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Paleoecology and paleobiogeography of the latest Miocene site of Shuitangba, Zhaotong, China

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ABSTRACT

Apart from northern and central China, the fossil record of the latest Miocene and Early Pliocene of Asia is not well documented and the record of South China during this interval is especially poor. Shuitangba, a site in Yunnan Province, offers a rare window into the paleoenvironment of the latest Miocene in southwestern China. Over 2400 vertebrate and macrobotanical specimens have been recovered from the site. The faunal assemblage is dominated by aquatic avian taxa and many of the mammalian taxa are those that indicate densely vegetated, water-margin habitats. Pollen and carpological remains indicate a temperate to subtropical, broad-leaved/coniferous forest around standing water, with more open areas containing grasses and herbs. Analyses of clay minerals, chemical weathering, and enamel stable isotopes suggest that Shuitangba was warmer and more humid than today, possibly with more pronounced seasonality. Results of community structure analysis indicate that the Shuitangba mammalian community was different from those of other Late Miocene Chinese sites in the high proportions of aquatic-dependent mammalian taxa. While Shuitangba shared mammalian faunal elements with other Late Miocene sites in Yunnan, it was still faunally distinct. Further, Shuitangba was depauperate in its mammalian fauna, which may have been a result of the depositional setting rather than a true reflection of regional faunal diversity.

1. Introduction

Yunnan Province in southwestern China is one of the most biodiverse regions on earth because of its subtropical location and extreme topographical and geological complexity. As sequelae of the deformation subsequent to the India-Eurasia collision, the many sedimentary basins of Yunnan record a detailed history of Cenozoic paleoenvironmental

change and act as snapshots of both regional tectonic and palaeobiological evolution (Tian et al., 2021).

The site of Shuitangba (STB) in the Zhaotong Basin of northeastern Yunnan (Fig. 1) initially attracted our attention because of the recovery of large mammal fossils during mining operations, indicating its potential for producing well-preserved Late Miocene primate fossils. After nearly two decades of work devoted to the retrieval of fossils at the site

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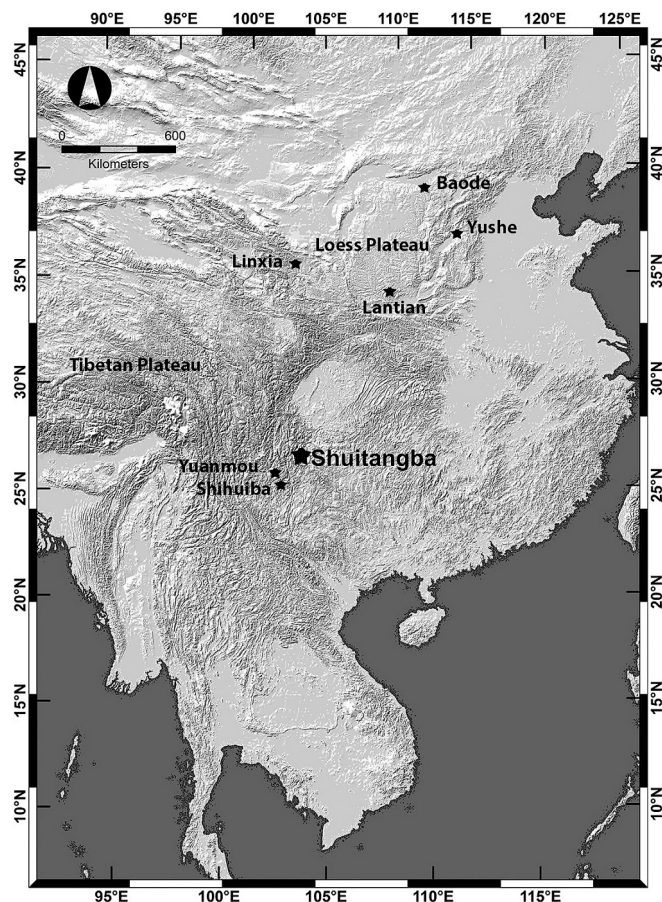


Fig. 1. Map showing the location of Shuitangba (STB) and other significant Chinese Late Miocene sites (Yushe, Baode, Linxia, Shihuiba, Yuanmou) mentioned in the text. Modified from Jablonski et al. (2020).

and the study of its biota, we have come to recognize STB more generally as a unique paleobiological window on the Late Miocene of southern China.

The lignite mines in the Zhaotong area were known to be highly fossiliferous, but only a few cursory studies of the area and its fossils had been attempted (Chow and Zhai, 1962; Zheng, 1985; Zhang et al., 1989) until 2007 when the original team (NGJ, XPJ, JK, and DFS) conducted preliminary fieldwork at STB with subsequent field seasons in 2009 and 2010. A final field season was carried out in 2015 by NGJ, TD, LJF and XPJ. Altogether, over 2400 vertebrate and macrobotanical specimens were recovered, in addition to a large number of pollen grains (over 10,000), resulting in rich and diverse floral and faunal assemblages that add new evidence and perspectives to our understanding of the Late Miocene environment of the STB region and its impact on the biota.

2. Geographical, geological, and geochronological context

The Zhaotong Basin in southwestern China is one of many coal-bearing basins in the western South China fold belt (Wang et al., 1998), formed by the Xianshuihe-Xiaojiang and Sagaing left-lateral strike-slip fault system as well as associated dip-slip extensions (Wang et al., 1998; Li et al., 2015b). It is located near the southeastern margin of the Tibetan Plateau with an elevation of ~2000 m. Late Miocene STB may have achieved a similar elevation; paleoaltimetric estimates indicate that NW and SE Yunnan reached their current elevations by the Middle Miocene (~13 Ma; Li et al., 2015a). It should be noted, however, that the Zhaotong Basin, like the rest of the Yunnan region, has been tectonically active and subject to changes of elevation since the Oligocene, owing to the continued uplift of the Tibetan Plateau and its effects

on the region's underlying complex fault structure and the pace of river incision (He et al., 2023).

The site is within the Zhaotong Formation, which consists of fluvial, lacustrine and fluvio-lacustrine clays, peaty clays and silts interbedded with lignite layers and underlain by Permian limestone and Emeishan basalt (Fig. 2; Jablonski et al., 2014; Zhang et al., 2016). While the Zhaotong Basin sedimentary sequence ranges up to several hundred meters thick, it is only 18 m thick at the STB excavation site, which is on the periphery of the basin. A borehole of 120 m was drilled several hundred meters away where the section is thicker, which allowed for both paleomagnetic dating and a longer record for certain analyses; the borehole and excavation site are correlated by a distinctive lignite-peaty-clay-lignite triplet (Jablonski et al., 2014). Three superposed lignite beds typify the Zhaotong Formation (Dai and Chou, 2007), the youngest of which is absent at STB (Fig. 2; Jablonski et al., 2014).

Early biostratigraphic age estimates of the Zhaotong Basin sedimentary sequence provided a coarse chronological framework for STB in the absence of radiometric constraints (Chow and Zhai, 1962; Zhang et al., 1989). This early fossil evidence included two proboscideans (*Sinomastodon* and *Stegodon*) and a large beaver then thought to be like *Sinocastor* of North China (Shi et al., 1981), suggesting a Late Miocene age. More recent collections from STB include other biochronologically useful taxa (Ji et al., 2013; Jablonski et al., 2014) that allow for better age estimation. Included are key faunal elements, such as *Miorhizomys* and *Muntiacus*, indicating that STB is of the Baodean Stage/Age, a standard terrestrial biochron for the Late Miocene of Asia with a range of 7.25 to 5.3 Ma (Zhu et al., 2008). However, while the STB fauna includes typically Baodean faunal elements, it also has the distinctive character of other assemblages of South China, described below, in contrast to the classic Late Miocene Baodean faunas of North China. Local magnetostratigraphic age correlation further constrains the age of STB to 6.5–6.0 Ma (Fig. 2; Jablonski et al., 2014).

3. Depositional environment and taphonomy

The STB excavated sedimentary sequence (Fig. 2) represents a series of lacustrine sedimentary facies, including swamp-shore and shore-shallow lake subfacies (Zhang et al., 2016) consisting of water-lain peaty clays found between layers of lignite (Jablonski et al., 2014). Vertebrate fossils at STB are found in-situ as isolated elements scattered throughout the peaty clay layer (Fig. 2; Jablonski et al., 2014).

The nature of the lacustrine facies of STB suggests that the site was at least intermittently a series of marshy embayments created by beaver dams, indicated by the plentiful remains of the semi-aquatic beaver, "*Steneofiber*" *zhaotongensis*, as discussed below, and by the presence of masses of preserved leaves and branches of varying diameters consistent with accumulations made by beavers (Davies et al., 2022). There is no obvious evidence of beaver-gnawing on the wood, but the pattern of bone deposition and minimal indications of weathering or environmental modification suggest deposition in pond-like confines consistent with those created by beaver dams.

Previous observations of large mammal bone surface modifications ($n = 428$) by Jablonski et al. (2014) suggest that STB large mammals were buried relatively quickly and were relatively undisturbed after burial. A particularly dramatic although atypical example is a proboscidean death assemblage that consists of at least three individuals, including an infant (Fig. 3). These remains, unusual for STB in their degree of close association, were found in a separate outcrop roughly 150 m from the main excavation area and likely record a catastrophic event during which the individuals were killed and buried quickly in-situ. Specimens of proboscideans and rhinocerotids otherwise show more advanced stages of weathering compared to non-megaherbivores, and a few specimens also bear evidence of trampling, likely due to being deposited in shallow water (Jablonski et al., 2014).

One of the most striking features of the STB faunal assemblage is the dominance and diversity of the avifauna, which accounts for over 60%

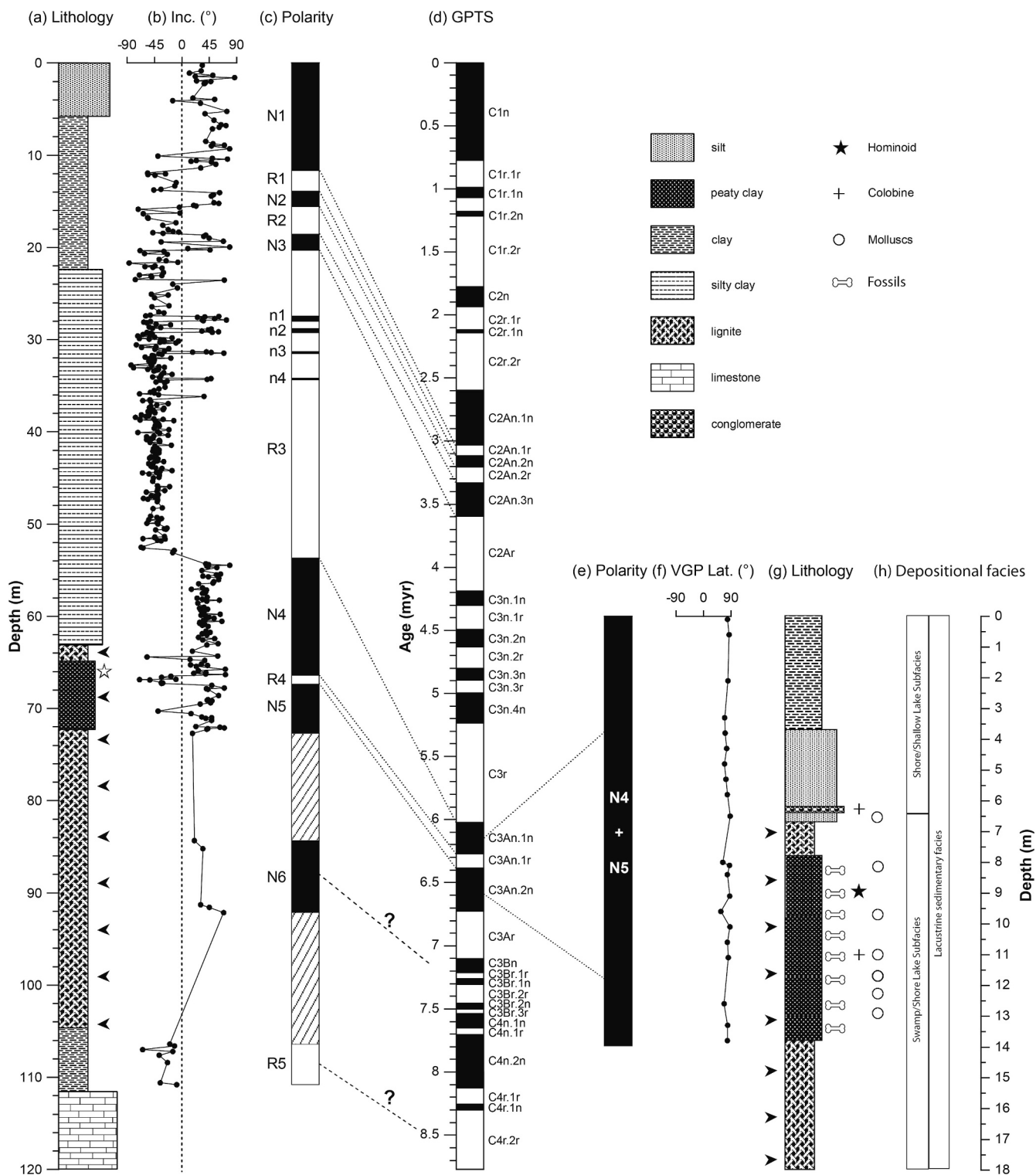


Fig. 2. Lithostratigraphy and magnetostratigraphy of the borehole core (a-c) and Shuitangba excavation (e-h), respectively. (a) and (g), lithology; (b) and (e), inclination; (c) and (e), magnetic polarity zonation; (d), geomagnetic polarity timescale (GPTS) to show correlation; (f), VGP latitudes; (h), depositional facies and subfacies. The hatched areas in (c) indicate intervals with no data. The hominoid-bearing layer in the outcrop indicated by the solid star in (g) corresponds to the layer in the core indicated by the open star shown in (a), which plots at the base of subchron C3An.1n. The colobine indicated above the fossil layer in (g) was recovered from a preliminary excavation in another area from that represented by the primary STB excavation. The borehole core is located several hundred meters away from the excavation site (Jablonski et al., 2014). The correlation between the stratigraphic sequence in the core and at the site itself was established by the lignite-peaty-clay-lignite triplet associated with the hominoid, indicated by solid arrows. Modified from Jablonski et al. (2014).



Fig. 3. Excavation of a proboscidean death assemblage at STB. This was likely created by a catastrophic event that killed and quickly buried at least three individuals (two adults and one infant) at or near the water margin; it illustrates a particularly graphic example of the lack of transport at STB that resulted in the recovered faunal assemblage.

of the vertebrate specimens other than fish and represents eighteen families (Zhang et al., 2013; Jablonski et al., 2014). Avian bones tend to express similar taphonomic surface modifications as those of mammalian bones (Behrensmeier et al., 2003; Prassack, 2011, 2014), but are particularly sensitive to taphonomic factors due to their delicate nature (Mitchell, 2015). Preliminary analysis of the avian bone surface modifications ($n = 495$, observed under 10x magnification) indicates higher

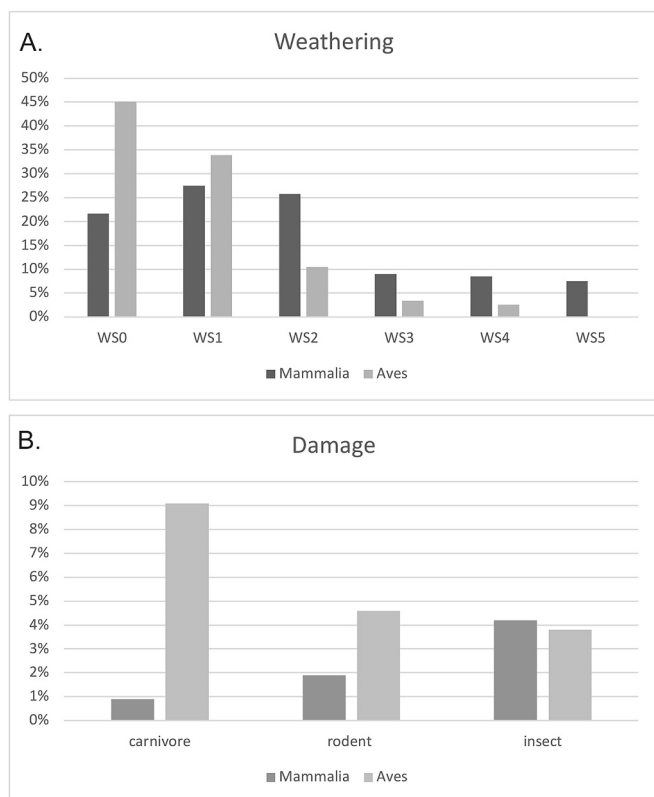


Fig. 4. Comparison of surface modifications between STB mammalian and avian assemblages. A. Percentage of specimens recorded as weathering stages (WS) 0–5. Majority of specimens have little (WS1) to no (WS0) weathering. See Behrensmeier (1978) for definitions of weathering stages. B. Percentage of specimens with carnivore, rodent, and insect damage.

levels of carnivoran (birds: 9.1%, mammals: 0.9%) and rodent (birds: 4.6%, mammals: 1.9%) activity (Fig. 4) than on the mammalian bones. The percentage of carnivoran-marked avian bones shows that STB small carnivorans had an impact on the avian assemblage through a combination of scavenging and possibly hunting. Their modern relatives are known to include birds as a significant part of their diets (Guy, 1977; Yensen and Tarifa, 2003; Simcharoen et al., 2020). Even if they were largely opportunistically scavenging the available avian remains, these small carnivorans would have contributed to the avian accumulation to some extent, particularly when compared to the mammalian assemblage, in which very few carnivoran surface modifications were found. In addition, the majority of the avian specimens exhibit very little to no weathering (79%) or abrasion (2.2%), indicating relatively rapid burial and lack of transport. This suggests that the abundance and diversity of the avian assemblage are mostly due to the combination of a favorable depositional environment for preservation of delicate bones and a local habitat (see below) preferred by the species in the the avian assemblage.

Sedimentological data (Zhang et al., 2016), a high proportion of postcranial to craniodental specimens in the mammalian assemblage (Jablonski et al., 2014), the lack of or minimal weathering, and low occurrence of animal damage (Fig. 4) all suggest that the STB faunal assemblage is autochthonous, with remains quickly buried and not widely dispersed, except for some vertical displacement as the bones disarticulated (Jablonski et al., 2014). Although impossible to conclude with certainty due to the scattered nature of the specimens, some may represent single individuals based on proximity, similar preservation, and non-duplication of elements (Jablonski et al., 2014).

4. Paleoclimate and paleoenvironment

Since our first field season in 2007, numerous lines of evidence, ranging from sedimentological to faunal and floral data, have been assembled by our team and others to reconstruct the paleoenvironment at STB.

4.1. Clay minerals and chemical weathering

Mineral sampling was carried out on the entire extent of the borehole core taken from near the STB site. Individual clay minerals such as kaolinite and smectite form by weathering under specific conditions, kaolinite in warm, humid climates with acidic weathering and strong leaching, smectite in areas of low relief where poor drainage prevents the removal of silica and alkaline/alkaline-earth ions, being generally linked to a warm climate with alternating humid and dry seasons (Li et al., 2019). At STB, the kaolinite percentage gradually falls as that for smectite increases, suggesting a somewhat more seasonal climate over time (Fig. 5; Li et al., 2019).

Chemical weathering indices are also used to infer aspects of climate, particularly temperature and humidity (Chen et al., 1997; Zhang et al., 2015). Three silicate chemical weathering indices based on elemental ratios of aluminum, calcium, potassium, and sodium (Nesbitt and Young, 1982; Harnois, 1988; Fedo et al., 1995) were utilized to evaluate climatic conditions at STB. Values for all three indices show a marked and progressive decrease upward through the section (Fig. 5), indicating progressively decreasing temperature and humidity, albeit in a still predominantly warm and humid environment (Zhang et al., 2016). The cooling phase appears to have begun ca. 6.7 Ma and reached a nadir by ca. 6.0 Ma, followed by a partial recovery over the ensuing ~200,000 years, but not to the temperature and humidity levels that preceded the cooling (see also Li S. et al., 2020). The excavated section at STB, from about 6.5–6.0 Ma, is centered within this cooling phase and partial recovery (Fig. 5).

Such proxies consistently indicate that the climate in the Zhaotong Basin during the period of deposition at STB was broadly warm and humid, but that the climate changed directionally throughout the period to become somewhat cooler, less humid and perhaps more seasonal,

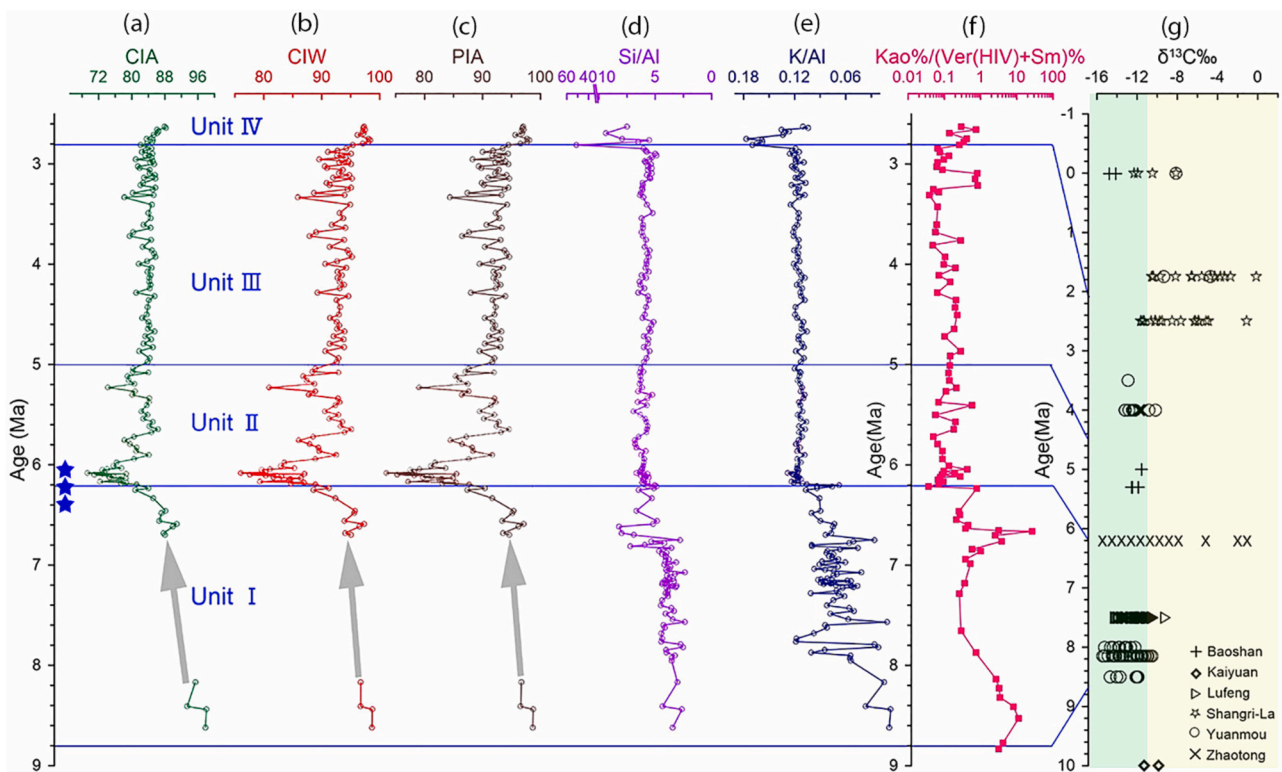


Fig. 5. Paleoenvironmental indicators for STB: silicate chemical weathering indices (a,b,c), Si/Al and K/Al ratios (d,e), clay mineral composition (f); carbon isotope ratios from mammalian tooth enamel (g: data from [Biasatti et al., 2012](#); [Sun et al., 2021](#)), include localities outside the Zhaotong Basin to show herbivore dietary trends over time against temporal trends in clay minerals and chemical weathering at STB and the Zhaotong Basin. For (g), green = more closed habitat, yellow = more open habitat (demarcation between closed and open from [Sun et al., 2021](#)). Unit 1 = 8.8–6.2 Ma, Unit 2 = 6.2–5.0 Ma, Unit 3 = 5.0–2.8, Unit 4 = 2.8–2.6 Ma (Unit age ranges from [Li P. et al. 2020](#)). Gray arrows substitute for the silicate weathering index values in the lignite layer of Unit 1 because these values are on a different scale (see [Li P. et al. 2020](#) for explanation). Series of blue stars indicate the interval of the STB excavation. See text for discussion of paleoenvironmental indicators. Modified from ([Li P. et al. 2020](#)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with temperature reaching a minimum near the Pliocene at the top of the section.

4.2. Stable isotopes

$\delta^{13}\text{C}$ values from tooth enamel of STB mammals (-29.4‰ to -15.0‰) suggest C_3 -dominated diets ([Fig. 5](#)), with some taxa consuming small amounts of C_4 plants, about 11% on average ([Sun et al., 2021](#)). The STB enamel $\delta^{18}\text{O}$ values range from -14.2‰ to -4.6‰ (average -9.7 ± 2.2‰), substantially lower than those from modern enamel samples (-9.2 to -4.8‰, average -7.5 ± 1.2‰; ([Sun et al., 2021](#))). The reconstructed paleo-water $\delta^{18}\text{O}$ values range from -17.3‰ to 7.4‰ (average 12.4 ± 2.4‰), substantially lower than those of modern enamel samples (-11.7 to -6.8‰, average -9.8 ± 1.4‰), and also lower than the weighted average $\delta^{18}\text{O}_w$ value (-10.3‰) of modern precipitation recorded at the nearest International Atomic Energy Agency station in the region, suggesting a wetter climate and possibly stronger Asian Monsoon in the Late Miocene than today ([Sun et al., 2021](#)). In addition, both the time-series $\delta^{18}\text{O}$ data from serial enamel samples collected along the growth axes of individual teeth and $\delta^{18}\text{O}$ data from STB fossil freshwater shells indicate greater seasonal variation in precipitation compared to today ([Sun et al., 2021](#)). Temperature estimations using carbonate clumped isotope thermometry suggest that the STB paleotemperature was about 15–16 °C, warmer than today, conceivably by about 3–4 °C ([Sun et al., 2021](#)). Combined, the stable isotope data indicate that STB was dominated by C_3 plants with a small proportion of C_4 biomass, likely in patches of open areas where forest canopies were broken. It was also warmer and wetter, possibly with stronger precipitation seasonality compared to today.

4.3. Fauna

The fauna of STB includes diverse mammalian, avian, reptilian, amphibian, piscine, and invertebrate taxa. Certain vertebrates, particularly among mammals and birds, exhibit important ecological and environmental signals.

Aves. STB has produced the most diverse Late Miocene avifauna known from southeastern Asia ([Table 1](#)), which is still undergoing study. The avian diversity at STB represents a wide range of body sizes from large geese (Anserinae) and a vulture (Accipitridae) to very small songbirds (Passeriformes), and various ecologies distributed across terrestrial, arboreal, aquatic, and aerial habitats, with aquatic birds being the most common ([Jablonski et al., 2014](#)). Some birds, such as geese, were possibly only seasonal migrants to the area, but others, such as the darter and pheasants, were likely year-round residents, suggesting that the avian fossil assemblage might represent the accumulation of taxa across seasons. No juvenile individuals, and only a few eggshells, have been recovered, indicating a potential wintering or non-breeding-season occurrence of at least some of the more abundant aquatic taxa.

STB hosts the oldest known ecological guild of piscivorous foot-propelled diving birds from a single site, comprising members of the clades of grebes (Podicipedidae), cormorants (Phalacrocoracidae), darters (Anhingidae), and diving ducks (Anatidae). There are also fossils of a pelican (Pelecanidae), adding to the overall piscivorous avian diversity. This combination of bird groups is similar to avifauna from tropical aquatic sites in southern Asia today, with the STB fossils of the subtropical to tropically distributed darters being the first records in China. The waterbird assemblage suggests the availability of various water depths, ranging from less than one meter to as much as several

Table 1
Shuitangba bird and mammal faunal list.

Aves	
Anseriformes	Anatidae*
Galliformes	Phasianidae
Falconiformes	Accipitridae
Ciconiiformes	Ciconiidae* Ardeidae*
Passeriformes	Fringillidae Corvidae
Charadriiformes	Charadriidae* Haematopodidae* Scolopacidae*
Pelecaniformes	Pelecanidae* Phalacrocoracidae* Anhingidae*
Gaviiformes	Gaviidae*
Strigiformes	Strigidae
Gruiformes	Gruidae*
Podicipediformes	Podicipedidae*
Mammalia	
Eulipotyphla	Talpidae <i>Yunosaptor scalprum</i> Soricidae <i>Soriculus</i> sp. <i>Anourosorex</i> cf. <i>A. squamipes</i> Erinaceidae <i>Lantanotherium sanmigueli</i>
Rodentia	Muridae <i>Linomys</i> sp. nov. Murinae cf. <i>Yunomys</i> sp. nov. Sciuridae <i>Albanensia</i> sp. nov. <i>Sciurotamias</i> sp. Cricetidae <i>Kowalskia hanae</i> Rhizomyidae <i>Miorhizomys gigas</i> <i>Miorhizomys</i> cf. <i>M. tetracharax</i> Castoridae "Steneofiber" <i>zhaotongensis</i> *
Lagomorpha	Leporidae <i>Nesolagus longisinuus</i>
Primates	Hominoidea <i>Lufengpithecus</i> cf. <i>L. lufengensis</i> Cercopithecoidea <i>Mesopithecus pentelicus</i>
Carnivora	Mustelidae cf. <i>Cernictis</i> sp. <i>Siamogale melilutra</i> * Ursidae <i>Ailurarcos</i> cf. <i>A. lufengensis</i> Felidae <i>Amphimachairodus</i> sp. gen. et sp. indet., small Viverridae cf. <i>Viverra</i> sp.
Perissodactyla	Tapiridae <i>Tapirus yunnanensis</i>

(continued on next page)

Table 1 (continued)

	Rhinocerotidae <i>Acerorhinus lufengensis</i> Rhinocerotini gen. et sp. indet.
Artiodactyla	Cervidae <i>Muntiacus zhaotongensis</i> Bovidae <i>Gazella</i> sp. Suidae <i>Propotamochoerus hyotherioides</i> *
Proboscidea	Mammutidae <i>Sinomastodon praeintermedius</i> Stegodontidae <i>Stegodon zhaotongensis</i>

* Taxa that are dependent on aquatic resources.

meters, as well as the presence of areas of open water. Emergent vegetation near the aquatic margins and elevated areas for the cormorants and darters to dry their feathers were also likely. Rails (Rallidae) and shorebirds (Charadriiformes) also point to the presence of vegetated lacustrine or fluvial margins along with shallow water habitats (likely under ~30 cm).

The STB avian fauna also indicates a diversity of terrestrial habitats, although the fossils of aquatic taxa far outnumber those of terrestrial clades. While deriving from a largely aquatic group (Anatidae), geese (Anserinae) are primarily terrestrial grazers and their occurrence indicates the presence of non-forest grass/herb covered habitats near or at STB. This is further supported by the presence of medium-sized pheasants (Phasianidae). Arboreal habitats are indicated by a woodpecker (Picidae), a medium-sized *Strix*-like owl (Strigidae), and a variety of small songbirds (Passeriformes), possibly including starlings. However, these are not informative regarding either the density or height of the woodlands or forests.

Together, the avifauna represents a set of habitats consistent with a tropical, mountainous, mixed woodland/forest, grassland, and aquatic mosaic. The included taxa represent a diversity of diets, including piscivores, carnivores, herbivores, insectivores, and omnivores. Fossils of soaring vultures (Accipitridae) add to the wide diversity of available dietary and habitat resources in the vicinity of STB.

Primates. Primates are relatively rare at STB, represented by just a handful of specimens of an ape, *Lufengpithecus* (perhaps only one individual), and a monkey, *Mesopithecus* (Ji et al., 2013; Jablonski et al., 2020). Most extant apes are ripe-fruit specialists, but can tolerate seasonal and other periods of scarcity in these preferred foods, shifting to lower quality fallback foods of various kinds (Wrangham et al., 1998; Marshall and Wrangham, 2007; Knott et al., 2009; Marshall et al., 2009). The presence of multiple severe hypoplasias on the upper third premolar of the juvenile hominoid cranium ZT299 (Fig. 6) demonstrates repeated episodes of physiological stress, most likely related to nutrition (Gua-telli-Steinberg et al., 2012), suggesting regular episodes of low food availability and/or quality. There are three hypoplastic episodes and perhaps the beginning of a fourth, likely to have initiated soon after weaning based on a chimpanzee model of dental development (Smith et al., 2013; Boughner et al., 2015; Machanda et al., 2015). They appear to be highly regular but not annual since the amount of developmental time over which they occur would have been considerably less than three years (Smith et al., 2007), and probably less than two. If the hypoplasias represent seasonal episodes, they would be most compatible with a semi-annual cycle rather than the annual cycle usually implied in discussions of seasonality.

The inferred biology of *Mesopithecus*, as well as the geography of its fossil record, suggest an organism capable of exploiting a variety of habitats (Jablonski et al., 2020). *Mesopithecus*, like all colobine monkeys, likely was able to tolerate a wider range of foods and be less susceptible to seasonal food stress than apes. STB *Mesopithecus* specimens include a



Fig. 6. Upper third premolar of the *Lufengpithecus* partial cranium, ZT299, showing severe and repetitive enamel hypoplasias.

mandible, a probably associated right proximal femur and a left calcaneus (Jablonski et al., 2014; Jablonski et al., 2020). The femur and calcaneus show adaptations to arboreal activities, perhaps including occasional leaping between tree crowns (Jablonski et al., 2020; Ji et al., 2020), as well as some terrestrial quadrupedal activities (Ji et al., 2020). This behavioral reconstruction is compatible with a forested habitat interspersed with more open areas.

Carnivora. Modern relatives of the STB small carnivorans (*Viverra* sp. and cf. *Cernictis* sp.) inhabit forest or other closed habitats (Chutipong et al., 2014; Gray et al., 2014; Jiangzuo and Wang, 2023) and in the case of *Cernictis*, water-margin habitats (Jiangzuo and Wang, 2023).

Ailuroides cf. *A. lufengensis*, an early panda, is represented by isolated teeth and a radial sesamoid. In the extant panda, the enlarged wrist radial sesamoid functions as an opposable false thumb for manipulating bamboo. Despite having a relatively primitive upper second molar, the STB panda has a radial sesamoid that is slightly longer than that in the extant panda, which suggests a grasping false thumb that was already fully functional as an opposable “thumb” as in modern pandas (Wang et al., 2022). Thus, it is likely that the STB *Ailuroides* was already a dedicated bamboo-feeder with bamboo widely available in the STB flora (Wang et al., 2022; Fig. 8), although it is not represented among the floral remains (see below).

Siamogale melilutra, a basal otter belonging to an East-Southeast Asian clade of primitive otters, is unusual in its giant size, estimated to approach 50 kg, and in its badger-like upper molars (Wang et al., 2017). The jaw of *S. melilutra* possesses exceptional biomechanical strength, presumably for crushing large mollusks that are frequently found in STB sediments (Tseng et al., 2017). The postcranial skeleton, still under study, indicates both aquatic and digging capabilities.

Perissodactyla. Several specimens of tapir (*Tapirus yunnanensis*) have been recovered from STB (Jablonski et al., 2014; Ji et al., 2015). Tapirs are commonly found in humid and densely vegetated tropical forest environments (Eisenmann and Guerin, 1992). Their food mainly includes leaves, buds, twigs and aquatic plants, as well as some fruit (Janis, 1984). Enamel carbon isotopic data indicate that *T. yunnanensis* at STB consumed some C4 resources in addition to their primarily C3 diet (Sun et al., 2021). While the dental morphology of the STB rhinocerotid, *Acerorhinus lufengensis*, indicates a grazing diet, and the rhinocerotid postcranials suggest open habitat adaptations (Lu et al., 2017), the enamel carbon isotopic data indicate that it was consuming largely C3 resources (Sun et al., 2021). This suggests a plasticity to

dietary strategies that may be related to resource availability.

Artiodactyla. Most STB suid specimens are referred to *Propotamochoerus hyotherioides* (Hou et al., 2019), which is morphologically similar to extant *Potamochoerus* and considered to have similar habits. The living red river hog, *Potamochoerus porcus*, occurs mainly in moist tropical forests with dense cover and frequents swamps and reed beds (Woodhouse, 1911). It is omnivorous and feeds on a variety of food items including tubers and roots, seeds, fruits, grass, and aquatic plants. Unpublished microwear data for *Pr. hyotherioides* suggest that it was a mixed feeder, supported by enamel carbon isotopic data (Sun et al., 2021). STB cervid specimens belong to *Muntiacus zhaotongensis* (Dong et al., 2014). The living species of *Muntiacus* tends to be found in rocky mountain forests and forest-grassland ecotonal habitats, grazing on grass along forest edges and browsing on leaves, flowers, and fruits (Sheng and Liu, 2007). Unpublished microwear and mesowear data suggest that *M. zhaotongensis* was also a mixed feeder.

Proboscidea. Proboscidean taxa from STB include *Stegodon zhaotongensis* and *Sinomastodon praeintermedius* (Jablonski et al., 2014; Wang et al., 2016; Sanders et al., 2022). The occlusal morphology of *Si. praeintermedius* and mammutids in general suggests a browsing diet overall (includes leaves and other parts of dicotyledonous plants) and a more strictly folivorous diet in younger individuals (Von Koenigswald, 2016). Microwear and dental isotopic studies of mammutids, including *Sinomastodon* (e.g., Koch, 1998; Domingo et al., 2013; Dotsika et al., 2014; Zhang et al., 2017; Smith and Desantis, 2018; Loponen, 2020), indicate that they were browsers that may have eaten a wide range of food items, including tough, fibrous plants (but see Puspaningrum, 2016). Limited dental isotopic investigation of *Si. praeintermedius* from STB indicates a primarily browsing diet (Sun et al., 2021).

Stegodon zhaotongensis (Stegodontidae) is represented by most elements of the skeleton at STB. Its molars are very brachydont and its close set of straight, downturned tusks is consistent with forest or closed woodland environments. Isotopic analyses of stegodonts suggest that they were either mixed feeders or grazers (Sanders et al., 2010; Puspaningrum, 2016), or browsers (Cerling et al., 1999), and most dental microwear studies indicate C3-dominated feeding, possibly including C3 grass such as bamboo, along with other tough, abrasive C3 plants (Zhang et al., 2017; Saegusa, 2020). At STB, isotopic records from stegodont teeth show a range of individual dietary preferences ranging from pure C3 to mixed diets with C4 grasses comprising <20% of the total intake (Sun et al., 2021). Oxygen isotopic results show that *Stegodon* and *Sinomastodon* from STB were obligate drinkers, indicating habitats with abundant sources of water (Sun et al., 2021).

Micromammals. The STB microfauna as known through 2015 includes fossil representatives of three mammalian orders. Among Eulypotyphla, members of the hedgehog, mole, and shrew families all indicate a moist paleoenvironment. Compared to extant hedgehogs, *Lantanothereum* from STB is most like the lesser gymnure *Hylomys*, which prefers dense undergrowth in hilly terrain. The fossil mole, *Yunosceptor* is represented by a humerus and dentition and is thought to be associated with humid forests with dense undergrowth (Storch and Qiu, 1991). Shrews (Soricidae) include species of two genera. The extant members of *Soriculus* inhabit damp forests in China. Several specimens of the mole shrew *Anourosorex* are indistinguishable from the living species *A. squamipes*, which prefers montane forests above 1500 m. Lagomorpha at STB is represented by the rabbit *Nesolagus longisinuus*; the extant *Nesolagus* is nocturnal and exploits upland forest.

The majority of paleohabitat indicators of the STB Rodentia are of moist forest, but there are exceptions. For example, while the extinct flying squirrel *Albanensia* suggests forest, extant members of the rock squirrel *Sciurotamias* typically inhabit dry uplands, particularly rocky habitats. The extinct hamster, *Kowalskia*, also suggests open terrain. Two unnamed new species of murines are most likely consistent with subtropical forest. The remaining rodents are of medium to large body size and suggest pond or moist forest habitat. There are two species of bamboo rat belonging to the extinct genus *Miorhizomys*. Extant species

of bamboo rat in China are found mostly in bamboo thickets and feed on the roots and stems of bamboo (Smith et al., 2010). Based on skull material from the Siwaliks of the Indian subcontinent and from Lufeng (Flynn, 2009), *Miorhizomys* was subterranean and likely exploited underground plant resources in moist, dense undergrowth. One of the two species (Flynn et al., 2019, 2023) was large (probably several kilograms). It would have required emergent ground at least a half meter above the water table for its burrows. The last rodent, a large semi-aquatic beaver previously assigned to *Sinocastor zhaotungensis* but now recognized as *Steneofiber*, likely engaged in dam-building that may have contributed to creating the pond setting of STB. It is perhaps the most distinctive rodent in the fauna because of its abundance (several specimens were recovered while quarrying) and large size – it was much larger than the mid-Miocene beaver from Thailand, *Steneofiber siamensis* (Suraprasit et al., 2011).

4.4. Flora

Plant remains at STB are abundant and comprise pollen, fruits, seeds, spores, masses of leaves, branches of various sizes, and large tree trunks. Pollen and spores were recovered from 16 m of the 18 m STB excavation section (Chang et al., 2015), while fruits and seeds were collected only from layers of peaty clay in the middle of the section (7.6–12.3 m; Huang et al., 2017). The pollen record is dominated by broad-leaved trees, mostly oak (*Quercus*) – both evergreen and deciduous – and alder (*Alnus*), with hickory (*Carya*), elm (*Ulmus*) and chestnut (*Castanea*) being present but much less common. Also common are conifers, including pines (*Pinus*) and hemlock (*Tsuga*). Grasses are present throughout the pollen record, although minimally represented in the upper several meters. Carpological remains (fruits and seeds) are overwhelmingly dominated by floating aquatic plants, mostly water lilies (*Euryale*) and some water chestnut (*Trapa*), but with the broad-leaved Indian prickly ash (*Zanthoxylum*) also relatively well represented. Various other broad-leaved trees and shrubs, floating aquatic plants, herbs, and lianas are represented in small amounts in both categories of floral remains. Lastly, fern spores are common, making up ~10% of the combined pollen/spore record.

Of the 25 most common genera or higher taxa represented by either pollen or carpological remains, only five are represented by both. However, sample sizes for seeds and fruits of most taxa are quite small. Of the 16 taxa represented by carpological remains, only the aquatic genera *Euryale* and *Trapa* (the former ~85% of all carpological remains, but not represented by pollen), and the broad-leaved tree/shrub *Zanthoxylum*, have sample sizes greater than five (Huang et al., 2017). Among the most common pollen taxa (including *Quercus*, which comprises nearly 50% of recovered pollen), only *Alnus* is also represented by carpological remains. As noted by Huang et al. (2017), these distributions likely reflect a strong taphonomic bias since fruits and seeds mostly alight near where they are produced, in this case in the pond or small lake represented by the peaty clay layer from which the large number of aquatic fruits and seeds were recovered, whereas pollen dispersal is quite varied (Matthias et al., 2015).

The picture of the STB paleoenvironment based on plant remains is consistent with that derived from other lines of evidence: a warm temperate to subtropical forest surrounding bodies of quiet, standing water, and including more open areas in which grasses and herbs were present. By examining the temperature and rainfall tolerances associated with the nearest living relatives of each of the fossil taxa, Huang et al. (2017) were able to propose an associated climate profile for this setting as being moderately warm and humid, with both the mean annual temperature and mean annual rainfall higher than at present in the region. The modern comparisons also suggest pronounced seasonality in both temperature and precipitation, with warm, dry summers and cool, wet winters.

Within these overall parameters, and based on shifts in the proportions of types and taxa of pollen, there were both long and shorter

term variations in the makeup of the vegetation, which most likely reflect fluctuations in regional climate. In some cases, though, variation may also express responses to more local factors, such as possible fluctuations in the amount of standing water over the period of deposition. A principal longer-term variation is evident in the proportions of broad-leaved versus coniferous trees, which fluctuated roughly inversely through time, and which probably reveal responses to relatively warmer and colder periods (Chang et al., 2015). Within this variation, one brief period within the peaty clay facies stands out as particularly warm, coming at the end of a progressive increase in the proportion of broad-leaved tree pollen and a corresponding decrease in that of conifers. Among the broad-leaved trees during this brief interval, the proportion of evergreen *Quercus* pollen increased greatly while that of *Alnus* showed a corresponding decline. Also notable are increases in the proportions of herbs, grasses, aquatic plants, and other broad-leaved tree species (Chang et al., 2015). It is from this interval that the few hominoid remains were recovered.

4.5. Summary of STB Paleoenvironment

Much of the evidence documented above, particularly the flora and a predominance of water-dependent avian and mammalian taxa, suggests a wetland environment where standing water is surrounded by forest and areas of grasses and herbs. The avian assemblage further indicates the presence of various water depths from less than one meter to several meters, probably connecting with areas of deep, open water. Pollen and some faunal elements, both birds and mammals, suggest the presence of drier and more open habitats as well, which were likely peripheral to the area of the excavated STB section given the wide dispersal range of pollen and more typically open-habitat faunal elements being much less common. Some of the mammal taxa, particularly among micro-mammals, suggest an upland setting, in accord with the geological evidence (Li et al., 2015b) for topography and paleo-altitude for the Yunnan region being similar to that at present. Environmental proxies from the floral assemblage, chemical weathering, clay minerals, and enamel oxygen stable isotopes all indicate that STB was generally warm and humid, probably warmer and more humid than today, but likely with more pronounced seasonality. Finally, while chemical weathering and clay mineralogy indicate gradual cooling over the period represented by the STB section, albeit within still predominantly warm and humid conditions, the pollen record in particular reveals a more nuanced picture of oscillation between warmer and cooler periods, perhaps reflected as well by the restricted presence of the more environmentally sensitive hominoid, *Lufengpithecus*, to a particularly warm phase.

5. Biogeography and comparative paleoecology

The STB small mammal composition resembles predecessor assemblages from Yunnan Province in its diverse insectivores, bamboo rats, and the beaver *Steneofiber*, rather than the coeval small mammal faunas of North China, which are dominated by xeric hamsters, gerbils, dipodoids, and steppe-adapted mice. For example, Late Miocene-Early Pliocene assemblages of the Yushe Basin (Mahui and Gaozhuang formations) are dominated by dipodoid rodents, a gerbil and hamsters, a chipmunk, and the burrowing *Prosilphneus*. Murines in North China assemblages show high diversity, as do lagomorphs, which had diversified after entry into Eurasia by about 8 Ma (Flynn et al., 2014). Yushe moles and shrews show diversity comparable to that of STB, but the Yushe bamboo rat (living genus *Rhizomys*) and advanced beaver, *Sinocastor*, are different. Paleoecological reconstruction for Yushe suggests inland habitat with seasonal precipitation, but less xeric conditions than regions to the west.

The latest Miocene of the Baode-Lantian area west of Yushe was dominated by hamsters, gerbils, and dipodoids, as well as by diverse murines and chipmunks, but no bamboo rats. The mice (Murinae) of

Baode Locality 30, close in age to STB, were steppe-adapted, unlike the subtropical murines of STB. The differences between STB and these Shanxi Province assemblages were profound and even more accentuated in drier faunas farther west in Gansu Province; they share no species but perhaps one genus (*Kowalskia*), likely due to paleoecological differences. In contrast to STB, the Pliocene Tianzhu and early Late Miocene Linxia small mammal assemblages of Gansu show dominance of hamsters, gerbils and dipodoids; Linxia also supported several kinds of squirrels and a dormouse (Qiu et al., 2023). The lower stratigraphic levels of Lingtai, Gansu, close in age to STB, show the dominant hamster-gerbil-dipodoid assemblage plus *Prosiphneus*, a dormouse and diverse mice (Zheng and Zhang, 2001).

The regional- and age-related differences seen in small mammals are also reflected in the large mammal community. When compared to other Late Miocene sites in China (5–10 Ma) using a modified Forbes similarity coefficient (see Supplementary Information for methodology), STB and the other Yunnan Late Miocene sites are distinct in taxa >500 g, even from sites of similar age (Fig. 7). Further, the STB fauna, while most similar to those of other Late Miocene sites in Yunnan, appears to differ even from these, with Shihuiba clustering with Yuanmou (Fig. 7).

The presence of primates at STB is associated with two episodes of dispersal into southwestern China that differ in time and possibly represent two different pathways. The *Lufengpithecus* lineage was present in southern China by early Late Miocene, as evidenced by hominoids from Kaiyuan (Woo, 1957; Zhang, 1987; Dong and Qi, 2013), which have been assigned to *Lufengpithecus* but perhaps represent a different genus. Kelley and Gao (2012) have shown that the large mammal faunas of both Shihuiba and Yuanmou differ markedly at the family level from those from hominoid-bearing sites in Southeast Asia (Thailand, Myanmar) and South Asia (Siwaliks), and that *Lufengpithecus* from the two Chinese sites bears no affinity to Late Miocene fossil apes found in South and Southeast Asia, nor to fossil and extant *Pongo* in Southeast Asia. They suggested instead that the *Lufengpithecus* lineage arrived from Europe, most likely following a route through southcentral Asia prior to major uplift of the northern portion of the Tibetan Plateau. In contrast, STB represents the earliest occurrence of *Mesopithecus* in East Asia. Its immigration, most likely from southeastern Europe, proceeded rapidly during the Late Miocene across Southwest Asia and into South Asia south of the Tibetan Plateau, and then into China (Jablonski et al., 2020).

STB shares widely distributed ungulate taxa such as *Propotamochoerus*, *Acerorhinus*, *Muntiacus*, and *Gazella* with other Late Miocene Chinese sites, but compared with elsewhere, such as the Baode and

Mahui assemblages in North China (Kaakinen et al., 2013; Qiu et al., 2013), the diversity of ungulates is low. This is also the case when comparing STB to the Late Miocene South China Shihuiba and Yuanmou faunas. For example, hipparionine equids are ubiquitous throughout the Late Miocene of Eurasia (Garcés et al., 1997) and occur at Shihuiba and Yuanmou (Qi, 1993; Qi and Dong, 2006; Sun, 2013) but are absent from the STB fauna. This absence may point to a key difference in the environmental conditions at STB.

The carnivoran guild at STB is similarly impoverished compared to those of Shihuiba and Yuanmou, which sample diverse species of ursids, mustelids, hyaenids, viverrids, and felids (Qi, 1993; Qi and Dong, 2006). STB carnivorans are represented by two species of mustelid, including the giant otter *Siamogale*, a single species of ailuropodine, a single viverrid, and two species of felids, one large and the other small (Table 1). However, given the relatively close proximity of all the Late Miocene sites of Yunnan, the low carnivoran diversity at STB, rather than reflecting biogeography, may instead be related to the low ungulate diversity, as predator richness is linked to prey richness (Sandom et al., 2013). However, this simply shifts the question to the reasons for the low ungulate diversity, which is most probably due to the particular habitat represented by the STB depositional environment (see further below). It is notable that the large carnivorans at STB are *Siamogale*, an aquatic form that likely preyed on fish and mollusks, the herbivorous *Ailuartcos* specializing on bamboo, and a single specimen of *Amphimachairodus*. The last is a likely ambush predator and the only STB large carnivoran with a diet based on terrestrial prey.

Faunal community structure can be characterized according to ‘functional’ traits of the constituent animals such as body size, diet and locomotion. Faunal communities that exhibit similar proportions of particular traits for each category are from similar habitats, regardless of species composition (Andrews et al., 1979). The large mammal community structure at STB was compared to those of other Late Miocene Chinese sites using Correspondence Analysis (see Supplementary Information for methodology). The distinctiveness of STB from these other Chinese sites reveals that it was different in its community structure (Fig. 8). The position and angle of the STB functional traits, “T-AQ” (terrestrial-aquatic) and “AqF” (aquatic food), in the plot indicate that they are associated and are important discriminators of STB from other Late Miocene Chinese sites. This is due to the higher proportion of aquatic-dependent taxa at STB (Supplementary Table 4).

The results of the community structure analysis indicate that, concordant with paleobotanical evidence, the paleoenvironment at STB was wet and wooded. As such, it might be supposed that STB would have represented an ideal habitat for primates, particularly apes given their reliance on ripe fruit for much of the year. However, as is the case for ungulates and carnivorans, the STB primate community is depauperate, in contrast with the abundant and diverse primate communities at the other major Late Miocene sites in Yunnan, Yuanmou and Shihuiba (Dong and Qi, 2013). The difference with Shihuiba in particular is notable because it overlaps in age with STB by several hundred thousand years according to paleomagnetic records (Yue and Zhang, 2006; Jablonski et al., 2014) and the sites share a broadly similar depositional environment (Badgley, 1988; Jablonski et al., 2014). Particularly notable is the absence at STB of smaller-bodied primates (pliopithecids, sivaladapids, hylobatids), which are common at both Yuanmou and Shihuiba (Pan, 1988; Pan, 2006; Ji et al., 2022), and the presence at STB of the cercopithecid, *Mesopithecus*, absent from the other two sites. However, *Mesopithecus* might owe its singular presence at STB to the younger age of this site rather than to any aspect of the environment, irrespective of the temporal overlap with Shihuiba. As noted above, this is the earliest occurrence of the genus in East Asia as it spread from southeastern Europe (Jablonski et al., 2020). *Mesopithecus* at STB is represented by just a handful of specimens (Jablonski et al., 2014; Jablonski et al., 2020), indicating rarity on the landscape (or at least in the STB depositional environment; see below); fossil monkeys are typically found in large numbers reflecting high population densities.

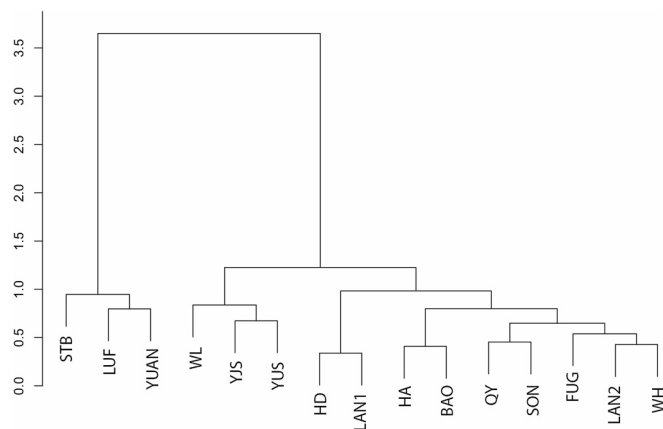


Fig. 7. Dendrogram of the results from hierarchical clustering analysis of the faunal dissimilarity index based on the modified Forbes faunal similarity coefficient. Dendrogram drawn from the dissimilarity matrix in Supplementary Table 3. Abbrev: STB, Shuitangba; YUAN, Yuanmou; LUF, Lufeng-Shihuiba; FUG, Fugu; HD, Hezheng-Dashengou; HA, Hsin-An; LAN1, Lantian >8 Ma; LAN2, Lantian <8 Ma; BAO, Baode; QY, Qingyang; SON, Songshan; WH, Wu-Hsiang; WL, Wudu-Longjiagou; YJS, Yangjiashan.

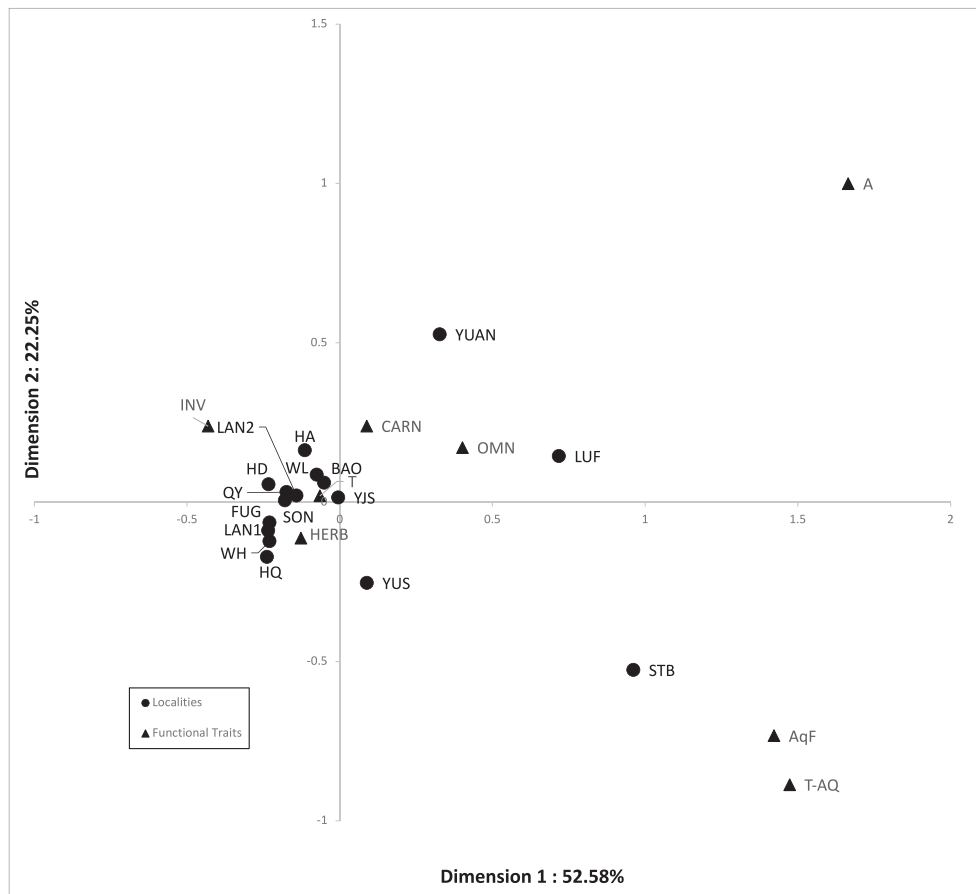


Fig. 8. Results of correspondence analysis of the mammal community structures of STB and comparative Late Miocene (5–10 Ma) Chinese sites. See Supplementary Table 1 (5–10 Ma) for comparative sites. Abbrev: Localities - STB, Shuitangba; YUAN, Yuanmou; LUF, Lufeng-Shihuiba; FUG, Fugu; HD, Hezheng-Dashengou; HA, Hsin-An; LAN1, Lantian >8 Ma; LAN2, Lantian <8 Ma; BAO, Baode; QY, Qingyang; SON, Songshan; WH, Wu-Hsiang; WL, Wudu-Longjiagou; YJS, Yangjiashan. Functional Traits - T: Terrestrial; A: Arboreal; AQ: Terrestrial-Aquatic; Herb, Herbivore; AqF, Aquatic Foods; FL, Leaves plus; C, Meat plus; OM, Omnivorous; I, Insects.

The overall faunal numbers at STB, as well as an abundance of small vertebrate and delicate bird remains, make it unlikely that the rarity of primates is a sampling artifact, particularly concerning the complete absence of smaller taxa. What this impoverished but compositionally unique primate fauna indicates about the STB paleoenvironment is not clear. Concerning the two larger-bodied taxa, it could reflect a habitat that was only capable of supporting large primates at low population densities. As noted, the STB clay mineralogy and chemical weathering data suggest a gradual cooling phase within a generally warm and humid climate over the period of deposition (Zhang et al., 2016; Li et al., 2019; Li P. et al., 2020), while the pollen record suggests a brief, warmer period within this phase coinciding with the presence of *Lufengpithecus*. Coincidentally, enamel carbon isotope records reveal a moderate shift toward more C4 plants in ungulate diets at STB compared to the somewhat earlier and primate-rich sites of Yuanmou and Shihuiba (Fig. 5; Sun et al., 2021), suggesting a more open habitat at STB. The beginning of a similar but earlier isotope shift in the Siwaliks of South Asia saw the last appearance of lorises, followed shortly thereafter by the hominid *Sivapithecus* (Nelson, 2003; Badgley et al., 2008). Thus, apes and many other primates appear to be sensitive indicators of environmental change toward more open habitats. The regular, strong expression of enamel hypoplasias seen in the dentition of the hominoid cranium, ZT299, suggests periods of nutritional stress, perhaps semi-annual seasonal cycles. This may indicate seasonal interruptions in the availability of ripe fruit at STB, and thus signal an environment that is only marginally able to support primates dependent upon a denser forest and the availability of ripe fruit for much of the year. The absence from

the pollen record at STB of trees that would produce the types of fruits preferred by apes in particular is perhaps notable in this regard.

Alternatively, the depositional setting at STB may simply represent a particular habitat that was rarely visited by primates. STB is unusual in having such a high proportion of avian remains relative to those of mammals, with the avifauna dominated by aquatic birds. In contrast, the much smaller avian assemblages from Shihuiba and Linxia consist of, respectively, mostly ground and perching birds (Hou, 1985), or arid-adapted ground birds (Li et al., 2018; Li Z. et al. 2020, 2021). As noted, the diversity of large mammals at STB is also low compared to other Late Miocene sites in Yunnan, and the most abundant large mammals are, for the most part, those with either a strong association with aquatic or water-margin habitats (“*Steneofiber*”, *Siamogale*, *Propotamochoerus*), or that can easily navigate such habitats (Proboscidea). Finally, the near absence of indicators of bone transport and modification reveal that the source area of the preserved remains was limited largely to the immediate vicinity of the excavated area. All of these features of the STB fauna suggest that the wetland depositional environment it samples has played an outsized role in faunal preservation, and that comparisons with faunas from other sites must be interpreted in light of this.

Given the diversity and abundances of large mammals at the other principal Late Miocene sites in Yunnan, Yuanmou and Shihuiba, it therefore seems more likely that the recovered large mammal fauna from STB greatly underrepresents the regional or even more local fauna in both diversity and abundance, rather than the fauna being genuinely as depauperate as the recovered remains might indicate. It may be that

individuals of many taxa infrequently ventured into the part of the local habitat represented by the excavated sediments, and that only those larger mammals for which the pond or lake was part of their habitus, or that could comfortably move into the water or along its margins to feed or drink, are commonly preserved.

6. Shuitangba and East Asian Miocene tectonics, climate and environment

After the Middle Miocene climatic optimum (~17–15 Ma), global climate experienced a general long-term cooling trend (Zachos et al., 2001; Herbert et al., 2016), which altered terrestrial environments and over time led to changes in mammalian communities worldwide (Nelson, 2007; Merceron et al., 2010). Like other regions, the Zhaotong Basin was subject to progressive cooling during the Neogene. The paleoclimate reconstruction of STB detailed above indicates that, as conditions became less warm and humid (Xia et al., 2009; Sun et al., 2021) – although still within a generally warmer and more humid climate than the present – environmental seasonality was likely accentuated, most notably after the Late Miocene, with warmer and drier summers and cooler, wetter winters (Xia et al., 2009; Huang et al., 2016). However, climate change was not linear through time in the vicinity of STB. The general cooling trend through the late Miocene was punctuated by episodes of milder climate, reflected in the changes to the vegetation described above that likely would have impacted the fauna as well (Chang et al., 2015; Li Z. et al. 2020).

The primary driver of environmental change between the Middle and Late Miocene was the uplift of the Higher Himalayas and Tibetan (Qinghai-Xizang) Plateau, resulting in changes in global atmospheric circulation and the initiation of the worldwide long-term cooling trend (An et al., 2001; Quade et al., 1989; Sanyal et al., 2004; Sun and Wang, 2005). This had far-reaching consequences, including some affecting the topography of Yunnan. The impact of the Indian subcontinent led to predominantly northward compression and the eastward and southward extrusion of parts of the Qiangtang Terrane (Tapponnier et al., 1982; Li S. et al. 2020), which today forms large parts of eastern Tibet and the Hengduan Mountains in Yunnan. The accompanying deformation throughout Yunnan created >150 Cenozoic sedimentary basins (Huang et al., 2016), which increased biodiversity in Yunnan by compartmentalization of landscapes, thus creating isolated habitats in which endemic faunas evolved (Ruddiman and Kutzbach, 1989; An et al., 2001; Guo et al., 2002; Chaplin, 2005; Huang et al., 2016). The importance of topographic complexity, including basin creation, in the generation of biodiversity has been emphasized by Badgley et al. (2017) and has been recognized as a particular driving force in the generation of high levels of biodiversity in Yunnan (Huang et al., 2016; Badgley et al., 2017; Tian et al., 2021).

Such factors likely exerted a strong influence on the composition of mammalian faunas in the region. However, it is difficult to reconstruct the biogeographical histories of most of the taxa at STB to make meaningful inferences about the STB assemblage. Exceptions are the primate taxa. As noted, *Lufengpithecus* shows affinity to lineages that are otherwise known from older strata in Europe (Kelley and Gao, 2012). These lineages were once widely distributed and *Lufengpithecus* therefore may be considered as a late Miocene subtropical-tropical relic. *Mesopithecus* dispersed to East Asia through South Asia not long before STB times (Jablonski et al., 2020) and was able to survive the cooler and increasingly seasonal environmental conditions of the region.

The impact of tectonics and basin formation on the fauna is also illustrated by the taxonomic novelty among the mammals at STB. Despite the relatively impoverished taxonomic composition of the mammalian fauna and the small number of taxa identified to species (Jablonski et al., 2014), four new species have so far been recognized among a diverse array of genera, including *Muntiacus zhaotongensis* (Dong et al., 2014), *Sinomastodon praeintermedius* (Wang et al., 2016), *Siamogale melilutra* (Wang et al., 2017), and *Miorhizomys gigas* (Flynn

et al., 2023), with only *S. melilutra* recorded outside the Zhaotong Basin. Several other new species have yet to be named (Table 1; see also Jablonski et al., 2014). Species of three further genera, *Stegodon zhaotongensis* (Chow and Zhai, 1962), *Tapirus yunnanensis* (Shi et al., 1981), and "*Steneofiber*" *zhaotongensis* (Shi et al., 1981) were earlier named from material recovered from the Zhaotong Basin, although a specific locality was only provided for one (*S. zhaotongensis*). None of these has been definitively identified from other sedimentary basins of Yunnan (Dong and Qi, 2013).

7. Conclusion

The site of STB is particularly important as a window on the terminal Miocene of South China. Apart from northern and central China, the latest Miocene and early Pliocene of Asia are not well documented and the record of South China during this interval is especially poor (Barry et al., 2002; Wang et al., 2013). STB offers a view of one ecosystem from this period near the northern limit of the South China biogeographic region. The biotic record from the site is remarkable in its breadth, which has permitted a reconstruction of the paleoenvironment of the area that is exceptional in its detail. The multiplicity of evidence suggests a wetland environment where standing water is surrounded by forest and areas of grasses and herbs and paleoclimatic conditions that were likely warmer and more humid than today with more pronounced seasonality.

CRediT authorship contribution statement

D.F. Su: Conceptualization, Data curation, Funding acquisition, Writing – original draft, Writing – review & editing, Formal analysis, Investigation. **J. Kelley:** Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing, Investigation. **X.P. Ji:** Data curation, Funding acquisition, Project administration. **L.J. Flynn:** Funding acquisition, Writing – original draft, Writing – review & editing, Investigation. **C.L. Deng:** Writing – original draft, Writing – review & editing, Investigation. **T. Deng:** Writing – original draft, Investigation. **P. Li:** Writing – original draft, Investigation. **Z. Li:** Writing – original draft, Investigation. **W.J. Sanders:** Writing – original draft, Writing – review & editing, Investigation. **T.A. Stidham:** Writing – original draft, Investigation. **F. Sun:** Writing – original draft, Investigation. **X. Wang:** Writing – original draft, Writing – review & editing, Investigation. **Y. Wang:** Writing – original draft, Writing – review & editing, Investigation. **D. Youlatos:** Writing – original draft, Writing – review & editing, Investigation. **N.G. Jablonski:** Conceptualization, Funding acquisition, Project administration, Writing – original draft, Writing – review & editing, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data used in the research is available in Supplementary Materials.

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Appendix A. Supplementary data

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