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EDITED AND REVIEWED BY
Laura Parducci,
Sapienza University of Rome, Italy

*CORRESPONDENCE

Eduardo Jiménez-Hidalgo
✉ eduardojihi@gmail.com
Ferran Estebaranz-Sánchez
✉ estebaranz@protonmail.com
Maciej T. Krajcarz
✉ mkrajcarz@twarda.pan.pl
Carlo Meloro
✉ c.meloro@lmu.ac.uk
Larisa DeSantis
✉ la.risa.desantis@vanderbilt.edu

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Editorial: Reconstructing paleodiets: challenges and advances

Eduardo Jiménez-Hidalgo^{1*}, Ferran Estebaranz-Sánchez^{2*},
Maciej T. Krajcarz^{3*}, Carlo Meloro^{4*} and Larisa DeSantis^{5,6*}

¹Laboratorio de Paleobiología, Instituto de Recursos, Campus Puerto Escondido, Universidad del Mar, Puerto Escondido, Oaxaca, Mexico, ²Archaeology of Social Dynamics (2021 SGR501), Institució Milà i Fontanals de Recerca en Humanitats (IMF-CSIC), Barcelona, Spain, ³Institute of Geological Sciences, Polish Academy of Sciences, Warszawa, Poland, ⁴Research Centre in Evolutionary Anthropology and Palaeoecology, School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, United Kingdom, ⁵Department of Biological Sciences, Vanderbilt University, Nashville, TN, United States, ⁶Department of Earth and Environmental Sciences, Vanderbilt University, Nashville, TN, United States

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Editorial on the Research Topic

Reconstructing paleodiets: challenges and advances

Reconstruction of past diets allows tracking numerous ecological and behavioral aspects through time and across diverse geographic areas, such as the trophic position of species, niche sharing and niche partitioning; it also provides information about the structure of past vegetation and its change, migration patterns, ontogenetic and individual food preferences, and adaptations to environmental changes (Clementz, 2012; Pineda-Munoz et al., 2017). These insights are also key to reconstructing and understanding past ecosystems' structure, composition, and function, and extracting lessons learned of direct relevance to modern conservation.

One of the most widely used techniques to reconstruct diets of fossil mammals is dental microwear texture analysis (DMTA, Kaiser and Brinkmann, 2006) and in this Research Topic, Sato et al. provide an interesting case study on the dietary habits of a 6,000 years ago population of sika deer (*Cervus nippon*) from Torihama Shell Midden, Japan. Their results showed that fossil sika deer had a mixed diet based on herbaceous vegetation, which may reflect its flexible ecological adaptations. By elucidating the diet of this ancient herbivore population, their study also informed on prehistoric human communities' hunting practices and their dietary habits. Miyamoto et al. equally applied DMT to the study of wild boars (*Sus scrofa*) from Toyama Prefecture, Japan. Results indicated that tooth surfaces of boarlets were rougher than those of juvenile or adult animals. A comparison of boars from different habitats showed that mainland boars inhabiting deciduous broad-leaved forests had flatter and less rough tooth surfaces than those in the subtropical evergreen broad-leaved forest. This study gives important information about microwear texture data of an underrepresented ungulate group such as suids.

Standardised *in vitro* experiments with controlled diets to associate specific microtexture patterns with the ingestion of specific food types or their mechanical properties is another methodological aspect that has recently gained importance. Martin

et al. analysed the effect of DMT on adding or not adding various extrinsic abrasives to pelleted diets compared to natural diets in guinea pigs (*Cavia porcellus*). Specimens fed a natural diet had a lower range of DMT values. The normalised DMT data range of guinea pigs and sheep (*Ovis aries*) fed identical diets were also compared: while the DMT data range was higher in sheep, the absolute Spearman's correlation coefficient between the different variables was lower in sheep than in pigs. This suggests that DMT is species specific and its variation between species must be interpreted with caution.

Winkler et al. conducted a pilot feeding experiment with five juvenile *Alligator mississippiensis*. Each individual received a diet of different hardness: crocodylian pellets (control), sardines, quails, rats, or crawfish. DMT showed similar dental microwear texture patterns before they were switched to their designated experimental diet, but from the first feeding bout on, dental microwear textures differed across the diets. The crawfish-feeder showed consistently higher surface complexity, followed by the rat-feeder. Quail- and fish-feeding resulted in similar wear signatures, with low complexity. Such patterns can support the identification of hard-object feeding in the Crocodylia fossil record.

Winkler et al. investigated which objects or food items can produce high-complexity DMT patterns (in the absence of external abrasives). A feeding trial on a sample of 36 laboratory rats separated into six distinct groups, each receiving a different diet indicated that seeds are the main cause of complex microwear textures, but that hard insect parts may also be a major factor causing high complexity in the enamel surface of small mammals.

The increase in the number of published microtexture studies is associated with the use of different commercial resins by different researchers. Sawaura et al. analysed the accuracy of using different types of commercial silicone resins on dental microtexture variables to improve the reproducibility of studies and ensure comparability of data between different studies. Results showed that silicones with rapid completion and showing steep viscoelastic curves and those that had a delayed change in shrinkage show better reproducibility and accuracy of microwear features with less blurring and air bubble contamination.

Avià et al. explored the relationship between wear-related dental functional morphology and dietary ecological constraints within Papionini primates. Their results indicate that hard-object feeders and grass eaters papionines exhibit a pattern of occlusal complexity, surface curvature, relief, and morphological wear resistance that is significantly different from the omnivores and folivore-frugivore species despite the overall homogeneity of the bilophodont dentition. In another multiproxy analysis of papionini, Ramírez-Pedraza et al. inferred the feeding habits of *Macaca cf. sylvanus* from the Plio-Pleistocene site Guefât-4.2 (eastern Morocco). The occlusal microwear results showed that *M. cf. sylvanus* had a pattern similar to the extant *Cercocebus atys* and *Lophocebus albigena*, African forest-dwelling species characterized by a durophagous diet. Buccal microtexture results also supported the consumption of some grasses and the exploitation of more open habitats. At the same time, stable isotopes of *M. cf. sylvanus* indicated a C3-based diet without the presence of C4 plants.

Stable isotopes provide valuable information on animal physiology and dietary adaptations (Ehleringer et al., 1986). By

collating data from over 24 studies with an additional sample of 80 teeth specimens, Wang and Badgley provided in this Research Topic an extensive overview of carbon isotopic variation ($\delta^{13}\text{C}$ diet) within living terrestrial artiodactyls. Because most species of this clade are primary consumers, the interpretation of carbon data is linked to their consumption of C3 or C4 plants. Variation in C3 within and between artiodactyl species exhibits similar shifts following plant distribution across different continents.

DeSantis et al. equally offered an interesting application of stable isotope to clarify diet of carnivorous mammals, by analyzing bone collagen (carbon and nitrogen) and enamel carbonate (carbon) of extinct and extant North American felids and canids, supplementing it with data from African wild dog (*Lycaon pictus*) and African lion (*Panthera leo*). Their results revealed that $\Delta_{\text{ca-co}}$ values are positively related to enamel carbonate values in secondary consumers and are less predictive of trophic level. Foraging habitat and diet of prey affect $\Delta_{\text{ca-co}}$ in carnivores, like in herbivore species. Average $\Delta_{\text{ca-co}}$ values in Pleistocene canids ($8.7 \pm 1\%$) and felids ($7.0 \pm 0.7\%$) overlap with previously documented extant herbivore $\Delta_{\text{ca-co}}$ values, suggesting that trophic level estimates may be relative to herbivore $\Delta_{\text{ca-co}}$ values in each ecosystem and not directly comparable between disparate ecosystems.

In another paper, Pardi and DeSantis presented an approach in which species distribution modeling allows interpreting variation in stable isotope and dental microwear texture data. They investigated the resource use over space and time from the last glacial maximum to the end of the Pleistocene in North American mastodon (*Mammuthus americanum*) and mammoths of the genus *Mammuthus*. Mammoth dietary behavior varied by context across north american geographic range while dietary preferences of mastodon are less resolved and isotopic data does not allow to identify significant geographical changes in its diet.

Ecomorphological variation of terrestrial herbivores is further explored in the work of Mühbachler et al. that present an interesting application of the geometric morphometric techniques (GMM, Adams et al., 2013) to 2D images of the second upper molar from 91 ruminant species. Two landmarks and twenty semi-landmarks that slide along the cusp curvy surface were used. A substantial degree of covariation between cusp shape data generated with GMM and more traditional mesowear scoring was validated by Mühbachler et al. and supported its further biological interpretation for dietary reconstruction. Discriminant Function Analysis applied to cusp shape data improved dietary classification from 56.1% of the traditional mesowear method to 67.2%, showing the potential of GMM to accomplish a more comprehensive understanding of tooth-wearing biological processes.

Regarding studies involving hominins, Estalrich and Krueger analyzed prehistoric and historic children through DMTA of deciduous anterior teeth. Their results showed that DMTA successfully differentiated the samples by all texture variables examined. The Neanderthal and Point Hope children had similar mean values across all the texture variables, and both groups were significantly different from the Amarna, Egyptian children. These results suggest diversity in abrasive load exposure and participation in non-dietary anterior tooth-use behaviors. They also showed that

some prehistoric and historic children took part in similar behaviors as their adult counterparts.

Rendú et al. reported new zooarchaeological data analyses on the site of Chez-Pinaud, Jonzac (France). Previous recognition of the Quina Mousterian techno-complex supported adaptations to reindeer (*Rangifer tarandus*) hunting in Neanderthals from Jonzac. However, Rendú et al. new data indicate that the contribution of the horse and bison to Neanderthal economy was higher than expected by previous interpretations and that the reindeer was overestimated in the faunal spectrum. Horses and bovids were significant sources of protein for the Quina Neanderthals population.

The studies presented in this Research Topic are either aimed at improving our understanding of how dietary behavior is recorded in extant taxa or clarifying how we can reconstruct dietary behavior in ancient ecosystems. By applying different methodologies, this topic demonstrates the myriad of ways in which we can improve accuracy and precision in palaeodietary reconstruction, a discipline that is progressing rapidly with novel technological applications.

Author contributions

EJ-H: Writing – original draft, Writing – review & editing. FE-S: Writing – original draft, Writing – review & editing. MK: Writing –

original draft, Writing – review & editing. CM: Writing – original draft, Writing – review & editing. LD: Writing – original draft, Writing – review & editing.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The authors declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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