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Pliocene bone-cracking Hyaeninae (Carnivora, Mammalia) from the Zanda Basin, Tibet Autonomous Region, China

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We dedicate this paper to Yuki Tomida, whose welcomed company in our fieldwork in Neogene localities of northern China has produced long-lasting memories of an enthusiastic and always curious mind at work.

The Zanda Basin in the western Tibet Autonomous Region, China, produces fossils of Miocene–Pleistocene age. Proximity of the basin to the Himalaya Range makes Zanda an important region for understanding vertebrate evolution and dispersal in and around the Tibetan Plateau. Five field seasons of prospecting in the basin have resulted in a rich collection of fossil mammals, with highest abundance and taxonomic richness in the Pliocene section of the Zanda Formation. In this report, we describe the first Tibetan Plateau record of the bone-cracking hyaenine carnivoran *Pliocrocota perrieri* from early Pliocene (4.1 Ma) deposits in Zanda. The Zanda *Pliocrocota* specimen is the smallest known *Pliocrocota* in China. In both morphology and size, it is similar to other early occurrences of *Pliocrocota* in Spain and northern China. Materials from Zanda and Yushe represent the earliest and least robust Asian specimens of a highly variable Pliocene hyaenid species, and indicate that *Pliocrocota* were already widespread across diverse environments at their first appearance. The presence of two fossil hyaenid species along with at least three canids and one felid in the Plio-Pleistocene Zanda fauna indicates a less deteriorated large predator guild in the Himalayan foothills compared to extant ecological communities in western Tibet.

Keywords: Pliocene; mammals; fossil; Himalaya; Carnivora

1. Introduction

Members of the carnivoran family Hyaenidae were distributed throughout the Neogene of Africa, Eurasia and North America (Werdelin and Solounias 1991). The early hyaenid species were mongoose- and jackal-like, whereas later species exhibit the more typical features for hypercarnivory and bone-cracking seen in the extant sub-Saharan African spotted hyenas (Werdelin and Solounias 1996). Living bone-cracking hyenas are highly adaptable predators that are found from a wide range of habitats, including coastal to high mountain environments, with both open- and closed-vegetation coverage (Kruuk 1972). In this study, we report the first occurrence of the late Neogene bone-cracking hyaenid, *Pliocrocota perrieri*, from the Tibetan Plateau, with a comparison to other early occurrences of this species in Eurasia.

Although the Tibetan Plateau has been shown to constitute a major barrier to Neogene mammal dispersal, as indicated by the presence of endemic bovids and carnivorans through the Neogene (Wang, Wang, et al., *in press*), a significant representation of different hyaenid ecomorphs is shared by the plateau and the rest of Eurasia.

The scansorial, mongoose-like early hyaenid genera such as *Plioviverrops* and *Protictitherium* are found from early and middle Miocene sites around the Tibetan Plateau, but not within (Wang 2004). The earliest hyaenid occurrences within the Tibetan Plateau were wolf-like *ictitheres* (Wang et al. 2007). By the time the cursorial *Chasmaporthetes* clade and the more robust bone-cracking hyaenine clade evolved, both dispersed to the Tibetan Plateau shortly after. The hyaenine *Adcrocuta eximia* is known from the early late Miocene of the Qaidam Basin (Wang et al. 2007), and the cursorial *Chasmaporthetes gangsiensis* is known from the Pliocene of the Zanda Basin (Tseng et al. 2013). The *Pliocrocota* specimens from Zanda Basin described herein represent the only late Cenozoic occurrence of large bone-cracking hyaenids on the Tibetan Plateau; no Pleistocene *Pachycrocota* or *Crocota* are yet known from the Plateau, although their fossil records are widespread in the rest of Eurasia from England to Southeast Asia (Werdelin and Solounias 1991).

The Zanda Basin contains Mio-Pleistocene lacustrine and fluvial deposits that preserve fossil fishes, birds and mammals (Wang et al. 2013). Many elements of the faunas

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are currently under study, but the carnivorans are by far the best known thus far (Figure 1). Recently published descriptions include the oldest known pantherine felid *Panthera blytheae* (Tseng et al. 2014), a putative arctic fox relative *Vulpes qiuzhudingi* (Wang et al. 2014), a hunting-dog-like hypercarnivorous canid *Sinicuon* cf. *Sinicuon dubius* (Wang, Li, et al., 2015) and the cursorial hyaenid *Chasmaporthetes gangsriensis* (Tseng et al. 2013). In addition, the most ancestral woolly rhino, *Coelodonta thibetana*, was also described from Zanda and forms the first of a series of fossil evidence favouring the 'out of Tibet' hypothesis (Deng et al. 2011; Wang, Wang, et al., in press). Description of the micromammals collected from five field seasons in Zanda Basin is underway, and preliminarily indicates four species of lagomorphs and nine species of rodents. By comparison, modern-day western Tibet has three canids and two felid species, and lacks hyaenids, although the striped hyena is still found to the west and south of the Himalayan Range (Feng et al. 1984).

2. Materials and methods

Measurements on the newly collected specimens of *Pliocrocota perrieri* were taken using vernier calipers to

the nearest 0.02 mm. Measurements of other *Pliocrocota* occurrences included for comparison were taken directly from the publications referenced. Log ratio diagrams were constructed as in Werdelin (1988b).

3. Systematic paleontology

Class **Mammalia** Linnaeus, 1758

Infraclass **Eutheria** Huxley, 1880

Order **Carnivora** Bowdich, 1821

Family **Hyaenidae** Gray, 1869

Genus ***Pliocrocota*** Kretzoi, 1938

Pliocrocota perrieri (Croizet and Jobert, 1828)

(Figures 3 and 4, Table 1)

Diagnosis: p1 absent, unlike *Adcrocuta*; earlier occurrences of *Pliocrocota* retain m1 metaconid, similar to *Adcrocuta* where the m1 metaconid is variably present; p3 and p4 anterior accessory cusps lingually deflected, unlike aligned cusps down the midline of the tooth in *Chasmaporthetes*; m1 paraconid swollen, longer than protoconid and is the same height as the protoconid, unlike in *ictitheres* which have higher crowned m1 protoconid

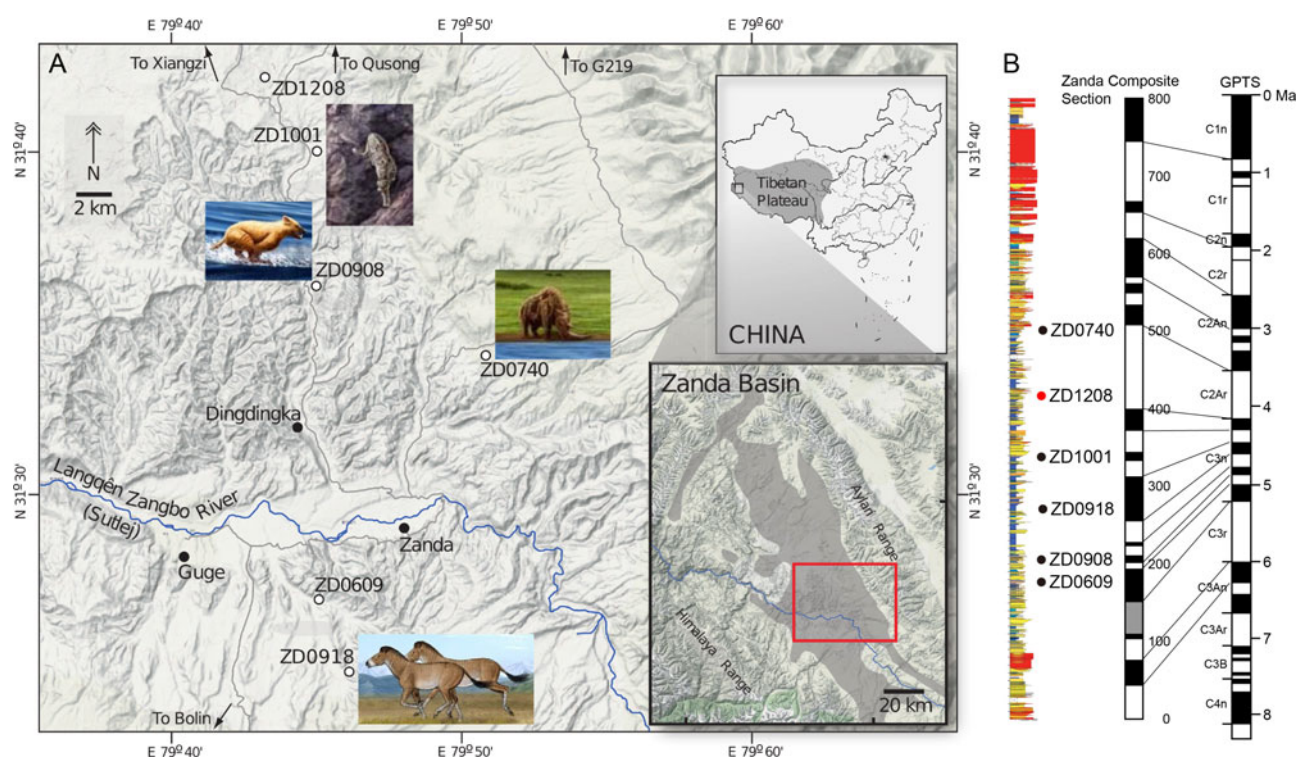


Figure 1. (Colour online) (A) Locality map and (B) stratigraphic column of Zanda Basin, showing IVPP locality ZD1208, where the presently described specimens were discovered, relative to type localities of described mammal fauna nearby, local towns and topological features: *Panthera blytheae* and *Vulpes qiuzhudingi* from ZD1001 (Tseng et al. 2014; Wang et al. 2014), *Chasmaporthetes gangsriensis* from ZD0908 (Tseng et al. 2013), *Coelodonta thibetana* from ZD0740 (Deng et al. 2011) and *Hipparion zandaense* from ZD0918 (Deng et al. 2012). ZD0609 is a screen-washed micromammal locality. Artwork by Julie Selan. Stratigraphic column modified from Wang et al. (2013).

Table 1. Linear measurements of lower dentition of *Pliocrocota perrieri* from the Zanda Basin (IVPP V20801) and several early occurrences of Eurasian *Pliocrocota perrieri* specimens.

	Zanda	Malancun		Wangjiagou	Malancun		Xiachuang	Changwakou	Perpignan	La Calera II
	IVPP V20801	IVPP V7285.rt	IVPP V7285.lt	IVPP V7289	IVPP V7290.rt	IVPP V7290.lt	F:AM (n = 5)	F:AM (n = 8)	Holotype	Multiple
c.l	14.7	17.3	17.3	17.8	16.9	17.3	17.5	17.16	16.2	16.4
c.w	11.62	13.1	13.2	14	13.6	14	14.3	12.1	12.5	11
p2.l	15.9	15.9	16.1	15.4	15.2	14.7	17.1	15.5	16.3	16.8
p2.w	9.5	10	10	9.9	11.1	11.1	13	10.41	9.4	10.5
p3.l	19	20.6	20.1	21.2	20.1	20.3	21.5	19.57	20	–
p3.w	11.38	13.3	13.3	13	14	14.1	15.3	13.4	13	–
p4.l	20.64	21.9	21.8	22.4	22.8	22.6	24.05	22.7	24	23.2
p4.w	12.06	13.3	13.3	13.3	14.5	14.6	15.4	13.26	13	13
m1.l	23.3	–	25.9	25.2	24.5	24.3	26.75	24.07	24.7	23.1
m1.w	11.2	12.2	–	12	12.9	12.8	14.3	12.37	12.6	10.6

Note: Comparative measurements for European and F:AM specimens were taken from Howell and Petter (1980), measurements for other specimens were taken from Qiu (1987): c, lower canine; p, lower premolar; m, lower molar; l, length; w, width; rt, right side; lt, left side; F:AM, Frick Fossil Mammal Collection, American Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, China.

compared to paraconid; p3 and p4 rhomboid in outline, not greatly inflated as in *Pachycrocota* and *Crocota*.

Referred material: IVPP V20801, right partial dentary with c1, p2-m1. IVPP V20802, right partial I3. IVPP V20803, left ramus fragment with p2 roots and p3.

Locality and age: IVPP locality ZD1208, Zanda Basin, Tibet Autonomous Region, China. ZD1208 was initially discovered by one of us (G. Xie) on 7 July 2012 within a yellow sandstone lens, presumably sourced from a nearby basement exposure to the west. Sediments are mostly weathered into loose sand, and subsequent dry screening of the site has yielded a rich collection of fossil mammals (Figure 2). The locality has an elevation of 4195 m above sea level and has been correlated with the geomagnetic polarity time scale chron C2Ar, with an age of ~4.1 Ma (Figure 1(B); Wang et al. 2013).

Description: IVPP V20801 is of a partial right dentary missing the portion posterior to m1, and the area around

the mental foramen. The anterodorsal half of the mandibular symphysis is preserved, exhibiting a highly rugose articular surface with interdigitations, and trending 45° overall relative to the long axis of the ramus (Figure 3 (A)). The preserved section of the ramus is deepest below m1, measuring 38 mm. All of the preserved teeth show moderate to heavy wear, and the premolars and molar exhibit strong surface crenulations typical of bone-cracking hyaenids (Stefen and Rensberger 2002). The lower canine exhibits a large elongate patch of medial wear facet where it would contact the upper canine; the canine crown has fresh breaking edges, indicating that it was broken post-mortem, perhaps from post-fossilisation weathering. Both p2 and p3 exhibit moderate wear on the occlusal surface of the main cusp, and light wear on the posterior accessory cusps; no wear is present on the anterior accessory cusp of either p2 or p3, and compared to the posterior accessory cusps, the anterior ones are smaller

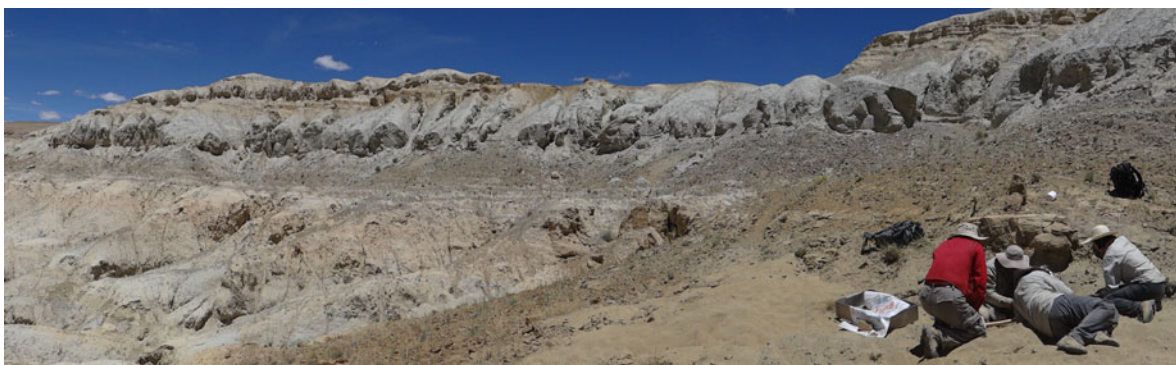


Figure 2. (Colour online) Panoramic view of IVPP ZD1208 locality with field team (at right-hand corner) collecting fossils. Weathered sandstone in the foreground is rich with fossil mammals. Fossils were collected by both hand-picking and dry screening. Photograph by Xiaoming Wang on 8 July 2012.

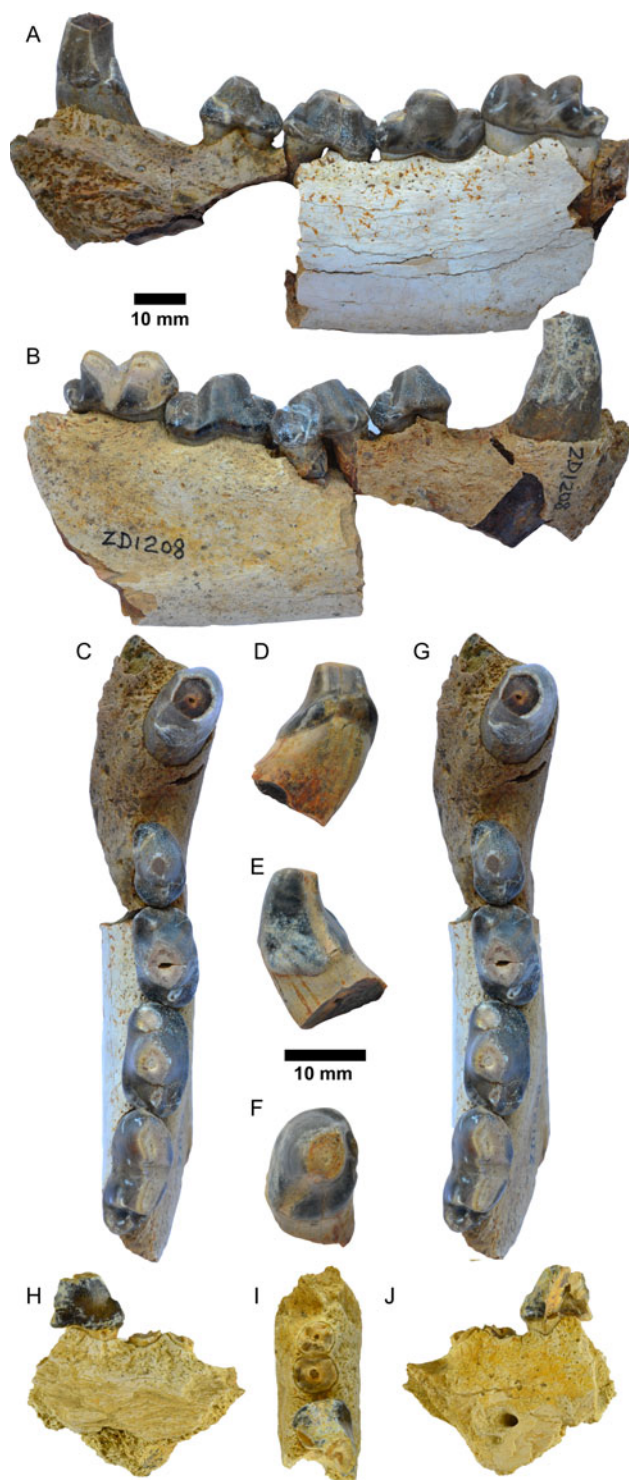


Figure 3. (Colour online) *Pliocrocota perrieri* from Zanda Basin, Tibet Autonomous Region, China. (A) Medial view; (B) lateral view; (C) occlusal view of stereopair left of IVPP V20801, partial lower right dentary with canine, p2-m1; (D) medial view; (E) lateral view; (F) occlusal view of IVPP V20802, partial upper right I3; (G) occlusal view of stereopair right of IVPP V20801; (H) medial view; (I) occlusal view and (J) lateral view of IVPP V20803, left ramus fragment with left p2 roots and partial p3. Top scale bar is for A-C, G. Bottom scale bar for the rest.

and more pressed into the base of the main cusp. The m1 carnassial has a heavily worn shearing surface on the trigonid, with exposure of the dentin all the way from the top to the base of the crown. There is a single, centrally positioned hypoconid on the m1 talonid basin, which is reduced and forms only a minor portion of the total length of the tooth. A continuous but cusped cingulum surrounds the centrally positioned hypoconid. A small metaconid, about the same size as the hypoconid, is present at the posterolingual corner of the protoconid (Figure 3(C),(G)).

The isolated right I3 represented by IVPP V20802 is moderately worn, with a longitudinal wear facet on the posterolabial face of the crown, where the tooth would have occluded with the medial edge of the lower right canine (Figure 3(E)). Both the characteristic wear and the robust appearance of the tooth indicate that it comes from a hyaenid, and given the close proximity of the find to IVPP V20801 and the same size range, we referred this specimen also to *Pliocrocota perrieri*.

A third specimen (IVPP V20803), that of a ramus fragment with p2 roots and p3, also exhibits morphology and size consistent with *Pliocrocota perrieri* (Figure 3(H)–(J)). The broken edges of the jaw fragments exhibit heavy pitting and flaking, indicating significant weathering prior to discovery. This specimen possibly belongs to the same individual as IVPP V20801. The fresh breaking edge at the p2 roots also indicates that tooth breakage occurred post-fossilisation, most likely from subsequent exposure and weathering. A large mental foramen is present on the bone fragment, directly under the position of the posterior p2 root (Figure 3(J)). A smaller, secondary mental foramen is located ventral and anterior to the larger one. The robustness of the jaw fragment, together with the lack of p1 indicated by a large diastema anterior to the p2 roots, are consistent with assignment to *Pliocrocota*.

Comparison: Werdelin and Solounias (1991) grouped specimens previously referred to *Pliocrocota pyrenaica* and *Pliocrocota perrieri* together as *Pliocrocota perrieri* based on a more or less continuous range of metric variations in tooth measurements across the Eurasian samples. We follow their opinion in this study because we also fail to see significant morphological differences that would justify keeping the two samples as distinct species. In fact, the observed variations could be attributed to a combination of geologic age and geographic differences in a variable species sample (Werdelin and Solounias 1991). We therefore restrict our comparisons to both the geologically older and smaller-sized specimens in our comparison to *Pliocrocota perrieri* from Zanda (Figures 4 and 5).

The holotype of *Pliocrocota pyrenaica* (= *Pliocrocota perrieri*) described from Serrat d'En Vacquer (in Perpignan) by Deperet (1890) serves as the standard in our metric comparisons (Figure 4). Compared to the Serrat d'En Vacquer specimen, IVPP V20801 has smaller teeth

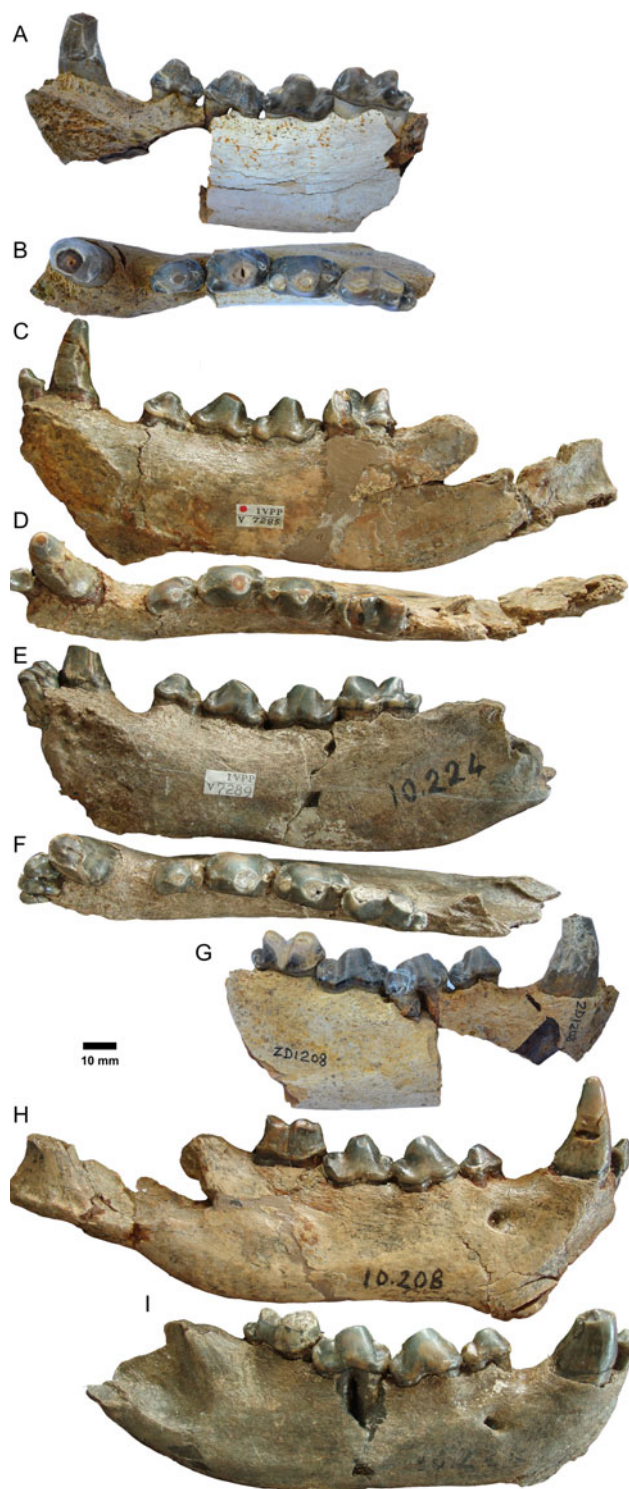


Figure 4. (Colour online) Lower dentitions of the earliest *Pliocrocota perrieri* specimens from China. (A) Medial view; (B) occlusal view of IVPP V20801 (Zanda Basin); (C) medial view; (D) occlusal view of IVPP V7285 (Damalan/Malancun, Yushe Basin); (E) medial view; (F) occlusal view of IVPP V7289 (Wangjiagou, Yushe Basin); (G) lateral view of IVPP V20801; (H) lateral view of IVPP V7285; (I) lateral view of IVPP V7289.

overall, with the exception of a similarly sized p2. This difference is also true between IVPP V20801 and Chinese *Pliocrocota perrieri* samples from Yushe Basin. The larger-sized *Pliocrocota* samples compared generally tend to increase cheek tooth width relative to its length, and in this respect the Zanda *Pliocrocota* is less derived given its relatively narrow premolars and molar. In addition, earlier *Pliocrocota* specimens also tend to exhibit less reduced anterior and posterior accessory cusps compared to younger, larger specimens. The relatively wider cusps and smaller accessory cusps can be seen even by comparing two specimens from the same sub-basin at Yushe (Figure 4: Malancun specimens; also see Qiu 1987).

4. Discussion

The binning of a geographically widespread Eurasian sample of *Pliocrocota*-like specimens by Werdelin and Solounias (1991) into *Pliocrocota perrieri* was based on the intraspecific differences observed in other fossil hyaenid genera for which large samples were available (Werdelin 1988a; Werdelin and Solounias 1990). Given the limited material described in this new study, there are no significant new data to reject or support their interpretation. Our own analyses of metric characters among samples of *Pliocrocota* (*sensu lato*) in China also show that there is no obvious separation of species-level differences that cannot be attributed to geologic age differences, at least based on the lower dentition (Figures 4 and 5). However, we note that alternative interpretations for Eurasian specimens previously assigned to *Pliocrocota perrieri* and *Pliocrocota pyrenaica* exist (Howell and Petter 1980), particularly pertaining to Chinese specimens which have been classified either as *Pachycrocota*/*Pliohyaena* (Qiu 1987; Qiu et al. 2004) or *Pliocrocota* (Qiu et al. 2013). Therefore, it is important in the discussion of taxonomic assignment of *Pliocrocota*-like specimens to provide comparisons to specific specimens (e.g. Figure 4), so the morphological concept with which new specimens are referred to existing species is as unambiguous as possible.

Metrically, the Zanda *Pliocrocota* has a relatively smaller canine compared to *Pliocrocota* fossils from other Chinese localities. The Zanda occurrence is also among the smallest Chinese *Pliocrocota* in overall size. Other than that, the relative dimensions of the cheek teeth in the Zanda *Pliocrocota* are similar to samples from the Yushe Basin (Qiu 1987) and from 'Chang Wa Kou' (Howell and Petter 1980; Figures 4 and 5). In contrast, the sample from 'Hsia Chwang' (Pinyin: Xiachuang according to Tedford et al. 2013) is larger in overall size than the other Chinese *Pliocrocota* occurrences, in addition the Hsia Chwang specimens tend to have relatively widened teeth (Figure 5).

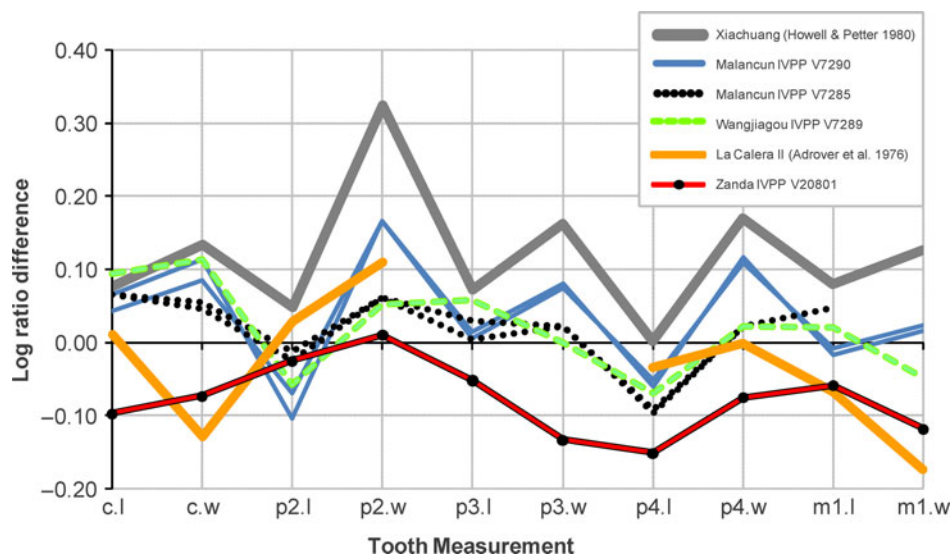


Figure 5. (Colour online) Log ratio diagram of the earliest *Pliocrocota perrieri* specimens relative to the specimen of *Pliocrocota perrieri* (= holotype of *Pliocrocota pyrenaica*) from Perpignan (Serrat d'en Vacquer). Abbreviations as in Table 1.

These differences may be attributed to populational variation (Werdelin and Solounias 1991), differences in geologic age, or more likely a combination of both. An explanation using population variation requires larger samples than is currently available; similarly, the lack of well-constrained locality information in earlier Chinese fossil collections prevents more rigorous biostratigraphic analyses to be conducted (see Table 2). While it is true that geologically younger *Pliocrocota* specimens tend to have larger size and more widened teeth in the Chinese sample, such pattern is not consistent across other Eurasian samples. For example, geologically younger specimens in the Spanish localities La Puebla de Valverde and Villaroya are similar in size to the earliest occurrences in that region at La Calera and La Gloria. A review of size trends in *Pliocrocota* over time and geographic region is needed, but is beyond the scope of this study.

The hyaenines *Pliocrocota*, *Pachycrocota*, *Adrocota*, *Crocota*, *Hyaena* and *Parahyaena* are all considered to be specialised bone-cracking hypercarnivores in a previous ecomorphological classification of hyaenids (Werdelin and Solounias 1996). The occurrence of *Pliocrocota* in Zanda represents a new addition to this bone-cracking guild for the Tibetan Plateau. Previously, bone-cracking ecomorphs *Adrocota* are known from the late Miocene of the Qaidam Basin in the northern plateau (Wang et al. 2007) and perocrotid *Dinocrocota* from the late Miocene of Bulong Basin in eastern Tibet (Zheng 1980). The Pliocene occurrence of this hyaenid ecomorph indicates that the plateau continued to host faunas that supplied enough vertebrate prey for these large hypercarnivores through much of the late Neogene, even though no bone-cracking carnivorans are found there in recent times. The Zanda

Pliocrocota was also contemporaneous with a cursorial member of the Hyaenidae, *Chasmaporthetes* (Tseng et al. 2013), suggesting that Pliocene Zanda Basin was home to a more diverse and cosmopolitan (*Chasmaporthetes* and *Pliocrocota* both being very geographically widespread genera) carnivoran guild compared to the current lower diversity community, in which *Canis lupus* and *Panthera uncia* represent the largest living hypercarnivores there (Feng et al. 1984). Both occurrences of *Chasmaporthetes* and *Pliocrocota* in the Zanda Basin exhibit relatively large anterior premolars compared to other Eurasian specimens in the respective genera (Tseng et al. 2013, this paper), and such an 'under-differentiated' tooth row contrasts with the hypertrophied p3-p4 and reduced p2 in bone-cracking ecomorphs such as *Crocota*. Whether the retention of large p2 has any functional or palaeoecological significance will require further testing, but could be correlated with a relatively less-specialised niche within the bone-cracking ecomorphology.

The overall similarity in both morphology and dimensions of the Zanda *Pliocrocota perrieri* to the early Pliocene *Parahyaena howelli* from Kenya (Werdelin 2003; Werdelin and Manthi 2012) is new evidence supporting the old idea that *Pliocrocota perrieri* was ancestral to the extant brown hyena (*Parahyaena*) lineage (Howell and Pether 1980). Compared to the wide distribution of the *Crocota* lineage across the entire Old World during Quaternary times, those for *Parahyaena* were restricted to Africa, although their putative ancestral species *Pliocrocota perrieri* were similarly widespread in Eurasia as *Crocota*. Mechanisms behind such stark differences in zoogeographical evolution of two closely related bone-cracking hypercarnivores remain to be elucidated.

Table 2. Geographic and stratigraphic occurrence of *Pliocrocota perrieri*, localities compiled from Werdelin and Solounias (1991) and Turner et al. (2008).

Locality	Country	Age	MN13	MN14	MN15	MN16a	MN16b	MN17	MN18
Furninha	Portugal	Late Pleistocene/MN18							•
Mauer	Germany	0.5 Ma/MN18							•
Mosbach	Germany	Middle Pleistocene/MN17–18							•
Petralona	Greece	0.8 Ma/MN18							•
Olivola	Italy	1.8 Ma/MN18							•
Tasso	Italy	1.8 Ma/MN18							•
Seneze	France	2.21–2.09 Ma/MN18							•
Erpfinger Höhle	Germany	Pleistocene/MN18							•
Gerakarou	Greece	MN18							•
Hollabrunn	Austria	Mid/Late Pleistocene/MN17–18						•	•
La Puebla de Valverde	Spain	2.14–1.95 Ma/MN17–18						•	•
Haiyan, Yushe	China	2.5–2.2 Ma/MN17–18						•	•
Nihewan	China	MN17–18						•	•
Es-Taliens	France	Middle Pleistocene/MN17–18						•	•
L'Escafe	France	Middle Pleistocene/MN17–18						•	•
Lunel-Viel	France	Middle Pleistocene/MN17–18						•	•
Montmaurin	France	Middle Pleistocene/MN17–18						•	•
Montsaunes	France	Middle Pleistocene/MN17–18						•	•
Greusnach	Germany	Middle Pleistocene/MN17–18						•	•
Chilhac	France	2.375 Ma/MN17						•	
Pardines	France	MN17						•	
St Vallier	France	MN17						•	
Gundersheim	Germany	MN17						•	
Sesklon	Greece	MN17						•	
Tegelen	Netherlands	MN17						•	
Khapry	Russia	MN17						•	
Kuruksai	Tadjikistan	MN17						•	
Red Crag	England	Early Pleistocene/MN17						•	
Ahl al Oughlam	Marocco	2.5 Ma/MN16–17				•	•	•	
AinBrimba	Tunisia	~ 2.5 Ma/MN16–17				•	•	•	
Montopoli	Italy	2.588 Ma/MN16b				•	•	•	
El Rincon	Spain	2.7–2.6 Ma/MN16a-b				•	•	•	
Etouaires	France	2.78 Ma/MN16a				•	•	•	
Villaroya	Spain	3.04–2.58 Ma/MN16a				•	•	•	
Niuwagou	China	3.0 Ma/MN16				•	•	•	
Hajnacka	Czech	3.5–2.6 Ma/MN16a				•	•	•	
Zhaozhuang	China	3.5–3.0 Ma/MN16				•	•	•	
Zhangwagou	China	3.6–3.0 Ma/MN16				•	•	•	
Arde	France	MN16				•	•	•	
Gulyazi	Turkey	MN16				•	•	•	
Odessa Catacombs	Ukraine	MN16				•	•	•	
Viallete	France	3.8 Ma/MN15–16			•	•	•	•	
Layna	Spain	3.912 Ma/MN15			•	•	•	•	
Perpignan	France	MN15			•	•	•	•	
Xiachuang	China	Plio-Pleistocene/MN14–18		•	•	•	•	•	•
Yinjiao	China	'Pliocene'/MN14–16		•	•	•	•	•	•
Zanda ZD1208	China	4.1 Ma/MN14		•	•	•	•	•	•
La Calera II	Spain	4.186 Ma/MN14		•	•	•	•	•	•
La Gloria 4	Spain	4.186 Ma/MN14		•	•	•	•	•	•
Wangjiagou	China	5.0–4.5 Ma/MN14		•	•	•	•	•	•
Taoyang	China	5.6–5.0 Ma/MN13–14	•	•	•	•	•	•	•
Damalan	China	Unavailable							

Note: Bold values indicate locality described in this study. Darker shades in stratigraphic ranges indicate localities compared in the numerical analysis. Younger localities are at the top of the list, older localities at the bottom. Locality ages were taken from the literature (Thenius 1964; Savage and Curtis 1970; Kurtén and Werdelin 1988; Mourer-Chauvire 1989; Qiu and Qiu 1995; Steininger et al. 1996; Caloi and Palombo 1997; Geraads 1997; Turner and Anton 1997; Sotnikova et al. 2002; Van Couvering 2004; Fosse and Quiles 2005; Vislobokova 2005; Antón et al. 2006; Koufos 2006; Domingo et al. 2007; Rightmire 2007; Herrera 2008; Turner et al. 2008; Baryshnikov and Tsoukala 2010; Tedford et al. 2013; Wang et al. 2013; Nomade et al. 2014; Vinuesa et al. 2014).

Lastly, updated biostratigraphic ranges across Eurasia for *Pliocrocota* (Table 2), and incorporation of better stratigraphic correlation of classic localities in the Yushe Basin, Shanxi, indicate that the most ancestral population of *Pliocrocota* may be in China (Tedford et al. 2013). Although early Pliocene Spanish localities La Calera II and La Gloria 4 both produce *Pliocrocota*, those from Yushe localities predate them (Table 2). In addition, early *Pliocrocota* distribution was largely clustered within China, prior to appearing in Eurasian localities elsewhere (with the exception of Spain). Together with the earliest occurrence of the cursorial hyaenid *Chasmaporthetes* from Qingyang, China (Kurtén and Werdelin 1988), these evidence suggest China, and East Asia in general, as the starting point of dispersal and diversification for both *Pliocrocota* and *Chasmaporthetes*, a pair often found in sympatry across Eurasian Plio-Pleistocene localities (Turner et al. 2008). Additional tests of this biogeographic hypothesis require both better records of *Pliocrocota* in central Asia in order to understand possible routes of dispersal, as well as a more comprehensive review and study of all available Old World material to include yet unidentified or misidentified occurrences.

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Disclosure statement

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References

- Antón M, Turner A, Salesa MJ, Morales J. 2006. A complete skull of *Chasmaporthetes lunensis* (Carnivora, Hyaenidae) from the Spanish Pliocene site of La Puebla de Valverde (Teruel). *Estud geol (Madr.)*. 62:375–388.
- Baryshnikov G, Tsoukala E. 2010. New analysis of the Pleistocene carnivores from petralona cave (macedonia, greece) based on the collection of the Thessaloniki Aristotle University. *Geobios*. 43(4): 389–402, doi:10.1016/j.geobios.2010.01.003.
- Caloi L, Palombo M. 1997. Biochronology of large mammals in the early and middle Pleistocene of the Italian Peninsula. *Hystrix*. 9:3–12.
- Deng T, Li Q, Tseng ZJ, Takeuchi GT, Wang Y, Xie G, Wang S, Hou S, Wang X. 2012. Locomotive implication of a Pliocene three-toed horse skeleton from Tibet and its paleo-altimetry significance. *Proc Nat Acad Sci*. 109(19):7374–7378, doi:10.1073/pnas.1201052109.
- Deng T, Wang X, Fortelius M, Li Q, Wang Y, Tseng ZJ, Takeuchi GT, Saylor J, Sällä LK, Xie G. 2011. Out of Tibet: Pliocene woolly rhino suggests high-plateau origin of Ice Age megaherbivores. *Science*. 333(6047):1285–1288, doi:10.1126/science.1206594.
- Deperet CJ. 1890. Les animaux Pliocenes de Roussillon [The Pliocene animals of Roussillon]. *Mém Soc géol Fr*. 3:1–164.
- Domingo MS, Alberdi MT, Azanza B. 2007. A new quantitative biochronological ordination for the Upper Neogene mammalian localities of Spain. *Palaeogeogr Palaeoclimatol Palaeoecol*. 255(3–4): 361–376, doi:10.1016/j.palaeo.2007.08.004.
- Feng Z, Cai G, Zheng C. 1984. A checklist of the mammals of Xizang (Tibet). *Acta Theriologica Sinica*. 4:341–358.
- Fosse P, Quiles J. 2005. Tafonomía y arqueozoología comparadas de algunos yacimientos de los Pirineos franceses y de Cantabria [Comparisons of taphonomy and archaeozoology of some deposits of the French Pyrenees and Cantabria]. *Munibe (Antropología-Arkeología)*. 57:163–181.
- Geraads D. 1997. Carnivores du Pliocène Terminal de Ahl al Oughlam (Casablanca, Maroc). *Geobios*. 30(1):127–164, doi:10.1016/S0016-6995(97)80263-X.
- Herrera AA, ed. 2008. Vertebrados del Plioceno superior terminal en el suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas. Vol. 10. Madrid: Instituto Geológico y Minero de España.
- Howell FC, Pether G. 1980. The pachycrocuta and hyaena lineages (plio-pleistocene and extant species of the hyaenidae). Their relationships with miocene icittheres: palhyaena and hyaenictitherium. *Geobios*. 13(4):579–623, doi:10.1016/S0016-6995(80)80004-0.
- Koufos GD. 2006. The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. *Hellenic J Geosci*. 41:183–214.
- Kruuk H. 1972. The spotted hyena: a study of predation and social behavior. In: Shaller GB, editor. *Wildlife behavior and ecology series*. 335 p. Chicago, IL: The University of Chicago Press.
- Kurtén B, Werdelin L. 1988. A review of the genus *Chasmaporthetes* Hay, 1921 (Carnivora, Hyaenidae). *J Vert Paleontol*. 8:46–66.
- Mourer-Chauvire C. 1989. A peafowl from the Pliocene of Perpignan, France. *Palaeontology*. 32:439–446.
- Nomade S, Pastre JF, Guillou H, Faure M, Guérin C, Delson E, Debard E, Voinchet P, Messager E. 2014. 40Ar/39Ar constraints on some French landmark Late Pliocene to Early Pleistocene large mammalian paleofaunas: Paleoenvironmental and paleoecological implications. *Quat Geochronol*. 21:2–15, doi:10.1016/j.quageo.2012.12.006.
- Qiu Z-x. 1987. Die Hyaeniden aus dem Ruscium und Villafranchium Chinas [Ruscinian and Villafranchian hyaenids of China], *Münchner Geowissenschaftliche Abhandlungen Reihe A: Geologie und Paläontologie* [Munich Geoscience treatises Series A: Geology and Paleontology].
- Qiu Z, Deng T, Wang B. 2004. Early Pleistocene mammalian fauna from Longdan, Dongxiang, Gansu, China. *Palaeontol Sin Ser C*. 191: 1–198, with 39 plates.
- Qiu Z-x, Qiu Z-d. 1995. Chronological sequence and subdivision of Chinese Neogene mammalian faunas. *Palaeogeogr Palaeoclimatol Palaeoecol*. 116(1–2):41–70, doi:10.1016/0031-0182(94)00095-P.
- Qiu ZX, Qiu ZD, Deng T, Li CK, Zhang ZQ, Wang BY, Wang X. 2013. Chapter 1. Neogene land mammal stages/ages of China. In: Wang X, Flynn LJ, Fortelius M, editors. *Fossil mammals of Asia: neogene biostratigraphy and chronology*. New York, NY: Columbia University Press; p. 29–90.
- Rightmire GP. 2007. Chapter 12. Later Middle Pleistocene *Homo*. In: HENKE W, Tattersall I, editors. *Handbook of paleoanthropology*. New York, NY: Springer; p. 1695–1715.
- Savage DE, Curtis GH. 1970. The Villafranchian Stage-Age and its radiometric dating. *Geol Soc Am Spec Pap*. 124:207–231.
- Sotnikova MV, Baigusheva VS, Titov VV. 2002. Carnivores of the Khapry faunal assemblage and their stratigraphic implications. *Stratigr Geol Correlat*. 10:375–390.
- Stefen C, Rensberger JM. 2002. The specialized enamel structure of hyaenids (Mammalia, Hyaenidae): description and development within the lineage – including percrocutids. *Zoologische Abhandlungen*. 52:127–147.

- Steininger F, Berggren WA, Kent DV, Bernor RL, Sen S, Agustí J. 1996. Circum-Mediterranean Neogene (Miocene and Pliocene) marine-continental chronologic correlations of European mammal units. In: Bernor RL, Fahlbusch V, Mittmann H-W, editors. The evolution of western Eurasian Neogene mammal faunas. New York, NY: Columbia University Press.
- Tedford RH, Qiu ZX, Flynn LJ. 2013. Late Cenozoic Yushe Basin, Shanxi Province, China: geology and fossil mammals. New York, NY: Springer; p. 109.
- Thenius E. 1964. Über das Vorkommen von Streifenhyänen (Carnivora, Mammalia) im Pleistozän Niederösterreichs [On the occurrence of striped hyenas (Carnivora, Mammalia) in the Lower Pleistocene of Austria]. *Ann Naturhist Mus Wien*. 68:263–268.
- Tseng ZJ, Li Q, Wang X. 2013. A new cursorial hyaena from Tibet, and analysis of biostratigraphy, paleozoogeography, and dental morphology of chasmaporthetes (mammalia, carnivora). *J Vert Paleontol*. 33(6):1457–1471, doi:10.1080/02724634.2013.775142.
- Tseng ZJ, Wang X, Slater G, Takeuchi GT, Li Q, Liu J, Xie G. 2014. Himalayan fossils of the oldest known pantherine establish ancient origin of big cats. *Proc Roy Soc B Biol Sci*. 281(1774):20132686, doi:10.1098/rspb.2013.2686.
- Turner A, Anton M. 1997. The Big Cats and their fossil relatives. New York, NY: Columbia University Press.
- Turner A, Antón M, Werdelin L. 2008. Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios*. 41(5):677–687, doi:10.1016/j.geobios.2008.01.001.
- Van Couvering JA, ed. 2004. The Pleistocene Boundary and the beginning of the quaternary. Cambridge: Cambridge University Press.
- Vinuesa V, Madurell Malapeira J, Anson M, Alba DM. 2014. New cranial remains of *Pliocrocuta perrieri* (Carnivora, Hyaenidae) from the Villafranchian of the Iberian Peninsula. *B Soc Paleontol Ital*. 53: 39–47.
- Vislobokova I. 2005. On Pliocene faunas with Proboscideans in the territory of the former Soviet Union. *Quat Int*. 126–128:93–105, doi: 10.1016/j.quaint.2004.04.017.
- Wang X. 2004. New materials of *Tungurictis* (Hyaenidae, Carnivora) from Tungur Formation, Nei Mongol. *Vert PalAsia*. 42:144–153.
- Wang X, Li Q, Xie G. 2015. Earliest record of *Sinicuon* in Zanda Basin, southern Tibet and implications for hypercarnivores in cold environments. *Quat Int*. 355:3–10, doi:10.1016/j.quaint.2014.03.028.
- Wang X, Li Q, Xie G, Saylor J, Tseng ZJ, Takeuchi GT, Deng T, Wang Y, Hou S, Liu J, et al. 2013. Mio-Pleistocene Zanda Basin biostratigraphy and geochronology, pre-Ice Age fauna, and mammalian evolution in western Himalaya. *Palaeogeogr Palaeoclimatol Palaeoecol*. 374:81–95, doi:10.1016/j.palaeo.2013.01.007.
- Wang X, Qiu Z, Li Q, Wang B, Qiu Z, Downs WR, Xie G, Xie J, Deng T, Takeuchi GT, et al. 2007. Vertebrate paleontology, biostratigraphy, geochronology, and paleoenvironment of Qaidam Basin in northern Tibetan Plateau. *Palaeogeogr Palaeoclimatol Palaeoecol*. 254(3–4): 363–385, doi:10.1016/j.palaeo.2007.06.007.
- Wang X, Tseng ZJ, Li Q, Takeuchi GT, Xie G. 2014. From ‘third pole’ to north pole: a Himalayan origin for the arctic fox. *Proc Roy Soc B Biol Sci*. 281(1787):20140893, doi:10.1098/rspb.2014.0893.
- Wang X, Wang Y, Li Q, Tseng ZJ, Takeuchi GT, Deng T, Xie G, Chang M, Wang N. in press. Cenozoic vertebrate evolution and paleoenvironment in Tibetan Plateau: Progress and prospects. *Gondwana Res*. doi:10.1016/j.gr.2014.10.014.
- Werdelin L. 1988a. Studies of fossil hyaenids: the genera *Ictitherium* Roth & Wagner and *Sinictitherium kretzoi* and a new species of *Ictitherium*. *Zool J Linn Soc*. 93(2):93–105, doi:10.1111/j.1096-3642.1988.tb01528.x.
- Werdelin L. 1988b. Studies of fossil hyaenas: the genera *Thalassictis* Gervais ex Nordmann, *Palhyaena* Gervais, *Hyaenictitherium* Kretzoi, *Lycyaena* Hensel and *Palinhyaena* Qiu, Huang & Guo. *Zool J Linn Soc*. 92(3):211–265, doi:10.1111/j.1096-3642.1988.tb01512.x.
- Werdelin L. 2003. Carnivora from the Kanapoi Hominid site, Turkana Basin, Northern Kenya. *Contrib Sci*. 498:115–132.
- Werdelin L, Manthi FK. 2012. Carnivora from the Kanapoi hominin site, northern Kenya. *J Afr Earth Sci*. 64:1–8, doi:10.1016/j.jafrearsci.2011.11.003.
- Werdelin L, Solounias N. 1990. Studies of fossil hyaenids: the genus *Adcrocuta* Kretzoi and the interrelationships of some hyaenid taxa. *Zool J Linn Soc*. 98(4):363–386, doi:10.1111/j.1096-3642.1990.tb01206.x.
- Werdelin L, Solounias N. 1991. The Hyaenidae: taxonomy, systematics and evolution. *Fossils Strata*. 30:1–104.
- Werdelin L, Solounias N. 1996. The evolutionary history of hyenas in Europe and western Asia during the Miocene. In: Bernor RL, Fahlbusch V, Rietschel S, editors. Later Neogene European biotic evolution and stratigraphic correlation. New York, NY: Columbia University Press.
- Zheng SH. 1980. A *Hipparion* fauna from the Bulong Basin, Biru, Tibet. In: Paleontology of Tibet, collected works on research on the Qinghai Tibetan Plateau. I. Beijing: Science Press; p. 33–47.