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Reply to "Comment on "Isotopic insight on paleodiet of …" by Bocherens et al. (Gondwana Research, 48(1), 7–14)"

Fariña and Varela (2018) consider that the observed pattern of difference between $\delta^{13}C$ in the carbonate fraction of bioapatite and bone collagen ($\Delta\delta^{13}C_{carb\text{-}coll}$) presented for extinct giant Xenarthrans, especially the giant ground sloth *Megatherium*, do not demonstrate an herbivorous diet, as concluded by Bocherens et al. (2017). The main argument is that the influence of body mass on $\Delta\delta^{13}C_{carb\text{-}coll}$ values would not have been considered in Bocherens et al. (2017). However, contrary to the assertion by Fariña and Varela (2018), the possible influence of body mass on $\Delta\delta^{13}C_{carb\text{-}coll}$ was actually considered in this work. Indeed, small and large herbivorous as well as small and large carnivorous mammals were considered separately among the modern mammals used as reference to compare the fossil specimens (Fig. 2 and Table 2 in Bocherens et al., 2017). Small and large carnivores on the one hand, and small and large herbivores on the other hand, presented statistically significant differences. Despite these differences linked to size, small herbivores and small carnivores presented statistically significant differences ($p < 0.0001$), as did large carnivores and large herbivores ($p = 0.008$) (Table 2 in Bocherens et al., 2017). Therefore, the possibility to infer dietary preferences from $\Delta\delta^{13}C_{carb\text{-}coll}$ in each size class was checked on modern specimens with known diets before inferring the paleodiet of extinct Xenarthrans using the same approach.

When considering a continuous variation in body mass as done by Fariña and Varela (2018, Fig. 1B), it is noticeable that the correlation for extant mammals, though statistically significant, has a r^2 value of only 0.17 (Fariña and Varela, 2018), meaning that only 17% of the correlation is explained by body mass, and 83% by other factors. Moreover, the lack of any carnivorous species with a body mass higher than 300 kg leads to a very large confidence interval that overlaps with that of herbivores in the range of Log Body Mass above 3 (corresponding to body masses above 1000 kg). The fact that one value for *Megatherium* falls at the margin of this very wide confidence interval for carnivores is probably a statistical artefact. To test if this is the case, we included into the same type of graph the data from the late Pleistocene of Beringia (from Clementz et al., 2009) and combined them with data from Bocherens et al. (2017) for large modern mammals with different trophic ecologies (herbivores, insectivores, omnivores and carnivores) and the data for the late Pleistocene Pampean mammals from the same publication. The body masses were taken from Smith et al. (2003). The graph shows that all $\Delta\delta^{13}C_{carb\text{-}coll}$ values of carnivores, insectivores and omnivores in the selected body mass have average values lower than those of herbivores in the same body mass range (Fig. 1). There is a slight overlap when considering the standard-deviations in the range of $\Delta\delta^{13}C_{carb\text{-}coll}$ values between 5 and 6, but the overwhelming majority of large herbivores exhibit $\Delta\delta^{13}C_{carb\text{-}coll}$ values well above those of large carnivores (Fig. 1). As noted before, there is no large carnivore or omnivore in a similar body mass range as *Megatherium*, but interestingly, the woolly mammoth from Beringia exhibits an average a $\Delta\delta^{13}C_{carb\text{-}coll}$ value even lower than that of *Megatherium*, and there is no doubt that this proboscidean was purely herbivore (e.g. Bocherens, 2003; Schwartz-Narbonne et al., 2015; Naito et al., 2016). Also, *Macrauchenia*, a pure herbivore with a body weight reaching 1 ton, has a $\Delta\delta^{13}C_{carb\text{-}coll}$ value similar to that of *Megatherium*, so not all very large late Pleistocene South American extinct herbivorous mammals had $\Delta\delta^{13}C_{carb\text{-}coll}$ values above those of *Megatherium*. The whole range of $\Delta\delta^{13}C_{carb\text{-}coll}$ values should be considered in the discussion on *Megatherium* diet, not only the highest ones.

Another argument used by Fariña and Varela (2018) to support a carnivorous diet for *Megatherium* is the similar range of $\delta^{15}N$ values of bone collagen between this ground sloth and the sabretooth cat *Smilodon* as published in Bocherens et al. (2016) for the same fossil material. However, in the same paper, *Macrauchenia* also falls in the same range of $\delta^{15}N$ values as *Smilodon*, therefore a carnivorous diet should be also considered for this extinct species if we follow the reasoning of Fariña and Varela (2018). Such an option is absolutely not supported by morphology and mechanical analysis (e.g. Varela and Fariña, 2015). This is not the only case of an herbivore with $\delta^{15}N$ values of bone collagen overlapping with those of some carnivores in the same context. Indeed, this is the case of the woolly mammoth in its distribution area from western Europe to north-western North America (Bocherens, 2015). Such a pattern has also been documented for mammals from modern ecosystems (e.g. Davie et al., 2014). The reasons for such a pattern are a combination of dietary preference of these herbivores for plants with high $\delta^{15}N$ values (such as graminoids and forbs) and the prey choice of the predator focused on herbivorous prey with rather low $\delta^{15}N$ values, caused by the consumption of plants such as shrubs and tree leaves or legumes (e.g. Yeakel et al., 2009; Bocherens et al., 2015).

In conclusion, we consider that the carbon and nitrogen isotopic composition of the collagen and carbonate fraction of the bones of the *Megatherium* specimens analyzed so far do not support the hypothesis that they consumed animal resources. When more isotopic data become available for *Megatherium* and coeval fauna, it will be possible to evaluate the variability of the dietary ecology of this fascinating extinct species.

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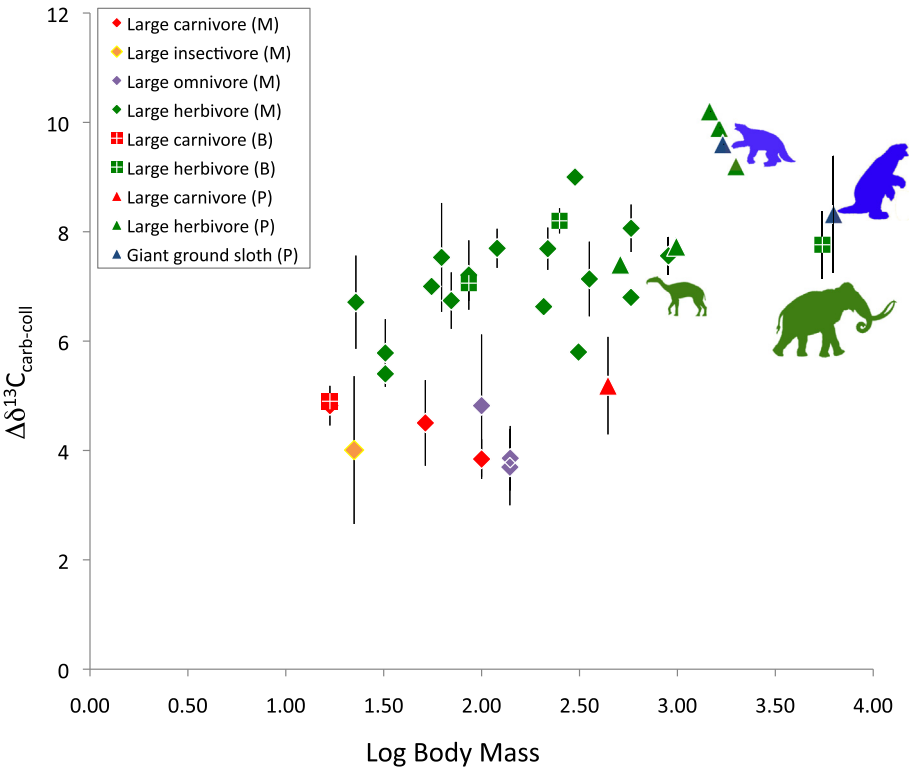

Fig. 1. Scatter-plot of the difference between $\delta^{13}C$ of carbonate and collagen of bone ($\Delta\delta^{13}C_{carb\text{-}coll}$) and Log body mass for Modern and Pleistocene mammals. The vertical bars indicate one standard-deviation for each considered species.

References

Bocherens, H., 2003. Isotopic biogeochemistry and the paleoecology of the mammoth steppe fauna. In: Reumer, W.F., Braber, F., Mol, D., de Vos, J. (Eds.), Advances in Mammoth Research. 9. Deinsea, Rotterdam, pp. 57–76.

Bocherens, H., 2015. Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. Quaternary Science Reviews 117, 42–71.

Bocherens, H., Drucker, D.G., Germonpré, M., Lázničková-Galetová, M., Naito, Y., Wißing, C., Brůžek, J., Oliva, M., 2015. Reconstruction of the Gravettian food-web at Předmostí I using isotopic tracking of bone collagen. Quaternary International 359–360, 211–228.

Bocherens, H., Cotte, M., Bonini, R., Scian, D., Straccia, P., Soibelzon, L., Prevosti, F.J., 2016. Paleobiology of sabretooth cat *Smilodon populator* in the Pampean Region (Buenos Aires Province, Argentina) around the Last Glacial Maximum: insights from carbon and nitrogen stable isotopes in bone collagen. Palaeogeography, Palaeoclimatology, Palaeoecology 449, 463–474.

Bocherens, H., Cotte, M., Bonini, R.A., Straccia, P., Scian, D., Soibelzon, L., Prevosti, F.J., 2017. Isotopic insight on paleodiet of extinct Pleistocene megafaunal Xenarthrans from Argentina. Gondwana Research 48, 7–14.

Clementz, M.T., Fox-Dobbs, K., Wheatley, P.V., Koch, P.L., Doak, D.F., 2009. Revisiting old bones: coupled carbon isotope analysis of bioapatite and collagen as an ecologicaland palaeoecological tool. Geological Journal 44, 605–620.

Davie, H., Murdoch, J.D., Lini, A., Ankhbayar, L., Batdorj, S., 2014. Carbon and nitrogen stable isotope values for plants and mammals in a semi-desert region of Mongolia. Mongolian Journal of Biological Sciences 12, 33–43.

Fariña, R.A., Varela, L., 2018. Comment on "Isotopic insight on paleodiet of extinct Pleistocene megafaunal Xenarthrans from Argentina" by H. Bocherens, M. Cotte, R. A. Bonini, P. Straccia, D. Scian, L. Soibelzon and F. J. Prevosti, Gondwana Research, Volume 48, Issue 1, Pages 7–14. Gondwana Research (in press).

Naito, Y.I., Drucker, D.G., Chikaraishi, Y., Ohkouchi, N., Wißing, C., Semal, P., Bocherens, H., 2016. Ecological niche of Neanderthals from Spy Cave revealed by nitrogen isotopes of individual amino acids in collagen. Journal of Human Evolution 93, 82–90.

Schwartz-Narbonne, R., Longstaffe, F.J., Metcalfe, J.Z., Zazula, G., 2015. Solving the woolly mammoth conundrum: amino acid ^{15}N-enrichment suggests a distinct forage or habitat. Scientific Reports 5, 9791.

Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H., Haskell, J.P., 2003. Body mass of Late Quaternary mammals. Ecology 84, 3403.

Varela, L., Fariña, R.A., 2015. Masseter moment arm as a dietary proxy in herbivorous ungulates. Journal of Zoology 296, 295–304.

Yeakel, J.D., Patterson, B.D., Fox-Dobbs, K., Okumura, M.M., Cerling, T.E., Moore, J.W., Koch, P.L., Dominy, N.J., 2009. Cooperation and individuality among man-eating lions. Proceedings of the National Academy of Science 106, 19040–19043.

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