



# An investigation of palaeodietary variability in European Pleistocene canids



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## ABSTRACT

Temporal and interspecific dietary variability were investigated in three canid taxa, *Canis lupus*, *Canis mosbachensis* and *Canis etruscus*, across a range of British and mainland European wolf assemblages from the Early Pleistocene to Recent periods. Using established cranio-dental indicators to reveal dietary specialisations towards bone eating, flesh slicing, and non-flesh food crushing, inferences were made concerning the proportions of flesh to non-flesh foods in the diet, and hence the level of carnivory adopted by each taxon. Significant temporal differences were found in the diet and frequency of tooth wear of *C. lupus* from MIS 3, 5a and 7 in Britain. Relative body size comparisons based on lower carnassial length also revealed variation in body size for the Pleistocene age groups, correlating with differences in diet. Stepwise Discriminant Function Analyses revealed large-bodied MIS 5a *C. lupus* to be hyper-carnivorous and specialised in fast flesh slicing and to some extent bone consumption, whereas relatively smaller-bodied MIS 3 and 7 *C. lupus* were both less carnivorous and more specialised in crushing non-meat foods. Modern wolves from central Sweden are smaller than those of MIS 5a and hyper-carnivorous, although with greater specialisation towards crushing of non-meat foods. Temporal variations in diet were related to changes in prey diversity, competition from other carnivores, openness of the environment, and ultimately climate, and reflect the cranio-dental plasticity of *C. lupus*. In contrast, no temporal differences in diet were found in age groups of *C. mosbachensis* and *C. etruscus*, which may relate to more stable overall conditions in comparison to the later Pleistocene. The cranio-dental characteristics of the smaller-bodied mesocarnivore *C. etruscus* indicate adaptations to non-meat food crushing, whereas in the similarly small *C. mosbachensis*, enhanced flesh slicing capabilities and reduced crushing abilities indicate that it was more carnivorous than *C. etruscus*. *C. etruscus* and *C. mosbachensis* were both more specialised than *C. lupus*.

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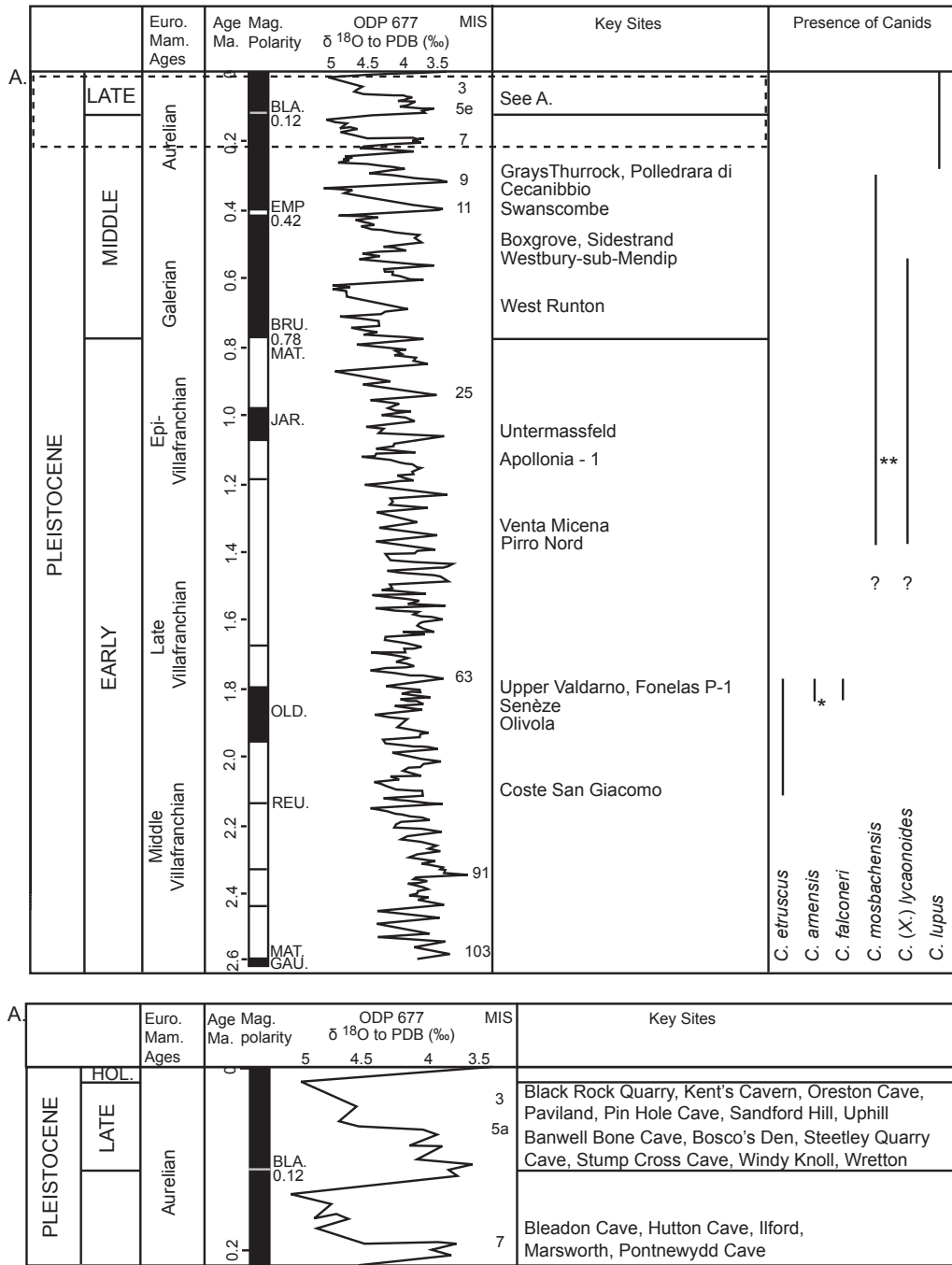
## 1. Introduction

This paper aims to investigate temporal variation in the diet of one of the most successful Pleistocene predators, the grey wolf *Canis lupus* L., 1758, as well as analysing potential dietary variability between *C. lupus* and two other Pleistocene canids, the Early Pleistocene *Canis etruscus* Forsyth-Major, 1877, and the Early to Middle Pleistocene *Canis mosbachensis* Soergel, 1925. Establishing the relative ecological roles of the different canids within a changing carnivore guild is critical for our understanding of Pleistocene palaeoecology and in particular, the importance of intra- and inter-specific competition. Changing dietary behaviour can be traced in different aspects of cranio-dental morphology, including

the morphology of the premolars and molars, depth of the mandible and degree of tooth wear (Van Valkenburgh, 1988a,b; Van Valkenburgh, 1991; Van Valkenburgh and Koepfli, 1993). It is therefore anticipated that any morphological changes identified may shed light on temporal and geographical variation in the diet of Pleistocene wolves, which may in turn be linked to changes in prey diversity, competition, environment and climate. By using the ecology and subsistence behaviour of modern *C. lupus* as an analogue, inferences may be drawn concerning the palaeoecology and palaeodiet of Pleistocene *C. lupus*, as well as allowing comparison with extinct canid taxa in order to establish ecological niches of individual species. Finally, dietary information from modern Palaearctic wolf specimens will be compared to the Pleistocene dataset, in order to see whether there are differences in morphology that might equally be explained by environmental or other parameters. The paper adopts an explicitly British perspective for much of the palaeodietary component, in order to maximise

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**Fig. 1.** Chronostratigraphy of indicative sites (2.6 Ma to the present) from Europe mentioned in the text, and the chronological range of key canids. **A:** Detailed view of the chronostratigraphy of indicative sites of the late Middle to Late Pleistocene from Britain. Uncertainties with taxonomic status indicated by \* for *C. senezensis* = *C. arvensis*, \*\* for *C. apolloniensis* = *C. mosbachensis*. Age, magnetic polarity and oxygen isotope calibration from Shackleton et al. (1990).

information from well-dated Middle and Late Pleistocene localities. These data are then compared with an extensive range of northern and southern European wolf assemblages in order to address wider questions of changing palaeodiet through time, competition and niche differentiation by individual species.

**2. History and chronology of the Pleistocene canids in Europe**

The genus *Canis* had an enduring presence in the European Pleistocene (2.6 Ma–11.5 ka). Its early history in western and southern Europe is fairly well established (see Sardella and

Palombo, 2007; Sotnikova and Rook, 2010 for a review), although there are considerable hiatuses in the fossil record, particularly in the Early Pleistocene. The oldest remains currently attributed to *Canis* are from the Late Pliocene early Villafranchian site of Viallette, France, dated to 3.1 Ma (Lacombat et al., 2008), followed by Early Pleistocene middle Villafranchian material attributed to *Canis* cf. *etruscus* from the site of Coste San Giacomo, Italy, dated to 2.2–2.1 Ma (Fig. 1) (Rook and Torre, 1996a; Sardella and Palombo, 2007; Rook and Martinez-Navarro, 2010; Bellucci et al., 2012). Taken together, it is clear that these new records place the dispersal of the genus into Europe much earlier than the so-called ‘Wolf Event’

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