Journal of Archaeological Science 167 (2024) 106148

Contents lists available at ScienceDirect

Journal of Archaeological Science

journal homepage: www.elsevier.com/locate/jas

How to ethically and effectively sample human hair

Daniel R. Gleeson [a,b,*], Tanya M. Smith [c,d], Gerrit Dusseldorp [e], Kasha N. Willis [f], Benjamin T. Laffoon [g], Jean-Albert C. Colman [h,i,1], Kevin T. Uno [a,b,1]

[a] Department of Environmental Biology, University of Arizona, USA
[b] Lamont-Doherty Earth Observatory, Columbia University, USA
[c] Griffith School of Social and Cultural Research, Griffith University, Australia
[d] Australian Research Centre for Human Evolution, Griffith University, Australia
[e] The Department of Geography, Geology and Environment, University of Hull, UK
[f] Research School of Earth Sciences, Australian National University, Australia
[g] European Research Council, Belgium
[h] Department of Earth and Environmental Sciences, University of Rochester, USA
[i] Department of Earth and Environmental Sciences, University of Rochester, USA

ARTICLE INFO

Keywords:
Dicing microsampling
Enamel oxygen isotope
Inner enamel
Oxygen isotopes
Seasonality and paleoecology

ABSTRACT

Variations in oxygen isotope ratios in human tissues can be used to reconstruct changes in climate, water availability, and diet. Previous studies have shown that oxygen isotope ratios in human hair can be used to reconstruct seasonal changes in environmental conditions and diet. However, there is a lack of information on how to effectively sample hair for oxygen isotope analysis. Here we present a simple and inexpensive method for sampling hair for oxygen isotope analysis. We test the method on hair samples from 10 individuals and find that the method is reproducible and can be used to reconstruct seasonal changes in environmental conditions and diet. We also provide recommendations for sampling hair for oxygen isotope analysis, including the number of hairs to sample, the length of hair to sample, and the sampling interval. Our results suggest that hair can be a useful tissue for reconstructing seasonal changes in environmental conditions and diet, and that our method can be used to sample hair for oxygen isotope analysis in a variety of archaeological and forensic contexts.

* Corresponding author. 1215 E. Lowell St., Bldg. 77, Tucson, AZ 85721, USA.
E-mail address: dgleeson@email.arizona.edu (D.R. Gleeson).
[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.jas.2024.106148
Received 14 December 2023; Received in revised form 8 April 2024; Accepted 14 April 2024
0305-4403/

1. Introduction

1.1. Seasonal variation in the biosphere

Rainsfeaalsloossstaalpitesetructfuiofreardcent, erminoixnyggen-bmeaeicsugeaocileossreelsyemthloesfeApphos-biongeogr(Sphayeear2.0,1;Higgeinls2.0,1)6vegetatploadmodearmdvelprsefrovsetsdeiel(Charlaim&gharp,(Mayarnkdhaly2a0n1;Vi,ieeta2l.0,1)7,antdhteimaingature4.99;Blumenethla2l.0,1;Smieta2l.0,1)8Becauseeftohrmofanimbaehav(Mieolreiaml2.0,1;Shpagneeldael2.0,1;Wesslingcremeonvetarhloeyuosdleaymso,ntansyleaarsayefis-eta2l.0,1)3Seasoniastlhiotuytgdutrisvpeeci(Thionmassscremeen-HAtpealanlseocpaldteefseasohiamh(Maeeha l.,eta2l.0,1)3,andsimplicahtuemdaonrig(Simsnheeimaer,198;Bala2006;Passaenyer2l.0,0;Passeetayl2.0,0;52.0,0;Wesleianlg2.0,1)3dhise(Aaseweiteyh2t0,0)8;subsis-Pederaand&Birit2.0,0)9Seriemamoe-Oscillaarteionsten(Geel1.9,9)5,ocsitarlucatnudriet(Wangraon&GraebdirectlyattoeedasemavironmaneteVaalue-Beasl-asse2.0,1)5Undersatsthoeeqduiasltriobfuatioinmoenhnoeuosfeethyee(Walahdawl1e9r8;Heinegal2.0,1;Bianklijmans-istoifcIsimiantcelurdaiimngsfeaalslon(Allieetayl2.0,1;Green2.0,1)7,seasoniasalmiatyiccompnoefocotntempoIriamayteeeta2l.0,2;Vaigledavla2.0,2)4Fofurtdhiesrcuosfsioneral-changeg(erch1e9r9;tB,atezal2.0,0;Barceitaal2.0,1;Mobrezatisoe-Tex-,“Mineral”ization.eta2.0,1;Schwæratl2.0,2;Poleteale2r0,2)2Ovelrortgimescaleseas,soriaanIfluegnrcoessriaotmeetsm,osphcheremicasntdly1,.4Accoufnoti-ngvariaibeinlviityronmleonatdadlo,othglaciadnitoni,tosulitiifmthgeEarstchlimsattaeeta-euegal.,enamel2.0,1;Wulefal2.0,1)0.

1.2. Oxygen isotope fossil archive of local to global climate

Variabineinvtiyronmtemperaatruirdeaistdye,ograpanydyadiveosfiotoiydtemea,whitthoiwrmataensdmpli-aree fecbtyetdlexygæmdhydroigseontcoompmeposiotfiotnusdcefsisotopaiorgeelattcpvrecip(teaKtoi.hon1.9,9)6.environmaen(Gaal1.9,9;Bowe2n0,1)COxygiesnotcoompme-Thesseasovnarliaylpeoidsbwimeahtmospchxeygiaecmd,positaiderypicdaeslcyraiseOdvaluewhse,reatRoofthebodwyateesermvioxiurscroexnytgiemnpuwtstthoisrecorpo-heavy-toox-ylgiiesnhottopeS1i8ma1m6polfientesease,ratiendthpeasFtur.thearmgrivelenoncaitnoonetrhamheals-meaasurredattoaiseteandsatrsdu,cthha1t8Os = (Rs/Rst)d - 1formtehdromighearadditimounltiwpaveesvetrimoef,ten(Friedmaan&ONei1l9,7;Cop2e0n1;Shap2l0,1)7nthgeloba-characaesmiinzieslderaelvtaivoelmeennamsetIrucitsursethydrocygtlheies,sotcoompmipcosoifaitonmosspwhaetrveiacpor-wihtthsetrucgtruoiwemas(Sug1a9,8;Passaenyer&Cerling,precipiintahteioormnfraiamdsnovsan,dlrinkwiantgein-1967;Gat1,99;Bowe2n0,1;Boweenta2l.0,1)9Inatmosphe2r0ic;Balumenethla2l.0,1)5Somreegiofmosoetrhamreelmaain-streamsevandslakaesvlarsypatiaaldvetrim(Deansgaa2d0,0;Passeetayl2.0,0;Bodleestalk2.0,0;Greeenta2l.0,1,7moisturaen,sapropdotogrelsosstuperecipirteastuihotnincomphieneteavolievzyeedaraftthemoensoefetnamseelcretionisotopliicgadplrkeycipaiathaghemiaandesi(dcdoes(Uneta2l.0,1)3.cootemperaatnuarlteosn)gieststafmrcotemsecaeSnesa.sonalAsaconsequeemacsesingcaalosedistodratmepde,moerd,pattenthesotcoompmipcosoifitaionafnadlolnIntinseumrtfaaceenttilroeisntyeedtehs,ptihtieecremeanttuarfthefiorrmationwaterusecomplicmartepdlicvaalt,ietnuvdieronamendmotrse,Oneegiofmtheirsehsiennemroasmtærle:gioofmarwoiwdthinfuebyfeudctuaitmriaimsafmaolulthtatmpera(Gaur,eadjactehenamel-jduemnct(tiEDthh)achieigmsineral1.99;Bowe2n0,0;2012;Bedaestal2.0,2)0Seasoinsaoltopdiecnsisthioerastfltyeercre(Zaiaoneta2l.0,0;5Taffoeeta2u,compsiatrieompsacbtyeadmosphieriducaanthioinsture2.0,0;Smiah&Taffo2.0,6;Greeenta2l.0,1;Menegeotal.,sourceelytheartveaipoaftaionafsiatranfsriotms2.0,1)7.ItremaiumsleawevheorwthitchkeonefhighlycloutchsrowghmaerdrilearyefastmosphiesfeurthemrinerailnzeerdenoamsmiesW,ithrepsorretpsorratnsgfiingmsinfuenbcysedgnifacaninstotopfircaclliyoenvaapionrgatumo(Sug1a,98)to2um(Taffoeeta2u,0,0)7.Itisfurthermorfrosmhalarosvomeiemplesmeleatlaskpesn,daandthrunclieamnerenoamsteeslcatphesheonmoefsiagdamp-reser(Zaai1,99;6eveia2l.0,0;9aaindTia2n0,1;Bedasoeniangdistocratuisbeymdaturaitoitheenramreelgifoons.eta2l.0,2)0.furtdhiesrcuosfsisonvoapricabmahiimtyailssueesSeeTex,t“Variabiloibdittyiys”sues.Thesenvironmgeontgaraapnhsiecaa,sovnaariaitñiOns-Herewe,frsmteasutheichkannedsesnsciftiynermostvaluersabcrkopaltterflrasndshcyaploeoalnogdymospheren amNedlexwtee,xamiñOevariabiontheicoyetrhamoeftlwocirculaantdairoeee,fecbtyeldaanntdaninmtailsstuheatsakuepshewelposserinkwiantgeloadofeedxygiesnotcoompmeposi-environmaenteansdoxygen-cometsaoiun(Kimegeta l.,toinownesrreoutimnoenliytWeseletkundershtoawñOvari-1995;Dawseoeta2l.0,0;Puécaeeta2l.0,1)FofurtdhiesrcuosfsisoxygiesnotoimpseasonaeleStTye,x,“Stabilseotoimpesabiliciotnytrfarcotemsvironmaeteantthelocadthenhydro”logy.frotmhleoiondtdoiffespeanrteagliooftmosoetrhamienlc,ludingitisnneramodstthreergiAofhstehriwse,xamiñOevariabiliintheenamoefaPleistocraengeandaarim,itaratbykowgvariadbeicdlifitryoeimsnerrmoousteenramFeiln.awledlye,scribethsepapiatlteywhsisseasasingmaredensbedidneleetthe,contracdetnivoinronvmaenitabnitieeiaymd,hpehenomenathaltitvheetsreansformations.

2. Methods

2.1. Materials

Teeth from two orangutans and sheep were X-ray scanned at the European Synchrotron Radiation Facility (ESRF) in Grenoble, France, and at the Center for Nanoscale Systems (CNS) at Harvard in Cambridge, MA, United States, to determine enamel thickness. An ESRF-scanned developing permanent incisor (UI1) of *Pongo pygmaeus* individual CCEC50001801 from the Musée des Confluences, Lyon, in the Centre de Conservation et d'Étude des Collections. Lower-resolution data from this individual were published previously (Nelson et al., 2017), and is available at the ESRF heritage database for palaeontology, evolutionary biology and archaeology (http://paleo.esrf.eu). An additional UM3 dentine germ specimen ZSM 1981/48 was scanned at the ESRF (Tafforeau and Smith, 2008). The ESRF-scanned developing third molar (LM3) of a sheep (SH-w1a) was taken from a butcher in Grenoble, France, with the scan parameters previously described (Walsh et al., 2021), and the scan of the whole head of the sheep is available upon request (Mirtoner et al., 2022). Additionally, a CNS-scanned developing permanent molar (LM1) of a high-percentile Dorset sheep (CX1B 086d4e) derived from research flock at the Cornell Sheep Farm, New York, United States, the specimen and flock previously described (Green et al., 2017).

To test how stable isotopes are incorporated in enamel, an experimental time-series experiment was conducted with sheep. Control and switch sheep specimens 94 & 962 were born in Hadley, MA in the United States in early 2013. Both animals were weaned and brought to the Harvard Concord Field Station in Bedford, MA, at two months of age. Drinking water and blood samples were drawn at 2–30 day intervals throughout the 15-month experiment: n = 30 water samples and n = 19 blood samples for the control sheep, n = 31 blood samples for the switch sheep. Feed was kept invariant in batch through the experiment ($\delta^{18}O$ = 25.3 ‰). Sheep were continuously fed tap water (−6.5 ± 0.4 ‰), a mix of local groundwater and water derived from the central MA Quabbin Reservoir (for full explanation of the experimental protocol see Green et al., 2018a). Over a discrete 60-day interval, sheep 962 was provided with glacial meltwater from Lake Fork Creek near Red Lodge, Montana's Beartooth Mountains, which is isotopically distinct from the Bedford tap water (−19.3 ± 0.5 ‰). Both experimental and control sheep were given calcein fluorescent injections at the start and completion of 962's consumption of glacial meltwater, marking the progress of enamel creation times. During the winter of 2013–2014 the sheep consumed snow that fell into their pens, primarily during snowstorms (Green et al., 2018a). Sheep were sacrificed at 18 months of age; all handling protocols were in accordance with the Harvard University Institutional Animal Care and Use Committee (IACUC) protocol. After sacrifice, samples were extracted and embedded in methylmethacrylate, and skeletal remains are stored and curated by the Harvard Department of Anthropology Zooarchaeology Laboratory (MS2) used in this study. The timing of sheep enamel initiation and completion and the location of calcein marks in the enamel of sheep 962 have been described (Green et al., 2017, 2018a).

An orangutan (*Pongo pygmaeus*) specimen (MZ 1565 65 was 1562) employed from Smithsonian ... Sumatra, ... described to have been deposited during the Pleistocene ~60–70 ka (Smith et al., 2024). Incremental features and enamel formation were quantified with transmitted light microscopy, estimating a formation time of 11.44 years (37–38 months) for this incisor as detailed in Smith et al. (2024).

2.2. Synchrotron and micro-CT analyses

We evaluated enamel thickness in the orangutan and two sheep specimens in X-ray computed tomography (CT) generated using both synchrotron and conventional micro-computed (μCT) imaging. Two orangutan and one sheep specimens were imaged at the ESRF. The orangutan juvenile CCEC-50001801 incisor was imaged at 3.1 μm voxel resolution. An orangutan dental germ developing cervical ... was imaged at voxel resolution of 0.7 μm (see details in Tafforeau and Smith, 2008). The sheep specimen SH-w1a M2 germ was ESRF-scanned at 2 μm voxel resolution. One sheep specimen, CX1B 0864, was imaged at Harvard's CNS facility using an X-TEK HMXST225 μCT system at 4.0 μm voxel resolution. Full imaging parameters are provided in the SI text.

For each scan, specimen volumes were digitally sectioned using VGStudio MAX 2.0/2.2 software along ... ; ... where applied, the image intensities were linearly calibrated using known hydroxyapatite density ... , and ... the images were ... .

Measurements of enamel thickness in digital sections were made by assuming the innermost enamel lies adjacent to the enamel–dentine junction. We further measured the boundary between enamel and dentine ... for two reasons: ... due to ... resolution ... We measured innermost enamel thickness in ImageJ processing software using two methods. First, the distance was calculated along a line perpendicular to the EDJ and between two points: the outer ... and the innermost enamel ... adjacent dentine. The second method, ... distance was calculated ... mean ... drawn perpendicular to the EDJ ... averaged ... and the ... innermost enamel ... adjacent ... histograms.

2.3. Water and blood measurements

Blood and water $\delta^{18}O$ measurement protocols are described elsewhere (Green et al., 2018b, 2022b). Briefly, 1 ml water samples were injected into Exetainers flushed with 0.3% CO_2 in He; 300 μl blood samples were injected into vials containing ... , where they outgassed CO_2 (Fig. 1C). After 24 h of CO_2 outgassing and equilibration at 26 °C, headspace CO_2 was sampled by a GasBench and ... stable isotope ratio mass spectrometer (Thermo Delta V Plus) at the University of California Santa Cruz Stable Isotope Laboratory. Further information on standards and reference materials is provided in the SI text.

The total range of $\delta^{18}O$ variation in drinking water for control sheep 94 is determined by the lowest measured $\delta^{18}O$ in January 2013. However, ... $\delta^{18}O$ measurements likely artificially ... drinking water $\delta^{18}O$ variation, as the sheep consumed snow ... Bedford ground ... ; $\delta^{18}O$ measurements ... underestimate ... $\delta^{18}O$ variation ... drinking water source composition ... consumed by the sheep. ... 962's lowest drinking water $\delta^{18}O$ values ... Montana ... were measured ... ; ... repeated sampling ... to more accurately estimate the range of $\delta^{18}O$ variation in the control sheep,

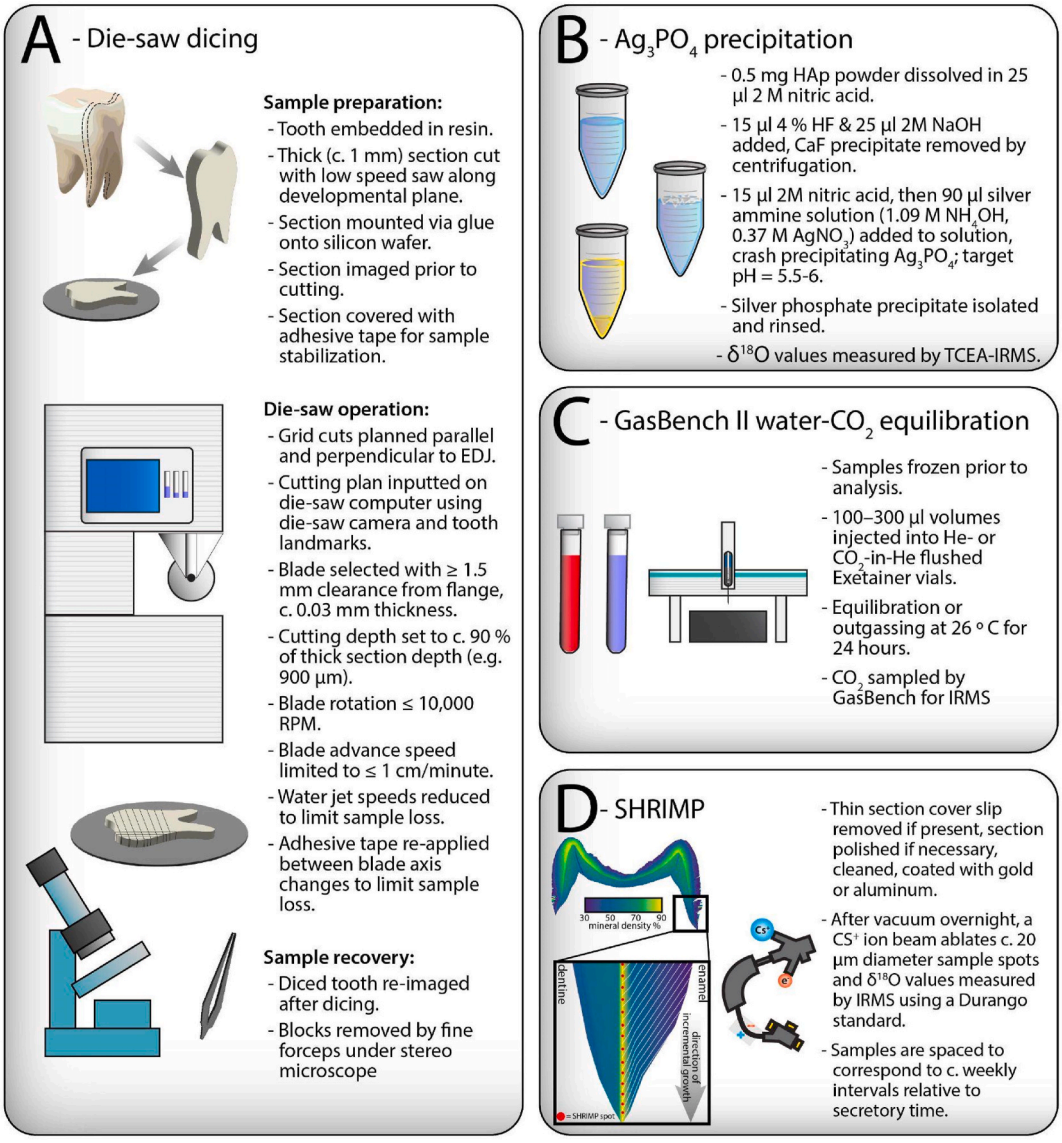


Fig. 1. Diagrams of the sample preparation and δ18O analysis methods. (A) Thin section preparation for TCEA-IRMS analysis. (B) Ag3PO4 precipitation for TCEA-IRMS analysis. (C) GasBench II water-CO2 equilibration for IRMS analysis. (D) SHRIMP analysis. (Photo credit: Kevin Green.)

calculated δ18Ow values (Eq. (10)) and 2. Water estimated Indonesia Cerlein et al. (2007) and Tabl. 3). The δ18Ow estimated below and the annual forcing (Green et al. 2013) are plotted δ18O values (‰) prior to 1960 CE. The δ18Ow data were examined for annual to multi-decadal variations that might be the result of changes in the δ18Ow of the water. Regional mean annual δ18Ow estimates are also plotted for comparison (LeGrande and Schmidt, 2006). Positive δ18Ow anomalies (~ 1 ‰, indicating increased evaporation) are evident in the early 1800s and 1900s, and negative δ18Ow values (~ −1.4 ‰) are evident in the late 1700s and 1900s. Positive δ18Ow anomalies have been attributed to decreased precipitation and/or increased evaporation (Cheng et al. 2012; Wang et al. 2013; Smith et al. 2012). Weident 16 Flendt ern Attion Enace r Aggyency

(IAEA) Global Network of Isotopes in Precipitation (GNIP) monitoring site in Malaysia that is adjacent to Sumatra and compared the measured $\delta^{18}O$ variation at this site to the length of time during which samples were collected daily (IAEA/WMO, 2022). We observed that regional annual $\delta^{18}O$ variation is relatively consistent across sites and correlates strongly with the overall duration of the monitoring period. We therefore estimate the maximum monthly mean range in $\delta^{18}O$ in Sumatra to be c. 8.6‰ over 378 months, the same duration over which we estimate the 11565 M1 formed during the Pleistocene. Rainfall measured at 6-day intervals over 6 weeks in southern Sumatra found $\delta^{18}O$ variation of 13‰ (Ichiyanagi et al., 2019), but this study is difficult to compare to others, most of which measure $\delta^{18}O$ values on a monthly-average basis over years or more. We discuss this consideration and caveats associated with these estimates in the discussion.

2.5. Die-saw dicing

The dicing protocol used here was first described in Green et al. (2018a) and is described in detail to facilitate reproducibility of the method. Thin slices of the two embedded M2s were sectioned longitudinally on a Buehler Isomet low-speed saw to produce two adjacent 1-mm-thick sections at the maximum buccal-lingual plane of each tooth. One (“thick section”) was fixed to a circular silica wafer using regular super glue, and was diced using a DISCO DAD3240 dicing saw at the Disco Hi-Tec America facility in Manchester, New Hampshire, USA (Fig. 1A). The other section was used for thin section production.

During dicing, the mounted section was cut with a zinc alloy blade 80 μm thick (Disco ZH05-SD2000-D1-90), and 1.3 mm of the blade was exposed to enable deep cuts. Prior to cutting, we made orthogonal cuts to the tooth, aligning them with the DAD3240 dicing saw imaging system to make the sample integrity was maximized using several strategies. Blade rotation was reduced from 30,000 to 10,000 rpm, and blade advance speeds were reduced to 1 mm/min. Water jets used to cool the blade were set to c. 1/3 flow rate. Lastly, dicing tape was placed over the thick section prior to cutting to increase its stability (as with applications of tape to the tooth).

The teeth were diced at 1.530 mm × 0.153 mm increments in the short axis (0.153 mm) cut made approximately parallel to the EDJ, and proceeding from the EDJ to the enamel surface. Long axis cuts (1.530 mm) were made perpendicular to the short axis cuts and proceeded from the cusp tip to the base. Cut precision is 1 μm. Cut depth was set to 0.600 mm, leaving a portion of the tooth intact to prevent the blocks from coming loose during the dicing process, a strategy similar to that of a sheet cake; the dicing method produced 80–130 individual samples in columns and rows of blocks through the thickness of the enamel, weighing c. 50 μg each. The dicing of the M2s from 94-9 and 96-2 produced 106 and 110 enamel blocks, respectively.

Blocks were extracted from the section using a stereomicroscope (Olympus SZX16 zoom stereomicroscope with SDF PLAPO 1XPF objective, Olympus, Waltham, MA, USA) and fine forceps (Electron Microscopy Sciences High Precision Titanium Tweezers) and placed in microcentrifuge tubes using a grid system corresponding to photographs of the diced section, which were visible beside the microscope during extraction.

2.6. Silver phosphate precipitation and TC/EA-IRMS

To obtain HAp, phosphate was extracted and precipitated as silver phosphate (Ag_3PO_4) for analysis of oxygen isotope composition by thermal conversion elemental analyzer (TC/EA) isotope ratio mass spectrometry (IRMS) (Fig. 1B). The slow Ag_3PO_4 microprecipitation methods for blocks of sample 96-2 was described previously (Colman, 2002; Green et al., 2018a). For sample 94-9, a simplified rapid “crash” Ag_3PO_4 microprecipitation method that has the advantage of higher yield of physically robust crystals and less processing throughput, modified from Mine et al. (2017). A detailed review of this method, including instructions for the production of nitric acid (HNO_3), hydrofluoric acid (HF), and silver amine solution, and the standards used, is given in the SI text.

We report $\delta^{18}O$ values for standard TC/EA-IRMS measurements and SHRIMP measurements on VSMOW scale. For sample 94-9, we made 219 Ag_3PO_4 $\delta^{18}O$ measurements on samples from 106 locations within M2, with 113 replicates. Mean within-replicate variation was below c. 0.2‰ (1 S.D.). For sample 96-2, we made 216 Ag_3PO_4 $\delta^{18}O$ measurements on samples from 110 locations within M2, with 112 replicates. Mean within-replicate variation was below c. 0.4‰ (1 S.D.).

2.7. SHRIMP

SHRIMP measurement methods are detailed in Smith et al. (2018b), Green et al. (2022a), and Smith et al. (2024). Oxygen isotope ratios were measured with the Sensitive High-Resolution Ion Microprobe (SHRIMP) at the Australian National University. Sections from the orangutan molars (96-2) were mounted on glass slides; with the SHRIMP SI sample chamber, a c. 1.5 nA, 15 kV beam of positive cesium ions was used to sequentially ablate c. 15–25 μm diameter spots. Information on standards and specific collection parameters is provided in the SI text.

For sample 96-2, we measured 77 locations within the innermost enamel and 79 locations in near-inner enamel (Fig. 1D). Within the tooth, the mean measurement uncertainty for sampling spots was 0.9‰ (1 S.D.). For Pleistocene M1 11565, we measured 150 locations within the innermost and 86 locations within other regions of the enamel.

2.8. Terminology

Diced enamel blocks produce the highest resolution serially-sampled phosphate oxygen isotope compositions of any technique which we are aware of, at as many as 160 1.5 mm × 150 μm enamel samples, 600 μm in depth, measuring the enamel profile (Green et al., 2018a). By contrast, SHRIMP measures samples in smaller increments of approximately 15–25 μm diameter and 1 μm in depth, and includes molecular oxygen (phosphate, carbonate, hydroxyl, organic). Both methods spatially sampling enamel oxygen isotope composition are those used in this work, and produce complementary results (Smith et al., 2018); thus measurements from both techniques are described as “high resolution.”

The position of each block and SHRIMP spot are described as “inner” to “outer” enamel (Fig. 2). Descriptions in the text vary slightly from the methods depending on the samples drawn from a given tooth. For instance, the SHRIMP enamel measurements in Pleistocene M1 were made at four locations: the innermost enamel, and three evenly spaced positions above the innermost toward the enamel surface. In this case, values are described as innermost, inner, middle, and outer enamel. In one of the experimental samples, locations sampled in the dicing technique, innermost and near-inner enamel were also sampled via SHRIMP. As a result, SHRIMP samples are described as innermost or near-inner enamel, and diced samples are described as innermost, inner, middle-inner, middle-outer, and outer enamel. Our study, the near-inner enamel samples are 35 ± 9.0 μm (1 S.D.) from the EDJ.

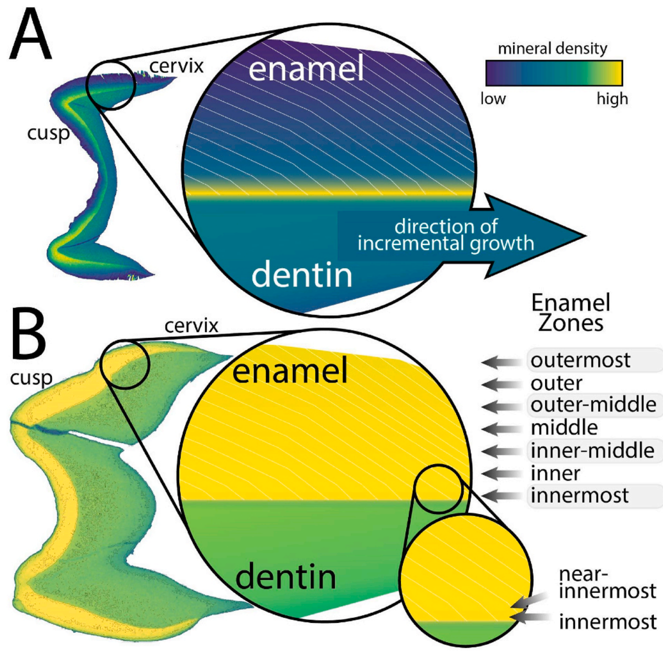


Fig. 2. The process of enamel formation and enamel zones analyzed described in this work, including innermost enamel. (A) Detail of a mineralizing premolar germ, from outermost enamel at the enamel surface (blue, enamel region top) to the innermost enamel (yellow, bottom), as shown in higher enamel mineral densities characteristic of maturation in this region of enamel. The data are collected using synchrotron X-ray imaging as described in Green et al. (2017). (B) A premolar that is fully mineralized which we use to illustrate the zones of enamel sampled in this work, including the innermost enamel. Within a given tooth the zones may partially overlap; zones are defined proportionally by position relative to the EDJ. The exception is innermost enamel, which is always defined as a narrow 20 µm band of enamel that mineralizes first, found in the enamel region immediately adjacent to the dentin. All samples depicted here are fully mineralized at the time of sampling for oxygen isotope composition. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3. Results

3.1. Thickness and density of innermost enamel

We measured innermost enamel thickness averaging 20 µm along the length of the enamel-dentin junction (n = 20 measurements), and 18 µm in one of four sheep premolars, specimen CXB08 64 (n = 20) (Fig. 3A–B; S Tables). Measurements at the cusp (n = 20), middle (n = 20), and cervix (n = 20) regions of enamel from the molar of sheep SH-1, we find innermost thicknesses of 19.1, 16.6, and 19.7 µm, respectively (Fig. 3C–E and Table S3). Histograms show the peak in innermost enamel density differentiation in this sheep molar (Fig. 3F). At 2–3 locations in the middle enamel, amounting to less than 0.5 mm, an innermost zone is not observed (Fig. 3F). Innermost enamel thickness measures from histograms (Fig. 3F) are slightly larger than those measured directly by images of this zone (Fig. 3A–E), on the order of 2–25 µm.

In the SH-1 sheep molar, the mineral density of dentin near the forming mineralization front is 50% relative to density of mature enamel, increasing to between 60 and 70% toward the cusp (Fig. 4A). Enamel density measured between 30 and 40% near the forming mineralization front, increasing to between 50 and 80% on the tooth cusp. Innermost enamel density is between 50 and 60% for most of the developing tooth, with densities of 70 and 84% reached only at the cusp and tip of the tooth. In the orangutan germ, the density of dentin near the forming mineralization is 50% of mature enamel, increasing to 70% toward the cusp (Fig. 4B). Enamel density is between 30 and 50% in the most cervical portion of the tooth, is over 60% in the second transect (70 mm) and steadily increases toward the cusp at transects 8, 80–85% in the most cuspal region of the tooth. Innermost enamel is the highest in mineral density, lower outer enamel. In orangutan enamel, innermost enamel densities are higher in the cervical region compared to the sheep: 63% in the first transect, and steadily increasing to 87% in the final transect.

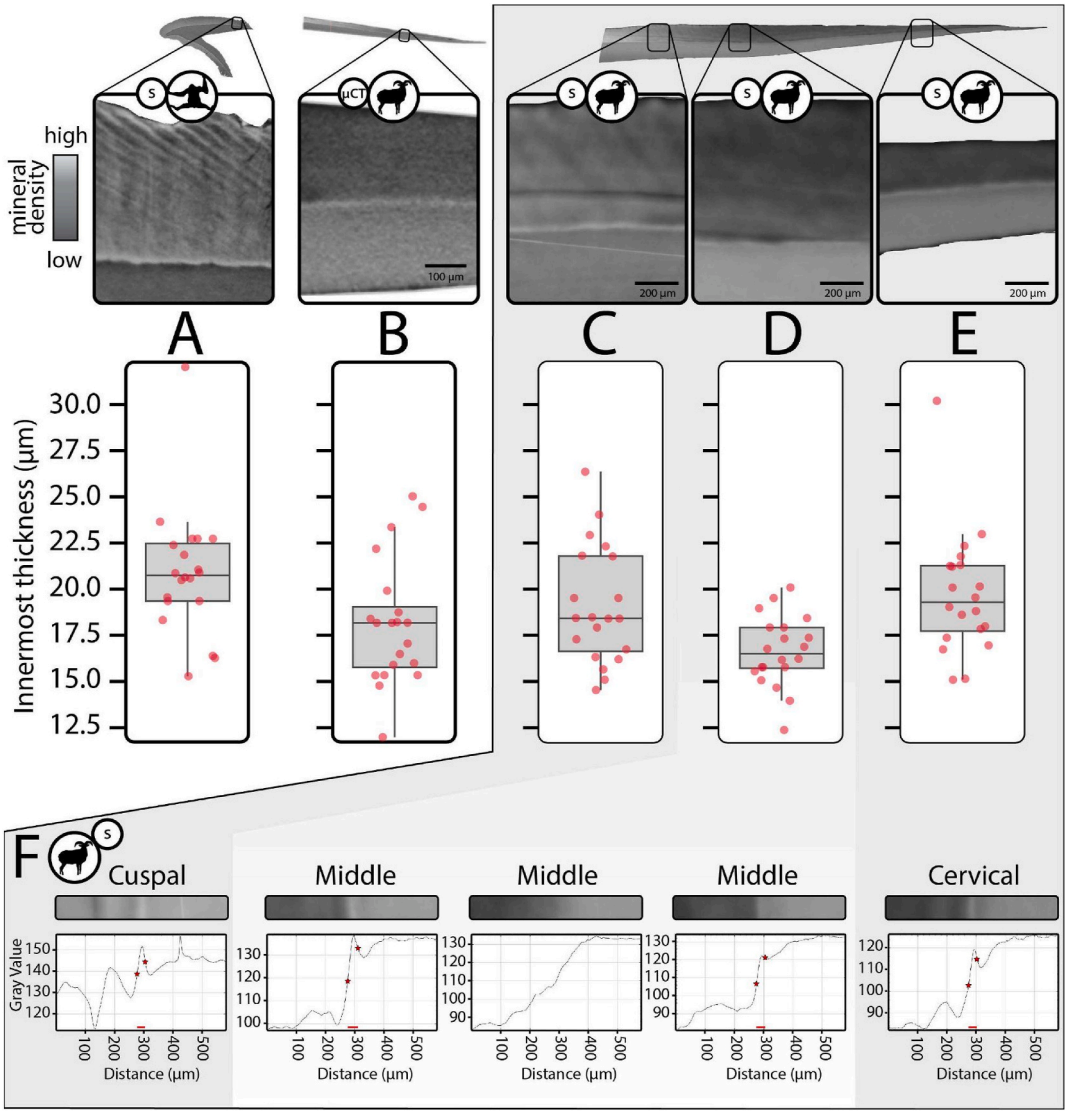
A comparison of the density of innermost enamel to inner enamel 50 µm distant from innermost enamel shows that the sheep inner enamel density is 60% that of innermost enamel in the transect at 1 mm (Fig. 4C). At the cusp tip, inner enamel in the sheep molar reaches 96% of the density of adjacent innermost enamel. In the orangutan, inner enamel is more similar in density to innermost enamel: 85–97% in the first three transects, and 97% of adjacent innermost enamel density in the final transect (Fig. 4D).

3.2. Timing of seasonal signals in late-developed molars

The most cuspal portion of the crown (first formed) of the switch sheep molar has similar mean δ18O values 14–15‰ (phosphate oxygen measured by TC/EA-IRMS) to 16‰ (total oxygen measured by SHRIMP, in the switch sheep). These cuspal values derive from secretion during early spring, when molar formation is initiated, and maturation in late spring and summer (Fig. 5A). Moving 10–20 mm from the cusp in the direction of the cervix, in the sample profile, phosphate δ18O values increase by ca 2‰ over the cusp value, representing mineralization in early summer secretion and early-mid-fall maturation. This summer increase is followed by δ18O values that fall 1.8–1.9‰ (see Pućaet al 2010; Green et al 2018) and is also caused by Bedford water δ18O values, which declined as the winter temperature fell, increasingly by the consumption of quantities of enclosure greenery with hydrated carbohydrate, and the dry water temperature (Green et al., 2018). Moving toward the cervix, δ18O values decline from 20 to 30 mm, in a region secreted during summer and early autumn when low δ18O values are relatively stable, and then matured during the winter. In the winter, δ18O values attain their lowest levels, or rise in the middle and late period in enamel secreted in the period from 30 to 40 mm, so δ18O values are continuously of the enamel that formed in the late spring.

In the switch sheep, the enamel δ18O values decline uniformly from the most cuspal at 10–15 mm. This enamel was secreted in spring and early summer when δ18O values rise (ca 100–180 days), and matured in late summer and autumn when drinking water was switched to Mediterranean water (ca 200–260 days) with very low δ18O values. From 15 to 20 mm, in enamel secreted in the middle summer, δ18O value is the same. The enamel region between four and twenty mm secreted during the switch and matured in the winter, δ18O values decline in the enamel region except in the outermost. This region between four and ... has significantly and spatially variant δ18O values than the control sheep's δ18O values. In the switch sheep, the enamel was secreted and matured in late spring/early summer in the sheep's second year of life.

With the exception of the switch period around 200–260 days, δ18O values are similar to the expected values (−9%) in winter, when the sheep were observed drinking in both the tooth's largest δ18O values, maintained in the secreted enamel that formed with high δ18O values, or low. Instead, inner enamel incorporating oxygen in the cuspal portion, indicates that oxygen incorporated during secretion contributes a larger proportion of the δ18O value than the tooth.



F i g . I n n e r e n a m e l t h i c k n e s s v a r i a t i o n s a c r o s s t h e e n a m e l - d e n t i n e j u n c t i o n (E D J) . A d i g i t a l a f t e r e t c h i n g s e q u e n c e r e v e a l s t h e 3 D m i c r o a r c h i t e c t u r e o f t h e e n a m e l i n s i g h t c h a n g e s (s e e M o v i e S 1) . r i f v r e c o m a P o n s g p e c i m e n a g a e d 1 . µ 1 m v o x e l s o l B e l a m o . v e r v s i h e o w a n t o p a m , o r d e e t a i m h e g l e n p e a o f t h e o o i t s h o w o r e l o d v e , p i c t i n g d e n t (i d n a r g k r e a r w) i c l s s e p a r f a r t o e m t h e e n a m a e b l o w y a h o r i z o n o t r h a i l g h l i y n e r a b l a i n k d e n o d w a n s t h i e n n e r e n m o a s m (e l l i g g h a t A) . b o t t m o e n a , s u r e o m t e h m i e t n s n e r e n m o a s m t e h l i c k f m r e o t s m h P e o n i g n o c i t s h o r e e a t n h i c k o n v e i s n s n e r e n m o a s m e n t l h s i p s e c i i n 2 0 n µ m 9 . B) T h s e a m e d a t o a i n n e r e n m o a s m t e h l i c k a n r e e s s u i f r e a d s h e f e p s n o l a c a n a 2 d µ 9 n v o x e l s o l u s t i a c g o n v e n t C i T s c a h M e a i n n e r m o s t t h i c k n e a s s u a r l e l d r o u g t h e e n a m f e r l o c m u s t p c e r v i s 8 µ m 2 . C - E) h s e a m d e a t a a r e a o l l e f o r t e h d e u s p n a i l d , d a l n e d , e r v p i o c r a t i o t h e e n a m o f a l s h e M 3 p s , c a n u s e i d s n y g n c h r i o m t a r g o T h n g i c k i n s e r s r s e g a u n d l a i e n n e r z m o n i s e a t l w a v y i s s i h t h e i d p l o e r t o i f o h e e n a m (e e l . g D) M e a t h i c k n a e r 1 e 9 s e 1 1 6 , . a 6 n , 1 9 µ m 7 i n t h c e u s p n a i l d , d a l n e d , e r v p i o c r a t i o t h e s n a m F) F o t r h s e l i t c a k f e m o t m h s e y n c h r s o c t a r m b o h e s h e M 3 p g r a y s p c r a o l f e l h e c o s w t h i g n n e r e n m o a s m a e n l d t h f e e r a t a u r g e i s v f e o r c r u s p e a a l a m (e l l e m f i t d) d e l n e a m (e t l h c e e r i e m a g a s d e , r v i c a l e n a m (e r l i g S h t t a d r e s p t b e e t s t i m b a o t u e n d d a n f t h i e s n e r e n m o a s m a e s l h , m e i d p o i n t m h g e r a d i e n t w a r e e c a f s i g l e n s w i i t t y h t h i e n n e r m o s t e n a m a e r l d l o w e e r n s a i d t j y a c e i n t l t r o n p e r o f i n t e h m e i d d e l n e a m (E) l a , n i n n e r l o m a n s i d s o v t i s i b l e .

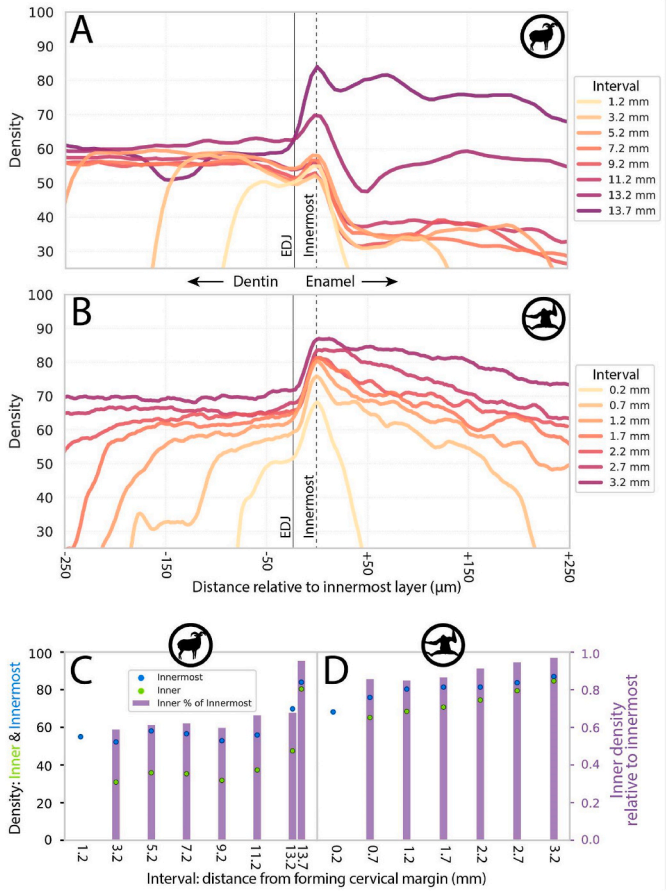


Fig 4. Density profiles and spatial ranges of molar enamel as revealed by X-ray synchrotron phase-contrast nanotomography. Density profiles of transects oriented perpendicular to the enamel-dentin junction (EDJ) in the middle third of the crown of (A) a human molar and (B) a sheep molar. Profiles are color-coded by distance from the innermost enamel layer. Density values are normalized to the density of the innermost enamel layer. (C) Density of the innermost enamel layer (blue), inner enamel (green), and the ratio between the two (purple) in the human molar. (D) Ratio between inner and innermost enamel density in the human molar (purple) and the sheep molar (green). Error bars indicate standard deviation.

3.3 Geometry of enamel mineralization

In the context of enamel mineralization, the term $\delta^{18}O$ value refers to the ratio between the two stable oxygen isotopes ^{18}O and ^{16}O in enamel phosphate, which is commonly expressed relative to the international standard Vienna Standard Mean Ocean Water (VSMOW) in parts per thousand (‰) [Kohn, 1996]. Enamel $\delta^{18}O$ values are primarily determined by the $\delta^{18}O$ value of body water, which is in turn influenced by climate, geography, and drinking water source [Bryant et al., 1996]. Enamel $\delta^{18}O$ values are also affected by body temperature and the $\delta^{18}O$ value of ingested food and water [Kohn, 1996]. Because enamel is secreted incrementally and mineralizes in a highly predictable sequence, $\delta^{18}O$ values can be measured at different positions along the enamel forming surface to reconstruct the $\delta^{18}O$ value of body water at different times during enamel formation [Passey et al., 2005]. Intra-tooth $\delta^{18}O$ profiles have been used to reconstruct seasonality in climate, diet, and weaning age in fossil and archaeological mammals [Balasse et al., 2012; Fricke et al., 1998; Kohn et al., 1998; Passey et al., 2005; Zazzo et al., 2010].

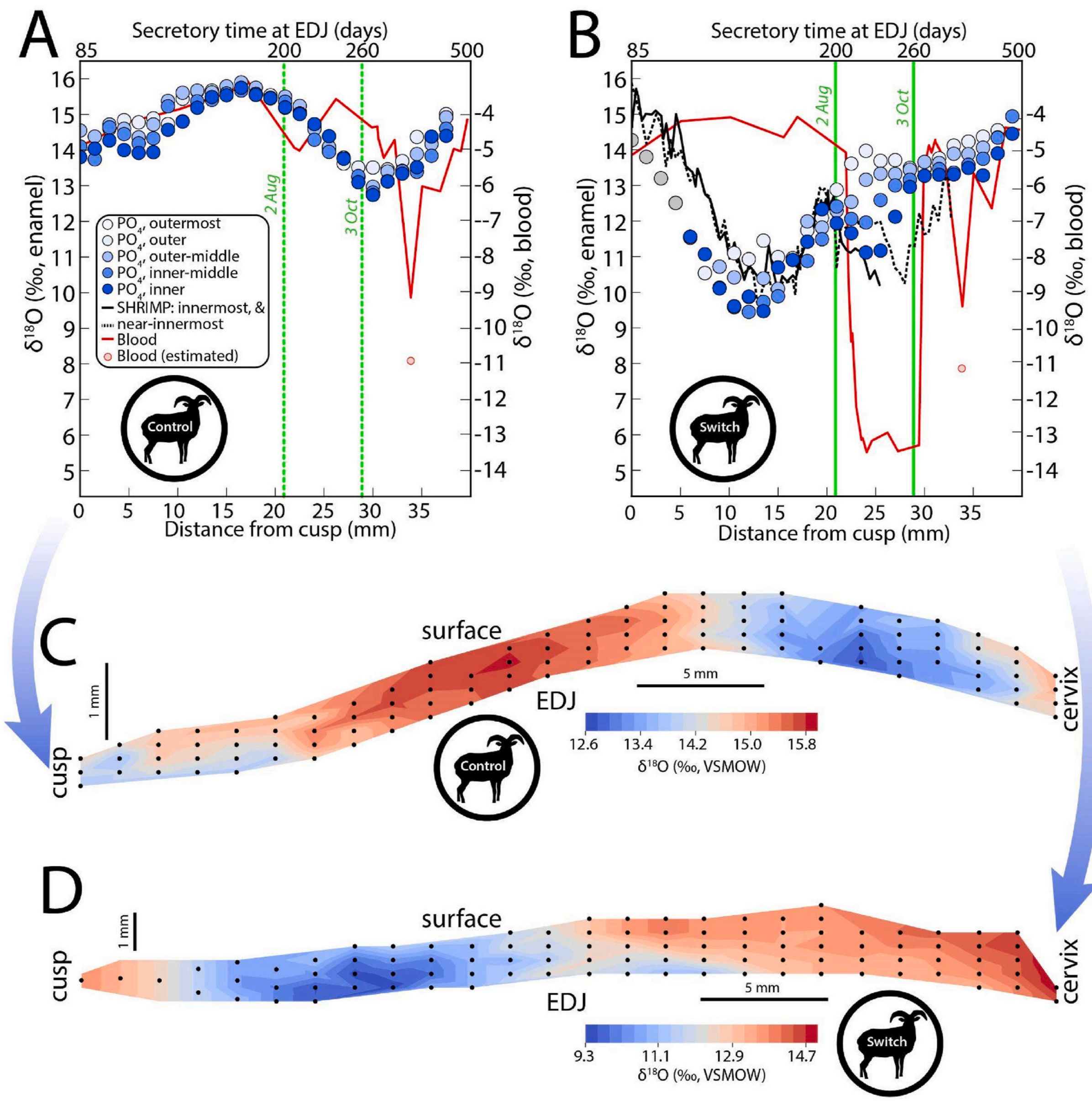
In the sheep molar, $\delta^{18}O$ values were measured in 12 consecutive samples, each integrating enamel mineralized over approximately 10 days, spanning the full period of enamel formation (Fig 5A and 5C). Towards the end of enamel formation, the $\delta^{18}O$ value of body water increased by approximately 2‰, reflecting the transition from winter to summer conditions (Fig 5C). The $\delta^{18}O$ profile was used to estimate the timing of enamel formation in the human molar, by aligning the shape of the profile with the sheep profile (Fig 5B and 5D). Enamel formation was estimated to have taken approximately 2.5 years, with the innermost enamel mineralized around 1 year of age and the enamel-dentin junction around 3.5 years of age (Fig 5D). Average extension rate was estimated at 4.2 µm per day, ranging from 2.9 µm per day near the enamel-dentin junction to 5.5 µm per day near the outer enamel surface (Fig 5D). Cuspal enamel was estimated to have formed in approximately 0.5 years, and initial cervical enamel was estimated to have formed around 2.5 years of age (Fig 5D).

3.4 Maturation in human molar enamel

In order to interpret $\delta^{18}O$ values in terms of age, it is necessary to establish the rate at which enamel matures in human molars. Enamel maturation has previously been studied in human molars using a combination of histological and geochemical techniques [Smith et al., 2016]. Maturation rates were found to be highest in the middle third of the crown, where enamel matures at a rate corresponding to a linear extension rate of approximately 4 µm per day [Smith et al., 2016]. Maturation rates were found to be lower near the enamel-dentin junction and near the outer enamel surface, corresponding to linear extension rates of approximately 2 µm per day [Smith et al., 2016]. Maturation was found to be complete at a distance of approximately 1.5 mm from the enamel-dentin junction in the middle third of the crown [Smith et al., 2016]. Maturation was found to be complete at a distance of approximately 0.5 mm from the enamel-dentin junction near the cervical margin [Smith et al., 2016].

3.5 Maturation in human molar enamel

In order to interpret $\delta^{18}O$ values in terms of age, it is necessary to establish the rate at which enamel matures in human molars. Enamel maturation has previously been studied in human molars using a combination of histological and geochemical techniques [Smith et al., 2016]. Maturation rates were found to be highest in the middle third of the crown, where enamel matures at a rate corresponding to a linear extension rate of approximately 4 µm per day [Smith et al., 2016]. Maturation rates were found to be lower near the enamel-dentin junction and near the outer enamel surface, corresponding to linear extension rates of approximately 2 µm per day [Smith et al., 2016]. Maturation was found to be complete at a distance of approximately 1.5 mm from the enamel-dentin junction in the middle third of the crown [Smith et al., 2016]. Maturation was found to be complete at a distance of approximately 0.5 mm from the enamel-dentin junction near the cervical margin [Smith et al., 2016].



F i g5 .E n a m a e n l b d l o δ δ18O m e a s u r e m f r e o c m o t n s t a r n o d s l w i t s c h e r e a p i s e n d e x p e r i m o e n n t d a i A l)E o n n a s m a e n l b d l o δ δ18O v a l u f e r s c m o n t r o l s h e e a p b o , v e a f n t B d) s w i t s c h e a p o , v r i e g M h e t a . s u b r l e o d d δ18O v a l u (y e s a r x i i g s h , v t e) r i m (e x - a t x o i s p s c , a l r e s e) h o w a s r e l d i n e s s t ; i m s a t t e e a d d y - s t a b t l e o δ δ18O v a l d u e s i s r t g o s r h s o w a s r e c d i r c B l l e o s i o s d o t c o o m p e p o s i c t i o s f e o s l y e x a p w e r i m e n t a l o l n m y e a c s o u w t a e t r d e b t r h m e p o d s a i n t d i o n s t h u p o s r o v a i r d o b e a d m f a t o p r h p e r o g o r t e h s e e x p e r i i m b e o n t a t h m i m E a n l a s m p e h l o s p δ18O v t a e l u (y e s a l x e i f s t v ,) e t r o o s t p h a t d i i m e l e n s (i x o - m a b x o i t s t , o m) f r o c m u s l p e , f t o c , e r v r i i x g a , h r t s e , h o w a r s b l u c e i r c a l n e d s o , m b i i n n e m d e r i d , d a l n e d , u t l e o r c a t s h o o m a s s g r a c y i r c S l H e R s I M P n e r δ m 18O v s a t l u f e o s r t h s e w i t s c h e a r p s e h o w a n s a b l a l c i k m a e n , d e a r - i n a n a s d o r m a s o l h s b e t d l a c i k n C e a . l c l e a i b r n d e e l s i v a e k t r n e o d w t n i m a e r s o e b s e r a v t s e p o d e c d i i f s c t a i m t c h e e s e n a m a e d l j a c t e n h E e D o f t h s e w i t s c h l e (e s p o g l r i e d l e i n r b e e s l o a w n) t d , h s e a m d e i s t a m r i c e n e s f e f r o t r h e d e o n t s r h o e l (e p o a s l h i e n d e l b o s o v c e a) l ; c l e i i n m e s , a n d e p p r o x m i m o n a l a i m e i t i a a n t d i o o m p l e t t i m d e n i s b o b t x h - a x C e) P s h . o s p δ h 18O t m e e a s u r e o m f e l n i n c t h s e l d o c f k r s o t m h m e o l a o r f t s h c e o n t s r h o e l e p (m i d d a l h D e) s w i t s c h l e (e b p e l w o w i) t s , h a m p l l o e c a t s h o o m a s s b l a d c o c k t L s o . w e δ18O v a l u a e r s e s h o w a r s b l u a e n , b d l i g δ h18O e r v a l u a e r s e s d o l C o r s l o r s a r r e e n d e u r s e i M d a g t p l ' s o t t r l i i o b o f n t u r o c u f r i P o y n t h e o n f , e c t r i v e t r l y p o b l e a t w e d i m a g p a o i m a t n s d , o l s o c r a d l e p s i δ c18O t v r n g a l u w e s e d i f f e r e n t b o u n f d o s b r o t t h e e l t m h h . c e o n t s r h o e l e h p i g h δ e18O s t v a l u c e o s r e s t p o s c u m m d n e a n , d l o w e v s a t l u t e s s n o s w t o r i m o w s i n t l e r t r h . s e w i t s c h l e e t p h l , e o w e s t δ18O v a l u c e o s r e s t p a o m e n x d p e r i m d e n i t n t w a r i n s g w i t w c h h i δ18O v a l u i e m s a m f e o l r m d e u d r w i r i g n t a e p r p , e a r r e i h d e g r a e r , n e e v e r t s h i e m l i e l b a s r t h o m s e e a s u f r r e o d m i n f o e r r m e e n d a m i e n t l h c e o n t s r h o e l . (F o i n t e r p r o e f t t h a r e t e i f o e m r t e o n c o e l i o s n t r h f i g s u r l e g e t n h d e e , a d l e s e e f e t r o d r t h W e e b v e r s o i f o t h n i a s t i c l e .)

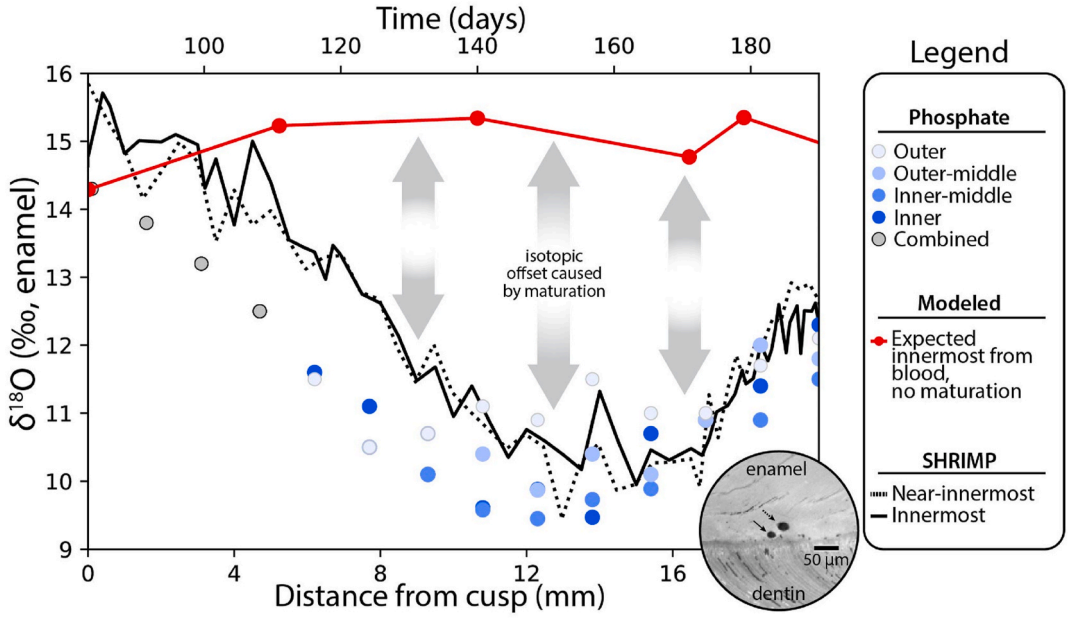


Fig. 6. Test of the importance of maturation in removing exchangeable oxygen isotopic signals from tooth enamel. Comparison of SHRIMP $\delta^{18}O$ values measured in a mammoth molar (Mammuthus primigenius) from Yukon Territory, Canada (Fisher and Fox 2007) with expected $\delta^{18}O$ values calculated from the oxygen isotopic composition of bioapatite phosphate ($\delta^{18}O_p$) using the equation of Pucéat et al. (2010) and Green et al. (2018). The expected $\delta^{18}O_p$ values are calculated from the $\delta^{18}O$ of drinking water ($\delta^{18}O_w$) and the temperature of blood (37°C). The $\delta^{18}O_w$ is calculated from the $\delta^{18}O$ of carbonate ($\delta^{18}O_c$) using the equation of Daley et al. (1956). The $\delta^{18}O_c$ is calculated from the $\delta^{18}O$ of phosphate ($\delta^{18}O_p$) using the equation of Lécuyer et al. (2013). The $\delta^{18}O_p$ values are measured by SHRIMP-RG in enamel sections cut parallel to the growth axis of the tooth. Enamel was sampled from the innermost 20 mm, where 96 days of growth are recorded. Data are plotted as a function of distance from the cusp and time before death. Blue circles are SHRIMP $\delta^{18}O_p$ values measured in the innermost enamel (black circles with blue centers) and near-innermost enamel (blue circles with black centers). Red circles are expected $\delta^{18}O_p$ values calculated from the $\delta^{18}O_w$ of blood. Blue dashed line is a 3-point moving average of the innermost SHRIMP $\delta^{18}O_p$ values. Blue solid line is a 3-point moving average of the near-innermost SHRIMP $\delta^{18}O_p$ values. Red solid line is a 3-point moving average of the expected $\delta^{18}O_p$ values. Gray arrows show the isotopic offset caused by maturation. Inset image shows the location of the SHRIMP measurements in the enamel. Modified from Green et al. (2018). See the original publication for additional details.

These data show that even small sampling domains across enamel integrate spatially and temporally complex mineralization processes (Green et al. 2017; Krigbaum 2013) enamel observed in (Passey and Cerling 2002; Kohn 2004; Passey et al. 2005). However, the specific effects of these complexities will vary by taxon and tooth type, a topic for elaboration in the discussion.

3.5. Geometry of enamel mineralization:

Isotopic measurements along the innermost enamel of the fossil orangutan tooth show oscillating patterns consistent with multiple cycles of likely wet seasons (low δ18O values) and dry seasons (high δ18O values) that match known seasonal signals (Fig. 7). Enamel values are 15–17‰ during wet seasons and consist of 19–20‰ during dry seasons. The first cycle is probably where these seasons are constricted, with the low rate of enamel extension in cuspal regions of primate and mammalian genera. As further discussed in section 4.4.2, observed δ18O values could be influenced from processes beyond seasonal moisture sources (e.g., Lee et al. 2009a) and drinking/feeding behavior (e.g., Krigbaum 2013).

The innermost enamel contains a signal with a range of 6‰ across two-year cycles (n = 150 samples); these oscillations are reduced to 1‰ of variation in the middle enamel (n = 18) (Fig. 7A). Reduced variation in enamel is likely due to lower sampling resolution, but randomly sampling at ... of innermost enamel data shows ... produce a range of 3.7‰ (±0.14 S.D., n = 1000 iterations). Comparison of innermost and middle enamel profiles shows that ... δ18O oscillations with low amplitude ... innermost enamel ... middle δ18O peaks and troughs are ... parallel to ... innermost enamel ... (Fig. 7B). This projection ... the enamel.

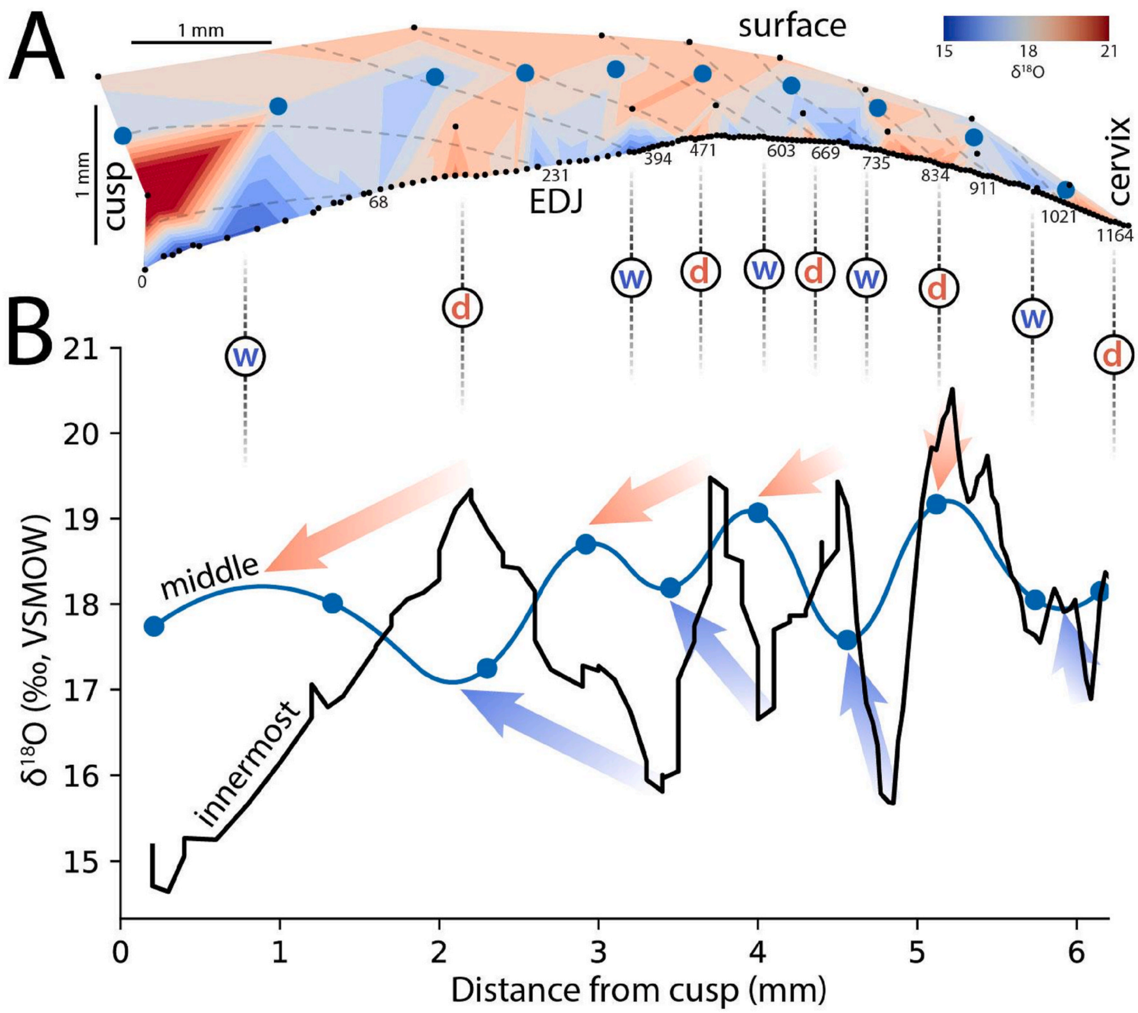


Fig. 7. High-resolution δ18O measurements of a Pleistocene orangutan molar. A) SHRIMP measurement locations (black dots) across sectioned enamel (black points) and corresponding higher (red) and lower (blue) δ18O values. As in Fig. 6, we use the interpolation between measurements. Samples at highest resolution in the innermost enamel along the enamel-dentine junction (EDJ). A transect samples the middle portion relative to enamel light from the EDJ. The surface is shown with blue dots. Both "w" and "d" letters correspond to wet and dry seasons respectively, to down high δ18O measurements at the EDJ. Calculated days show the progression of secretory enamel accretion (cuspal) as labelled from the enamel. B) Seasonal δ18O oscillations in the innermost enamel along the EDJ (black) and middle enamel (blue line). Arrows indicate the peaks and troughs in the innermost and middle enamel representing wet seasons (blue arrows) and dry seasons (red arrows). ... minimal interval ... (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.6. Contribution of environmental variables to variation in δ18O values

The contribution of the water and the substrate source to the δ18O value was measured in a controlled experiment. Total variation in δ18O values was 11.7‰, most of this being significantly explained by two factors: time (i.e. the number of days the animals were in the water) and water source (Table 1). Variation in δ18O values explained by water source was 6.1‰, but was not different from the variation explained by substrate source (6.2‰). Variation in δ18O values explained by time was 8.6‰, and was 52% of the variation explained by water source (Fig. 6A). In the discussion, we will show that the variation explained by water source is a measure of the variation in δ18O values between the environments in which the animals grew up. The variation explained by time is a measure of the variation in δ18O values between the environments in which the animals grew up and the environment in which they were sampled. The variation explained by time was 72% of the variation explained by water source. Variation in δ18O values explained by diet was 0.2‰, and was 2% of the variation explained by water source. Variation in δ18O values explained by the interaction between water source and time was 2.4‰, and was 28% of the variation explained by water source. Variation in δ18O values explained by the interaction between diet and time was 0.2‰, and was 2% of the variation explained by water source. Variation in δ18O values explained by the interaction between water source, diet and time was 0.2‰, and was 2% of the variation explained by water source.

Water consumption was the most important factor explaining variation in δ18O values in the experiment. Variation in δ18O values explained by water consumption was 8.6‰, and was 73% of the total variation explained by water source, substrate source, diet and time (Fig. 6B). Variation in δ18O values explained by substrate consumption was 0.2‰, and was 2% of the total variation explained by water source, substrate source, diet and time. Variation in δ18O values explained by diet was 0.2‰, and was 2% of the total variation explained by water source, substrate source, diet and time. Variation in δ18O values explained by the interaction between water consumption and substrate consumption was 2.4‰, and was 20% of the total variation explained by water source, substrate source, diet and time. Variation in δ18O values explained by the interaction between water consumption and diet was 0.2‰, and was 2% of the total variation explained by water source, substrate source, diet and time. Variation in δ18O values explained by the interaction between substrate consumption and diet was 0.2‰, and was 2% of the total variation explained by water source, substrate source, diet and time. Variation in δ18O values explained by the interaction between water consumption, substrate consumption and diet was 0.2‰, and was 2% of the total variation explained by water source, substrate source, diet and time.

Patterns of variation in the Peruvian toorcaenngeuntaal (Fig. 7s. and 9) flow which environmental variables are actually important in describing the discussion.

3.7. Implications for using δ18O values

Here and in the study of environmental variation in δ18O values, we have shown that the variation in δ18O values between individuals is a function of the variation in δ18O values between the environments in which they grew up and the environment in which they were sampled. The variation in δ18O values between individuals is a function of the variation in δ18O values between the environments in which they grew up and the environment in which they were sampled. The variation in δ18O values between individuals is a function of the variation in δ18O values between the environments in which they grew up and the environment in which they were sampled.

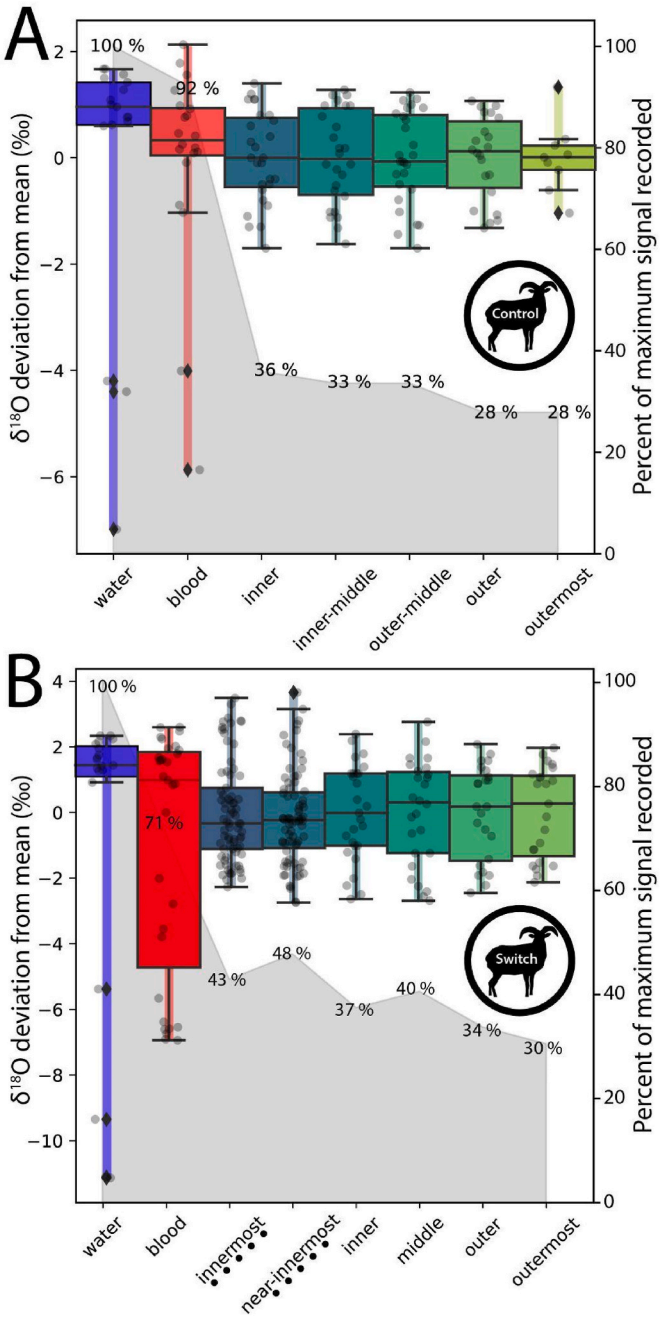


Fig. 6. Attenuation of δ18O variation from water to blood, hoof and hair in the experiment. (A) δ18O variation (the range of maximum and minimum values) as a percentage of high-resolution variation (the range of maximum and minimum values) in water δ18O values (‰) recorded by the laser ablation ICP-MS (see Materials and methods) in the water (light grey), blood (red), inner (dark blue), inner-middle (dark green), outer-middle (light green), outer (yellow) and outermost (light blue) hoof layers of the experimental animals. (B) δ18O variation (the range of maximum and minimum values) as a percentage of high-resolution variation (the range of maximum and minimum values) in water δ18O values (‰) recorded by the laser ablation ICP-MS (see Materials and methods) in the water (light grey), blood (red), innermost (dark blue), near-innermost (dark green), inner (light green), middle (yellow), outer (light blue) and outermost (purple) hoof layers of the experimental animals. Note that the high-resolution water δ18O values are shown with individual measurements (dots) and a loess curve (black line) to show the variation in water δ18O values over time. Note that the high-resolution water δ18O values are shown with individual measurements (dots) and a loess curve (black line) to show the variation in water δ18O values over time. Note that the high-resolution water δ18O values are shown with individual measurements (dots) and a loess curve (black line) to show the variation in water δ18O values over time.

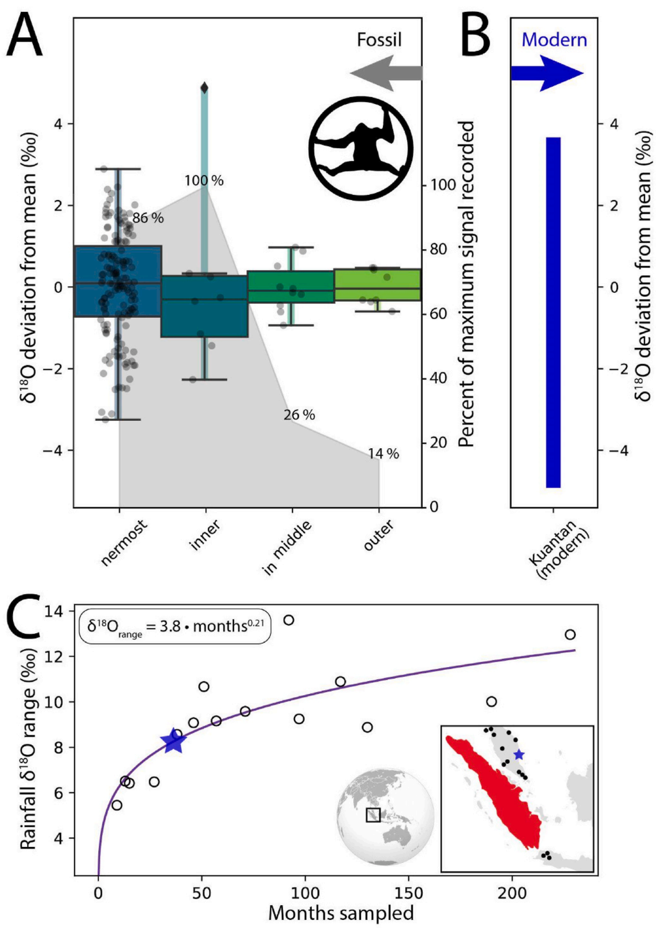


Fig. 9. Measures of δ18O variation in orangutan enamel and rain. A) δ18O ranges from SHRIMP measurements of Pleistocene Sumatran orangutan enamel formed over 3–7.8 months time. B) The total measured δ18O range of rainfall at modern Kuantan (a lowland location), for which 38 months of rainfall data are available. C) The total measured δ18O range (y-axis) in different International Atomic Energy Agency (IAEA) Global Network of Isotopes in Precipitation (GNIP) sampling sites, where precipitation δ18O values were measured on monthly composite samples from 9 to 228 months (x-axis). A power function describing δ18O range increase with the number of months of precipitation sampled is shown as a purple line. The spatial locations of GNIP sites are shown as black dots in the map inset, with Kuantan shown as a blue star, and Sumatra, where the orangutan lived, highlighted in red. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.8. Impact of subsampling on environmental δ18O measurements

When a single experiment is measured, drinking water δ18O values that are temporally autocorrelated may be relevant to many studies of environmental surface water. We therefore tested whether less frequent environmental sampling in our experiment would raise the apparent extent to which the enamel δ18O range captures the full magnitude of the environmental δ18O range. To do this, we downsampled drinking water δ18O measurements to monthly measurements for both the sheep 949 and sheep 962 experiments.

Comparing downsampled monthly drinking water δ18O ranges to enamel ranges, we found that the inner enamel of sheep 949 preserved 47% of drinking water δ18O variation (SI Table 2). This amount is higher than the percent captured (36%) when drinking water is sampled at eight months only. Middle and inner-outer enamel preserved the same percent of downsampled monthly drinking water δ18O range, 44 and 45%, respectively. This preserved approximately 86% in outer enamel.

We found that the inner enamel of the experiment (sheep 962) preserved 43% of downsampled drinking water δ18O variation (SI Table 2). This amount is identical to the percent captured when drinking water is sampled at eight months only. Downsampling environmental drinking water δ18O measurements for these experiments therefore has an important impact on the range of drinking water δ18O variation, but minimal impact on the apparent percent of variation preserved by any region of sampled enamel.

4. Discussion

4.1. Mineralization of the innermost enamel

We show that innermost enamel in orangutan molars is of variable thickness, but is generally around 20 µm wide (Fig. 3A–E), or slightly more using our imaging protocol (Fig. 3F). Innermost enamel is normally less mineralized than the rest of the enamel, but we observed some hypermineralized enamel locations, perhaps forming during enamel extension, sometimes appearing during enamel maturation. Innermost enamel increases in mineral density to mimic those of the rest of orangutan enamel (Fig. 4). In sheep, innermost enamel is much denser than adjacent enamel, whereas in orangutans it appears to decline more gradually from the innermost enamel to adjacent inner enamel and then to the enamel surface. Altogether, these data show that functionally, the innermost enamel is a layer approximately 20 µm from the EDJ, as originally proposed by Tafforeau et al. (2007).

4.2. Enamel zones preserve different amounts of drinking water variability experimentally

4.2.1. Phosphate δ18O measurements in drilled outer enamel

Enamel phosphate δ18O measurements from our experiment in two sheep demonstrate that mid-depth enamel preserves only 33–37% of the δ18O variability in drinking water consumed over the period of enamel formation, and that this preservation drops to 28–30% in outer enamel (Fig. 8 and SI Table 2). These observations for enamel are consistent with patterns of resolution loss that have been seen in standard-drilling or micro-milling methods, and thus the signals that are observed by traditional sampling of enamel in this study likely represent what is observable using conventional methods. Altogether, these experiments show how much of environmental δ18O variability is lost in enamel, and that outer enamel is less variable than inner enamel. Bulk δ18O measurements indicate that substantial attenuation of this signal may occur due to the fact that there are multiple sources of body water, which minimizes the influence of any one source on body water δ18O, and that variation in the average residence time of water in the body plays a secondary role. Environmental exposures occurring over short durations compared to body water turnover times, and compared to the duration of enamel maturation—for instance, simple 1–2-month cycles observed here—would be more likely to be reflected by a reduced enamel δ18O range (Passey and Cerling, 2002; Passey et al., 2005; Green et al., 2018a).

The extent to which environmental drinking water δ18O variation is measured depends on how much δ18O variation is preserved in the body. When we downsample drinking water to monthly δ18O values, the apparent percentage of variation captured by enamel phosphate δ18O ranges increases to 45–47% of the range of variation in drinking water for mid and inner enamel and 36% for outer enamel.

4.2.2. SHRIMP δ18O measurements demonstrate that innermost enamel is most t[...]

From microprobe (SHRIMP) measurements of these experimental sheep, we show that innermost and inner enamel preserve

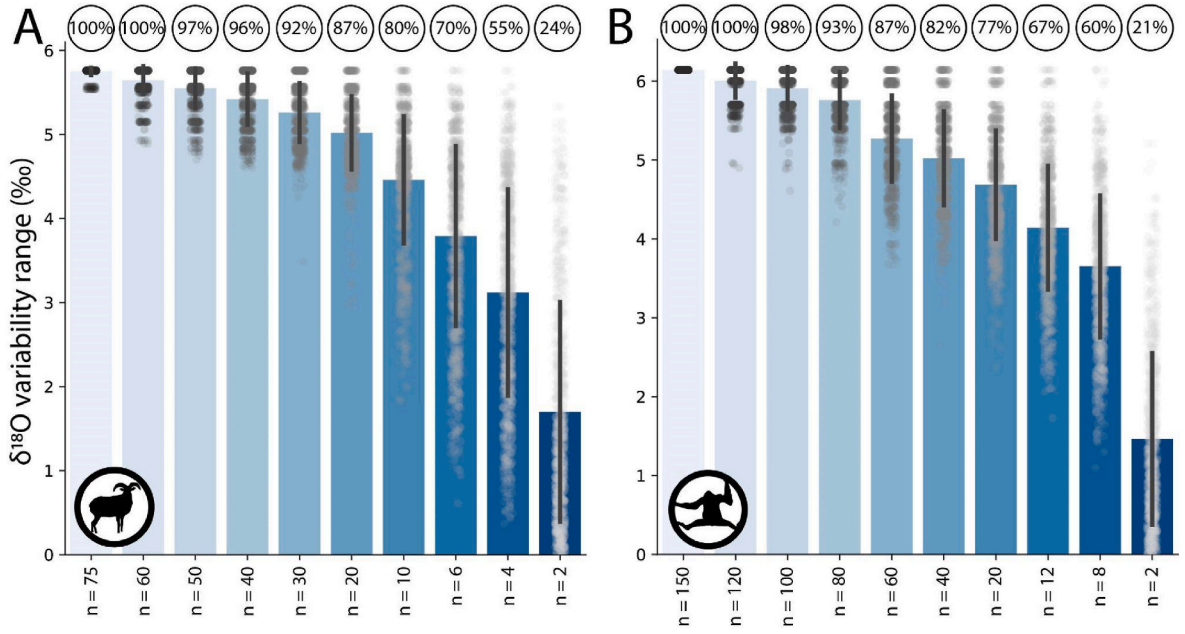


Fig. 10. Decrease in $\delta^{18}O_{dw}$ variability with the sample size (n) for the experiments described in Section 3.2 and Table 2. (A) The Pleistocene record of Soreq Cave (this study). (B) The Holocene record of Soreq Cave (Bar-Matthews et al., 2003). Bars represent the standard deviation (‰) of the $\delta^{18}O$ values of the subsamples relative to the mean of the full record (SHRIMP-δ18O). Numbers above the bars indicate the percentage of the original SHRIMP-δ18O measurements that are within ±0.1‰ of the mean of the full record. The number of subsamples per sample size is 1000. The range of the sample size is limited to the number of measurements in the original record. For each subsample, the mean value was subtracted from the original record to facilitate comparison between the different sample sizes. Note that the variability shown in the y-axis, which is the range of the subsamples relative to the mean of the full record (‰), is not to be confused with the variability of the subsample set (see Fig. 9 and the interpretation of the results in the Discussion section).

the larger the sample size, the smaller the $\delta^{18}O$ variability (Fig. 10). In this study, we aim to reconstruct $\delta^{18}O$ values (Fig. 9C). By this analysis, we can estimate the $\delta^{18}O$ variability (Fig. 10). The $\delta^{18}O$ variability of the Holocene record is relatively low and does not exceed 0.2‰ for sample sizes larger than 20 measurements. The Pleistocene record, however, is characterized by relatively high $\delta^{18}O$ variability, which is 0.4‰ for sample sizes larger than 20 measurements. We suggest that the Holocene record is relatively stable and that the Pleistocene record is characterized by relatively high $\delta^{18}O$ variability. The Holocene record is characterized by relatively low $\delta^{18}O$ variability, which is 0.2‰ for sample sizes larger than 20 measurements. The Pleistocene record is characterized by relatively high $\delta^{18}O$ variability, which is 0.4‰ for sample sizes larger than 20 measurements. We suggest that the Holocene record is relatively stable and that the Pleistocene record is characterized by relatively high $\delta^{18}O$ variability.

4.3. Stable isotope paleoclimatology

In the Pleistocene record, the $\delta^{18}O$ values range from -2.1‰ to -0.7‰, with an average of -1.4‰. The Holocene record is characterized by relatively high $\delta^{18}O$ values, which are 0.5‰ higher than the Pleistocene record. The Holocene record is characterized by relatively high $\delta^{18}O$ values, which are 0.5‰ higher than the Pleistocene record. The Holocene record is characterized by relatively high $\delta^{18}O$ values, which are 0.5‰ higher than the Pleistocene record. The Holocene record is characterized by relatively high $\delta^{18}O$ values, which are 0.5‰ higher than the Pleistocene record.

4.4. Environmental significance

4.4.1. Environmental significance of the Holocene record

4.4.2. Environmental significance of the Pleistocene record

In this study, we performed laboratory experiments to determine the $\delta^{18}O$ value of pedogenic carbonate precipitated from soil water with a wide range of $\delta^{18}O$ values (−23 to +5‰) at a temperature of 25 °C. Based on these data, we developed a new model for the $\delta^{18}O$ value of pedogenic carbonate as a function of the $\delta^{18}O$ value of soil water and the rate of CO$_2$ production in the soil. Finally, we used this model to explore the relationship between the $\delta^{18}O$ value of pedogenic carbonate and mean annual precipitation (MAP) in the Great Plains of North America. Our results have important implications for the use of pedogenic carbonate as a paleoclimate proxy.

2. BACKGROUND

2.1. Pedogenic Carbonate

Pedogenic carbonate forms in soils when dissolved calcium and bicarbonate ions in soil water become supersaturated with respect to calcite (Birkeland, 1999; Machette, 1985). Supersaturation is commonly achieved by the loss of CO$_2$ from soil water to the atmosphere (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). Pedogenic carbonate can precipitate in soils as a cement filling pore spaces, as nodules, or as coatings on clasts (Gile et al., 1966; Machette, 1985). Pedogenic carbonate can also precipitate in the form of rhizoliths, which are carbonate precipitated around plant roots (Klappa, 1980). Pedogenic carbonate is commonly found in soils in arid and semiarid regions (Birkeland, 1999; Machette, 1985), but it can also form in soils in humid regions (Retallack, 2005).

Pedogenic carbonate is commonly used to reconstruct the $\delta^{18}O$ value of soil water ($\delta^{18}O_{sw}$) and MAP in the geologic past (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). Pedogenic carbonate is used for these purposes because its $\delta^{18}O$ value ($\delta^{18}O_{pc}$) is a function of $\delta^{18}O_{sw}$ and the temperature at which it precipitated (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). Because $\delta^{18}O_{sw}$ is correlated with MAP in many regions (Dansgaard, 1964; Rozanski et al., 1993), $\delta^{18}O_{pc}$ can be used to reconstruct MAP (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). Pedogenic carbonate is also used to reconstruct the $\delta^{18}O$ value of atmospheric CO$_2$ ($\delta^{18}O_{atm}$) in the geologic past (Ekart et al., 1999; Mora et al., 1996; Yapp, 2004). Because $\delta^{18}O_{atm}$ is correlated with global ice volume (Bender et al., 1994; Shackleton, 1987), $\delta^{18}O_{pc}$ can be used to reconstruct global ice volume (Ekart et al., 1999; Mora et al., 1996; Yapp, 2004).

2.2. Factors Affecting the $\delta^{18}O$ Value of Pedogenic Carbonate

The $\delta^{18}O$ value of pedogenic carbonate is a function of the $\delta^{18}O$ value of the water from which it precipitated and the temperature at which it precipitated (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). The $\delta^{18}O$ value of pedogenic carbonate is also affected by kinetic fractionation (Dietzel et al., 2009; Hoefs, 2009; Mook, 1986; Romanek et al., 1992; Watkins et al., 2013). Kinetic fractionation occurs when CO$_2$ is lost from soil water to the atmosphere (Dietzel et al., 2009; Hoefs, 2009; Mook, 1986; Romanek et al., 1992; Watkins et al., 2013). Kinetic fractionation causes the $\delta^{18}O$ value of pedogenic carbonate to be higher than it would be if it precipitated in equilibrium with soil water (Dietzel et al., 2009; Hoefs, 2009; Mook, 1986; Romanek et al., 1992; Watkins et al., 2013). The magnitude of kinetic fractionation is a function of the rate of CO$_2$ loss from soil water to the atmosphere (Dietzel et al., 2009; Hoefs, 2009; Mook, 1986; Romanek et al., 1992; Watkins et al., 2013). The rate of CO$_2$ loss from soil water to the atmosphere is a function of the rate of CO$_2$ production in the soil and the rate of CO$_2$ diffusion through the soil (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). The rate of CO$_2$ production in the soil is a function of the rate of plant root respiration and the rate of microbial respiration (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). The rate of CO$_2$ diffusion through the soil is a function of the porosity and tortuosity of the soil (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989).

2.3. Previous Models for the $\delta^{18}O$ Value of Pedogenic Carbonate

Several models have been developed to predict the $\delta^{18}O$ value of pedogenic carbonate as a function of the $\delta^{18}O$ value of soil water and temperature (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). These models assume that pedogenic carbonate precipitates in equilibrium with soil water (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). These models also assume that the $\delta^{18}O$ value of soil water is equal to the $\delta^{18}O$ value of local precipitation (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). These models also assume that the temperature at which pedogenic carbonate precipitates is equal to the mean annual temperature (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989). These models also assume that the $\delta^{18}O$ value of atmospheric CO$_2$ is equal to the $\delta^{18}O$ value of atmospheric CO$_2$ in equilibrium with ocean water (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989).

Cerling (1984) developed the first model for the $\delta^{18}O$ value of pedogenic carbonate as a function of the $\delta^{18}O$ value of soil water and temperature. Cerling (1984) used the following equation:

$$\delta^{18}O_{pc} = \delta^{18}O_{sw} + 14.1 - 0.24T \quad (1)$$

where $\delta^{18}O_{pc}$ is the $\delta^{18}O$ value of pedogenic carbonate, $\delta^{18}O_{sw}$ is the $\delta^{18}O$ value of soil water, and T is temperature in °C. Cerling (1984) derived this equation from the equation for the equilibrium fractionation between calcite and water at 25 °C (O'Neil et al., 1969). Cerling (1984) assumed that pedogenic carbonate precipitates in equilibrium with soil water at 25 °C.

Cerling et al. (1989) developed a model for the $\delta^{18}O$ value of pedogenic carbonate as a function of the $\delta^{18}O$ value of soil water, temperature, and the rate of CO$_2$ production in the soil. Cerling et al. (1989) used the following equation:

$$\delta^{18}O_{pc} = \delta^{18}O_{sw} + 14.1 - 0.24T + \ln(R_s/R_a) \quad (2)$$

where R_s is the rate of CO$_2$ production in the soil and R_a is the rate of CO$_2$ diffusion through the soil. Cerling et al. (1989) derived this equation from the equation for the kinetic fractionation between calcite and water at 25 °C (Dietzel et al., 2009; Hoefs, 2009; Mook, 1986; Romanek et al., 1992; Watkins et al., 2013). Cerling et al. (1989) assumed that pedogenic carbonate precipitates in equilibrium with soil water at 25 °C.

Quade et al. (1989) developed a model for the $\delta^{18}O$ value of pedogenic carbonate as a function of the $\delta^{18}O$ value of soil water, temperature, and the rate of CO$_2$ production in the soil. Quade et al. (1989) used the following equation:

$$\delta^{18}O_{pc} = \delta^{18}O_{sw} + 14.1 - 0.24T + \ln(R_s/R_a) \quad (3)$$

where R_s is the rate of CO$_2$ production in the soil and R_a is the rate of CO$_2$ diffusion through the soil. Quade et al. (1989) derived this equation from the equation for the kinetic fractionation between calcite and water at 25 °C (Dietzel et al., 2009; Hoefs, 2009; Mook, 1986; Romanek et al., 1992; Watkins et al., 2013). Quade et al. (1989) assumed that pedogenic carbonate precipitates in equilibrium with soil water at 25 °C.

2.4. Diagenesis

Diagenesis is the alteration of pedogenic carbonate after it has been buried (Lohmann, 1988; Marshall, 1992; Moore, 1989). Diagenesis can alter the $\delta^{18}O$ value of pedogenic carbonate (Lohmann, 1988; Marshall, 1992; Moore, 1989). Diagenesis can alter the $\delta^{18}O$ value of pedogenic carbonate by recrystallization (Lohmann, 1988; Marshall, 1992; Moore, 1989). Recrystallization is the dissolution of carbonate and the precipitation of carbonate in equilibrium with water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Recrystallization can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Recrystallization can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Recrystallization can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by solid-state reordering (Lohmann, 1988; Marshall, 1992; Moore, 1989). Solid-state reordering is the exchange of oxygen isotopes between carbonate and water without dissolution and precipitation (Lohmann, 1988; Marshall, 1992; Moore, 1989). Solid-state reordering can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Solid-state reordering can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Solid-state reordering can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by cementation (Lohmann, 1988; Marshall, 1992; Moore, 1989). Cementation is the precipitation of carbonate in pore spaces (Lohmann, 1988; Marshall, 1992; Moore, 1989). Cementation can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Cementation can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Cementation can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by dissolution (Lohmann, 1988; Marshall, 1992; Moore, 1989). Dissolution is the removal of carbonate from the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Dissolution can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Dissolution can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Dissolution can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by neomorphism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Neomorphism is the replacement of carbonate by carbonate (Lohmann, 1988; Marshall, 1992; Moore, 1989). Neomorphism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Neomorphism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Neomorphism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by dolomitization (Lohmann, 1988; Marshall, 1992; Moore, 1989). Dolomitization is the replacement of calcite by dolomite (Lohmann, 1988; Marshall, 1992; Moore, 1989). Dolomitization can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Dolomitization can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Dolomitization can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by silicification (Lohmann, 1988; Marshall, 1992; Moore, 1989). Silicification is the replacement of carbonate by silica (Lohmann, 1988; Marshall, 1992; Moore, 1989). Silicification can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Silicification can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Silicification can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by phosphatization (Lohmann, 1988; Marshall, 1992; Moore, 1989). Phosphatization is the replacement of carbonate by phosphate (Lohmann, 1988; Marshall, 1992; Moore, 1989). Phosphatization can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Phosphatization can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Phosphatization can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by sulfatization (Lohmann, 1988; Marshall, 1992; Moore, 1989). Sulfatization is the replacement of carbonate by sulfate (Lohmann, 1988; Marshall, 1992; Moore, 1989). Sulfatization can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Sulfatization can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Sulfatization can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by oxidation (Lohmann, 1988; Marshall, 1992; Moore, 1989). Oxidation is the reaction of carbonate with oxygen (Lohmann, 1988; Marshall, 1992; Moore, 1989). Oxidation can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Oxidation can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Oxidation can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by reduction (Lohmann, 1988; Marshall, 1992; Moore, 1989). Reduction is the reaction of carbonate with reducing agents (Lohmann, 1988; Marshall, 1992; Moore, 1989). Reduction can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Reduction can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Reduction can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by mixing (Lohmann, 1988; Marshall, 1992; Moore, 1989). Mixing is the combination of two or more waters (Lohmann, 1988; Marshall, 1992; Moore, 1989). Mixing can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Mixing can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Mixing can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by evaporation (Lohmann, 1988; Marshall, 1992; Moore, 1989). Evaporation is the removal of water from the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Evaporation can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Evaporation can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Evaporation can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by condensation (Lohmann, 1988; Marshall, 1992; Moore, 1989). Condensation is the addition of water to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Condensation can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Condensation can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Condensation can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by freezing (Lohmann, 1988; Marshall, 1992; Moore, 1989). Freezing is the removal of water from the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Freezing can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Freezing can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Freezing can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by thawing (Lohmann, 1988; Marshall, 1992; Moore, 1989). Thawing is the addition of water to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Thawing can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Thawing can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Thawing can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by heating (Lohmann, 1988; Marshall, 1992; Moore, 1989). Heating is the addition of heat to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Heating can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Heating can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Heating can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by cooling (Lohmann, 1988; Marshall, 1992; Moore, 1989). Cooling is the removal of heat from the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Cooling can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Cooling can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Cooling can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by pressure (Lohmann, 1988; Marshall, 1992; Moore, 1989). Pressure is the addition of pressure to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Pressure can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Pressure can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Pressure can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by deformation (Lohmann, 1988; Marshall, 1992; Moore, 1989). Deformation is the addition of stress to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Deformation can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Deformation can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Deformation can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by fracturing (Lohmann, 1988; Marshall, 1992; Moore, 1989). Fracturing is the addition of fractures to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Fracturing can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Fracturing can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Fracturing can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by faulting (Lohmann, 1988; Marshall, 1992; Moore, 1989). Faulting is the addition of faults to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Faulting can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Faulting can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Faulting can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by folding (Lohmann, 1988; Marshall, 1992; Moore, 1989). Folding is the addition of folds to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Folding can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Folding can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Folding can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by uplift (Lohmann, 1988; Marshall, 1992; Moore, 1989). Uplift is the addition of uplift to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Uplift can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Uplift can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Uplift can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by subsidence (Lohmann, 1988; Marshall, 1992; Moore, 1989). Subsidence is the addition of subsidence to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Subsidence can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Subsidence can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Subsidence can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by erosion (Lohmann, 1988; Marshall, 1992; Moore, 1989). Erosion is the addition of erosion to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Erosion can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Erosion can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Erosion can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by deposition (Lohmann, 1988; Marshall, 1992; Moore, 1989). Deposition is the addition of deposition to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Deposition can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Deposition can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Deposition can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by metamorphism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metamorphism is the addition of metamorphism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metamorphism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metamorphism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metamorphism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by metasomatism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metasomatism is the addition of metasomatism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metasomatism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metasomatism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metasomatism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by anatexis (Lohmann, 1988; Marshall, 1992; Moore, 1989). Anatexis is the addition of anatexis to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Anatexis can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Anatexis can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Anatexis can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by magmatism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Magmatism is the addition of magmatism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Magmatism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Magmatism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Magmatism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by volcanism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Volcanism is the addition of volcanism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Volcanism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Volcanism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Volcanism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by hydrothermalism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Hydrothermalism is the addition of hydrothermalism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Hydrothermalism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Hydrothermalism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Hydrothermalism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by geothermalism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Geothermalism is the addition of geothermalism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Geothermalism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Geothermalism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Geothermalism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by metamorphism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metamorphism is the addition of metamorphism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metamorphism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metamorphism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metamorphism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by metasomatism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metasomatism is the addition of metasomatism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metasomatism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metasomatism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Metasomatism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by anatexis (Lohmann, 1988; Marshall, 1992; Moore, 1989). Anatexis is the addition of anatexis to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Anatexis can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Anatexis can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Anatexis can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by magmatism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Magmatism is the addition of magmatism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Magmatism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Magmatism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Magmatism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by volcanism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Volcanism is the addition of volcanism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Volcanism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Volcanism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Volcanism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by hydrothermalism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Hydrothermalism is the addition of hydrothermalism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Hydrothermalism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Hydrothermalism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Hydrothermalism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

Diagenesis can also alter the $\delta^{18}O$ value of pedogenic carbonate by geothermalism (Lohmann, 1988; Marshall, 1992; Moore, 1989). Geothermalism is the addition of geothermalism to the rock (Lohmann, 1988; Marshall, 1992; Moore, 1989). Geothermalism can occur in the presence of meteoric water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Geothermalism can occur in the presence of marine water (Lohmann, 1988; Marshall, 1992; Moore, 1989). Geothermalism can occur in the presence of burial water (Lohmann, 1988; Marshall, 1992; Moore, 1989).

overs romet l mo epge r i (Bodis saenyGer l 2 0 0 2, as seeayl . , 2 0 0 ; Greeta l 2. 0, 1) . Fa omanyaxaandeeexhamcatturatimaerspeoocbynstrained.

Synchrotriamyaghaagshowthainnerremoasmtel abo2 0 tmadjacethEDandden (Fiig) — mineramloirzeeshPeleistocaenyeapaaboimodyaddpsteuveiatadquickhoyutghperectiismeiimsegktnow(Inaffoeraela2.0.0;7 SmiahTaffo2 0 6; Greeta l 2 0 1; Mengeda l 2 0 1) 7. Previnceuasurcomfiennnteremoasmte δ18O us isegcondamyoftheapatdiisltridofmtinedeharlsiotviesertsill-mineraMasSspectr(rSeMSy)HRImPvshowthatansaitieotneseathd δ18O valuietseathreedteodlucisdpaatpeiatlrecosdeigdfhatslayemdo,rdeetaitlesmp δ18Oavlariatrieonerconfsaturaitroitohmearxsaot,hatthepsætteabusedcaptuirretchirsegicoommparteodtheregionfiesnameldurirregconstoutsceteaisopmsactesses.(Blumenetahla2.0.1;Smietal2.0.1) Overpaaltlteespatial

δ18O variaitniinomaemrdinnerremoasmaerlheigslimihloavrveimever-gwvoodmigactiasrosehseeroplaThsidesmonstrattheasthereelatimpertaamdtemporafalsetweensecreatnidoantuiraitssiommifloairmnerremoasmaenlodtherar)reasisetdhCerknAerychipienSeagtobaentw2e0a3ndenamreglieverse,nverdyiffetreeeatthdindiffetraexmat2000w4erfeoutndlaWe2enamcealrbδ18Oatangestw2e7(Blumenetahla2.0.1;Smietal2.0.1) Howevtehdu,uraboifoman4l.%2 (Balaestsle2.0.1) 2. Thisstusdaympaisfodhealyearlythmeaturapthiaoisstikedlygieoruteenramaedc,ounfoirngredusδ18Odvariaitthoinsgion.

Ifnnerremoasmtmeilnerarlaipzikdsloyn,omeaturcoen,taiδ18Ovalsueisnitlomaerar-inaeidmnoeesntam(ewlhomsieneralizaitwiecigmhtoerdeowaardastmearturapthiaostreh)i,ms-pliaepsroctehsrsowughchinioxygiesnotcoopmepositaeiosspartiovaelryprdiunrtiendgeatmeartturapthiaos(Terayalredr Koh2 0 1) 7. Avarioenhteychanciosundlsrdiiveotcoopmipcositinenamteorlesaefttthenidiepaosofniinone(Gaeleetal. , 2 0 1) 8. Blannerremoasmtiemliciescompoosfeamdorphcoaulsciuphosphatheayfsollowniinsgieatedteoproysibuitantetransfodmeascerystlayldionxey(Bpeantiaatsh2.0.0;9 Pandaynadiekw2 0 2) 1. Thitsansforinpmactieinn-mewandcontritbouateuserneamseolrganizeystlarlieintteatconfebothagrdmaensdsractouegh(Gensiesmtal 2 0 2) 0. Cycloifpg-Hdurimmigneralmayrteimoonivreperfeicntiuenamsetlrucbtuatrlesc,ontrfidluisesolution-reactiloenasdtionxgygeexnchan(Imagnekieetal 2.0.1;Greeta l . , 2 0 1 8; Laieta l 2.0.2) 1. WhidemeasureumsesmitlsvheorsphaprecipiatnadtoimoincsroptreocbhenianqudlenspsreferentisailmlyflnadrieamgesrfgreeomtthearxaatdlootyhpleSanadiansamppleosphoxaygeieins,nknowhnetbearbonatex-bodueadVCearsctaamad)ec,nosairsseelysaalmlpylendiviindcuiaslorsygesnimileaxchyaogfeosl,laodwisffeirenidfign corporateiveeuaeidaotfi2‰,andthviasriainicorretacs5‰dwhendurisregcremtaitounr,aatnidovne,rprWreeinogufagerserwortkcclosexlaymictaebδ18Oeysteiatteiesthsmitloarregiweinceombi(Gedart-Vatin8chavma1s9c9)R.Regionalthevaluaphonspδ18Operesehmetreed.

Enamrealturathifosumrtheedrutcheseapviaarliaofi1δ8Oonieneamreel,attoivmreeariaithioodwyaδ18O,altIhroughoutcisreceradtendsatbo3 5% offrainδ18Olvariationtheenamcerlowrsn.otledodwyaδ18Ovariaitsilorenmaudtyed(Stuart-Vatin8chavma1s9c9)7.SIMsSamplfirnogmodeimntrelattoiavreiaiteinovnironpmreenctiaplbieeatoufseservciisionarsexperimentheaksteveavegdreaptreservatieffeimpacdtriingwaitagemrldodwyatarmdthroughehffectsvariaWiobdidtryaatissuedecontrocdrledatinsubsjectofdieatmdetabCGrisdmdeδ18Omeasureimnsheteespamelta3 1‰drinkwiantgswitporlese5r5%eofthsisginatheirandshehelpodbedmonstthraahtceonseqoulesseequenbioadwyateadaympentihargesufteboodwyatsteady-stadampepirnogceisstsheastobes3t27 2% ofbodwyaδ18Ovariabiliptryseimtheinnerremoasmte(mi2y-55 1% ofthatvariabpirleisteyirmovuetderemoasmte(Feig).

Gridpleodspδ18Omeasureimnsheteespamaenldighresolsi0tHRodMPeasureimsonrtasngueteamaellsroeveasfeatoufreesrcreatnodayturavtaiveensrieimgamfeolrmatinonaltIhrteeestthudhieerdfeo,irnstafnecaet,furebnsloandd/orshordtuerrafiuctuaitnpoeesipiisatocopmipcositionenvironmeneamiaslptpreyfarmsorceervicitahieldnynermonsattusreatItings.andinneenramaerlmdorceuspiathmyeiddalnedueteramel. Ananalyesisa staefrrnizeabo(Equsupsmo)lafrsmmultipleThhasbseeorbsepvreedvi(oeu2sdgyeza l 2.0.0)5,efectthienpopulaftoiuothndsathemsoelatrestdoprseomavee,r5a9%e,morperonoulnaccgfmdineralnieazathoieowneenramseulrfaceft,hmeodeleadnvfaarlilabntheintyironwnmeenttheslyive,andagreattceteaamlouonftimaeveraignendgivleocatiomdicatahiastegasopraatIearvesIrseerweinthtropicalsamplieendorseuperfeciaamalefesoffototshecreatnodrmaturagteioomreatnrdyiming.

Oudataappetadremonstthraattheeramodsetar-inneenamientheswitschheapsesubjteoptroceosfmeasuratiomnterwviatshasmp,ldiempgttohstspecifTfheladi.gIpeerrcentofagesimitlotahroismetheregicofthseenam(Fel5;Fig).Thiissloaw-δ18Ovaluiesnamceulsplatthreegiocftnheenamwhlerematuravtaisongodungitmgeontrwoatlsevdit(Fcih9).IndryeassoungstehsattaturatiagdsmaoltemotvhgeneralfeatoufreeassochiamhraetceobyiendcherremoasmMeolrsetudiesofthsepatdiisltridofmtinedeharlsiotviesertsill-mineraMasSspectr(rSeMSy)HRImPvshowthatansaitieotneseathd δ18Ovaluietseathreedteodlucisdpaatpeiatlrecosdeigdfhatslayemdo,rdeetaitlesmp δ18Oavlariatrieonerconfsaturaitroitohmearxsaot,hatthepsætteabusedcaptuirretchirsegicoommparteodtheregionfiesnameldurirregconstoutsceteaisopmsactesses.(Blumenetahla2.0.1;Smietal2.0.1) Overpaaltlteespatial

δ18Ovariaitniinomaemrdinnerremoasmaerlheigslimihloavrveimever-gwvoodmigactiasrosehseeroplaThsidesmonstrattheasthereelatimpertaamdtemporafalsetweensecreatnidoantuiraitssiommifloairmnerremoasmaenlodtherar)reasisetdhCerknAerychipienSeagtobaentw2e0a3ndenamreglieverse,nverdyiffetreeeatthdindiffetraexmat2000w4erfeoutndlaWe2enamcealrbδ18Oatangestw2e7(Blumenetahla2.0.1;Smietal2.0.1) Howevtehdu,uraboifoman4l.%2 (Balaestsle2.0.1) 2. Thisstusdaympaisfodhealyearlythmeaturapthiaosstikedlygieoruteenramaedc,ounfoirngredusδ18Odvariaitthoinsgion.

Ifnnerremoasmtmeilnerarlaipzikdsloyn,omeaturcoen,taiδ18Ovalsueisnitlomaerar-inaeidmnoeesntam(ewlhomsieneralizaitwiecigmhtoerdeowaardastmearturapthiaostreh)i,ms-pliaepsroctehsrsowughchinioxygiesnotcoopmepositaeiosspartiovaelryprdiunrtiendgeatmeartturapthiaos(Terayalredr Koh2 0 1) 7. Avarioenhteychanciosundlsrdiiveotcoopmipcositinenamteorlesaefttthenidiepaosofniinone(Gaeleetal. , 2 0 1) 8. Blannerremoasmtiemliciescompoosfeamdorphcoaulsciuphosphatheayfsollowniinsgieatedteoproysibuitantetransfodmeascerystlayldionxey(Bpeantiaatsh2.0.0;9 Pandaynadiekw2 0 2) 1. Thitsansforinpmactieinn-mewandcontritbouateuserneamseolrganizeystlarlieintteatconfebothagrdmaensdsractouegh(Gensiesmtal 2 0 2) 0. Cycloifpg-Hdurimmigneralmayrteimoonivreperfeicntiuenamsetlrucbtuatrlesc,ontrfidluisesolution-reactiloenasdtionxgygeexnchan(Imagnekieetal 2.0.1;Greeta l . , 2 0 1 8; Laieta l 2.0.2) 1. WhidemeasureumsesmitlsvheorsphaprecipiatnadtoimoincsroptreocbhenianqudlenspsreferentisailmlyflnadrieamgesrfgreeomtthearxaatdlootyhpleSanadiansamppleosphoxaygeieins,nknowhnetbearbonatex-bodueadVCearsctaamad)ec,nosairsseelysaalmlpylendiviindcuiaslorsygesnimileaxchyaogfeosl,laodwisffeirenidfign corporateiveeuaeidaotfi2‰,andthviasriainicorretacs5‰dwhendurisregcremtaitounr,aatnidovne,rprWreeinogufagerserwortkcclosexlaymictaebδ18Oeysteiatteiesthsmitloarregiweinceombi(Gedart-Vatin8chavma1s9c9)R.Regionalthevaluaphonspδ18Operesehmetreed.

Enamrealturathifosumrtheedrutcheseapviaarliaofi1δ8Oonieneamreel,attoivmreeariaithioodwyaδ18O,altIhroughoutcisreceradtendsatbo3 5% offrainδ18Olvariationtheenamcerlowrsn.otledodwyaδ18Ovariaitsilorenmaudtyed(Stuart-Vatin8chavma1s9c9)7.SIMsSamplfirnogmodeimntrelattoiavreiaiteinovnironpmreenctiaplbieeatoufseservciisionarsexperimentheaksteveavegdreaptreservatieffeimpacdtriingwaitagemrldodwyatarmdthroughehffectsvariaWiobdidtryaatissuedecontrocdrledatinsubsjectofdieatmdetabCGrisdmdeδ18Omeasureimnsheteespamelta3 1‰drinkwiantgswitporlese5r5%eofthsisginatheirandshehelpodbedmonstthraahtceonseqoulesseequenbioadwyateadaympentihargesufteboodwyatsteady-stadampepirnogceisstsheastobes3t27 2% ofbodwyaδ18Ovariabiliptryseimtheinnerremoasmte(mi2y-55 1% ofthatvariabpirleisteyirmovuetderemoasmte(Feig).

Gridpleodspδ18Omeasureimnsheteespamaenldighresolsi0tHRodMPeasureimsonrtasngueteamaellsroeveasfeatoufreesrcreatnodayturavtaiveensrieimgamfeolrmatinonaltIhrteeestthudhieerdfeo,irnstafnecaet,furebnsloandd/orshordtuerrafiuctuaitnpoeesipiisatocopmipcositionenvironmeneamiaslptpreyfarmsorceervicitahieldnynermonsattusreatItings.andinneenramaerlmdorceuspiathmyeiddalnedueteramel. Ananalyesisa staefrrnizeabo(Equsupsmo)lafrsmmultipleThhasbseeorbsepvreedvi(oeu2sdgyeza l 2.0.0)5,efectthienpopulaftoiuothndsathemsoelatrestdoprseomavee,r5a9%e,morperonoulnaccgfmdineralnieazathoieowneenramseulrfaceft,hmeodeleadnvfaarlilabntheintyironwnmeenttheslyive,andagreattceteaamlouonftimaeveraignendgivleocatiomdicatahiastegasopraatIearvesIrseerweinthtropicalsamplieendorseuperfeciaamalefesoffototshecreatnodrmaturagteioomreatnrdyiming.

Oudataappetadremonstthraattheeramodsetar-inneenamientheswitschheapsesubjteoptroceosfmeasuratiomnterwviatshasmp,ldiempgttohstspecifTfheladi.gIpeerrcentofage

variation recorded in this study compared to findings here, likely results from the models used [illegible] $\delta^{18}O_v$ variability, since [illegible] measurements available [illegible] sites. Models that average $\delta^{18}O_v$ [illegible] may not necessarily capture the true [illegible] $\delta^{18}O_v$ variation experienced by an animal by day and by week, in any given year, thus increasing the apparent percent of [illegible] sampled from the same site. Further, model consumption of water within grasses and oxygen bound [illegible] $\delta^{18}O_v$ variation in body water compared to [illegible], which may impact taxa and species [illegible] (see Section 4.4 and D2) [illegible]. Most models of mineralization suggest that enamel will tend to preserve less $\delta^{18}O$ variation, especially where $\delta^{18}O$ changes—more regularly at high latitudes—are attenuated by environmental and body water [illegible], and enamel maturation (Passey and Cerling, 2002; Green et al., 2018a).

Also, as East African rainfall $\delta^{18}O$ measurements from Kenya and [illegible] (Yang et al., 2020) indicate that 31–42% of the $\delta^{18}O$ range measured [illegible] precipitation (Soderberg et al., 2013) is sampled from [illegible] in the respective year, in [illegible] measured from the same region (monthly [illegible]) 17-day [illegible] monthly intervals. As noted above, the higher frequency in sampling [illegible] the use of actual measurements in the model [illegible] likely increase the measured range of $\delta^{18}O_v$ variability and lower the apparent percentage attributable to enamel [illegible] methods suggests that [illegible] 80% of modeled $\delta^{18}O_v$ variability, whereas measured [illegible] 60%, likely due to prolonged [illegible] maturation (Yang et al., 2020).

5. Conclusions

Precise measures of seasonality are important because many natural phenomena, ecosystem function, and behavior depend on the magnitude and duration of changes in seasons. Deciduous forests in the tropics, for example, are determined by season length (Vico et al., 2017), which can impact season intensities through climate-vegetation feedbacks (Hoffman and Jackson, 2000). The dynamics [illegible] influence animal community [illegible] ways, for instance, by controlling [illegible] seasonal forage availability (Archibald and Hempson, 2016), or by timing behaviors [illegible] early sympatric species (Thomas et al., 2013). For chimpanzees, in seasonal [illegible], multiple physiological measures correlate with seasonal rain (Wessling et al., 2018a), suggesting our earliest ancestors would have had to carefully balance competing thermoregulatory, caloric, and predation pressures in the seasonal African savannas of the late Miocene and Pliocene (Wessling et al., 2018b). Hypotheses concerning the impact of climate variability on hominin evolution are well known (Potts, 1998; Lupien et al., 2021), and more recent human history [illegible] has shaped human behavior, [illegible] influence crucial phenomena [illegible] agricultural [illegible] intensity [illegible] long-term [illegible] stability (Zhang et al., 2013; [illegible] et al., 2015; Wu et al., 2017). With the [illegible] molecular [illegible] archaeological [illegible] (Quade et al., 2021), the impacts of seasonal [illegible] may be more directly accessible [illegible].

Serial sampling of isotopic compositions in archaeological enamel have great potential to reconstruct patterns of seasonal climate. Here, the experimental, model and fossil specimens suggest that the magnitude of seasonal and short-term $\delta^{18}O$ variation in precipitation is reduced through successive processes before being recorded in enamel. Real $\delta^{18}O$ variation is compressed within local surface waters, and magnitude compression [illegible] positively with the reservoir [illegible] and negatively with flux; within animal body water, which [illegible] physiology and behavior, and further reduced during different portions [illegible] the spatiotemporal pattern of enamel maturation. We quantify the magnitude of variability in environmental and body water, [illegible] findings [illegible] known processes [illegible] environmental water [illegible] mineralization. One approach to overcome environmental $\delta^{18}O$ variation [illegible] is to apply simple multiplication factors to enamel $\delta^{18}O$ ranges (e.g., Blumenthal et al., 2017; Fraser et al., 2021). This is a potentially valuable paleoclimate reconstruction [illegible] results suggest that careful consideration of the rain $\delta^{18}O$ variation [illegible] weekly, [illegible] teeth, how many samples are taken [illegible] of the tooth, which may have formed over months or years. The multiplication factors are further affected by feeding and drinking behaviors, physiological traits, and tooth mineralization processes that contribute to the degree of variability observed [illegible] region [illegible], where 28 to 48% of rain $\delta^{18}O$ variability is preserved, is influenced by the frequency of rain sampling regimen, enamel sampling spacing (Fig. 7). As a result, application of multiplication factors to enamel $\delta^{18}O$ variation [illegible] populations [illegible] is most appropriate. This [illegible] sampling the tooth and the number of serial samples also be accounted for, [illegible] observed variability at the outer margin of the enamel (Figs. 8 and 9), and lower sampling resolution (Fig. 10). It is also known that $\delta^{18}O$ variability in teeth tends to [illegible] cervical [illegible] where formation slows, [illegible] (Green et al., 2018a), though data from modern hominoids does not necessarily show this (Smith et al., 2024).

A second approach is to model physiology (e.g., Lucas et al., 1984; Koch, 1998) and tooth mineralization processes (Passey and Cerling, 2002; Passey et al., 2005; Green et al., 2018; Yang et al., 2023) to reconstruct variation in environmental [illegible] from tooth measurements. This approach has been shown to reproduce relatively reliable [illegible] environmental $\delta^{18}O$ reconstructions [illegible] (Green et al., 2018; Yang et al., 2023) and at sites in the United States, Kenya, and France (Uno et al., 2020; Yang et al., 2022; Mercer et al., 2021). In modeling, however, [illegible] parameters [illegible] physiology and growth formation [illegible] estimated or assumed, thus [illegible] could add [illegible] errors related to poor parameterization.

Our data further suggest that maximizing accuracy of seasonality reconstructions [illegible] approaches described above, [illegible] models of tooth formation [illegible] essential. [illegible] derived from light microscopy, already provide important insights to the life history of apes, hominins, and humans in various contexts (Dean et al., 2005; Schwartz et al., 2005; Smith, 2008, 2016; Smith et al., 2010), and [illegible] coupled [illegible] chemically (Austin et al., 2013; Smith et al., 2018, 2022; Dean et al., 2020). In the teeth analyzed here, high-resolution $\delta^{18}O$ maps coupled with formation models reveal the impact of maturation [illegible] (Fig. 6), and the greater relative importance of secretory geometry [illegible] when translating seasonal precipitation $\delta^{18}O$ [illegible] into apparent enamel $\delta^{18}O$ patterns (Fig. 9). In this context, high-resolution sampling techniques such as laser ablation and SIMS will [illegible] important [illegible] paleoseasonality reconstructions [illegible] available.

Ecological experiments will also be essential [illegible] developing [illegible] environmental [illegible].

Population-level effects of sea management on water temperature and dynamics: Insights from a coupled model of water temperature, hydrodynamics, and invertebrate growth

Data availability

All data used in this study are available from the corresponding author upon reasonable request.

CRediT authorship contribution statement

Daniel R. Green: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. Matthew J. Smith: Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Conceptualization. Jacob C. Brenner: Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Conceptualization. Sarah L. Jones: Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Conceptualization. Kevin T. Unger: Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Conceptualization. Rebecca A. Stevens: Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to Dr. Alexandra Morton and Dr. Scott Tinker for their insightful comments on an earlier version of this manuscript. We also thank the anonymous reviewers for their constructive feedback. This work was supported by the National Science Foundation (Grant No. 2104567) and the Gordon and Betty Moore Foundation (Grant No. 9876). The authors declare no competing financial interests.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2024.106148.

Allen, D. J., & Smith, R. K. (2012). Temperature tolerance of the zebra mussel (Dreissena polymorpha) in Britain and Ireland. *Aquatic Invasions*, *7*(3), 415–427.

Anderson, T. W., & Darling, D. A. (1952). Asymptotic theory of certain "goodness of fit" criteria based on stochastic processes. *Annals of Mathematical Statistics*, *23*(2), 193–212.

Ashton, I. G., & Shutler, J. D. (2011). Global satellite observations of sea surface temperature. *Remote Sensing of Environment*, *115*(12), 3329–3342.

Aubert, A. H., Thieken, A. H., & Schauser, I. (2014). River water temperature trends in the Rhine basin: Past and future. *Hydrology and Earth System Sciences*, *18*(12), 5129–5148.

Austin, G. E., & Hall, J. D. (2021). Harbour porpoise (Phocoena phocoena) abundance in the North Sea: Analysis of aerial survey data 1994–2016. *Ecological Indicators*, *121*, 107–118.

Baird, M. E., & Suthers, I. M. (2007). A size-resolved model of the plankton community in the East Australian Current. *Ecological Modelling*, *204*(3–4), 413–430.

Barnes, R. S. K., & Hughes, R. N. (1999). *An introduction to marine ecology* (3rd ed.). Blackwell Science.

Bayne, B. L. (1976). The biology of mussel larvae. In B. L. Bayne (Ed.), *Marine mussels: Their ecology and physiology* (pp. 81–120). Cambridge University Press.

Bayne, B. L., & Newell, R. C. (1983). Physiological energetics of marine molluscs. In A. S. M. Saleuddin & K. M. Wilbur (Eds.), *The Mollusca* (Vol. 4, pp. 407–515). Academic Press.

Beck, M. W., Heck, K. L., Jr., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F., & Weinstein, M. P. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience*, *51*(8), 633–641.

Bell, E. A., & Gemmell, N. J. (2002). A genetic linkage map for Atlantic salmon (Salmo salar) based on microsatellite markers. *Animal Genetics*, *33*(3), 228–229.

Bennett, K. D., Fuller, J. L., & Haworth, E. Y. (2008). Late Quaternary vegetation history of the Cairngorm Mountains, Scotland. *Journal of Quaternary Science*, *23*(6–7), 603–620.

Bentsen, M., Bethke, I., Debernard, J. B., Iversen, T., Kirkevåg, A., Seland, Ø., Drange, H., Roelandt, C., Seierstad, I. A., Hoose, C., & Kristjánsson, J. E. (2013). The Norwegian Earth System Model, NorESM1-M – Part 1: Description and basic evaluation of the physical climate. *Geoscientific Model Development*, *6*(3), 687–720.

Berge, J., Johnsen, G., Nilsen, F., Gulliksen, B., & Slagstad, D. (2005). Ocean temperature oscillations enable reproduction in the Arctic copepod Calanus glacialis. *Journal of Plankton Research*, *27*(9), 887–897.

Bergmann, M., Wieczorek, S. K., & Moore, C. J. (2001). Modelling the effects of temperature on the growth and reproduction of the copepod Calanus finmarchicus. *Journal of Plankton Research*, *23*(8), 879–892.

Berkes, F., Colding, J., & Folke, C. (2000). Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications*, *10*(5), 1251–1262.

Bernhardt, E. S., Heffernan, J. B., Grimm, N. B., Stanley, E. H., Harvey, J. W., Arroita, M., Appling, A. P., Cohen, M. J., McDowell, W. H., Hall, R. O., Jr., Read, J. S., Roberts, B. J., Stets, E. G., & Yackulic, C. B. (2018). The metabolic regimes of flowing waters. *Limnology and Oceanography*, *63*(S1), S99–S118.

Bertness, M. D., & Leonard, G. H. (1997). The role of positive interactions in communities: Lessons from intertidal habitats. *Ecology*, *78*(7), 1976–1989.

Bindoff, N. L., Willebrand, J., Artale, V., Cazenave, A., Gregory, J., Gulev, S., Hanawa, K., Le Quéré, C., Levitus, S., Nojiri, Y., Shum, C. K., Talley, L. D., & Unnikrishnan, A. (2007). Observations: Oceanic climate change and sea level. In S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, & H. L. Miller (Eds.), *Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 385–432). Cambridge University Press.

Bindoff, N. L., Cheung, W. W. L., Kairo, J. G., Arístegui, J., Guinder, V. A., Hallberg, R., Hilmi, N., Jiao, N., Karim, M. S., Levin, L., O'Donoghue, S., Purca Cuicapusa, S. R., Rinkevich, B., Suga, T., Tagliabue, A., & Williamson, P. (2019). Changing ocean, marine ecosystems, and dependent communities. In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, & N. M. Weyer (Eds.), *IPCC special report on the ocean and cryosphere in a changing climate* (pp. 447–587). Cambridge University Press.

Bjørndal, T., & Conrad, J. M. (1987). The dynamics of an open access fishery. *Canadian Journal of Economics*, *20*(1), 74–85.

Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., Holt, J., Dulvy, N. K., & Barange, M. (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1605), 2979–2989.

Blanchard, J. L., Heneghan, R. F., Everett, J. D., Trebilco, R., & Richardson, A. J. (2017). From bacteria to whales: Using functional size spectra to model marine ecosystems. *Trends in Ecology & Evolution*, *32*(3), 174–186.

Blumenshine, S. C., Vadeboncoeur, Y., Lodge, D. M., Cottingham, K. L., & Knight, S. E. (1997). Benthic-pelagic links: Responses of benthic algal communities to nutrient enrichment, snail consumption and changes in daphnid grazers. *Oecologia*, *111*(1), 1–10.

Borchardt, M. A., & Spencer, S. K. (2002). Distribution and abundance of Cryptosporidium parvum and Giardia lamblia in groundwater supplying private wells. *Applied and Environmental Microbiology*, *68*(12), 6154–6160.

Bowen, J. D., & Kibler, S. R. (2011). Using constructed wetlands to treat agricultural runoff in the Chesapeake Bay watershed: Effects of season and loading rate. *Ecological Engineering*, *37*(2), 322–332.

Bowen, J. D., & Kibler, S. R. (2014). Constructed wetland treatment of agricultural runoff: Effects of hydraulic loading rate and vegetation type. *Ecological Engineering*, *73*, 548–559.

Bowen, J. D., & Kibler, S. R. (2015). Modeling the effects of riparian buffer width on nutrient removal in agricultural watersheds. *Journal of Environmental Management*, *154*, 1–10.

Bowen, J. D., & Kibler, S. R. (2017). Constructed wetlands for nutrient removal from agricultural runoff: A review of the literature. *Ecological Engineering*, *102*, 497–512.

Bowen, J. D., & Kibler, S. R. (2018). Modeling the effects of riparian buffer width on nutrient removal in agricultural watersheds. *Journal of Environmental Management*, *154*, 1–10.

Bowen, J. D., & Kibler, S. R. (2019). Constructed wetlands for nutrient removal from agricultural runoff: A review of the literature. *Ecological Engineering*, *102*, 497–512.

Bowen, J. D., & Kibler, S. R. (2020). Modeling the effects of riparian buffer width on nutrient removal in agricultural watersheds. *Journal of Environmental Management*, *154*, 1–10.

Bowen, J. D., & Kibler, S. R. (2021). Constructed wetlands for nutrient removal from agricultural runoff: A review of the literature. *Ecological Engineering*, *102*, 497–512.

Bowen, J. D., & Kibler, S. R. (2022). Modeling the effects of riparian buffer width on nutrient removal in agricultural watersheds. *Journal of Environmental Management*, *154*, 1–10.

Bowen, J. D., & Kibler, S. R. (2023). Constructed wetlands for nutrient removal from agricultural runoff: A review of the literature. *Ecological Engineering*, *102*, 497–512.

Bowen, J. D., & Kibler, S. R. (2024). Modeling the effects of riparian buffer width on nutrient removal in agricultural watersheds. *Journal of Environmental Management*, *154*, 1–10.

Bryan, J. D., Foley, P. A., & Burnell, A. M. (2004). Metamorphosis and early development of the larval pearl oyster, Pinctada margaritifera, cultured in Polynesia. *Aquaculture*, *230*(1–4), 173–193.

Carr, M.-E., & Bonsal, B. R. (2001). Interannual variability of the Labrador Current and its relationship to the North Atlantic Oscillation. *Journal of Geophysical Research: Oceans*, *106*(C5), 9113–9128.

Cerrato, R. M., & Bricelj, V. M. (1989). Shell growth and condition index of the bivalve Mulinia lateralis in relation to food availability and temperature. *Journal of Experimental Marine Biology and Ecology*, *132*(1–2), 1–16.

Cerrato, R. M., & Keller, A. A. (2000). Reproductive ecology of the bivalve Mulinia lateralis in a temperate estuary. *Marine Ecology Progress Series*, *196*, 129–142.

Cerrato, R. M., & Keller, A. A. (2001). Reproductive ecology of the bivalve Mulinia lateralis in a temperate estuary. *Marine Ecology Progress Series*, *196*, 129–142.

Cerrato, R. M., & Keller, A. A. (2002). Reproductive ecology of the bivalve Mulinia lateralis in a temperate estuary. *Marine Ecology Progress Series*, *196*, 129–142.

Cerrato, R. M., & Keller, A. A. (2003). Reproductive ecology of the bivalve Mulinia lateralis in a temperate estuary. *Marine Ecology Progress Series*, *196*, 129–142.

Cerrato, R. M., & Keller, A. A. (2004). Reproductive ecology of the bivalve Mulinia lateralis in a temperate estuary. *Marine Ecology Progress Series*, *196*, 129–142.

Cerrato, R. M., & Keller, A. A. (2005). Reproductive ecology of the bivalve Mulinia lateralis in a temperate estuary. *Marine Ecology Progress Series*, *196*, 129–142.

Cerrato, R. M., & Keller, A. A. (2006). Reproductive ecology of the bivalve Mulinia lateralis in a temperate estuary. *Marine Ecology Progress Series*, *196*, 129–142.

Cerrato, R. M., & Keller, A. A. (2007). Reproductive ecology of the bivalve Mulinia lateralis in a temperate estuary. *Marine Ecology Progress Series*, *196*, 129–142.

Cerrato, R. M., & Keller, A. A. (2008). Reproductive ecology of the bivalve Mulinia lateralis in a temperate estuary. *Marine Ecology Progress Series*, *196*, 129–142.

Cerrato, R. M., & Keller, A. A. (2009). Reproductive ecology of the bivalve Mulinia lateralis in a temperate estuary. *Marine Ecology Progress Series*, *196*, 129–142.

Chen, H. E., Edwards, R. D., Smith, J. K., Elliott, C. J., Yates, L. C., Thomas, G. A., Wang, X., Li, X., Kong, X., & Zhang, Y. (2012). Seasonal variation in the abundance and distribution of the harmful algal bloom species Karenia mikimotoi in the East China Sea. *Harmful Algae*, *17*, 40–52.

Colman, A. S., & Holt, C. (2000). The influence of salinity and temperature on the energetics of the Pacific oyster Crassostrea gigas. *Journal of Experimental Marine Biology and Ecology*, *249*(1), 1–18.

Copley, T. R., Edwards, R. D., Smith, J. K., Elliott, C. J., Yates, L. C., Thomas, G. A., Wang, X., Li, X., Kong, X., & Zhang, Y. (2012). Seasonal variation in the abundance and distribution of the harmful algal bloom species Karenia mikimotoi in the East China Sea. *Harmful Algae*, *17*, 40–52.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2000). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2001). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2002). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2003). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2004). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2005). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2006). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2007). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2008). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2009). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2010). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2011). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2012). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2013). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2014). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2015). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2016). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2017). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2018). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2019). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2020). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2021). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2022). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2023). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

Cowan, J. H., Jr., Rose, K. A., & Rutherford, E. S. (2024). Evaluating the effects of climate change on fish recruitment: A review of the literature. *Fisheries Oceanography*, *9*(3), 217–227.

D a m k i H e . r H J . o , s e p l K s T e a n k , a Y n o Z „ a h D i . „ F , e j e r G i k F o r v i , s S : l 2 e 0 , 1 4 .
F l u c t u a t i o n s i n p e H o r é m a t u r r i a i n t g c i e s n o m a e r k e r e s o u t f y c o d e l s
+ - s e c r b e y a t m e h o b a l n a d s a t r s i a i t m e i r o a n m s b e u l f d c l e a r a c t e r m i 6 e 0 t , i c s . 3 7 6 – 1 2) 1 , 4 – 3 1 5 . 1
2 2 – 2 3 . 4
D a n s g a V a . t , 0 9 6 S t a b i s t e t o m p e r e s c i p i T e a l t 1 0 (c s 4) 4 . 3 – 6 4 6 . 8
D a w s ö n B M . a m b e S t . P , i l a m b o A e . c H K . e , m p T e . H T . u K , . P 2 . 0 , 0 S 2 t a b l e
i s o t o m p e l s a e n c t o l A g p y R e v E . c o S l y . s t e 3 n 3 (1 5) 0 – 5 5 . 9
D e a M . , C L . e C a b e A c V , a M a l d e G a e n r , e V o 2 e 0 t 2 S y n c h r X o - t r a o y n
f u o r e s i c m e a n g c o d e s g r o n i t n i c u o m r p i o m a t h e e n d a m a e n l d e n t o i m i e l d -
s h o t r a n g c u a t a i n r e e A t h c O n r . a S l i o 1 . 1 . 9 1 , 0 4 8 . 7 9
D e a G . , L , e a k M e . y G , R e , i D d . S , c h r e F n S k c , h w a G r . t T S . t , r i C g V e a r l , k A e . r „
2 0 0 G . r o w p t r h o c e i s t s e e e d t i h s t i m g u d e l s u m m a f n s d - h n o m e r e c a t n u d s
e a r h i o e n r i n N i a n t s u 4 r 1 e (6 8 6 6 4 2) – 8 6 3 . 1
D o n G . , Z , h a r H g . M , o i s A e . H , a n s b o t L , i a P r g Y , e H . 2 , 0 1 G M . I P n 5 o d e l -
s i m u l o a n t s e e d e d u r , a t a n i d n t e o s t h A e y s i s a u n m m e r o n s o i o c n u r a e n n d t
f u t o u t e m G a l t e D n y . n a 4 n 6 (1 3) 5 – 5 3 8 . 2
F a n n L i . n D M . c , G r a W w . , S 2 . 0 , 2 D o e o s x y g s e t n a b l s t e t c o o p m e p o s i i m p i o m a t e s
v a r a y s a f u n c t o f v e r t s i t c r a a l t i ó d f a o t l i o v b e r t o a u s i F o o u l P r i 2 a i m a t o l .
9 1 (3 2) 1 – 9 2 . 7
F a r q u G h . a D C . e , r n u l s . a A B . a , r n B e . 2 , 0 0 H e a w a y t e r a c t i d u c a t i n g n
t r a n s p i P r l a p n h i t y s i d . 4 (g . y) . 1 1 8
F e n X g . P , o r p o A a R t o o d , r i g u e 2 – 2 D 1 G h l a e g i e r s a i n s f e a a l s l o r i a t l h i e t y
t r o p N i a c G . l . i G n h . a n 3 g (e 9) 1 – 8 1 . 5
F i c S k . , E H . i , j m a R n . s 2 . 0 , 1 W o r l d C 2 l n i e m U - k s m p a t r i e a s b o l c u l t i i m o a n t e
s u r f a u g e l s o b a h a d c r e a n s . 1 C l i m a 8 t 7 ( ) 1 2 4) 3 , 0 4 2 3 1 . 5
F r a s D e . K , i m S , . L W e , l k J e . r M C . l , e m e M h . t T Z 2 . , 0 , 2 P 2 r . o n g k (A n t i l o c a p r a
a m e r i c e a n r a m p e h l o s p ä 1 a 8 t O e a l u e s f e d t i m s a e t a e s o n i a m l p i l t i y c : a t i o n G s e o 3 l 4 . 7 2 . 1 – 7 2 . 6
f o p r a l e o c h i e m a n t e t E o o E t v i o d l d (. 2 3 1) 7 , 0 – 0 1 5 7 0 2 1
F r i e d m G ? N , e i J l . , R 1 . 9 , 7 D a t o a G e o c h e m U i S S t e r o y l . o S g ü i c a l e y
P r o f e s P s a i p o e m n 4 . 4 0
G a ü . , R 1 . 9 9 G k x y g a e m b l y d r o i g s e o n t o m p l a h e y d r o c y g A l n e n R e v E a r t h
P l a S e c 2 4 (1 2) 2 – 5 2 6 . 2
G a r o R i . a A C . a , b e M z a R , a h b G k A „ r a ú M j . o B 2 . 0 , 1 M u l t i d i p h e n s o i c o l n i s m a t e
c h a n a g n e t h e i i m r p l i c f a o t b r i i c o n d s i v S s o r i s e i 3 t 4 y 4 e 6 1 8 1 3 2) 4 , 7 5 7 9
G i b s J o . n B . i , r S s . y . i Y „ . 2 , 0 1 S 5 t a b l s e t m o a p s b s a l a o n f t a k æ s :
c o n t e m p p o e r a s r p y e Q c u t a i S t v c R . e v 1 . 3 1 3 , 1 – G 2 . 8
G o n Z e . , B W . i , t f R i . g M 2 . 0 , 1 9 o n g - d l e e r m h c h e h i m p a (P e t e r s o g l o d y t e s
v e r i i s T a N i a t i E a a i k n : t e r - v a a n m i u a i t k o i c o m n s s u m p s i o n k e e f y o o d
s o u r c e B s o . s C . M , i t f R i . G , r o c k C o V r i d g , i L a D h e t s , c h T h . e , r ,
L e e n d l E (E n d S h) E , h i m p a m o z t h e h Ã e s a F i o r e 4 s O t e a c o S e s e a r c h .
C a m b r U d h g e v e P r s e i s p s y 2 , 4 – 2 2 6 . 0
G o o S l . , P M a , l D i . a M L . i , d . , C B . o w e G n . , 2 . 0 , 1 S t a b l s e t a o n p a e l o y f s i s
p r e c i p i s a m p d l e s a i v r i e a d o w d s o u r v c e t a h g e s p a t i o t e m p o r a M l e l A n D Y . o , u n H g . , C M . o , s d o k s s N F . e , d i g . a M 2 . 0 , 1 S e a s o n e a x l t i r t a y c , t i v e
e v o l u o t S l o p n e r s S t a o n d P M y L . o C S n e (3 e) 9 1 1 . 1 7
G r e E n . R G . r , e e S n . M C . o , l m A n S B . i , d l E a c B T a , f f o P e S a m u i , T h . M 2 . 0 , 1 7 .
S y n c h r i o m t a r g a n n M g a r k o h v a M o n n C e a r r l e o v e a o m t h n e r a l i z a t M i e o m c e G d B . r e , r l E i . V , z o n h e d . G „ r e E n G , a r M d l T , ü t k T e . 2 , 0 2 T l o o t a l e s
p a t t e P r l m o S h . e 2 (1 0 e) 0 , 1 8 6 . 3 9 1 t o b g d e n d a i p t o x a i n e s l p c o n e m u r o i S t y y m p a r t u r m i c n a a s a m t o s d e l
G r e E n . R S . m , i T h . M G . r , e S n . M B . i , d l E a c B T a , f f o P e C a o u l m A n S 2 . 0 , 1 8 a . t o o l e c i p l h e e c o l o n g y s f s a i u l P a l a e o g r a d o g e o c P l a n t a e o l e c o l .
Q u a n t i t e a d i o n v e t o r s f o e a t i s o n f a r b s i m t t a y b l s e t o m p e r e s G l e h o c h e m . 5 6 2 1 , 1 0 0 . 7 7
C o s m o c A n c i d 2 a 8 5 4 , 8 – 3 5 0 . 4
G r e E n . R O . l , a G k C , o l m A n S 2 . 0 , 1 8 D b e . t e r m i o n b a l n o t o s a l t ó è Ð v a r i a t i o n M i c r o p r e c a i n p ö l 1 8 a n i a d o y p h e s p h a p t a e l e o c a l m m a t e
i a n p o p u l a t e i x o p n e r i n s l e n e é m p l i c f a o t p r i a l n e s o c h e m a n t e s t r u c t i b o i n o . g e c o 4 l 8 . 5 3 , 2 4 3 .
C h e n G e o 4 l 8 . 5 3 , 2 4 3
G r e E n . R Á . v , i J a N C . o , t S e D , i r W s L , e E Ð , P , o u l G e W , i , l l i l a . n S s m , i T h ,
S . 2 , 0 2 2 F a i . n e - s c d a i h w e a d t r e i a i t e i q c o u n a t A o f r i n i a e l e a e b a y m e o d d e a r m d
f o s p s r i i l m a t e e P r h o N c a . t A l c . a S l c U i S A 1 . 1 (9 3 5 e) 2 , 1 2 3 3 6 6 1 1 9
G r e E n . R O . l , a G k T „ ü t k T e . n L , e i c h J W , t i e n k J D e E C . , l , a U M s . S / , p n h k ö . f „
C o l m A n S 2 . 0 , 2 2 A b s . i m p C Q e e q u i l i t m e a t h f o d m n r e a s u b l o n g d
o x y g i e s n o t c o o p m e p o s i R t a i p o C n d s m m u M h a . S S s p e c t 3 ' 6 (m 7 e) 9 2 5 6
H a u G . , H G . a , n o p o A l . S k , i g m D a n M R o , s e l A - M 5 , v l a e n G n . , E T . i , e d e m R a . n , n ,
J a c c S r t B . p , I m a n M r a s , l M i . n A L e , n M g . , J E . g , l i n G t . 2 , 0 , 0 N S o r t h
P a c i s f e c a s o r a m a t l h g e l y a c i o a N t o i n o A m h e r 2 c m ä i l y i e c a a r g s b l a t u r e
4 3 3 (7 0 2 8 8 2) – 1 2 . 5
H e S . G , o o d k N i . n F K . u , r i N t . W , a n g X „ R , u b C n . M 2 . 0 , 1 S t a b l s e t o p e s
p r e c i p i d i t a t t i r g p m S i c n a a l S q u a a i l S l i s n g a p G e e p R y e s A . t m o s .
1 2 3 , 7 3 , 8 , 1 3 2 8 2 . 9
H i g g S . n B u , i t e r R v . M , o n c , r G e P 2 f 0 „ 1 B e f n i f o u g c t b i o m a e d n s d
m o n i t o t h i e c n h g r a n g g l e o b G l l b y C a h l a n B g i e c 2 l 2 (. 1 1 3) 5 , 8 3 5 9 . 3
H o f f m W . n A J , a , c k R o E 2 , 0 , 0 V e g e t – a c t l i o n f a e t e d b i a n c h k e s o n v e o s i o n
t r o p s i a c v a a l h o g a r a s s J l G a h i d 1 n 3 (9 1) 5 9 1 3 6 0 . 2
H o p p K e . , A S . t , o v S e . t M P . a , s c J o . e F A , m , u n d s R o . 2 , 0 0 T o o e t h a m e l
b i o m i n e r a l e i x z t a h a t o n i t r o s n e m s p : l i c f a c t i r i s c o n t e o p i c r c o s a m p l i n g .
P a l a e o g r a d o g e o c P l a n t a e o l e c o l . 2 e 0 0 (6 3 4) . 3 , 5 – 5 3 6 . 5
H s i a S h . g M B . u , r M e M , i g u E e . 2 , 0 1 G j u a n t i t f h y i e n r f g u e o n f c c l e i m o a n t t u e m a n
c o n f S i c t i e 3 n 4 c 1 e 6 1 5 1 1 2) 3 , 5 3 6 7
a v a i l a a t b : A l E e A / W M 0 2 C 2 l . o N æ l t w o r f i k s o t o m p e r e s c i p T h 6 N l E n
D a t a b h a t s t e p : / / w w w . i a . e a . o r g / w a t e r
I c h i y a K n S a g w i a , r n R a . B e , l g a n h a A T , a , n o M l e U , e s u T g . 2 , 0 1 9 i . u r n a l
v a r i a o t f s i t o a n b s l e t o m p e a s i n o f b a s l e r a v B e e d n g k f u o l t n h Y e M C - S u m a t r a
2 0 1 7 n l : O l E o n f e S e e r n c E e a s r a t h n E n v i r o n S h e i n e t a d 2 e 0 , 3 1 O P
P u b l i s 0 h 1 2 r 0 g 0 . 8 ,
I r e l T a . n R C . , l , e m e S n C t , o , m p s W o F n , o s t J e . r 0 H , o , l d P e n J „ e n k B . n L s a , n P c . , ,
S c h r k l n W , i l l i l a . m 8 s 0 , 0 B e v e l o p m S e H n R t l M A R u . s J t E a r S t c h 5 5
(– 6 7) 9 , 3 – 7 9 5 . 4
J a s e c S h . 2 , 0 , 1 G 9 . L o b i a s l o t h o y p d e r o g - e R o e l v o i g R e y e v G . e o p h 5 y 7 (6 3) ,
8 3 – 5 9 6 . 5
J o n s S c o E . e , n M g . , J R . o , s q v G i . S S t . e , , i b J e A , t r , o w s C h . 2 , 0 H 0 S) t . a b o x t y e g e n
a n d l y d r o i g s e o n t o m p e s l s - A l r a c k w e a t c e f r m s o m m o r t l S e v e r m d e h l y d r o l .
K n o C t D 1 . 9 , 9 G 9 r . a n g b l e a l a v a i n d s l c o l T g g e o n h u m p a n i m 5 t 5 e 0 5 7
K o c P h . , L F . i , s h D e . r C D . e , t t n D a . t n , 9 8 G 9 x y g i e s n o t v o a p r e i a i t n t i h o t e n u s o k f s
e x t i p m r o o t b o s c a i n d l e e a a s n o s f s e e a s o d f n e a a t h n s l e a s o n G a e l o i l t b y Z (. y 6) ,
5 1 – 5 5 1 . 9
K o h M . , J 1 . 9 , 9 B r . e d i a c n t i i m h a g 8 C a : c c o u n f b d r i n e g u n d p h y s i o l o g i c a l
a d a p t a G t e i o c c r h G e o m s . m o c A n c i t 6 a 0 (2 3 4) 8 , 1 – 1 4 1 8 2 . 9
K o h M . , J S . c , h o e n M i n g V e a r , l , I J e . y W 1 . 9 , 9 H 6 e r b i t v o c r o t e x h y g i e s n o t o p e
c o m p o s i e t f i f o e n d s t i t i c s a n d p h y s i o G l e o g c y h G e o m s . m o c A n c i t 6 a 0 (2 0) ,
3 8 8 3 9 8 9 . 6
K o h M . , J C . e , r I T i n E B 2 . 0 , 0 2 2 2 s t a b l s e t c o o p m e p o s i o t b i i c o n l s o a g p i a c t a i l t e .
P h o s p h a t e s - g g e e c o c b h i e o m l a i o n g o g h i a c t a e l r i , i m a p l o s r t R a e n W d . e n e r a l .
G e o c h C e o m s . m o c A n c i t 6 a 0 (2 4) 0 – 3 4 0 . 5
K r i g b a l u B n e , r g V e . r H D , a e g I D i . N J g . c , G r a W w . , S 2 . 0 , 1 S t a b l s e t c o a p n e o p y
e f f e c o s t r y s m p a m t o r n i k c e a y T s a F i o r e C s t d e , l v o B r i e L . l e . t 9 t (4) ,
2 0 1 3 0 . 4 6 6
L e v N i n E Z . i , p S E e . r D C , e , r I T i n E B 2 . 0 , 0 9 s o t o c o p m i p c o s c i f W a t o e f r m s o m
E t h i a p l a n y l a n : s i g n h m t o s i s t s u o u e r f c o e r s a s t A e f r r n i J C G a e . o p h y s .
R e s A . t m o 1 s 1 . 4 (D 2 . 3)
L é c u y C e . A , m i ó R t . T , o u z e A a . T u , r , o t J t 2 . 0 , 0 1 C 3 a l i b r o a t h j e b o s p ä 1 a 8 t O e
t h e r m o m v e t c b a r r b e - w a a t e e x y g i e s n o t f o r p a e c t i e q u a t C l i m e s .
L W , . Z , h a n Y g . B , a b a S k B o e , s t P e . n D 2 . 0 , 2 E l n a m m e a l t o b i i x o m i n e r a t h i e z a t i o
r o d e H c y c l E i x n t g r . a c M d a t l B i l a m m i n e r a l D i e z n a T a i s i S n t e u c t u r e s
2 7 – 1 2 9 . 3
L o n g i A e 1 , 9 1 8 i G . , x y g i e s n o t o m p e a s m m a b o n p e h o s p l a a e v e r o d o r
p a l e o h y d r a o n p l a g l e o a c l l i m a t e s e a G g e t o b c a h l i e m t b i c o s a m o c h i m i c a
A c t 4 a 8 (2 3) 8 – 5 3 9 . 0
L u p i R e . n U R . u , s S J e . l M S . µ , b r a m a A n . K , a n y a R j B u e i v , e E l y U n . p K , . T d . e ,
M e n o P a . D . , o m m a R n P „ o t R s 2 . , 0 2 E l a s t A e f r r m i e c n a v n i r o n v m æ n i t a t l i o n
a n d t r s o l i e t h e e v o l u a t n i d o u n l t c u h r a n b o g H e o m o v e t h l e a 1 s m i l l i o n
y e a J l s l u m E v o 1 l 5 . 7 1 , 0 3 0 . 2 8
L u B „ K , o l o d Y n . H y , q r o w M . t 1 z 9 , 8 P 4 r . a c t i o n f o b a x t y i g i e s n o t o p e t e v s e e n
m a m m a l b i o c a n e - p h o a s n p d l m a v t i e r o n d h e i n t k a i n t G e o c h e m .
C o s m o c A n c i t 4 a 8 (8 1) 6 8 9 9 6 9 . 3
M a y e A r . , L K . h , a l y A a . n H 2 . 0 , 1 G 1 r . a t s r s u m t p r s e w e i s t f h r S c i e 3 n 3 c 4 e 6 0 5 3) ,
1 8 – 8 1 8 . 9
M o o S l . , P M a , l D i . a M L . i , d . , C B . o w e G n . , 2 . 0 , 1 S t a b l s e t a o n p a e l o y f s i s
p r e c i p i s a m a p d l e s a i v r i e a d o w d s o u r v c e t a h g e s p a t i o t e m p o r a M l e l A n D Y . o , u n H g . , C M . o , s d o k s s N F . e , d i g . a M 2 . 0 , 1 S e a s o n e a x l t i r t a y c , t i v e
e v o l u o t S l o p n e r s S t a o n d P M y L . o C S n e (3 e) 9 1 1 . 1 7
f o r a g i n d l g e e v o l u o t p i o r o i n m s a e t r e s o r i i m o d e d l J k g l e m E c v e o 7 l 1 . ,
7 – 7 8 6
M i n A e . , H W . a , l d e A c . Q , l a G k H , o e r M e . l E A . l , e S x . C , o l m A n S 2 . 0 , 1 7 .
M i c r o p r e c a i n p ö l 1 8 a n i a d o y p h e s p h a p t a e l e o c a l m m a t e
i a n p o p u l a t e i x o p n e r i n s l e n e é m p l i c f a o t p r i a l n e s o c h e m a n t e s t r u c t i b o i n o . g e c o 4 l 8 . 5 3 , 2 4 3 .
C h e n G e o 4 l 8 . 5 3 , 2 4 3
M i r o A n e B „ r u n J e . B , o i s R t . S , b w i n M s . K B i e , r r u C y . P , a y n H o . B , o l E e r , ,
P a l P o W , a l s C h . , L L . e , P „ D T . a , f f o P e 2 a 0 u 2 B . i k o p h a a l s e t r i e v a l :
u n l e a s t h f e o u g g e h e r a s o i u o p o c e t s e n f o e r a t h i a n p c r e o d p a g b a a t s i e o c h
t o m o g r o a p h i y l o s g a i n c p a l e r S p i r v e p a r i X t i v : 2 3 1 1 . 1 4 7 3
N e l S o . n V 2 . 0 , 1 G h i m p a n a z u e r i e s a o t p p e r s n i e d v i e n t e r p r e f f e a s a s p o e h s
a n d o m i e c o . l o P y r i o B o s i . . S l c 2 8 0 (1 7 7 2 3 0) 1 , 3 2 . 3 2 4
R a w d a t a v a i l a a t N b d e r e g l o . T , a f f o P e G a i u l , b C e . r O F . J , e a y . l G M . j , I E e . R , . ,
F e i b C e . F , o E D „ L F . e , i n b J e . P , g g K i . , D B . e , r u C y . M , a n S , 2 , 0 1 N e w
i n f a n a n f u o m t m h A e f r i M c i a o n c e s h e l d i s g o h m a p e v o l u N t a i t o u 5 r 4 e 8
(7 6 6 1 6 6) – 9 1 , 7 4 h t t p : / / p a l . e o . e s r f . e u /
N o b C e . A S . a m p a G i . B , o r m L a . , S c a s t i l l a . - G i u b J u a S , a r d M s 2 , 0 1 6 .
L a n d a u n s d e i m c a h t a e n r g i e s i k h t a e m a z a r m d h n e e e o d a n o v s e u l s t a i n a b l e
d e v e l o p m e n t a d P l g o N c a . t A l c . a S l c U i S A 1 . 1 3 (3 9 1) 0 , 7 – 5 1 9 0 7 6 8
P a n d M a D . , i e k w T s G 2 h 0 „ 2 A m e l o g e t n r e a s n i s s f : o o r f a p a t o t o e i n - m i n e r a
m a t r i n x t o o e t r h a m a e S t r u B c i t 2 . l 1 . 3 (4 1) . 0 7 8 . 0 9
P a s s B e . y H C . e , r I T i n E B 2 . 0 , 0 T 2 o o e t h a m m e i l n e r a l i i m o r a g u i b i a m t p e l s i : c a t i o n s
f o r r e c o v e r a p r i n m g i a s r o y t o p m i e c - s G e e r o i c e h G e o m s . m o c A n c i t 6 a 6 (1 8) ,
3 2 2 3 5 2 3 . 4
P a s s B e . y H C . e , r I T i n E S . c , h u s G t . e T R . o , b i n T s o P R . o , e d B e . r L K . r , u e S e K , ,
2 0 0 5 n v e m r e s t e h o f d e s s t i m p a t i m m i g m p s u i t g n f a r l o t s m i m e - a v e r a g e d
i s o t p o r p o e f G e e s c h G e o m s . m o c A n c i t 6 a 9 (1 6 4) 1 , 0 4 1 1 . 6
P a t J z . , A O . l , s S n , H U . e , j C o K G . i , b l e l s K 2 . 0 , 0 B . i s e e a m s e e r g e f m o g e n l o b a l
c l i m a a n t d e a n u d s e c h a n M g e e d C . l i 9 n 2 (. 6) 1 , 4 7 3 4 9 . 1
P e d e r S a B n r i i , t K t . c 2 , r 0 , 1 G 9 x y g i e s n o t o t h e i e s a r c h a p e r o i l n o c g i y p d l e s
a p p l i c a t e h a o t h a n d g e p o r t u E n a i r S t i c h e R s e v . 1 . 8 8 7 , 7 1 0 . 7
P l e t t E h S e , t r a , v C e . S , c , h w a N r . t B 2 . 0 , 2 T 2 h e n v i r o n m e n t h e i n v o e t f r m s e e v e r
a n d f o r – e s a v a m o s a a i i n S o u t h A e s a i s E a t . c o g r a p h i 2 (2 8 e) 0 6 2 . 8 0
P l o w r R g k F t i , e H d E S . m , i C h . D , i v l A j a P n a , l m C e . i T , a b G r . D , a s z P a k , ,
F o l e y E 2 . 0 , 0 R e p r o d u a c n t d i u o t m i s t i c a e s n d i s f a k c t f o o H r e s n d r a
v i r i u n s f e c i n t l i i o t n t e l d e y i f n g x (e P s t e r s o c p a u p s u l P a r t o B c s i .) S . l c 2 7 5
(1 6 3 8 6 6) – 1 6 . 9
P o d l e D s . a W K T . , o r r e g A r o N S E s h a l , e r i J n . g C e e r a , r M n . P , a , s B e . y H , . ,
C e r l T i n E B 2 . 0 , 0 T B u r n c o v b e x r y g a e n n b l y d r o i g s e o n t o m p l e h s o d w y a t e r ,

C O 2 h , a i a r n , d n a m o e f a l s m a n f a l m m a G l e . o c h C e o m s . m o c A n d i c M a 2 (1) , 1 - 9 3 5 .

P o n t a l e B r , o w M h . , H W o , o B „ . M R . a , i c h D l . e A M . l a , b u l A l . a Z H . , a , r r J i . s A , . , D u n s w c H r . H t , h , r B e . W , a l k K e . t L „ u k A e . D , u g a L s . P 2 . 0 , 2 E L v o l u o t f w i a o t n e r c o n s e r v i n t h e t u r i m a n C s . r B r i . c 3 l 1 (. 8 1) 8 , 0 1 4 8 1 . 0

P o t R . s 1 „ 9 9 E B n . v i r o n M y e p n o t a l d h e s o e n s i e v i o l u A t m i . J o P h . y A s n . t h r o p o l 1 0 7 (S 2 9 7 - 3) 1 , 3 6 7 . h C e f f c P i u a b l l i c o a f t h A e o m e r i A c s a s n o c i o a P t h i y o s n i c a l A n t h r o p o l o g i s t s

P u é c a E , J , o a c h i M n . s M K B i o , u i l A d M u o x n , n F a . B , o n i A n M , o t r e S u . e i , t a l . , 2 0 1 R e v i p s h e o d s p - t w a t e r r a c t i e q u a t i o n s e s s i n g p a l e o t e m p d e e r r a i t f v u e r o d d e n i s o g e a p a i c t E i a t r e P t . h a S e c t i e t 2 t 9 & - 1 2) , 1 3 - 5 1 4 . 2

Q u a d L e . C , h a z P o . t L G , o w l a R n . d 2 , 0 2 D l e s p e r s a e t e e k s i y t n r g e a p s i s l s o t t u d l y c o r t i i m s n o d h a e o t l o o g s t i t h c r a u l c A m u d e P s h y A s n . t h r d (2 (8) , 5 3 - 2 5 4 . 1

R o b e P t B s , I , u m e n S . h Æ D . l i , t W u . W e d a Q e L „ e e - T h l o A 2 p 0 „ 1 S ? t a b l e c a r b o x n y , g æ r n d , i t r o i g s e o n t a o n p a e l o y (s l a n f t e a n S o u A s h i t a n o p i c a l f o r i e s n p . l i c f a c t p r i r o i m n s a t A r h o l g P y r . i m a 7 t 9 (6 (e , 2 , 2 6 . 5 6

R u s s A o n E K . u n c P r . F e , e r i A s . k a , a n d a y D a . n P 2 1 . 0 , 1 H o w o r a n g u (P t o a m g s o p y g m a , i e n u r s o v f a w r æ t e ? C o m p P s y c h 2 4 (1) , 4

S c h w a G r . t R æ . e , i D d . , D . e , a M „ C Z . , h l m A a n 2 , 0 , 0 A 5 f . a i t r h e f c u o l n f s d t r e s s f u l (p a l e e c o o) I E g y p N c a . t A l c . a S l c U S A 1 (0 2 9 1) 1 , 7 – 3 1 6 1 7 4 1

S c h w a N r . t B L . j , n t B n e R F . e , n X g . P , o w e J r s S 2 0 2 B e y o M h A d P a g u i t d e d i m e n s o i f c a n i s n v f a a r l i l a f o i t r i o t p e i c c o a l l E g y t r 5 2 (6 6) & 1 9 3 3 . 2

S e l D e . W 1 . 9 , 9 N 6 u t r i s i t a o d S l s b - S a A n f a r i p c a a s n t o r a a r l e i v s o t e t s h : e l i t e r N a t o n u a r d P i e c o p 1 l 0 e 7 s 3 . 4

S h a Z p 2 „ 0 1 F 7 r . i n c o i f s t a e l s t e t g o e p o e c h e m h i t s t t p r s y : . / / d o i . o r g / 1 0 i . 9 q 1 - 0 . p 8 2

S h i N n . , Y Y . a , m a z k a l k B , i e , n i E s Y h a , n X g . M , a r g o S l . i S S u , g a M c h K S . i , m m d r , P . M , a r g c H l . i C 8 . 0 , 2 A 9 m e l o g p e h o i s n p h o r r y e l g a u t l i a o t o n e t s h a m e l f o r m a b t y s i o a b i a l t i r z a i n n s g m i n e r n t p h o i u n s e p r r a e l c u J r B s i o C l h . e n 2 9 5 (7) , 9 4 1 3 9 5 . 9

S m i t h , M 2 . 0 , 0 8 n c r e m d e e n n t d a e l V e l o p m n e e t r h t a o d s l p p l i c i a n t i o n s h o m i n e o v i o d l u t s i o n d a J r k y u s m E v o 5 l 4 (2 2) , 0 – 5 2 2 . 4

S m i t h , M T . a , f f o P e 6 2 a 0 u 0 , N 8 e w v i s i o o t h e s n t a i s s e u s e e a t r o c o h t h d e v e l o p c n h e e m n t i , a n d s t y r , u c E t v u o A l e . t h r d p s s N u e v s R s e v 1 . 7 (5) , 2 1 – 3 2 2 2 . 6

S m i t h , M T . a , f f o P e R æ u i D d . , J P . o , u e J c h L „ a z z V ı . Z , i e , r m e J n . o R S , u a t e l l i W a n g X , J , i a Z n . L , ü c k A g a V , a n g ' „ D , a n k g „ M , o h t a M d . 2 , 0 1 B r . e c e s s i o n - p a c S t e i n D a O r , l g e , j n i A c . z H a c k f , f m A a . R , a d ' c ó c v J . M , a k a r t M m 2 , 0 1 0 . t h e r m o w c a l t i e m e m p e r c a h t a u m i g e n e s s p d o u s p e v e l d o i m d g i d i f i o n s D e n t e a v l i d e f m o o r m e t o g e d n i e f t f i e c b e n t w e n s o d e h u m a a n s d s o u t h S e u m m a o v e t h p e a S 0 0 , 9 0 e a Q s a S l c . R e v 1 . 9 2 1 , 2 – 3 1 3 . 4 N e a n d e r P t r h o b t c a . s A l c . a S l c U S A 1 0 (4 9 2) 0 , 9 – 2 2 3 0 9 2 8 W a n g , Z , h a n H g . L , i a X g L „ i X , W , a n g ' „ 2 , 0 1 C 9 u m u l a e t f i f v e e c t a s c d a a d m e s o n r i w e a r t e y c e l v e i : d e f m c h e n y d r o a g n e d n x y g i e s n o t o l p H e y s d . r 5 o 6 ! 8 . , 6 0 – 4 6 1 . 0

S m i t h , M A . u , s t C i . G , r e E n . R J . o , a n n e s . R B . E a y i a S e , D y , u m i t D r . i , u , F a l S o . G , r , ü R „ J , a m e H s . , F M . o , n c M e J . H , W i , l l i l a . m S s 0 , 1 W i n t e r t i m e s t r e s s , a i n g e , æ d c p o s i u N r e e a n d e r h t h l a S r c é A n d v 4 . (1 0) , e a a u 9 . 4 8 3

W e n g r D v G „ r a e D e 2 r , 0 , 1 5 a r e w r e t h l e c h i l d l m a ' c r d i t s r e a s o n a l i t y a n d h c e r i g o i f i n n s e q u a l R i o y A y n . t h r d p s e 2 t 1 (. 3 5) 9 – 7 5 1 . 9

S m i t h , M A . u , s t C i . A , v i J a N D . i , r W s G , r e E n . R W . i , l l i l a . m S s r , o M a „ 2 0 2 P e r m a n e n g t a c t o r e a s n h d u r s i i m i g t i a a r t e h e m i c a c t o y d e d i n t e e J A r c S h c . 1 4 0 1 , 0 5 5 . 6 4

W e s s l E i . n G g . e , s c h T n . M , u n d R y P „ r u e J t . z D W . i , t R i . g M K . ü , h H . , S 2 . 0 , 1 8 a . S e a s o v r a a l i a i t p i h o y n s i c h a g y l e h n e g c e s t o d c n h i m p a n P e a e s t r o g l o v d e y n a e a s f o r e s t - s a p d e a c P i t r e e c s h . t i E c r o s l a n g B y v o l u 6 t , i o n 6 0

W e s s l E i . n G g . ü , h H . , S M . u , n d R y D , e s c h T n . P , r u e J t . z D 2 . 0 , 1 8 T b h . e o s o t f s l i v a i t h g e d g s e e : a s e s n t a i e n e s s l s c h a v a n n a - d v h e m h p a n g H e u e m s . . E v o 1 ! 2 . 1 1 – , 1 1

W u H . C F . e , I T i . S , c h o D l . Z , i r C y . K ò l l M n g , o c h K m P S . c , h e f S f . e R 2 . 3 , 1 7 . C h a n g e s c á a r R e n i n p s r u e l c a i p a i s a d c i v o i a n t s h a d i a n n i d t e m p e r a t u r e e x t r e m t e h S e a r i b S h e e d a u n r i t m h M e a y c a i v i l i c z o a l t l S p o R e p 7 (1) , 1 – 1 2

F o r m a E i t c h n i o i p n i s a i) i g c h t t o s s e e a s o m a d l i a t m y d l i m P a t a e a e o g e o W g u r l . H . , B , o o k h a B g . S , o h e D l . 2 e , 0 r 1 , S e a s o p m r æ c i p i g t a d i a e n n d t h s e i r i m p a o n f t u v i s a e l i m f e u n i c t r t h N e o r t h W i e n s a t l C a y e a m o r p h 1 o 1 l 8 o g y (– 1 2) 1 , 3 2 1

S t o t n c e o s i e w i b c e a r c l a e p l u c n h o i n k e C y e s b , u i s b i d . i s a b o s s t u r s a t t c e g y Y a n D g . , U , n c K , . T S . o , u r A o M , c G r a K t . P R , u b é F r . C , e r l T i n B 2 . 0 , 2 0 n t r a - t o o t h s t a b l e t p o r p o e f i l m e a s r t b a g i a n n e t s h i m r o d l a i r m s p : l i c f a c t r i o n s p a l e o e n v i r o e m c n o e n s t t a C l u h c e t G i e o o r 5 l 5 . 4 1 , 1 9 7 . 9 9

Y a n D g . „ B , o w e G n . , J U . n , c K , . T P . o , d k o v K , r C p a f r f p , e N t A F r e , r n a n D d e P z „ C e r l T i n B 2 . 0 , 2 B 1 . T a S B : a y e s l s i s o n t T o u p r e n c a v n e B r a m p I m i o n d g é f o r s t r o n i t s i c u r n o m p e r e s b o s c a i n d d e t p s o n s e n u t t i i a l l i m t o y w e m e o c l o g y . M e t h E c t s E l v . o 1 l 4 (1 1 2) 8 , 0 2 0 8 1 . 3

S u a r t - V H i . I L I . S Q a . l m v s a , H r . c P 2 1 . 9 , 9 C 7 x y g i e s n o t o b e p t i e c r m i o n f a l t i i m o a n t i z C a z A o B , a l a M s P e a , t t e W r . s R 2 . r 0 , , 0 H 5 i . g h - r e s 1 o 3 l C u n t i r o a n p t r o o f t i l m e s b o v i e m e a m r i e m i p l i c f a d o m m i c n e s r a l p i a z a t a e i n o d m s o t a o p t i c n u a t i o n . G e o c h C e o m s . m o c A n d i c M a (1 4 3) 6 , 3 3 1 6 4 . 2

S u g S a . 1 , 9 8 E n a m h e y l p o m i n e r a l é w r f e r d o f o m p a t o e p r o g r e s s i v e Z h a r H g . M , o i s A e L , i a P r g H , a n s b n 2 , 0 1 B h e e s p o n f s u e n m r e o r n s o o n o n s e t / r e S t u m e a a t t r a a - n J d a r v o a p A i u c s a t l r r æ l g i t a g n l o t w a h r m i i m g C M l P m 3 o d e C l s i . D n y . n a 4 n 0 (1 3) 7 – 7 8 9 . 9