM technology in

**Table 2** Completeness of mitochondrial DNA data of living animals on the Tibetan Plateau

Taxa	Number of recorded species	Number of counted species	MtDNA database			Notes
			Complete	Partial	None	
Mammal	ca. 190	149	119	15	13	The animal species that lack mtDNA data are primarily Vespertilionidae, Muridae, Columbidae, and Caprimulgidae, and only <i>Moschus fuscus</i> in Artiodactyla has no complete mtDNA data
Fish	159	152	112	20	20	Species without data are distributed in all families, but other species of the same genus always have data
Bird	817	234	152	71	11	Most of the data are not available for Rallidae, Scolopacidae, Scolopacidae, and Caprimulgidae among others.

species classification. BBM is capable of amplifying only a single class of organisms in a biota, such as fish, birds, and mammals, resulting in challenges in determining the relative proportions of multiple taxa in a single DNA extract (Taberlet *et al.*, 2012). Furthermore, identifying species from single organelle markers presents certain issues, such as low specificity on the barcode for relatively young species in the evolutionary process or gene introgression between species, which can lead to incorrect species identification (Taberlet *et al.*, 2012).

As an emerging technology, the implementation of BBM in animal archaeology demonstrates significant potential. In the future, using this technology to analyze DNA from bone fragments retrieved from archaeological sites could efficiently and accurately identify a vast array of species, substantially enhancing work efficiency. Furthermore, cross-validating BBM analysis results with traditional animal archaeology morphological results enhance BBM research accuracy and opens up additional avenues for expansion.

## 4.2 Seasonality analysis of archaeological sites

Seasonality analysis provides direct evidence of whether an archaeological site was inhabited throughout the year and reflects human resources utilization strategies. The growth, reproduction, and behavior of animals in temperate regions are influenced by seasonal changes, and the animal remains discovered at a site are important materials for conducting seasonality analysis. The criteria used to determine seasonality include, but are not limited to: (1) the presence of species that only appear at specific times, such as migratory birds, migratory fish, and mammals with migratory habits, and insect pupae (Yeomans and Richter, 2020); (2) the presence of bones with seasonal characteristics, such as antlers that annually grow and shed, and the medullary bone formed only during the breeding season in female birds (Serjeantson, 2009); (3) determining the age at death of mammals through their teeth and bones to calculate the season of death, as the birth season of animals is usually fixed (Hillson, 2005); (4) observing growth rings in materials such as shells, fish vertebrae, opercula, otoliths, and dental cementum of mammals to determine the season of death (O'Connor, 2008); and (5) determining the season of death by changes in the enamel oxygen isotope of herbivorous animal teeth (Henton, 2012). By analyzing the season of death of each individual animal, the seasonal distribution of a species can be obtained. By summarizing the season of death of all species and individuals, the occupation seasons of a site can be determined. To obtain a more comprehensive and objective understanding, species that entered the site de-

posits through natural forces should be eliminated as much as possible when using animal remains to discuss seasonality, and only specimens that are clearly due to human activity entering the site deposits should be selected.

Appropriate research methodologies must be chosen for each archaeological site, considering the animal remains excavated from the site. The Tibetan Plateau, the origin of numerous major rivers in Asia, boasts a plethora of lakes, with more than 417 lakes exceeding 10 km<sup>2</sup> in size, covering a total area of approximately 44,993.4 km<sup>2</sup> (Dong *et al.*, 2014). This region thus provides abundant aquatic resources (Wu and Wu, 1992). Additionally, wild mammalian remains have been uncovered in archaeological sites throughout the area (Figure 2). Accordingly, the following two methodologies have potential to determine the seasonal usage patterns of sites in this region.

#### 4.2.1 Cementum increment analysis in mammals

In zooarchaeology, the techniques used to determine the age of death of mammals mainly comprise of evaluating the fusion condition of bone epiphysis and the eruption sequence and degree of dental abrasion, as well as measuring crown height (Hillson, 2005). Due to enamel's resilience and ease of preservation, the order of tooth eruption and the degree of abrasion is frequently employed to estimate the age of death of animals, and, in conjunction with the species' birth season, the season of death may be deduced. However, as the age of death and season of birth of animals tend to be distributed in time intervals, this method is less accurate in determining seasonality (Li and Zhang, 2014).

Cementum, a concentric layer of mineralized tissue surrounding the tooth root, is generated through the mineralization of collagen fiber bundles in the periodontal ligament. It measures around 30–50 µm in thickness and consists of 60% collagen, 40% hydroxyapatite, and trace quantities of non-collagenous proteins (Burke and Castanet, 1995). Cementum is generally situated below the gum line on the tooth's cervical area and around the root. In perissodactyls, such as horses, cementum not only covers the root surface but also extends to the entire cheek teeth, except for the occlusal surface. Histological investigations have demonstrated that cementum cell growth is linked to food, climate, and environment. When the environment is warm and food is abundant, cementum cell growth is rapid and densely packed. Conversely, in dry and cold environments with low nutrition, cementum cell growth is slow and sparsely distributed (Fišáková, 2013). Controlled experiments conducted on goats have shown that the alternation of translucent and opaque bands in cementum growth is determined by two factors. First, the frequency and intensity of chewing various foods affect the direction of protein bands in cementum. Second, alterations in nutrient intake trigger changes in the relative rate of mineralization and deposition of cementum bands (Lieberman, 1994). Both of these factors relate to the seasonal dietary alterations of animals, which, in turn, give rise to the alternating translucent and opaque bands in cementum growth. Cementum grows continuously from the emergence of a tooth and does not undergo remodeling or resorption. Under polarized light, the opaque bands in mammalian cementum sections indicate slow growth rates in seasons such as winter (which may also be broad), while the translucent bands indicate sustained rapid growth. The transparency of the sections under reflected light is the opposite: the opaque bands under transmitted light become translucent under reflected light, and the transparent bands under transmitted light become opaque. The animal's age at death may be determined by counting the bands and adding the tooth's

emergence time, while the type of the outermost band can be used to determine the animal's season of death.

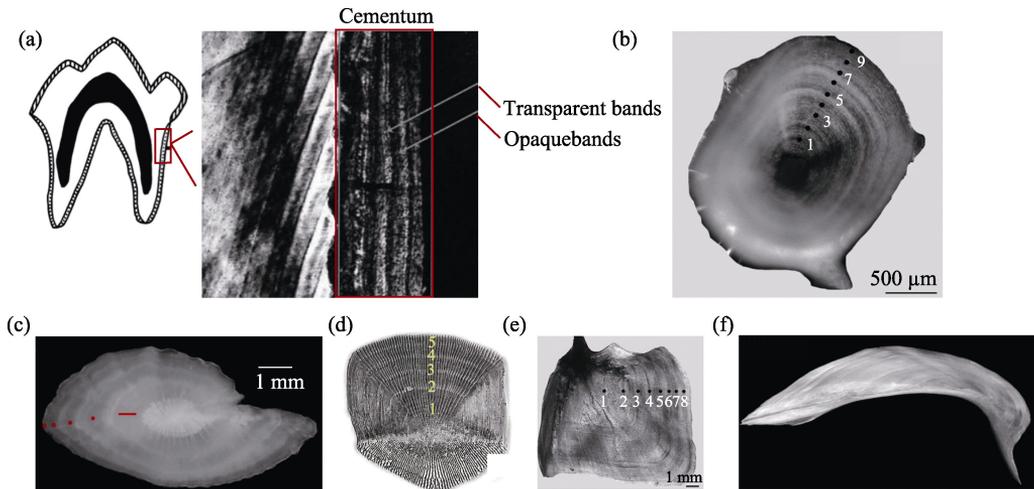
Research into the periodic deposition of dental cementum dates back to the 1950s, exemplified by Laws' investigation into the age estimation of walrus (*Mirounga leonina*) through the computation of cementum annuli (Laws, 1952). In the late 1960s, cementum increment analysis was employed to examine animal remains discovered at archaeological sites (Saxon and Higham, 1968). By comparing the teeth of modern and Iron Age sheep, it was posited that the Iron Age sheep died during the summer. Subsequently, this method was extensively employed worldwide, encompassing animals such as deer, goats, and horses, and proved invaluable in the investigation of issues such as hunting strategies, seasonal usage of sites, and sedentary patterns (Saxon and Higham, 1968; Jones, 2012; Schmaus *et al.*, 2020; Azorit *et al.*, 2021). However, this method has been less used in Chinese archaeological sites, with comparable analyses only conducted on horse teeth excavated from the Xujiayao site in the early and late Pleistocene strata (Li *et al.*, 2017).

The widespread application of cementum growth analysis in archaeology is limited by a major factor, which is its destructive sampling method. Prior to making dental cementum sections, it is necessary to conduct zooarchaeological analysis, take photographs, and even create three-dimensional scanning models. In addition, the production of tissue slices requires a complete set of hard tissue slicing equipment to minimize errors, and the production process is relatively complex. It is best to have professional personnel perform the operation to ensure the accuracy of the results. Kay borrowed the method of making fragile rock slices from geologists to make animal fossil slices that more clearly display the chalky annual rings. Using a polarizing microscope, false growth rings formed by burial can be further distinguished, which improves the accuracy of determining the season of animal death (Kay and Hiiemae, 1974; Stutz, 2002).

#### 4.2.2 Marginal type analysis of fish vertebrae

Fish are ectothermic creatures with characteristic growth patterns that are periodically distinct. Calcified structures, including scales, bones, and otoliths, grow continuously throughout the lifespan of a fish without undergoing remodeling or resorption (Bagenal, 1974). It is generally assumed that fish growth is impeded during winter, resulting in narrow, semi-transparent growth bands that appear dark in reflected light and light in transmitted light. During periods of rapid growth, a relatively wider region (summer band) forms, appearing opaque in transmitted light and white in reflected light. A single annulus is made up of one summer band and one winter band, and typically one annulus is formed per year. Consequently, the number of growth rings serves as a measure of a fish's age (Bagenal, 1974; Van Neer *et al.*, 1999). The mechanism underlying the formation of calcified structures and growth rings in fish is not yet fully understood, but it is commonly assumed that it is related to seasonal fluctuations in temperature (Andrus, 2011). Nonetheless, other factors, such as internal circumstances (reproduction, gender reversal, migration, sexual maturity) and external circumstances (food or water abundance, water quality, salinity), are also linked to the development of growth rings in fish (Vitale *et al.*, 2019). In tropical fish, the alternation of dry and rainy seasons may have a greater impact (Gabriela *et al.*, 2021). Based on the principles of growth-ring formation, contemporary fisheries science typically uses marginal analysis to determine fish age and examine fish growth, generally using fish scales and oto-

liths. Fish scales are the simplest to acquire, while otoliths have the greatest precision and accuracy. Additionally, vertebrae, cleithrum, pectoral fin, opercula, and fin spines are frequently used (Figures 4b–4f). The Marginal Increment Ratio Analysis can be employed to reflect fish growth by measuring the ratio of the outermost ring to the secondary ring, generating a complete annual edge growth curve through monthly measurement. However, this technique cannot accurately detect small increments and has a significant error in slow-growing and older individuals (Smith, 2014).



**Figure 4** Animal bone materials used for seasonality analysis (a. Position of cementum and microstructure of cementum under polarizing microscope (Fišáková, 2013); b. fish vertebra (Ma *et al.*, 2017); c. otolith (Van Neer *et al.*, 1999); d. fish scale; e. opercular (Ma *et al.*, 2017); f. cleithrum (Faust *et al.*, 2013))

Marginal growth analysis is a valuable tool in determining the season of death for fish remains in zooarchaeology. This method relies on the seasonal formation of annual rings in living specimens of the target species. However, since the formation of annual rings is influenced by various factors such as fish species, gender, collection location, and water conditions, it is crucial to conduct detailed studies on the fish fauna and resource status of the site area (Casteel, 1972). Additionally, it is important to study the growth patterns of annual rings in relevant living fish species, especially in otoliths and vertebrae, to provide a reliable basis for determining the age and season of death of fish remains excavated from archaeological sites (Walters, 1992; Van Neer *et al.*, 1999; Gabriela *et al.*, 2021).

An illustrative case is found along the Yarlung Tsangpo, which has a diverse range of living fish species, with a total of 25 species distributed in the middle and upper reaches and major tributaries of the river. These fish belong to 3 orders, 5 families, and 17 genera, of which 16 species are endemic to the Tibetan Plateau (Yang *et al.*, 2011). The main economic fish species include *Schizopygopsis younghusbandi*, *Schizothorax o'connori*, *Racoma waltoni*, *Schizothorax macropogon*, *Ptychobarbus dipogon*, *Oxygymnocypris stewartii*, and *Glyptosternum maculatum*, which account for over 99% of the catch weight. Notably, *Schizopygopsis younghusbandi*, *Schizothorax o'connori*, and *Schizothorax macropogon* alone account for 82% of the catches (Yang *et al.*, 2010). Additionally, *Gymnocypris waddellii* is widely distributed in the Yarlung Tsangpo basin near the lakes Yamzhog Yumco and Duoxing Co (Yang and Huang, 2011) (Table 3).

**Table 3** Timing of the winter-summer boundary of dominant fish in the middle reaches of Yarlung Zangbo

Species	Number of ring cycles per year	Month	Analyzed material	Reference
<i>Ptychobarbus dipogon</i>	1	3–5	Otolith	Li <i>et al.</i> , 2009
	1	3–6	Otolith	Yang, 2015
<i>Oxygymnocypris stewartii</i>	1	3–6	Otolith and vertebra	Huo, 2014
		3–5		
<i>Schizopygopsis younghusbandi</i>	1	3–5	Otolith	Duan, 2015
<i>Glyptosternum maculatum</i>	1	4–6	Vertebra	Ding <i>et al.</i> , 2008
<i>Schizothorax o'connori</i>	1	3–5	Otolith	Ma <i>et al.</i> , 2011
		3–6	Vertebra	
<i>Schizothorax waltoni</i>	1	3–5	Otolith and vertebra	Hao, 2005; Zhou, 2014
<i>Schizothorax macropogon</i>	1	3–6	Otolith	Liu, 2016
<i>Gymnocypris waddellii</i>	1	–	Anal scale and dorsal fin ray	Yang <i>et al.</i> , 2011

The economically significant fish species inhabiting the middle reaches of the Yarlung Tsangpo have been thoroughly studied with respect to their individual biology, particularly focusing on the use of otoliths and vertebral bones in determining their growth season. Investigations on the growth and age of indigenous fish species on the Tibetan Plateau have evinced the high precision and dependability of otoliths and vertebrae as tools for animal age determination, with otoliths displaying a slightly greater degree of accuracy than vertebrae. Table 3 presents an outline of the winter and summer rings, their periodicity and timing, formed on the otoliths and vertebrae of major fish species in the middle reaches of the Yarlung Tsangpo. The analysis has shown that the vertebral rings of *Oxygymnocypris stewartii*, *Glyptosternum maculatum*, *Schizothorax o'connori*, and *Racoma waltoni* have a formation period of one year, beginning in March to May, with the exception of *Glyptosternum maculatum*, which forms its rings from April to June. The otolith rings of *Ptychobarbus dipogon*, *Schizopygopsis younghusbandi*, and *Schizothorax macropogon* are formed from March to May/June. However, there are currently no data regarding the formation time of each bone ring of *Gymnocypris waddellii*. From the analysis of the types of edge rings of fish vertebrae discovered at archaeological sites on the Tibetan Plateau, it is possible to ascertain their death seasons, and thus can indicate the occupation seasons of the site.

## 5 Problems and prospects

The chronology and driving mechanisms of prehistoric human sedentism on the Tibetan Plateau remain obscure. What was the role of hunter-gatherers in the early sedentary process? How significant was the use of animal resources in Tibetan Plateau sedentism? To address these questions, systematic zooarchaeology research needs to be undertaken on the Tibetan Plateau.

The extant archaeological work has provided initial insights into prehistoric animal resource use on the Tibetan Plateau. However, systematic zooarchaeological research has only been conducted at a few sites, and most animal remains were collected from the ground sur-

face, lacking archaeological context. Animal remains were merely identified and simply counted, lacking quantitative analysis. Current research primarily focuses on the northeast region, leaving vast geographical gaps. Due to current limitations, the unearthed animal remains are not thoroughly studied. Many studies have only discussed ancient environments and the proportion of domestic animals in the economic system. Issues such as animal resource use, cull patterns, sex ratios, and taphonomic analysis require further investigation. Moreover, the domestication and spread of the major livestock on the Tibetan Plateau are still unclear, and their significance in the subsistence economy of each time period and their impact on human behavior and social development are also unclear. Significantly, except for a few sites with evident sedentary features (such as Zongri, Karuo, and Qugong), the seasonal analysis of other sites is lacking, making it challenging to comprehend fully the occurrence and development of early sedentism.

Henceforth, a more systematic and interdisciplinary approach is required to advance zooarchaeological research on the Tibetan Plateau. It requires the use of diverse techniques to determine the species, sex, and age of animal remains unearthed from archaeological sites, in addition to morphometrics, quantification, and taphonomic analysis. Based on this information, the use of animal resources, animal domestication and dissemination, their contributions to the Plateau's sedentary lifestyle, prehistoric subsistence economy, and ancient humans' survival skills can be explored. Simultaneously, suitable methods for seasonality analysis must be employed to account for the circumstances at each site. Alongside other archaeological objects and features, economic characteristics, and environmental conditions, a comprehensive and objective examination of the seasonality of the different animal remains discovered at the sites should be conducted to enhance our understanding of when and how prehistoric humans established sedentism on the Tibetan Plateau. While sedentism's emergence worldwide is thought to be the result of natural environmental and socio-economic factors, such as climate change, population growth, resource pressures, and technological innovation, the discussion of the factors driving prehistoric sedentism on the Tibetan Plateau primarily revolves around animal and crop domestication and diffusion, which form the foundation of the subsistence economy. As a result, a comprehensive analysis of economic, paleoclimatic, environmental, and socio-economic factors will help us gain a more profound understanding of the mechanisms driving prehistoric human sedentism on the Plateau.

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