1.4 Using X-ray Microtomography to Discriminate Between Dogs' and Wolves' Lower Carnassial Tooth

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Abstract

Dogs and wolves exhibit similar dental features since they belong to the same species. Here we explore a new method to discriminate between wild and domestic forms, based on the analysis of the internal structure of the teeth. We analysed the lower first molar of 21 dogs and 17 wolves. X-ray microtomographic analyses were performed and tooth tissue proportions were assessed by the proportion of the dentine volume. As a result, dog molars show a lower percentage of dentine than those of wolves. This analysis offers promising applications in the study of dog domestication origins.

Keywords: dog domestication, wolf, lower carnassial tooth, X-ray microtomography, tooth tissue proportions.

1 Introduction

Dogs and wolves show similar skeletal features since they belong to the same species. Distinctions between the two groups can be related to different body proportions (e.g. length of limbs in relation to total body length) as well as to other specific features of peculiar skeletal elements. More diagnostic traits are located in the head region (skull and mandible) (Pluskowski 2006): for instance, dogs can show tooth crowding (even if this characteristic was also found in wolves and should be critically re-evaluated, e.g. Ameen *et al.* 2017), a lower orbital angle (e.g. Aaris-Sørensen 1977), smaller, compressed and crumpled tympanic bullae (e.g. Lawrence and Bossert 1967), a shortened facial part of the skull (and a consequently shortened mandible) (e.g. Clark 1996; Davis 1995), a steep frontal region (e.g. Lawrence and Bossert 1967) and a reduction of the relative length of both upper and lower carnassial teeth (e.g. Clark 1996; Davis 2003).

In spite of the above mentioned characteristics, the identification of prehistoric dogs is sometimes challenging due to the absence of clear diagnostic features or to the presence of a mosaic pattern of characteristics in the initial phases of domestication. In addition, diagnostic skeletal differences between dogs and wolves were often observed using modern individuals as a reference, but it has to be kept in mind that wolf populations lost both genetic and phenotypic variability through time. For instance, skulls of Late Pleistocene wolves from Beringia show a shortened rostrum (Leonard *et al.* 2007), and an overlap in carnassial tooth size was observed among wolves and dogs (e.g. Davis 2003). Difficulties in identifying the earliest domesticated populations is testified for instance by the scientific debate about the taxonomy of some *Canis* populations from a number of central and northern European Late Pleistocene archaeological sites (e.g. Crockford and Kuzmin 2012; Germonpré *et al.* 2009, 2012, 2015; Morey 2014). Since dogs were the first animals to be domesticated by humans, their history has great implications in the evolution of past human cultures and societies, and the identification of the first domestication centres and of the different domestication waves is of pivotal importance from an archaeological perspective (Frantz *et al.* 2016; Larson *et al.* 2012; Shannon 2015; Skoglund *et al.* 2015; Thalmann *et al.* 2013). For this reason, we propose here a new method to discriminate between wild and domesticated forms, based on the analysis of the internal structure of the lower carnassial teeth. In particular, this paper presents the study of the ratio between dentine volume and total volume in two selected parts of the tooth.

Table 1. Specimens considered in this work. Unisi: University of Siena; MNHT: Civic Museum of Natural History, Trieste; FA: Fisiocritici, Siena Academy of Science; PM: Bioarchaeology Lab. of the Museo delle Civiltà, Rome; L: length of the carnassial, measured at the cingulum (von den Driesch 1976).

Taxonomy	ID	Sample location	Sample provenance/chronology	L	% of dentine	
					Slice 1	Slice 2
dog	1	Unisi	extant	22.4	86.0	68.4
dog	2	Unisi	extant	22.2	85.6	69.7
dog	70	Unisi	extant	21.3	87.1	74.6
dog	196	Unisi	extant	25.3	87.3	73.0
dog	757	MNHT	extant	27.5	87.7	75.5
dog	1359	Unisi	extant	21.4	86.6	72.6
dog	95F	Unisi	extant	24.0	87.0	77.2
dog	chiostraccio	Unisi	extant	20.5	88.6	74.5
dog	M766	MNHT	extant	25.2	87.1	72.9
dog	TS nonum	Unisi	extant	19.9	86.4	71.3
dog	TS3	Unisi	extant	22.0	85.6	74.9
dog	TS6	Unisi	extant	22.7	87.9	71.9
dog	TS7	Unisi	extant	23.5	88.7	73.9
dog	TS8	Unisi	extant	25.6	87.1	72.9
dog	TS9	Unisi	extant	23.8	87.4	74.4
dog	TS10	Unisi	extant	23.0	88.6	76.3
dog	TS11	Unisi	extant	25.0	87.8	75.7
dog	TS13	Unisi	extant	18.5	88.7	74.2
dog	SC1	MNHT	Holocene - Slovenia	19.8	86.6	71.8
dog	SC3	MNHT	Holocene - Slovenia	21.4	-	74.9
dog	Vpa6831	MNHT	Holocene - Slovenia	23.2	86.8	74.4
wolf	52	Unisi	extant - Zoo	30.0	89.1	77.8
wolf	353	Unisi	extant - Central/Southern Italy	27.3	91.6	79.2
wolf	357	Unisi	extant - Central/Southern Italy	30.4	90.2	-
wolf	358	Unisi	extant - Central/Southern Italy	28.0	90.2	79.1
wolf	359	Unisi	extant - Central/Southern Italy	28.6	91.0	84.5
wolf	375	Unisi	extant - Central/Southern Italy	26.4	90.7	78.5
wolf	376	Unisi	extant - Central/Southern Italy	29.5	90.1	79.7
wolf	377	Unisi	extant - Central/Southern Italy	27.0	90.4	81.1
wolf	378	Unisi	extant - Central/Southern Italy	27.5	89.0	78.9
wolf	fis_139	FA	extant - Central/Southern Italy	26.5	88.8	78.9
wolf	fis_135	FA	extant - Central/Southern Italy	26.5	89.9	80.2
wolf	551	MNHT	extant - North-eastern Italy	25.0	89.0	79.8
wolf	17775	Unisi	Grotta Paglicci - MIS 2 (layer 12d)	31.3	90.5	-
wolf	R38	Unisi	Grotta Paglicci - MIS 2	29.8	88.8	77.4
wolf	P6265	PM	Grotta Romanelli - MIS 2	30.4	88.8	77.6
wolf	877	Unisi	Grotta Paglicci - Middle Palaeolithic	26.4	-	80.7
wolf	3596_3	PM	Grotta Romanelli - Terre Rosse	24.7	-	82.1

2 Materials and Methods

In this exploratory study, the lower first molar of 18 recent dogs, three archaeological Holocene dogs from Slovenia, 11 extant Italian wolves, one extant zoo-wolf originating from a population of northern Europe and five Middle to Upper Palaeolithic wolves from Southern Italy were analysed (Table 1).

Almost all of present-day dogs were collected in the field; two specimens are from the zoological collection of the Civic Museum of Natural History of Trieste; the breed of all specimens is unknown. The three archaeological dog remains are stored at the Civic Museum of Natural History of Trieste and are from Holocene archaeological sites near Škocjan in South-western Slovenia; two are from old excavations and the context is unknown; one (Vpa6831) is from Grotta delle Ossa (Riedel 1977). Among present-day wild wolves, 8 are from Central-southern Italy and are part of the osteological collection of the Research Unit in Prehistory and Anthropology of the University of Siena; two are from Central Italy and are part of the zoological collection of the Siena Academy of Science (Accademia dei Fisiocritici), whilst one is from North-eastern Italy and is part of the zoological collection of the Civic Museum of Natural History of Trieste. Among archaeological wolves, all of them are from Apulia (Southern Italy) and in particular from two well-known sites: Grotta Paglicci and Grotta Romanelli.

The Paglicci site is located on the Gargano promontory (Foggia) and the remains studied in this paper come from three distinct excavated areas: one tooth (R38) is from the present-day cave and it was discovered in a Late Glacial context between the atrium and an inner room. Even if sediments from this area were reworked by looters, only Epigravettian remains were yielded (Arrighi *et al.* 2008; Ricci *et al.* 2016). One tooth, discovered in the main trench excavated in the cave's atrium, is from the Early Epigravettian layer 12d (Boschin 2019); this layer is dated between about 18–19 ky cal. BP (Boschin *et al.* 2018); The third tooth (877) is from a Middle Palaeolithic context (layer 1d) from the external rock shelter (Crezzini *et al.* 2016; Mezzena and Palma di Cesnola 1971). These remains are stored at the University of Siena.

Grotta Romanelli is located in Southern Apulia and is characterised by a stratigraphy composed of an upper part called 'Terre Brune', where Late Upper Palaeolithic evidence was detected (dated between about 13,800 and at least 8,600 cal. BP) (Calcagnile *et al.* 2019; Sardella *et al.* 2018; Tagliacozzo 2003), and a lower part called 'Terre Rosse', that lays under a stalagmite dated to 40,000+/-3,250 with the 230Th/238U method (Cassoli *et al.* 2003; Sardella *et al.* 2018). Among specimens analysed in this paper, two teeth are from the 'Terre Brune' and one is from the 'Terre Rosse'. All specimens are stored at the Bioarchaeology Lab of the Museo delle Civiltà in Rome. Wolves from the Upper Palaeolithic (MIS2) of Apulia (Epigravettian contexts at Grotta Paglicci and 'Terre Brune' at Romanelli) are generally characterised by a large size, whilst those from Middle Palaeolithic contexts (the external rock shelter at Grotta Paglicci and the 'Terre Rosse' at Grotta Romanelli) are characterised by a reduced size. This pattern was confirmed by matching together the evidence from other Apulian sites (Mecozzi and Lucenti 2018). It has to be highlighted that older (and smaller) Apulian wolves were previously considered as possibly belonging to *Canis mosbachensis*. Recently they were reassessed to belong to *Canis lupus* (Sardella *et al.* 2014). Given the fact that these small wolves overlap in size with dogs, their analysis is of great interest to understand if some differences in the lower carnassial tooth internal structural signature can be found between domesticated and wild individuals of similar body size.

The specimens were analysed by means of microfocus X-ray computed tomography using a system designed for the study of cultural heritage at the Multidisciplinary Lab of the 'Abdus Salam' International Centre for Theoretical Physics of Trieste (Italy) (Tuniz *et al.* 2013). The microCT acquisitions of the teeth were performed using a Hamamatsu L8121-03 sealed X-ray source with a focal spot size of 5µm. Sets of 1440 or 2400 projections, depending of the sample's characteristics, were recorded over a total scan angle of 360° using a Hamamatsu C7942SK-25 flat panel detector. The resulting microCT slices were reconstructed using the software DigiXCT (DIGISENS) in a 32-bit format. Once the 3D reconstruction of each specimen was completed, different tissues (enamel and dentine) were separated carrying out a semi-automatic threshold-based segmentation (e.g. Coleman and Colbert 2007).

Since the ratio between the volume of different tissues composing the tooth's structure can be affected by wear, a first effort was attempted to avoid this problem and to analyse all teeth in a homogeneous and reproducible way. For this reason, it was decided to analyse selected sub-volumes of each tooth, located in those portions not affected or less affected by use-wear. Starting from protocols already developed in virtual palaeoanthropology (e.g. Zanolli *et al.* 2018, 2019), we fitted a tooth cross-section to the cervix and we set it as a reference to extract two sub-volumes (hereafter volumes 1 and 2). Moving the reference cross-section through the tooth's crown, we selected four plans to extract the two volumes: a first plane (cross-section 1) was set tangent to the uppermost part of the cervix; a second plane (cross-section 2) was set at the point when the hypoconulid is closed; a third plane (cross-section 3) was set at the bottom of the fossa between the paraconid and the protoconid; finally, a fourth plane (cross-section 4) was set at the separation between the paraconid and the protoconid (Figure 1). Volume 1 is the part of the tooth comprised between cross-sections 1 and 2, whilst volume 2 is the part of the tooth comprised between cross-sections 3 and 4. A standardised ratio (expressed in percentage) between dentine volume and total volume was recorded for both volumes. Due to the presence of contact facets on the cingulum, or to the presence of worn surfaces on the paraconid and protoconid, the ratio wasn't calculated for both volumes in all samples (Table 1). In addition, the length (L) of each tooth (von den Driesch 1976) was measured with a calliper (Table 1).

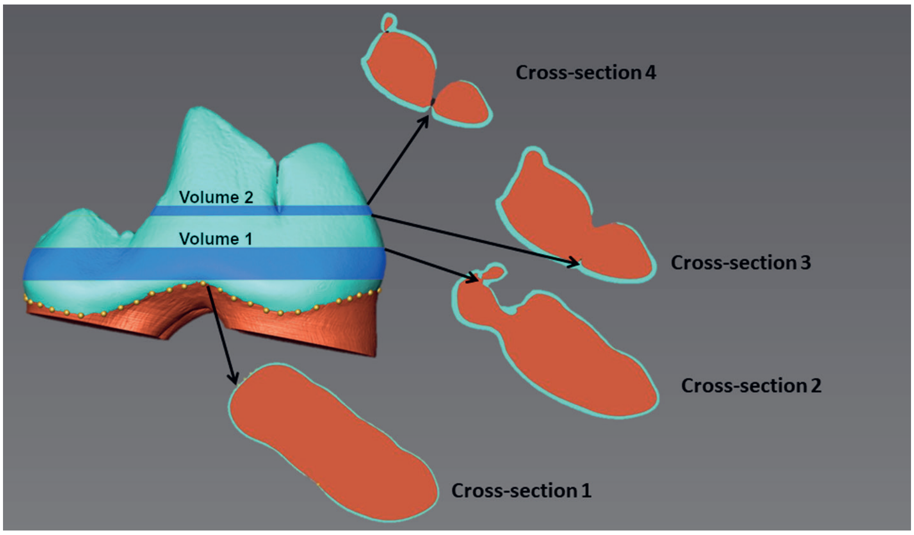

Figure 1. Cross-sections used to extract the two sub-volumes. Volume 1 located on the cingulum; volume 2 located on the cusps (by F. Boschin).

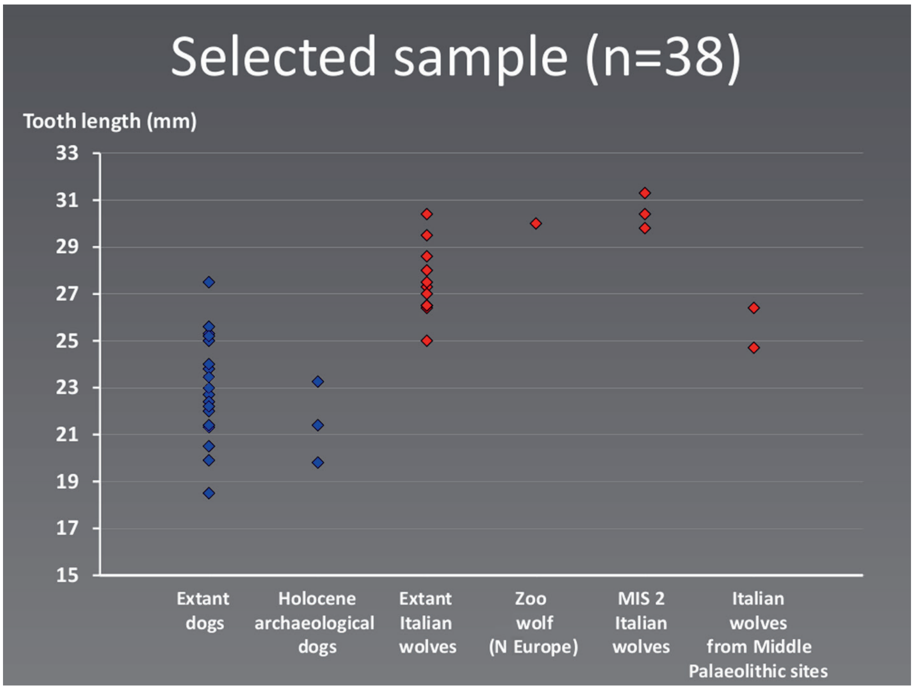

Figure 2. Length of teeth analysed in this paper. Image by one of the authors (by F. Boschin).

3 Results

Metric analysis reveals an overlap between wolves and dogs (Figure 2). In particular, larger dogs' teeth show a size that is comparable with that of both smaller extant Italian wolves and small-sized individuals from Middle Palaeolithic contexts. The teeth of the zoo-wolf originating from Northern Europe, as well as of the Italian wolves from the MIS 2 are larger than those of all considered dogs. If the analysis moves to the tooth internal structural signature the picture changes: the proportions of dentine are different, both in volume 1 and 2, between the wild and the domestic form. Considering volume 1, dogs show a lower proportion of dentine, thus indicating a thicker enamel. The values range between 85.6% and 88.7% in dogs and between 88.8% and 89.9% in wolves. As for volume 2, the distinction between the two groups is even clearer, as the ratio falls between 68.4% and 77.2% in dogs and between 77.4% and 84.5% in wolves (Figure 3). Also in this case wolves show a thinner enamel, as expressed by a higher proportion of dentine. Considering dogs and wolves as separate groups, the enamel thickness was tested in relation to the size of the teeth. Neither in domesticated, nor in wild individuals, was a clear correlation between the two parameters found. Linear correlation is very low in dogs both in volume 1 ($p=0.79$, $r2=0.003$) and in volume 2 ($p=0.28$, $r2=0.05$). In wolves the picture is similar: there is no correlation in volume 1 ($p=0.94$, $r2=0.0004$), and a not significant result was also found in volume 2 ($p=0.15$, $r2=0.14$). Even if statistics reject the hypothesis of a correlation between tooth size and enamel thickness, a negative trend can be observed in the volume 2 among wolves

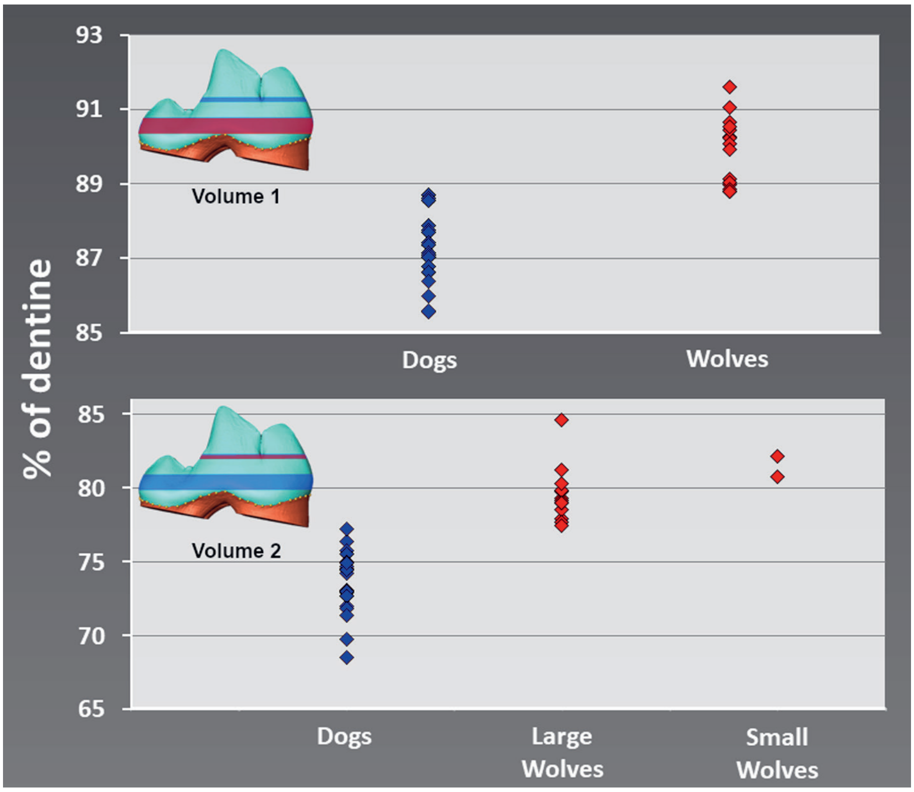

Figure 3. Proportion of dentine (% dentine volume/ total volume) in each volume (indicated in red on the tooth model). Image by one of the authors (by F. Boschin).

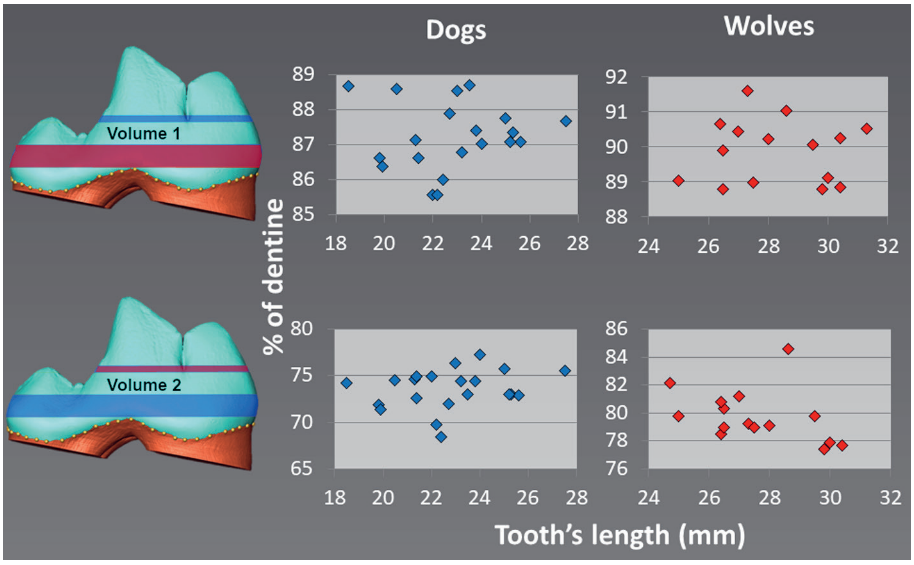

Figure 4. Correlation between tooth length (X-axis) and % of dentine (Y-axis) in dogs and wolves in volume 1 (top) and volume 2 (bottom). Image by one of the authors (by F. Boschin).

(Figure 4), with smaller individuals showing a thinner enamel. This is relevant from a taxonomic perspective, since wild individuals closer to dogs from a biometric point of view, can be better discriminated observing the proportion of dental tissues.

4 Discussion and Conclusions

Our results demonstrate that the wolf domestication process did not only affect the relative size of the lower carnassial tooth but also its internal structure. An increase in enamel thickness is visible both in the area of the cingulum and in the main cusps. In particular, it seems that the difference is more pronounced in the latter region, where the minimum percentage of dentine volume reached by dogs is 68.4% and the maximum reached by wolves is 84.5%. In the cingulum, the range of variability is more compressed and varies from a minimum of 85.6% in dogs and a maximum of 89.9% in wolves. At the present stage of research it is difficult to assess whether the different tooth internal structure between dogs and wolves is related to a different masticatory behaviour or if it has been triggered by the shortened rostrum and mandible. The latter option could be argued due to the greater difference in enamel thickness observed between dogs and wolves in the 'more functional' area of the tooth (i.e. the cusps). Even if the breed of studied dogs is unknown, the great variability of the tooth's length (from 18.5 to 27.5 mm) could reflect a high canine diversity in the sample, and the absence of clear trends in the pattern of enamel thickness could reject a relation between the internal structural signal and masticatory mechanics. Also the structural difference detected in the cingulum, a region less involved in mastication, could suggest that changes in enamel thickness could be more related to a reorganisation of the tooth internal structure due to the reduction of the tooth's size triggered by domestication. Only further analysis of teeth belonging to dogs of known breeds could shed light on this issue. At the present stage of research, it can only be highlighted the valuable help given by microCT studies to the problem of the identification of domesticated individuals among faunal remains; indeed, regardless of whether the changes in enamel thickness from wolves to dogs are a matter of masticatory/feeding behaviour or not, the difference observed between the two groups is very clear, also when small wild individuals are analysed.

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