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Taxonomical revision of fossil *Canis* in Middle Pleistocene sites of Zhoukoudian, Beijing, China and a review of fossil records of *Canis* mosbachensis variabilis in China

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ABSTRACT

Canis mosbachensis is a widely distributed species from the Early to Middle Pleistocene in Europe. In Eastern Asia, Canis variabilis was supposed to be a local subspecies of C. mosbachensis, but such hypothesis has never been tested in details. Here we restudied the Canis materials from type locality, Loc.1 of ZKD (Zhoukoudian) of Middle Pleistocene, as well as other localities that produced important materials of this taxon (e.g. Loc.13 of ZKD). To better evaluate the variability of the Pleistocene Canis, a series of morphotypes are described. Based on morphotype and morphometric, the present study reveals there is only one species present at Loc.1 and Loc.13 of ZKD, which is quite similar to European C. mosbachensis and should be revised as a subspecies of C. mosbachensis, namely C. mosbachensis variabilis. C. m. variabilis is more derived and less hypercarnivorous than the Early Pleistocene Canis chihliensis (as well as European Canis etruscus and Canis arnensis) in craniodental characters, whereas it is less derived and less hypercarnivorous than *Canis lupus*. A review of fossil records of *C. m. variabilis* in China was made based on these different characters. Canids from Gongwangling, Lantian of Shaanxi Province (middle or late Early Pleistocene) are the earliest known representatives of C. mosbachensis in China, which are still more primitive than C. m. variabilis from the Middle Pleistocene sites of ZKD. Reliable records of C. mosbachensis are only known from the Early Pleistocene to the late Middle Pleistocene in Northern China. C. m. variabilis is not direct ancestor to C. lupus but a close relative of the latter, while it is far from the Early Pleistocene C. chihliensis. The latter remains more primitive characters that are more similar to those of European Canis etruscus and Canis arnensis.

1. Introduction

Canis is one of most important members in the Pleistocene faunas. It first appeared in late Hemphillian in North America, but entered Eurasia much later (Sotnikova and Rook, 2010; Tedford et al., 2009). The earliest record of *Canis* in Eurasia is from the Late Pliocene localities in Yushe Basin of China (Flynn et al., 1991) and Vialette in France (Lacombat et al., 2008). During the early to middle Early Pleistocene (2.58–1.2 Ma), the diversity of *Canis* in Eurasia arrived at its peak (Bartolini Lucenti et al., 2017; Brugal and Boudadi-Maligne, 2011; Sotnikova and Rook, 2010), with numerous species in both Europe (*Canis etruscus* Major, 1877, *Canis arnensis* Del Campana, 1913, *Canis* mosbachensis Soergel, 1925, Canis apolloniensis Koufos and Kostopoulos, 1997, Canis accitanus, Garrido and Arribas, 2008 and hypercarnivorous members derived from Canis, namely Xenocyon falconeri Major, 1877 and Xenocyon lycaonoides, Kretzoi, 1938) and Eastern Asia (Canis chihliensis, Zdansky, 1924, Canis palmidens, Teilhard de Chardin and Piveteau, 1930, Canis teilhardi, Qiu et al., 2004, Canis longdanensis, Qiu et al., 2004, Canis brevicephalus, Qiu et al., 2004 and hypercarnivorous Xenocyon antonii, Zdansky, 1924, Xenocyon dubius, Teilhard de Chardin and Piveteau, 1930, Xenocyon yuanmouensis, You and Qi, 1973). Some of these taxa might be invalid and can be assigned to other species, but a high diversity is widely accepted (Brugal and Boudadi-Maligne, 2011; Sotnikova and Rook, 2010). During the late Early Pleistocene and early

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Middle Pleistocene (1.2–0.4 Ma), the diversity of *Canis* was markedly reduced, with probably only *C. mosbachensis* in Europe (except hypercarnivorous members). In Asia, three species were reported during the late Early Pleistocene and early Middle Pleistocene: *Canis variabilis, Canis cyonoides* and *Canis lupus* (Hu and Qi, 1978; Pei, 1934), but some later authors thought that these species may be conspecific and only *Canis variabilis* is present (Tedford et al., 2009; Teilhard de Chardin and Pei, 1941).

C. mosbachensis is the most frequently found canid in the late Early Pleistocene and early Middle Pleistocene European fauna. It first appeared in the Middle Early Pleistocene (late Villafranchian) in southern Europe, such as Pirro Nord of Italy and Venta Micena of Spain (Bartolini Lucenti et al., 2017; Petrucci et al., 2013; Sardella et al., 2014). The late Early Pleistocene C. mosbachensis dispersed to more Northern part of Europe. Materials from German site Untermassfeld (Sotnikova, 2001) are the best representatives of C. mosbachensis in this period. The middle and late Early Pleistocene Canis from Southern Europe were thought to be closely related to C. arnensis by some authors (e.g. Rook and Torre, 1996). However recent revision of Southern Europe carnivores (Bartolini Lucenti et al., 2017; Petrucci et al., 2013) revealed that this canid was closer to materials from Untermassfeld and should be assigned to C. mosbachensis. In the early Middle Pleistocene, C. mosbachensis became more abundant and widely distributed, known from many sites, such as L' Escale of France (Bonifay, 1971), Stränskä skäla of Czech Republic (Musil, 1972), Mosbach 2 of Germany (Soergel, 1925) and Petralona Cave of Greece (Kurtén and Poulianos, 1977). For a review of C. mosbachensis records in Middle Pleistocene sites see Kahlke (1975). So far, the most informative descriptions of C. mosbachensis are materials from Untermassfeld by Sotnikova (2001). She thought this canid was close to C. etruscus and the living Indian wolf C. lupus pallipes, but far from the Early Pleistocene C. arnensis. Sotnikova (2001) didn't directly give the phylogenetic relationships of these canids, but those of C. arnensis - C. latrans and C. etruscus - C. mosbachensis - C. lupus are supported by her morphological analysis.

Compared with rich studies on Pleistocene fossil Canis in Europe, the studies on Chinese Pleistocene fossil Canis are much fewer in recent decades. Most studies concentrated on only brief description of the materials without any discussion. Qiu et al. (2004) made a comprehensive study of rich Canis materials from the Early Pleistocene site Longdan, Gansu Province, which greatly enriched our understanding about the early evolution of Canis in Eastern Asia. However no comprehensive study about the Middle Pleistocene Canis in China was made yet. Most Middle Pleistocene Canis in China were assigned to Canis variabilis, Pei, 1934 with no discussion. Canid from Loc.1 of ZKD (Zhoukoudian, previously spelled as Choukoutien) was firstly described by Zdansky (1928) as Canis cf. dingo according to its small size compared with the living wolf. Pei (1934) established C. lupus var. variabilis based on more materials from Loc.1 of ZKD. Pei (1934) distinguished Canis materials from Loc.1 of ZKD into three types: the large one as C. lupus, the small mesocarnivorous one as C. lupus var. variabilis and the small but slightly hypercarnivorous one as C. cyonoides. Among these three taxa, C. lupus var. variabilis is the dominant one, while fossils of C. lupus and C. cyonoides are much fewer (e.g., they are absent at Loc. 3, 6 and 9 of ZKD). In his monograph about Carnivora at Loc.1 of ZKD, Pei (1934) thought that C. lupus var. variabilis differed from the materials of C. lupus in this locality by smaller size, slenderer muzzle and weaker sagittal crest, though he admitted that the materials assigned to C. lupus were also different from the living wolf by some tooth characters and smaller size. Pei didn't give detailed comparison about C. cyonoides, thinking that it differs from other materials by hypercarnivorous characters: reduced metaconule and cingulum of M1, as well as reduced metaconid and entoconid of m1, but the degree of hypercarnivore is less than that of Cuon in retaining m3 and entoconid of m1. Later on, Teilhard de Chardin and Pei (1941) described materials from Loc.13 of ZKD. The age of Loc.13 of ZKD is probably equivalent to the age of lower part of Loc.1 of ZKD. The materials of fossil canids are less

abundant than those of Loc.1 but comprise better preserved craniums. Based on these new materials, Teilhard de Chardin and Pei (1941) reviewed the Chinese Canis materials and concluded that all specimens from Loc.1 and Loc.13 belongs to the same type. They upgraded C. lupus var. variabilis to species level as C. variabilis, and assigned materials previously assigned to C. lupus to this species, representing the extreme variants of the species. Later Teilhard de Chardin and Leroy (1942) also assigned C. cyonoides to C. variabilis. These opinions were widely accepted by most later Chinese authors. They regarded all early Middle Pleistocene Canis specimens as C. variabilis if their size were smaller than living C. lupus. Teilhard de Chardin and Pei (1941) thought the canids from Nihewan were also not different from C. variabilis and can be assigned to this species. This opinion was less accepted, but some later authors followed this opinion and assigned some Early Pleistocene canids to C. variabilis. Sotnikova (2001) stressed the similarities between ZKD C. variabilis and European C. mosbachensis. She thought C. variabilis and European C. mosbachensis together with medium sized canids from Russia formed a Palearctic distributed species (though she admitted a more detailed study of Asia materials was needed to draw the conclusion). Tedford et al. (2009) briefly reviewed the materials from ZKD, and concluded that C. variabilis was only different from European C. mosbachensis by short nasal bone (posterior tip of nasal lies rostral to maxilla-frontal suture). They agreed with Sotnikova (2001) that C. variabilis and C. mosbachensis represented a geographically widespread mid-Pleistocene wolf, but retained the specific level of C. variabilis. The phylogenetic analysis by Tedford et al. (2009) suggested C. variabilis was sister group to C. mosbachensis, and they thought both species were closer to C. arnensis and C. latrans than to C. etruscus and C. lupus, which is in conflict with the opinions of Sotnikova (2001).

In summary, there are still many unclear questions about the Middle Pleistocene *Canis* in China:

- 1. Are there multiple species at Loc.1 of ZKD?
- 2. Could *C. variabilis* be assigned to *C. mosbachensis* and are there any differences between these two taxa?
- 3. If there is only one species (*C. variabilis*) at Loc.1 of ZKD, what are the differences between *C. variabilis* and *C. lupus*?
- 4. What are the differences between *Canis* from ZKD and similar sized Early Pleistocene *Canis* in China (mainly *C. chihliensis* and *C. palmidens*)?
- 5. Phylogenetic position of *C. variabilis* and *C. mosbachensis*, whether they are closer to *C. arnensis* or *C. etruscus/C. lupus*?

2. Materials and methods

In present analysis, materials of Locs.1, 3, 6, 9 and 13 of ZKD that are still preserved in IVPP (it is a great pity that most specimens were lost during World War II, but the remained specimens are sufficient for understanding the characters and their variability of the species) are restudied. Great morphological variability (especially in teeth) are known in *Canis* (Tong et al., 2012), and it is impossible to use one state to describe the whole population. Therefore a series of morphotypes (cranium, mandible and teeth) are defined here based on character matrix of Tedford et al. (2009) and description of fossil canids by Sotnikova (2001), Qiu et al. (2004), Bartolini Lucenti and Rook (2016), Bartolini Lucenti et al. (2017) as well as our own observations. To better analyse the interrelationship of different *Canis*, the morphotypes are defined to cover the morphology of all the known species including *Xenocyon, Cuon* and *Lycaon*.

Age framework: The Early Pleistocene was subdivided into early Early Pleistocene (Gelasian, from 2.58 to 1.80 Ma), middle Early Pleistocene (early Calabrian, from 1.80 to 1.20 Ma) and late Early Pleistocene (late Calabrian, from 1.20 to 0.78 Ma). Download English Version:

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