Palaeolithic dogs and the early domestication of the wolf: a reply to the comments of Crockford and Kuzmin (2012)

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ABSTRACT

This is a response to the comments of Crockford and Kuzmin (2012) on our identification of Palaeolithic dogs from different European Palaeolithic sites. In their comments Crockford and Kuzmin (2012) present some errors, misunderstandings and misrepresentations that we remedy here. In our opinion, the early wolf domestication must be regarded as an intimate relationship between humans and canids including the breeding of the latter by prehistoric people, resulting in the European Palaeolithic dogs.

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1. Introduction

Based on multivariate statistics, we argued that canid skulls from Goyet, Belgium, Předmostí, the Czech Republic, and Mezin and Mezhirich, the Ukraine, were Palaeolithic dogs (Germonpré et al., 2009, 2012a). Crockford and Kuzmin (2012) conjecture that these studies have some serious deficiencies. Hence, we would like to offer a few comments in response. We will address each of the points of criticism raised by Crockford and Kuzmin (2012) to remedy some errors, misunderstandings and misrepresentations and to further bolster our previous interpretations. Below we will follow the structure of their paper.

2. Main issues

2.1. Is the Razboinichya canid also a Palaeolithic dog?

Crockford and Kuzmin (2012) remark that we did not include the Razboinichya dog published by Ovodov et al. (2011), a paper

on which Crockford and Kuzmin are co-authors, in our recent paper on large canids skulls from the Předmostí site, the Czech Republic (Germonpré et al., 2012a). The Ovodov et al. (2011) paper was available online on 28 July 2011, after we had submitted our initial draft of the Předmostí paper for peer review, but before our resubmission following these reviews. We chose not to integrate the Razboinichya dog into our paper at this late stage as comments relating to this specimen would not have been peer reviewed and this would have involved introducing data to readers that had not been given to the reviewers of our original manuscript. The Razboinichya canid will be compared here with the Palaeolithic dogs.

2.2. Issues with the analysis

Crockford and Kuzmin remarked that Předmostí OK 1063 is missing from Table 2 in Germonpré et al. (2012a). However, no data are missing; the confusion is due to a typographic error. Skull Předmostí OK 1063 (=Předmostí 3) and Předmostí OK 1069 are actually one specimen. This skull was identified as a Palaeolithic dog in Germonpré et al. (2012a) and will be included in our reanalyses presented here.

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Crockford and Kuzmin (2012) do not agree with our choice of European Epipalaeolithic and Mesolithic dogs skulls as reference material because they consider the small size of these skulls as problematic. They further add that prehistoric dogs of roughly similar size are known from Europe and elsewhere, without, however, giving references. In Ovodov et al. (2011), the only reference dogs that are used as a comparison group (only the means, not the individual measurements) are Greenland dogs dating to the Thule period (they are less than 1000 years old). We chose the much older prehistoric dog skulls from the Epipalaeolithic and the Mesolithic because we wanted a prehistoric comparison group as close as possible in time and in space to the unknown Palaeolithic canid skulls, all from European sites. In our first paper, the measurements used in the Discriminant Function Analyses (DFA) were size-adjusted because of the size differences between the reference groups (Germonpré et al., 2009, p. 476). In Germonpré et al. (2012a), a first DFA used log$_{10}$-transformed dimensions, permitting size to be taken into account (Germonpré et al., 2012a, p. 189). The second DFA was carried out on size-adjusted variables (Germonpré et al., 2012a, p. 190). The use of size-adjusted data may allow the identification of differently sized individuals that have the same shape (Jungers et al., 1995). In Germonpré et al. (2012a), contrary to the remarks of Crockford and Kuzmin (2012), none of the unknown cases were added to the very large modern dogs group. First, we did not define a very large modern dog group. We infer that Crockford and Kuzmin (2012) are referring here to our Recent Other Dog group (RDo). Only in the PCA plot based on the log$_{10}$-transformed measurements do some of the unknown specimens fall within the range of the RDo group where it overlaps with the range of the Palaeolithic dogs (Germonpré et al., 2012a: Fig. 9). In the DFA plot (Germonpré et al., 2012a: Fig. 10) based on the log$_{10}$-transformed dimensions, none of the unknown specimens fall in the range of the RDo group, contrary to what Crockford and Kuzmin claim. In the size-adjusted DFA plot (Germonpré et al., 2012a: Fig. 12) only two unknown cases fall within the range of the RDo and, contrary to what Crockford and Kuzmin (2012) assert, none were grouped with the RDo because their probabilities are too low to confidently add them to this group. All Palaeolithic dogs identified by us were found in European Palaeolithic sites: Goyet (Germonpré et al., 2009) in Western Europe, Předmostí (Germonpré et al., 2012a) in Central Europe, Mezin, Mezhirichi (Germonpré et al., 2009) and Eliseevichi (Sablin and Khlopachev, 2002) in Eastern Europe.

Crockford and Kuzmin (2012) write that the Palaeolithic dogs tend to group together in our statistical analyses but that they do not group with other dogs, except for very large modern breeds. This is not correct. None of the Palaeolithic dogs were assigned to the RDo group, while one specimen (Předmostí (−)) resembles with equal probability both the recent Archaic dogs (RDa) and the Palaeolithic dogs (Germonpré et al., 2012a; Table 9).

Here, we rerun our analysis with only the Palaeolithic dogs, the Recent Archaic dogs, the Recent wolves and the Pleistocene wolves as comparative material, in order to eliminate confusion that could occur due to the presence of the RDo and the small prehistoric dogs. We add as unknown specimens the Předmostí and Avdeevo skulls which could not be assigned to a group in Germonpré et al. (2012a), the four zoo wolves and the F1 hybrid used in Germonpré et al. (2012a) and add also the *Razboinichya canid* (Ovodov et al., 2011) and a large dog skull (Total Length: 202.7 mm) discovered in a prehistoric ritual site near Cambridge (U.K.) dating from the Bronze Age (Baxter, 2007, Table 1). For the methodology the reader is referred to Germonpré et al. (2012a, pp. 189–190).

The DFA based on log$_{10}$-transformed dimensions has a very low Wilks' lambda (0.029, $P < 0.0001$), denoting high discrimination between the groups. Table 1 gives the eigenvalues and the

Table 1

First and second canonical functions observed from the Discriminant Function Analysis based on log$_{10}$-transformed dimensions; measurements, according to von den Driesch (1976), of the fossil large canids skulls used in this study; TL: total skull length (1), VL: viscerocranium length (8), ALP1-M2: alveolar tooth row length P1-M2 (15), P4CL: carnassial crown length (18), GWbrc: greatest braincase width (29), GWpal: greatest palatal width (34), MWpal: minimal palatal width (35).

	Canon 1	Canon 2
Eigenvalue	8.67	1.47
% Explained	81.90	13.89
% Cumulative	81.90	95.79
Eigenvectors		
Log TL (1)	−2.43	−27.86
Log VL (8)	11.23	−39.21
Log ALP1-M2 (15)	17.31	38.45
Log P4CL (18)	33.73	−6.84
Log GWBrc (29)	0.48	36.26
Log GWPal (34)	−8.94	12.13
Log MWPal (35)	−6.82	19.72

eigenvectors of the first two functions, which together account for 95.8% of the variation among the groups. This DFA allows a clear separation of the canids, with a correct classification of 97.2%. Only two skulls are misclassified: two recent wolf skulls are identified as Pleistocene wolf skulls. The centroids of the reference groups are well separated although the range of the Pleistocene wolves overlaps partly with that of the recent wolves (Fig. 1). The probabilities of the Předmostí and Avdeevo skulls once again are too ambiguous to assign them to one of the reference groups (Table 2). We therefore proposed that a possible explanation for their mixed characteristics is that they are captive wolves or hybrids between Palaeolithic dogs and Pleistocene wolves (Germonpré et al., 2012a, p. 195). Interestingly, the "incipient" Razboinichya dog cannot be assigned to the group of the Palaeolithic dogs as its typicality probability is very low (Table 2). The Bronze Age dog also has rather low probabilities in this DFA preventing it being assigned to any group (Table 2).

The DFA based on the size-adjusted variables also has a very low Wilks' lambda, which indicates high discrimination between groups (0.069, $P < 0.0001$). Table 3 gives the eigenvalues and the eigenvectors of the first two functions, which together account for 92.8% of the variation among the groups. This DFA has a high rate of correct classification (91.8%). Only six skulls were misclassified: one Palaeolithic dog (Předmostí (−)) was assigned to the Archaic dog group, two Archaic dogs (two Siberian huskies) were assigned to the Palaeolithic dogs, and three recent wolves were assigned to the group of the Pleistocene wolves. All group centroids are well separated, although the range of the Pleistocene wolves falls almost completely inside the range of the recent wolves and there is an overlap in the ranges of the Palaeolithic dogs and Archaic dogs (Fig. 2). The probabilities of the unassigned Předmostí and Avdeevo skulls are once again too ambiguous to add them to one of the reference groups (Table 4). The "incipient" Razboinichya dog has a low typicality probability (Table 4) for the Palaeolithic dogs group: it has only about 10% chance of actually belonging to the European Palaeolithic dogs group. It is possible that in the future, when increasing the size and variability of the Palaeolithic dog group, the probability of assigning the Razboinichya canid to this group will be higher. On the other hand, the fact that the Razboinichya dog does not fit well with the European Palaeolithic dogs could indicate that it has another origin. Interestingly, the Bronze Age dog from Cambridge (U.K.) that in the first DFA presented low probabilities has in the size-adjusted DFA clear-cut probabilities assigning this dog to both the Palaeolithic dog group and the Archaic dog group, suggesting that its skull shape has characteristics resembling both groups. This together with the overlap