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OXYGEN ISOTOPE FRACTIONATION BETWEEN DENTAL ENAMEL PHOSPHATE AND CARBONATE IN CARNIVORANS – IMPLICATIONS FOR THE PRESERVATION ASSESSMENT IN PALEOECOLOGICAL STUDIES

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Abstract:
The relationship between $\delta^{18}O$ values in phosphate ($\delta^{18}O_P$) and carbonate ($\delta^{18}O_C$) fractions of the dental enamel bioapatite is a tool allowing for evaluation of the preservation of isotopic signal in fossil teeth. In modern mammals, used as a reference, it was recognized until now nearly exclusively in ungulates. To expand the database on the statistically representative set of carnivorans, we analyzed $\delta^{18}O_P$ and $\delta^{18}O_C$ in 32 samples collected from modern dogs and foxes from Poland. We found our data obtained for canids to be similar to that for all other mammals presented in the literature. This observation points toward a universal model of oxygen fractionation between enamel phosphate and carbonate in mammals (at least, in carnivorans, artiodactyls, and perissodactyls).

Key words: Stable isotopes, biogeochemistry, teeth, carnivores, apatite, preservation state.

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INTRODUCTION

Oxygen isotope composition of dental enamel bioapatite is widely used in Quaternary studies, paleontology and archaeology as a proxy of paleoenvironmental conditions (Koch, 2007). It was used, among others, as paleothermometer (Longinelli, 1984; Fox and Fisher, 2001; Skrzypek *et al.*, 2011; Kovács *et al.*, 2015; Britton *et al.*, 2019), paleohumidity indicator (Shahack-Gross *et al.*, 1999; Hoppe, 2006), proxy of drinking water source and ecological niche width (Koch, 1998; Chenery *et al.*, 2012; Baryshnikov, 2014; Trindade Dantas *et al.*, 2020; Asevedo *et al.*, 2021; Lüdecke *et al.*, 2022; Habinger *et al.*, 2023), predictor of geolocation and migrations (Münzel *et al.*, 2014; Ueda and Bell, 2021), tracker of transhumance and husbandry practices (Buchan *et al.*, 2016; Morandi *et al.*, 2021), and record of physiology (Kohn *et al.*, 1998; Robu *et al.*, 2019).

All these studies use numeric $\delta^{18}O$ values, either absolute values of relative differences, and therefore need a well-preserved isotopic signal, not altered by weathering or diagenesis. Several tests for the evaluation of $\delta^{18}O$ preservation state were proposed, such as: intra-population isotopic variability, apatite crystallinity, or carbonate-to-phosphate ratio (Kohn and Cerling, 2002; Marshall *et al.*, 2007; Roche *et al.*, 2010; Trayler and Kohn, 2017; Stefaniak *et al.*, 2021; Toffolo and Richard, 2024). The most direct test, i.e., the one based directly on the $\delta^{18}O$ values within a sample, is the comparison of $\delta^{18}O$ signal between phosphate ($\delta^{18}O_P$) and carbonate ($\delta^{18}O_C$) fractions of the bioapatite (Iacumin *et al.*, 1996; Pellegrini *et al.*, 2011). The test relies on the presence of two oxygen-bearing and relatively easy-to-extract anion groups in the bioapatite, $Ca_{10}[\underline{PO_4},\underline{CO_3}]_6[OH]_2$ (groups underlined; another one is the hydroxyl group that is, however, more difficult to extract; see Wang and Cerling, 1994). It has been found that in many recent (i.e., well preserved) mammalian enamel or bone bioapatite there is a constant shift between the $\delta^{18}O_P$ and $\delta^{18}O_C$ values (Bryant *et al.*, 1996; Iacumin *et al.*, 1996; Shahack-Gross *et al.*, 1999; Zazzo *et al.*, 2004; Martin *et al.*, 2008), and, in a consequence, high correlation between them.

Bryant *et al.* (1996) explained this phenomenon as a consequence of constant metabolic fractionation rate between phosphate and carbonate oxygen due to stable body temperature in homeothermic animals. This hypothesis allows to extrapolate the found $\delta^{18}O_P$–$\delta^{18}O_C$ shift to all mammals of similar body temperature. However, the only modern mammal taxa studied until now in statistically representative number were ungulate herbivores of two orders: perissodactyls and artiodactyls (Bryant *et al.*, 1996; Iacumin *et al.*, 1996; Shahack-Gross *et al.*, 1999; Zazzo *et al.*, 2004; Martin *et al.*, 2008). Many phylogenetic groups were understudied or not studied at all (e.g., marsupials, rodents, lagomorphs, cetaceans, bats, or carnivorans). This makes the all-mammal hypothesis difficult to confirm. The goal of this study is to widen the set of studied mammals by adding a group of another trophic ecology and another phylogeny: the omni- or carnivores of the order Carnivora, whose remains are common in the Pleistocene and Holocene fossil record.

MATERIALS AND METHODS

Our research material were dental enamel samples collected from modern (i.e., not altered by diagenesis or weathering) carnivorans: domestic dog (*Canis familiaris*; 8 specimens, 20 teeth) and red fox (*Vulpes vulpes*; 10 specimens, 12 teeth) (Table 1). All were adult individuals. The studied specimens originate from Poland (obtained from hunters and road kills in 2008–2018) and were selected from the reference osteological collection of the Department of Environmental Archaeology and Human Paleoecology of the Institute of Archaeology, Nicolaus Copernicus University in Toruń, Poland.

Sampling

In each studied tooth, the best-preserved surface of enamel was selected for sampling (the flat area with the least visible cracking, see Table 1). Prior to sampling, the surface was carefully washed with acetone, blown with compressed air, and mechanically cleaned by drilling-off the surficial part with a Dremel diamond-coated bit. We removed dental plaque and any dirt if present. Around 0.3–0.5 mm of the external enamel layer was also removed, because this outer part was reported to be isotopically biased by later mineralization (Reade *et al.*, 2015; Trayler and Kohn, 2017). The exposed surface was washed with Millipore water and dried. To avoid contamination during sampling, the skull/mandible and the sampled tooth outside the sampling surface were covered with parafilm. Enamel samples were collected by careful drilling about 10–20 mg of powder (with care to avoid sampling the dentin).

Chemical pretreatment

The chemical pretreatment method followed Koch *et al.* (1997) and Bocherens *et al.* (1996). Although not needed in our modern material, we applied the elimination of exogenous carbonates and organic contaminants protocol that would be used in the case of any fossil material. The powder was soaked in 1.5 mL of 0.1M acetic acid for 48 h; then it was centrifuged, a supernatant carefully removed with a pipette, and the powder rinsed and vortexed with Millipore water (at least 3× or more, until neutral pH, checked with a universal indicator paper). The powder was then treated with 1.5 mL of 30% H_2O_2 for 24 h; then 4× centrifuged, supernatant removed, and rinsed-vortexed. It was dried in 60°C for 48 h. Loss was determined as the percentage ratio of sample weights before and after the pretreatment subtracted from 100%.

Each sample was then divided into two subsamples: one for the phosphate extraction (around 4 mg) and another one for the direct isotopic measurement of the carbonate fraction (a remaining part, >2 mg, usually around 10 mg). The phosphate extraction procedure followed Koch *et al.* (1997) and Tütken *et al.* (2006). The powder was dissolved in 1.5 mL of 2M HF for 24 h, then neutralized with 25% NH_4OH with bromothymol blue used for pH control. A 0.8 mL aliquot of 2M $AgNO_3$ (i.e., an excess) was then added to precipitate the Ag_3PO_4. The precipitate was centrifuged, a supernatant carefully removed with a pipette, and the solid phase rinsed and vortexed with Millipore water (all repeated 5×). It was dried in 60°C for 72 h. Yield was determined as the ratio of sample weights before and after the pretreatment.

A spit of internal lab standard (powdered enamel of a modern cattle, sample Bos A) followed the entire procedure to control the pretreatment conditions. To identify any possible contamination of the isotopic signal from Paraloid B-72, used as a preserver in the osteological collection (although it was carefully removed with acetone from the sampled teeth), a piece of this preserver was also pretreated and analyzed likewise the samples.

Isotopic analyses

Isotopic analyzes of the phosphate fraction ($\delta^{18}O_P$) were conducted at the Stable Isotopes Lab of the Institute of Geological Sciences, Polish Academy of Sciences in Warsaw (Poland), in a Thermo Flash EA 1112HT elemental analyzer interfaced with Thermo Delta V Advantage IRMS in a continuous flow system. The analytical molecule was

Table 1. Sampled teeth and stable isotope results.

Sample	Collection ID	Taxon	Tooth anatomy	Loss[a] %	CO_3 %	$\delta^{18}O_C$ ‰ VPDB	$\delta^{18}O_C$[b] ‰ VSMOW	$\delta^{13}C$ ‰ VPDB	Yield[c] %	$\delta^{18}O_P$ ‰ VSMOW	$\Delta^{18}O_{C-P}$[d] ‰ VSMOW
H1	CAFA-10	*Canis familiaris*	m1 dex. lab.	43.2	3.32	-9.30	21.32	-13.88	199.8	13.89	7.43
H2	CAFA-10	*Canis familiaris*	c dex. lab.	42.7	3.44	-9.04	21.59	-13.87	208.8	14.81	6.91
H3	CAFA-06	*Canis familiaris*	m1 sin. lab.	35.9	3.82	-10.16	20.43	-14.12	221.9	13.72	6.71
H4	CAFA-06	*Canis familiaris*	c sin. lab.	41.6	3.08	-9.60	21.01	-13.89	157.6	13.57	7.44
H5	CAFA-08	*Canis familiaris*	m1 dex. lab.	42.8	3.55	-9.04	21.60	-11.55	213.3	13.53	8.06
H6	CAFA-08	*Canis familiaris*	c dex. lab.	14.7	3.33	-10.10	20.49	-11.87	218.4	14.06	6.44
H7	CAFA-05	*Canis familiaris*	m1 dex. lab.	38.1	3.94	-9.29	21.34	-15.26	193.1	14.25	7.09
H8	CAFA-05	*Canis familiaris*	c dex. lab.	36.8	3.75	-9.55	21.07	-15.34	211.0	14.74	6.33
H9	CAFA-09	*Canis familiaris*	m1 sin. lab.	24.3	3.74	-9.27	21.36	-15.50	219.1	15.22	6.13
H10	CAFA-09	*Canis familiaris*	c sin. lab.	32.1	4.43	-8.52	22.13	-15.37	219.5	15.14	6.99
H11	CAFA-03	*Canis familiaris*	m1 dex. lab.	33.5	3.27	-8.87	21.77	-14.64	223.2	14.62	7.15
H12	CAFA-03	*Canis familiaris*	c dex. lab.	39.6	3.82	-8.65	22.00	-14.97	221.9	15.16	6.84
H13	CAFA-04	*Canis familiaris*	m1 sin. lab.*	26.6	3.60	-9.94	20.67	-13.82	217.5	13.79	6.88
H14	CAFA-04	*Canis familiaris*	m1 sin. lab.*	32.5	2.99	-9.35	21.27	-14.16	215.9	13.41	7.86
H15	CAFA-04	*Canis familiaris*	p4 sin. lab.	39.1	2.90	-9.44	21.17	-13.93	222.6	13.37	7.14
H16	CAFA-04	*Canis familiaris*	p3 sin. lab.	44.0	3.22	-8.95	21.68	-14.06	220.3	13.74	7.95
H17	CAFA-04	*Canis familiaris*	c sin. lab.†	31.9	3.49	-9.01	21.62	-14.12	209.3	13.79	8.94
H18	CAFA-04	*Canis familiaris*	c sin. lab.†	44.8	3.44	-8.98	21.66	-14.18	208.0	13.74	7.92
H19	CAFA-01	*Canis familiaris*	m1 sin. lab.	33.7	2.21	-9.99	20.61	-14.35	134.2	11.93	8.68
H20	CAFA-01	*Canis familiaris*	c1 sin. lab.	34.8	4.33	-10.29	20.30	-14.27	217.9	11.96	8.34
H21	VUVU-04	*Vulpes vulpes*	C sin. ar.	47.7	3.28	-7.83	22.84	-14.66	201.3	16.17	6.67
H22	VUVU-05	*Vulpes vulpes*	C sin. ar.	45.5	4.48	-8.00	22.66	-15.08	204.3	16.16	6.50
H23	VUVU-08	*Vulpes vulpes*	C sin. ar.	44.3	2.66	-8.00	22.66	-14.89	204.4	14.61	8.05
H24	VUVU-09	*Vulpes vulpes*	C sin. ar.	40.8	2.97	-7.44	23.24	-15.49	215.4	15.57	7.67
H25	VUVU-10	*Vulpes vulpes*	C dex. ar.	43.7	2.41	-6.83	23.87	-14.99	217.0	16.38	7.50
H26	VUVU-11	*Vulpes vulpes*	C sin. ar.	41.1	2.31	-7.98	22.68	-14.56	215.1	15.86	6.82
H27	VUVU-12	*Vulpes vulpes*	C dex. ar.	36.9	3.75	-7.47	23.21	-13.18	226.2	15.68	7.54
H28	VUVU-13	*Vulpes vulpes*	C sin. ar.	40.2	2.45	-8.09	22.57	-16.26	214.1	15.05	7.53
H29	VUVU-14	*Vulpes vulpes*	C dex. ar.	34.2	2.65	-8.07	22.59	-17.15	210.5	15.91	6.68
H30	VUVU-15	*Vulpes vulpes*	C sin. ar.	38.7	3.36	-8.83	21.81	-13.84	219.2	15.33	6.48
H31	VUVU-15	*Vulpes vulpes*	c sin. ar.	35.5	3.16	-9.47	21.15	-13.87	223.8	15.20	5.95
H32	VUVU-14	*Vulpes vulpes*	c dex. ar.	38.8	3.32	-7.44	23.24	-17.17	218.7	15.79	7.45
H33[e]	Bos A	*Bos taurus*	p3 dex. lab.	37.7	4.05	-9.73	20.88	-12.69	227.2	14.07	6.86
H34[f]	–	–	–	0.3	n.s.	n.s.	–	n.s.	0.0	n.s.	–

Tooth anatomy symbols: c – lower canine; C – upper canine; m1 – lower first molar; p3 – lower third premolar; p4 – lower fourth premolar; sin. – left; dex. – right; lab. – labial side; ar. – around (labial and lingual sides); *, † – the same symbol and color marks the same tooth.

[a] after the acetic acid–hydrogen peroxide pretreatment; [b] calculated from the $\delta^{18}O_C$ (‰ VPDB) data; [c] after the HF–NH_4OH–$AgNO_3$ pretreatment; [d] calculated from the $\delta^{18}O_C$ (‰ VSMOW) and ($\delta^{18}O_P$ ‰ VSMOW) data; [e] internal lab standard; [f] Paraloid B-72; n.s. – no signal.

CO, released from the 1450°C pyrolysis of 0.4 mg (±0.03 mg) Ag_3PO_4. The measurements were calibrated using the USGS 80, USGS 81, and B 2207 reference materials. Repeatability of results was 0.3‰ (standard deviation, sd). Each sample was measured in duplicates, and their average was the final value.

Isotopic analyzes of the carbonate fraction ($\delta^{18}O_C$) were conducted at the Biogeology Work Group lab, Department of Geosciences, University of Tübingen (Germany), in the MultiFlow-Geo (automatic CO_2 extraction device) interfaced with Elementar IsoPrime 100 IRMS. The analytical molecule was CO_2, released in the reaction of 2.7 mg (±0.15 mg) of pretreated powder with 99% H_3PO_4 (in excess) in 70°C lasting for 4 h. The measurements were calibrated using the IAEA-603 and NBS18 reference materials. Repeatability of results was 0.2‰ (sd). The $\delta^{13}C$ was also measured, with 0.1‰ repeatability (sd). The CO_3 content (%) was also measured as a ratio of IRMS CO_2 peak area to sample weight, normalized to the known percentage in a standard.

The isotopic ratios are expressed as delta (δ) notation, a deviation in per mil from the standard value (which was VPDB for $\delta^{13}C_C$ and $\delta^{18}O_C$, and VSMOW for $\delta^{18}O_P$). For making the results in variable scales comparable, the $\delta^{18}O_C$ results in a VPDB scale were transformed to VSMOW scale using an equation of Coplen *et al.* (1983): $\delta^{18}O_C(VSMOW) = 1.03091 \cdot \delta^{18}O_C(VPDB) + 30.91$.

Statistics

Ordinary least square regression model was used to determine the linear regression between paired datasets [in a form: y = a(±std. error) x + b(±std. error)]. The analysis of covariance (ANCOVA) was applied to test for equality of slopes, to determine whether two or more $\delta^{18}O_C/\delta^{18}O_P$ trends significantly differed from each other. The Pearson's correlation was used to test for correlation between the parametric (normal distribution) carbonate and phosphate $\delta^{18}O$ values; alternatively, the nonparametric Spearman's correlation was applied. To test for normal distribution, we used Shapiro-Wilk test (with confidence level 0.05). All statistical analyses were performed with the PAST software, version 4.05 (Hammer *et al.*, 2001).

RESULTS

All quality control parameters were stable and acceptable: consequent loss in pretreatment (37.5±6.8%; for comparison it was 37.7% in our bovine internal standard); consequent yield of Ag_3PO_4 precipitation (210.1±18.7%, with 227.2% in the internal standard); and consequent CO_3 content (3.3±0.6%, with 4.1% in the internal standard) (Table 1).

The isotopic results are presented in Table 1 and Fig. 1. The ANCOVA shown no significant differences between foxes' and dogs' $\delta^{18}O_C/\delta^{18}O_P$ linear regressions ($F[1, 29] = 2.838$, $p = 0.1032$) that allows regarding them as one group. The measured $\delta^{18}O_C$ values of the entire dataset ranged between -10.3‰ and -6.8‰ (VPDB), and the $\delta^{18}O_P$ values ranged between 11.9‰ and 16.4‰ (VSMOW), both with normal distribution (Shapiro-Wilk test for normality hypothesis: W = 0.9614 and 0.9518, p = 0.3002 and 0.1624, respectively), which is an appropriate range to test for any linear trends. Pearson's correlation between the $\delta^{18}O_C$ and $\delta^{18}O_P$ values was moderately strong ($r = 0.80798$, $r^2 = 0.65282$) and significant ($p < 10^{-7}$ for the uncorrelated hypothesis). The $\delta^{18}O_C/\delta^{18}O_P$ linear regression followed the equation:

$$\delta^{18}O_P(\text{VSMOW}) = 1.0055(\pm 0.13388) \cdot \delta^{18}O_C(\text{VSMOW}) - 7.3549(\pm 2.9219) \quad \text{[Equation 1]}$$

Paraloid B-72 preserver gave no IRMS signal (Table 1), so we assume that even in the case it had not been fully removed at the cleaning step, it had no impact on isotopic measurements.

DISCUSSION

Intra-individual variability

Intra-individual and inter-tooth variability in dental enamel isotopic record is expected due to incremental growth of enamel that takes (Hillson, 2005), thus reflecting isotopic changes in animal's environment, diet, and drinking water (Fricke *et al.*, 1998; Balasse, 2002; Reade *et al.*, 2015; Pederzani and Britton, 2019). In large-toothed mammals, enamel growth time window may reach >1 year for an individual tooth and several years for the entire tooth row (Hoppe *et al.*, 2004; Feranec *et al.*, 2009; Pawlak *et al.*, 2025), and even longer periods in proboscideans (Müller and Anczkiewicz, 2016). In carnivorans, enamel mineralization and tooth eruption are usually faster than in ungulates, but still the enamel formation process may last for several seasons (Klevezal, 1996; Hillson, 2005). It was found to be reflected in isotopic variability of carnivoran enamel (Feranec, 2004; Czernielewski *et al.*, 2020). Intra-individual differences found in our study (Table 1) are relatively small (0.2‰ on avarage, with a maximum difference of 1.1‰ in a dog CAFA-08) and do not exceed those noticed in other carnivorans. This indicates either a low isotopic variability of ingested water or short periods of mineralization. We checked also within-tooth variability in two teeth (Table 1, sample pairs H13-H14 and H17-H18). Samples were drilled from different elevations of the crown, thus representing different moments of mineralization. The difference was found greater in a molar (0.7‰ on average for both $\delta^{18}O_C$ and $\delta^{18}O_P$) than in a canine (0.0‰ on average), likely idicating different growth rates.

Dogs and foxes against other mammals

Our literature survey found only artiodactyls and perissodactyls, plus three carnivoran specimens, studied so far for the $\delta^{18}O_P/\delta^{18}O_C$ relationship in dental enamel (Supplementary Table). This dataset includes families: bovids, cervids, hippopotamids, equids, and rhinocerotids (Bryant *et al.*, 1996; Iacumin *et al.*, 1996; Shahack-Gross *et al.*, 1999; Zazzo *et al.*, 2004; Martin *et al.*, 2008; Trayler and Kohn, 2017; Miller *et al.*, 2019); and herpestids, ursids, and canids that are discussed below. This bias toward ungulates derives from both research focus (most of studies are focused on herbivores) and analytical issues (ungulate teeth are usually bigger and have thicker enamel than carnivoran ones, so it is easier to sample them).

Our data obtained for canids are within the variability of all other mammals (Fig. 2). The ANCOVA test for equality of the $\delta^{18}O_C/\delta^{18}O_P$ regression slopes of our new data vs. all other mammals revealed no statistical difference ($F[1, 230] = 0.03356$, $p = 0.8548$ for the equality of slopes hypothesis). Literature data allows for modelling dental enamel $\delta^{18}O_P/\delta^{18}O_C$ linear regressions for several families (Table 2). The ANCOVA test reveals that our new regression for canids (Equation 1) is similar (with p values in most cases > 0.7 for the equality of slopes hypothesis) with that of bovids, cervids, hippopotamids, and equids (Bryant *et al.*, 1996; Iacumin *et al.*, 1996; Zazzo *et al.*, 2004; Trayler and Kohn, 2017; Miller *et al.*, 2019). Among tested co-variances, only a pair of canids vs. rhinocerotids exhibits low ANCOVA p-value. However, the rhinocerotid dataset represents only two specimens (Martin *et al.*, 2008), so it has low variance, unequal with the canid dataset, non-normal distribution, and weak linearity, making both datasets not truly comparable.

Dogs and foxes against other carnivorans

Our literature survey revealed only three carnivoran specimens that were studied so far for $\delta^{18}O_P/\delta^{18}O_C$ relation-

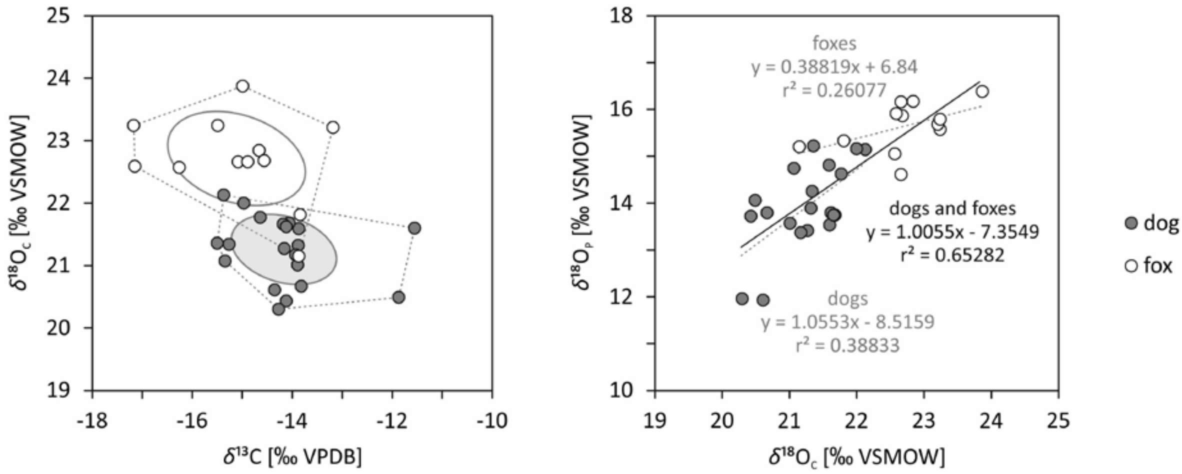

Fig. 1. Results of δ^{13}C, $\delta^{18}O_C$, and $\delta^{18}O_P$ measurements in studied dog and fox enamel. Left panel: $\delta^{13}C/\delta^{18}O_C$ isotopic niches (dashed line for convex hulls; continuous line for 40% probability ellipses). Right panel: newly obtained dog and fox $\delta^{18}O_C/\delta^{18}O_P$ relationship (gray dashed lines for trend lines, separately for dogs and foxes; a continuous line for the overall trend).

ship in dental enamel (Iacumin *et al.*, 1996). These belong to: white-tailed mongoose (*Ichneumon albicauda*), American black bear (*Ursus americanus*), and gray wolf (*Canis lupus*). While mongoose, coming from tropical climate, and wolf, from boreal climate, gave δ^{18}O absolute values that are very different from our dataset, they all form a linear trend (Fig. 2) that follows the trend in ungulates. The correlation between carbonate and phosphate δ^{18}O values in the entire dataset of carnivorans is very good (Spearman's correlation: $\rho = 0.77773$, $p < 10^{-7}$ for the uncorrelated hypothesis). This points toward the same oxygen fractionation model in carnivorans, regardless of the phylogeny (canids, ursids, herpestids) or trophic ecology (hypercarnivores: wolf, mongoose; opportunistic carni-/omnivore: fox; omnivores: black bear, dog).

Phosphate-carbonate oxygen isotope fractionation in mammals

According to the observations presented above, carnivorans (in particular, canids) exhibit the same $\delta^{18}O_C/\delta^{18}O_P$ relationship as artiodactyls and perissodactyls. It is thus justified to use the same linear regression to test for the preservation state of dental enamel isotopic record, regardless of taxonomy. The overall linear regression model, including our new data and all modern mammals studied so far (N = 233; Bryant *et al.*, 1996; Iacumin *et al.*, 1996; Shahack-Gross *et al.*, 1999; Zazzo *et al.*, 2004; Martin *et al.*, 2008; Trayler and Kohn, 2017; Miller *et al.*, 2019), follows the equation:

$$\delta^{18}O_P(\text{VSMOW}) = 0.95893(\pm 0.014443)\ \delta^{18}O_C(\text{VSMOW}) - 7.5694(\pm 0.34496) \quad \text{[Equation 2]}$$

with very strong correlation. Pearson's correlation provides $r = 0.97478$, $r^2 = 0.95019$, with $p < 10^{-100}$, however, the test for normal distribution is slightly violated for the confidence level 0.05 (Shapiro-Wilk $p = 0.04154$ for $\delta^{18}O_C$ and 0.0565 for $\delta^{18}O_P$ – a consequence of different isotopic values between animals from different climates). Nonparametric Spearman's correlation provides $\rho = 0.96869$, $p < 10^{-100}$. The reverse equation is:

$$\delta^{18}O_C(\text{VSMOW}) = 0.9909(\pm 0.014925) \cdot \delta^{18}O_P(\text{VSMOW}) + 8.6684(\pm 0.23232) \quad \text{[Equation 3]}$$

Spacing between the $\delta^{18}O_C$ and $\delta^{18}O_P$ values (known as $\Delta^{18}O_{C\text{-}P}$) for our canid dataset is 7.2±0.7‰ (data in the VSMOW scale), while for all mammals, including our new data, it is 8.5±1.0‰. We recommend using the presented

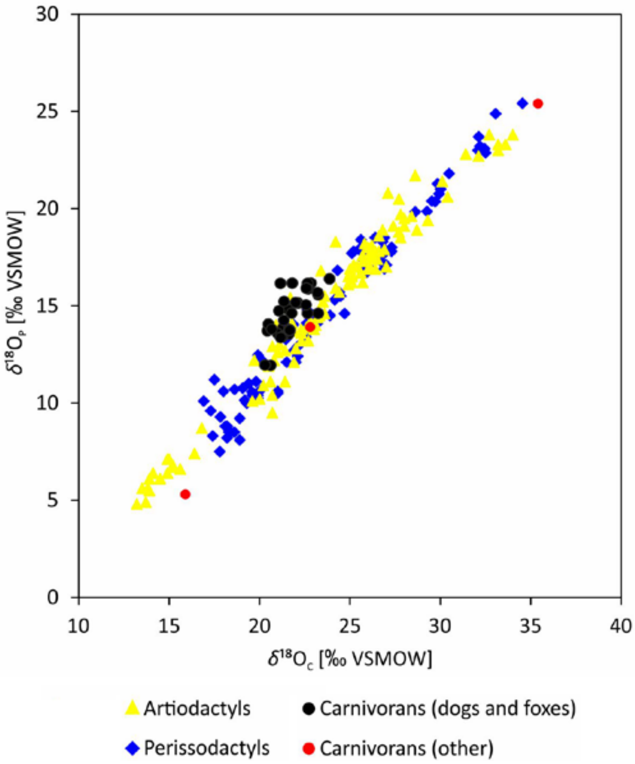

Fig. 2. Comparison of newly obtained dog and fox $\delta^{18}O_C/\delta^{18}O_P$ relationship with those known for modern perissodactyls, artiodactyls, and carnivorans (literature data from: Bryant *et al.*, 1996; Iacumin *et al.*, 1996; Shahack-Gross *et al.*, 1999; Zazzo *et al.*, 2004; Martin *et al.*, 2008).

Table 2. Comparison of $\delta^{18}O_P/\delta^{18}O_C$ linear regressions for variable phylogenetic groups (families) of mammals.

Family	N	Linear regression model	Reference for data	ANCOVA		
				F	df	*p* (same)
Canids	32	$\delta^{18}O_P = 1.0055(\pm0.13388) \cdot \delta^{18}O_C - 7.3549(\pm2.9219)$	new data	–	–	–
Bovids[a]	21	$\delta^{18}O_P = 1.2027(\pm0.14825) \cdot \delta^{18}O_C - 13.557(\pm3.2324)$	Iacumin *et al.* (1996); Trayler and Kohn (2017)	1.001	1.50	0.3219
Cervids[b]	58	$\delta^{18}O_P = 0.97565(\pm0.02064) \cdot \delta^{18}O_C - 7.7954(\pm0.46571)$	Trayler and Kohn (2017); Miller *et al.* (2019)	0.04457	1.87	0.8333
Cervids[c]	12	$\delta^{18}O_P = 1.0854(\pm0.27433) \cdot \delta^{18}O_C - 10.452(\pm7.4529)$	Miller *et al.* (2019)	0.08954	1.41	0.7663
Hippopotamids	7	$\delta^{18}O_P = 0.96811(\pm0.048738) \cdot \delta^{18}O_C - 8.9345(\pm1.5023)$	Zazzo *et al.* (2004)	0.05345	1.36	0.8185
Equids[d]	52	$\delta^{18}O_P = 0.97712(\pm0.054482) \cdot \delta^{18}O_C - 8.4597(\pm1.1328)$	Bryant *et al.* (1996); Trayler and Kohn (2017)	0.02603	1.81	0.8722
Equids[e]	15	$\delta^{18}O_P = 1.035(\pm0.07205) \cdot \delta^{18}O_C - 10.102(\pm2.2553)$	Bryant *et al.* (1996)	0.03326	1.43	0.8562
Rhinocerotids	26	$\delta^{18}O_P = 0.2165(\pm0.17814) \cdot \delta^{18}O_C + 12.032(\pm4.6872)$	Martin *et al.* (2008)	11.45	1.55	0.001339

Only data from similar climate are included into each group, to keep datasets' normality and variance homogeneity. ANCOVA is presented for the new dataset of dogs and foxes vs. the compared groups. All δ^{18}Ovalues in VSMOW scale. [a] temperate climates only (*Bos taurus*, *Capra hircus*); [b] temperate climates only (*Cervus elaphus*, *Dama dama*); [c] subtropical climates only (*Dama dama*); [d] temperate climates only (*Equus caballus*); [e] tropical climates only (*Equus burchelli*).

linear regressions and spacings as references in studies of the preservation of isotopic signal in fossil tooth enamel.

CONCLUSIONS

We found the dental enamel $\delta^{18}O_C/\delta^{18}O_P$ relationship in modern dogs and foxes similar (statistically significant) to that known for modern ungulates. This observation points toward a universal model of oxygen fractionation between enamel phosphate and carbonate in mammals (at least, in carnivorans, artiodactyls, and perissodactyls); this further justifies to apply the model for other phylogenetic groups. The data allows to refine the expected $\delta^{18}O_C/\delta^{18}O_P$ regression and $\delta^{18}O_C$–$\delta^{18}O_P$ spacing that are used as parameters to check the isotopic preservation in fossil teeth.

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Supplementary materials

This paper is supplemented by a Supplementary Table (an Excel file).

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Supplementary Table – database of the used data.

Order	Family	Species	Climate	tooth	$\delta^{18}O_C$	$\delta^{18}O_P$	Ref.	$\Delta^{18}O_{C-P}$
Artiodactyla	bovid	*Alcephalus major*	subtropical		30.1	21.4	Iacumin et al. (1996)	8.7
Artiodactyla	bovid	*Bos taurus*	temperate		24.4	15.7	Iacumin et al. (1996)	8.7
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	20.6	11.1	Trayler and Kohn (2017)	9.5
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	20.8	12.2	Trayler and Kohn (2017)	8.6
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	20.7	12.9	Trayler and Kohn (2017)	7.8
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	21.1	13.0	Trayler and Kohn (2017)	8.1
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	21.4	12.7	Trayler and Kohn (2017)	8.7
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	21.9	13.7	Trayler and Kohn (2017)	8.2
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	22.3	13.8	Trayler and Kohn (2017)	8.5
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	22.3	13.2	Trayler and Kohn (2017)	9.1
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	22.8	14.2	Trayler and Kohn (2017)	8.6
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	22.6	13.9	Trayler and Kohn (2017)	8.7
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	23.2	14.4	Trayler and Kohn (2017)	8.8
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	23.1	14.0	Trayler and Kohn (2017)	9.1
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	23.0	13.8	Trayler and Kohn (2017)	9.2
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	22.7	13.2	Trayler and Kohn (2017)	9.5
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	21.9	12.1	Trayler and Kohn (2017)	9.8
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	21.4	11.1	Trayler and Kohn (2017)	10.3
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	20.7	10.4	Trayler and Kohn (2017)	10.3
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	20.0	10.2	Trayler and Kohn (2017)	9.8
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	20.7	9.5	Trayler and Kohn (2017)	11.2
Artiodactyla	bovid	*Capra hircus*	temperate?	M3	19.6	10.1	Trayler and Kohn (2017)	9.5
Artiodactyla	bovid	*Gazella gazella*	subtropical		33.2	23.3	Shahack-Gross et al. (1990)	9.9
Artiodactyla	bovid	*Kobus* sp.	tropical		32.7	23.8	Iacumin et al. (1996)	8.9
Artiodactyla	bovid	*Syncerus caffer*	tropical		31.4	22.8	Iacumin et al. (1996)	8.6
Artiodactyla	camelid	*Camelus dromaderius*	subtropical		33.2	23.0	Iacumin et al. (1996)	10.2
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	16.4	7.4	Trayler and Kohn (2017)	9.0
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	14.9	7.1	Trayler and Kohn (2017)	7.8
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	14.5	6.1	Trayler and Kohn (2017)	8.4
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	13.9	5.5	Trayler and Kohn (2017)	8.4
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	13.5	5.6	Trayler and Kohn (2017)	7.9
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	13.8	5.6	Trayler and Kohn (2017)	8.2
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	13.9	6.1	Trayler and Kohn (2017)	7.8
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	13.7	4.9	Trayler and Kohn (2017)	8.8
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	16.8	8.7	Trayler and Kohn (2017)	8.1
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	15.6	6.6	Trayler and Kohn (2017)	9.0
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	15.2	6.7	Trayler and Kohn (2017)	8.5
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	14.1	6.4	Trayler and Kohn (2017)	7.7
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	15.0	7.1	Trayler and Kohn (2017)	7.9
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	14.9	6.4	Trayler and Kohn (2017)	8.5
Artiodactyla	cervid	*Cervus elaphus*	temperate?	M3	15.2	6.8	Trayler and Kohn (2017)	8.4
Artiodactyla	cervid	*Dama dama*	subtropical	I	28.6	21.7	Miller et al. (2019)	6.9
Artiodactyla	cervid	*Dama dama*	subtropical	I	27.8	18.5	Miller et al. (2019)	9.3
Artiodactyla	cervid	*Dama dama*	subtropical	I	27.1	20.8	Miller et al. (2019)	6.3
Artiodactyla	cervid	*Dama dama*	subtropical	M3	26.4	17.8	Miller et al. (2019)	8.6

Artiodactyla	cervid	*Dama dama*	subtropical	M3	26.6	18.6	Miller et al. (2019)	8.0
Artiodactyla	cervid	*Dama dama*	subtropical	M3	28.4	19.6	Miller et al. (2019)	8.8
Artiodactyla	cervid	*Dama dama*	subtropical	M3	25.7	17.3	Miller et al. (2019)	8.4
Artiodactyla	cervid	*Dama dama*	subtropical	M3	26.1	17.5	Miller et al. (2019)	8.6
Artiodactyla	cervid	*Dama dama*	subtropical	M3	25.7	17.6	Miller et al. (2019)	8.1
Artiodactyla	cervid	*Dama dama*	subtropical	I	27.7	18.8	Miller et al. (2019)	8.9
Artiodactyla	cervid	*Dama dama*	subtropical	I	28.0	19.5	Miller et al. (2019)	8.5
Artiodactyla	cervid	*Dama dama*	subtropical	I	27.7	20.5	Miller et al. (2019)	7.2
Artiodactyla	cervid	*Dama dama*	temperate	M3	27.8	19.7	Miller et al. (2019)	8.1
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.8	17.3	Miller et al. (2019)	8.5
Artiodactyla	cervid	*Dama dama*	temperate	M3	26.1	17.7	Miller et al. (2019)	8.4
Artiodactyla	cervid	*Dama dama*	temperate	I	20.5	11.9	Miller et al. (2019)	8.6
Artiodactyla	cervid	*Dama dama*	temperate	I	21.7	15.4	Miller et al. (2019)	6.3
Artiodactyla	cervid	*Dama dama*	temperate	I	20.2	10.9	Miller et al. (2019)	9.3
Artiodactyla	cervid	*Dama dama*	temperate	M3	21.0	12.6	Miller et al. (2019)	8.4
Artiodactyla	cervid	*Dama dama*	temperate	M3	20.5	13.8	Miller et al. (2019)	6.7
Artiodactyla	cervid	*Dama dama*	temperate	M3	23.6	15.5	Miller et al. (2019)	8.1
Artiodactyla	cervid	*Dama dama*	temperate	M3	26.6	17.8	Miller et al. (2019)	8.8
Artiodactyla	cervid	*Dama dama*	temperate	M3	23.6	14.6	Miller et al. (2019)	9.0
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.1	16.2	Miller et al. (2019)	8.9
Artiodactyla	cervid	*Dama dama*	temperate	M3	20.9	14.0	Miller et al. (2019)	6.9
Artiodactyla	cervid	*Dama dama*	temperate	M3	21.8	14.1	Miller et al. (2019)	7.7
Artiodactyla	cervid	*Dama dama*	temperate	M3	22.3	13.6	Miller et al. (2019)	8.7
Artiodactyla	cervid	*Dama dama*	temperate	M3	26.8	18.9	Miller et al. (2019)	7.9
Artiodactyla	cervid	*Dama dama*	temperate	M3	27.4	19.1	Miller et al. (2019)	8.3
Artiodactyla	cervid	*Dama dama*	temperate	M3	24.2	18.3	Miller et al. (2019)	5.9
Artiodactyla	cervid	*Dama dama*	temperate	M3	23.3	14.5	Miller et al. (2019)	8.8
Artiodactyla	cervid	*Dama dama*	temperate	M3	24.9	16.5	Miller et al. (2019)	8.4
Artiodactyla	cervid	*Dama dama*	temperate	M3	22.0	12.8	Miller et al. (2019)	9.2
Artiodactyla	cervid	*Dama dama*	temperate	M3	24.2	15.9	Miller et al. (2019)	8.3
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.7	16.2	Miller et al. (2019)	9.5
Artiodactyla	cervid	*Dama dama*	temperate	M3	23.5	15.2	Miller et al. (2019)	8.3
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.9	17.3	Miller et al. (2019)	8.6
Artiodactyla	cervid	*Dama dama*	temperate	M3	24.9	16.1	Miller et al. (2019)	8.8
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.2	17.1	Miller et al. (2019)	8.1
Artiodactyla	cervid	*Dama dama*	temperate	M3	23.4	16.8	Miller et al. (2019)	6.6
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.1	16.6	Miller et al. (2019)	8.5
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.0	16.9	Miller et al. (2019)	8.1
Artiodactyla	cervid	*Dama dama*	temperate	M3	26.9	17.9	Miller et al. (2019)	9.0
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.4	17.0	Miller et al. (2019)	8.4
Artiodactyla	cervid	*Dama dama*	temperate	M3	26.2	18.1	Miller et al. (2019)	8.1
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.8	18.2	Miller et al. (2019)	7.6
Artiodactyla	cervid	*Dama dama*	temperate	M3	28.0	19.1	Miller et al. (2019)	8.9
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.1	16.5	Miller et al. (2019)	8.6
Artiodactyla	cervid	*Dama dama*	temperate	M3	26.0	18.0	Miller et al. (2019)	8.0
Artiodactyla	cervid	*Dama dama*	temperate	M3	26.0	16.9	Miller et al. (2019)	9.1
Artiodactyla	cervid	*Dama dama*	temperate	M3	25.6	16.7	Miller et al. (2019)	8.9
Artiodactyla	cervid	*Dama dama*	temperate	I	26.4	16.9	Miller et al. (2019)	9.5

Artiodactyla	cervid	*Dama dama*	temperate	I	25.6	16.7	Miller et al. (2019)	8.9
Artiodactyla	cervid	*Dama dama*	temperate	I	26.5	17.4	Miller et al. (2019)	9.1
Artiodactąyla	cervid	*Dama dama*	temperate	I	26.1	17.0	Miller et al. (2019)	9.1
Artiodactyąla	cervid	*Ragnifer tarandus*	boreal		13.2	4.8	Iacumin et al. (1996)	8.4
Artiodactyla	cervid	*Ragnifer tarandus*	temperate		19.7	12.2	Iacumin et al. (1996)	7.5
Artiodactyla	hippopotamid	*Hippopotamus amphibius*	tropical	C1	33.6	23.3	Zazzo et al. (2004)	10.3
Artiodactyla	hippopotamid	*Hippopotamus amphibius*	tropical	M1	32.1	22.7	Zazzo et al. (2004)	9.4
Artiodactyla	hippopotamid	*Hippopotamus amphibius*	tropical	M1	28.7	18.9	Zazzo et al. (2004)	9.8
Artiodactyla	hippopotamid	*Hippopotamus amphibius*	tropical	P4	29.3	19.4	Zazzo et al. (2004)	9.9
Artiodactyla	hippopotamid	*Hippopotamus amphibius*	tropical	p3	27.0	17.0	Zazzo et al. (2004)	10.0
Artiodactyla	hippopotamid	*Hippopotamus amphibius*	tropical	P3	34.0	23.8	Zazzo et al. (2004)	10.2
Artiodactyla	hippopotamid	*Hippopotamus amphibius*	tropical	C1	30.4	20.6	Zazzo et al. (2004)	9.8
Carnivora	canid	*Canis familiaris*	temperate	m1 dex. lab.	21.3	13.9	NEW DATA	7.4
Carnivora	canid	*Canis familiaris*	temperate	c dex. lab.	21.6	14.8	NEW DATA	6.8
Carnivora	canid	*Canis familiaris*	temperate	m1 sin. lab.	20.4	13.7	NEW DATA	6.7
Carnivora	canid	*Canis familiaris*	temperate	c sin. lab.	21.0	13.6	NEW DATA	7.4
Carnivora	canid	*Canis familiaris*	temperate	m1 dex. lab.	21.6	13.5	NEW DATA	8.1
Carnivora	canid	*Canis familiaris*	temperate	c dex. lab.	20.5	14.1	NEW DATA	6.4
Carnivora	canid	*Canis familiaris*	temperate	m1 dex. lab.	21.3	14.3	NEW DATA	7.1
Carnivora	canid	*Canis familiaris*	temperate	c dex. lab.	21.1	14.7	NEW DATA	6.3
Carnivora	canid	*Canis familiaris*	temperate	m1 sin. lab.	21.4	15.2	NEW DATA	6.1
Carnivora	canid	*Canis familiaris*	temperate	c sin. lab.	22.1	15.1	NEW DATA	7.0
Carnivora	canid	*Canis familiaris*	temperate	m1 dex. lab.	21.8	14.6	NEW DATA	7.2
Carnivora	canid	*Canis familiaris*	temperate	c dex. lab.	22.0	15.2	NEW DATA	6.8
Carnivora	canid	*Canis familiaris*	temperate	m1 sin. lab.*	20.7	13.8	NEW DATA	6.9
Carnivora	canid	*Canis familiaris*	temperate	m1 sin. lab.*	21.3	13.4	NEW DATA	7.9
Carnivora	canid	*Canis familiaris*	temperate	p4 sin. lab.	21.2	13.4	NEW DATA	7.8
Carnivora	canid	*Canis familiaris*	temperate	p3 sin. lab.	21.7	13.7	NEW DATA	7.9
Carnivora	canid	*Canis familiaris*	temperate	c sin. lab.†	21.6	13.8	NEW DATA	7.8
Carnivora	canid	*Canis familiaris*	temperate	c sin. lab.†	21.7	13.7	NEW DATA	7.9
Carnivora	canid	*Canis familiaris*	temperate	m1 sin. lab.	20.6	11.9	NEW DATA	8.7
Carnivora	canid	*Canis familiaris*	temperate	c1 sin. lab.	20.3	12.0	NEW DATA	8.3
Carnivora	canid	*Canis lupus*	boreal		15.9	5.3	Iacumin et al. (1996)	10.6
Carnivora	canid	*Vulpes vulpes*	temperate	C sin. ar.	22.8	16.2	NEW DATA	6.7
Carnivora	canid	*Vulpes vulpes*	temperate	C sin. ar.	22.7	16.2	NEW DATA	6.5
Carnivora	canid	*Vulpes vulpes*	temperate	C sin. ar.	22.7	14.6	NEW DATA	8.1
Carnivora	canid	*Vulpes vulpes*	temperate	C sin. ar.	23.2	15.6	NEW DATA	7.7
Carnivora	canid	*Vulpes vulpes*	temperate	C dex. ar.	23.9	16.4	NEW DATA	7.5
Carnivora	canid	*Vulpes vulpes*	temperate	C sin. ar.	22.7	15.9	NEW DATA	6.8
Carnivora	canid	*Vulpes vulpes*	temperate	C dex. ar.	23.2	15.7	NEW DATA	7.5
Carnivora	canid	*Vulpes vulpes*	temperate	C sin. ar.	22.6	15.1	NEW DATA	7.5
Carnivora	canid	*Vulpes vulpes*	temperate	C dex. ar.	22.6	15.9	NEW DATA	6.7
Carnivora	canid	*Vulpes vulpes*	temperate	C sin. ar.	21.8	15.3	NEW DATA	6.5
Carnivora	canid	*Vulpes vulpes*	temperate	c sin. ar.	21.2	15.2	NEW DATA	6.0
Carnivora	canid	*Vulpes vulpes*	temperate	c dex. ar.	23.2	15.8	NEW DATA	7.5
Carnivora	herpestid	*Ichneumon albicauda*	tropical		35.4	25.4	Iacumin et al. (1996)	10.0

Carnivora	ursid	*Ursus americanus*	boreal		22.8	13.9	Iacumin et al. (1996)	8.9
Perissodactyla	equid	*Equus burchelli*	subtropical	P4	26.0	17.0	Bryant et al. (1996)	9.0
Perissodactyla	equid	*Equus burchelli*	tropical	P2	29.9	20.8	Bryant et al. (1996)	9.2
Perissodactyla	equid	*Equus burchelli*	tropical	P3	29.5	20.4	Bryant et al. (1996)	9.1
Perissodactyla	equid	*Equus burchelli*	tropical	P4	30.0	21.0	Bryant et al. (1996)	9.0
Perissodactyla	equid	*Equus burchelli*	tropical	M1	29.7	20.4	Bryant et al. (1996)	9.4
Perissodactyla	equid	*Equus burchelli*	tropical	M2	29.3	19.9	Bryant et al. (1996)	9.4
Perissodactyla	equid	*Equus burchelli*	tropical	M3	29.8	21.3	Bryant et al. (1996)	8.6
Perissodactyla	equid	*Equus burchelli*	tropical	P2	32.5	23.1	Bryant et al. (1996)	9.4
Perissodactyla	equid	*Equus burchelli*	tropical	P3	32.1	23.7	Bryant et al. (1996)	8.4
Perissodactyla	equid	*Equus burchelli*	tropical	P4	32.2	23.2	Bryant et al. (1996)	9.0
Perissodactyla	equid	*Equus burchelli*	tropical	M1	33.1	24.9	Bryant et al. (1996)	8.2
Perissodactyla	equid	*Equus burchelli*	tropical	M2	32.1	23.0	Bryant et al. (1996)	9.1
Perissodactyla	equid	*Equus burchelli*	tropical	M3	32.5	22.9	Bryant et al. (1996)	9.6
Perissodactyla	equid	*Equus burchelli*	tropical	M2	30.5	21.8	Bryant et al. (1996)	8.7
Perissodactyla	equid	*Equus burchelli*	tropical	M2	34.5	25.4	Bryant et al. (1996)	9.1
Perissodactyla	equid	*Equus caballus*	temperate	P2	19.6	10.6	Bryant et al. (1996)	9.0
Perissodactyla	equid	*Equus caballus*	temperate	P3	19.1	10.8	Bryant et al. (1996)	8.3
Perissodactyla	equid	*Equus caballus*	temperate	P4	20.1	10.7	Bryant et al. (1996)	9.4
Perissodactyla	equid	*Equus caballus*	temperate	M1	20.1	12.2	Bryant et al. (1996)	7.8
Perissodactyla	equid	*Equus caballus*	temperate	M2	19.9	10.4	Bryant et al. (1996)	9.5
Perissodactyla	equid	*Equus caballus*	temperate	M3	19.9	10.3	Bryant et al. (1996)	9.6
Perissodactyla	equid	*Equus caballus*	temperate	p2	19.3	10.0	Bryant et al. (1996)	9.3
Perissodactyla	equid	*Equus caballus*	temperate	p3	19.2	10.1	Bryant et al. (1996)	9.0
Perissodactyla	equid	*Equus caballus*	temperate	p4	17.8	9.3	Bryant et al. (1996)	8.6
Perissodactyla	equid	*Equus caballus*	temperate	m1	19.9	12.5	Bryant et al. (1996)	7.5
Perissodactyla	equid	*Equus caballus*	temperate	m2	20.2	12.1	Bryant et al. (1996)	8.1
Perissodactyla	equid	*Equus caballus*	temperate	m3	18.6	10.7	Bryant et al. (1996)	7.9
Perissodactyla	equid	*Equus caballus*	temperate	dP2	24.5	15.5	Bryant et al. (1996)	9.0
Perissodactyla	equid	*Equus caballus*	temperate	dP3	22.6	13.4	Bryant et al. (1996)	9.2
Perissodactyla	equid	*Equus caballus*	temperate	dP4	24.2	15.3	Bryant et al. (1996)	8.9
Perissodactyla	equid	*Equus caballus*	temperate	P2(unerupted)	21.5	13.3	Bryant et al. (1996)	8.2
Perissodactyla	equid	*Equus caballus*	temperate	P3(unerupted)	22.7	14.8	Bryant et al. (1996)	7.9
Perissodactyla	equid	*Equus caballus*	temperate	P4(unerupted)	21.9	14.0	Bryant et al. (1996)	7.8
Perissodactyla	equid	*Equus caballus*	temperate	M1	23.2	14.3	Bryant et al. (1996)	8.8
Perissodactyla	equid	*Equus caballus*	temperate	M2	22.3	13.5	Bryant et al. (1996)	8.9
Perissodactyla	equid	*Equus caballus*	temperate	M3(unerupted)	24.3	16.8	Bryant et al. (1996)	7.5
Perissodactyla	equid	*Equus caballus*	temperate	M2	28.6	19.8	Bryant et al. (1996)	8.8
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	24.4	15.7	Trayler and Kohn (2017)	8.7
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	24.7	14.6	Trayler and Kohn (2017)	10.1
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	22.8	14.2	Trayler and Kohn (2017)	8.6
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	23.9	14.5	Trayler and Kohn (2017)	9.4
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	23.2	14.1	Trayler and Kohn (2017)	9.1
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	22.6	14.1	Trayler and Kohn (2017)	8.5
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	22.1	12.9	Trayler and Kohn (2017)	9.2
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	22.1	12.4	Trayler and Kohn (2017)	9.7
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	22.0	12.1	Trayler and Kohn (2017)	9.9
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	21.9	12.7	Trayler and Kohn (2017)	9.2

Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	21.5	12.1	Trayler and Kohn (2017)	9.4
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	21.0	10.6	Trayler and Kohn (2017)	10.4
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	21.0	10.5	Trayler and Kohn (2017)	10.5
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	19.6	10.4	Trayler and Kohn (2017)	9.2
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	18.9	9.2	Trayler and Kohn (2017)	9.7
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	18.6	8.5	Trayler and Kohn (2017)	10.1
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	18.1	8.8	Trayler and Kohn (2017)	9.3
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	18.9	8.1	Trayler and Kohn (2017)	10.8
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	18.4	8.5	Trayler and Kohn (2017)	9.9
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	17.8	7.5	Trayler and Kohn (2017)	10.3
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	18.2	8.2	Trayler and Kohn (2017)	10.0
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	17.4	8.3	Trayler and Kohn (2017)	9.1
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	17.3	9.6	Trayler and Kohn (2017)	7.7
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	18.3	8.5	Trayler and Kohn (2017)	9.8
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	18.2	8.8	Trayler and Kohn (2017)	9.4
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	16.9	10.1	Trayler and Kohn (2017)	6.8
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	18.0	10.6	Trayler and Kohn (2017)	7.4
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	17.5	11.2	Trayler and Kohn (2017)	6.3
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	19.4	11.0	Trayler and Kohn (2017)	8.4
Perissodactyla	equid	*Equus ferus caballus*	temperate?	M3	19.8	11.1	Trayler and Kohn (2017)	8.7
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.4	18.5	Martin et al. (2008)	7.9
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.9	17.7	Martin et al. (2008)	9.2
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.8	18.6	Martin et al. (2008)	8.2
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.8	18.5	Martin et al. (2008)	8.3
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.9	16.9	Martin et al. (2008)	10.0
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.9	18.5	Martin et al. (2008)	8.4
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.8	17.8	Martin et al. (2008)	9.0
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.8	18.3	Martin et al. (2008)	8.5
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.7	17.3	Martin et al. (2008)	9.4
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	27.3	18.0	Martin et al. (2008)	9.3
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	27.3	17.8	Martin et al. (2008)	9.5
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	27.0	17.1	Martin et al. (2008)	9.9
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.9	17.9	Martin et al. (2008)	9.0
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	26.4	18.5	Martin et al. (2008)	7.9
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M1	25.8	17.9	Martin et al. (2008)	7.9
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	26.0	17.0	Martin et al. (2008)	9.0
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	25.9	16.7	Martin et al. (2008)	9.2
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	25.7	16.9	Martin et al. (2008)	8.8
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	25.8	16.9	Martin et al. (2008)	8.9
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	25.8	17.3	Martin et al. (2008)	8.5
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	25.8	17.7	Martin et al. (2008)	8.1
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	25.8	17.3	Martin et al. (2008)	8.5
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	25.6	18.4	Martin et al. (2008)	7.2
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	25.5	17.9	Martin et al. (2008)	7.6
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	25.1	17.7	Martin et al. (2008)	7.4
Perissodactyla	rhinocerotid	*Rhinoceros unicornis*	tropical	M2	25.2	17.8	Martin et al. (2008)	7.4