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Biogeosciences Discussions

Interactive comment on "Chemical composition of modern and fossil Hippopotamid teeth and implications for paleoenvironmental reconstructions and enamel formation: 1. major and minor element variation" *by* G. Brügmann et al.

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Discussion of the referees comments

We are thankful for the thorough and thoughtful criticisms of the referees. We are pleased that they appreciate the extensive work put into this project and emphasize the importance of such systematic studies for understanding enamel biomineralization, diet and diagenetic processes and its implications for palaeoenvironmental studies.

The main comments

The main comments are related to two topics: one concerns the chemical composition of nutrition and drinking water intake of hippopotamus, its influence on tooth chemistry (MgO content, MgO/CaO or MgO/Na2O) and its interpretation with regard to the hippo habitat (Review #1, T. Tütken); the second concern centers on the sample types and their taxonomy (Review #2). In our following reply, we cite the comment of the referees between quotation marks, which is followed by our clarification; page numbers and lines refer to the discussion manuscript.

Referee #1

"I have only one critical point and some problems with the use of MgO/CaO and MgO/Na2O ratios to reconstruct the salinity changes of ambient water although this is an interesting approach. . . . From element concentrations of grass and lake waters one might be able to make a rough, back of the envelope calculation to see which intake controls the body fluid pool. "

In our manuscript, we do not restrict the interpretation of MgO distribution in enamel on water composition. We always discuss the use of MgO/CaO or MgO/Na2O in enamel to "distinguish saline lake from fresh water environments" (e.g. P5219, L9-13 or in the abstract P520, L 5-6). Thus, we try to emphasize that the environment or habitat, the interplay of vegetation cover, soils composition, bedrock, pore solution and lake or river water, determines the chemical fingerprint of the teeth. We actually discuss this complex interplay in our manuscript (P5200, L21-24). In fact, we select this more general phrase to meet the concerns about the ultimate source of MgO (or Sr, which we will discuss in an upcoming manuscript) in the diet: what is the contribution of the drinking water relative to the plant material? The Mg-concentrations in plants and terrestrial water reservoirs vary by several orders of magnitude. For example, in African fresh water lakes and rivers the Mg concentration varies from <1 μg/g to >100 μg/g (Talling and Talling, 1965). Along the River Nile dissolved Mg in river water varies from 5μg/g to

BGD

8, C4397–C4412, 2011

14 μg/g and ground water concentrations are up to 3 times higher (Dekov et al. 1997; Meybeck and Ragu, 1996). Vegetation on average contains about 0.2 dry wt.% of Mg, but concentrations in grass vary by more than a factor of ten depending on grass type and age, season, soil type, climate (Fleming and Murphy, 1968; Minson, 1990). For example, the Mg content in tropical grasses varies from 0.04 to 0.9 dry wt.% with an average of 0.35 dry wt.% (Skerman and Riveros, 1990). In summary, the grass/water ratio for the Mg concentration in fresh water environments varies enormously, somewhere between 4 and 9000. The Mg concentrations in plants from specifically saline environments are not well known. However, conditions of drought or high salinity reduce plant growth and nutrient uptake and may even cause nutrient deficiency (Hu and Schmidhalter, 2005). Dissolved Mg concentrations in saline lakes vary enormously (<1 μ/g to > 7 wt.%; Jones et al., 2003). This could mean that in saline Mg-rich environments, the proportion of Mg uptake derived from water intake is significant. This would explain the higher MgO content in teeth from saline environments. However, it is obvious that we cannot provide dependable numbers on the relative contribution of solid diet and water intake in saline environments. The uncertainties increase if we look at the food habits of hippopotamus, which have not been studied as well as those of other large herbivores. Hippopotamus daily consume about 50 kg of solid forage (about 2.5% of body weight, or in terms of dry weight forage, about 0.6% of body weight; Schwarm et al. (2006)). However, the amount of drinking water intake of Hippopotamus is unknown, even in captivity (personal communication with Dr. Sliwa, Curator of the Zoo at Cologne, Germany and Dr. Salz, operations manager of the Zoo at Basel, Switzerland, October 2011). A theoretic approach using the metabolic rate versus body mass relationship, would estimate 43 l to 72 l per day of water intake (Calder, 1984). These numbers would vary a great deal, depending on seasonality, vegetation type, animal weight and age, parameters that we do not know from our recent analogue specimen. As the discussion above indicates, we did evaluate mass balance calculations. However, this turned out to be so speculative, that we omitted this discussion: neither can we provide a reliable estimate of the concentration of MgO in the forage and drinking

BGD

8, C4397–C4412, 2011

water nor do we know food habits of Hippopotamus in different habitats well enough.

"Your new MgO/Na2O proxy to infer the Lake Albert hydrologic history suggests no significant evaporation between 7 and 1.5 Ma, which is, as you say, in contradiction to the oxygen isotope results, which indicate a continuous evaporation in this time interval. This already indicates some unambiguity of the element proxy, which needs explanation."

We actually discussed this "contradiction" in our manuscript (P219, L25-26.). One important aspect to understand is the sensitivity of the proxies regarding evaporation. The oxygen isotopic composition of water reacts sensitively to evaporation (LIT), however the sensitivity of the MgO/Na2O is not established. Thus, in the manuscript we suggested that oxygen reacts more sensitive to evaporation than MgO/Na2O. One must also consider that the oxygen isotopic composition of lake water does not only depend on evaporation, but also for example on altitude and mean annual temperature. It is not known whether and how much these factors contribute to the oxygen isotope trend observed by Brachert et al. (2010) in the fossil Lake Albert specimens between 7 and 1.5 Ma. Our MgO/Na2O data from Lake Albert indeed indicate a relatively broad range of MgO/Na2O in the fossil Lake Albert specimens (Fig. 6, 8). This could reflect salinity changes in the lake, but because of the considerable overlap of MgO/Na2O among samples, we did not emphasize these differences. Nevertheless, the modern Lake Albert has significantly a higher MgO/Na2O ratio (=0.41; Table 1) and higher oxygen isotope composition (δ18O = 5.5) than the fossil lake (MgO/Na2O=0.24, δ18O <2.0; Table 1; Brachert et al., 2010). This would support the idea that MgO/Na2O and oxygen isotope composition monitor aridity and salinity changes.

Anonymous Referee #2

"My only negative remarks are in certain ecological and biological assumptions that are made that are not clear, such as which molar is used for sampling and the taxonomic identification of certain fossil hippos" "It is not often clear which tooth is being

BGD

8, C4397–C4412, 2011

sampled (i.e., molar, canine, etc.) Please check back through the text and make sure the sampled tooth is clearly indicated (M1, M2 , etc.). Knowing which molar is used is critical because of differences in eruption/formation times for each tooth and whether or not there is an in utero effect on enamel composition."

We agree that it is important to know the taxonomic identification and which type of teeth have been studied in order to present reasonable reconstructions of individual hippo environments. Unfortunately, with regard to the taxonomy, it is not possible to provide more details. As we described in the text, all modern specimens belong to the species Hippopotamus amphibius. However, the classification of the fossil specimens from the Lake Albert is problematic. This has been discussed by Boisserie (2005), who dismissed the original categorization of Faure (1994). The most obvious difference we observe is that there are specimens with large and specimens with small teeth. Thus, we are left with a simple classification applied by Brachert et al. (2010): one group with large teeth having the size of modern Hippopotamus sp. is called “Large Hippopotamids” and the second group with small teeth is termed “Small Hippopotamids of the Albertine Rift”. It appears that in terms of the major element compositions discussed in our manuscript we do not need to distinguish between these two classes of Hippopotamus. For example, if we divide our major element or the stable isotope data of Brachert et al. (2010) from Lake Albert into groups corresponding to the two taxa, we cannot find any criteria that would distinguish these different taxa. Therefore, by ignoring the taxonomic differences we do not introduce a bias, which would compromise our conclusions regarding the environmental fingerprints.

"It is not often clear which tooth is being sampled (i.e., molar, canine, etc.) Please check back through the text and make sure the sampled tooth is clearly indicated (M1, M2 , etc.). Knowing which molar is used is critical because of differences in eruption/formation times for each tooth and whether or not there is an in utero effect on enamel composition."

In the section 2.1 (P5204, L12-15) we stated that our sample set comprises exclusively

BGD

8, C4397–C4412, 2011

molars. Within the text, we did not distinguish between M1, M2 or M3 molars, because we could not find significant differences in the distribution of the major elements among these tooth types. In addition, it is not always possible to distinguish the molar type, because there are only tooth fragments and splinters available. However, most of our specimens represent M3 molars, which should not show any weaning effects. Indeed, in none of our samples such effects could be identified. Weaning signals are easily recognized by increasing or decreasing Sr and Ca or Sr/Ca across the neonatal line. Along our profiles from the outside enamel rim towards the dentin, we would cross the neonatal line if present. However, no sudden concentration changes along the profiles do occur. This implies that potential in utero/weaning effects are not important. Nevertheless, we will emphasize in the text that we studied molars and in our final electronical supplement attached to the manuscript, we will provide detailed information related to taxa and tooth type, if available.

Specific comments

Referee #1:

"The order of authors of the references in the text is not consistent and there is no systematic order. Usually it should be in chronological order, rarely in alphabetical. Check with the journal guideline and adjust throughout the text accordingly." We have prepared the reference list according to the guidelines of the journal (Copernicus publication style). However, we also realized that the reference list in the discussion paper deviates from that of our submitted manuscript. This we also observed for journal titles and their abbreviations. We have to discuss this with the editor.

"Do you have any information about the diet of the zoo rhinoceros to explain the different Na/Ca, Cl and Mg/Na than its modern african counterparts? If not from this individual, may be you can check with the zoo in Frankfurt for information how they feed their rhinos. Is it by the way an animal that was raised in the zoo or may it be a wild capture? Probably not but may be worth checking, if it is an old museum speci-

BGD

8, C4397–C4412, 2011

men as in this case it might have formed its enamel before it was brought to the zoo. Might be in any case interesting to learn about the rhino diet to see how this may affect element concentrations and ratios."

We presume the reviewer means hippopotamus rather than rhinoceros. We cannot see systematic differences of Na/Ca, Cl and Mg/Na in enamel from the zoo specimen (S276) if compared with the fossil specimens (see Fig. 3 and 8). Even the MgO/Na2O is right within the range of fossil samples (Fig. 8). Unfortunately we do not know the origin of the specimen, whether it was a wild capture or born in captivity. In captivity, the forage of the Hippopotamus consists dominantly of grass and hay supplemented with fruits, vegetables, and bread cereals (Schwarm et al., 2006). No information on the major element budget of the food is available. However, this has not real bearing on our interpretations and conclusions. The importance of the zoo specimen lies in its modern age, which allows us to compare modern and fossil specimens in order to evaluate alteration effects.

"What is the pore space volume in modern enamel? How can the enamel contain up to 24wt.% FeO? Is there a replacement of apatite by FeO occuring?"

This high FeO content has not been measured in enamel but in dentin (P5210 L2-3), which has a much higher pore space volume (up to 30 vol.%) than enamel (2 vol. %; Glimcher et al., 1990).

Anonymous Referee #2

"Specific: Page 5199, line 15 – “secondary enrichments” - too vague, are they isotopic, mineral, or both? Please specify. line 21 – how can the concentration be 300% of the enamel? Is it a 300% increase? Please clarify."

Regarding line 15: we add "secondary enrichments of these components Regarding line 21: we believe this statement is unambiguous.

"Page 5202, lines 28-29 – “compare. . .sites” again, this is a very vague sentence.

BGD

8, C4397–C4412, 2011

Could you please provide a little more information on what was measured and what the conclusions were that differed, rather than driving the reader back to the original articles (if he or she isn't familiar with them)?"

We will omit this sentence in order to accommodate the following argument

"Page 5203, lines 4-6 – how do we account for the problem of time? i.e., environments are changing all the time, yet certain diagenetic conditions that result in a specific trace element distribution in fossil material might have only occurred during a very specific temporal window. Likewise, we're unsure of how long those conditions persisted. So, I suppose all we can say about past environments or climates based on diagenetically imposed trace element composition is that it may have occurred at some point, but how do we know when and for how long?"

This is a point well taken. There is new evidence that bones can exchange chemical components with the sedimentary environment on time scales of millions or even tens of millions years (Herwartz et al., 2011). We will include this aspect, although such a long-term open-system behavior has not been demonstrated for teeth.

"Page 5205, lines 14-17: I am concerned about analyses done on hippopotamids of unknown taxonomy. Hippopotamids have varied in the degree of their aquatic lifestyle and likely their ecology, which is essential for interpreting the isotopic composition of their enamel. If we don't know how reliant on an aquatic habitat these hippos are (as opposed to modern H. amphibius which is entirely reliant on a water source to live in), how can we draw conclusions on the reflection of trace elements in enamel and ancient habitats?"

This point we have already addressed above. Variation in lifestyle or ecology would influence the conclusions about ancient habitats. However, as we argued above, there are no systematic differences in isotopic and chemical composition of enamel from small and large Hippopotamids. Even if we look at the sedimentary record, teeth from small and large Hippopotamids have been found in similar lacustrine environments.

BGD

8, C4397–C4412, 2011

Thus, there is no evidence for different lifestyles or ecology among our specimens.

"Page 5206, lines 10-11 – “outer part” refers to where, spatially, on the tooth? I believe only lower canines are predominately dentine, with a lateral strip of enamel on each (see Hillson’s 2005 “Teeth” book for details). "

We will clarify this by adding "the outer part of the crown". We analyzed only molars not canines.

"Page 5206 Lines 13 “to cover. . .variability.” - it is important to acknowledge that there could be a considerable amount of isotopic variation recorded in the middle of the profile that you did not sample and that samples at only the apex and cervix might not be present all possible compositional variation within a tooth. See hippo tusk profile in Cerling et al. 2008, Stable isotope ecology of the common hippopotamus (Journal of Zoology)."

We agree that along a tusk profile we could observe considerable amount of chemical and isotopic variation, because this tooth type grows livelong. We studied molars, which are not remodeled after their eruption. We observe almost identical variations of concentrations and ratios along apical and cervical profiles. We also measured along profiles in-between (for example in specimen S276 or 5306) but there are no systematic differences. It is actually one unexpected observation of our study that along profiles from the apex to the cervix near the enamel-dentin junction no significant concentration and ratio changes do occur.

"Page 5210, line 20 – citation to a table with results from ANOVA, please, or list values in text"

We consider it not to be necessary to add a table that reveals no information except that there is no relationship. We will add to the text a value for the probability level at which a relationship would become significant.

"Page 5215, lines 12-15 – I think this is very likely a key factor in observed differences

BGD

8, C4397–C4412, 2011

in elemental variation, although it probably doesn't tell the whole story." "Page 5216, lines 25-26, "one important. . .enamel." - I would have been very interested in seeing this data for all specimens."

We agree that data on the carbonate content would perfectly complement our data set. However, we have no direct access to analytical instrumentation, which could determine this component with high spatial resolution. The "missing" data do not concern our interpretation or conclusions. Such data would be more important for the interpretation of for example stable isotope compositions; this is not the subject of this manuscript

"Page 5218, lines 1-2 – this surely would change depending on sampling frequency and the tooth used; i.e., many incremental samples of continuously growing canine enamel will reveal more sharp changes in enamel composition than a serial sample of a molar."

In continuously growing teeth, we can expect significant chemical changes. However, we analyzed molars. We will add this word to the sentence.

"Page 5219, lines 22-24 "However, oxygen. . .2Ma." – isotope data from pedogenic carbonates or tooth enamel?"

in tooth enamel

"Table 1-3: I would like to see standard deviations for all average values, especially for Lake Albert fossil value since it is an average of 18 specimens."

We add the standard deviation of the averages to the table

Technical corrections

We add additional references suggested by both reviewers to the reference list if they directly concern tooth compositions. Similarly, we corrected grammar and spelling errors in the text and reference list. We also implemented the suggestions to improve

BGD

8, C4397–C4412, 2011

tables and figures. However, most of such comments of referee #2 are due to the unfortunately far too small reproduction of our figures in the discussion version. We will address this problem with the journal editor. In the following, we cut the technical comments on these subjects, and focus on comments of referee #1 concerning the content of the manuscript.

Referee #1:

"P 5204, L 6: Can you give a number here how small in km2 is the average/range of hippopotamid home range size (I think territory is more a politcal term) "

This will be highly variable depending on climate (dry and wet season), vegetation type, animal age, and population size. Grazing is often confined within 2 to 5 km of the water body and about 5 hectares of pasture are necessary to maintain good body condition (Chansa et al., 2011). We will add this to the text.

"P 5204, L 14: Please be more specific and say which molars you analyzed, M1, M2 or M3? Always the same molars? Is there any information about the molar eruption sequence? E.g. in humans the first molar starts already mineralizing its enamel at birth, hence can be partily influenced by suckling. "

We addressed this comment above under "Main comments" replying to Referee #2.

"P 5209, L 20: here you should be more specific, not just stating very low but give the maximum concentrations of the respective element oxides <Xwt.% or range x-y wt.% alternatively give the detection limits for the respective oxides. "

We will add such figures to these lines. Detection limits are given in Table S1 in the electronic supplement.

"P 5215, L 4: Mg is an element that is mobile during diagenesis. Therefore it may well be possible that concentration differences between fossil dentin and cement specimens reflect effects of alteration and not necessarily of habitat. This would only be true if you are sure that original compositions are still preserved. Can you? "

BGD

8, C4397–C4412, 2011

We mentioned at the beginning of the section (P5214, L8-10) that we cannot evaluate the influence of alteration on major element distribution in dentin and cement because we did not systematically investigate the distribution in this tooth parts. We will clarify this part of the text by mentioning the potential influence of secondary alteration.

"P 5216, L 13: You say enamel at the EDJ is the least altered to sample, which is plauible and reasonable, however, you also mention U-shaped trace element profiles and in this case the enamel in the central part of the thickness would be the appropriate area to sample to retrieve pristine chemical compositions. "

The U-shaped pattern is the cumulative curve of two distribution trends: secondary element addition at the outer enamel rim overrides the normal trend (established by modern specimens) of increasing concentration from the outside rim towards the enamel-dentin junction. Thus, the high concentrations near the enamel-dentin junction are not due to secondary enrichment but reflect, like the central low concentration part, pristine chemical compositions.

"P 5216, L 26-28: You say that the carbonate content decreases from the EDJ outwards and may compensate for the increase of the total element concentration in the same direction. Can you give numbers to justify this statement mass-balance-wise? How much in wt.% does the CO3 content decrease? "

The mass-balance is about 2 to 2.5 wt.% as we have demonstrated in the text. This is also seen in Table 4, where we calculated element concentrations at the outer enamel rim und at the enamel-dentin junction applying linear regression analysis. The Total, thus the sum of all components (we used capital T to define this parameter) increases by this amount from the rim towards the dentin. Carbonate is the only major component we could not measure. Thus, we suggest that the mass difference of 2 to 2.5 wt.% reflects the CO3 content.

"5218, L 22-25: I like this argument and the Na and Cl distribution in enamel should hence be a good indicator of significant enamel alteration. Are there any indications

BGD

8, C4397–C4412, 2011

of deviations from the concentration trends, e.g. at the outer enamel rim or in clearly altered enamel areas? "

There are cases where the major element contents of the outside rim appear to be altered. This concerns the outside 100-300 μm. This might explain some spread in the results of the regression analysis of Table 4, but it did not override the overall trends. In some cases, we recognize chemical "anomalies" along crossing fissures. Such data have not been included when calculating the composition of fresh enamel.

"P 5220, L 2: White Nile enamel this is not correct enamel specimens from the White Nile " "P 5220, L 11: dito. Is the Mg concentration of White Nile river water higher than for the Blue and Upper Nile? "

Why should White Nile enamel not be the correct specimen? We do not know what the Mg concentrations in the Nile water is, however, the enamel from the White Nile River has significantly, almost a factor of 2, higher MgO contents than Blue und Upper Nile enamel (Table 1; Fig. 8).

"P 5223, L 18-19: are there any data on the enamel fluid composition measured that support this reasonable statement? "

Aoba and Moreno (1987) and Moreno and Aoba (1987) performed such analyses on piglet and porcupine incisors (P5222, L12-14). Unfortunately, these data represent just a snapshot of the evolution of the enamel fluid; we are not aware of studies investigating the evolution of the chemical composition of the dental fluid with time. The statement that the Cl concentration in the fluid is increasing with time is supported on P5224, L12-13, as the crystal chemistry of apatite tells us that the Cl ion is too big to fit into the lattice of hydroxyapatite. This argument is confirmed by the observation that even during alteration Cl is not incorporated into the dentin, cement and enamel apatite (Fig. 5, 6, 7).

"P 5223, L 27-29: What do you mean by recrystallisation? Dissolution and reprecipi-

BGD

8, C4397–C4412, 2011

tation? Why is this necessary to explain the observed element concentration patterns of Na, Mg and Cl, this is not perfectly clear to me. I suggest that you add a sentence explaining the reasoning. Furthermore, is this conclusion of partial dissolution of enamel supported by data from the literature? Does it mean that some of the 14% enamel formed during the secreation phase is dissolved and again precipitated in the maturation phase? If so how much of the preexisting enamel is affected? "

As mentioned in the text and supported by published studies, at the end of the secretory stage just about 14 wt.% of apatite have been deposited. This apatite consists of nm-sized crystallites, which are in equilibrium with organic material and dental fluid. Our model proposes that after the appositional growth maturation starts at the enamel-dentin junction and proceeds towards the outside enamel rim. Maturation involves the growth of existing secretory crystallites and we assume that during this stage the newly deposited apatite and the existing secretory apatite equilibrated with the evolving dental fluid at the crystallization front. Away from the front, the secretory apatite crystallites also continuously equilibrate with the evolving dental fluid until they become engulfed by the crystallization front. Equilibration continues until crystal growth and protein removal close the pore spaces. Because of the small size of the secretory crystallites, we argue that they readily equilibrate with surrounding dental fluid. The alternative view that the crystallites can preserve their original chemical composition and develop a chemical zonation is therefore unlikely. However, because the composition of such small crystallites is not measurable, this argument is currently not testable by analytical experiments. This is the process we termed recrystallization, which is not a process of dissolution and reprecipitation. In fact, it is a process of reequilibration, or equilibrium recrystallization in small increments at the crystallization front. Commonly, such a process is called fractional crystallization. Perfect equilibrium crystallization would produce apatite crystal with identical compositions in the whole enamel. This is in contrast to what we observe. We will change the text in order to clarify the meaning of recrystallization. âĂČ References

BGD

8, C4397–C4412, 2011

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BGD

8, C4397–C4412, 2011

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Interactive comment on Biogeosciences Discuss., 8, 5197, 2011.