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GENERA ARE OFTEN BETTER THAN SPECIES FOR DETECTING EVOLUTIONARY CHANGE IN THE FOSSIL RECORD: A REPLY TO SALESA ET AL.

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In their technical comment Salesa et al. (2011) raise several issues, including an important topic affecting most, or perhaps all, paleoecological studies—the difficulty of determining a reasonable way to deal with taxonomy. Specifically, Salesa et al. draw our attention to a taxonomic revision of Iberian *Anchitherium* (Sánchez et al. 1998), that we failed to follow in our study (Eronen et al. 2010), and express concerns that a different handling of *Anchitherium* taxonomy would have affected our results and conclusions.

KEY WORDS: **Anchitherium, genus-level, Miocene, tooth crown height, regional climate.**

In our study, we contrasted a classic *Anchitherium* locality from Germany to material collected from multiple localities in Spain. The reasons for examining multiple localities from Spain was to increase sample size and to ascertain that the more derived state of *Anchitherium* evolution, in this case dental morphologies showing incipient hypsodonty, was not restricted to a single Spanish locality. In contrast to the multiple species described from Spain, the Central European *Anchitherium* consists of one species (*A. aurelianense*) split into three subspecies (Abusch-Siewert 1983; Forsten 1991; Bernor & Armour-Chelu 1999). As our analyses (Eronen et al. 2010) and the analyses of Salesa et al. (2011) show, there is variation among Spanish localities but this is markedly more subtle than between German and Spanish specimens. We agree with the first point of Salesa et al. (2011) that there may have been environmental differences among Spanish localities, and discussed the "fragmentation of habitats" as a regional factor driving the evolution of hypsodonty in Spanish *Anchitherium*. However, we interpreted the ultimate driver of the difference between German and Spanish *Anchitherium* to be the way regions respond to large-scale climatic changes of the Miocene (Fortelius et al. 2002; Mosbrugger et al. 2005; Eronen et al. 2009).

In their second and third points, Salesa et al. (2011) point out the detailed nature of Spanish *Anchitherium* radiations. Although we agree that at the regional scale the patterns are indeed more nuanced, our aim was to look at the "prime" stage of radiation when *Anchitherium* as a genus had its broadest occupancy (Jernvall and Fortelius 2004).

The most extended discussion by Salesa et al. (2011) is focused on the taxonomy of Spanish *Anchitherium*. Most paleoecological analyses rely on taxa identified from each locality, and this information is also used to determine the biochronological order of localities relative to each other. Taxonomy of many fossil groups is often revised by various workers, and ideally these

revisions are reflected in museum collections and international publications. An additional challenge in fossil taxonomy is that the description and revision of taxonomy is often slow, and the fact that the relationship between fossil species and biological species is never entirely straightforward. To this end, large-scale paleoecological analyses preferentially use the genus level (e.g., Alroy 1996; Fortelius et al. 1996; Foote 2001). In cases where multiple levels of taxonomic hierarchy are compared, genus-level analyses provide similar patterns to species-level analyses (Roy et al. 1996; Jernvall and Fortelius 2002; Foote et al. 2007, but see also Krug et al. 2008). In our analyses, we contrasted all the Spanish *Anchitherium* with the single locality sample from Germany; thus we performed a genus-level analysis. We also examined Spanish specimens from Puente de Vallecas separately. This taxon was in our analyses *A. aurelianense* but is *A. matritense* according to Salesa et al. (2011). If we had used *A. castellanum* in the separate analyses, which according to Salesa et al. (2011) would be the most primitive and comparable to the German *Anchitherium*, the difference between Germany and Spain would have been even more pronounced. Finally, an added complication with the use of MN (Mammal Neogene) biochronological units is their potentially different absolute ages in different regions, a notable example being Spanish and Central European chronologies (e.g., Krijgsman et al. 1996; Steininger et al. 1996, 1999; Daams et al. 1999; Daxner-Höck 2001; Agusti et al. 2001; Aguilar et al. 2004). This alone calls for caution when making detailed temporal comparisons of faunas across regions or comparing global climate reconstructions based on deep-sea isotope records (Zachos et al. 2001) to detailed terrestrial evolutionary scenarios.

We do welcome the taxonomic revision by Sánchez et al. (1998), and would have been happy to use that taxonomy in our analyses. To this end, the advent of international collaborations in databases should eventually lead to a coherent view into extinct communities, allowing linking of high-resolution analyses of faunal dynamics across regions and continents.

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LITERATURE CITED

Abusch-Siewert, S. 1983. Gebissmorphologische Untersuchungen an Eurasiatischen Anchitherien (Equidae, Mammalia) unter besonderer Berücksichtigung der Fundstelle Sandelzhausen. Courier Forschungsinstituten Senckenberg 62:1–361.

Aguilar, J.-P., W. A. Berggren, M.-P. Aubry, D. V. Kent, G. Clauzon, M. Benammi, and J. Michaux. 2004. Mid-Neogene Mediterranean marine-continental correlations: an alternative interpretation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 204:165–186.

Agusti, J., L. Cabrera, M. Garces, W. Krijgsman, O. Oms, and J. M. Pares. 2001. A calibrated mammal scale for the Neogene of Western Europe: state of the art. Earth Sci. Rev. 52:247–260.

Alroy, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. Palaeogeogr. Palaeoclimatol. Palaeoecol. 127:285–311.

Bernor, R. L., and M. Armour Chelu. 1999. The family equidae. In The Miocene Land mammals of Europe. Pp. 193–202 *in* G. E. Rössner and K. Heissig, eds. The Miocene land mammals of Europe. Verlag Dr. Friedrich Pfeil, München.

Daams, R., A. J. Van Der Meulen, M. A. Alvarez-Sierra, P. Pelaez-Campomanes, and W. Krijgsman. 1999. Aragonian stratigraphy reconsidered, and a re-evaluation of the middle Miocene mammal biochronology in Europe. Earth Planetary Sci. Let. 165:287–294.

Daxner-Höck, G. 2001. Early and Late Miocene Correlation (Central Paratethys). Ber. Inst. Geol. Paläontol. Karl-Franzens-Univ. Graz 4:28–33.

Eronen, J. T., A. R. Evans, M. Fortelius, and J. Jernvall. 2010. The impact of regional climate on the evolution of mammals: a case study using fossil horses. Evolution 64:398–408.

Eronen, J. T., M. Mirzaie Ataabadi, A. Micheels, A. Karme, R. L. Bernor, and M. Fortelius. 2009. Distribution history and climatic controls of the Late Miocene Pikermian chronofauna. Proc. Natl. Acad. Sci. USA. 106:11867–11871.

Foote, M. 2001. Inferring temporal patterns of preservation, origination, and extinction from taxonomic survivorship analysis. Paleobiology 27:602–630.

Foote, M., J. S. Crampton, A. G. Beu, B. A. Marshall, R. A. Cooper, P. A. Maxwell, and I. Matcham. 2007. Rise and fall of species occupancy in Cenozoic marine molluscs. Science 318:1131–1134.

Fortelius, M., L. Werdelin, P. Andrews, R. L. Bernor, A. Gentry, L. Humphrey, W. Mittmann, and S. Viranta. 1996. Provinciality, diversity, turnover and paleoecology in land mammal faunas of the later Miocene of western Eurasia. Pp. 414–448 *in* R. Bernor, V. Fahlbusch, and W. Mittmann, eds. The evolution of Western Eurasian neogene mammal faunas. Columbia Univ. Press, New York.

Fortelius, M., J. T. Eronen, J. Jernvall, L. Liu, D. Pushkina, J. Rinne, A. Tesakov, I. A. Vislobokova, Z. Zhang, and L. Zhou. 2002. Fossil mammals resolve regional patterns of Eurasian climate change during 20 million years. Evol. Ecol. Res. 4:1005–1016.

Forsten, A. 1991. Size trends in Holarctic Anchitherines (Mammalia, Equidae). J. Paleontol. 65:147–159.

Jernvall, J., and M. Fortelius. 2002. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. Nature 417:538–540.

Jernvall, J., and M. Fortelius. 2004. Maintenance of trophic structure in fossil mammal communities: site occupancy and taxon resilience. Am. Nat. 164:614–624.

Krijgsman, M., M. Garces, C. G. Langereis, R. Daams, J. van Dam, A. Van Der Meulen, J. Agusti, and L. Cabrera. 1996. A new chronology for the middle to late Miocene continental record in Spain. Earth Planet. Sci. Lett. 142:367–380.

Krug, A. Z., D. Jablonski, and J. Valentine. 2008. Species-genus ratios reflect a global history of diversification and range expansion in marine bivalves. Proc. R. Soc. Lond. B. 275:1117–1123.

Mosbrugger, V., T. Utescher, and D. L. Dilcher. 2005. Cenozoic continental climatic evolution of Central Europe. Proc. Natl. Acad. Sci. USA. 102:14964–14969.

Roy, K., D. Jablonski, and J.Valentine. 1996. Higher taxa in biodiversity studies: patterns from eastern Pacific marine molluscs. Philos. Trans. R. Soc. Lond. B 351:1605–1613.

Salesa, M., I. Sanchez, B. Azanza, D. DeMiguel, and J. Morales. 2011. Systematics and taxonomy of the Spanish Anchitheriinae, and their relationship with regional climatic changes: a comment on Eronen et al.

Evolution. doi: 10.1111/j.1558-5646.2011.01219.x [Epub ahead of print].

Sánchez, I. M., M. J. Salesa, and J. Morales. 1998. Revisión Sistemática del género Anchitherium Meyer, 1834 (Equidae; Perrissodactyla) en España. Estudios Geol. 54:39–63.

Steininger, F. F., W. A. Berggren, D. V. Kent, R. L. Bernor, S. Sen, and J. Agusti. 1996. Circum-Mediterranean Neogene (Miocene and Pliocene) marine-continental chronologic correlations of European mammal units. Pp. 7–46 *in* R. L. Bernor et al., eds. The Evolution of Western Eurasian Neogene Mammal Faunas. Plenum, New York.

Steininger, F. F. 1999. Chronostratigraphy, Geochronology and Biochronology of the Miocene 'European Land Mammal Mega-Zones' (ELMMZ) and the Miocene 'Mammal-Zones (MN-Zones)'. Pp. 9–24. *in* G. E. Rössner and K. Heissig, eds. The Miocene land mammals of Europe. Verlag Dr. Friedrich Pfeil, München.

Zachos, J. C., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to Present. Science, 292:686–693.

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