Teeth reveal juvenile diet, health and neurotoxicant exposure retrospectively: What biological rhythms and chemical records tell us

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Abstract
Integrated developmental and elemental information in teeth provide a unique framework for documenting breastfeeding histories, physiological disruptions, and neurotoxicant exposure in humans and our primate relatives, including ancient hominins. Here we detail our method for detecting the consumption of mothers’ milk and exploring health history through the use of laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) mapping of sectioned nonhuman primate teeth. Calcium-normalized barium and lead concentrations in tooth enamel and dentine may reflect milk and formula consumption with minimal modification during subsequent tooth mineralization, particularly in dentine. However, skeletal resorption during severe illness, and bioavailable metals in nonmilk foods, can complicate interpretations of nursing behavior. We show that explorations of the patterning of multiple elements may aid in the distinction of these important etiologies. Targeted studies of skeletal chemistry, gastrointestinal maturation, and the dietary bioavailability of metals are needed to optimize these unique records of human health and behavior.

KEYWORDS
barium, breastfeeding, lead, nursing, strontium, tooth development, tooth mineralization

Abbreviations: Ba, barium; Ca, calcium; EDJ, enamel-dentine junction; GI, gastrointestinal; LA-ICP-MS, laser ablation-inductively coupled plasma-mass spectrometry; M1, first molar; M2, second molar; M3, third molar; Pb, lead; Sr, strontium

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INTRODUCTION

Tooth growth and mineralization: a microscopic archive of developmental information

Teeth are one of the most common anatomical units recovered in forensic, archeological, and paleontological contexts. Studies of their growth and composition play an especially important role in our understanding of ancient human behavior, development, and evolution.\(^1\) Teeth also serve as important records of toxic environmental exposures in living people,\(^5\) perhaps best exemplified by the detection of radioisotopes in American children following atomic testing in the 1950s.\(^9\) In this unprecedented situation, a “Baby Tooth Survey” was launched to assess the amount of a radioactive variant of strontium in children born in St. Louis, Missouri before, during, and after a period of especially heavy nuclear testing in 1953. The study leveraged the fact that strontium behaves similarly to calcium, becoming passively concentrated in mothers’ milk, and ultimately stored in the developing teeth and bone mineral of nursing children. By collecting and analyzing 300,000 “baby” (primary or deciduous) teeth, scientists were able to show that children whose teeth grew prior to 1953 had eight times less radioactive strontium (specifically the atomic variant, or isotope, Sr\(^{90}\)) than those born in 1957. All told, concentrations of Sr\(^{90}\)—a cancer-causing agent—increased by nearly 50 times over 13 years. Recent and on-going environmental crises such as the tragic lead contamination in Flint, Michigan will leave a similar permanent imprint in children reliant on municipal water.\(^1\)

Teeth are especially powerful for documenting early life experiences because enamel and dentine are secreted on a rhythmic basis, locking in precise temporal records that can be mined decades or even millions of years later.\(^1\) Experimental studies have proven that mammalian teeth have microscopic subdaily, daily, and supradaily structures in their hard tissues.\(^2\) These incremental features can be visualized by cutting a tooth lengthwise to expose an internal plane (Figure 1). Analyses of growth lines in well-preserved and well-sectioned teeth may provide estimates of tooth formation timing that is accurate to within a few weeks or, in some cases, days.\(^1\) For these reasons dental hard tissues serve as the body’s best retrospective information source, although thin section preparation and analysis is technical, laborious, and can be prone to error.

You are what you eat, with caveats

Over the past few decades, anthropologists have probed developmental and chemical information from teeth to estimate ancient nursing behavior and age at weaning (defined here as the cessation of suckling), postweaning diets, land-use patterns, and prehistoric climate variation.\(^1\) Technologies advances in imaging modalities and chemical characterization have allowed for recent progress,\(^1\) yet our understanding of ancient human diets, environments, and migrations has not achieved its full potential due to several theoretical and practical challenges. For example, while the increase of overall mineral density during tooth crown formation is well documented through radiographic studies, the timing of when specific elements (and isotopes) are locked into tooth enamel is less certain.\(^1\) Initial elemental secretion may be mixed with or overwritten by later additions, or an element of interest may only be incorporated as part of the maturation process that occurs after the formation of corresponding secretory increments (Box 1)—meaning that the elemental chemistry of incremental features could be asynchronous. This potential complication hinders studies that attempt to relate localized chemical records to growth rates or formation times.

A further complication stems from the fact that the chemical makeup of tooth crowns and roots may derive from one or more sources during childhood. Initial inputs come via the placenta and mothers’ milk, which includes elements stored in her own skeletal reserves. For example, 7%–39% of lead in the fetal skeleton of macaque monkeys may be derived from the maternal skeleton.\(^2\) Additional elemental sources in teeth include nonmilk liquids, solid foods, environmental dust, soil, and inhaled vapors.\(^2\) When relating tooth chemistry to nursing behavior, nonmilk dietary inputs, and health, it is ideal to know: 1) how effectively specific elements are absorbed during digestion; 2) whether elements are selectively filtered out...
FIGURE 1  Upper (maxillary) molar from a captive rhesus macaque (Macaca mulatta) shown from (A) front/mesial view and (B) top/occlusal view. White dotted line indicates the position of the cutting plane used to create the thin section in d). (C) Close up of birth line (white arrows) in the enamel. (D) Thin section used for developmental and chemical analysis,[18] showing the approximate position of enlarged/magnified images in C, E, and F. (E) Four daily growth lines (white arrows) in enamel, shown between regular long-period growth lines (dark nearly vertical lines). (F) Accentuated lines in dentine (white arrows) with finer-spaced long-period lines between in parallel. This information was used to estimate the timing of developmental disruptions and the monkey’s age at death, which was accurate to within 1 day of the true age[16]
of the blood; 3) and how interactions with other elements or compounds may impact these processes. Furthermore the absorption and filtration of nutrients and metals may change as the gastrointestinal (GI) tract matures, and these physiological processes can also be influenced by hormonal or metabolic transitions. Most research of this nature has been undertaken on calcium and other essential elements.\textsuperscript{[29–31]} Healthy adults typically absorb about 25\% of the calcium (Ca) they consume through both active and passive transport in the small intestine,\textsuperscript{[30]} of which 99\% is stored in the skeleton. Calcium absorption doubles for women during pregnancy, facilitating active transport to the fetus via the placenta. After parturition, maternal absorption of dietary Ca returns to baseline, but her skeletal stores of Ca are heavily mobilized to produce calcium-rich milk. Nursing infants absorb Ca passively prior to the maturation of their GI tract, a process that is enhanced by other chemicals in mothers’ milk. This dynamic process of Ca transportation is relevant to studies of infant nursing and metals exposure, as Ca shares several chemical characteristics with the “bone-seeking” elements barium, strontium, and lead. These double charged ions (M\textsuperscript{2+}) may substitute for one another in cellular transport processes, and with Ca\textsuperscript{2+} sites in the hydroxyapatite mineral of bones and teeth, which store more than 90\% of their total amounts retained in the body.\textsuperscript{[32–34]}

Considerations of non-essential metals further illustrate the complex relationship between elemental chemistry and physiology. Barium (Ba) can be absorbed via GI uptake with lethal effect when bound to soluble salts,\textsuperscript{[35,36]} but when bound to sulfate it forms insoluble barium sulfate and is excreted. In this form it is considered safe for use in clinical X-ray imaging as a GI contrast agent.\textsuperscript{[37]} Similarly, Brazil nuts, which contain an exceptionally high amount of Ba relative to most foods,\textsuperscript{[35]} are generally safe for human consumption since the compounded Ba is not absorbed in proportion to its concentration.\textsuperscript{[38]}

In these latter two instances, Ba is not considered highly bioavailable since the body largely excretes it. In contrast, the metal strontium (Sr) is routinely used to measure Ca uptake due to the general similarity of their intestinal absorption,\textsuperscript{[39,40]} although Sr absorption and excretion can vary with nutritional factors.\textsuperscript{[41,42]} Lead (Pb) is known to be preferentially absorbed by infants and young children.\textsuperscript{[43]} Isotopic studies have established that Pb can be transferred from maternal stores to the infant via the placenta and through breast milk, which is influenced by Ca levels as mothers mobilize their skeletal reserves.\textsuperscript{[44,45]}

Little is known about these physiological processes in nonhuman primates; observational research is most concerned with human health, whereas experimental studies typically employ rodent models.\textsuperscript{[30,34,46]} Studies of rodents and domesticated mammals have provided important insights, yet human physiology is more closely linked with primates,\textsuperscript{[47]} our evolutionary cousins. Below we show how the timing and patterning of these elements in nonhuman primate teeth provide retrospective access to consequential behaviors for human survival, reproduction, and health outcomes.

**MAIN TEXT**

**Birth and infant nursing are reflected in tooth structure and chemistry**

Deciduous teeth begin forming in utero, as does the first permanent molar (M1). This involves activation of adjacent enamel- and dentine-secreting cells at the future enamel-dentine junction (EDJ), which move apart while rhythmically secreting a protein-rich matrix that captures their spatial and temporal progression (Box 1). Deciduous teeth and M1s preserve important structural features that indicate the exact position of enamel- and dentine-forming cells at birth (Figure 1). Oral biologists discovered these neonatal lines by examining sections of hundreds of naturally shed deciduous teeth from children, finding similar dark lines in a comparable position in nearly all teeth.\textsuperscript{[14,48]} These structures serve as natural and permanent markers of the profound physiological and nutritional transition that occurs at birth.

Developments in laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS, Box 2) allow individual elemental concentrations to be measured across a tooth section from adjacent microscopic spots serially ablated in a linear progression,\textsuperscript{[49–52]} which is illustrated in Figure 1, p. 399 of ref\textsuperscript{[53]}. Most LA-ICP-MS studies that leverage incremental features in teeth investigate humans and other primates,\textsuperscript{[54]} perhaps inspired by a seminal reports of elemental transitions near the neonatal line in human teeth.\textsuperscript{[146]} Integrated developmental and elemental maps suggest that the initial consumption of mother’s milk can be identified after birth without a marked temporal delay.\textsuperscript{[18]}

**Which elemental marker of nursing works best?**

Our initial study focused on Ba, which is often elevated (enriched) in human milk compared to maternal sera,\textsuperscript{[56,57]} leading to a novel framework for documenting the process and duration of nursing in permanent teeth (Figure 2A).\textsuperscript{[18]} We drew upon knowledge of human maternal-fetal physiology; a key study of 29 healthy mothers demonstrated that certain elements vary in maternal blood shortly before delivery, in umbilical cord blood measured immediately after delivery, and in colostral collected 1–3 days later.\textsuperscript{[57]} Average barium concentrations in umbilical cord blood were reported to reflect only a quarter of maternal blood values; a trend interpreted as evidence that the placenta may act as a barrier for Ba transfer in utero.\textsuperscript{[58]} In contrast to this prenatal discrimination, Ba was elevated by a factor of seven in colostral relative to umbilical cord blood (Table S1). Consistent with this, we found that human deciduous teeth (n = 22/25) and macaque M1s (n = 4/4) showed a marked Ba increase (relative to Ca) in close association with the neonatal line (Figure 2B).\textsuperscript{[18]} Thus, despite marked variation of absolute Ba values in the milk of humans\textsuperscript{[56,57,59]} and macaques,\textsuperscript{[18]} patterns of Ba/Ca in teeth are a useful indicator of the initiation of milk intake.
Related attempts to document nursing in human deciduous teeth include studies of \( {\text{Sr/Ca}} \)\textsuperscript{[60,61]} and calcium isotope ratios \( (\text{\textsuperscript{44}/\textsuperscript{42}\text{Ca}}) \)\textsuperscript{[62]}. To test this first approach, we compared \( \text{Sr/Ca} \) and \( \text{Ba/Cl} \) ratios in teeth from the same subjects\textsuperscript{[18]}. We found that \( \text{Sr/Ca} \) mapping was complicated by proportionately smaller changes in \( \text{Sr} \) levels across nursing transitions, and observed patterns varied among human and macaque subjects. Both \( \text{Sr} \) and \( \text{Ca} \) concentrations exhibit similar prenatal-to-postnatal shifts as reflected in the two-fold increase of each element in colostrum relative to umbilical cord blood (Table S1); thus, calcium-normalized \( \text{Sr} \) values measured from teeth should be very similar prior to and after birth. Regarding the use of calcium isotope ratios \( (\text{\textsuperscript{44}/\textsuperscript{42}\text{Ca}}) \)\textsuperscript{[62]}, we note that comparisons of calcium iso-

topes and nitrogen isotopes did not yield consistent results in the same human subjects, and others have concluded that \( \text{\textsuperscript{44}/\textsuperscript{42}\text{Ca}} \) does not always change with the introduction of milk, possibly due to masking by other physiological effects\textsuperscript{[63]}. Moreover, retrospective reports of breastfeeding histories can be impacted by recall bias\textsuperscript{[64]}, which may impact tests of the efficacy of \( \text{Sr/Cl} \)\textsuperscript{[60]} and \( \text{\textsuperscript{44}/\textsuperscript{42}\text{Ca}} \)\textsuperscript{[62]}. Prospective studies of cohorts of mothers and their infants are needed to clarify inconsistencies amongst these elements and isotopes prior to and after the initiation of nursing.

### Natal tooth biomarkers confirm the fidelity of dietary transitions recorded by barium

Given that barium typically increases with the advent of nursing, the neonatal line provides an opportunity to test the degree and timing of elemental overprinting by post-secretory elemental diffusion in teeth (Box 1). We have previously shown that elevated \( \text{Ba/Cl} \) values were evident in the prenatal enamel of a mineralizing sheep tooth (illustrated in ref\textsuperscript{[21]}; Figure S8). This pattern established that high barium concentrations derived from milk consumption can influence low barium concentrations in earlier-formed enamel secreted prior to birth, although these enriched postnatal barium values impacted less than a month of enamel formation. A study of \( \text{Ba/Cl} \) in the enamel of primate M1s yielded similar evidence of relatively minor overprinting: cusps that initiated formation less than 3 weeks before birth \((n = 2/2) \) did not show an elemental transition near the birth line, whereas the majority \((n = 17/22) \) of earlier-initiating M1 cusps displayed the characteristic \( \text{Ba/Cl} \) rise (Figure 2B)\textsuperscript{[Smith, Austin, Arora: unpublished data]}. Humans begin M1 calcification in the final months of gestation; individuals who initiate M1 cusps in the final few weeks, or are born premature, may not show a prenatal-to-postnatal \( \text{Ba/Cl} \) transition in LA-ICP-MS maps due to subtle overprinting, particularly when M1 prenatal enamel is diminutive. However, \( \text{Ba/Cl} \) patterns in human pre- and postnatal deciduous enamel are similar to those of rapidly mineralizing dentine (illustrated in ref\textsuperscript{[18]}; Figure 1, p. 217), providing additional evidence that the duration and magnitude of barium overprinting by subsequent enamel formation is small.

It is likely that this relatively limited offset of \( \text{Ba/Cl} \) at birth is reflective of the broader pattern of barium incorporation throughout tooth development. For example, decreased \( \text{Ba/Cl} \) patterns appeared in two infant rhesus macaques’ M1s within a few weeks of premature weaning due to maternal separation; comparisons of \( \text{Ba/Cl} \) in the enamel and dentine adjacent to the EDJ revealed only slight offsets between regions of differing intensity, further confirming their approximate contemporaneity (e.g., ref\textsuperscript{[16]}; Figure 2, pp. 218; Figure S4). This elemental transition is also apparent with high fidelity in a pig-tailed macaque infant raised in captivity (Figure 3). As part of a 1970s study of developmental stress, this individual was separated from its mother at birth and fed commercial infant formula (Enfamil) until 112 days of age, followed by diluted apple juice for another week, which was then replaced by water and Purina Monkey Chow until sacrifice at

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**Box 2. LA-ICP-MS elemental imaging of teeth**

LA-ICP-MS is a sensitive, micro-spatial elemental and isotopic analysis technique that is increasingly applied to study the distribution of elements in biological and geological samples\textsuperscript{[153,49]}. Sampling occurs at environmental conditions (e.g., atmospheric pressure, humid air, room temperature) and therefore requires minimal preparation—only a flat surface. The method scans a laser (typically with a wavelength in the UV region) across the sample surface, aerosolizing small amounts of solid sample at precise locations. The material, which comprises gases and a plume of particles in the nm-\( \mu \text{m} \) range, is transported to the ICP-MS where the particles are volatilized, atomized, and ionized in high temperature plasma (up to 10,000 K) and measured by the mass spectrometer. LA-ICP-MS is one of the most sensitive elemental imaging technologies, and can simultaneously measure elements at trace, minor, and major levels. Detection limits for \( \text{Sr}, \text{Ba} \) and \( \text{Pb} \) are typically around 0.01–0.05 \( \mu \text{g/g} \). For tissue imaging, spatial resolutions are typically in the 20–60\( \mu \text{m} \) range; all maps depicted here have a spatial resolution (pixel size) of 35 × 35\( \mu \text{m} \) and acquisition time from 7 (Figure 3) to 25 h (Figure 4). Although higher resolutions (1\( \mu \text{m} \)) are possible, the small amounts of material ablated can be too low to measure trace elements. To account for variation in mineral density between samples and sensitivity across analyses, element intensities are typically normalized to a minor isotope of a major matrix element, such as \( \text{\textsuperscript{43}Ca} \); scales on maps depicted here are adjusted to optimize the contrast between high and low signal intensity ratios \((\text{\textsuperscript{88}Sr/\textsuperscript{43}Ca}, \text{\textsuperscript{138}Ba/\textsuperscript{43}Ca}, \text{\textsuperscript{206}Pb/\textsuperscript{43}Ca})\). A remaining challenge for LA-ICP-MS is the limited availability of matrix-matched standards for accurate quantification\textsuperscript{[46]}. Matrix matching is required to account for differences in laser coupling with different matrices, which leads to different amounts of mass ablated at the same laser conditions. These standards were not available for the analyses presented in this paper.
FIGURE 2  (A) Model of barium incorporation predicting chemical transitions in the enamel and dentine of a primate M1 following intake of elementally enriched mothers’ milk at birth (indicated by neonatal line [NL] and change from low to high values). After exclusive nursing ends, barium values are predicted to drop with the introduction of solid food, and again at the cessation of milk intake (weaning). Right: Growth (arrows) begins at the enamel-dentine junction (EDJ) and progresses as indicated by arrows; developmental patterning can be recognized in elemental maps from parallels with incremental growth line geometry. (B) Model confirmation in a captive macaque (Macaca mulatta) M1 cusp that began forming 47 days before birth (with corresponding low prenatal Ba/Ca value in this region [red arrows]). This macaque (515) was intensively nursed for ~3 months, and naturally weaned after 300 days of age.¹⁸ Note that all elemental maps depicted are relative high-low signal intensity ratios (warm to cool color scales), and subsequent elemental maps are not on the same scale, as each image is adjusted to optimize the contrast within a sample. It is often difficult to show comparable elemental increases in both enamel and dentine in a single elemental map due to absolute concentration differences between these tissues; our analyses consistently include multiple scaled maps that optimize each tissue individually.

361 days of age. Although the absolute Ba/Ca values are lower than rhesus macaques that consumed mothers’ milk for their first 5 to 10 months of life,¹⁸ developmental and elemental maps reveal distinct decreases in Ba/Ca (and Pb/Ca) in the enamel and dentine at ~112 days of age. This is consistent with experimental work showing that barium from ingested liquids is rapidly incorporated into hydroxyapatite, and cleared from the bloodstream within a day of dosing.³⁴ Thus, sustained decreases of Ba/Ca in tooth enamel are likely to correspond to the withdrawal of enriched milk-products or the cessation of nursing within days of the actual event.
Figure 3A developing macaque (Macaca nemestrina) lower M1: accentuated lines (including the white dotted neonatal line) were initially temporally charted without knowledge of age or feeding history. The individual’s age at death was later determined from medical records to have been underestimated by 10 days (<3% error). Concentrations of calcium-normalized (B) barium (Ba/Ca), (C) lead (Pb/Ca), and (D) strontium (Sr/Ca) in the enamel drop markedly with the cessation of formula (Enfamil) intake at 112 days of age (red arrows), which is even more apparent in the underlying dentine. Low intensity Ba/Ca signals are not clear in the earliest-formed enamel, despite cusp initiation approximately 62 days before birth. This may be due to the fact that the individual was fed Polycose (a corn-starch derivative) at birth, followed by 1:1 Polycose and Enfamil solution for the first few days of life—leading to low and/or slow barium input. Elemental intensities from high to low follow the color palette shown in Figure 2A, as is the case in all subsequent figures.

Figure 3D also shows a Sr/Ca transition at the end of artificial formula consumption, but it is slightly less defined compared to Ba and Pb, an observation that may reflect a more diffuse or delayed mineralization process for Sr, or longer retention in the bloodstream than Ba. A study of postnatal Sr/Ca bands in an orangutan canine also found only a minor amount of elemental modification after initial secretion of the enamel and dentine. These authors suggested that Sr overprinting may occur for approximately 1 to 2 months in each tissue, although the outermost enamel showed prolonged changes in Sr values that were not numerically quantified. We have also observed that the outer enamel may not reflect pronounced elemental transitions in concert with its secretion as minerals are added later and likely...
more slowly than in the innermost enamel.\[^{22,25,66}\] While this is not of particular concern for the identification of birth in human M1s from Ba/Ca patterns (due to the consistent position of the neonatal line in the inner enamel)—elemental measurements from tooth surfaces are unlikely to correspond to formation times of external growth increments, contra ref.\[^{67}\]

In summary, the neonatal line in human and nonhuman primate deciduous teeth and permanent M1s provides a reliable biomarker for the estimation of an individual’s age as well as their nursing history, including reliance on artificial infant formulas (Figure 3).\[^{18}\] By using this unique skeletal birth certificate as a focal point, we have shown that the continuous process of tooth mineralization does not greatly obscure the timing of known dietary transitions, and instead records the onset of nursing through an increase in Ba, as well as the end of milk intake through a decrease of Ba, which is discussed further below.

**From one to many teeth: reading the entire elemental record of childhood**

Primate dental development has been extensively studied through fine-scaled microscopic approaches and macro-level clinical radiography. As noted above, human permanent M1 crowns initiate calcification first, followed after birth by the incisors, canines, premolars, second molars, and finally the third molar crowns and roots—altogether yielding a ~20-year developmental window prior to adulthood. Importantly, for different tooth types, crown and root formation begins and ends at staggered times; thus, successively forming teeth must be registered, or temporally linked, in order to interrogate the full developmental period. An opportunistic study of tetracycline markers in a young man believed to have been lost at sea is illustrative; 30 antibiotic treatments—ultimately yielding an exact age of the juvenile.\[^{14}\]

The time between these fluorescent biomarkers was determined from microscopic growth lines to link each individual tooth and to determine their initiation and completion ages—effectively charting his adolescence dentally (illustrated in ref.\[^{68}\]: Figure 7, p. 260).

More commonly, patterns of natural microscopic disruptions termed accentuated lines (Figure 1) may be used as a kind of barcode to link overlapping periods of enamel or dentine formation within and across teeth (e.g., ref.\[^{69}\]: Figure 1, p. 94; ref.\[^{70}\]: Figure 5, p. 7). Concurrently-forming teeth often show synchronous accentuated lines, as is the case with fluorescent markers like tetracycline, which can help to provide accurate stress histories and ages at death for juveniles.\[^{14,15,71,72}\] Accentuated lines formed after birth are multifactorial in origin; dozens of illnesses and physiological stressors are believed to cause these structural irregularities.\[^{14}\] For example, the dentition of a deceased captive gorilla revealed generic accentuated lines coincident with dates of an eye injury, hospital visits, and enclosure transfers—ultimately yielding an exact age of the juvenile.\[^{14}\]

Unfortunately, this registration method is subject to error, particularly for individuals with limited or excessive stress, as it is difficult to identify multiple concurrent accentuated lines when they are either infrequent or exceedingly numerous across teeth.\[^{69}\]

Concurrently-forming teeth also record the same elemental information; Ba, Sr, and Pb dietary transitions in the lower M1 of the macaque in Figure 3 are all evident in whole crown elemental maps of its upper M1. Building on this fidelity, here we demonstrate how developmental (biogenic) patterns of trace elements can be used to identify concurrent elemental changes in order to register successively-forming teeth (Figure 4). Combined with analyses of time using growth increments, this method provides a verification of tooth crown and root registration that yields a continuous record of life from before birth into adolescence. Integration of the two approaches has yielded novel estimates of tooth formation timing, nursing histories, and age at death in wild orangutans.\[^{65,69}\] In the following section we extend this method to illustrate how nonhuman primates inform our understanding of early life diets.

**Why probe teeth for records of nursing history?**

Humans’ agricultural, pastoral, and industrial food production practices are hypothesized to have shortened nursing compared to our earlier ancestors, who relied on gathered and hunted foods.\[^{73,74}\] Because mothers in natural fertility populations have a longer pause between births when they nurse their infants for longer,\[^{75}\] broad-scale provisioning of soft, cultivated “weaning foods” may have allowed farming or pastoralist mothers to transition infants off milk more rapidly than hunter-gatherers, leading to a concomitant boost in fertility. This influential idea has underpinned numerous studies of weaning in human prehistory.

The most common approach employs drilling or cutting serial sections from tooth roots in order to measure carbon and nitrogen isotopes.\[^{76}\] Unfortunately the temporal resolution of this method is limited to the scale of several months, or possibly even years, meaning early-life dietary changes cannot be resolved without large confidence intervals.\[^{20}\] More precise developmentally-informed studies of nursing and weaning began with LA-ICP-MS spot-sampling of Sr/Ca in humans and baboons,\[^{60,77,78}\] followed by more comprehensive mapping of entire tooth crowns with an emphasis on Ba/Ca patterning (Figures 3 and 4).\[^{18}\]

**Barium and strontium patterns reveal dietary information beyond nursing behavior**

As detailed above, we initially validated the efficacy of Ba/Ca pattern analysis for revealing the cessation of milk intake (weaning) using four captive macaque infants that transitioned from mothers’ milk to a uniform commercial diet, showing corresponding sustained Ba/Ca decreases in each instance.\[^{18}\] This has underpinned recent studies of wild primates and fossil hominins, which may also show early-life biogenic patterns of Ba/Ca.\[^{21,65,79}\] Our model (Figure 2A) was predicated on the ideas that most supplemental foods contain less bioavailable barium than milk, as is the case with Ca,\[^{80}\] and that the absorption of barium decreases with age.\[^{35,43}\] Physiological
data in support of these points derive from human studies, although observations and experimental manipulations of rodents and dogs also show a decrease in the efficiency of barium absorption with age.\[81,82\]

In contrast to the expectations of our model, wild primate teeth may show sustained periods of elevated Ba/Ca after nursing is likely to have ended, complicating direct assessments of this consequential dietary change. For example, a wild South African baboon’s M1 root shows several unexpected Ba bands that likely formed after weaning (illustrated in ref\[79\]: Extended Data Figure 5F). A third molar crown from this same species shows sustained Ba/Ca banding long after the juvenile was likely to have last consumed milk (ref\[79\]: Extended Data Figure 5C). Broad barium bands also appear in two wild Ethiopian baboons’ dentitions (Figure 4) long after the average weaning age for this species.\[55\] These observations require us to revisit our framework for documenting weaning ages.
Soil can be an important repository for Ba,[43] and scholars have suggested that Ba derived from soil and dust leads to detectable levels in the teeth of terrestrial carnivores and omnivores.[28] South African mammals that subsist on grass and other low-lying vegetation show higher Ba values in their teeth than animals that feed on higher-growing non-grass vegetation.[83] Terrestrial baboons routinely consume plant parts located in close proximity to the ground, including underground resources that are known to preferentially concentrate Ba and Sr.[84,85] High levels of Ba have been measured in Acacia seeds and grass corms from Kenyan grasslands, although their bioavailability has not been established. Ethiopian baboons consume these same foods on a seasonal basis, at times constituting 90% of their total diets.[86]

The elevated Ba we have documented in Ethiopian baboons occurred during nursing as well as the first few years of their presumed maternal independence (Figure 4), including high concentrations during a sustained drought shortly before their deaths in 1973—suggesting that both animals were relying heavily on Ba-rich fallback foods. This information is relevant to studies of human prehistory, as it may also explain cyclical Ba/Ca bands in the teeth of Australopithecus africanus.[79] a South African hominin hypothesized to have consumed underground resources such as tubers.[87,88] If confirmed, these patterns may provide important insight into regional seasonality during key periods of human evolution, which has been implicated as an important driver of unique human adaptations.[89]

As noted above, Sr/Ca concentrations have also been measured from sequential ablated spots in tooth enamel. Studies of two Ugandan baboons built upon knowledge of the wide-scale abundance of Sr in plant foods to construct a model of the nursing and weaning process.[77,78] They found that two infants’ early-formed teeth show rises in Sr/Ca broadly consistent with the average ages of solid food supplementation and the cessation of suckling—as would be expected from decreased nursing and increased consumption of foods with bioavailable strontium. However, our examination of later-forming Ethiopian baboon teeth show episodic Sr/Ca rises and falls for several years after species-typical weaning ages (Figure S1). Variation of the adult diet appears to obscure identification of the cessation of suckling from Sr/Ca values; the initial model postulated that Sr/Ca values peak when milk access ends and then fall as digestive discrimination against strontium is maximized.[77] This does not appear to be the case in wild Ethiopian baboons, orangutans, or modern humans.[23,79] Moreover, captive macaques’ Sr/Ca patterns may reach peak values prior to the cessation of milk intake.[18] In one case Sr values measured directly from mothers’ milk nearly doubled from 1 to 5 months of infant age, suggesting a complex relationship between Sr patterns in teeth and dietary signals.

Barium and Sr concentrations may covary in foodwebs,[83,85] although Sr is far more abundant in the environment than Ba, and recent work has argued that exposure to soil and dust contribute more of these elemental inputs to mammalian teeth than directly-consumed foods.[26] Calcium-normalized ratios of both Ba and Sr are believed to be lower in the body than in the diet due to limited absorption in the digestive tract and preferential excretion by the kidneys (relative to Ca).[32,41] We suggest that Ba/Ca may be more effective for identifying the cessation of nursing as the elemental pattern for total replacement of milk at weaning should be low and sustained, while the Sr/Ca signal may or may not be high depending on the particular available adult diet. A complementary approach to document the cessation of nursing in wild primates is to consider multiple elemental patterns in tandem. For example, one Ethiopian baboon M1 shows a prolonged drop in Ba/Ca ∼1.3–1.8 years of age, which is consistent with reported ages at weaning in this species (Figure S2).[55,78] Patterns of Sr/Ca rise after crown completion at 1.7 years of age and peak somewhat later than expected, but are broadly similar to inferences of a non-milk diet from Ba/Ca patterns.

Novel whole-crown elemental analyses of wild baboon teeth provide unexpected evidence of a substantial presence of Ba derived from non-milk dietary sources, as well as a complex relationship between Ba/Ca and Sr/Ca bioavailability. Future studies of wild primates with associated behavioral and ecological records are needed to refine these approaches to reconstruct primate nursing histories, as well as for the exploration of weaning during human prehistory.

Developmental disruptions are reflected in tooth structure and chemistry

Experiences of stress during early life are an important predictor of women’s reproductive physiology and adult health outcomes in westernized societies,[90] and similar trends have been found in nonhuman primates and mammals more broadly.[91,92] Scholars have long understood that developing teeth are highly susceptible to physiological disruptions and stresses, resulting in permanent macroscopic defects and microscopic accentuated lines (Figure 1).[1,2,4] As highlighted above in the example of the captive gorilla,[14] these irregular structural features can be caused by numerous factors. Studies of captive primates with associated dietary and medical information are especially helpful for understanding cases with limited prospective information. Such studies indicate that Ba and other trace elements are mobilized from skeletal stores during extreme illness both prior to and after weaning.[93] Thus, Ba/Ca concentrations not only record dietary intake, but health histories as well.

We previously documented an instance where a young rhesus macaque required hospitalization at 166 days of age due to an inflamed leg abscess.[93] Elemental maps revealed several enriched bands of Ba/Ca (and Sr/Ca) after this age that corresponded with accentuated lines and marked weight losses, leading us to conclude that trace elements were being released from skeletal stores due to active calcium remobilization. Short-lived increases in Ba/Ca appear as thin discrete lines in dentine, in contrast to the more gradual pattern of elemental change seen during natural suckling transitions. We have since found similar acute Ba/Ca bands in a wild orangutan M2 that correspond with accentuated lines in its tooth root (Figure S3), suggesting that these lines are the result of developmental disruptions rather than a Ba-rich food source. Their fairly regular spacing may indicate a periodic etiology; unfortunately the cause of these specific disruptions
cannot be inferred from their structural appearance or chemistry alone. In the section that follows we illustrate a multi-elemental approach to strengthen such studies of health and behavior.

**Lead exposures during childhood are recorded in teeth**

In addition to physiological stress, elemental records in teeth can reveal exposure to toxic substances in the environment. As detailed in the introduction, studies of people living today often examine naturally-shed deciduous teeth in order to determine the frequency or timing of exposure to industrial neurotoxicants such as lead or manganese—providing a window into the first year or so of childhood. Recent work has also explored the presence of Pb in the permanent dentition of prehistoric children and nonhuman primates. Lead is common in nature, including in soils, dust, and vegetation, although concentrations vary greatly depending on local geology, seasonal growth, and plant parts. Teeth record Pb exposure very rapidly, particularly in dentine, leading to its use as an artificial time-maker in foundational studies of incremental tooth development.

We recently reported the oldest-known evidence of Pb exposure in two Neanderthal children who lived in southeastern France approximately 250,000 years ago. Broad bands of increasing lead intensity appeared in one child at about 2.5 months of age and continued throughout its first few years of life. By coupling LA-ICP-MS data with oxygen isotopes, we showed that the Neanderthal children were exposed to Pb repeatedly during the winter or spring of their first few years of life. Both children survived long enough to erupt and considerably wear down the respective molar teeth, but unfortunately these were found in isolation from the rest of their remains, which have not been recovered. The source of the Neanderthals’ exposure could not be identified from archaeological records, although at least two significant Pb deposits occur within 25 kilometers of their burial site, as they have been commercially mined in the past century. It is plausible that their social groups sought shelter, combustible materials, and/or food or water from nearby caves that included comparably-rich lead deposits. Reports of lead exposure in these Neanderthals, and possibly other hominins, give rise to the question of how often our direct ancestors were exposed to lead in the natural environment prior to its use for industrial or ancient metalworking practices.

Studies of wild primates can be illustrative for understanding natural exposure to Pb. Examination of the molar dentitions of six orangutans (three Sumatran, three Bornean) that lived more than a century ago in densely forested regions in Indonesia reveals biogenic lead lines or bands prior to ~8–10 years of age (e.g., Figure S3). We have also found low-level Pb banding in the canine root of a male Bornean orangutan from ~10 to 20 years of age [Smith, Austin, Arora, unpublished data]. In these wild orangutans inhabiting dense forests far from industrial contamination, biogenic Pb bands are more frequent and/or intense once infants begin supplementing mothers milk with solid foods (estimated from decreased Ba/Ca in early-formed enamel and field reports of infant behavior). These orangutans are likely to have integrated low-level Pb into their skeletal tissues naturally from plant consumption, although infrequent liquid, dust, or soil sources cannot be ruled out. Lead exposures have also been detected in two wild Ethiopian baboons. The baboon illustrated in Figure 4 obtained its drinking water from the Awash River in the Awash National Park from the late 1960s until July 1973. Recent sampling of this river reveals elevated lead levels due to agricultural and industrial pollution, although it is unclear if this would have been as pronounced 50 years ago.

Lead can also be transferred through mothers’ milk, and is commonly mobilized from mothers’ skeletal stores after pregnancy. This is not simply a problem unique to modern children; we have observed Pb in the M1s of captive rhesus macaques (n = 8/8), pig-tailed macaques (n = 2/2), and one Japanese macaque (n = 1/1) reared at the California National Primate Center, Washington National Primate Research Center, and the Primate Research Institute, Kyoto University, respectively. Captive monkeys may be exposed from leaded water pipes or paint, as lead may imbue paint with a sweet taste, and macaques have been observed licking their enclosure walls. Patterns of Pb/Ca parallel Ba/Ca in the captive macaque teeth we have examined (e.g., Figure S4), suggesting that the lead was derived from their mothers’ milk. Teeth from pig-tailed macaque infants provided Enfamil in 1976–77 (Figure 3) also implicate this commercial source, consistent with reports of metal contamination of various human infant formulas.

Studies of nonhuman primates in captivity also suggest that extreme illness may cause the release of Pb back into the bloodstream when an infant’s skeletal stores of calcium are resorbed. In one complex case, a rhesus macaque was initially hospitalized for several weeks with a life-threatening pathogenic diarrheal disease. During this time Pb/Ca and Ba/Ca fell as nursing ceased abruptly (Figure 5), again implicating mothers’ milk as the primary source of these metals. Seven months later, a marked increase in Pb/Ca (and Sr/Ca) coincided with severe weight loss due to a whipworm infection that did not respond to clinical treatment, leading to eventual euthanization. This increase in Pb/Ca was likely due to released skeletal stores as the individual was on a constant commercial diet with a stable municipal water supply. Case studies such as these reveal the remarkable processes of intergenerational metal transfer, skeletal storage, and remobilization—providing important context for the interpretation of health challenges and environmental exposures faced by children in global economies.

**CONCLUSIONS AND PROSPECTS**

Developmentally-informed analyses of the tooth chemistry of captive and wild nonhuman primates, as well as human children with prospective nursing and health records, reveal the retrospective nutritional and physiological experiences of individuals in unprecedented detail. Despite a suggestion that Ba/Ca patterns in teeth relate to dietary stress rather than dietary transitions, we have demonstrated Ba/Ca increases with the advent of milk intake and decreases with the cessation of nursing in multiple species, and this is not substantially altered
Rhesus macaque (Macaca mulatta) M1 showing correspondence between elemental concentration changes and the individual’s nursing and medical histories. During an initial 25-day hospitalization beginning at 257 days of age, the infant was given a blood acidity regulator (K-Phos), a blood serum transfusion due to low serum protein, and several antibiotic courses, which coincide with marked decreases in Pb/Ca and Sr/Ca, as well as a drop in Ba/Ca. Medical treatments, maternal separation leading to premature weaning, and a change in the water supply during this period influenced tooth mineralization and/or metal deposition. Elevated Pb/Ca levels prior to hospitalization parallel those of Ba/Ca, suggesting that the Pb was derived from its mother’s milk. At 469 days of age the individual was determined to have lost 20% of its body weight over the past month due to a whipworm infection, and was readmitted to the hospital. Pb/Ca and Sr/Ca rose sharply just prior to the second hospitalization, but Ba/Ca displayed only a minor increase. (Further details of individual 152 are given in ref. [18])

by mineral incorporation after initial secretion. Moreover by mapping the entirety of tooth crowns and roots we provide multiyear longitudinal developmental records of dietary behavior, health, and neurotoxicant exposure. These maps are superior to conventional LA-ICP-MS spot samples and isolated linear tracks, particularly for linking successive teeth and for examining buried samples that may show elemental modification (diagenesis). This is because developmental geometry can often be distinguished from diagenetic contamination with such comprehensive maps.[18,65,79]

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CONFLICT OF INTEREST
The authors have declared no conflicts of interest.

AUTHOR CONTRIBUTIONS
T.M.S. and C.A. conceptualized this review with input from L.C., W.D., and D.G., and wild primate samples provided by W.D. All authors contributed to the writing of this manuscript.

DATA AVAILABILITY STATEMENT
The data that supports the findings of this study are available in the main figures, text, and supplementary material of this article.

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**Supporting Information**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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