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Dance of the Cave Bear: Honouring the Scientific Legacy of Björn Kurtén

Application of Kurténian theories to non-analogue communities: dental traits in South America

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Dental ecometric traits in large herbivores have been used to reconstruct palaeoenvironments, given the known relationships that these traits have to modern environments (such as the negative correlation between hypsodonty and precipitation). These techniques have largely focused on environments in North America and particularly both Eurasia and Africa, and consequently ecometric models have been trained on groups of herbivores that are most significant in those regions today (Artiodactyla, Perissodactyla, Primates and Proboscidea). The extent to which these relationships are persistent in communities with other dominant herbivores has never been tested. Because South America has been isolated for most of its history, fossil assemblages in the continent contain other clades, which likely have different trait–environment relationships due to their evolutionary history. Quantitative testing of these relationships and tailored regional models for South America, particularly those incorporating dietary information, will improve palaeoenvironmental reconstructions in the continent using mammal communities.

Dental ecometrics

Ecometric traits are those which have a direct, quantifiable relationship with aspects of the environment (Vermillion *et al*. 2018) and the study of ecometrics uses these trait–environment relationships on a community level, through measurement of the distribution of trait values across the community (Eronen *et al*. 2010a, Polly *et al*. 2011, Polly & Head 2015, Vermillion *et al*. 2018). The first fully developed ecometric trait, which has been subsequently widely applied, is hypsodonty, the relative height of molar teeth in mammals (especially large herbivores), with which a relationship to precipitation has been quantified by a variety of authors (e.g. Fortelius *et al*. 2002, Eronen *et al*. 2010a, Liu *et al*. 2012, Žliobaitė *et al*. 2016, 2018, Oksanen *et al*. 2019, Schap *et al*. 2021, Short *et al*. 2021, Schap *et al.* 2024). Ecometric traits have been developed in other groups e.g. body mass in reptiles (Head *et al*. 2009, Parker *et al*. 2023) and leaf morphology (Wolfe 1990, Beerling *et al.* 2002).

Hypsodonty increases the durability of teeth in herbivorous mammals, with crown height increased to reduce the detrimental effect of abrasion on tooth function. Either hypsodonty or hypselodonty (ever-growing cheek teeth) have been identified in 78 families of mammalian herbivores, and elevated molar crown

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height is therefore the most widespread solution to increase durability (Janis & Fortelius 1988). Historically, the interpretation of the coincident evolution of hypsodonty in North American equids with the spread of grasslands in the Miocene (e.g. Stirton 1947, Simpson 1951, Janis *et al.* 2002) has been used as evidence supporting the belief that hypsodonty is an evolutionary consequence of grazing (Damuth & Janis 2011), and indeed, there is a positive correlation between grazing and hypsodonty (Janis 1988). To a large extent, the abrasion which has driven the evolution of hypsodonty in most groups relates more to ingested material than inherent properties of grasses. Grazers feed close to the ground and are more likely to ingest soil and grit than browsers, and in dry, open habitats dominated by grazing taxa, wind and rain can promote accumulation of sediment on plant material, in contrast to closed forest habitats (Damuth & Janis 2011). Because of this, the proportion of hypsodont taxa within a community can be used to estimate the relative aridity and openness of a habitat.

The use of hypsodonty has deep roots in Finland, with the master's thesis of Björn Kurtén using the trait to identify forest or steppe environments in Late Miocene China (Kurtén 1952). Here, Kurtén used the proportions of brachydont, intermediate and hypsodont forms within faunas in China as a proxy for environment, with proportionally more hypsodont faunas suggested to reflect steppe environments. The ideas introduced in studies such as this have formed the basis of subsequent works that have more quantitatively described the relationship between hypsodonty and precipitation in large herbivores (Fortelius *et al*. 2002, Eronen *et al*. 2010a, Liu *et al*. 2012, Žliobaitė *et al*. 2018, Oksanen *et al*. 2019, Short *et al*. 2021). In Finland, these studies have used mean ordinated hypsodonty, with taxa described as either brachydont, mesodont or hypsodont, suggesting an ongoing 'Kurténian' element to the methodology.

More recently, other dental traits have been identified as being related to other environmental variables. These include the number of longitudinal lophs (Liu *et al*. 2012) and the presence of acute cutting lophs (Oksanen *et al*. 2019), both of which are related to the ability to cut bark or branches during the cold season (and thus are negatively correlated with temperature). Bunodonty (the absence of lophs) is higher in warm, tropical, forested environments because this type of tooth is common in frugivores and omnivores (Liu *et al*. 2023), and structural fortification (Žliobaitė *et al*. 2018) is more common in wetland and forest grazers. Especially in combination, these types of dental traits can be used for palaeoenvironmental reconstruction, and the suite of dental traits that a herbivore possesses is referred to as the functional crown type (FCT) (Jernvall *et al*. 1996, Žliobaitė *et al*. 2016, 2018, Saarinen *et al*. 2021, Liu *et al*. 2023).

One of the key advantages of ecometrics is that they are taxon-free (Eronen *et al*. 2010b, Polly *et al*. 2011, Andrews & Hixson 2014, Polly & Head 2015, Polly *et al*. 2016, Vermillion *et al*. 2018), meaning that they can theoretically be applied across space and time, so long as trait–environment relationships remain constant, even when the same taxa are not present. However, trait–environment relationships are ever-evolving and must be tested (Polly & Head 2015). For example, structural fortification has never been identified in a non-artiodactyl and is consequently likely to be an inappropriate trait prior to the global origin of this group and in continents where they were absent for most of the Cenozoic.

Bias in dental ecometric studies

Largely as a consequence of the research questions they have been used to address, the use of dental ecometrics has been applied in a relatively geographically limited capacity. The intended use of these methods to reconstruct palaeoenvironments in Eurasia and Africa (often in the context of hominin evolution) (Fortelius *et al*. 2016, Saarinen *et al*. 2021) has necessitated the use of the dominant herbivorous taxa in these regions for trait coding. Subsequently, most dental ecometrics studies have used only artiodactyls, perissodactyls, primates and proboscideans (APPP) for community trait means (Liu *et al.* 2012, Galbrun *et al.* 2018, Žliobaitė *et al.* 2018, Oksanen *et al.* 2019, Liu *et al.* 2023). Whilst ecometrics are supposedly taxon-free, this small pool of taxa introduces an inherent bias to the method, such that its applicability to times and places where these taxa are not dominant requires much further investigation. For example, Australia never had these herbivorous taxa for most of its history so applications of models using solely the APPP taxa are likely inappropriate. The applicability of these models to the fossil record of Eurasia and Africa also requires testing. For example, the Paleogene faunas of the Fayum sequence in Egypt were dominated by hyracoids and embrithopods (Gagnon 1997), not included in the APPP taxa.

The key to the application of ecometrics is that trait–environment relationships can remain relatively constant through time and space, as well as across disparate taxa (Polly & Head 2015, Vermillion *et al*. 2018). However, these relationships cannot be universal. For ecometrics to be useful, the environment in which an organism lives should exert a selective pressure on the traits of that organism, so that species distributions are thereby controlled by the traits of individuals (Polly *et al.* 2011). Over regional scales, communities are then sorted according to their traits through processes including evolution, extinction, migration and clade sorting (Eronen *et al.* 2010b, Polly *et al.* 2011, Polly & Head 2015, Polly *et al.* 2016, Vermillion *et al.* 2018).

However, a variety of factors might influence trait means within a community beyond the environmental variable of interest for ecometric studies. The difference between the predicted community trait value based on ecometric relationships and actual trait values is termed ‘ecometric load’ (Polly *et al.* 2016), and a variety of factors can increase the ecometric load of a particular community (compared to global ecometric models). Biotic interactions can affect trait values (and consequently ecometric load), as illustrated by changes in carnivore calcaneum gear ratio in Bloomington, Indiana, related to anthropogenically driven hunting and habitat loss (Polly & Head 2015). Another factor is taxonomic identity, related to evolutionary history. A clear example of this would be communities of New Zealand, where the absence of herbivorous mammals resulted in communities where browsing niches are filled by large birds (Clout & Hay 1989), and subsequently where dental ecometrics are wholly inappropriate. The unique faunal composition and evolutionary history of South America provides an opportunity to test the applicability of these models in a non-analogue setting.

Faunal history of South American herbivores

The application of global dental ecometric models, constructed using modern-day communities, to modern South America reveals that the ecometric load is no more or less than in other continents (Žliobaitė *et al.* 2018, Oksanen *et al.* 2019, Wilson *et al.* 2022). The extent to which this holds true in the fossil record has never been explicitly tested. Modern South American herbivore communities contain a high proportion of APPP taxa (Wilson *et al.* 2022), though this has not been true for the majority of the history of the continent (Fig. 1).

The history of the fauna of South America is one of successive periods of migration and replacement, organised into four Cenozoic phases (Croft 2012, Goin *et al.* 2012). Undisputed therians are absent from the Mesozoic fossil record, and instead in the Late Cretaceous, mammal communities from high-latitude localities are almost exclusively dryolestoids and gondwanatherians (Rougier *et al.* 2009, 2011). These gondwanatherians of South America provide the earliest evidence of hypsodont cheek teeth in mammals, from the Late Cretaceous to the Early Paleocene (a period before open grasslands) (Bonaparte 1986, Von Koenigswald *et al.* 1999). Therians are recorded in the earliest Paleogene onwards, having seemingly migrated from North America through the Caribbean via the Aves Ridge in the Late Cretaceous or earliest Paleogene (Case *et al.* 2005). These therian immigrants ultimately gave rise to the groups that have been called the three “old-timers” (the marsupials, ungulates and xenarthrans) (Simpson 1980), of which the ungulates and xenarthrans are the groups that include the large herbivores relevant for dental ecometric studies. The time period where these early immigrant groups and the remaining endemic taxa are the only mammals in South America is called the ‘Early South American Phase’ (Goin *et al*. 2012).

The xenarthrans include two broad groups, each with herbivorous representatives: the cingu-

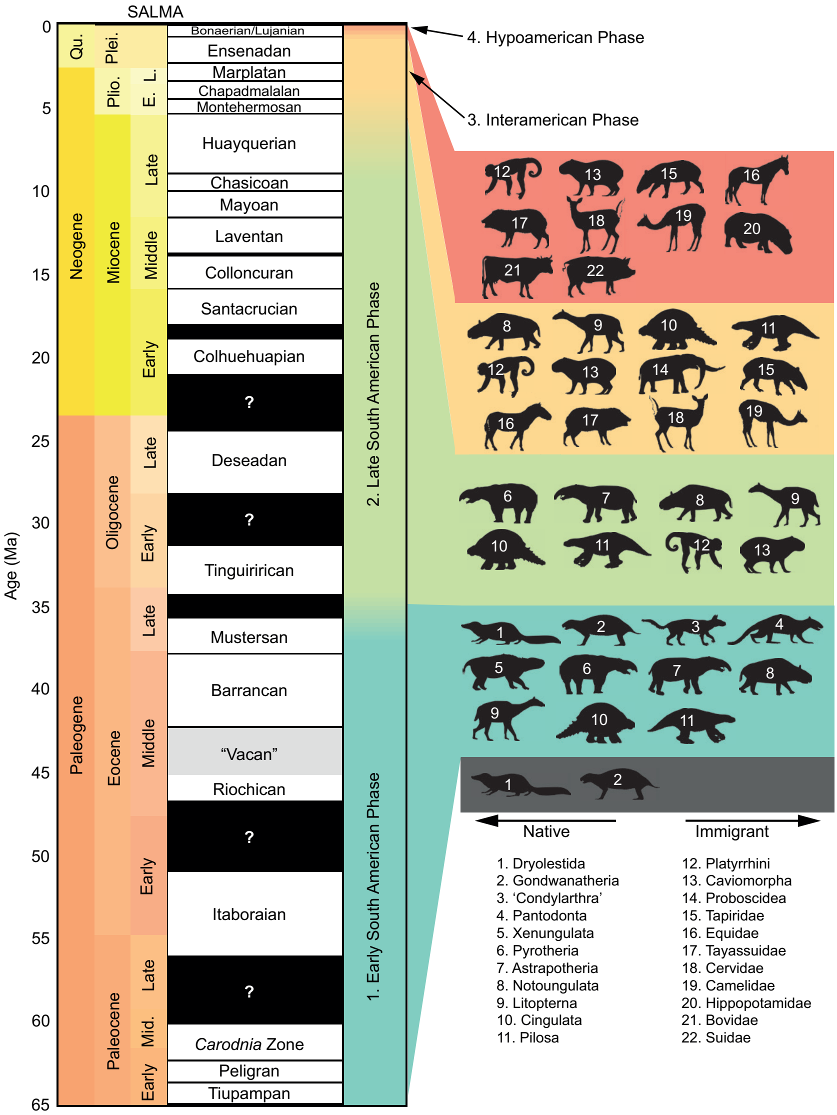

Fig. 1. Stratigraphic chart illustrating the different phases in South American mammal evolution, and the sequence and timing of the South American Land Mammal Ages, adapted from Croft (2016) and Krause *et al.* (2017). The grey shading of the "Vacan" reflects the fact that this is included within the Riochican, as defined by Krause *et al.* (2017). Gradients are used rather than sharp boundaries between the phases of mammal evolution because the timing is not consistent across the whole continent. The potential large (> ~0.5 kg) herbivore taxa in each phase are included as silhouettes. Silhouettes facing left are native during the phase, whilst silhouettes facing right immigrate to or are descended from immigrants into South America during the phase. A family level is used for Artiodactyla and Perissodactyla (in comparison to the ordinal level of other clades) to highlight the effect on the community composition of the anthropogenic impacts of the Hypoamerican Phase. SALMA = South American Land Mammal Age. Silhouettes from phylopic.org: *Dryolestes* (Elis Newham, CC0 1.0 DEED), *Adalatherium hui* (Scott Hartman, CC BY 3.0 DEED), *Hyopsodus*, *Carodnia vieirai* (T. Michael Keesey, CC0 1.0 DEED), *Alcidedorbignya inopinata*, *Hilarcotherium miyou*, *Nesodon*, *Xenorhinotherium*, *Notiomastodon platensis* (Zimices, CC BY-NC 3.0 DEED), *Pyrotherium*, *Tapirus pinchaque*, *Dicotyles tajacu*, *Hippopotamus amphibius*, *Bos primigenius taurus*, *Sus scrofa domestica* (Steven Traver, CC0 1.0 DEED), *Glyptodon* (Fabio Machado, CC0 1.0 DEED), *Magdalenabradys confusum* (Zimices, PDM 1.0 DEED), *Cebus* (Sarah Werning, CC BY 3.0 DEED), *Hydrochoerus hydrochaeris* (Skye McDavid, CC0 1.0 DEED), *Lama vicugna* (Kai Caspar, CC0 1.0 DEED), *Equus neogeus* (Zimices, CC BY-SA 3.0 DEED), *Odocoileus virginianus* (Gabriela Palomo-Munoz, CC BY-NC 3.0 DEED), *Equus ferus caballus* (Tamara L. Clark, CC BY-NC-SA 3.0 DEED).

lates (with predominantly herbivorous representatives from the Glyptodontidae and Pampatheriidae), and the pilosans (of which the sloths are the only herbivorous radiation). The Paleogene fossil record of xenarthrans is limited, because the earliest xenarthrans were probably burrowing myrmecophages in tropical environments, with low population densities and preservation potential (Gaudin & Croft 2015). The origin of the group is unclear. Some recent molecular phylogenetic studies suggest that Xenarthra is the sister taxon of Afrotheria, and that the split between these clades occurred in the Cretaceous (Murphy *et al.* 2021). This could suggest an origin in Gondwana rather than a northern origin for Xenarthra, but much more study of this biogeographic question is required.

The monophyly of the South American Native Ungulates (SANUs) is debated (de Muizon & Cifelli 2000, O'Leary *et al.* 2013, de Muizon *et al.* 2015, Carrillo & Asher 2017, Croft *et al.* 2020), but they are usually placed into seven groups: Kollpaniinae, Didolodontidae, Xenungulata, Pyrotheria, Astrapotheria, Litopterna and Notoungulata (Croft *et al.* 2020). The Kollpaniinae and Didolodontidae were small, bunodont 'condylarths' from the Paleocene and the Eocene. At the same time, xenungulates were also found across the continent. These were bilophodont taxa ranging from small (~2.9 kg) to large (~394 kg) (Gelfo *et al.* 2020). The pyrotheres of the Eocene and particularly the Oligocene were similarly wholly bilophodont (when the controversial Eocene taxa *Proticia* and *Colombitherium* are not considered) (Sánchez-Villagra *et al.* 2000, Billet *et al.* 2010) and included very large species like *Pyrotherium romeroi* (~3000 kg) (Croft 2016). Astrapotheres survived from the early Eocene until the Middle Miocene, with later forms like *Granastrapotherium* reaching similar sizes to the largest pyrotheres (~3142 kg) (Kramarz & Bond 2011).

The most diverse and most recent groups of SANUs are the notoungulates and the litopterns (both Early Paleocene-Late Pleistocene). Molecular evidence from both groups supports a northern origin as a sister group to the perissodactyls (Buckley 2015, Welker *et al.* 2015, Carrillo & Asher 2017, Westbury *et al.* 2017). The litopterns include a diverse range of forms which illustrate convergent evolution with herbivorous mammals on other continents e.g. pig-like, camel-like and horse-like ecomorphologies (Cifelli & Villarroel 1997, Croft *et al.* 2020). The most diverse group is the Notoungulata, which contained ~150 genera from 14 different families (Croft *et al.* 2020). There is a broad split in notoungulates between the generally larger toxodontians and the generally smaller typotherians (Billet 2011). As with the litopterns, there are ecomorphologies that align with those in other continents, particularly rabbit-like, large rodent-like, small horse-like and rhino-like forms (Giannini & García-López 2014).

Of the four APPP groups, primates were the first to arrive in South America. As is also true for caviomorph rodents, the primates of South America had their origins in Africa and dispersed across the Atlantic to eastern South America (Poux *et al.* 2006, Bond *et al.* 2015). There is evidence of several independent dispersals of primates from Africa to South America, from the Oligocene localities of western Amazonia (Bond *et al.* 2015, Seiffert *et al.* 2020, Marivaux *et al.* 2023). The timing of these dispersals is debated and depends on accurate dating of the known primate record (Seiffert *et al.* 2020, Campbell *et al.* 2021), but phylogenetic analyses have previously supported migration during periods of low sea level during the middle Eocene climatic optimum (Silvestro *et al.* 2019, Marivaux *et al.* 2023). The period after the arrival of primates and caviomorph rodents from Africa is called the 'Late South American Phase' (Goin *et al.* 2012).

Artiodactyls and perissodactyls (as well as proboscideans, now extinct in South America) arrived in the continent during the Great American Biotic Interchange (GABI), as the closure of the Isthmus of Panama allowed migration between North and South America (Webb 1991). The effect of GABI was that the relative diversity of northern immigrants in South America increased, while the relative proportion of southern taxa declined. This can be explained by the higher rate of extinction in the southern taxa (Carrillo *et al.* 2020), which has been suggested to be related to the naivety of the southern endemics to the northern predators who also entered South America during GABI (Faurby & Svenning 2016). However, the extent to which this pattern of competitive exclusion holds true has been debated. The sparassodont carnivores had already gone extinct before the arrival of most northern carnivores, and competition with these taxa does not seem to have driven their extinction (Engelman & Croft 2019, Tarquini *et al.* 2022). Similarly, many groups of SANUs were declining in diversity during the Late Miocene, prior to the arrival of artiodactyls and perissodactyls (Croft *et al.* 2020, Engelman *et al.* 2023). Whether these declines were due to climatic change, competition from other herbivores (e.g. sloths and rodents) or a combination of factors, as for sparassodonts (Tarquini *et al.* 2022), remains unclear.

GABI does not represent a single immigration event, and instead consisted of a series of migrations (both northwards and southwards) over millions of years (Webb 1991, Woodburne 2010, O'Dea *et al.* 2016, Jaramillo 2018). The main period of exchange was in the Late Pliocene and Early Pleistocene (~2.6 Ma) (O'Dea *et al.* 2016), but there is a body of evidence for earlier migrations. Procyonids are present from the Late Miocene, with abundant records from the Cerro Azul (Hontecillas *et al.* 2023), Chiquimil (Marshall *et al.* 1979, Reguero & Candela 2011), Huayquerias (Linares 1981) and Maimará (Candela *et al.* 2023) Formations in Argentina, the Camacho Formation in Uruguay (Soibelzon *et al.* 2019), the Tariquía Formation in Bolivia (Soibelzon *et al.* 2020) and the Pisco Formation in Peru (Tarquini *et al.* 2020). Similarly, there is evidence of early northwards migration of sloth taxa, with records of two genera (*Thinobadistes* and *Pliometanastes*) in North America from ~9 Ma (Morgan 2008, Woodburne 2010). Adding to the earlier records of interchange are curious dental remains of *Panamacebus transitus* from the Early Miocene Las Cascadas Formation of Panama (20.9 Ma) that record the first presence of a platyrrhine primate in Central America and pre-date other records of terrestrial mammalian migration (either northwards or southwards) by ~12 Ma (Bloch *et al.* 2016). Whether this represents a waif dispersal or an earlier record of a connection between South and Central America is unclear. Throughout the Late Miocene to the Early Pleistocene, the localities from South America record a general pattern of increasing proportions of northern immigrants in faunal lists. However, the pattern of immigration is not consistent across the whole continent. For example, the Pliocene locality of Inchasi, Bolivia, does not contain any North American immigrant taxa despite dating from around 4.0–3.3 Ma (MacFadden *et al.* 1993, Anaya & MacFadden 1995). The result of GABI was a shift in trait values resulting from this faunal turnover during the period referred to as the 'Interamerican Phase' (Goin *et al*. 2012).

The final period of faunal turnover in South America came during the Late Pleistocene, as humans arrived in the continent and had dramatic effects on the biota and particularly the large mammals. South America lost more genera of megafauna than any other continent (52 genera, 83%; Barnosky & Lindsey 2010). There is significant evidence of human hunting, through the presence of stone tools (Prates & Perez 2021, Prates *et al.* 2022), cut marks (Politis *et al.* 2019, Labarca *et al.* 2020) and cave art (Bigarella *et al.* 1984, Chahud *et al.* 2020), though climate change likely also had a significant impact in driving megafaunal decline (Cione *et al*. 2003, Araújo *et al*. 2021). More recently, anthropogenic activities have driven population declines in living South American mammals, with 67 large herbivores currently considered threatened by the IUCN (Faurby *et al.* 2018). Seven megafaunal species (largely in the form of domesticates) have also been added to South America by humans (Lundgren *et al.* 2018). The period after human arrival and impact in South America can be called the 'Hypoamerican Phase' (Croft 2012).

South American dental functional traits

The key question regarding the application of ecometrics to South America is to what extent the relationship between traits and environments that have been determined in other continents hold true through the four phases of South American history, particularly prior to the Hypoamerican Phase. To understand this, consideration of the functional traits of the large herbivores (particularly those outside of the APPP) is required. The dentition of the SANUs was diverse, but in many cases analogous to those of taxa on other continents. For example, the bilophodont dentitions of pyrotheres and xenungulates is comparable to modern tapirs, the bunodont dentition of megadolodine litopterns to pigs and the ectolophodont dentitions of astrapotheres and toxodontids to rhinoceroses (Croft *et al*. 2020) (Fig. 2).

The key difference between the molar dentition of herbivores in South America and in other continents is in the proportion of hypsodont and hypselodont taxa, and the timing of the evolution of these traits (Patterson & Pascual 1968). South America has been described as a "cradle of hypsodonty" (Madden 2015), with up to 26 clades evolving the trait, and half of those including a hypselodont member. The notoungulates in particular have a remarkable proportion of hypsodont and hypselodont members, with four major families possessing ever-growing molar dentition (Mesotheriidae, Hegetotheriidae, Interatheriidae and Toxodontidae) (Gomes Rodrigues *et al.* 2017). Both hypsodonty and hypselodonty are assumed to have evolved to increase the functional durability of the molar dentition (Janis & Fortelius 1988, Damuth & Janis 2011). However, in comparison to other continents, the increase in the proportion of hypsodont mammals in South America is comparatively early, with hypsodonty increasing in the Eocene in some clades (Scott 1937, Patterson & Pascual 1968, Shockey 1997, Madden 2015). In North America, a similar change in Miocene ungulates (particularly equids) has historically been associated with the spread of grasslands during this time (Stirton 1947, Simpson 1951, Janis *et al.* 2002) and whether the pattern observed in South America suggests an early presence of grassland environments is an open question.

There has been particular interest in the role of volcanic ash in the evolution of increased molar crown height in notoungulates in Patagonia. Strömberg *et al.* (2013) found that the evolution of hypsodonty in notoungulates in Patagonia is disconnected from the spread of grasslands, suggesting that habitat openness may not be the only selective pressure driving the evolution of this trait. During the Paleogene, three periods of increased frequency of volcanic eruption are correlated with increased rates of evolution of hypsodonty (Madden 2015). These periods of increased eruption would have blanketed vegetation with highly abrasive volcanic ash (Zobel & Antos 2017), and evidence from a population of howler monkeys on Isla de Ometepe, Nicaragua shows that consumption of vegetation covered in ash causes extreme levels of dental wear (Smith *et al.* 1977). Alongside these eruptions, it seems likely that the mountain building of the Andes would have further provided abrasive sediment in the western part of the continent (Solórzano & Núñez-Flores 2021). The small notoungulates living in these high-abrasion regions in the Paleogene would have fed close to the ground and been more likely to ingest ash and other sediment alongside their food (Saarinen *et al.* 2020). The argument of proponents of this theory is that the evolution of hypsodonty and hypselodonty in the notoungulates is less closely linked to precipitation or habitat type, and more to geological processes.

However, there is debate about the extent to which volcanism alone can account for the prevalence of hypselodonty in notoungulates. While increasing molar height is common in SANU lineages, it is not ubiquitous. For example, hypselodont molars are never observed in litopterns or several notoungulate families (e.g. Leontiniidae, Homalodotheriidae) (Madden 2015). Leontinids and homalodotheres are typically assumed to have been browsers on relatively high leaves and branches (Coombs 1983, Kay & Madden 1997a, 1997b, Elissamburu 2010, Cassini *et al.* 2012, Croft *et al.* 2020, Trayler *et al.* 2020, Sanz-Pérez *et al.* 2024, Wilson & Saarinen 2024), though quantitative dietary analyses are limited and some authors have suggested an abrasive component of the diet of some Oligocene leontinids for example (Shockey 2005). That brachydont taxa were able to survive and diversify would suggest that non-abrasive diets were possible during periods of Andean volcanism, potentially supporting the idea that there were both open and closed habitats available during the Paleogene, and that there were differences in the evolution of hypsodonty in clades inhabiting these different environments. It is possible that there was tiering of the canopy, with browsers feeding on higher leaves and branches (e.g.

Fig. 2. Examples of dentition in South American Native Ungulates (SANUs) (for institutional abbreviations *see* Appendix). — **A**: *Carodnia vieirai* (Carodniidae, Xenungulata) (MCT.M.333), Itaboraí, Brazil, Eocene. — **B**: *Carodnia inexpectans* (Carodniidae, Xenungulata) (MUSM-2025), Quebrada Cabeza de Vaca, Peru, Eocene. — **C**: *Etayoa bacatensis* (Etayoidae, Xenungulata) (UNC-GM-32), Bogotá, Colombia, Eocene. — **D**: *Colombitherium tolimense* (?Colombitheriidae, ?Pyrotheria) (MNHN.F-CLB.15), Gualanday, Colombia, Eocene. — **E**: *Baguatherium jaureguii* (Pyrotheriidae, Pyrotheria) (MUSM-436), Bagua, Peru, Oligocene. — **F**: *Pyrotherium romeroi* (Pyrotheriidae, Pyrotheria) (MNHN-F-DES.1243), Rio Deseado, Argentina, Oligocene. — **G**: *Tetragonostylops apthomasi* (Trigonostylopidae, Astrapotheria) (MCT.M.355), Itaboraí, Brazil, Eocene. — **H**: *Xenastrapotherium kraglievichi* (Astrapotheriidae, Astrapotheria) (MPV-12), La Venta, Colombia, Miocene. — **I**: *Xenorhinotherium bahiense* (Macraucheniidae, Litopterna) (UCV-VF-361), Muaco, Venezuela, Pleistocene. — **J**: *Huilatherium pluripicatum* (Leontiniidae, Notoungulata) (UCMP 40278), La Venta, Colombia, Miocene. — **K**: *Taubatherium paulacoutoi* (Leontiniidae, Notoungulata) (MHNT-VT-1403), Tremembé, Brazil, Oligocene. — **L**: *Andinotoxodon bolivarensis* (Toxodontidae, Notoungulata) (EPN(Q)-V-6382), Nabón, Ecuador, Miocene. — **M**: *Periphragnis vicentei* (Isotemnidae, Notoungulata) (SGO-PV-3107), Tinguiririca, Chile, Oligocene. — **N**: *Ernestokokenia chaishoer* (Didolodontidae, 'Condylarthra') (MGP-PD-29119), Bajo Palangana, Argentina, Eocene. — **O**: *Villarroelia totoyoi* (VPPLT-1264) (Proterotheriidae, Litopterna), La Venta, Colombia, Miocene. — **P**: *Ultrapithecus rutilans* (Oldfieldthomasiidae, Notoungulata) (MNHN.F-CAS.479). — **Q**: *Megadolodus molariformis* (Proterotheriidae, Litopterna) (UNC-TATAC-1), La Venta, Colombia, Miocene. — **R**: *Miocochilius anomopodus* (Interatheriidae, Notoungulata) (VPPLT-1584), La Venta, Colombia, Miocene. — **S**: *Microtypotherium choquecotense* (Mesotheriidae, Notoungulata) (MNHN-Bol-V-003410), Choquecota, Bolivia, Miocene. — **T**: *Proadinotherium saltoni* (Toxodontidae, Notoungulata) (UATF-V-000138), Salla, Bolivia, Oligocene. — **U**: *Archaeotypotherium tinguiriricaense* (Archaeohyracidae, Notoungulata) (SGO-PV-3080), Tinguiririca, Chile, Oligocene. Scale bar = 50 mm for **A**–**M**, 25 mm for **N**–**U**.

homalodotheres, leontinids) experiencing a less dramatic effect of any abrasive ash, although this would not explain the pattern in small litopterns, presumably feeding close to the ground.

While Strömberg *et al.* (2013) found that the increasing hypsodonty and hypselodonty in notoungulates in Patagonia was decoupled from the vegetation changes, subsequent studies have provided other interpretations of the relationships between these factors. Dunn *et al.* (2015) used phytolith morphology to reconstruct habitat openness through a metric called leaf area index (LAI) and found evidence of dry, open habitats in Patagonia since the Eocene. Similarly, Kohn *et al.* (2015) found that dry habitats in Patagonia were present and stable between 43 and 20 Ma. Recent syntheses therefore largely suggest that open habitats were present from the Eocene onwards in Patagonia (e.g. Bellosi *et al.* 2021). This does not preclude a role for volcanism in the widespread evolution of hypsodonty and hypselodonty, with Kohn *et al*. (2015) for example suggesting that the relatively slow evolution of these dental traits in the Eocene and Oligocene after their arrival ~43 Ma can be explained by a 'ratchet' model, with a stable climate not driving selection except for rapid perturbations to the environment, which might be either climatic shifts or volcanic activity. A similar 'ratchet' effect has been identified for the evolution of proboscidean dental traits in Africa during the Neogene (Saarinen & Lister 2023). Similarly, one conclusion of Dunn *et al.* (2015) was that any volcanic sediment influx would have a greater impact on dietary abrasion in more open environments and therefore provide an important selection pressure driving the evolution of hypsodonty and hypselodonty, with temporal correlation between declining LAI (indicating increased habitat openness), ash influx and increased hypsodonty index in notoungulates.

So far, largely because of spatiotemporal biases in the South American fossil record (e.g. Carrillo *et al.* 2015), any investigations into the question of molar crown height evolution in SANUs have focused on Patagonia or the well-sampled Oligocene localities of Tinguiririca, Chile (Early Oligocene, Tinguirirican SALMA) (e.g. Flynn *et al.* 2003), and Salla, Bolivia (Late Oligocene, Deseadan SALMA) (e.g. Shockey 1997). Further fieldwork in and incorporation of other localities from elsewhere in South America will be invaluable to further increasing our understanding of the evolution of these traits and the biogeographic history of the animals that possess them. It will also be important to consider the evolution of hypsodonty outside of the notoungulates. In 1968, Patterson and Pascual suggested that the evolution of hypsodonty in macraucheniid litopterns mirrored that of equids, with an increase in hypsodont forms in the Miocene. This shift might correspond to the increasing abundance of grasses at this time (Strömberg *et al.* 2013). Similar changes in hypsodonty in proterotheriid litopterns have also been identified in the Miocene (McGrath *et al.* 2020) and there is significant potential for the further investigation of the relationship between hypsodonty and environment in litopterns for the purpose of palaeoenvironmental reconstruction.

The other most abundant groups of herbivores have teeth that are similarly high-crowned (Fig. 3), with herbivorous xenarthrans, including the sloths, pampatheres and glyptodontids, all possessing ever-growing, rootless dentition (Vizcaino 2009). In the Early South American phase, records of xenarthrans are extremely rare (Gaudin & Croft 2015), so understanding their dental evolution is challenging, but a suite of dental characters is consistent, including hypselodonty, monophyodonty, absence of enamel and a secondarily non-tribosphenic molar pattern (Vizcaino 2009). The earliest xenarthrans were probably myrmecophagous (Gaudin & Croft 2015), and this myrmecophagy likely allowed for the loss of enamel due to relaxed selection (Emerling *et al.* 2023).

The evolution of ever-growing dentition in xenarthrans was probably a response to increased wear given the absence of enamel. Modern armadillos consume a large amount of sediment during foraging (Abba 2008) and given the ecological consistency between modern armadillos and the projected ancestor of xenarthrans, this sediment intake might be the driver of hypselodonty in this group (Vizcaino 2009). However, another possibility is that the movement towards herbivory caused the ingestion of more abrasive food material (Bargo *et al.*

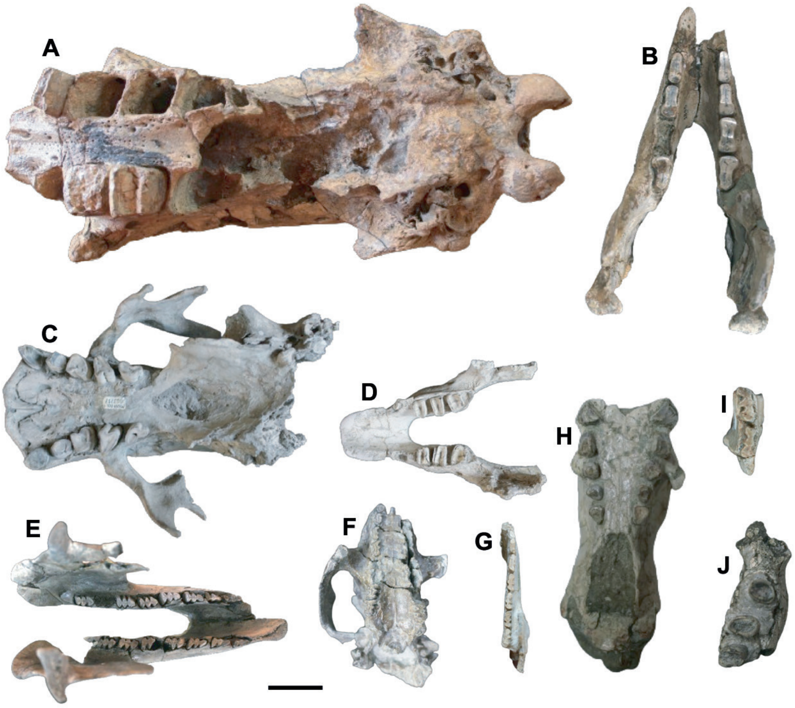

Fig. 3. Examples of dentition in South American xenarthrans (for institutional abbreviations *see* Appendix). — **A**: *Proeremotherium eljebe* (Megatheriidae, Pilosa) (AMU-CURS-126), Urumaco, Venezuela, Miocene. — **B**: *Octodontobradys puruensis* (Mylodontidae, Pilosa) (UFAC-1803-PV), Acre, Brazil, Miocene. — **C**: *Simomylodon uccasamamensis* (Mylodontidae, Pilosa) (MNHN-Bol-V-003717), Casira, Bolivia, Pliocene. — **D**: *Lakukullus anatirostratus* (Nothrotheriidae, Pilosa) (MNHN-Bol-006601), Quebrada Honda, Bolivia, Miocene. — **E**: cf. *Boreostemma acostae* (Glyptodontidae, Cingulata) (IGM-MGN-03012016), La Venta, Colombia, Miocene. — **F**: *Propalaeohoplophorus andinus* (Glyptodontidae, Cingulata) (MNHN-Bol-V-6352), Quebrada Honda, Bolivia, Miocene. — **G**: *Glyptotherium cylindricum* (Glyptodontidae, Cingulata) (UCV-VF-980-2), Muaco, Venezuela, Pleistocene. — **H**: *Brievabradys laventensis* (Mylodontidae, Pilosa) (UNC-LV-4-12), La Venta, Colombia, Miocene. — **I**: *Pseudoglyptodon sallaensis* (*incertae sedis*, Pilosa) (MNHN-Bol-V-009623), Salla, Bolivia, Oligocene. — **J**: *Eucholoeops* indet. (Megalonychidae, Pilosa) (UNC-1-V-89-2), La Venta, Colombia, Miocene. Scale bar = 50 mm for **A**–**G**, 25 mm for **H**–**J**.

2006). The shift to herbivory in these early xenarthrans was probably possible because of the absence of competitors in comparison to other continents but the unique dentition may also have offered some selective advantages for herbivorous xenarthrans, including earlier intake of solid food and possibly extended lifespans in the absence of molar wear (Vizcaino 2009). The dentition of sloths did have relatively significant morphological diversity however, with bilophodont, monolophodont and basin-like forms for example (Saarinen & Karme 2017).

After their arrival in the Eocene, the caviomorph rodents also became significant large herbivores in many parts of South America, with some very large rodents possibly occupying niches held by ungulates elsewhere (Vucetich *et al.* 2015, Álvarez *et al.* 2017, Pérez *et al.* 2017, Engelman 2022). Several groups of caviomorph rodents independently evolved hypsodonty (and hypselodonty), which as in notoungulates seems to be related to increased abrasion due to both increased volcanism and mountain building, alongside any shifts towards more open environments (Goin *et al.* 2012, Strömberg *et al.* 2013, Vucetich *et al.* 2015). Of the larger rodents (i.e. over 1 kg) in the Neogene, almost all are hypsodont or hypselodont, although there are some exceptions (e.g. *Steiromys*) (Walton 1997). Within the large rodents of South America, the functional diversity of their dentition was relatively low, with lophodont molar teeth consisting

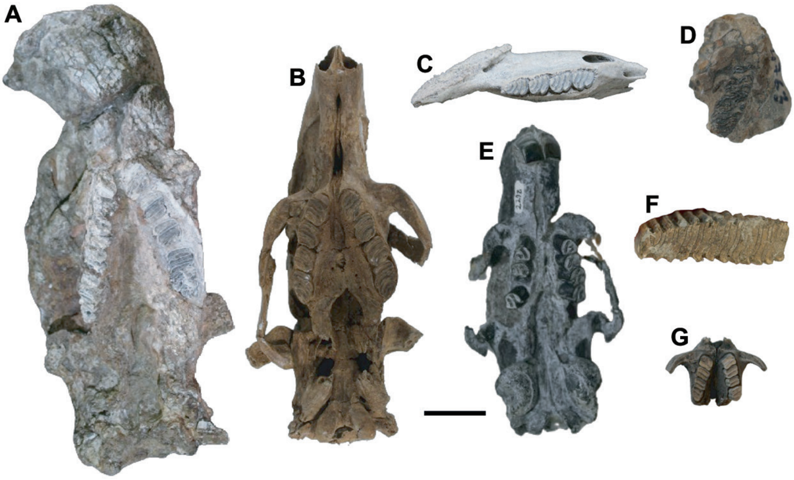

Fig. 4. Examples of the dentition of large caviomorph rodents from South America (for institutional abbreviations *see* Appendix). — **A**: *Phoberomys pattersoni* (Neoepiblemidae, Caviomorpha) (AMU-CURS-255), Urumaco, Venezuela, Miocene. — **B**: *Neoepiblema acreensis* (Neoepiblemidae, Caviomorpha) (UFAC-4515-PV), Acre, Brazil, ?Miocene. — **C**: *Tetrastylus* indet. (Dinomyidae, Caviomorpha) (MNHN-Bol-V-12614), Achiri, Bolivia, Miocene. — **D**: *Cardiatherium orientalis* (Hydrochoeridae, Caviomorpha) (UFAC-4763-PV), Acre, Brazil, ?Miocene. — **E**: *Neoreomys australis* (Cavioidea *sensu stricto*, Caviomorpha) (SGO-PV-2212), Pampa Castillo, Chile, Miocene. — **F**: Hydrochoeridae indet. (Hydrochoeridae, Caviomorpha) (MUN-STRI-16321), Ware, Colombia, Pliocene. — **G**: *Lagostomus angustidens* (Chinchillidae, Caviomorpha) (MNHN.F-PAM.723), Pampean, Argentina, Pleistocene. Scale bar = 50 mm for **A**–**C**, 25 mm for **E**–**G**.

of a series of transverse obtuse lophs (Vucetich *et al*. 2015) (Fig. 4).

The relatively early evolution of hypsodont and hypselodont dentition in the major groups of South American herbivores in many cases seems to have been at least somewhat decoupled from the spread of grasslands, though this is the subject of considerable debate, and it is clear that there were at least open habitats present in Patagonia from the Eocene onwards (e.g. Strömberg *et al.* 2013, Dunn *et al.* 2015, Kohn *et al.* 2015, Madden 2015, Bellosi *et al.* 2021), and further research is undoubtedly required on this topic. Regardless of the underlying cause, the fossil record of South America contains a high proportion of taxa with teeth which would be coded as hypsodont using the functional trait coding scheme (Liu *et al.* 2012, 2023, Žliobaitė *et al.* 2016, Oksanen *et al.* 2019).

As described by Kurtén, the evolution from brachydont to hypsodont forms "is easy to understand; but it is much more difficult to imagine the reverse process, a hypsodont tooth becoming secondarily brachydont" (Kurtén 1952). While he did not mention hypselodonty, the reversal of this process would presumably be even more developmentally challenging. Once a lineage has become hypsodont, or indeed hypselodont, there is limited selective pressure for reversal even when dietary abrasion is low, but the cost of abrasive wear for a brachydont is so extreme that shifts towards higher molar crowns are very strongly selected for (Damuth & Janis 2011). This suggests that a high community mean hypsodonty score could be the result of evolutionary history rather than necessarily because of environment. For example, the neotropical Middle Miocene localities of Fitzcarrald (Peru) and La Venta (Colombia) represent wet, forested environments (Kay & Madden 1997a, 1997b, Tejada-Lara *et al.* 2015, Spradley *et al.* 2019, Catena & Croft 2020, Wilson & Parker 2023) though they have a diversity of hypselodont taxa including *Pericotoxodon*, *Miocochilius*, *Boreostemma*, sloths and dinomyid rodents (Kay *et al.* 1997a, 1997b, Tejada-Lara *et al.* 2015). Applications of ecometric models trained on modern global communities using APPP taxa would reconstruct much drier environments than is likely, although the extent to which there were also open patches in these localities, possibly maintained through the action of megaherbivores, is debated (Kay & Madden 1997a, 1997b, Carrillo *et al.* 2023). Given there are differences in the relative hypsodonty of some groups of herbivores e.g. litopterns (Patterson & Pascual 1968, McGrath *et al.* 2020), we suspect that community hypsodonty averages would be informative for palaeoenvironmental comparison, but advocate for specific tailored models that can account for the abundance of hypsodont and hypselodont taxa relative to other continents.

The other dental ecometric traits (e.g. presence of acute lophs, number of longitudinal lophs) (Liu *et al.* 2012, Oksanen *et al.* 2019) have not yet been investigated in the South American fossil record. There is somewhat more variability in these other traits within the sloths and ungulates, but the large rodents show consistency in these traits (i.e. no longitudinal lophs and absence of acute lophs). More work on these other traits in a South American context is required to identify possible trait–environment relationships in the fossil records. We do not argue that dental traits do not represent a useful tool for palaeoenvironmental reconstruction in South America, but instead that for all dental traits, care should be taken to account for the unique taxonomic assemblages in South America, for example by applying focused ecometric models that have been trained on the past and which can therefore be more readily applied across taxonomic groups.

The role of diet

The principle of using dental functional traits is that the teeth represent the most direct interface of an organism with its environment, and indeed in most cases, they are the only part of a fossil that physically touched an animal's surroundings during its lifetime. However, functional traits like hypsodonty represent only an evolutionary response to abrasive material in the diet (which might be the combined effect of eating grass and from extraneous sediment) rather than direct evidence of diet. The extant pronghorn *Antilocapra americana* is hypsodont but has a diet containing limited grasses, for example (Damuth & Janis 2011).

For more detailed understanding of the environment, particularly vegetation, direct dietary proxies may be more appropriate. Mesowear arguably represents the most cost-effective and straightforward of these proxies. This represents the "average diet of a particular species from a particular location in space and time" (Fortelius & Solounias 2000). The idea behind mesowear is that when herbivores eat soft plant material (e.g. leaves and fruit), the greatest influence on tooth wear is the movement of teeth against each other (attrition), which produces sharp, well-developed facets, whereas when herbivores eat low-growing abrasive material, the food (and the exogenous grit ingested alongside it) has the greatest influence on wear (abrasion), which produces flat, poorly developed facets (Fortelius & Solounias 2000, Green & Croft 2018).

Traditionally, mesowear has been measured in taxa with selenodont, ectolophodont and plagiolophodont molars using two different metrics: cusp shape and relief. Cusps may be considered either sharp (1), rounded (2) or blunt (3), whilst relief describes the intercusp angle. High relief and sharp cusps are typical of attrition-dominated diets (i.e. browsing), whilst low-relief and blunt cusps are typical of abrasion-dominated diets (i.e. grazing) (Fortelius & Solounias 2000). By combining cusp shape and relief into a single score, it is possible to describe the diet of a particular species at a particular time (Rivals *et al.* 2007, Mihlbachler *et al.* 2011, Solounias *et al.* 2014, Saarinen *et al.* 2016).

For taxa with other molar types (e.g. lophodonts), mesowear angles can be used, as in proboscideans (Saarinen *et al.* 2015, Saarinen & Lister 2016, 2023, Xafis *et al.* 2020) and xenarthrans (Saarinen & Karme 2017). In most proboscideans, these angles are measured from the base of dentine valleys to the top of the enamel ridge. In grazers, the greatest effect of abrasion occurs at the topographically highest points on the occlusal surface, which grinds down these surfaces and makes the dentine valleys relatively shallower. In some taxa, these dentine valleys develop only in late wear stages, and in these cases, facet angles can be measured and converted to equivalent mesowear angles (Saarinen & Lister 2016, 2023, Xafis *et al.* 2020). The utility of these facet angles in particular suggests that mesowear angles could be applied across other taxonomic groups (Hernesniemi *et al.* 2011, Loffredo & DeSantis 2014, Saarinen & Karme 2017, Schap & Samuels 2020), and these angles have the advantage over traditional mesowear that because they use a continuous scale, it is possible to compare between specimens on a finer scale, and to use parametric methods for statistical analysis (Schap & Samuels 2020). In theory, these angles should be more directly comparable across dental morphologies (e.g. in primates, sloths and proboscideans, a mesowear angle of 90° is associated with a browsing diet (Saarinen *et al.* 2015, Saarinen & Karme 2017, Ungar *et al.* 2018, Saarinen & Lister 2023). Both mesowear scores and angles can be related to environment to act as a form of ecometric trait (Saarinen & Lister 2016, 2023, Saarinen *et al.* 2016, 2021, Xafis *et al.* 2020). An advantage of these dietary traits relative to other ecometric traits is that they have the potential to be more universal, being less constrained by different evolutionary histories in primary morphology) and given that they directly relate to the environment. However, for many fossil taxa, the relationships between mesowear and diet have not been quantitatively tested.

In South America, mesowear studies are extremely limited, with a single published study on mesowear in SANUs, investigating three notoungulates from the Late Oligocene locality of Salla, Bolivia (Croft & Weinstein 2008). These authors found that two of these taxa (*Trachytherus alloxus* and *Archaeohyrax suniensis*) were likely grazers (though *A. suniensis* likely included a small amount of browse in its diet), while the other (*Federicoanaya sallaensis*) was a mixed feeder. Additionally, they noted an abundance of individuals with low relief but sharp cusps, a feature not typically identified in modern ungulates. A mesowear angle technique has been developed in xenarthrans (Saarinen & Karme 2017), which shows significant differences between dietary categories, but this method has not been applied since.

Mesowear analysis has been able to capture differences between captive and wild diets in modern ungulates (Clauss *et al.* 2007, Kaiser *et al.* 2009, Taylor *et al.* 2014) that illustrates that hypsodonty does not necessarily predict the diet directly. Kaiser *et al.* (2013) argue that mesowear provides information on diet alone, whilst the hypsodonty signal includes both this dietary information and external abrasives (e.g. ash, grit, dust). It is also independent of other non-environmental factors like evolutionary history that affect hypsodonty and other traditional ecometric traits (Fig. 5). Despite this, in the cases where hypsodonty has been applied in palaeoenvironmental reconstructions in South America, it has been used without additional dietary information (e.g. Flynn *et al.* 2003, Strömberg *et al.* 2013, Dunn *et al.* 2015, Madden 2015, Bellosi *et al.* 2021). An example is Tinguiririca, from the Early Oligocene of Chile, where a high proportion of hypsodont notoungulates has been used as evidence to argue that the locality was one of the earliest open habitats in South America (Flynn *et al.* 2003). In Flynn *et al.* (2003), hypsodonty was compared with results from body mass analyses e.g. using cenograms, and included within broader ecological diversity analyses, so it was not used as the only proxy. Later analyses (Croft *et al.* 2008, Catena & Croft 2020) have attempted to remove the potential bias of hypsodonty by coding all non-frugivorous herbivores as folivores, so that they may be considered either grazers or browsers (Su & Croft 2018), but a quantitative dietary analysis of the mammals of Tinguiririca has not yet been attempted. The herbivore fauna contains taxa (e.g. the homalodothere *Trigonolophodon*; Bradham *et al.* 2015) that represent clades commonly considered as browsers. The mammals at Tinguiririca have been found in volcanic rocks (i.e. fine-grained volcaniclastics) (Flynn *et al.* 2003) and thus a role of ash in the evolution of hypsodonty here seems possible. Future studies may compare dietary signals to community hypsodonty to further test the open habitat hypothesis and our ongoing project aims to continue this work in South America through potential ecometric uses of South American mammal mesowear.

Conclusions

Large herbivore dental ecometrics is a rapid, simple, and cost-effective tool in palaeoenvironmental reconstruction, that has been successfully applied in Eurasia, Africa and North America to quantify environmental change (e.g. Fortelius *et*

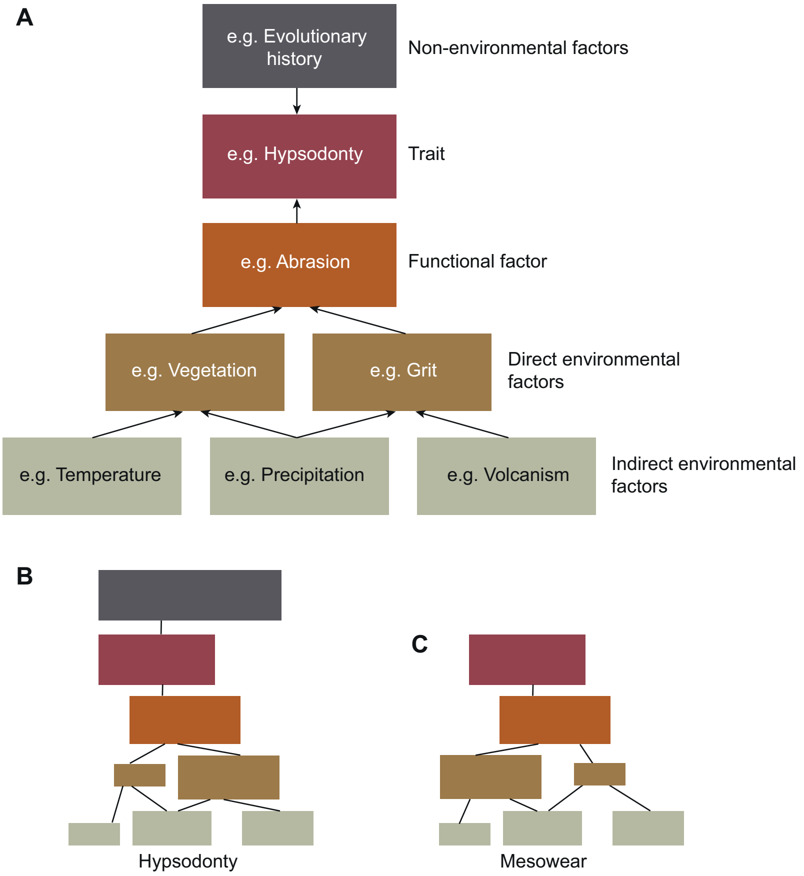

Fig. 5. Schematic diagram illustrating the direct and indirect factors that affect (**A**) ecometric traits and comparing the strength of the relationship between these factors and two dental traits: (**B**) hypsodonty and (**C**) mesowear. The size of each box represents the size of the effect of that factor. Arrows denote the direction of the effect of each factor. Modified from Polly and Head (2015).

al. 2002, 2016, Oksanen *et al.* 2019, Saarinen *et al.* 2021, Short *et al.* 2021, Lauer *et al.* 2023, Liu *et al.* 2023). However, the models that have been used for these analyses should be applied with caution to fossil localities containing large herbivores outside of the groups to which they were fitted, e.g. in Australasia and South America. For such communities, more work is required to code the functional traits of the large herbivores and to build more regional models relating these traits to alternative environmental proxies for the past.

Given the likely specific trait–environment relationships in the fossil record of South America (especially given the heightened incidence of hypsodonty), the incorporation of dietary information (e.g. through mesowear scores or angles) will provide additional, more direct information on the surrounding vegetation. Further study of the way that mesowear relates to diet in extinct groups e.g. SANUs and large rodents will be important in this regard. The extension of these methods to additional palaeontological contexts represents a logical but significant continuation of the work in Finland that builds on the ideas of Björn Kurtén.

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References

Abba, A. M. 2008: Ecología y conservación de los armadillos (Mammalia, Dasypodidae) en el noreste de la Provincia de Buenos Aires, Argentina. — Ph.D. thesis, Universidad Nacional de La Plata, http://sedici.unlp.edu.ar/handle/10915/4367.

Álvarez, A., Arévalo, R. L. M. & Verzi, D. H. 2017: Diversification patterns and size evolution in caviomorph rodents. — *Biological Journal of the Linnean Society* 121: 907–922.

Anaya, F. & MacFadden, B. J. 1995: Pliocene mammals from Inchasi, Bolivia: the endemic fauna just before the Great American Interchange. — *Bulletin of the Florida Museum of Natural History* 39: 87–140.

Andrews, P. & Hixson, S. 2014: Taxon-free methods of palaeoecology. — *Annales Zoologici Fennici* 51: 269–284.

Araújo, T., Machado, H., Mothé, D. & dos Santos Avilla, L. 2021: Species distribution modeling reveals the ecological niche of extinct megafauna from South America. — *Quaternary Research* 104: 151–158.

Bargo, M. S., De Iuliis, G. & Vizcaíno, S. F. 2006: Hypsodonty in Pleistocene ground sloths. — *Acta Palaeontologica Polonica* 51: 53–61.

Barnosky, A. D. & Lindsey, E. L. 2010: Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. — *Quaternary International* 217: 10–29.

Beerling, D. J., Lomax, B. H., Royer, D. L., Upchurch, G. R. & Kump, L. R. 2002: An atmospheric pCO_2 reconstruction across the Cretaceous–Tertiary boundary from leaf megafossils. — *Proceedings of the National Academy of Sciences* 99: 7836–7840.

Bellosi, E., Genise, J. F., Zucol, A., Bond, M., Kramarz, A. G., Victoria Sánchez, M. & Marcelo Krause, J. 2021: Diverse evidence for grasslands since the Eocene in Patagonia. — *Journal of South American Earth Sciences* 108, 103357, https://doi.org/10.1016/j.jsames.2021.103357.

Bigarella, J. J., Beltrão, M. da C. de M. C. & Töth, E. M. R. 1984: Registro de fauna na arte rupestre: possíveis implicações geológicas. — *Revista de Arqueologia* 2: 31–37.

Billet, G. 2011: Phylogeny of the Notoungulata (Mammalia) based on cranial and dental characters. — *Journal of Systematic Palaeontology* 9: 481–497.

Billet, G., Orliac, M., Antoine, P.-O. & Jaramillo, C. 2010: New observations and reinterpretation on the enigmatic taxon *Colombitherium* (?Pyrotheria, Mammalia) from Colombia. — *Palaeontology* 53: 319–325.

Bonaparte, J. F. 1986: A new and unusual Late Cretaceous mammal from Patagonia. — *Journal of Vertebrate Paleontology* 6: 264–270.

Bond, M., Tejedor, M. F., Campbell, K. E., Chornogubsky, L., Novo, N. & Goin, F. 2015: Eocene primates of South America and the African origins of New World monkeys. — *Nature* 520: 538–541.

Bradham, J., Flynn, J. J., Croft, D. A. & Wyss, A. R. 2015: New notoungulates (Notostylopidae and basal toxodontians) from the Early Oligocene Tinguiririca Fauna of the Andean Main Range, central Chile. — *American Museum Novitates* 3841, https://doi.org/10.1206/3841.1.

Buckley, M. 2015: Ancient collagen reveals evolutionary history of the endemic South American 'ungulates.' — *Proceedings of the Royal Society B* 282, 20142671, https://doi.org/10.1098/rspb.2014.2671.

Campbell, K. E., O'Sullivan, P. B., Fleagle, J. G., De Vries, D. & Seiffert, E. R. 2021: An early Oligocene age for the oldest known monkeys and rodents of South America. — *Proceedings of the National Academy of Sciences* 118, e2105956118, https://doi.org/10.1073/pnas.2105956118.

Candela, A. M., Abello, M. A., Reguero, M. A., García Esponda, C. M., Pardiñas, U. F. J., Zurita, A. A., Pujos, F., Miño Boilini, A., Quiñones, S., Galli, C. I., Luna, C., Voglino, D., De Los Reyes, M. & Cuaranta, P. 2023: The Late Miocene mammals from the Humahuaca basin (northwestern Argentina) provide new evidence on the initial stages of the great American biotic interchange. — *Papers in Palaeontology* 9, e1527, https://doi.org/10.1002/spp2.1527.

Carrillo, J. D., Forasiepi, A., Jaramillo, C. & Sánchez-Villagra, M. R. 2015: Neotropical mammal diversity and the Great American Biotic Interchange: spatial and temporal variation in South America's fossil record. — *Frontiers in Genetics* 5, 451, https://doi.org/10.3389/fgene.2014.00451.

Carrillo, J. D. & Asher, R. J. 2017: An exceptionally well-preserved skeleton of *Thomashuxleya externa* (Mammalia, Notoungulata), from the Eocene of Patagonia, Argentina. — *Palaeontologia Electronica* 20.2.34A, https://doi.org/10.26879/759.

Carrillo, J. D., Faurby, S., Silvestro, D., Jaramillo, C., Bacon, C. D. & Antonelli, A. 2020: Disproportionate extinction of South American mammals drove the asymmetry of the Great American Biotic Interchange. — *Proceedings of the National Academy of Sciences* 117: 26281–26287, https://doi.org/10.1073/pnas.2009397117.

Carrillo, J. D., Jaramillo, C., Abadía, F., Aguilera, O., Alfonso-Rojas, A., Billet, G., Benites-Palomino, A., Cadena, Edwin, A., Cárdenas, A., Carlini, A. A., Carrillo-Briceño, J. D., Carvalho, M., Cortés, D. Escobar, J., Herrera, F., Link, A., Luque, J., Martínez, C., Pérez-Lara, D. K., Salas-Gismondi, R., Suarez, C., Stiles, E., Urrea-Barreto, F. J. & Zapata, S. 2023: The Miocene La Venta Biome (Colombia): a century of research and future perspectives. — *Geodiversitas* 45: 739–767.

Case, J. A., Goin, F. J. & Woodburne M. O. 2005: "South American" marsupials from the Late Cretaceous of North America and the origin of marsupial cohorts. — *Journal of Mammalian Evolution* 12: 223–255.

Cassini, G., Cerdeño, E., Villafañe, A. & Muñoz, N. 2012: Paleobiology of Santacrucian native ungulates (Meridiungulata: Astrapotheria, Litopterna and Notoungulata). — In: Vizcaino, S. F., Kay, R. F. & Bargo, M. S. (eds.), *Early Miocene paleobiology in Patagonia: High-latitude paleocommunities of the Santa Cruz Formation*: 243–286. Cambridge University Press, Cambridge.

Catena, A. M. & Croft, D. A. 2020: What are the best modern analogs for ancient South American mammal communities? Evidence from ecological diversity analysis (EDA). — *Palaeontologia Electronica* 23, a03, https://doi.org/10.26879/962.

Chahud, A., Costa, P. R. de O. & Okumura, M. 2020: Caçando megafauna? Considerações sobre uma pintura rupestre de Lajedão do Riacho Largo, Central (BA), Brasil. — *Palaeoindian Archaeology* 2: 43–58.

Cifelli, R. L. & Villarroel, C. A. 1997: Paleobiology and Affinities of *Megadolodus*. — In: Kay, R. F., Madden, R. H., Cifelli, R. L. & Flynn, J. J. (eds.), *Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia*: 265–288. Smithsonian Institution Press, Washington D.C.

Cione, A. L., Tonni, E. P. & Soibelzon, L. 2003: The Broken Zig-Zag: Late Cenozoic large mammal and tortoise extinction in South America. — *Revista del Museo Argentino de Ciencias Naturales* 5: 1–19.

Clauss, M., Franz-Odendaal, T. A., Brasch, J., Castell, J. C. & Kaiser, T. 2007: Tooth wear in captive giraffes (*Giraffa camelopardalis*): mesowear analysis classifies free-ranging specimens as browsers but captive ones as grazers. — *Journal of Zoo and Wildlife Medicine* 38: 433–445.

Clout, M. N. & Hay, J. R. 1989: The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. — *New Zealand Journal of Ecology* 12: 27–33.

Coombs, M. C. 1983: Large mammalian clawed herbivores: a comparative study. — *Transactions of the American Philosophical Society* 73: 1–96.

Croft, D. A., Flynn, J. J. & Wyss, A. R. 2008: The Tinguiririca Fauna of Chile and the early stages of "modernization" of South American mammal faunas. — *Arquivos do Museu Nacional* 66: 191–211.

Croft, D. A. 2012: Punctuated isolation: the making and mixing of South America's mammals. — In: Patterson, B. D. & Costa, L. P. (eds.), *Bones, clones and biomes: The history and geography of recent Neotropical mammals*: 9–19. University of Chicago Press, Chicago.

Croft, D. A. 2016: *Horned armadillos and rafting monkeys*. — University of Indiana Press, Bloomington.

Croft, D. A. & Weinstein, D. 2008: The first application of the mesowear method to endemic South American ungulates (Notoungulata). — *Palaeogeography, Palaeoclimatology, Palaeoecology* 269: 103–114.

Croft, D. A., Gelfo, J. N. & López, G. M. 2020: Splendid innovation: the extinct South American native ungulates. — *Annual Review of Earth and Planetary Sciences* 48: 259–290.

Damuth, J. & Janis, C. M. 2011: On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. — *Biological Reviews* 86: 733–758.

de Muizon, C., Billet, G., Argot, C., Ladevèze, S. & Goussard, F. 2015: *Alcidedorbignya inopinata*, a basal pantodont (Placentalia, Mammalia) from the early Palaeocene of Bolivia: anatomy, phylogeny and palaeobiology. — *Geodiversitas* 37: 397–631.

de Muizon, C. & Cifelli, R. L. 2000: The condylarths (archaic Ungulata, Mammalia) from the early Palaeocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates. — *Geodiversitas* 22: 47–150.

Dunn, R. E., Strömberg, C. A. E., Madden, R. H., Kohn, M. J. & Carlini, A. A. 2015: Linked canopy, climate, and faunal change in the Cenozoic of Patagonia. — *Science* 347: 258–261.

Elissamburu, A. 2010: Estudio biomecánico y morfofuncional del esqueleto apendicular de *Homalodotherium* Flower 1873 (Mammalia, Notoungulata). — *Ameghiniana* 47: 25–43.

Emerling, C. A., Gibb, G. C., Tilak, M.-K., Hughes, J. J., Kuch, M., Duggan, A. T., Poinar, H. N., Nachman, M. W. & Delsuc, F. 2023: Genomic data suggest parallel dental vestigialization within the xenarthran radiation. — *Peer Community Journal* 3, e75, https://doi.org/10.24072/pcjournal.303.

Engelman, R. K. 2022: Resizing the largest known extinct rodents (Caviomorpha: Dinomyidae, Neoepiblemidae) using occipital condyle width. — *Royal Society Open Science* 9, 220370, https://doi.org/10.1098/rsos.220370.

Engelman, R. K. & Croft, D. A. 2019: Strangers in a strange land: ecological dissimilarity to metatherian carnivores may partly explain early colonization of South America by *Cyonasua*-group procyonids. — *Paleobiology* 45: 598–611.

Engelman, R. K., Beck, R. M., Potts, P. & Croft, D. A. 2023: No support for an interchange-driven extinction of notoungulates and litopterns based on diversification rates of South American native ungulates (SANUs). — *Journal of Vertebrate Paleontology, Program and Abstracts* 2023: 158–159.

Eronen, J. T., Liu, L., Lintulaakso, K., Damuth, J., Janis, C. M. & Fortelius, M. 2010a: Precipitation and large herbivorous mammals I: estimates from present-day communities. —*Evolutionary Ecology Research* 12: 217–233.

Eronen, J. T., Polly, P. D., Fred, M., Damuth, J., Frank, D. C., Scheidegger, C., Stenseth, N. C. & Fortelius, M. 2010b: Ecometrics: The traits that bind the past and present together. — *Integrative Zoology* 5: 88–101.

Faurby, S. & Svenning, J. C. 2016: The asymmetry in the Great American Biotic Interchange in mammals is consistent with differential susceptibility to mammalian predation. — *Global Ecology and Biogeography* 25: 1443–1453.

Faurby, S., Davis, M., Pedersen, R., Schowanek, S. D., Antonelli, A. & Svenning, J. C. 2018: PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology. — *Ecology* 99, 2626, https://doi.org/10.1002/ecy.2443.

Flynn, J. J., Wyss, A. R., Croft, D. A. & Charrier, R. 2003: The Tinguiririca Fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal "Age." — *Palaeogeography, Palaeoclimatology, Palaeoecology* 195: 229–259.

Fortelius, M. & Solounias, N. 2000: Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. — *American Museum Novitates* 3301: 1–36.

Fortelius, M., Eronen, J. T., Jernvall, J., Liu, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z. & Zhou, L. 2002: Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. — *Evolutionary Ecology Research* 4: 1005–1016.

Fortelius, M., Žliobaitė, I., Kaya, F., Bibi, F., Bobe, R., Leakey, L., Leakey, M., Patterson, D., Rannikko, J. & Werdelin, L. 2016: An ecometric analysis of the fossil mammal record of the Turkana basin. — *Philosophical Transactions of the Royal Society B* 371, 20150232, https://doi.org/10.1098/rstb.2015.0232.

Gagnon, M. 1997: Ecological diversity and community ecology in the Fayum sequence (Egypt). — *Journal of Human Evolution* 32: 133–160.

Galbrun, E., Tang, H., Fortelius, M. & Žliobaitė, I. 2018: Computational biomes: the ecometrics of large mammal teeth. — *Palaeontologia Electronica* 21.1.3A, https://doi.org/10.26879/786.

Gaudin, T. J. & Croft, D. A. 2015: Paleogene Xenarthra and the evolution of South American Mammals. — *Journal of Mammalogy* 96: 622–634.

Gelfo, J. N., García-López, D. A. & Bergqvist, L. P. 2020: Phylogenetic relationships and palaeobiology of a new xenungulate (Mammalia: Eutheria) from the Palaeogene of Argentina. — *Journal of Systematic Palaeontology* 18: 993–1007.

Giannini, N. P. & García-López, D. A. 2014: Ecomorphology of mammalian fossil lineages: identifying morphotypes in a case study of endemic South American ungulates. — *Journal of Mammalian Evolution* 21: 195–212.

Goin, F. J., Gelfo, J. N., Chornogubsky, L., Woodburne, M. O. & Martin, T. 2012: Origins, radiations and distribution of South American mammals: from greenhouse to icehouse worlds. — In: Patterson, B. D. & Costa, L. P. (eds.), *Bones, clones and biomes: the history and geography of recent Neotropical mammals*: 20–50. University of Chicago Press, Chicago.

Gomes Rodrigues, H., Herrel, A. & Billet, G. 2017: Ontogenetic and life history trait changes associated with convergent ecological specializations in extinct ungulate mammals. — *Proceedings of the National Academy of Sciences* 114: 1069–1074.

Green, J. L. & Croft, D. A. 2018: Using dental mesowear and microwear for dietary inference: a review of current techniques and applications. — In: Croft, D. A., Su, D. F. & Simpson, S. W. (eds.), *Methods in paleoecology: reconstructing Cenozoic terrestrial environments and ecological communities*: 53–73. Springer Nature, Cham.

Head, J. J., Bloch, J. I., Hastings, A. K., Bourque, J. R., Cadena, E. A., Herrera, F. A., Polly, P. D. & Jaramillo, C. A. 2009: Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. — *Nature* 457: 715–717.

Hernesniemi, E., Blomstedt, K. & Fortelius, M. 2011: Multiview stereo three-dimensional reconstruction of lower molars of Recent and Pleistocene rhinoceroses for mesowear analysis. — *Palaeontologia Electronica* 14, 2T, https://palaeo-electronica.org/2011_2/246/246.pdf.

Hontecillas, D., Soibelzon, L. H., Montalvo, C. I. & Bonini, R. A. 2023: *Cyonasua zettii* sp. nov. (Procyonidae, Mammalia) from the Late Miocene of Central Argentina and a review of the fossil record of Cerro Azul Formation. — *Historical Biology*, https://doi.org/10.1080/08912963.2023.2284421.

Janis, C. M. 1988: An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. — *Mémoires du Museum National d'Historie Naturelle* 53: 367–387.

Janis, C. M. & Fortelius, M. 1988: On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. — *Biological Reviews* 63: 197–230.

Janis, C. M., Damuth, J. & Theodor, J. M. 2002: The origins and evolution of the North American grassland biome: the story from the hoofed mammals. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 177: 183–198.

Jaramillo, C. 2018: Evolution of the Isthmus of Panama: biological, palaeoceanographic and palaeoclimatological implications. — In: Hoorn, C., Perrigo, A. & Antonelli,

A. (eds.), *Mountains, climate and biodiversity*: 323–338. John Wiley & Sons, Hoboken.

Jernvall, J., Hunter, J. P. & Fortelius, M. 1996: Molar tooth diversity, disparity, and ecology in Cenozoic ungulate radiations. — *Science* 274: 1489–1492.

Kaiser, T. M., Brasch, J., Castell, J. C., Schulz, E. & Clauss, M. 2009: Tooth wear in captive wild ruminant species differs from that of free-ranging conspecifics. — *Mammalian Biology* 74: 425–437.

Kaiser, T. M., Müller, D. W. H., Fortelius, M., Schulz, E., Codron, D. & Clauss, M. 2013: Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. — *Mammal Review* 43: 34–46.

Kay, R. F. & Madden, R. H. 1997a: Mammals and rainfall: paleoecology of the middle Miocene at La Venta (Colombia, South America). — *Journal of Human Evolution* 32: 161–199.

Kay, R. F. & Madden, R. H. 1997b: Paleogeography and Paleoecology. — In: Kay, R. F., Madden, R. H., Cifelli, R. L. & Flynn, J. J. (eds.), *Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia*: 520–550. Smithsonian Institution Press, Washington D.C.

Kay, R. F., Madden, R. H., Cifelli, R. L. & Flynn, J. J. 1997: *Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia*. — Smithsonian Institution Press, Washington D.C.

Kramarz, A. G. & Bond, M. 2011: A new early Miocene astrapotheriid (Mammalia, Astrapotheria) from Northern Patagonia, Argentina. — *Neues Jahrbuch für Geologie und Palaontologie-abhandlungen* 260: 277–287.

Krause, J. M., Clyde, W. C., Ibañez-Mejía, M., Schmitz, M. D., Barnum, T., Bellosi, E. S. & Wilf, P. 2017: New age constraints for early Paleogene strata of central Patagonia, Argentina: implications for the timing of South American Land Mammal Ages. — *Bulletin of the Geological Society of America* 129: 886–903.

Kurtén, B. 1952: The Chinese *Hipparion* fauna. — *Commentationes Biologicae, Societas Scientiarum Fennica* 13: 1–82.

Labarca, R., González-Guarda, E., Lizama-Catalán, Á., Villavicencio, N. A., Alarcón-Muñoz, J., Suazo-Lara, F., Oyanadel-Urbina, P., Soto-Huenchuman, P., Salazar, C., Soto-Acuña, S. & Buldrini, K. E. 2020: Taguatagua 1: New insights into the late Pleistocene fauna, paleoenvironment, and human subsistence in a unique lacustrine context in central Chile. —*Quaternary Science Reviews* 238, 106282, https://doi.org/10.1016/j.quascirev.2020.106282.

Lauer, D. A., Lawing, A. M., Short, R. A., Manthi, F. K., Müller, J., Head, J. J. & McGuire, J. L. 2023: Disruption of trait–environment relationships in African megafauna coincident with hominin emergence. — *Nature Communications* 14, 4016, https://doi.org/10.1038/s41467-023-39480-8.

Linares, O. J. 1981: Tres nuevos carnívoros prociónidos fósiles del Mioceno de Norte y Sudamérica. — *Ameghiniana* 18: 113–121.

Liu, L., Puolamäki, K., Eronen, J. T., Ataabadi, M. M., Hernesniemi, E. & Fortelius, M. 2012: Dental functional traits of mammals resolve productivity in terrestrial ecosystems past and present. — *Proceedings of the Royal Society B* 279: 2793–2799.

Liu, L., Galbrun, E., Tang, H., Kaakinen, A., Zhang, Z., Zhang, Z. & Žliobaitė, I. 2023: The emergence of modern zoogeographic regions in Asia examined through climate–dental trait association patterns. — *Nature Communications* 14, 8194, https://doi.org/10.1038/s41467-023-43807-w.

Loffredo, L. F. & DeSantis, L. R. G. 2014: Cautionary lessons from assessing dental mesowear observer variability and integrating paleoecological proxies of an extreme generalist *Cormohipparion emsliei*. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 395: 42–52.

Lundgren, E. J., Ramp, D., Ripple, W. J. & Wallach, A. D. 2018: Introduced megafauna are rewilding the Anthropocene. — *Ecography* 41: 857–866.

MacFadden, B. J., Anaya, F. & Argollo, J. 1993: Magnetic polarity stratigraphy of Inchasi: a Pliocene mammal-bearing locality from the Bolivian Andes deposited just before the Great American Interchange. — *Earth and Planetary Science Letters* 114: 229–241.

Madden, R. H. 2015: *Hypsodonty in mammals: evolution, geomorphology, and the role of Earth surface processes*. — Cambridge University Press, Cambridge.

Marivaux, L., Negri, F. R., Antoine, P.-O., Stutz, N. S., Condamine, F. L., Kerber, L., Pujos, F., Ventura Santos, R., Alvim, A. M. V., Hsiou, A. S., Bissaro, M. C., Adami-Rodrigues, K. & Ribeiro, A. M. 2023: An eosimiid primate of South Asian affinities in the Paleogene of Western Amazonia and the origin of New World monkeys. — *Proceedings of the National Academy of Sciences* 120, e2301338120, https://doi.org/10.1073/pnas.2301338120.

Marshall, L. G., Butler, R. F., Drake, R. E., Curtis, G. H. & Tedford, R. H. 1979: Calibration of the Great American Interchange. — *Science* 204: 272–279.

McGrath, A. J., Flynn, J. J. & Wyss, A. R. 2020: Proterotheriids and macraucheniids (Litopterna: Mammalia) from the Pampa Castillo Fauna, Chile (early Miocene, Santacrucian SALMA) and a new phylogeny of Proterotheriidae. — *Journal of Systematic Palaeontology* 18: 717–738

Mihlbachler, M. C., Rivals, F., Solounias, N., Semprebon, G. M. 2011: Dietary change and evolution of horses in North America. — *Science* 331: 1178–1181.

Morgan, G. S. 2008: Vertebrate fauna and geochronology of the Great American Biotic Interchange in North America. — *New Mexico Museum of Natural History & Science Bulletin* 44: 93–140.

Murphy, W. J., Foley, N. M., Bredemeyer, K. R., Gatesy, J. & Springer, M. S. 2021: Phylogenomics and the genetic architecture of the placental mammal radiation. — *Annual Review of Animal Biosciences* 9: 29–53.

O'Dea, A., Lessios, H. A., Coates, A. G., Eytan, R. I., Restrepo-Moreno, S. A., Cione, A. L., Collins, L. S., de Queiroz, A., Farris, D. W., Norris, R. D., Stallard, R. F., Woodburne, M. O., Aguilera, O., Aubry, M.-P., Berggren, W. A., Budd, A. F., Cozzuol, M. A., Coppard, S. E., Duque-Caro, H., Finnegan, S., Gasparini, G. M., Grossman, E. L., Johnson, K. G., Keigwin, L. D., Knowlton, N., Leigh, E. G., Leonard-Pingel, J. S., Marko, P. B., Pyenson, N. D., Rachello-Dolmen, P. G., Soibelzon, E., Soibelzon, L., Todd, J. A., Vermeij, G. J. & Jackson, J. B. C. 2016: Formation of the Isthmus of Panama. — *Science Advances* 2, e1600883, https://doi.org/10.1126/sciadv.1600883.

O'Leary, M. A., Bloch, J. I., Flynn, J. J., Gaudin, T. J., Giallombardo, A., Giannini, N. P., Goldberg, S. L., Kraatz, B. P., Luo, Z.-X., Meng, J., Ni, X., Novacek, M. J., Perini, F. A., Randall, Z. S., Rougier, G. W., Sargis, E. J., Silcox, M. T., Simmons, N. B., Spaulding, M., Velazco, P. M., Weksler, M., Wible, J. R. & Cirranello, A. L. 2013: The placental mammal ancestor and the post-K-Pg radiation of placentals. — *Science* 339: 662–667.

Oksanen, O., Žliobaitė, I., Saarinen, J., Lawing, A. M. & Fortelius, M. 2019: A Humboldtian approach to life and climate of the geological past: estimating palaeotemperature from dental traits of mammalian communities. — *Journal of Biogeography* 46: 1760–1776.

Parker, A. K., Müller, J., Boisserie, J. R. & Head, J. J. 2023: The utility of body size as a functional trait to link the past and present in a diverse reptile clade. — *Proceedings of the National Academy of Sciences* 120, e2201948119, https://doi.org/10.1073/pnas.2201948119.

Patterson, B. & Pascual, R. 1968: The fossil mammal fauna of South America. — *Quarterly Review of Biology* 43: 409–451.

Pérez, M. E., Vallejo-Pareja, M. C., Carrillo, J. D. & Jaramillo, C. 2017: A new Pliocene capybara (Rodentia, Caviidae) from northern South America (Guajira, Colombia), and its implications for the Great American Biotic Interchange. — *Journal of Mammalian Evolution* 24: 111–125.

Politis, G. G., Messineo, P. G., Stafford, T. W. & Lindsey, E. L. 2019: Campo Laborde: a Late Pleistocene giant ground sloth kill and butchering site in the Pampas. — *Science Advances* 5, eaau4546, https://doi.org/10.1126/sciadv.aau4546.

Polly, P. D., Eronen, J. T., Fred, M., Dietl, G. P., Mosbrugger, V., Scheidegger, C., Frank, D. C., Damuth, J., Stenseth, N. C. & Fortelius, M. 2011: History matters: ecometrics and integrative climate change biology. — *Proceedings of the Royal Society B* 278: 1131–1140.

Polly, P. D. & Head, J. J. 2015: Measuring Earth-life transitions: ecometric analysis of functional traits from Late Cenozoic vertebrates. — *The Paleontological Society Papers* 21: 21–46.

Polly, P. D., Lawing, A. M., Eronen, J. T. & Schnitzler, J. A. N. 2016: Processes of ecometric patterning: modelling functional traits, environments, and clade dynamics in deep time. — *Biological Journal of the Linnean Society* 118: 39–63.

Poux, C., Chevret, P., Huchon, D., De Jong, W. W. & Douzery, E. J. P. 2006: Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. — *Systematic Biology* 55: 228–244.

Prates, L. & Perez, S. I. 2021: Late Pleistocene South American megafaunal extinctions associated with rise of Fishtail points and human population. — *Nature Communications* 12, 2175, https://doi.org/10.1038/s41467-021-22506-4.

Prates, L., Rivero, D. & Perez, S. I. 2022: Changes in projectile design and size of prey reveal the central role of Fishtail points in megafauna hunting in South America. — *Scientific Reports* 12, 16964, https://doi.org/10.1038/s41598-022-21287-0.

Reguero, M. A. & Candela, A. M. 2011: Late Cenozoic mammals from the Northwest of Argentina. — In: Salfity, J. & Marquillas, R. A. (eds.), *Cenozoic geology of the Central Andes of Argentina*: 411–426. SCS Publisher, Salta.

Rivals, F., Solounias, N. & Mihlbachler, M. C. 2007: Evidence for geographic variation in the diets of late Pleistocene and early Holocene bison in North America, and differences from the diets of recent Bison. — *Quaternary Research* 68: 338–346.

Rougier, G. W., Forasiepi, A. M., Hill, R. V. & Novacek, M. 2009: New mammalian remains from the Late Cretaceous La Colonia Formation, Patagonia, Argentina. — *Acta Palaeontologica Polonica* 54: 195–212.

Rougier, G. W., Gaetano, L. C., Drury, B. R., Gómez, R. O. & Arango, N. P. 2011: A review of the Mesozoic mammalian record of South America. — In: Calvo, J., Porfiri, J., González Riga, B. & Dos Santos, D. (eds.) *Paleontología y dinosaurios desde América Latina*: 195–213. Editorial de la Universidad Nacional de Cuyo, Mendoza.

Saarinen, J. & Karme, A. 2017: Tooth wear and diets of extant and fossil xenarthrans (Mammalia, Xenarthra) – Applying a new mesowear approach. — *Palaeogeography Palaeoclimatology Palaeoecoogy* 476: 42–54.

Saarinen, J. & Lister, A. M. 2016: Dental mesowear reflects local vegetation and niche separation in Pleistocene proboscideans from Britain. — *Journal of Quaternary Science* 31: 799–808.

Saarinen, J. & Lister, A. M. 2023: Fluctuating climate and dietary innovation drove ratcheted evolution of proboscidean dental traits. — *Nature Ecology and Evolution* 7: 1490–1502.

Saarinen, J., Mantzouka, D. & Sakala, J. 2020: Aridity, cooling, open vegetation, and the evolution of plants and animals during the Cenozoic. — In: Martinetto, E., Tschopp, E. & Gastaldo, R. A. (eds.), *Nature through time*: 83–107. Springer Nature, Cham.

Saarinen, J., Eronen, J. T., Fortelius, M., Seppä, H. & Lister, A. M. 2016: Patterns of diet and body mass of large ungulates from the Pleistocene of western Europe, and their relation to vegetation. — *Palaeontologia Electronica* 19.3.32A, https://doi.org/10.26879/443.

Saarinen, J., Karme, A., Cerling, T., Uno, K., Säilä L., Kasiki, S., Ngene, S., Obari, T., Mbua, E., Manthi, F. K. & Fortelius, M. 2015: A new tooth wear-based dietary analysis method for Proboscidea (Mammalia). — *Journal of Vertebrate Paleontology* 35, e918546, https://doi.org/10.1080/02724634.2014.918546.

Saarinen, J., Oksanen, O., Žliobaitė, I., Fortelius, M., DeMiguel, D., Azanza, B., Bocherens, H., Luzón, C., Solano-García, J., Yravedra, J., Courtenay, L. A., Blain, H. A., Sánchez-Bandera, C., Serrano-Ramos, A., Rodriguez-Alba, J. J., Viranta, S., Barsky, D., Tallavaara, M., Oms, O., Agustí, J., Ochando, J., Carrión, J. S. &

Jiménez-Arenas, J. M. 2021: Pliocene to Middle Pleistocene climate history in the Guadix-Baza Basin, and the environmental conditions of early *Homo* dispersal in Europe. — *Quaternary Science Reviews* 268, 107132, https://doi.org/10.1016/j.quascirev.2021.107132.

Sánchez-Villagra, M. R., Burnham, R. J., Campbell, D. C., Feldmann, R. M., Gaffney, E. S., Kay, R. F., Lozsán, R., Purdy, R. & Thewissen, J. G. M. 2000: A new near-shore marine fauna and flora from the early Neogene of northwestern Venezuela. — *Journal of Paleontology* 74: 957–968.

Sanz-Pérez, D., Montalvo, C. I., Mehl, A. E., Tomassini, R. L., Hernández Fernández, M. & Domingo, L. 2024: Paleoenvironment and paleoecology associated with the early phases of the Great American Biotic Interchange based on stable isotope analysis of fossil mammals and new U-Pb ages from the Pampas of Argentina. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 634, 111917, https://doi.org/10.1016/j.palaeo.2023.111917.

Scott, W. B. 1937: *A history of land mammals in the western hemisphere*. — MacMillan Co., New York.

Schap, J. A. & Samuels, J. X. 2020: Mesowear analysis of the *Tapirus polkensis* population from the Gray fossil site, Tennessee, USA. — *Palaeontologia Electronica* 23(2), a26, https://doi.org/10.26879/875.

Schap, J. A., Samuels, J. X. & Joyner, T. A. 2021: Ecometric estimation of present and past climate of North America using crown heights of rodents and lagomorphs. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 562, 110144, https://doi.org/10.1016/j.palaeo.2020.110144.

Schap, J. A., McGuire, J. L., Lawing, A. M., Manthi, F. K. & Short, R. A. 2024: Ecometric models of small mammal hypsodonty can estimate paleoprecipitation across eastern Africa. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 643, 112181, https://doi.org/10.1016/j.palaeo.2024.112181.

Seiffert, E. R., Tejedor, M. F., Fleagle, J. G., Novo, N. M., Cornejo, F. M., Bond, M., de Vries, D. & Campbell, K. E. 2020: A parapithecid stem anthropoid of African origin in the Paleogene of South America. — *Science* 368: 194–197.

Shockey, B. J. 1997: Two new notoungulates (Family Notohippidae) from the Salla Beds of Bolivia (Deseadan: late Oligocene): systematics and functional morphology. — *Journal of Vertebrate Paleontology* 17: 584–599.

Shockey, B. J. 2005: New leontinidids (Class Mammalia, Order Notoungulata, Family Leontiniidae) from the Salla Beds of Bolivia (Deseadan, Late Oligocene) — *Bulletin of the Florida Museum of Natural History* 45: 249–260.

Short, R. A., Pinson, K. & Lawing, A. M. 2021: Comparison of environmental inference approaches for ecometric analyses: using hypsodonty to estimate precipitation. — *Ecology and Evolution* 11: 587–598.

Silvestro, D., Tejedor, M. F., Serrano-Serrano, M. L., Loiseau, O., Rossier, V., Rolland, J., Zizka, A., Höhna, S., Antonelli, A. & Salamin, N. 2019: Early arrival and climatically-linked geographic expansion of New World monkeys from tiny African ancestors. — *Systematic Biology* 68: 78–92.

Simpson, G. G. 1951: *Horses: the story of the horse family in the modern world and through sixty million years of evolution*. — Oxford University Press, Oxford.

Simpson, G. G. 1980: *Splendid isolation: the curious history of South American mammals.* — Yale University Press, New Haven and London.

Smith, J. D., Genoways, H. H. & Jones, J. K. Jr. 1977: Cranial and dental anomalies in three species of platyrrhine monkeys from Nicaragua. — *Folia Primatologica* 28: 1–42.

Soibelzon, L. H., Rinderknecht, A., Tarquini, J. & Ugalde, R. 2019: First record of fossil procyonid (Mammalia, Carnivora) from Uruguay. — *Journal of South American Earth Sciences* 92: 368–373.

Soibelzon, L. H., De Los Reyes, M., Tarquini, J., Tineo, D. E., Poiré, D. G., González, G. & Vergani, G. D. 2020: First record of a fossil procyonid (*Cyonasua* cf. *C. pascuali*), Mammalia, Procyonidae) in Bolivia, Tariquía Fm., Late Miocene. — *Journal of South American Earth Sciences* 99, 102492, https://doi.org/10.1016/j.jsames.2019.102492.

Solórzano, A. & Núñez-Flores, M. 2021: Evolutionary trends of body size and hypsodonty in notoungulates and their probable drivers. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 568, 110306, https://doi.org/10.1016/j.palaeo.2021.110306.

Solounias, N., Tariq, M., Hou, S., Danowitz, M. & Harrison, M. 2014: A new method of tooth mesowear and a test of it on domestic goats. — *Annales Zoologici Fennici* 51: 111–118.

Spradley, J. P., Glazer, B. J. & Kay, R. F. 2019: Mammalian faunas, ecological indices, and machine-learning regression for the purpose of paleoenvironment reconstruction in the Miocene of South America. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 518: 155–171

Stirton, R. A. 1947: Observations on evolutionary rates in hypsodonty. — *Evolution* 1: 32–41.

Strömberg, C. A. E., Dunn, R. E., Madden, R. H., Kohn, M. J. & Carlini, A. A. 2013: Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America. — *Nature Communications* 4, 1478, https://doi.org/10.1038/ncomms2508.

Su, D. F. & Croft, D. A. 2018: Synthesizing paleoecological data. — In: Croft, D. A., Su, D. F. & Simpson, S. W. (eds.), *Methods in paleoecology: reconstructing Cenozoic terrestrial environments and ecological communities*: 395–404. Springer Nature, Cham.

Tarquini, J., Soibelzon, L. H., Salas-Gismondi, R. & De Muizon, C. 2020: *Cyonasua* (Carnivora, Procyonidae) from Late Miocene of Peru shed light on the early dispersal of carnivorans in South America. — *Journal of Vertebrate Paleontology* 40, e1834406, https://doi.org/10.1080/02724634.2020.1834406.

Tarquini, S. D., Ladevèze, S. & Prevosti, F. J. 2022: The multicausal twilight of South American native mammalian predators (Metatheria, Sparassodonta). — *Scientific reports* 12, 1224, https://doi.org/10.1038/s41598-022-05266-z.

Taylor, L. A., Müller, D. W. H., Schwitzer, C., Kaiser, T. M., Codron, D., Schulz, E. & Clauss, M. 2014: Tooth wear in captive rhinoceroses (*Diceros*, *Rhinoceros*, *Ceratotherium*: Perissodactyla) differs from that of free-ranging conspecifics. — *Contributions to Zoology* 83: 107–117.

Tejada-Lara, J. V., Salas-Gismondi, R., Pujos, F., Baby, P., Benammi, M., Brusset, S., de Franceschi, D., Espurt, N., Urbina, M. & Antoine, P.-O. 2015: Life in proto-Amazonia: Middle Miocene mammals from the Fitzcarrald Arch (Peruvian Amazonia). — *Palaeontology* 58: 341–378.

Trayler, R. B., Kohn, M. J., Bargo, M. S., Cuitiño, J. I., Kay, R. F., Strömberg, C. A. E. & Vizcaíno, S. F. 2020: Patagonian aridification at the onset of the mid-Miocene Climatic Optimum. — *Paleoceanography and Paleoclimatology* 35, e2020PA003956, https://doi.org/10.1029/2020PA003956.

Ungar, P. S., Healy, C., Karme, A., Teaford, M. & Fortelius, M. 2018: Dental topography and diets of platyrrhine primates. — *Historical Biology* 30: 64–75.

Vermillion, W. A., Polly, P. D., Head, J. J., Eronen, J. T. & Lawing, A. M. 2018: Ecometrics: a trait-based approach to paleoclimate and paleoenvironmental reconstruction. — In: Croft, D. A., Su, D. F. & Simpson, S. W. (eds.), *Methods in paleoecology: reconstructing Cenozoic terrestrial environments and ecological communities*: 373–394. Springer Nature, Cham.

Vizcaino, S. F. 2009: The teeth of the “toothless”: novelties and key innovations in the evolution of xenarthrans (Mammalia, Xenarthra). — *Paleobiology* 35: 343–366.

Von Koenigswald, W., Goin, F. J. & Pascual, R. 1999: Hypsodonty and enamel microstructure in the Paleocene gondwanatherian mammal *Sudamerica ameghinoi*. — *Acta Palaeontologica Polonica* 44: 263–300.

Vucetich, M. G., Arnal, M., Deschamps, C. M., Pérez, M. E. & Vieytes, E. C. 2015: A brief history of caviomorph rodents as told by the fossil record. — In: Vassallo, A. I. & Antenucci, D. (eds.), *Biology of caviomorph rodents: diversity and evolution*: 11–62. SAREM Series A, Mammalogical Research.

Walton, A. H. 1997: Rodents. — In: Kay, R. F., Madden, R. M., Cifelli, R. L. & Flynn, J. J. (eds.), *Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia*: 392–409. Smithsonian Institution Press, Washington D.C.

Webb, S. D. 1991: Ecogeography and the Great American Interchange. — *Paleobiology* 17: 266–280.

Welker, F., Collins, M. J., Thomas, J. A., Wadsley, M., Brace, S., Cappellini, E., Turvey, S. T., Reguero, M., Gelfo, J. N., Kramarz, A., Burger, J., Thomas-Oates, J., Ashford, D. A., Ashton, P. D., Rowsell, K., Porter, D. M., Kessler, B., Fischer, R., Baessmann, C., Kaspar, S., Olsen, J. V., Kiley, P., Elliott, J. A., Kelstrup, C. D., Mullin, V., Hofreiter, M., Willerslev, E., Hublin, J.-J., Orlando, L., Barnes, I. & MacPhee, R. D. E. 2015: Ancient proteins resolve the evolutionary history of Darwin’s South American ungulates. — *Nature* 522: 81–84.

Westbury, M., Baleka, S., Barlow, A., Hartmann, S., Paijmans, J. L. A., Kramarz, A., Forasiepi, A. M., Bond, M., Gelfo, J. N., Reguero, M. A., López-Mendoza, P., Taglioretti, M., Scaglia, F., Rinderknecht, A., Jones, W., Mena, F., Billet, G., de Muizon, C., Aguilar, J. L., MacPhee, R. D. E. & Hofreiter, M. 2017: A mitogenomic timetree for Darwin’s enigmatic South American mammal *Macrauchenia patachonica*. — *Nature Communications* 8, 15951, https://doi.org/10.1038/ncomms15951.

Wilson, O. E. & Parker, A. K. 2023: Low predator competition indicates occupation of macro-predatory niches by giant Miocene reptiles at La Venta, Colombia. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 632, 111843, https://doi.org/10.1016/j.palaeo.2023.111843.

Wilson, O. E. & Saarinen, J. 2024. Mesowear analysis of *Taubatherium paulacoutoi* (Late Oligocene Tremembé Formation, São Paulo State, Brazil). — *Revista Brasileira de Paleontologia* 27. [In press].

Wilson, O. E., Fortelius, M. & Saarinen, J. 2022: Species discovery and dental ecometrics: good news, bad news and recommendations for the future. — *Historical Biology* 35: 678–692.

Wolfe, J. A. 1990: Palaeobotanical evidence for a marked temperature increase following the Cretaceous/Tertiary boundary. — *Nature* 343: 153–156.

Woodburne, M. O. 2010: The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. — *Journal of Mammalian Evolution* 17: 245–264.

Xafis, A., Saarinen, J., Bastl, K., Nagel, D. & Grímsson, F. 2020: Palaeodietary traits of large mammals from the middle Miocene of Gračanica (Bugojno Basin, Bosnia-Herzegovina). —*Palaeobiodiversity and Palaeoenvironments* 100: 457–477.

Žliobaitė, I., Rinne, J., Tóth, A. B., Mechenich, M., Liu, L., Behrensmeyer, A. K. & Fortelius, M. 2016: Herbivore teeth predict climatic limits in Kenyan ecosystems. — *Proceedings of the National Academy of Sciences* 113: 12751–12756.

Žliobaitė, I., Tang, H., Saarinen, J., Fortelius, M., Rinne, J. & Rannikko, J. 2018: Dental ecometrics of tropical Africa: linking vegetation types and communities of large plant-eating mammals. — *Evolutionary Ecology Research* 19: 127–147.

Zobel, D. B. & Antos, J. A. 2017: Community reorganization in forest understories buried by volcanic tephra. — *Ecosphere* 8, e02045, https://doi.org/10.1002/ecs2.2045.

Appendix. Institutional abbreviations.

AMU-CURS = Alcaldía Bolivariana de Urumaco, Urumaco, Venezuela.
EPN(Q) = Escuela Politécnica Nacional, Quito, Ecuador.
IGM = Museo Geológico José Royo y Gómez, Servicio Geológico Colombiano, Bogotá, Colombia.
MCT = Museu de Ciências da Terra, Serviço Geológico do Brasil, Rio de Janeiro, Brazil.
MGP-PD = Sezione di Geologia e Paleontologia del MNU, Università degli Studi di Padova, Italy.
MHNT = Museu de História Natural de Taubaté Doutor Herculano Alvarenga, Taubaté, Brazil.
MNHN = Muséum National d'Histoire Naturelle, Paris, France.
MNHN-Bol = Museo Nacional de Historia Natural, La Paz, Bolivia.
MPV = Museo Paleontológico Villavieja, Villavieja, Colombia.
MUN-STRI = The Mapuka Museum of Universidad del Norte, Barranquilla, Colombia.
MUSM = Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru.
SGO-PV = Fossil vertebrates collection of the Museo Nacional de Historia Natural de Santiago, Santiago, Chile.
UATF-V = Vertebrate Palaeontology Collection, Universidad Autónoma "Tomás Frías", Potosí, Bolivia.
UCMP = University of California Museum of Paleontology, Berkeley, USA.
UCV-VF = Museo Dr. José Royo y Gómez de la Escuela de Geología, Minas y Geofísica de la Universidad Central de Venezuela, Caracas, Venezuela.
UFAC = Universidade Federal do Acre, Rio Branco, Brazil.
UNC = Departamento de Geociencias, Universidad Nacional de Colombia, Bogotá, Colombia.
VPPLT = Vigías del Patrimonio Paleontológico, Museo de Historia Natural La Tatacoa, Villavieja, Colombia.