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Journal

Historical Biology, 33(10)

ISSN

0891-2963

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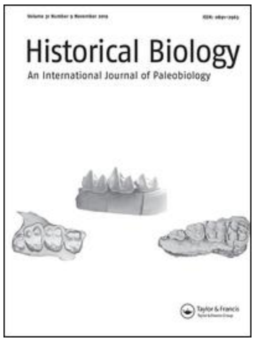
Publication Date

2021-10-03

DOI

10.1080/08912963.2020.1777551

Peer reviewed



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Historical Biology
An International Journal of Paleobiology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/ghbi20

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ARTICLE

Dragon bones from the heavens: European explorations and early palaeontology in Zanda Basin of Tibet, retracing type locality of *Qurliqnoria hundesiensis* and *Hipparion* (*Plesiohipparion*) *zandaense*

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ABSTRACT

More than 200 years since its initial exploration, Zanda Basin, a high-elevation (3,800–4,500 m above sea), intermountain basin at the foothills of the Himalaya, is the site to some of the earliest fossil discoveries, including the holotype of extinct Tibetan antelope, *Qurliqnoria hundesiensis*. These fossils also hold the record, in 1823, as the first vertebrate fossils from Tibet in the scientific literature. Unfortunately, these tantalising early records have become all but forgotten for more than 100 years due to a lack of information about their localities. Our recent explorations in the 2000s revive the interests in Zanda Basin and establish a unique Zanda mammal assemblage important in the evolution of Tibetan Neogene mammals. In this paper, we retrace the expedition routes by early explorers and attempt to establish, to the extent possible, the type locality of two key mammals in the Zanda fauna: *Q. hundesiensis* and *Hipparion* (*Plesiohipparion*) *zandaense*. We highlight the pivotal role Zanda fossil mammals play in the early discourse of mountain building, climate change, and mammal adaptation in high Himalaya, more than a hundred years before Chinese palaeontologists made a similar argument upon the discovery of three-toed horses, in the 1980s, at different basins in Tibet.

ARTICLE HISTORY
Received 30 April 2020
Accepted 31 May 2020

KEYWORDS
Qurliqnoria; *Plesiohipparion*; Zanda Basin; Cenozoic; Tibet; history of exploration

Introduction

As the capital of ancient Guge Kingdom (912–1630), Zanda (Zhada, Tuoling, Tsaparang) in the Ngari District of southwestern Tibet is perhaps the most extraordinary in the annals of explorations in Tibet. At the northern foothills of the Himalaya Range and with three mountain passes, Mana, Niti, and Lampiya, along its southern edge, the Zanda Basin is located at an elevation of 3,800–4,500 m above sea level and was often the first entry point to Tibetan Plateau for westerners venturing through these passes. This was especially true for explorations in the 16–18th centuries. Being the political, cultural and religious centre in western Tibet and a major transit town to the holy Mount Kailas (Kangrinpoche) and sacred Lake Mansarovar (Mapam Yumco), Zanda occupies a central place in the history of western Tibet. Equally remarkable is a unique set of sedimentary sequences in the basin incised by the Langqên Zangbo River (upper reach of the Sutlej), forming fantastic mesas, which preserve exquisite late Cenozoic fossils. Often produced from steep cliffs ('falling from the cloud', as early travellers described them) and traded by the locals as medicine or charms, these fossils attracted the attention of early explorers and became the source of the earliest palaeontological discoveries in Tibet. Most surprisingly, these earliest western scientific descriptions of Zanda vertebrate fossils even predate those from China, where a deep history of dragon bone trading as traditional Chinese medicines went back thousands of years earlier, and also spread to Tibet (McCormick and Parascandola 1981). Moreover, these reports were made before the discovery of late Cenozoic vertebrate fossils in the Siwalik Hills by Falconer, Cautley, and other officers of the British East Indian Company.

The significance of the discoveries of seemingly low-elevation fauna, which included extinct horses, antelopes, and rhinoceros, was not lost on early palaeontologists like Hugh Falconer and Richard Lydekker. These discoveries sparked a debate about the paleo-elevation and ancient environments in the high plateau, during the pre-tectonics era when there were few ways to fathom plateau paleo-elevation (Falconer 1868; Lydekker 1881). A hundred years later, a similar argument was independently advanced by Chinese vertebrate palaeontologists when three-toed horses were discovered in Gyirong and Bulong basins (Huang et al. 1980; Ji et al. 1980).

Despite this fascinating history, knowledge of the early discoveries of Zanda fossils was overlooked in the literature for the last 130 years. As a result, geological and geographic information about the principal localities for the Zanda fossils remained unknown. A particularly important specimen is the holotype of '*Pantholops*' *hundesiensis* (Lydekker 1881), housed in the Natural History Museum, London (NHMUK PV M10888), but tracing its type locality was not possible due to difficulties of access to remote locations and lack of knowledge about the basin sediments. Only recently, during five field seasons that our palaeontological team conducted from 2006 to 2012, have we finally been able to establish a biostratigraphic framework of the basin sediments (Wang et al. 2013a). Here, we review the early collecting history in the Zanda Basin by bringing together accounts of discoveries and re-examining the original specimens in the Natural History Museum, London, presenting photographs of the neglected collections, where appropriate. In re-examining historical materials in light of our own fieldwork in recent years and new insights from

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Published online 12 Jun 2020

our new collections, we present an argument for the type localities for two key Zanda Basin species, '*Pantholops*' *hundesiensis* and *Hipparion* (*Plesiohipparion*) *zandaense*.

Institutional abbreviations

NHMUK, Natural History Museum, London.

Etymology of the Zanda Basin

Zanda (Zhada) area was first referred to as Tsaparang (Chaparangue or Rtsa pa rang) in western literature, in reference to the ancient capital of Guge Kingdom. The modern usage of Tuolin (Tooling) refers to the main temple in Zanda County, but it was also an occasional substitute for Tsaparang. Moorcroft (1816) was the first European to use the term 'Ún-dés Plain' (= Hundes, Undés, Híundes, and Hioondès) (Figure 1), referring to the upper alluvium of the Zanda Basin and broad valleys extending to the sacred Lake Mansarovar, as viewed from the top of the Niti Pass (Webber 1902). Strachey (1851b, p. 62) began to use 'Elevated Plain', or 'Him-des', that is, snow country (Traill 1832, p. 34) but Hundes may also refer to the land of Huns (i.e. Xiong-nu) (Anonymous 1852, p. 92).

Early European explorations in the Zanda Basin

The first recorded visits of Zanda by European explorers were made by the Portuguese Jesuit António de Andrade and his brother Manuel Marques. In March 1624 de Andrade, while in search of the fabled (but false, see Gaborieau 2011; Bray 2014) 'lost Christian communities in Tibet', joined a Hindu pilgrimage to cross the Mana Pass and arrived at Tsaparang (Chaparangue or Rtsa pa rang, then capital of Guge Kingdom in Zanda) (Wessels 1924, 1937; Jina 1995, p. 14). In two separate visits, he established a short-lived Christian mission in the Guge Kingdom. Shortly thereafter in 1631, two other missionaries, fathers Francesco de Azevedo and Giovanni de Oliveiro, also arrived at Tsaparang and established a mission (Jina 1995, p. 15). In 1635, a six-person expedition led by Father Nuño Coresma made another attempt, but only two of the travellers (Coresma himself and Father Correa) made it to Tsaparang. They encountered hostility and were expelled (Wessels 1937, p. 12). Through 1641, a handful of additional missionaries had brief stays in Tsaparang and were met by physical difficulties and/or hostility from the Guge Kingdom. Since the first wave of missionary adventures, no records suggest that westerners succeeded in visiting Zanda area in the ensuing 170 years. The closest that a European reached Zanda was Father Ippolito Desideri, an Italian Jesuit and the only

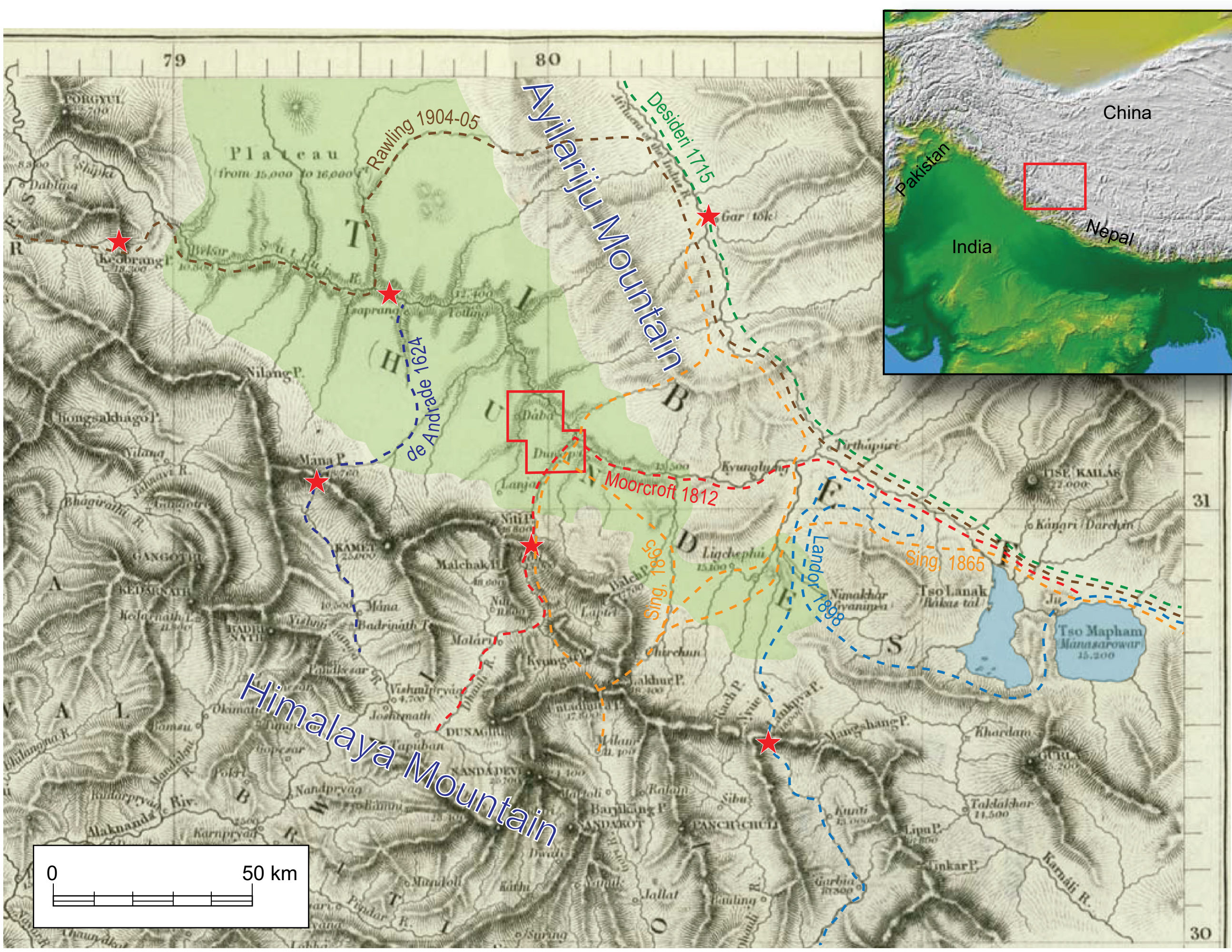

Figure 1. First western map of the Zanda Basin; modified from Strachey (1851b). The Keobrang, Mana, Niti, and Lankpya (Lampiya) passes, Tsaprang (Tsaparang), and the Gartok trading post are major landmarks highlighted by red stars, and the villages of Daba and Dungpu by red boxes, which are the source area of early discoveries of fossils. Coloured dash lines are routes of early explorers, mostly reconstructed from their narratives. We add a green and blue overlay to highlight the extent of Zanda Basin and large lakes to the east. The dark blue labels, Himalaya and Ayilariju, are our own. Inset topographic image is modified from NASA Earth Observatory (https://earthobservatory.nasa.gov/images/3741/topography-of-the-world).

westerner fluent in the Tibetan language at the time, who passed by Gartok (Gar Yasha) in the Ngari valley less than 40 km east of Zanda Basin in September 1715 (Desideri 1937, p. 81). One of Desideri's original goals was to re-establish de Andrade's Tsaparang mission. However, by early 1700 s, previous knowledge about the de Andrade route had been lost (Sweet 2006), causing Desideri to miss Tsaparang by a narrow mountain range (Ayilariju) (Figure 1).

With the exception of Desideri's posthumous book (1937, 2010), only letters of correspondence by the missionaries are preserved about their pioneering efforts (Sweet 2006; Andrade 2017), and the 17–18th Century missionaries in Tibet made little or no contributions to the local natural history. Formal scientific explorations of Tibet did not begin until the 1800s. In 1812, accompanied by Captain Hyder Young Hearsey, William Moorcroft, a British veterinarian and explorer, made a daring expedition into the western Himalaya. On 4 June, the Moorcroft party arrived at Niti, a small village of 14 to 16 houses and ~20 km south of the Niti Pass (about 45 km east of Mana Pass) (Moorcroft 1816). The southwestern rim of Zanda Basin is only a few kilometres from the pass (Figures 1 and 2). Motivated by his desire to bring back, albeit unsuccessfully, legendary horses from Central Asia to strengthen the horse stock in British India, and to trace the sources of Indus and Ganges rivers, the English explorers were probably some of the first western people to cross the western Himalaya via Niti Pass. He was also the first European to use the term 'Ún-dés Plain' (Hundes, Undés, Híundes, and Hioondès) (Figure 1), a term broadly overlapping with the modern concept of Zanda Basin but in circulation mainly in the 1800s and ceased to be used since (another reason for the disconnect between modern usage and historical literature). Moorcroft's adventure ushered in subsequent scientific expeditions, which also helped to initiate the 'Great Game' geopolitical rivalry between imperial Russia and the newly industrialised British Empire.

Figure 2. Upper, village of Niti, pencil on the back inscribed: 'Neetee – called also Leetee – frontier Village of Bootan – 1812', original was 370 × 463 mm (slightly cropped); lower, scene on the road to sacred Lake Mansarovar, on the back was inscribed in pencil: 'Kylass [Kailas] Mt. Road to Mansarovar Lake. Mr Moorcroft and Capt. H. and Chinese Horsemen', original was 354 × 515 mm (slightly cropped). Watercolours by Captain Hyder Young Hearsey in June (upper) and July (lower) 1812. Images owned by and reproduction with permission from the British Library.

Although Moorcroft recorded the rocks, river, and weather near Niti (Moorcroft 1816, p. 397–401), he failed to personally find any fossils (Moorcroft 1816, p. 435). Reports of vertebrate fossils traded at Niti and Mana began to circulate sporadically shortly after the Moorcroft expedition (reviewed chronologically below), but there are no reports of large-scale excavations in the basin.

In 1848 and 1849, Captain Richard Strachey, knowledgeable in geology and geography, visited the Hundes by way of the Niti Pass. Strachey (1851b) correctly recognised that the Hundes Plain, that is, the modern-day Zanda Basin, was a former alluvial plain about 60 × 170 km that completely filled the basin, which is later deeply incised by Langqên Zangbo River. This 'Elevated Plain' (Strachey 1851b, p. 62) had also been attributed to 'Him-des', i.e. snow country (Traill 1832, p. 34) but Hundes may also refer to the land of Huns (i.e. Xiong-nu) (Anonymous 1852, p. 92) or simply the Ngari region of Great Tibet (Landor 1898, p. 45).

By the mid-1800s, British imperial ambitions to survey Tibet were restrained by travel bans – European travellers were frequently expelled from Tibet due to the seclusionary policies of the central Chinese and local Tibetan governments. The solution was to train native Indian surveyors, known as the pundits, who would secretly record geographic data while disguised as pilgrims to various holy sites (Walker 1990). While crossings of the Mana Pass in 1865 by Indian pundits did much to advance the Great Trigonometric Survey by the British East India Company (among its accomplishments was the establishment of the elevation of Mount Everest, or Chomolungma, as the highest peak of the world), fossils and geology were not their main objective (Montgomerie 1868). Carl Ludolf Griesbach, a British palaeontologist and geologist, reported Zanda fossil collections but nothing was described (Griesbach 1880). In 1897, Arnold Henry Savage Landor, an English artist and photographer, entered Tibet via Lampiya (Lumpiya, Lankpya) Pass and skirted the southern edge of the Hundes Plain on his way to Lhasa (but failed to reach his destination) (Landor 1898). In 1904–1905, Cecil Godfrey Rawling, a British military officer, travelled from Gyangze to Gartok and after crossing the Ayilariju Mountain, arriving at Tooling (Tuoling, i.e. Zanda) on his way back to India (Rawling 1905). A long hiatus in scientific explorations of Zanda Basin ensued for nearly a century due to wars (both in China and Europe), political upheavals, and physical inaccessibility.

Modern palaeontologic exploration of the Zanda Basin began with the First Comprehensive Tibetan Plateau Scientific Expedition by the Chinese Academy of Sciences in 1973–1980. Despite the large-scale endeavour, Zanda fossils, in particular, were the subjects of only two papers resulting from this expedition: Zhang et al. (1981) published an extinct giraffe palate, *Palaeotragus microdon*, from Xiangzi area, and a new species of three-toed horse, *Hipparion* (*Plesiohipparion*) *zandaense*, was named by Li and Li (1990) from the Daba area (acquired from local villagers). In both publications, there is no indication that the Chinese palaeontologists were aware of prior fossil records discussed in this paper. The Zanda Basin was finally extensively surveyed by palaeontologists in the 2000s – five field seasons were conducted by our team of Chinese and American vertebrate palaeontologists and geochemists (Deng et al. 2011, 2012; Tseng et al. 2013a, 2013b, 2016; Wang et al. 2013; Wang et al. 2013a; Wang et al. 2014a, 2014b, 2016; Li and Wang 2015; Li et al. 2018).

Early fossil collecting in the Zanda Basin

Little more than 10 years after Moorcroft's 1812 Zanda Basin expedition (Early explorations above), the first vertebrate fossils were published based on specimens acquired from local traders at Niti village. Reverend William Buckland (1823, p. 222), an English theologian, was the first to mention fossils from Zanda Basin acquired by W. S. Webb:

> ... bones of horses and deer have been found at an elevation of 16,000 feet above the sea, in the Hymalaya [*sic*] mountains. The bones I am now speaking of are at the Royal College of Surgeons in London, and were sent last year to Sir E. [Everard] Home, by Captain W. S. Webb, who procured them from the Chinese Tartars of Daba, who assured him that they were found in the north face of the snowy ridge of Kylas [*sic*], in lat. 32°, at a spot which Captain [W. S.] Webb calculates to be not less than 16,000 feet high: they are only obtained from the masses that fall with the avalanches from the regions of perpetual snow, and are therefore said by the natives to have fallen from the clouds, and to be the bones of genii

Here, Mt. Kailas, which is visible standing on top of the Niti Pass, was obviously confused with the Himalayas (see Figure 1). By 1832, George William Traill, the then Commissioner of the affairs of Kumaon, British India, wrote of fossils called 'Bijli Hár' or lightning bones by the native traders occurring at the crest of the Niti Pass (Traill 1832, p. 17). He also noted that 'Chakar Patar' or wheel rocks (now known to be ammonites) were found in a ravine on the northern face of the Mana Pass. Traill's vertebrate fossils were presented to the Geological Society of London by Henry Colebrooke and included bones of a variety of sizes, fragments of crania, and a partial cranium of a goat or deer-like mammal (Herbert 1831). This latter specimen was later described by Lydekker (1881) as '*Pantholops*' *hundesiensis*. Herbert made additional collections with Traill's assistance (most likely acquired from Bhotea traders), from what he notes are the same localities as Traill's fossil sites. He states the localities (as described to him):

> ... were on the northern face of the ridge which separates the basin of the Ganges from that of the Sutluj [Sutlej], and not far from the town of Dumpu. This ridge is several days journey beyond the line of snowy peaks forming the zone of greatest elevation. (*Herbert 1831*, p. 270)

The village of Dumpu (= Dungpo, Dongpo, Dongbocun) is 22 km southeast of the village of Daba (Figure 1). Herbert was unfortunately unable to present his collection to European scientific society, and their whereabouts remain unknown. A few years after, on 11 October 1837, J. H. Batten (1838, p. 314) made it to the Niti Pass from where he described the Hundes Plains as, '... broken into ravines and river courses running down to the Satlej [Sutlej, i.e. Langqên Zangbo River]'. In a letter dated 22 December 1837 and addressed to P. T. Cautley (of Siwalik fossil fame), Batten mentions the fossils he encountered north of the Niti Pass and later sent to Cautley:

> I descended into this ravine, saw the source of the Siánki river and some green ponds on one side of it, thence ascended the opposite banks, keeping to the northwest for two miles till I came to what was called the fossil ground, (Charka patharke makán) ... I found the ammonites lying about in hundreds on the top of a small ascent just as the road wound through a kind of pass between two hillocks, before it descended into a ravine. (*Batten 1838*, p. 315)
>
> I have a good many fossil bones brought from the interior of Thibet, and from the Mána pass. They are however very broken and small. (Batten 1838, p. 316)

The first illustrations of vertebrate fossils from Zanda were made by the botanist John Forbes Royle. Royle illustrated Traill's partial skull, a left maxilla of an antelope-like animal, and a rhinoceros tooth (Figure 3) in his *Illustrations of the Botany and Other Branches of the Natural History of the Himalayan Mountains* to indicate the presence of Tertiary strata from the '... elevated land on the N.E. of the line of snowy peaks ... all from the northern face, beyond what may be considered the true Himalayas' (Royle 1839: xxix, pl. III). Royle (1839) reiterated Traill's observation that these fossils were referred to as 'Bijli ke har, or Lightning Bones' by native Indians and traded as medicine or charms.

Regarding Zanda fossils, Richard Strachey correctly determined that the vertebrate fossils were not derived from the Niti Pass, but from across the Himalayas (Strachey 1851b). While he published extensively on Palaeozoic and Mesozoic invertebrates from the basin (Salter and Blanford 1865), Strachey also procured vertebrate fossils, presumably from local traders. His collections include a metacarpal and distal tibia of '*Hippotherium*' (most likely *Hipparion* [*Plesiohipparion*] *zandaense*), a distal radius, and distal tibia of seemingly larger equids, a partial metacarpal of an equid, the proximal end of a tibia from a bovine ruminant, a dorsal vertebra from a ruminant, a partial cranium of a caprine bovid, very similar to the partial skull discovered by Traill ('*Pantholops*' *hundesiensis*), a partial atlas of a rhinoceros, a phalanx from the hindfoot of a rhinoceros, and possible proboscidean molar. To our knowledge,

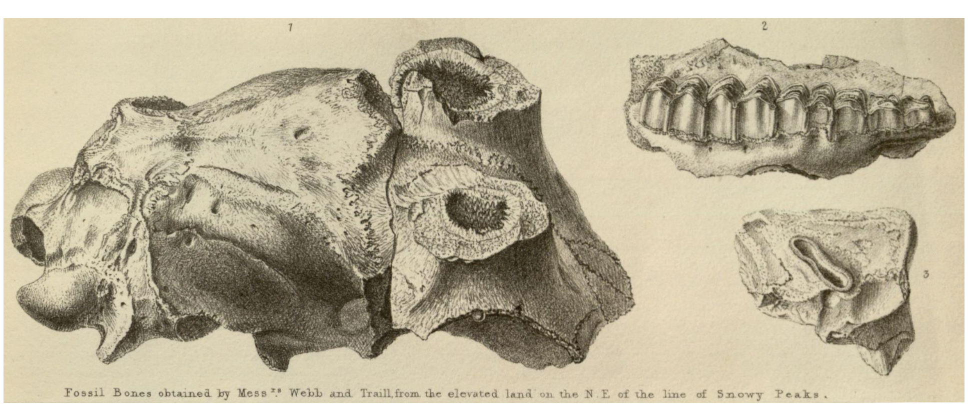

Figure 3. First illustrated vertebrate fossils from Tibet, adopted from Royle (1839:xxix, pl. III). 1, holotype, a partial skull and 2, referred specimen, left maxillary, later named '*Pantholops*' *hundesiensis* by Lydekker (1881), with cheek teeth (see Figure 5 for a photograph of the specimens); 3, a partial cheek tooth of a rhinoceros (likely *Coelodonta thibetana*).

these specimens were never described formally and their whereabouts remain unknown.

Falconer (1868) was the first to describe mammalian fossils from the Zanda Basin. In a manuscript, probably written in 1839, but published posthumously in 1868 by Charles Murchison in Falconer's Palaeontological Memoirs, Falconer mentions the various sources of the specimens in the collection he examined. These included fossils from Cautley's collection sent by Captain Corbet of Almorah, from Batten's collection (specimens procured from a 'Bhoteah merchant', presumably referring to the merchant from the 'Hioondès'), and from Pl. III of Royle's 'Illustrations', which featured Webb's and Traill's fossils presented to the Geological Society of London. In the same manuscript, Falconer described the remains of a rhinoceros but did not formally name the species. He also provides a very rudimentary description of the Traill's specimen of '*Pantholops*' *hundesiensis* and the maxillary fragment illustrated by Royle (1839), refraining from naming it, and lastly mentions a femoral head (not illustrated) of a large bovid, a caprine horn core (not illustrated), and a tooth from a hyaena (not illustrated). He later commissioned illustrations of the rhinoceros specimens and specimens of equids (most likely hipparionines) in the Fauna Antiqua Sivalensis (Falconer 1867) but did not describe the horses. According to Lydekker (1886a), the rhinoceros and equid specimens were given to Cautley by traders (most likely the 'Bhoteah merchant' that Falconer mentioned) over the Niti Pass.

The last 19th century European fossil collection in the region was made by Carl Ludolf Griesbach in 1880. He was also the first European to personally collect fossils from the Zanda Basin (Griesbach 1880) and states that the fossils were collected from a deposit near the town of Dongpo. This interestingly is the same town mentioned by both Traill and Herbert as the source of their fossils (Herbert 1831).

The first systematic treatments of Zanda Basin species were made by Richard Lydekker (1881). Lydekker tentatively named '*Pantholops*' *hundesiensis* as a new species of the Tibetan antelope based on Royle's illustration, even though he did not have a chance to see the original specimens. Twenty years later, Lydekker (1901) finally had the opportunity to examine the original specimen and re-figured it, but maintained the taxonomic nomenclature he originally proposed in 1881. These specimens are now believed to belong to the more primitive genus *Qurliqnoria* first described from late Miocene of Qaidam Basin on the northern Tibetan Plateau (Bohlin 1937; Gentry 1968). Lydekker (1886a), in his third part of the Catalogue of Fossil Mammalia in the British Museum (Natural History) classified the equid remains illustrated by Falconer (1867) as '*Hipparion*', and the rhinoceros specimens as *Rhinoceros* sp. b, but did not provide any further descriptions or nomenclatural notes. He does, however, in a subsequent publication on the Maragha fauna from Iran in 1886, mention that the Tibetan rhinos illustrated by Falconer might be '*Rhinoceros*' *blanfordi* (Lydekker 1886b). Modern taxonomic studies have shown that these rhinos are likely *Coelodonta thibetana* (Deng et al. 2011), which is the only known rhinoceros in the Zanda Basin (Wang et al. 2013a). In 1897, Landor (1898, p. 256), while exploring the narrow land between Mansarovar and Raksas Tal lakes, mentioned 'gigantic fossils' about 'one hundred feet above lake-level, imbedded in the mountain side'. However, owing to their size and weight, he was unable to collect these. Since the above early discoveries, diverse high-altitude mammalian fauna has been discovered and described by Sino-American expeditions (see summary in Wang et al. 2014c). To simplify the convoluted history of fossil discoveries in Zanda Basin, we summarise major events in a timeline (Figure 4).

It is surprising the above early discoveries of vertebrate fossils from Zanda published from the 1820 s through 1860 s considerably predate palaeontological literature on dragon bones from China. The West has known about China probably well before the days of Marco Polo in the 12–13th Century, but western palaeontologists did not begin to describe fossils purchased from traditional Chinese apothecaries until British anatomist Richard Owen (1870) named several new species of *Stegodon, Hyaena, Rhinoceros,* and others,

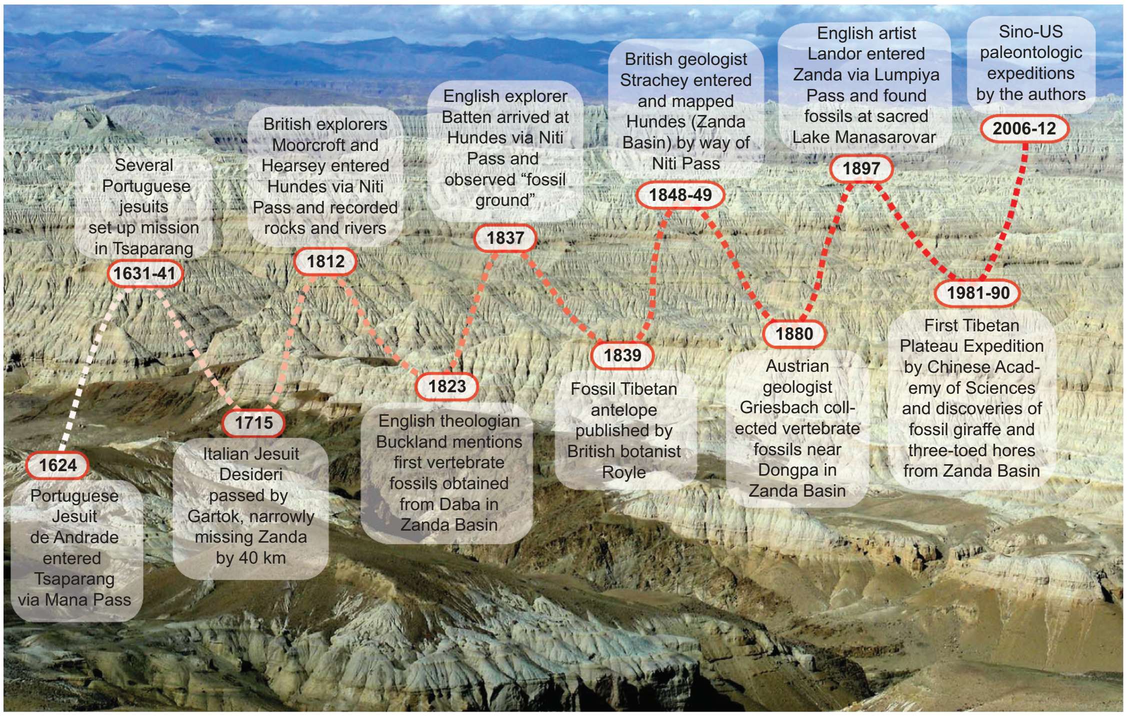

Figure 4. Waves of discoveries: timeline of Zanda Basin explorations and vertebrate fossils found by early expeditions. Background photo of Zanda Basin by Xiaoming Wang on 28 July 2007.

and later also by Koken (1885) and Schlosser (1903), despite the fact that earlier missionaries had long recorded the Chinese use of dragon bones as medicines (McCormick and Parascandola 1981). It is perhaps more remarkable that the provenance of these Tibetan fossils can be traced to Zanda Basin or possibly even to a single village (see below), whereas the geographical origins of Chinese dragon bone fossils acquired from drug stores in big cities are far less certain (thus causing considerable difficulties in the usage of fossil taxa based on 'dragon bones'). It is also remarkable that Tibetan mammalian fossils were known to western explorers before the discovery of the famous Upper Siwalik fossil beds by Falconer, Cautley, and other British explorers and scientists, despite the Siwalik beds being present in a densely populated part of the Indian Subcontinent.

Source area for historical collections

The Zanda Basin has the only appropriate historical and stratigraphic context to be the source of the holotypes of *Qurliqnoria hundesiensis* and *Hipparion* (*Plesiohipparion*) *zandaense*. Not only the Hundes was often the first encountered by early explorers of Tibet but also Zanda has the only known Pliocene age strata to produce vertebrate fossils in southern Tibet. Two other Tibetan localities are known to produce *Qurliqnoria* and *Hipparion*, one from the late Miocene of Qaidam Basin (Bohlin 1937; Wang et al. 2007) and another from the Pliocene of Kunlun Pass Basin (Li et al. 2014), but their geographic locations and timing of their explorations are too far apart from Zanda to be relevant.

Despite there being very little information on the exact geographic location of the early fossil finds from the Zanda Basin, the reports from western explorers offer some clues to where the fossils were extracted. Throughout the early explorations, fossil mammals were mostly acquired at the Niti village or Mana Pass, and these fossils were traded by merchants as curiosities or medicines with supernatural power (Royle 1839, p. xxix; Falconer 1868), presumably following the ancient Chinese practice of dragon bone trades. While their provenance was not clear, it was speculated that they came from the Hundes (Strachey 1851a). Strachey (1851a, p. 306) remarked that the 'existence of such fossil remains in the northern parts of these mountains had been long known, but we were altogether ignorant of the precise locality whence they came'. He pointed out that 'the Niti Pass, from which it was said that the bones had been brought, was not the place where they were found, but one of the routes only by which they came across the great Himalayan chain from unknown regions beyond'. Explorers like Herbert and Traill named the village of 'Dungpo' as a potential locality from which the traders were collecting their fossils. Partial confirmation by a professional geologist did not occur until 1880, when, near the village of 'Dongpa' (Dungpu in Strachey's map; Dongbocun in modern Chinese maps), Carl Ludolf Griesbach (1880, p. 91) found 'fragments of mammalian bones, which makes it reasonably certain that the former finds of bones (Strachey) were also derived from the same source'. Griesbach was thus the first scientist to have personally collected fossils from Zanda Basin.

The nearby village of Daba (Dhapa, Dápa), located in the southeastern part of the Zanda Basin 22 km northwest of Dongpo (Figure 1), also frequently appears in the writings of early explorers. Indeed, the holotype of *Hipparion* (*Plesiohipparion*) *zandaense* was obtained from near this village (Li and Li 1990). Therefore, it is likely that fossils traded at the Niti village were sourced from the vicinity of the villages of Daba and Dongpo. The fact that the specimens were acquired from people coming from Daba is tantalising (Buckland 1823, p. 222). However, Herbert's (1831, p. 270) remark that the specimens were 'found in caves' is also intriguing.

In general, native Tibetans do not have a tradition of dragon bone trade, prominent among the Chinese. Even when Tibetans do excavate caves, as have the Zanda Tibetans, the purpose is not for commercial exploitation but for religious meditation. Our own observation suggests that numerous caves in every village in Zanda Basin exist (Figure 5), and the caves are mostly dug in conglomerate beds (which are more abundant in the basal and upper strata in the basin). Falconer (1868, p. 176) remarked that

Figure 5. An example of religious ceremonial caves dug into walls of steep exposures of Zanda Formation strata. This site is near the village of Baidongpo (not the same as Dongpo elsewhere in this paper), 10 km northeast of Zanda County seat, at N31° 31′ 48.9″ E79° 54′ 21.2″. Photo by Xiaoming Wang on 12 July 2012.

matrices surrounding Tibetan fossils are typically coarse sand or gravel, consistent with lithology of cave-dwelling layers. It seems unlikely that these cave-digging activities would yield substantial numbers of fossils, as the conglomerates are typically less fossiliferous than finer-grained, sandier layers. Occasional encounters of fossils, however, are inevitable given the large-scale cave-digging activities in Zanda. Therefore, native Tibetans in Zanda Basin more than likely have been aware of their fossil heritage for as long as Buddhism had been flourishing in Tibet. In fact, the well-preserved partial skulls of *Qurliqnoria hundesiensis* and *Hipparion* (*Plesiohipparion*) *zandaense*are likely dug from fresh matrix in caves, as is the case for almost all Chinese dragon bone operations, because inexperienced collectors would not have the skill to properly preserve specimens weathered out on surface exposures.

During our visit to the village of Daba in 2006, although we were not permitted to look for fossils near the village due to religious sensibilities (private caves dug into cliffs, where family shrines are located and worshipped, are off-limits), we were able to confirm that, as elsewhere in Zanda Basin, numerous caves dug for religious purposes are scattered on steep exposures at Daba village (Figure 6). As for the holotype of *Hipparion* (*Plesiohipparion*) *zandaense*, it was acquired by Liang Dingyi in July 1982 with the help of local villagers and a Tibetan doctor (Liang had learned in 1981 that fossils were produced in Zanda area). Li and Li (1990, p. 187) stated that the type locality for *Hipparion* (*Plesiohipparion*) *zandaense* is from 'near top of the hill northwest of the Daba area, … at an elevation of ~4,250 m'. As seen in Google Earth, the ridgeline northwest of the Daba village has an elevation of 4,225–4,240 m. If our inference that the fossil came from the caves is correct (Figure 6), then actual elevation of the holotype should be slightly lower, around 4,220 m.

As for the holotype of '*Pantholops*' *hundesiensis*, its hypodigm can be traced to Dongpo area, a fortunate circumstance for fossils that were collected nearly 200 years ago. The holotype, NHMUK PV M10888, is the posterior part of skull with basal parts of left and right horncores. This along with referred specimens, NHMUK PV M10889, partial left and right maxillae with P2-M3, most likely belong to the same individual (Figures 3 and 7). The hypodigm was acquired by George Traill and presented by Henry Colebrooke to the Geological Society, London. According to Herbert (1831), Traill's specimens came from near Dongpo. The specimens, initially deposited in the Museum of the Geological Society, London, were subsequently acquired by the Natural History Museum, London in 1911, where they have resided since.

Remains of three-toed horse, *Hipparion* (*Plesiohipparion*) *zandaense*, were also acquired by Traill. As in the case of the holotype of *Qurliqnoria hundesiensis*, the horse materials most likely came from near Dongpo, and are part of the Colebrooke collection, now accessioned at the Natural History Museum, London (Figure 8).

Within the 800 m basin sediments, *Qurliqnoria* is known in the 100–400 m section, whereas our biostratigraphy for *Hipparion* is in the 70–530 m range (Wang et al. 2013a: Figure 4), i.e. much of the middle, fine-grained section where the vast majority of Zanda fossils were found. Although we were not permitted to collect at the village of Daba (see above), we did find fossils within 2 km west of Daba (solid red circle on lower right corner on Figure 2 in Wang et al. 2013a) as well as a few km north of Daba (Wang et al. 2014a). Therefore, we think it likely that the holotype of '*Pantholops*' *hundesiensis*, as that for *Hipparion* (*Plesiohipparion*) *zandaense*, came from similar caves in Dongpo and Daba. In any case, our suggested Daba–Dongpo occurrence for these specimens is parsimonious, similar to an assumption for Chinese dragon bones from historical localities, as from Yushe Basin (Qiu and Tedford 2013; Tedford et al. 2013).

Early debate on faunas, paleoenvironments, and elevations in Tibet

As the first geologist to Zanda Basin, Strachey (1851a, p. 306) was astonished by the lack of disturbance to Zanda strata: 'the most striking feature of the geology of these mountains is probably that which I have next to mention, viz. the existence of a great Tertiary

Figure 6. Exposures of Zanda Formation at the village of Daba. Cave entrances (dark holes in the middle section) are excavated on steep cliff, as is customary in all caves from villages of Zanda Basin. Note that caves are more concentrated in rusty-yellow or dark grey conglomeratic horizons. Although these layers are less fossiliferous due to their high-energy deposits, we think well-preserved specimens such as the holotypes of '*Pantholops*' *hundesiensis* and *Hipparion* (*Plesiohipparion*) *zandaense* were likely produced from caves such as these. The top of the ridge line is about 4,225–4,240 m. Photo by Xiaoming Wang on September 3, 2006.

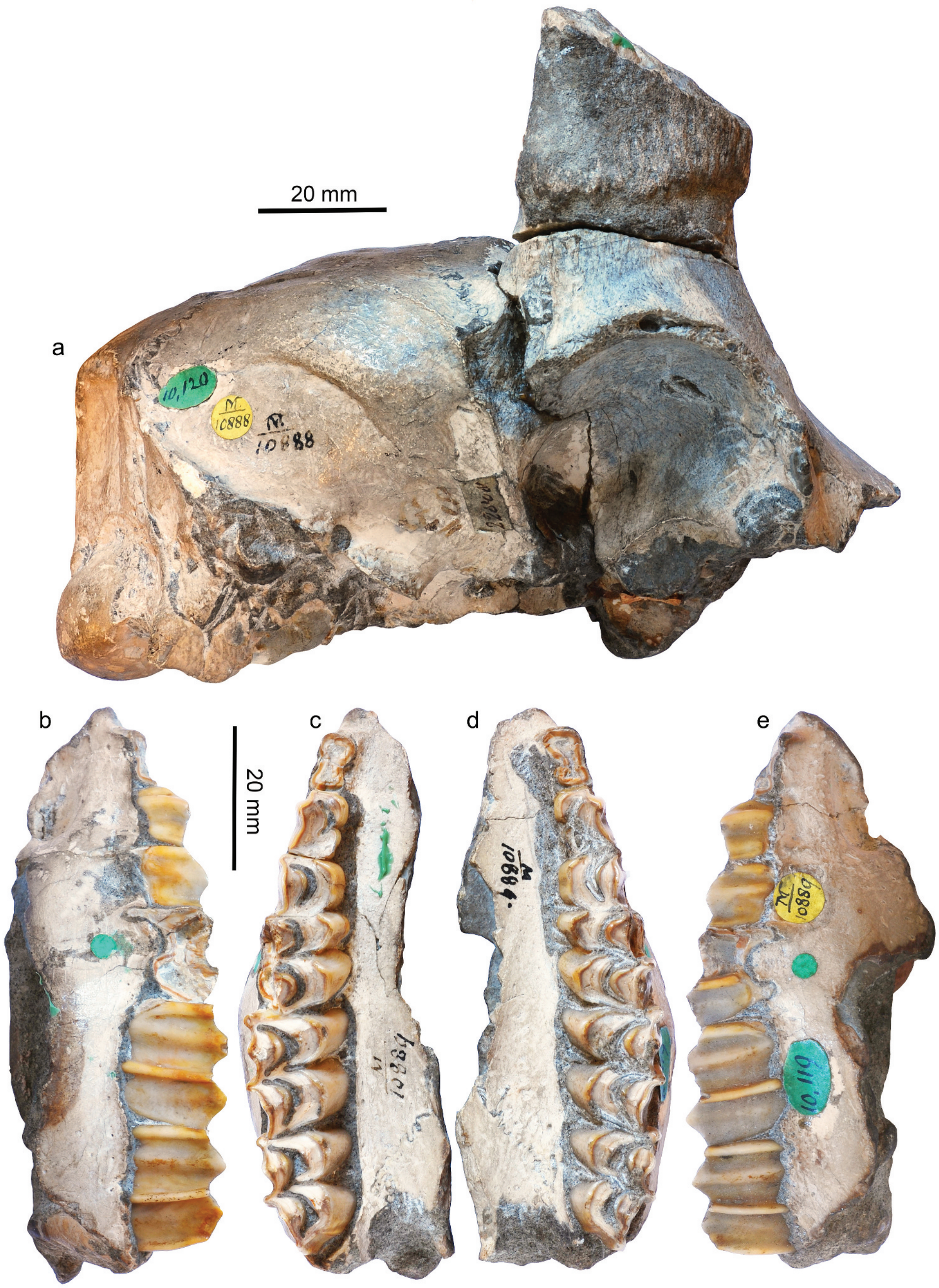

Figure 7. *Qurliqnoria hundesiensis* (Lydekker 1881) from Zanda Basin. A, holotype, partial skull, NHMUK PV M10888, right lateral view; B-E, referred specimen, left and right maxillary with left and right P2 s (broken)-M3 s, NHMUK PV M10889, right lateral (B) and occlusal (C) views of right maxilla, left occlusal (D) and left lateral (E) views of left maxilla. Photos by Xiaoming Wang.

deposit at an elevation of from 14,000 to 16,000 feet above the sea, still preserving an almost perfectly horizontal surface'. Although Strachey's elevations (~4,200–4,800 m), likely based on the top surface of Zanda Basin at the depo-centre to alluvial fans at the base of the Himalaya, differ from valley bottom at Langqên Zangbo River to the terminal surface (3,800–4,500 m) of modern understanding, his sense of incongruence between almost perfectly flat-lying beds in Zanda Basin (Figure 9) and violent tectonic upheavals in the Himalayas proved prescient and astute. After more than 160 years, Saylor et al. (2010) were the only authors to address this issue by invoking a delicate balance among several detachment faults.

The Zanda Basin also occupies a unique place in the annals of vertebrate palaeontology because at the time of its discovery Zanda fossil mammals were from a late Cenozoic basin of the highest then known elevation in the world. Such a lofty elevation did not escape the attention of early geologists and vertebrate palaeontologists, who began to speculate about its environmental consequences. The first attempt at accounting for such a lofty height was by Buckland (1823, p. 223) who proposed an antediluvian origin of the Zanda fossils, reasoning that the 'carcases [*sic*] of the animals were drifted to their present place, and lodged in sand, by the diluvial waters'. Such a religious overtone was perhaps not uncommon at a time when a Darwinian lens to interpreting and understanding evolution did not exist, nor the notion of mountain uplift by plate tectonics.

Discovery of an extinct rhinoceros from so high an elevation quickly caught the attention of palaeontologists. Although the

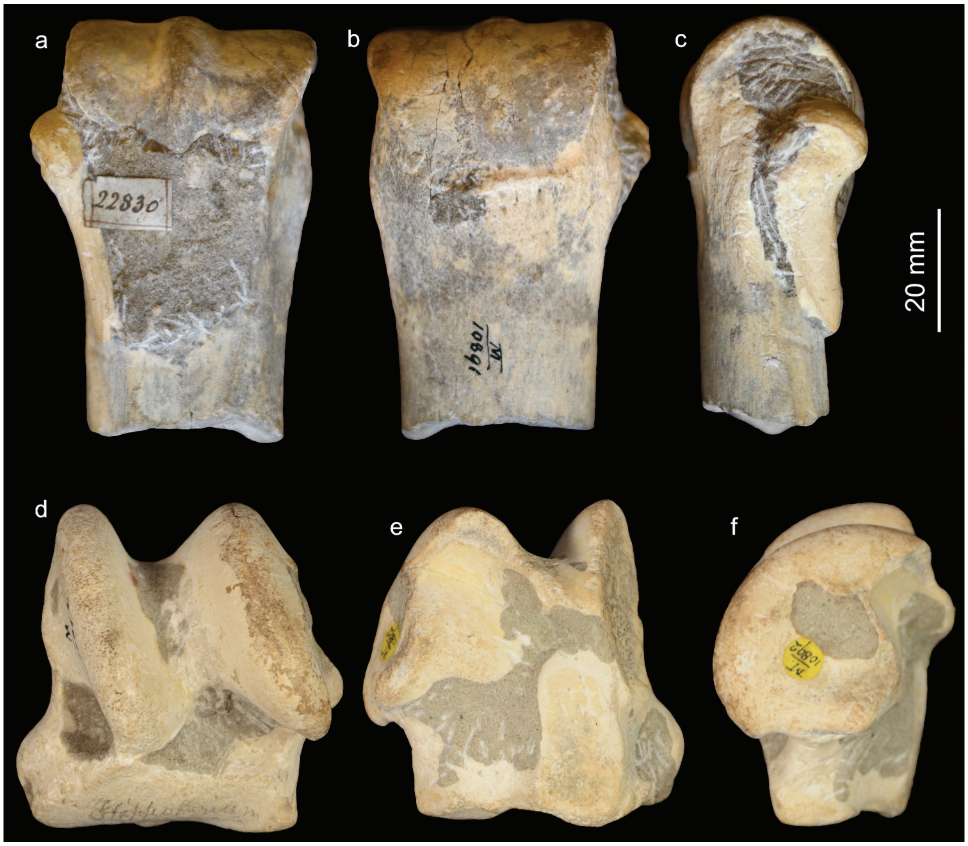

Figure 8. A partial metapodial and a left astragalus of *Hipparion* (*Plesiohipparion*) *zandaense* from Dongpo, Zanda Basin in the Colebrooke collection of the Natural History Museum, London. A, caudal, B, cranial, and C, lateral views of distal metapodials (III plus II or IV), NHMUK PV M10891, note presence of a lateral metapodial to indicate tridactylar condition; C, cranial, D, caudal, and E, left lateral views of a left astragalus, NHMUK PV M10892. Photos by Advait Jukar.

Figure 9. A typical exposure of nearly perfectly flat-lying Zanda Formation strata deeply incised by the Langqên Zangbo River (not visible in this view). Mesozoic basement is visible in the middle of the picture as dark brown, unstratified rocks. Located about 7 km southeast of Zanda County seat at N31°26′48.2″ E79°52′06.7″, road near this exposure was likely to have been travelled by early explorers such as the de Andrade 1624 expedition. Picture looking northeast and distant dark blue mountains in the background is Mt. Ayilariju (Figure 1). Photo by Xiaoming Wang on 13 July 2012.

fragmentary nature of the Zanda rhinoceros did not permit Falconer (1868) to determine its precise taxonomy, he was sure that the fossils represented a distinct species from the living Indian rhinoceros, *Rhinoceros unicornis* (he referred the Zanda materials as simply 'fossil rhinoceros'). Despite such a limitation, he took a considerable interest in its paleoenvironmental implications. He

Figure 10. Silent witness. This ancient cantilever bridge just east of the Tsaparang (Zanda) crosses the Langqên Zangbo River (upper reach of the Sutlej) and was probably used by several early western explorers. This bridge is now replaced by a concrete structure. Drawing by Xiaoming Wang based on a photograph in Rawling (1905, p. 287).

inferred that no living rhinoceros could have lived in the present environment of Zanda Basin at an elevation of ~4,500 m and above tree line, let alone scaling the steep, snow-covered mountain passes to get into Tibet. In a startling prescience, Falconer (1868) envisioned that the rhinoceroses from Hundes must have sported a thick coat of hair like those in the woolly rhinoceros frozen in Siberian tundra. Even then, he concluded that a much lower elevation, as much as 7,000 ft (2,133 m) below current elevation, must have existed in Zanda Basin for the rhinoceros to survive. Consequently, he argued, the 'Plains of Hundes' must have been uplifted by 2,000 m since the time of the rhinoceros (earlier in 1851, Strachey even speculated that Zanda strata were marine beds and therefore below sea level!).

Lydekker (1881), however, revisited the above question of rising elevations. He argued that many of the faunal elements from Zanda Basin are comparable to modern mammals still living in the high plateau, including his newly named '*Pantholops*' *hundesiensis*, a close relative of modern Tibetan antelope, *P. hodgsonii*. Given that Zanda strata remain perfectly flat, Lydekker considered it unlikely that the entire basin has been uplifted en mass without slight disturbance to its horizontal bedding. This, along with the similarity to living fauna, convinced him that invoking a lower elevation for the ancient Zanda biota is unnecessary. Lydekker (1881, p. 181) concluded that Zanda fauna is Pleistocene in age, and 'almost certainly not older than upper Pliocene'. As for the presence of Zanda rhinoceros, he conceded that rhinoceros is probably incapable of surviving in current vegetation in Zanda Basin, but he envisions a previously milder climate, perhaps with trees, in Zanda Basin that could sustain a great rhinoceros.

Falconer and Lydekker were ahead of their time. A similar argument was advanced during the Tibetan Plateau Scientific Expedition by the Chinese Academy of Sciences in 1973–1980. Hipparionine (three-toed) horses discovered in the Gyirong and Bulong basins had prompted Chinese vertebrate palaeontologists to conclude that the paleoelevation must have been substantially lower than the present (Huang et al. 1980; Ji et al. 1980). Interestingly, Huang and Ji were apparently unaware of the debates between Falconer and Lydekker, which had gone unnoticed for almost 100 years. More recently, a renewed debate on paleoaltimetry of Zanda Basin has brought to bear evidences from functional morphology of horse limbs (Deng et al. 2012), mammalian enamel stable isotopes (Wang et al. 2013b), and geochemistry of gastropod shells (Huntington et al. 2015). These studies suggest estimates ranging from ~1,000 m below present elevation to ~1,000 m above.

Conclusions

Despite its remote location surrounded by formidable mountains, the Zanda Basin has yielded the earliest vertebrate records in Tibet, predating even scientific literature about Chinese dragon bones (Figure 10). Sufficient documentations exist to suggest that extinct mammals were collected from the fantastically exposed, highly fossiliferous strata in Zanda Basin and were traded in villages near surrounding mountain passes. These fortunate circumstances gave rise to the early description of the holotype of '*Pantholops*' *hundesiensis* from Zanda Basin. The occurrences of fossils in a high-elevation basin also sparked a controversy over the uplift of the Himalaya and its paleoenvironments during the 1800s, when altitudes of the mighty Himalaya were just beginning to be surveyed but elevations in its geologic past were almost unfathomable. Despite this unusually early start, systematic efforts in vertebrate palaeontology of Zanda Basin did not resume until the 2000s. With our recent establishment of a biostratigraphic framework, we are finally in a position to infer the type locality of '*P*'. *hundesiensis* and *Hipparion* (*Plesiohipparion*) *zandaense*, as from the villages of Dongpo and Daba.

Acknowledgments

XW has benefited from conversations with Prof. Qiu Zhanxiang regarding early records of Zanda fossils. We greatly appreciate team members and drivers, both Chinese and Tibetan, of our Zanda expeditions, without whose dedication this project would not be possible. We would also like to thank P. Brewer, and N. Gabriel for access to the fossil mammal collection at the Natural History Museum, London. Ms. Bruna Lago-Fazolo has kindly assisted in granting permission to publish Captain Hearsey's watercolours in the collection of the

British Library. We greatly appreciate the comments and suggestions by three anonymous reviewers. We also thank Editor-in-Chief Gareth Dyke for his encouragement to submit this paper.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Funding for fieldwork and travel are provided by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26030304), CAS/SAFEA International Partnership Program for Creative Research Teams, Chinese National Natural Science Foundation (nos. 40702004 to Q.L., 40730210 to T. D., 49872011, 40128004), Chinese Academy of Science Outstanding Overseas Scholar Fund (KL205208), National Science Foundation (US) (EAR-0446699, 0444073, 0958704, 1227212 to X.W.), and National Geographic Society (no. W22-08 to Q.L.).

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