Earliest record of *Sinicuon* in Zanda Basin, southern Tibet and implications for hypercarnivores in cold environments

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**Abstract**

The “out of Tibet” hypothesis envisions late Cenozoic Tibetan mammals acquiring adaptations to cold environments and being ancestral to several Eurasian megafaunal species in the Pleistocene. Here we report an early record of a hypercarnivorous canid, *Sinicuon cf. Sinicuon dubius*, from Zanda Basin in the Himalaya Range. Although the new record is recovered from reworked sediments in a Pleistocene alluvium, we can constrain the fossil to within a narrow age range of 3.8–3.4 Ma in the middle Pliocene. Presence of this hypercarnivorous canid in the Pliocene of Tibet, along with the recently described pantherine cat and arctic fox, suggests a predator guild with predominately carnivorous diet characteristic of modern arctic carnivorans such as the arctic fox and polar bear. Wintering in extremely cold climates may have been the cause of such adaptations. *Sinicuon* shows transitional morphology to modern hypercarnivorous hunting dogs in southern Asia (*Cuon*), suggesting linkage of the high Tibetan Plateau to the southern continents.

1. Introduction

Based on an ancestral woolly rhinoceros, *Coelodonta thibetana*, we proposed an “out of Tibet” hypothesis postulating that the high Tibetan Plateau was a cradle of evolution for cold-loving Ice Age mammals (Deng et al., 2011). We have subsequently expanded this idea to include the big cats *Panthera blytheae* (Tseng et al., 2013b), the running hyena *Chasmaporthetes gangsriensis* (Tseng et al., 2013a), and the arctic fox *Vulpes* new species (Wang et al., in review). To these, we now add a hypercarnivorous canid, *Sinicuon cf. Sinicuon dubius*, from Zanda Basin, southern Tibet (Fig. 1).

The new Tibetan record predates all known occurrences of this taxon in Eurasia, and seems to suggest an “out of Tibet” scenario. Morphologically the various lineages of *Xenocyon* and *Sinicuon* are transitional to the modern hunting dogs, the Asian dhole *Cuon* and the African painted dog *Lycaon*. If *Sinicuon* is indeed ancestral to these living hypercarnivores, then the “out of Tibet” hypothesis can also be expanded to forms in warmer climates in South Asia and Africa.

2. Materials and method

Our usage of Plio-Pleistocene boundary follows the recent decision by the International Commission on Stratigraphy at 2.6 Ma (Gibbard et al., 2010; Pillans and Gibbard, 2012).

Abbreviations: F:AM, Frick Collection, American Museum of Natural History, New York; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

3. Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Family Canidae Fischer von Waldheim, 1817
Subfamily Caninae Fischer von Waldheim, 1817
Tribe Canini Fischer von Waldheim, 1817
Subtribe Canina Fischer von Waldheim, 1817
*Sinicuon* Kretzoi, 1941
Sinicuon cf. S. dubius (Teilhard de Chardin, 1940)
Xenocyon sp.: Wang et al., 2013a:93
Xenocyon: Wang et al., 2013b:234

Referred specimen. IVPP V18925, left ramal fragment with m1 and m2 alveolus, from IVPP locality ZD1205, 2 km north of the village of Dongsha, N31°19′29.77″ E79°54′30.1″, elevation 4045 m a.s.l., Zanda Basin in Zanda County, Ali District, Tibetan Autonomous Region, China; correlated to 3.81–3.42 Ma (see below) in the Geomagnetic Polarity Time Scale. IVPP locality ZD1205 is close to the boundary between Gaozhuangshan-Mazegouan Chinese land mammal stage/age (Qiu et al., 2013); collected by Xiaoming Wang on July 6, 2012.

Stratigraphic and age relationship. Because IVPP V18925 is clearly a reworked specimen secondarily deposited within Quaternary alluvium, it is a matter of some importance to document in detail the stratigraphic relationships. IVPP ZD1205 locality is located in the southeastern Zanda Basin, about 2 km north of the village of Dongsha, and is at the edge of a large alluvium deposit of presumably Quaternary age (younger than 0.5 Ma). The Mio-Pliocene Zanda Formation was cut into a broad valley (Fig. 2), which was filled with Quaternary alluvial gravels and finer sediments from nearby sources. This alluvium was itself being cut by a modern seasonal braided stream, sourced from the Himalaya, which flows northward (Fig. 2). IVPP locality ZD1205 is within a small tongue of the Quaternary alluvium, extending southeastward, that cuts into the Zanda Formation siltstone next to a small exposure of the basement rock (Fig. 3). The basement is composed of serpentines, schist, and quartz veins.

Within this small tongue, interbedded gravels and siltstones form the top 5 m of the Quaternary alluvium, which is underlain by a sequence of dark gray coarse gravels of approximately 20–30 m thick (Fig. 3A). IVPP locality ZD1205 is within the upper buff interbedded silt and gravel layer, about 2 m above the dark gray gravel unit (Fig. 3A and B). Gravels consist of mostly dark clasts of basement rocks that are poorly sorted, poorly rounded, and matrix supported. The light buff colored matrix is largely consisted of eroded siltstones from the Zanda Formation in the surrounding hills. Both gravels and matrix suggest a nearby source.

Although IVPP ZD1205 locality was clearly within the Quaternary alluvium, we think the canid specimen was reworked from the surrounding hills of Zanda Formation for the following three reasons: 1, the geometry of the alluvial cover is controlled by the local eroded hills of the Zanda Formation sediments (Fig. 2) such that the only possible source of the Quaternary alluvium is nearby hills; 2, both the matrix (eroded Zanda Formation siltstones) and the gravel clasts (eroded basement rocks) suggest local, nearby sources, probably no more than a few meters to a few hundred meters in transport distance; 3, a partial cheek tooth of Hipparion (probably Hipparion zandaense) (Deng et al., 2012; Wang et al., 2013a), IVPP V18926 (Fig. 4A and B), was also found in the top alluvial beds (within the upper buff interbedded silt and gravel layer); its preservation of strongly permineralized enamel and dentine with dark, rust-iron colored stains is very similar to that on IVPP V18925; the three-toed horse is not known to occur above Pliocene sediments, (within the upper buff interbedded silt and gravel layer); its presence in the IVPP locality ZD1205 is 4045 m a.s.l. For the flat-lying Zanda Formation, this means IVPP V18925 could not have been eroded from beds below the level of the Zanda Formation. The upper limit of the local Zanda Formation as a source for ZD1205 sediments is more conjectural. Although the local topographic highs (ridges surrounding the local basin) can be as high as 4279 m to the southeast of ZD1205, there is reason to believe that IVPP V18925 was from somewhere much closer, i.e., from an original horizon of much lower relative elevation, because of the pristine condition of the tooth and fragile nature of the lower jaw, which probably did not undergo long distance transport. Assuming a less than 50 m drop in elevation during the erosion and transport process, i.e., less than 300 m of horizontal transport from nearest hills with elevation of about 4100 m, IVPP V18925 was thus estimated to come from the 4045–4095 m level of the local Zanda Formation. The assumption of less than 50 m vertical drop in surface transport before re-burial of the specimen is justified given our frequent field observations that most fossils from the Zanda Formation are destroyed within a few meters of their original points of erosion, and that the poorly preserved Hipparion cheek tooth (IVPP V18926; Fig. 4A and B) from IVPP ZD1206 locality was horizontally transported by at least 200 m from the nearest edge of the Quaternary alluvium. Using the same correlation scheme as in Wang et al. (2013a), the above estimates translate to approximately the 469–525 m level of the South Zanda section by Saylor et al. (2010) that correspond to the middle part of C2Ar to the middle of C2An.3n of the Geomagnetic Polarity Time Scale (GPSTS); the estimated age of 3.8–3.4 Ma in the ATNTS2012 scale in Hilgen et al. (2012), middle Pliocene. The fact that the youngest in situ Hipparion in Zanda Formation is 3.36 Ma (Wang et al., 2013a) is also consistent with the above age estimates.

Description (Fig. 4C–E; Table 1). Represented by a single jaw fragment, this specimen is nonetheless highly distinct in its very hypercarnivorous lower first molar. The horizontal ramus does not preserve the ventral border, and the jaw depth cannot be observed. The perfectly preserved m1 is the most diagnostic tooth for this canid. The hypercarnivorous characters are shown in its elongated, narrow, sharply bladed trigonid that are mainly formed by a tall-crowned paraconid-protoconid blade. The metaconid is much reduced, with its apex barely above the hypocoonid. There is a distinct ridge at the posterior mediast of the trigonid leading down from the tip of the protoconid to the metaconid. The talonid is narrow and tapers posteriorly. The hypocoonid is almost centrally located as the only cusp in the talonid, flanked medially by a low and narrow cingulum that runs along much of the length of the talonid. A conical entoconid is absent, although it is conceivable that the lingual cingulum may potentially represent a reduced remnant of this cusp.

Table 1

| Dental measurements (in mm) of Sinicuon dubius and Xenocyon lycaonoides. Measurements for m1 length and width of Nihewan specimens are from Hu (2011) and Tong et al. (2012) and the trigonid length is by the authors; those from Yunxian are from Echassoux et al. (2008). |
|-----------------|-----------------|-----------------|-----------------|
|                | m1 length  | m1 width | m1 Trigonid length |
| Zanda Basin, Tibet | IVPP V18925 | 22.5 | 8.4 | 16.1 |
| Huuy (Zhoukoudian locality 18) | Uncatalogued | 26.5 | 9.5 | |
| Nihewan (Shanshenmaozui locality) | | | | |
| IVPP V17755.05 | 24.9 | 10.3 | 17.1 |
| IVPP V17755.04 | 25.5 | 10.4 | 18.7 |
| IVPP V17755.03 | 24.8 | 10.5 | 18.4 |
| IVPP V17755.21 | 27.7 | 10.6 | 20.0 |
| IVPP V17755.06 | 25.3 | 10.1 | 17.7 |
| IVPP V17755.10 | 24.7 | 9.6 | 17.0 |
| Yunxian | | | | |
| Yunxian 743-326 | 22.5 | 9.3 | |
| Yunxian 743-274 | 25.2 | 9.8 | |
| Yunxian 743-265 | 25.5 | 9.9 | |
| Yunxian 743-260 | 24.0 | 9.2 | |
| Yunxian 743-258 | 24.0 | 9.1 | |
Fig. 1. Map of Zanda Basin and fossil canid locality (black star) described in this study, modified from Wang et al. (2013a).

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The m2 is represented by its double-rooted alveoli, which suggest a reduced size compared to those in Canis. Presence or absence of an m3 cannot be ascertained because of the damage to bones behind the m2.

Taxonomic remarks. Taxonomic status of large hypercarnivorous canids of Eurasia and Africa is much debated. Fossils with various development of trenchant lower carnassials and loss of digits span the entire taxonomic spectrum of hypercarnivorous canids: Xenocyon (Kretzoi, 1938; Musil, 1972; Schütt, 1973; Moulle et al., 2006; Echassoux et al., 2008; Tedford et al., 2009; Hartstone-Rose et al., 2010), Sinicuon (Kretzoi, 1941; Qiu et al., 2004), Lycaon (Martínez-Navarro and Rook, 2003; Madurell-Malapeira et al., 2013), Cuon (Pei, 1939, 1987; Teilhard de Chardin, 1940; Baryshnikov, 1995, 1996), Canis (Hong Kong, 2002), or a subgenus Canis (Xenocyon) (Rook, 1994; Sotnikova, 2001; Sotnikova and Rook, 2010). Not surprisingly, each of the above authors has their own notions of relationships, or lack thereof, of the fossil taxa with the living Asian hunting dog (Dhole) Cuon and/or African hunting dog Lycaon, with no convergence of views in sight. While we cannot hope to settle matters with our limited material in hand, we only note that recent evidence from South Africa suggested that a chronospecies progression from Eurasian species to the African hunting dogs, as suggested by Martinez-Navarro and Rook (2003), is perhaps not so simple, as dental and limb structures were apparently evolved independently and are thus difficult to reconcile (Hartstone-Rose et al., 2010). In the Cuon lineage, geographic distribution alone can also mislead because an apparently true dhole, Cuon prisicus of European middle Pleistocene, co-exists with Xenocyon lycaonoides in Mosbach II, Germany (Thenius, 1954; Schütt, 1973). In their phylogenetic analysis, Tedford et al. (2009; Fig. 65) showed that a substantial morphological gap exists between modern African and Asian hunting dogs on the one hand and extinct forms in the Xenocyon grade on the other. This suggests that the transitional Xenocyon still serves a useful function of capturing the stage of morphological development in the Plio-Pleistocene hypercarnivores. A similar case also appears to be true for the genus Sinicuon.

In China, Pei (1939) first identified a dhole-like form ["?Cuon (Cyon) sp. (sp. nov.")] from Hujiu in Mentougou area (Mentougou, or Locality 18 of Zhoukoudian), about 25 km southwest of the (then) city limit of Beijing. A "lowermost Pleistocene" or "Villafranchian" age has been attributed to this site by Teilhard de Chardin (1938), Teilhard de Chardin (1940) erected a new species, Cuon dubius, based on these materials, recognizing, among other features, its unique combination of highly trenchant m1 talonid but with the presence of a metaconid; such a combination matches that of the Zanda form. As alluded to in his new name, Teilhard de Chardin did not really believe this species was ancestral to the dhole. Rather, he thought it probably belongs to an intermediate genus. Apparently unaware of Teilhard de Chardin’s 1940 paper, Kretzoi (1941) named a new genus and species, Sinicuon peii, based on Pei’s description. Kretzoi’s name did not gain currency in subsequent decades. In his description of the Liucheng Gigantopithecus Cave carnivores, Pei (1987) adopted the name C. dubius, ignoring Sinicuon. Recognizing the availability of Kretzoi’s name, Qiu et al. (2004) proposed to recombine Sinicuon with Teilhard de Chardin’s species with priority, i.e., S. dubius. They also referred to the latter a single left m1 from the Longdan loess deposits in Gansu Province, thus extending its age range into the early Pleistocene. However, Qiu et al. (2004) did not provide a generic diagnosis for Sinicuon with regard to Xenocyon, except by hinting that Xenocyon may possibly be related to Lycaon, despite their recognition that both Xenocyon and Sinicuon are transitional in morphology between Canis and modern hunting dogs. Qiu et al.’s new combination did not gain immediate acceptance, either. Following Schütt (1973), who preferred a more strict definition of Cuon without an m3, Tedford et al. (2009) placed the Hujiu form in Xenocyon dubius. Similarly, a large sample of X. dubius was recently recovered from the early Pleistocene (~1 Ma~800 ka) hominine-bearing Yunnan Man site in Hubei Province (Echassoux et al., 2008). The French
authors chose to use the genus *Xenocyon* despite their proposed ancestral relationship to the extant *Cuon* because of its possession of a metacarpal I.

To further complicate matters, Tedford et al. (2009:152) thought that by middle Pleistocene *X. lycaonoides* was present throughout Eurasia and occasionally, North America, although they did not list in detail East Asian occurrences. For example, a large series of individuals from the Shanshenmiaozui Site (Nihewan Basin) Tong et al. (2012), referred to *Canis chihliensis* (Teilhard de Chardin and Piveteau, 1930), is rather similar to *X. lycaonoides* described by Sotnikova (2001), Brugal and Boudadi-Maligne (2011) and Petrucci et al. (2012) provide recent summaries of European forms of *Cuon*. The critical question is therefore whether or not one can distinguish the *Cuon* clade among the earliest East Asian hypercarnivorous forms. If the answer is yes, then genus *Sinicuon* would serve as its earliest transitional form toward the *Cuon* clade.

The Zanda form shows tendencies toward a *Cuon*-like morphology, such as the nearly complete absence of entoconid and

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*Fig. 3. A, photograph of IVPP ZD1205 locality area, looking southeast along a small wash leading toward basement, showing contact relationships of basement rock, siltstones from Zanda Formation, and Quaternary alluvium (upper and lower units); location of fossil site (white arrow) is hidden from view by bluff. B, schematic stratigraphic profile X-Y (see Fig. 2 for location); vertically exaggerated; although fossils within the Quaternary alluvium are secondarily deposited, the only source rock where the fossils must have been reworked from is the Pliocene Zanda Formation.*
4. Zoogeographic comments

In a separate report, we documented a new fox from the Zanda Basin that is closely related to the modern arctic fox Vulpes lagopus (Wang et al., in review). Discovery of two hypercarnivorous canids in the Pliocene of high Tibet, well before their records elsewhere in northern Eurasia, may have ecologic and environmental implications. Modern terrestrial carnivorans in the arctic regions, such as the arctic fox, grey wolf, and polar bear, subsist almost exclusively on a carnivorous diet (e.g., Mech, 1974; DeMaster and Stirling, 1981; Audet et al., 2002). Such a highly predatory life style seems likely a consequence of availability of food resources, especially during the cold winters, and energetic requirements in freezing temperatures. It is thus of interest to speculate that the predominance of predatory canids in the Pliocene of Tibet may also be related to wintering in extreme coldness. The fact that Tibetan forms predate records elsewhere further lends support for the “Out-of-Tibet” hypothesis (Deng et al., 2011), i.e., earlier and more primitive forms in high Tibet being the ancestral stock, at a time when high arctic regions was much warmer (Ballantyne et al., 2010; Csank et al., 2011; Brigham-Grette et al., 2013), that subsequently gave rise to Ice Age descendants in northern Eurasia.

Recent molecular studies placed Cuon and Lycaon near the base of the Canis clade (Lindblad-Toh et al., 2005), in contrast to morphological analysis suggesting that hypercarnivorous forms are at the terminal end of the canine phylogeny (Tedford et al., 2009). If the molecular relationship is correct, then records of Cuon and Lycaon are expected to be at least as old as, if not older than, that of Canis. The arrival of large wolves (genus Canis) in Europe is termed the “wolf event” (Azzariol, 1983). Although records of early wolves have been pushed back slightly (Sardella and Palombo, 2007; Martínez-Navarro et al., 2009; Rook and Martínez-Navarro, 2010), the wolf event is essentially confined to the early Pleistocene (late Pliocene before recent redefinition; see Gibbard et al., 2010). The hypercarnivorous Sinicuon is more derived dentally and thus far its records tend to postdate the appearance of Canis. Our new Tibetan record demonstrates that hypercarnivorous canids may have predated the genus Canis.

Our Himalaya record thus shed new light not only in its highly hypercarnivorous morphology but also in its much older age than the previous known range. Our earlier Tibetan record is consistent with the “out of Tibet” hypothesis (Deng et al., 2011). Morphologically the various lineages of Xenocyon and Sinicuon are transitional to the modern hunting dogs, i.e., the Asian dhole Cuon and the African painted dog Lycaon. If Sinicuon is indeed ancestral to these

![Fig. 4. A, lateral and B, occlusal views of Hipparion zandaense, IVPP V18926 from locality ZD1206; C, medial, D, lateral, and E, occlusal (in stereo) views of Sinicuon cf. S. dubius, IVPP V18925 from locality ZD1205. Scales are in mm.](image-url)
living hypercarnivores, then the “out of Tibet” concept can also be expanded to megafaunas in warmer climates in South Asia.

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