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Reading children's teeth to reconstruct life history and the evolution of human cooperation and cognition: The role of dental enamel microstructure and chemistry

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ABSTRACT

Studying infants in the past is crucial for understanding the evolution of human life history and the evolution of cooperation, cognition, and communication. An infant's growth, health, and mortality can provide information about the dynamics and structure of a population, their cultural practices, and the adaptive capacity of a community. Skeletal remains provide one way of accessing this information for humans recovered prior to the historical periods. Teeth in particular, are retrospective archives of information that can be accessed through morphological, micromorphological, and biogeochemical methods. This review discusses how the microanatomy and formation of teeth, and particularly enamel, serve as archives of somatic growth, stress, and the environment. Examining their role in the broader context of human evolution, we discuss dental biogeochemistry and emphasize how the incremental growth of tooth microstructure facilitates the reconstruction of temporal data related to health, diet, mobility, and stress in past societies. The review concludes by considering tooth microstructure as a biomarker and the potential clinical applications.

1. Introduction

The period encompassing intra-uterine life and early childhood, extending post-conception to approximately 1000 days constitutes a pivotal phase in an individual's development. This developmental period significantly shapes our adult life trajectory, impacting facets of our health, susceptibility to specific diseases, longevity, and socio-cognitive abilities (Barker, 2001, 2004; Burkart and Van Schaik, 2010; Juster et al., 2011; Lupien et al., 2009; McEwen, 2012). Beyond factors inherent to pregnancy, such as maternal well-being, health, and nutrition, early childhood is profoundly shaped by an individual's social identity, cooperative caregiving, community dynamics, and

environmental influences (Fig. 1). Living conditions throughout intra-uterine life and during growth are reflected in frailty and mortality in adulthood, as well as in susceptibility to mental illnesses (McEwen, 2003). Consequently, early childhood and its subphases are commonly denoted as 'sensitive periods' (Knudsen, 2004).

In recent years there has been increased attention, from a medical and social perspective, on the importance of the earliest moments of an individual life (Brüne and Schiefenhövel, 2019; Kendall et al., 2020). This has cascaded into historical and evolutionary reconstructions of the mother-infant (and alloparent – infant) dyad and how this relationship has changed through time and between cultures (Gowland and Halcrow, 2019; Halcrow et al., 2020; Martin et al., 2020; Miller et al., 2020; Nava,

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2024; Page et al., 2019; Rebay-Salisbury and Pany-Kucera, 2020; Stefanović et al. 2019). Understanding the life histories of infants in the past is critical for understanding how humans and their societies have evolved.

Human life history is characterized by unusually short inter-birth intervals and early weaning (Nava et al., 2020; Robson and Wood, 2008). Hence, from a very young age, human children can be typically cared for by multiple caregivers (alloparents) in addition to the mother – making the evolution of our life history linked to that of our cooperative breeding behaviors and associated socio-cognitive and communicative abilities (Van Schaik and Burkart, 2010). Indeed, human development occurs within a social environment rich in interpersonal relationships, such as those with parents, siblings, and extended family members. This setting provides the backdrop for the emergence of strong social cognition and prosocial behaviors in young children (Hrdy and Burkart, 2020). During this crucial period, neural networks underlying advanced social, emotional, and communicative skills are established (Courchesne et al., 2007; Grossmann and Johnson, 2007; Hawkes and Finlay, 2018; Leppänen and Nelson, 2009). Multiple disciplines, including neuroscience, primatology, and psychiatry, converge to emphasize the critical temporal interplay between brain maturation and social experiences in shaping social cognition and prosocial tendencies (Grossmann and Johnson, 2007). In sum, reconstructing the evolutionary history of the unusually early age at weaning and characteristically short interbirth intervals of humans (Kuzawa and Bragg, 2012), means reconstructing the adaptations of our reproductive strategy that have led human infants to be exposed to a plurality of interactions during early brain ontogeny which have been shown to “tune” the social brain (Hawkes and Finlay, 2018).

Investigating individual life trajectories allows us to grasp the interplay between societies and their societal and ecological milieu (Fig. 1) (Agarwal, 2016; Halcrow, 2020). Many aspects of reproduction, child-rearing, care, and socialisation are central to archaeological and anthropological questions about the organisation of past societies, including division of labour, mobility, resource scheduling, and birth spacing (Baxter, 2022; Gowland, 2015). The study of infant growth, health and mortality is therefore essential in teasing apart lived experiences of health and disease in the past, including insights into infant feeding practices, fertility, family and social structure, population size (Gowland, 2015; Halcrow, 2020) and the adaptive capacity of a community (Kubat et al., 2023; Nava et al., 2020).

The study of human remains from archaeological contexts is known as human bioarchaeology. Human skeletal and dental remains are an excellent archive from which to study the human past. Teeth are often the most direct route for gaining insights into the lives of our ancestors (de Vareilles et al., 2021; Hardy, 2010; Zohar et al., 2022). Moreover, studies of dental and skeletal remains enable reconstructions of population dynamics. However, human skeletal remains rarely represent a true cross-section sample of a living society at a given time, because large-scale skeletal assemblages predominantly originate from funerary contexts. Indeed, the funerary record represents those who perished rather than those who were alive, which has been referred to as the Osteological Paradox (DeWitte and Stojanowski, 2015; Wood et al., 1992). The analyses of teeth provide one way of overcoming this limitation because they retain a longitudinal record of their formation.

Traditionally, human bioarchaeology has focused more on the adult segment of ancient populations, while studies of subadults have attracted less attention (Bondioli et al., 2016, 2020; Kamp, 2001). Less is

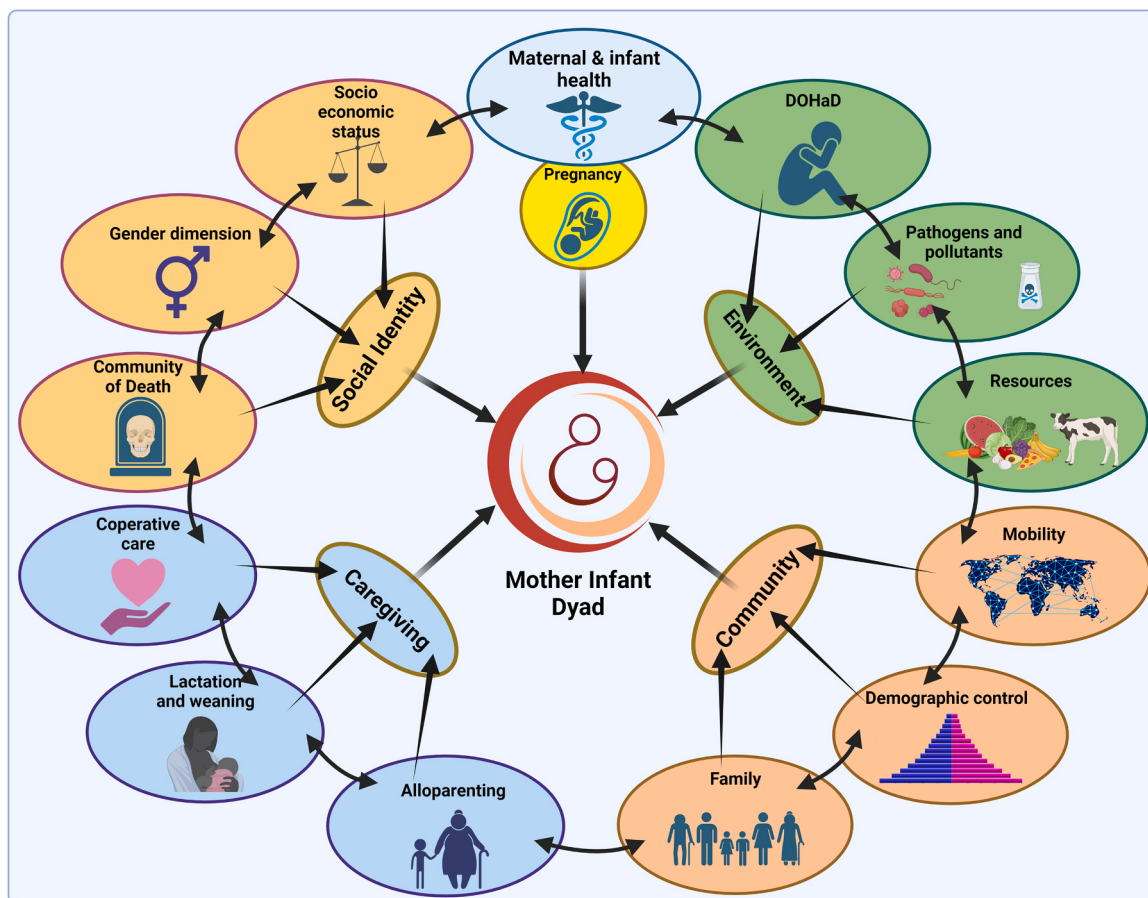


Fig. 1. The mother-infant nexus and bioarchaeology model of infancy and childcare (adapted from Halcrow et al. 2020). DOHaD = Developmental Origin of Health and Disease hypothesis.

known about child development, nutrition and their place in past societies, which is partly due to the scarcity of archaeological and historical records (Bondioli et al., 2020; Kamp, 2001). However, in recent years, attention has started to shift and the field is gradually becoming more focused towards infants and subadults in the past (e.g. Halcrow, 2020; Halcrow et al., 2020). These studies have started to address the role childhood development can play in the reconstruction of past population dynamics and social organization. Studies of teeth, both deciduous and permanent, are central to this developing aspect of human bioarchaeology.

2. Reconstructing life in the past from teeth

Teeth are of particular interest to bioarchaeologists because they can provide insights into the health, stress and mortality of subadults in past societies (e.g. FitzGerald et al., 2006; Kierdorf et al., 2021; Lorentz et al., 2019; Nava et al., 2017a; Sipovac et al., 2023). Teeth are the most durable of human remains and preserve well after death. They are a rich source of human life history (Stearns and Rodrigues, 2020), its evolution, as well as individual life stories that can be accessed through

micromorphological (histological) and biogeochemical methods (e.g. Austin et al., 2023; Fleming, 2009; Montgomery, 2010; Müller et al. under revision; Nava et al., 2020; Smith et al., 2021). Although all dental tissues (i.e. enamel, dentine and cementum) can preserve valuable information about an individual's biology, our review focuses on dental enamel. Indeed, tooth enamel microstructure becomes visible from the second trimester and continues to form until early adolescence. Unlike bone, enamel does not remodel once formed (Hillson, 2023). Therefore, a single tooth crown can capture a specific period of a child's development, and in this sense, teeth can be thought of as 'time capsules'. Forming enamel retains signatures of physiological growth, nutrition, and disruptions to an individual's homeostasis. As such, researchers are able to access these aspects of a child's life and recreate longitudinal records rather than reconstructing just a single point in time. This means that investigations of teeth can provide a way of partially overcoming many of the limitations that are typically inherent in mortality sample studies. Furthermore, the appositional growth process that governs tooth enamel formation preserves a time-resolved signal of such events (Dean, 2006). If extracted at sufficiently high spatial resolution, this process allows for daily to weekly temporal resolution. Therefore, the

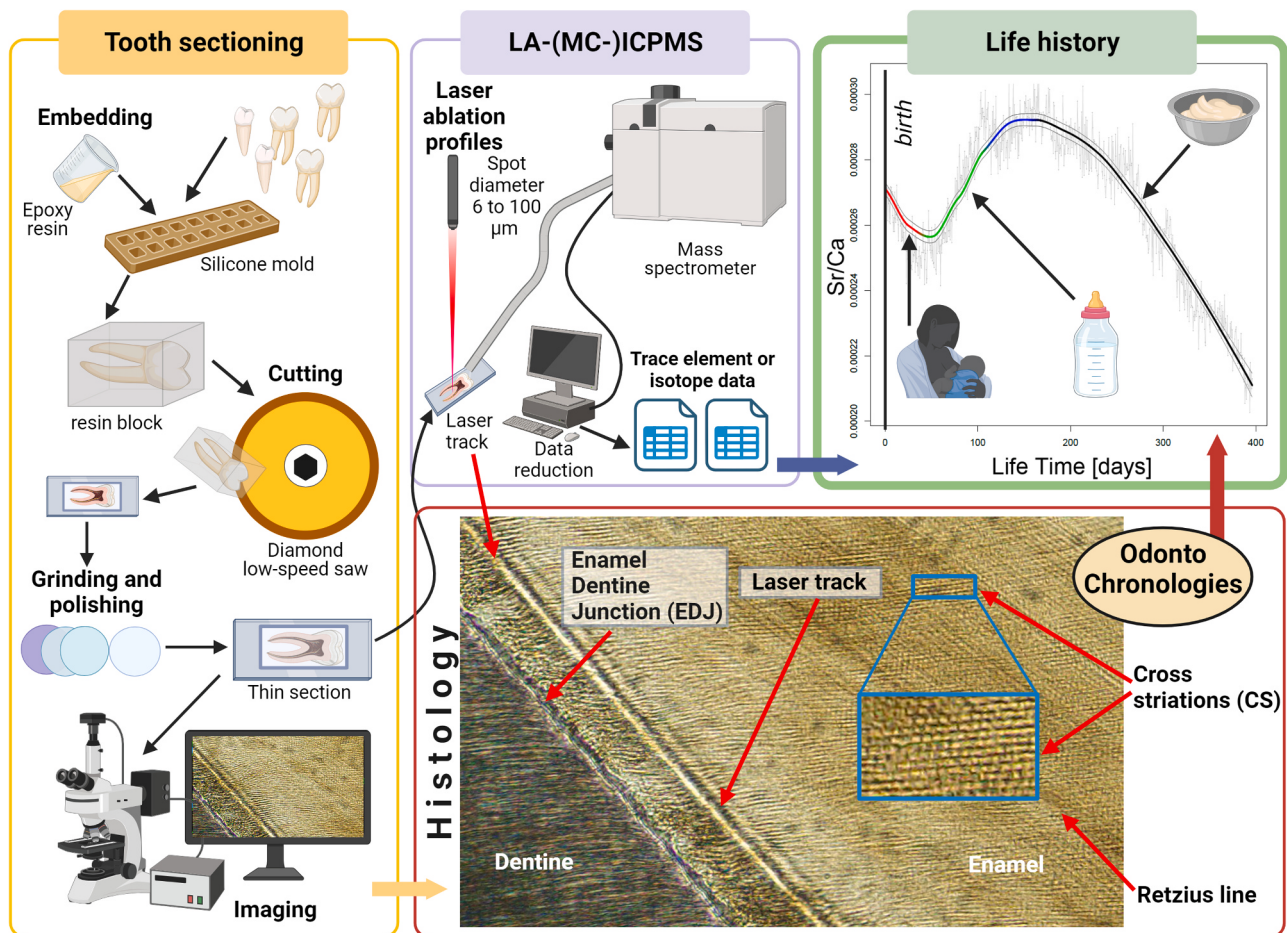


Fig. 2. Schematic representation of the analytical workflow for the reconstruction of individual life histories from dental histology coupled with spatially-resolved laser-based biogeochemical analysis. The workflow foresees the tooth sectioning (yellow box). After photographic documentation, the tooth is sectioned using a standard histological protocol (Nava et al. 2019). The tooth is first embedded in epoxy resin to prevent fractures during sectioning. It is then sectioned using a low-speed diamond blade saw. After the first cut, a microscope slide is attached to the exposed surface using the epoxy resin and a single longitudinal bucco-lingual thin section is cut from the specimen. Each thin section is then reduced to the appropriate thickness (~150 µm) using water-resistant abrasive paper and polished with a micro-tissue and diamond paste. The thin section is digitally recorded with a high-resolution digital camera paired with a transmitted light microscope to assemble the single frames into a photomosaic of the entire crown. The photomosaic is analysed to retrieve dental growth parameters (red box, see later in the main text and caption Fig. 3). The same thin section is subjected to biogeochemical analysis using a laser ablation instrument coupled to an ICPMS or an MC-ICPMS to measure elemental ratios (Müller et al. 2019) and isotope ratios (Lugli et al. 2022b; Müller and Anczkiewicz, 2016) respectively (purple box). The determination of odontochronologies along the laser track allows for the reconstruction of the individual life history during the period of tooth formation, for example, the reconstruction of the early life dietary history (green box).

microscopic and high-resolution biogeochemical analyses of tooth enamel properties are emerging as potent tools for obtaining highly detailed information about specific life histories (e.g. Dean et al., 2019; Joannes-Boyau et al., 2019; Kubat et al., 2023; Li et al., 2022; Müller et al., 2019; Nava et al., 2020; Smith et al., 2018a)(Fig. 2).

By harnessing the temporal growth of dental microstructures alongside their remarkable durability, researchers have started to achieve unprecedented advancements in the exploration of childhood also in the past (Aris et al., 2020; Austin et al., 2013; Dean, 2016, 2017; Dean and Cole, 2013; Dean and Elamin, 2014; Dean and Liversidge, 2015; Dean et al., 2019; Joannes-Boyau et al., 2019; Kubat et al., 2023; Mahoney et al., 2022; Mahoney et al., 2021; Nava et al., 2017a; Nava et al., 2020; Rosas et al., 2017; Smith et al., 2018a; Smith et al., 2021). These methodological strides, coupled with the introduction of novel interpretative frameworks, contribute to a more profound understanding of the intricate interplay among subadult health, parental care, mortality, and morbidity. Here, we discuss the current methodological advancements for investigating sub-adult life histories from teeth, with a specific focus on infancy and childhood. We also consider the challenges within the subject and the new opportunities and technological developments that are currently underway.

1) First, we discuss the fundamentals of dental growth and tooth microanatomy. The way that dental tissue is deposited is crucial to

understanding the type of information that teeth can contain, how the information is preserved and how it can be extracted.

- 2) Next, we discuss how teeth reflect and preserve somatic growth and its role in the deeper context of human evolution, and how such information is extracted using measurements and calculations of dental microstructure.
- 3) We then proceed to discuss dental biogeochemistry and how the incremental deposition of tooth microstructure allows us to reconstruct high-temporal resolution individual life history data in relation to health, diet, mobility and stress signatures.
- 4) Finally, we conclude by outlining how such intricate details about teeth and human life history can help us to understand the evolution of uniquely human socio-cognitive abilities, modern human variation, the interaction cross-overs archaeological studies of dental remains can have with modern medical approaches and hinting towards future approaches for the field.

3. A schematic overview of dental development and microanatomy

Tooth growth in humans is influenced by individual biological rhythms that are expressed in the microstructures of enamel, dentine and cementum (Boyde, 1989). The appositional formation of teeth makes it possible to relate growth, stress and biochemical aspects of development to a chronology.

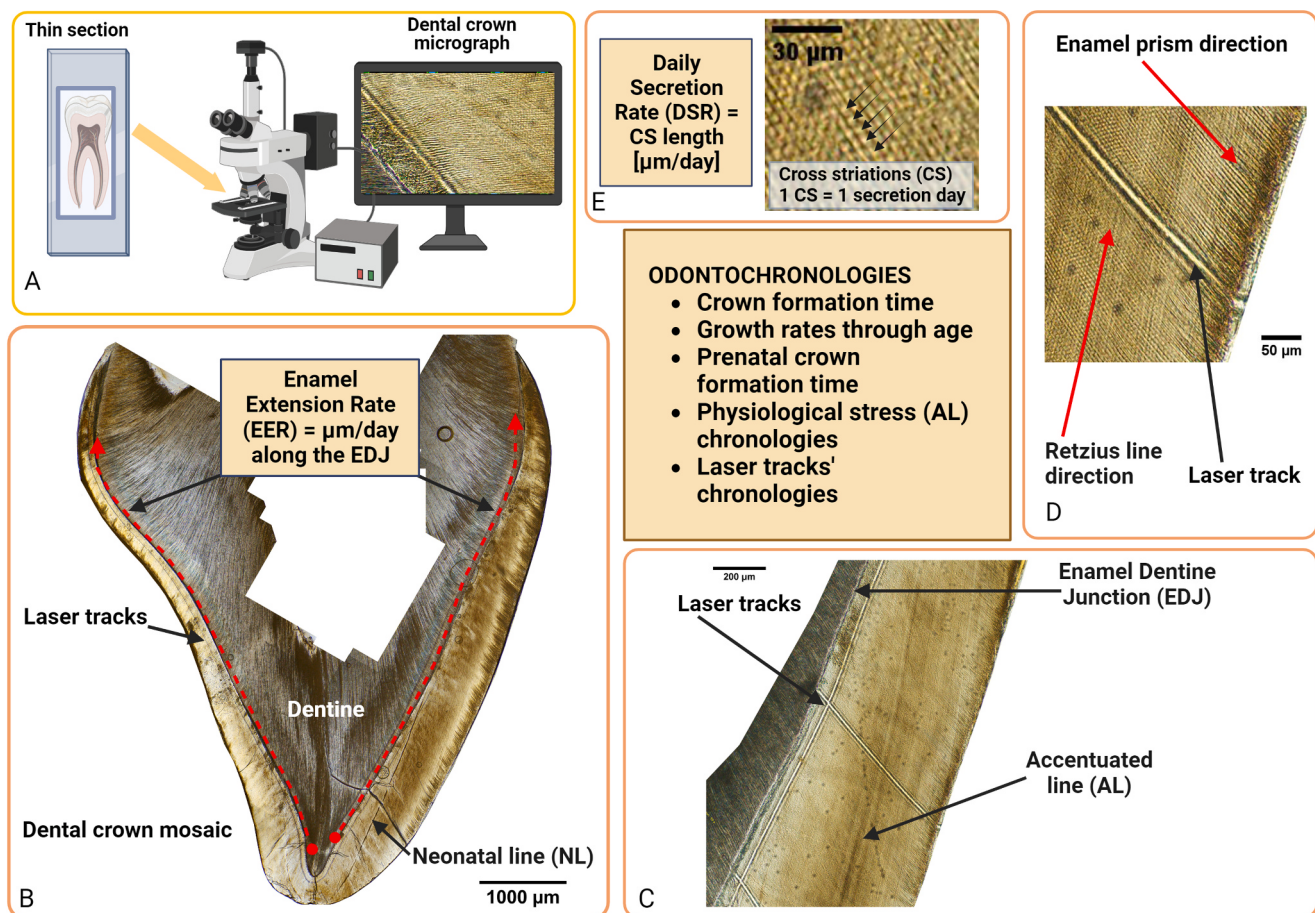


Fig. 3. Schematic overview of dental enamel microstructures and developmental parameters. A) Optical microscopy analysis of a dental thin section used to produce the photomosaics of the entire dental crown. B) Photomosaic of the thin section of a human deciduous upper canine crown. The black arrow points at the neonatal line, the birth marker. The red dotted lines highlight the direction of the enamel extension, i.e. the crown growth in height, from which EER is calculated as the rate of differentiation of secretory ameloblasts recruited along the enamel-dentine junction. C) Portion of the same photomosaic in B highlighting the laser tracks after LA-ICPMS analysis, the enamel dentine junction, and an accentuated stress line (AL). D) Further magnification of the photomosaic in B and C showing the enamel prisms and Retzius lines directions and the laser track.

Dental enamel, which is our focus here, starts developing in utero (at the beginning of the second trimester of pregnancy) forming the primary, deciduous dentition (Nanci, 2007). Around birth, all of the deciduous teeth, and a small portion of the first permanent molar, have usually commenced formation. The permanent teeth then continue to form sequentially until adolescence. Therefore, the study of dental enamel structure and chemistry can relate to an individual's life history roughly between late pregnancy and about 15 years of age.

The study of enamel growth dates back to the earliest moments of microscopy (Leeuwenhoek, 1677). The early part of the 20th century saw the first use of enamel incremental structures to reconstruct the chronology of tooth crown formation in clinical dentistry by Kajiyama (1965), Schour and Massler (1940), Tagiguchi (1966). However, Schour (1936) was the first to fully describe a marker of birth in teeth (see later in the text and Fig. 3B) and Boyde (1963) was the first to use enamel incremental markings to establish an age at death in archaeological material. The history of these early studies has been fully reviewed by Boyde (1964), Dean (1987), FitzGerald (1998), Smith (2006), and most comprehensively by Hillson (2023).

Markers of biological rhythms essentially follow two different time series with different frequencies. The first has a daily rhythm that relates to the day-night alternation (Zheng et al., 2014, 2013). The daily rhythm is expressed in enamel microstructure as cross striations that are visible along enamel prisms (Antoine et al., 2009; Bromage, 1991; Lacruz et al., 2012) (Fig. 3 D, E). The second rhythm in humans is characterized by a circaseptan (nearly weekly) periodicity, probably related to oscillations of biological rhythms over a longer period that are specific to each individual (Mahoney et al., 2022, 2018, 2017, 2016). These longer period rhythms appear to change between the anterior and posterior dentition of a single individual, at least for some individuals (McFarlane et al., 2020). The long-period rhythm becomes visible microscopically on dental thin sections as brown striae that are known as Retzius lines (Fig. 3, C) (Dean, 2019; FitzGerald, 1998; Retzius, 1837). Retzius lines demarcate 'layers' that emerge on the outer surface of the dental crown, where they are expressed as perikymata (Nanci, 2007).

There are other types of marking that occur in enamel, but these typically do not have a consistent rhythm over the course of enamel formation. One of these is named accentuated brown striae of Retzius, which are also known as Wilson bands or accentuated lines (ALs, Nava et al., 2019; Witzel et al., 2008). These ALs reflect disruptions of the metabolic equilibrium due to physiological stresses (but see also Goodman and Rose, 1990; Lemmers et al., 2021; Schwartz et al., 2006, for psychological stresses in primates). One well-documented example of an AL occurs at birth. Birth is recorded in the form of a peculiar accentuated line called the neonatal line (Dean et al., 2019; Sabel et al., 2008). The neonatal line demarcates the pre-, and post-natal environment and as such is a critical landmark in studies of enamel microstructure that reconstruct timelines related to life history.

The microstructure of a dental crown that becomes visible through a thin section (Fig. 3B), represents a calendar of all the individual's life moments from the beginning of crown formation to its completion.

4. Developmental trajectories revealed in dental microstructure

Individual rates of somatic growth can be represented, albeit not perfectly, by dental tissues (Sešelj, 2017). It follows that the reconstruction of individual ontogenetic trajectories in both *Homo* and extant and fossil primates (Austin et al., 2023, 2013; Cerrito et al., 2022; Craig et al., 2009; Dean, 2010, 2016, 2017; Dean and Cole, 2013; Dean et al., 2020; Dean and Smith, 2009; Kubat et al., 2023; Li et al., 2022; Mahoney et al., 2022; Mahoney et al., 2021; Müller et al., 2019; Nava et al., 2017b; Nava et al., 2019; Nava et al., 2020; Olejniczak et al., 2008; Rosas et al., 2017; Smith et al., 2022; Smith et al., 2018b; Smith and Tafforeau, 2008) is made possible by the comparative study of the histology of mineralised dental tissues.

Human life history (our pattern of growth, maintenance, and

reproduction) is unique. Compared to our closest living relatives, some aspects of it are accelerated (i.e. short spacing between births and early weaning) while others are decelerated (i.e. slow growth and delayed development). To understand its evolutionary history we can leverage the observation that our slow developmental trajectory is faithfully recorded in mineralized tissues (i.e. enamel, dentine and bone) and is reflected in a prolonged period of development and delayed dental and skeletal maturity (Dean and Smith, 2009; Guatelli-Steinberg, 2016; Leigh, 2001; Rosas et al., 2017; Sešelj, 2017; Smith, 1992). This slow growth in humans is probably an adaptation which permitted the growth and development of larger brains, which are energetically extremely expensive and therefore require an ontogenetic trade-off between neural development and skeletal development (Kuzawa et al., 2014). While across mammals there is a general trade-off between fertility and brain size (as both test the limit of maternal and allomaternal energetic input), humans stand out comparing to other mammals in that there is no brain size/fertility trade-off, and this is most likely a consequence of both paternal and alloparental care (Heldstab et al., 2019) and of increased fat storages (Heldstab et al., 2016; Navarrete et al., 2011).

Evidence about this trend of delayed development is derived from studies of infancy and childhood in the bioarchaeological and fossil record (Aiello and Dean, 1990; Aris et al., 2020; Bromage and Dean, 1985; Dean, 2000, 2006, 2009, 2010; Dean et al., 2001; Dean and Liversidge, 2015; Dean and Smith, 2009; Macchiarelli et al., 2006; Mahoney, 2015; Mahoney et al., 2021; Nava et al., 2017a; Nava et al., 2020; Smith, 1991; Smith, 2004; Smith, 2013), particularly with the study of the first permanent molar, which develops from birth till the end of the brain growth (Hillson, 2023). The chemical composition, the formation timing and the eruption age of permanent molars are effective proxies for some of life history benchmarks, like age at weaning, age at sexual maturity, age at first reproduction, inter-birth interval, natural life span (Humphrey et al., 2008a; Smith, 1991, 1992). To date, most dental paleoanthropologists recognize that some limitations exist about these correlations, especially when comparing living species with the fossil record, and some authors have questioned the validity of dental development and some aspects of eruption as a reliable proxy from which to infer life history variables (Robson and Wood, 2008). The relationship among the benchmarks, indeed, may have changed over time and the complex interplay between extrinsic (ecological niches) and intrinsic (physiology, somatic development) factors should be taken into account when inferring life history traits from the emergence of the first permanent molar (Guatelli-Steinberg, 2016; Smith, 2013).

The trend of delayed growth and development in humans is well known from the skeletal and dental analyses of a number of fossil and archaeological specimens, throughout the entire period of human natural history (e.g. Dean and Smith, 2009; Le Cabec et al., 2017; Rosas et al., 2017; Smith, 1992; Smith et al., 2004), as well as from the study of the extant great apes (Charnov and Berrigan, 1993; Walker et al., 2006). Conversely, very little has been explored on the critical period represented by intra-uterine life with few exceptions (Kierdorf et al., 2021; Mahoney, 2015; Mahoney et al., 2021; Nava et al., 2017a; Nava et al., 2017b; Witzel, 2014). Life in utero is a sheltered period when the selective forces driven by the environment are mediated and buffered to some extent by the maternal body and immune system, even if they are still acting on the mother-fetus relationship (Almond and Currie, 2011; Barker et al., 2002). Therefore, any attempt to reconstruct the prenatal and early postnatal growth trajectories can be of seminal importance for the understanding of the general pattern of slow growth and development of present-day humans. Moreover, recent evidence points out that the rate of adaptive evolution from the Neolithic is more than one hundred times higher than the rate that characterizes most of human evolution (Hawks et al., 2007). Not surprisingly, new genetic evidence shows that human adaptation continued well into historical times, with polygenic adaptation being an important force shaping both genotypic and phenotypic variation (Field et al., 2016). Consequently, the

expectation is to observe population-specific differences in fetal development and rapid and consistent changes through time. In addition, this model of fetal development appears to be supported by the Genome-Wide Association Study (GWAS), which points to a rapid selection in human recent past (Boyle et al., 2017; Field et al., 2016; Krapohl et al., 2017).

As teeth are the most frequent and best-preserved findings in the fossil and archaeological record, is it not surprising that some dental growth parameters are critical for assessing differential growth in past hominins. The daily enamel secretion rate (DSR, Fig. 3E) is the linear measure of enamel matrix secreted in one day by ameloblasts - the enamel-forming cells (Birch and Dean, 2014; FitzGerald and Hillson, 2009; Huda and Bowman, 1994; Macchiarelli et al., 2006; Mahoney, 2011, 2012, 2015; McFarlane et al., 2021; Nava et al., 2017a; Towle and Loch, 2024). This velocity is the basic parameter in evaluating dental growth trajectories and is calculated by dividing the lengths of prism segments by the corresponding number of daily increments (cross striations, CS) along them and is equivalent to the average length of a CS (Hillson, 2014). DSR varies along the crown profile and increases from the EDJ toward the outer enamel surface while decreasing from the tooth tip toward the neck (Beynon et al., 1991; Birch and Dean, 2009; Hillson, 2014; Mahoney, 2012; Massler and Schour, 1946; Nava et al., 2017a; Schour and Massler, 1937; Schour and Poncher, 1937). Fig. 4 shows the topographic distribution of DSR in a deciduous tooth, calculated by collecting randomly distributed DSR measurements ($N > 100$) across the entire crown portion (Nava et al., 2017a; Peripoli et al., 2023).

Enamel extension rate (EER) is the rate of differentiation of secretory ameloblasts, or the rate at which secretory front ameloblasts are recruited along the enamel-dentine junction (EDJ, Fig. 3C) between the dentine horn and the neck (Dean, 2009; Guatelli-Steinberg et al., 2012; Shellis, 1984). Extension rates vary along the EDJ, decreasing from the tip of the dentine horn toward the neck (Dean, 2009, 2010; Nava et al., 2017a). Crowns of deciduous teeth have higher initial EERs than permanent teeth (Mahoney, 2015; Shellis, 1984). Enamel extension rates are negatively correlated with overall crown formation time.

Retzius periodicity (RP) is the number of cross striations between two adjacent Retzius lines (Dean, 1987; FitzGerald, 1998). This interval is believed to reflect a basic biorhythm (Bromage et al., 2009; Dean, 1987; Mahoney et al., 2016). In modern humans, RP of permanent teeth can vary between 5 and 12 days when compared between individuals (FitzGerald, 1995, 1998). Typically, RP remains constant within an individual, but RP can sometimes change between the anterior and posterior dentition of some individuals (McFarlane et al., 2020), and within a tooth that preserves evidence of an extreme stress event (Mahoney et al., 2017). Population mean values are generally centred around 7, 8, or 9 days (see McFarlane et al., 2020 for a review of the topic).

5. Inferring stress exposure from dental microstructures

The mortality profile and physiological stress exposure of children in any human population is a measure of the biocultural adaptability of the community (Goodman and Armelagos, 1989; Lewis, 2018). As evidenced by several epidemiological studies on modern populations (for a

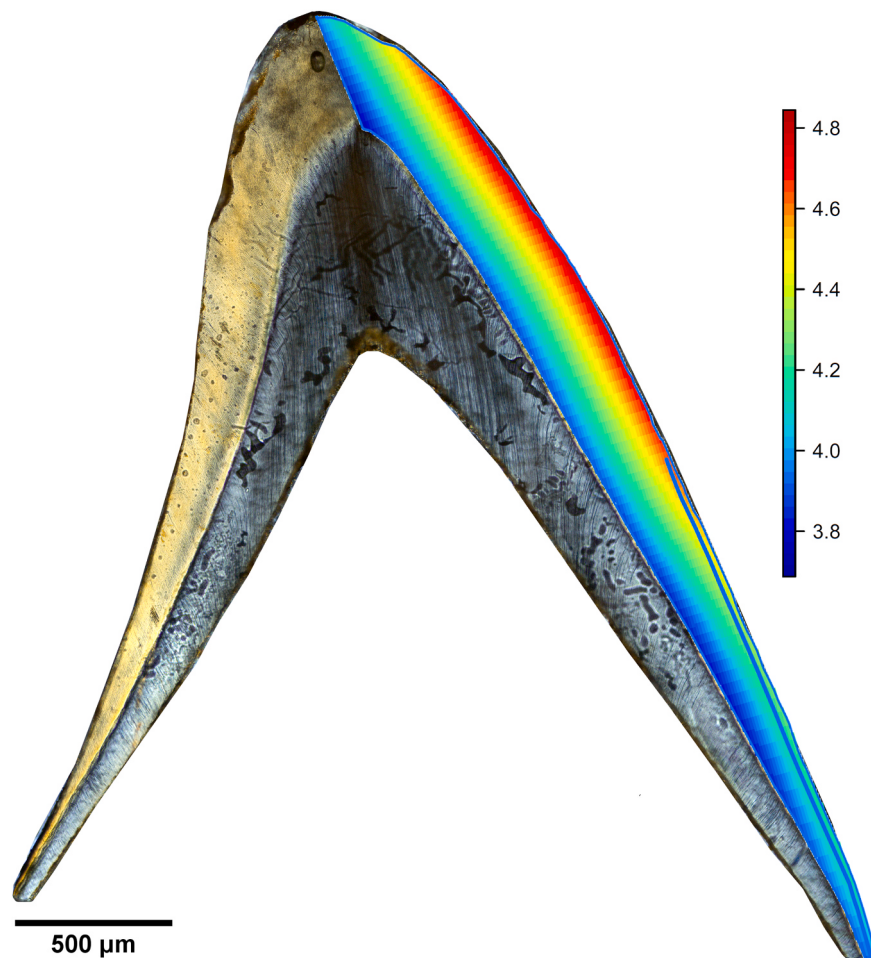


Fig. 4. The distribution of the daily secretion rates (DSR) represented as a pseudo-colour density map is superimposed on the photomosaic of the dental crown of a human deciduous incisor of an infant that died soon after birth. The neonatal line is highlighted by a thick blue line.

review see [Humphrey and King, 2000](#)), conditions during the early years of life - from intrauterine life to infancy - often affect poor health and early mortality in adulthood ([Armstrong et al., 2009](#); [Barker, 2004](#)).

The study of the dental and skeletal remains of human archaeological populations allows us to infer their lifestyle in the past and to determine the degree of adaptation to the environment in which they lived. Life-span may be considered the simplest and most direct indicator of such adaptation, but the frequency and chronology of non-fatal stressful events, such as disease or nutritional deficiencies, can provide important indications of the biological success of a population and are also unique tools in the context of palaeoepidemiological analyses ([Armstrong et al., 1981](#); [Goodman et al., 1988](#)). The prevalence in a population of both microscopic (ALs) and macroscopic (linear enamel hypoplasia) enamel defects is often interpreted as a measure of general health during childhood ([Larsen, 2015](#); [Lorentz et al., 2019](#); [Nava et al., 2019](#); [Peripoli et al., 2023](#); [Simpson, 1999](#); [Żądzińska et al., 2015](#)). Indeed, dental enamel is a highly specialised tissue that is very sensitive to physiological and environmental changes ([Klein et al., 2017](#)). Consequently, amelogenesis can be disrupted by systemic external stressors, producing permanent enamel defects ([FitzGerald and Rose, 2000](#); [FitzGerald and Saunders, 2005](#); [Witzel et al., 2008](#)). Stresses causing metabolic disturbances have been associated with a range of infant morbidity events, including malnutrition, low birth weight, maternal infections during pregnancy, infections and malnutrition during weaning, and many common childhood febrile illnesses ([Birch and Dean, 2014](#); [Hillson, 2023](#); [Schultz et al., 1998](#); [Seow, 1992](#); [Skinner and Goodman, 1992](#); [Teivens et al., 1996](#); [Witzel et al., 2008](#)). In addition, by calculating crown formation times, the relative chronology of ALs can be determined by directly counting daily cross-striations or Retzius lines (for a methodological review see [FitzGerald and Saunders, 2005](#); [Guatelli-Steinberg et al., 2012](#); [Lemmers et al., 2021](#); [Nava et al., 2017b](#); [Nava et al., 2019](#)). In teeth that possess the neonatal line, it is also possible to reconstruct the absolute chronology of stresses in an individual's life, and, considering several teeth from the same individual (since portions of dental crowns that are formed at the same time usually have the same AL patterns), it is possible to identify chronological intervals of homologous ALs on two or more teeth ([Lemmers et al., 2021](#); [Nava et al., 2017b, 2019](#)).

In [Nava et al. \(2019\)](#), the chronology of ALs in an Imperial Roman

sample has been derived by matching homologous intervals between ALs on several teeth of the same individual. The approach can be likened to a longitudinal approach, in that each individual is 'followed' throughout the formation of the selected teeth. A sample of 18 individuals with a total of 84 teeth (17 deciduous and 67 permanent) from the Roman Imperial necropolis of Isola Sacra (2nd to 4th century CE, Italy) were selected in [Nava et al. \(2019\)](#) study. [Fig. 5](#) shows the contribution (density lines) of the individual tooth classes superimposed on the general trend (histogram) of the crude count of ALs in the sample during the first 69 months of life (corresponding to 5 years/9 months). The whole sample distribution is asymmetrical with a mode around the 11th month of life. In the first month, the frequency of stresses is rather low, then, the frequencies grow rapidly until the 11th - 13th month, with a slight peak at the 4th month. After the modal months, the distribution decreases until the 22nd month. Between the 22nd and the 44th month, the distribution is mostly stable with some wavering toward the end of the distribution. The last 24 months are characterized by a very low frequency of stress events. A possible interpretation of this general trend is that the first months of life are usually protected by the presence of maternally derived antibodies ([Glezen, 2003](#)) that directly relate to the low ALs prevalence figures observed during this period of life. When comparing the ALs profile with previously published stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotopes bulk bone collagen data derived from the children's ribs of the same necropolis ([Prowse et al., 2008](#)), the authors hypothesize weaning as the main factor shaping the stress distribution around one year of life in the sample.

It is possible to see how the contribution of the different tooth classes weigh differently during the period of their formation. In fact, the different tooth types considered do not seem to record physiological stress in the same way, and the location of the stressor on the crown is important as well. The central part of the crown consistently is more likely to preserve evidence of stressor, compared to the cuspal and cervical regions. It, therefore follows that an effective reconstruction of the health status of a population in the past using accentuated lines, but also enamel hypoplasias, cannot be based on the evidence of a single tooth, which will always tend to underestimate the number of stress events in the initial period of its formation and the final period.

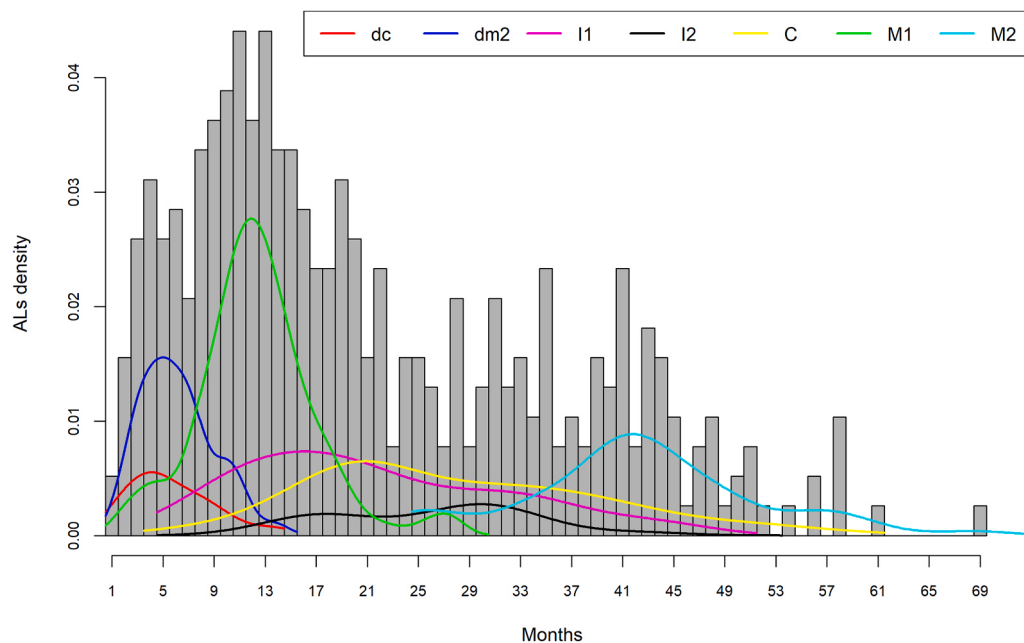


Fig. 5. Disaggregation of the raw ALs' count by tooth classes, approximated by the density estimates. The density curves are superimposed to the crude count distribution during the first 69 months of life (from [Nava et al. 2019 Fig. 4](#)).

6. Diet and mobility inferred from the biogeochemical analysis of dental mineralised tissues

In recent decades, the use of ‘bulk isotope analyses’, i.e. those utilizing several mg-sized samples thus averaging the signal over a broad time range, has played a crucial role in elucidating aspects such as diet, mobility and the broader interaction between humans and their environment. Such geochemical analyses commonly target either the collagenous (i.e. organic) portion of skeletal remains or the mineral phases (i.e. hydroxylapatite). Specifically, carbon ($^{13}\text{C}/^{12}\text{C}$), nitrogen ($^{15}\text{N}/^{14}\text{N}$) and sulfur ($^{34}\text{S}/^{32}\text{S}$) stable isotopes (commonly expressed in ‰ in δ -notation (e.g. $\delta^{13}\text{C}$...) vs. international standards) are measured on the collagen of human and animal bones/teeth and can reveal the trophic position (Schwarcz and Schoeninger, 2012) and, in case of S, the mobility of the individual (Richards et al., 2001). Oxygen ($^{18}\text{O}/^{16}\text{O}$), carbon, strontium ($^{87}\text{Sr}/^{86}\text{Sr}$) and lead isotopes ($^{206}\text{Pb}/^{204}\text{Pb}$; $x=8, 7$ or 6) are measured on the mineral phase(s) of tooth enamel – both the phosphate and the carbonate moiety depending on the analyte and the technique – and provide information on mobility (O, Sr, Pb) (Alt et al., 2014; Eckardt et al., 2009; Evans et al., 2022; Lugli et al., 2022b; Müller et al., 2003), diet (C) (Ambrose and Norr, 1993) and the environment (O, C) (Pederzani and Britton, 2019) where the individual lived. Recently, N isotopes have been also measured on the organic matter (~1 %) encapsulated in tooth enamel (Leichtler et al., 2021), as a novel method to obtain biogenic N isotope ratios in case of poor collagen preservation, e.g. in ‘deep time’.

Yet, two main issues arise from the use of ‘bulk’ isotopes for life-history reconstruction, namely 1) the lack of intra-life temporal resolution and 2) the poor preservation of collagen in fossil remains. While the latter issue can be (partially) solved by focusing on dental enamel only, also exploiting novel non-traditional stable isotope systematics (e.g. Zn, Jaouen et al., 2022, Ca, Dodat et al., 2021; Li et al., 2022; Li et al., 2016; Tacail et al., 2017), the former issue is more challenging to address. In this sense, much work has been devoted to measuring the isotope composition of incremental tissues – such as e.g. dentine and enamel – by exploiting intra-tooth sampling strategies, for example, analysing enamel (Zazzo et al., 2012) or dentine (Cheung et al., 2022) serial samples drilled/sawed from tooth specimens. However, even though these methods are suitable for various contexts, they still suffer from insufficient temporal resolution (Tsutaya, 2020), being able to solve diet and mobility changes at about multi-monthly/sub-annual scale, due to either instrumental limits (sample size and collection) or chronologization problems. There have been attempts to improve bulk sampling techniques that should reduce the impact of this issue (Beaumont et al., 2014; Curtis et al., 2022). When combined with dental histomorphometry, micro-sampling techniques – above all laser ablation (LA) – applied to incremental tissues can help improve the achievable spatial resolution and possibly resolve individual life histories at a sub-monthly scale (Kubat et al., 2023; Müller et al., 2019, 2009; Nava et al., 2020). In particular, LA can be coupled with ICPMS and MC-ICPMS to measure elemental ratios (Müller et al., 2019) – as e.g. Sr/Ca, Ba/Ca and Pb/Ca – and isotope ratios (Lugli et al., 2022b; Müller and Anczkiewicz, 2016) – as e.g. $^{87}\text{Sr}/^{86}\text{Sr}$ – with a lateral resolution of few μm ($< 10 \mu\text{m}$) and a spot size ranging between 10 and 100 μm .

In recent years, high spatial resolution elemental analyses of Sr/Ca and Ba/Ca ratios (Arora and Austin, 2013; Austin et al., 2013; Humphrey et al., 2008a, 2008b; Joannes-Boyau et al., 2019; Müller and Eggins, 2003; Müller et al., 2019; Nava et al., 2020; Smith et al., 2023) have been successfully used to reconstruct feeding behaviour in early life and weaning practices of past and recent hominins (Kubat et al., 2023; Lugli et al., 2022b; Müller et al., 2019; Nava et al., 2020; Smith et al., 2023, 2022). Sr and Ba share similarities with calcium (Ca) being alkaline earth elements with a divalent charge, but they have larger ionic radii (Sr: 1.18, Ba: 1.35, Ca: 1.00 Å) (Shannon, 1976) and no known major biological function in the body (Burton et al., 1999). Although they follow calcium metabolism, their larger size results in

discrimination (i.e. Ca is preferentially selected) in the gastrointestinal tract (Elias et al., 1982). From there, ions are mainly fixed via plasma in the skeletal tissue, with further discrimination relative to Ca (Balter, 2004). This leads to ~5-fold lower Sr/Ca and Ba/Ca ratios in bones and teeth compared to the diet, a phenomenon known as *biopurification* (Burton et al., 1999). Interestingly, during human growth, discrimination against Sr and Ba relative to Ca ions progressively increases, becoming significant at around one year of age (Price et al., 1986). This suggests that the Sr/Ca and Ba/Ca ratios in infant plasma should closely align with the values of the dietary inputs. Published data indicates that mammary glands exhibit greater discrimination for strontium (2.5-fold) compared to the placenta (1.7-fold), resulting in average strontium-to-calcium values in breastmilk being lower than those in the umbilical cord (fetal) values (Nava et al., 2020; Rossipal et al., 2000). Importantly, the chemical composition of fetal blood is preserved in prenatal dental enamel, while postnatal enamel reflects breastmilk consumption. Consequently, elevated Sr/Ca signals in prenatal areas, followed by reduced postnatal Sr/Ca levels, serve as indicators of breastmilk consumption (Humphrey, 2014; Humphrey et al., 2008a; Nava et al., 2020).

Unlike Sr, interpreting Ba/Ca data is challenging due to conflicting data in the literature and a lack of studies on barium metabolism (Krachler et al., 1999a; Peek and Clementz, 2012). Research on dental enamel indicates that barium generally behaves similarly to strontium, decreasing with breast milk consumption and increasing with the introduction of transitional foods (Peek and Clementz, 2012). However, barium's behaviour in tooth enamel appears to be less predictable than that of strontium, possibly due to the high variability of barium content in human milk, colostrum, and formulas (Krachler et al., 1999b; Müller et al., 2019).

In addition to dietary shifts, conducting multi-elemental analyses on teeth using LA-ICPMS (Fig. 2) can provide insights into health issues and exposures to toxic trace metal(loid)s, such as cadmium (Cd), mercury (Hg) and lead (Pb), during in-utero development, infancy, and childhood (Gerbi et al., 2022; Maret, 2022; Needleman et al., 1979; Schilfroth et al., 2023). This helps identify exposure events during critical life stages, such as, for example, brain development. Moreover, peaks of specific trace elements are expected within dentine and enamel during stress and/or pathological events, due to the rebuffing of elemental stores from the skeleton or deficiency (Austin et al., 2016; Müller et al., 2009; Obtel et al., 2022).

The study of the spatial distribution of trace elements by LA-ICPMS can be achieved with two main different approaches: 1) histologically-driven profile analysis, according to specific tooth growth trajectories previously determined by histomorphometry (e.g. Fig. 6) (Linscott et al., 2023; Müller et al., 2019) or 2) distribution maps across the tooth cross-section (Arora and Austin, 2013; Austin et al., 2013; Dean et al., 2019; Hare et al., 2011; Joannes-Boyau et al., 2019; Smith et al., 2018a).

Both methodologies retain their merits and limits. For example, while the former method does not yield a broad overview of the element distribution across the tooth, it does provide better lateral resolution coupled with much faster analytical time. In this sense, the method defined by Müller et al. (2019) proposes to analyze at least two LA traces along the EDJ of both buccal and lingual aspects, in which the enamel maturation overprint is minimal and the contribution of the secretion signal is maximal. In addition, at least two LA tracks are analyzed along two different enamel prisms. These serve as a control for an evaluation of the EDJ signal – although prisms are partially overprinted by maturation and thus monitor the topographic changes in enamel, e.g. the expected increase of Zn that is upregulated toward the outer enamel (Müller et al., 2019). On the other hand, the 2D-mapping approach offers a better overall view of the elemental distribution of the sample, but it is time-consuming and less spatially resolved; also, elemental images are difficult to convert to days of life due to the non-linear time of secretion across the enamel (Austin et al., 2016). Ultimately time-resolved profiles remain the gold standard for life history

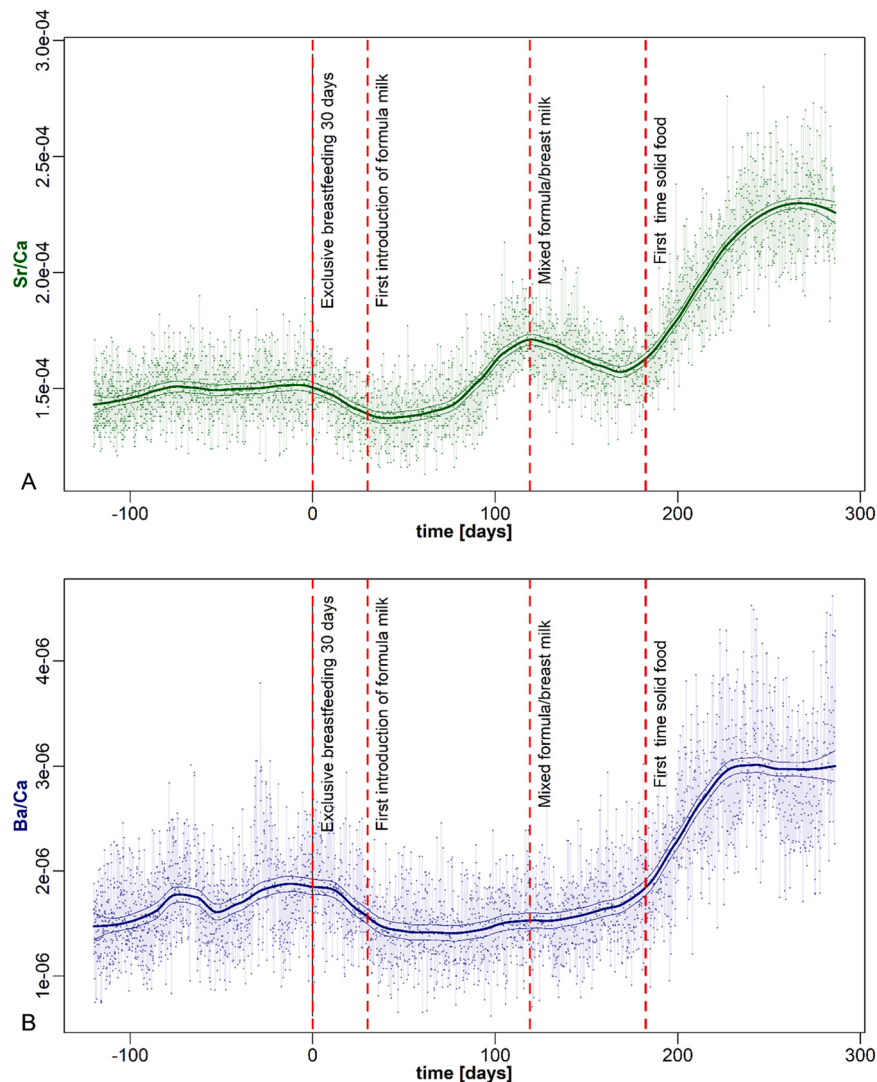


Fig. 6. Sr/Ca (A) and Ba/Ca (B) profiles along the EDJ in a contemporary individual with a known dietary history. The vertical black lines indicate the major events in the first 9 months after birth. Data from [Nava et al. \(2020\)](#).

reconstructions whether directly analysed or reconstructed from 2D maps.

When coupled with a multi-collector ICPMS, laser ablation sampling allows the reconstruction of high-temporally resolved (sub-monthly) mobility histories of individuals. This is accomplished by measuring the $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratio – a common proxy for provenance due to its link with the local geology (see e.g. [Bentley, 2006](#) for a review) – along the EDJ, thus obtaining isotope profiles that represent (possible) mobility events during specific stages of life ([Lugli et al., 2022b](#); [Müller and Anczkiewicz, 2016](#)). These data can be compared with local proxies and regional/national scale *isoscapes* (i.e. isotope maps, [Bataille et al., 2020](#); [Lugli et al., 2022a](#)), to possibly resolve the movements of the individual across the landscape ([Lugli et al., 2022b](#)) (see as an example [Fig. 7](#)). Moreover, examining deciduous teeth or permanent first molars that develop during pregnancy and early childhood provides insights into maternal movements. This information, especially among hunter-gatherer groups, can be extrapolated to encompass the entire human group or family, which is important to study the life histories of prehistoric communities ([Lugli et al., 2017, 2022b](#); [Nava et al., 2020](#)).

7. Conclusions: dental microstructure, life history, evolution of human cooperation and cognition, and clinical relevance - looking forward

Dental enamel, which is the focus of the present review, tells us about early nursing history and childhood life history events which are unquestionably vital demographic components that help reveal how population structure comes to be. Additionally, the other dental tissues, i.e. dentine and cementum, can record other human life history benchmarks like age at first reproduction, parturition and interbirth intervals. Human permanent enamel formation continues into the adolescent years, root dentine is complete at about 23 years of age ([AlQahtani et al., 2010](#)), while cementum grows continuously from tooth eruption until death. Accentuated lines in the third molar tooth (wisdom tooth) root can record evidence of parturition during adolescence ([Dean and Elamin, 2014](#)), although there are challenges in accurately accessing this information ([Liversidge, 2008](#); [Zandi et al., 2015](#)).

Cementum coats the external surface of the root, starting its deposition after a tooth has erupted, ([Perrone et al., 2022](#)). Unlike enamel and dentine, which form with a circadian rhythm, cementum increments form over an annual cycle and because this continues throughout an individual's life it can be drawn upon to estimate adult age-at-death.

Additionally, cementum can inform on important adult life history

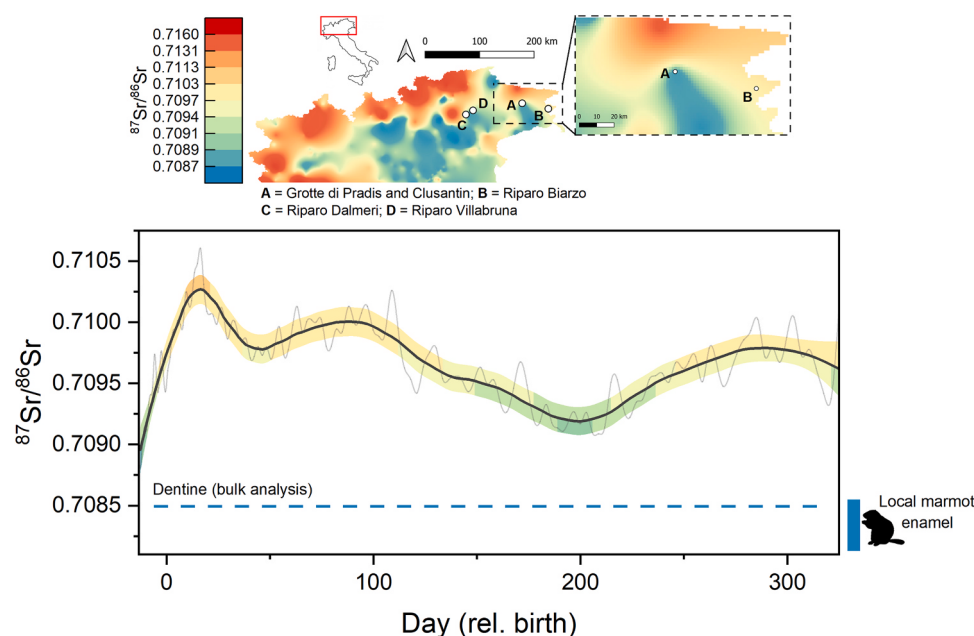


Fig. 7. Time-resolved Sr isotope profile measured along the EDJ of Pradis 1 tooth enamel (top panel); the signal is smoothed through a locally weighted polynomial regression fit (LOWESS), with its associated standard error (± 2 SE); the 2 SE bands are color-coded according to the isoscape ranges of the bottom panel. Reference local values (marmots' enamel and Pradis 1 dentine) are also reported in the graph as a comparison. The Sr isoscape model reported in the bottom panel is from [Lugli et al. \(2022a\)](#) and represents the isotope variability of the bioavailable Sr pool in Northern Italy. Overall, the human group from Grotte di Pradis was seasonally mobile, with Sr isotope values not compatible with the site. This figure is modified from [Lugli et al. \(2022b\)](#).

events such as parturition ([Newham and Naji, 2022](#)) and menopause ([Cerrito et al., 2020; Newham and Naji, 2022](#)) and therefore holds great potential for studying the evolution of these events.

Reconstructing the evolution of human life history through the analysis of dental microstructure has implications for our understanding of the evolution of human cooperation cognition and communication ([Hrdy and Burkart, 2020; Van Schaik and Burkart, 2010](#)). As reviewed above, teeth contain a faithful record of an infant's age at weaning, which in humans is much earlier (both chronologically and in terms of neural development) than expected for a primate of our body size ([Hawkes and Finlay, 2018; Robson et al., 2006](#)). Such early age at

weaning is correlated, both in humans ([Kramer, 2010](#)) and across mammals ([Cerrito and Spear, 2022](#)), with the presence of alloparental care: if help is available, mothers can wean their infants earlier and resume cycling, thus increasing their reproductive frequency. In turn, the reliance on alloparental care during a critical period in brain development exposes the maturing brain to a variety of social interactions on which the infant's life depends upon – making the infant also susceptible to develop impairments in adult socio-cognitive abilities shall it experience social adversities during childhood (e.g. [Dunn et al., 2013; Germine et al., 2015](#)). The developing infant must learn to elicit care from non-maternal caregivers who are not hormonally primed to do

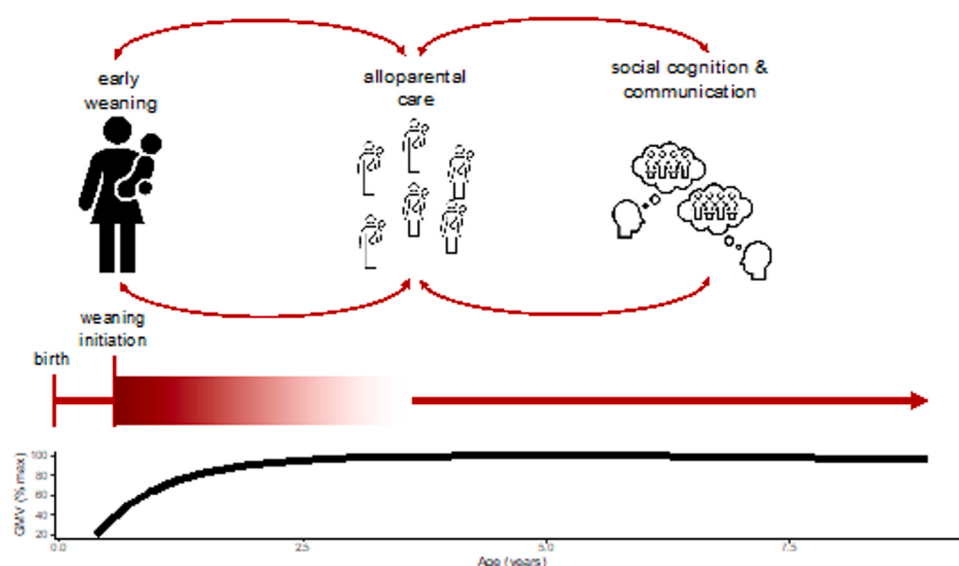


Fig. 8. Developmental trajectory of gray matter volume (GMV) in humans (data from [Bethlehem et al. 2022](#)) in relation to age at weaning and consequent infant-caregiver interactions. Age at weaning initiation is reported as 6 months (based on [World Health Organization, 2023](#)) while the transitional period is extremely variable between cultures ([Sellen, 2009](#)) and is represented here by a shaded area terminating between 2 and 3 years of age. After weaning initiation, and exactly during a critical period of brain development, human infants begin engaging in care-eliciting behaviors with a multitude of adults, thus “tuning” their social brain.

so. Comparative research has shown that the elicitation of care from non-maternal caregivers has co-evolved with brain structures involved in both non-verbal communication (Cerrito and DeCasien, 2021) and emotion regulation (Cerrito and Burkart, 2023). It is therefore during the earliest stage of postnatal development (0–2 years) that the brain circuitries involved in social cognition are “tuned” (Grossmann and Johnson, 2007). It is the interaction between “nature” (neurodevelopmental trajectory) and “nurture” (presence of alloparents as functionally correlated with early weaning) that sets the stage for the development of the social brain (Kenkel et al., 2017) (Fig. 8). However, despite the importance of understanding our unusually-early age at weaning, little is known regarding its evolution during the process of hominization (last 6–8 million years). Indeed, while it seems that Neanderthal age at weaning was similar to that of modern humans (Nava et al., 2020) almost nothing is known regarding other hominin species (but see Joannes-Boyau et al., 2019). Future work on fossil deciduous teeth will therefore be instrumental for the reconstruction not only of our early life-history events but also of our cooperative and cognitive traits that likely co-evolved with our nursing practices.

Besides reconstructing past individuals' life histories, teeth also can function as a retrospective archive of somatic growth trajectories, stress, and environmental exposures for contemporary individuals, with clinical relevance. Perinatal exposure to toxins and other environmental chemicals is linked to health issues in children, including impaired neurodevelopment and metabolic syndrome (Salazar et al., 2021; Sanders et al., 2018; Wang et al., 2014). Prenatal exposure to increased testosterone concentrations such as in mothers affected by polycystic ovary syndrome (Cherskov et al., 2018), has been linked to the development of autism spectrum disorder (Baron-Cohen et al., 2006). Given the potential of teeth in maintaining a record of systemic levels of steroid hormones (Quade et al., 2021), future research can shed light on both the evolution of the maternal endocrine system during gestation, and on the potential implications that this had on neurodiversity in past populations. Aside from chemical exposure, other early life circumstances, including stress and adversity, have a proven effect on an individual's brain development (Scheinost et al., 2016), with possible adverse effects on mental health later in life (Ben-Shlomo and Kuh, 2002; Dunn et al., 2018). As such, monitoring, prevention and intervention during sensitive periods of development are crucial to paediatricians and epidemiologists. While clinicians routinely have access to biomarkers like blood, saliva, and urine for health monitoring of both mothers and perinates, such markers often lack the precision required to study crucial vulnerability windows. Additionally, such samples merely offer a snapshot in time rather than recording an incremental record, the former potentially not being fully representative given the well-documented seasonal variability of blood Pb levels (e.g. Filippelli et al., 2005). Teeth however can register both prenatal and postnatal exposure histories of individuals, and in the last decade, there has been a growing recognition among clinical researchers of the temporal registration and archival potential of teeth in such contexts (Andra et al., 2015; Arora and Austin, 2013; Davis et al., 2020; Dunn et al., 2022). Additionally, the non-invasive nature of deciduous tooth sample collection, as they are naturally exfoliated starting around the age of 6, makes them a powerful potential biomarker for retrospective assessment of maternal and fetal health during pregnancy and early life.

Recent work by Davis et al. (2020) pointed out how specifically insights learned from biological anthropology could be applied to establish new lines of clinical research on the use of teeth as biomarkers to guide disease prevention (Davis et al., 2020), serving as a first-line asset for early screening and interventions to prevent future illness (Davis et al., 2020; Dunn et al., 2022). For example, Mahoney et al. (2022) observed a link between the RP of deciduous molars, maturation rates and obesity in a prospective cohort study of young adolescents. As such, biological anthropological studies contribute both to the study of the human past as well as modern human environmental adaptation and interaction. In return, if clinical studies of dental microstructure can be

implemented on a large scale, combining histological and chemical temporal registered data with fine-grained life history data from well-documented cohort studies (e.g. Dunn et al., 2019; Fraser et al., 2013; Stein et al., 2015) there is great potential to put archaeological and bioanthropological studies of teeth in a broader context: Modern cohort studies can contain a wealth of highly detailed life history and demographic details of individuals to whom the deciduous teeth belonged before being naturally exfoliated. Such detailed information can give us a much better understanding of the underlying drivers of individual variation in dental development and pathways in which chemical and stress signatures get integrated into an individual's dental microstructure. The level of detail available via cohort studies could never be obtained from the archaeological record alone, and as such, teeth are a truly versatile medium to study life history with implications for human evolution in deep and recent times.

Declaration of Competing Interest

None

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