

# Methods and Perspectives on the Study of Hominin Adult Life History

## Methoden und Perspektiven zur Erforschung der Lebensgeschichte erwachsener Homininen

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### ABSTRACT

Human life history is distinct from that of our closest living relatives, the great apes. In some regards it has slowed down (e.g., increased longevity, later age at first reproduction), while in others it has accelerated (e.g., earlier age at weaning). However, the evolution of our specific patterns of growth, development, and reproduction remains poorly understood. This paper first reviews the salient features of human life history. It then highlights key unresolved questions regarding its evolution, such as that of short interbirth intervals and significant female post-reproductive lifespan. Lastly, it provides an overview of the biological structures—mainly bone and dental cementum—that can be used to reconstruct and estimate the timing of adult life events, and it outlines promising directions for future research on this subject.

**Keywords:** Life history, mineralized tissues, dental histology

### ZUSAMMENFASSUNG

Die Lebensgeschichte des Menschen unterscheidet sich von der unserer nächsten lebenden Verwandten, den Menschenaffen. In mancher Hinsicht hat sie sich verlangsamt durch z.B. erhöhte Langlebigkeit oder dem späteren Alter bei der ersten Fortpflanzung, während sie sich in anderer Hinsicht beschleunigt hat wie beim früheren Alter der Mutter beim Abstillen. Die Evolution unserer spezifischen Muster von Wachstum, Entwicklung und Fortpflanzung ist jedoch nach wie vor unzureichend verstanden. In diesem Artikel möchte ich zunächst die offensichtlichen Merkmale der menschlichen Lebensgeschichte überprüfen. Anschließend hebe ich wichtige ungelöste Fragen bezüglich ihrer Evolution hervor, beispielsweise die von kurzen Geburtenabständen oder einer signifikanten postreproduktiven Lebensspanne von Frauen. Abschließend möchte ich einen Überblick über die biologischen Strukturen – hauptsächlich Kno-

chen und Zahnzement – geben, die zur Rekonstruktion und Schätzung des Zeitpunkts von Ereignissen im Erwachsenenleben verwendet werden können, und vielversprechende Richtungen für zukünftige Forschungen zu diesem Thema skizzieren.

**Schlagwörter:** Lebensgeschichte, mineralisiertes Gewebe, Zahn Histologie

## Human life history

Humans are part of the great ape clade and are the only extant species of the genus *Homo*. Although there is some variation within our species, the life history profile of *Homo sapiens* is notably distinct from that of our closest living relatives, chimpanzees and bonobos, and is likely derived from our last common ancestor (LCA) (Bribiescas 2020; Hill and Kaplan 1999; Kaplan et al. 2000; Mace 2000; Robson et al. 2006; Robson and Wood 2008; B. H. Smith and Tompkins 1995; Volk 2023). Understanding how, when, and in response to which selective pressures this unique life history profile evolved remains a key question in evolutionary anthropology.

Over the years, research on hunter-gatherer populations has provided valuable insights into the human life history profile in conditions that resemble those predating agriculture and modern medicine (Volk 2023). These populations offer a glimpse into the reproductive profiles, population densities, and mortality patterns that shaped our species' development before the advent of agriculture and medical advancements (Mace 2000; Page et al. 2018, 2024, 2025; Robson et al. 2006; Walker et al. 2006).

One of the most striking features of human life history is our extended lifespan, which cannot be explained by an increase in body size. Hunter-gatherer populations have a modal observed lifespan ranging from 68 to 79 years (Gurven and Kaplan 2007), while other great apes typically have maximum lifespans of 50 years in bonobos to 58 years in orangutans (Robson et al. 2006). Human longevity is primarily the result of reduced adult mortality, which derives from a combination of genes, environment, resiliency, and chance (Pignolo 2019), and it has been argued to being a self-reinforcing and positively-selected life-history trait (Carey and Judge 2001). However, for selection to favor slower rates of aging—characterized by declining physiological performance—the fitness benefits of maintaining physical performance must outweigh the costs of increased energy expenditure for maintenance and repair. While comparative primate data on aging progression is still limited, recent studies are expanding rapidly (Colchero et al. 2021; Emery Thompson et al. 2020). These studies highlight the need for caution when making cross-species inferences, as similarities in aging processes across species, such as humans and chimpanzees, do not necessarily correspond to similar functional outcomes (e.g., musculoskeletal aging may differ based on species' physical demands).

With increased human longevity comes a delayed age at first birth (AFR) relative to great apes (Konner 2017). This delay is relatively constant even in post-agricultural societies, according to historical records (Le Bourg et al. 1993; Pettay et al. 2005). In nomadic foragers with natural fertility, the average AFR is about 19 years, while AFR in great apes ranges from 10 years in gorillas to 15 years in orangutans (Emery Thompson and Sabbi 2019). Similarly, human gestation

is 10 to 30 days longer than in other great apes, which correlates with the larger infant size at birth (Emery Thompson and Sabbi 2019).

While AFR and gestation duration align with the increase in body mass and longevity, a derived aspect of human life history that contradicts these trends is the relatively short interbirth interval (IBI). In human hunter-gatherers, the mean IBI is 3.7 years, and the average age at weaning is approximately 2.5 years (Konner 2017; Mace 2000; Robson et al. 2006; Walker et al. 2006). In comparison, chimpanzees and orangutans have IBIs that are roughly twice as long: 4.5 years for chimpanzees, 7 years for orangutans (Robson et al. 2006). This is remarkable because, in all other aspects, human life history has slowed relative to the presumed ancestral (ape-like) state. Thus, human life history cannot be reduced to a simple shift, comparing to great apes, towards the K-end of the r/K spectrum (MacArthur and Wilson 1967).

Another unique life history trait of humans, shared with only a few non-terrestrial mammals, is the presence of a significant post-reproductive lifespan (PRLS) (Ellis et al. 2018). Theoretical work over the past 50 years has provided a framework for understanding senescence (the gradual deterioration of functional characteristics) in general, but it remains difficult to explain the decoupling of somatic and reproductive senescence (Kirkwood and Shanley 2010). Typically, somatic and reproductive senescence are linked: maintaining a functional germline is unlikely to be advantageous if somatic decline hinders the production of fertile offspring (Jones et al. 2014). However, in a few species, the two processes are decoupled—either somatic senescence is delayed or reproductive senescence is accelerated. This results in an extended PRLS, which has evolved independently at least three times in mammals, including primates (Ellis et al. 2018). In humans, the most plausible explanation for the evolution of a significant PRLS is the delay of somatic senescence, with reproductive decline proceeding at a constant rate, as it occurs at a similar age than in chimpanzees (Wood et al. 2023). Given the limited comparative sample, phylogenetically informed studies of the evolution and adaptive significance of PRLS are challenging. Some argue that PRLS is an adaptive trait (Brent et al. 2015; Cant and Johnstone 2008; Hawkes et al. 1998; Lahdenperä et al. 2004), while others consider it either widespread across species (Austad 1997; Cohen 2004; Tully and Lambert 2011) or unique to humans but consistent with life history allometries (Judge and Carey 2000).

Finally, many researchers (Bogin 1997; Konner 2017; Leigh 2001) contend that childhood is a distinct and unique ontogenetic phase in humans. In other primates, newborns transition from infants to juveniles when weaning is complete, meaning that nutritional independence coincides with the end of nursing (Pereira and Leigh 2003). In contrast, human children are weaned before they achieve the anatomical traits (e.g., mature dentition and full motor dexterity) that would allow them to become nutritionally independent. Childhood, therefore, is the period between the end of infancy (~2.5 years) and the beginning of the juvenile stage, during which children are still nutritionally dependent on other group members.

In summary, humans exhibit derived life history traits that deviate from the great ape trend: some traits have slowed down (prolonged lifespan, delayed AFR), others have accelerated (shortened IBI), and still others are entirely novel (childhood and PRLS). While there is consensus

about the emergence of modern human skeletal anatomy in Africa (Hublin et al. 2017) and the dispersal of *Homo sapiens* out of Africa in the late Pleistocene (Harvati et al. 2019), the evolution of the human life history strategy remains an intriguing puzzle that has yet to be fully understood. Our current limited data restricts our ability to test the various hypotheses surrounding this evolution. The following sections will focus explicitly on our current understanding of growth, development, reproduction, and lifespan in fossil hominins.

## Hominin life history

Until now, attempts to understand hominin life history have primarily relied on comparisons between living species, by leveraging phylogenetically conserved relationships between the timing of some life history events (e.g. weaning, AFR) and the value of other variables that can more easily be inferred in the hominin fossil record (e.g., body mass, brain mass, dental eruption times). However, recent advances in methodology offer the potential to reconstruct the changes that occurred during human evolution, allowing us to better understand which traits evolved together, and the timing and potential selective pressures behind their emergence. Following Robson and Wood (2008), a distinction is made between two types of variables (Table 1) that are often confused: life history variables (LHVs) and life history related variables (LHRVs).

## Longevity

The accuracy of estimating chronological age from hard tissues (bones and teeth) declines significantly once growth is complete. This is because most methods of skeletal aging rely on assessing the degree of formation of structures, such as dental development or cranial suture obliteration (Martrille et al. 2007), where the timing of these processes is well characterized in

Variable	Type	Available for extinct taxa
Gestation length	LHV	No
Age at first reproduction	LHV	No
Age at weaning	LHV	Yes
Interbirth Intervals	LHV	No – but is related to Age at weaning
Mean lifespan	LHV	No – but yes for Upper Paleolithic <i>H. sapiens</i>
Maximum lifespan	LHV	No
Adult body mass	LHRV	Yes
Dental formation times	LHRV	Yes
Dental eruption times	LHRV	Yes

**Table 1:** Availability of LHVs and LHRVs for fossil hominin taxa. Modified from Robson and Wood 2008.

**Tabelle 1:** Verfügbarkeit von LHVs (Lebensgeschichtsvariablen) und LHRVs (Lebensgeschichtsratenvariablen) für fossile Homininentaxa. Modifiziert nach Robson and Wood 2008.

modern populations. In contrast, aging adults is based on degenerative processes, such as dental wear, which have much more interindividual variation than developmental processes (McFadden et al. 2019). Evidence suggests that the pace of development in extinct hominins differed from that of modern humans (Bromage and Dean 1985; Dean et al. 2001). Thus, while anatomical developmental milestones can indicate a particular ontogenetic phase, they do not provide a precise estimate of the chronological age at which these milestones are reached.

Current hypotheses on the evolution of human longevity are based on the assumption that body and brain mass are closely linked to lifespan (Robson and Wood 2008; Schwartz 2012). Regressions linking lifespan and body mass in extant primates (Judge and Carey 2000) suggest a significant increase in longevity between *Homo habilis* (52-56 years) and *H. erectus* (60-63 years) around 1.7 to 2 million years ago (Lieberman et al. 2021; Tobias 2006), coinciding with a rapid increase in brain size (Gómez-Robles et al. 2017). However, caution is needed when accepting values inferred from these regressions, as modern humans deviate from such patterns. A demographic approach to understanding longevity, focused on age-structure pyramids (with just two age categories: young and old), based on dental wear in four broadly-defined hominin groups (australopithecines, Early *Homo*, Neanderthals, and Upper Paleolithic humans), suggests that old age only became relatively common in human evolution around 50,000 years ago, particularly among Upper Paleolithic *Homo sapiens* (Caspari and Lee 2004). This finding supports previous research on Neanderthal mortality patterns (Trinkaus 1995).

## Ontogeny

Our current understanding of hominin life history largely depends on patterns of growth and development. Research on this topic falls into two main categories: studies based on known correlations between dental development and the achievement of ontogenetic milestones (e.g., first molar emergence and weaning) (T. M. Smith 2013), which provide relative data, and studies using histological methods, which offer absolute chronological values (reviewed in: Dean 2006).

Several studies examining the correlation between molar emergence and life history variables have been conducted since Adolph Schultz's pioneering work in (Schultz 1949). These studies typically focus on extant humans and great apes (Jeanson et al. 2016; B. H. Smith 1984, 1989; B. H. Smith et al. 1994), so the regressions derived from them are not directly applicable to extinct hominins. Indeed, early radiographic studies and more recent virtual histological analyses have demonstrated that the dental ontogeny of early hominins—such as *Paranthropus*, *Australopithecus* (Bromage 1987; T. M. Smith et al. 2015), early *Homo* (T. M. Smith et al. 2015), *H. erectus* (Dean 2016; Zollikofer et al. 2024), and Neanderthals (T. M. Smith, Tafforeau, et al. 2010) —was distinct, and not simply intermediate between modern apes and humans.

With the introduction of histological methods in dental anthropology, researchers can now assign an absolute chronology to dental ontogeny in individual fossil specimens. This approach reduces the uncertainty associated with inferences drawn from comparative datasets. Since Bromage and Dean's foundational work in 1985, studies on hominin growth and development have rapidly proliferated. Based on dental development, we now know that the maturation rate in

*Paranthropus* (Dean et al. 2020), *Australopithecus*, and *H. erectus* was faster than in modern humans (Dean et al. 2001; Dean and Smith 2009; Zollikofer et al. 2024). Specifically, the age at first molar emergence is estimated to be about 3 years in *Paranthropus boisei*, 3.2 years in *Australopithecus africanus* (Kelley and Schwartz 2012), and 4.5 years in *Homo erectus* (Dean et al. 2001), while in modern humans it is about 6 years. Ontogenetic studies of cranial morphology ontogeny (Antón and Leigh 2003) suggest that *H. erectus* lacked a clear adolescent growth spurt, a hallmark of modern human development. However, the significant morphological variation within *H. erectus*, despite its large geographic and temporal spread, is seen as indicative of developmental plasticity—greater than that of Neanderthals but still not as advanced as in modern humans (Antón et al. 2016).

Recent research on ontogenetic patterns has predominantly focused on Neanderthals (Dean et al. 1986; Guatelli-Steinberg 2009; Hogg et al. 2020; Macchiarelli et al. 2006; Mahoney et al. 2021; McGrath et al. 2021; Nava et al. 2020; Rozzi and De Castro 2004; T. M. Smith et al. 2007, 2018; T. M. Smith, Tafforeau, et al. 2010). These studies collectively suggest that Neanderthal ontogeny was faster than that of modern humans. In summary, no extinct hominin species exhibits growth patterns similar to those of modern humans. The earliest evidence of modern human life history is found in a specimen of *H. sapiens* from around 300,000 years ago at Jebel Irhoud, Morocco (T. M. Smith et al. 2007), which also represents one of the earliest known sites of *H. sapiens*.

### Age at weaning

The earliest hominin species for which we have evidence regarding the age of weaning is *Australopithecus africanus*. Recent work suggests that, in at least one individual, the transition away from a predominantly maternal-milk diet occurred at around one year of age (Joannes-Boyau et al. 2019). After this point, cyclical patterns of elemental composition are observed in the dental enamel, likely reflecting irregular food availability. This supports the long-standing hypothesis that, over the course of hominin evolution, there has been a trend toward an earlier weaning age, with modern humans weaning earlier than extant *Pan* species. In wild chimpanzees, for example, while there is variation within the species, a significant increase in solid food intake typically begins at around one year of age (Lonsdorf et al. 2020).

Direct evidence for weaning age is also available for Neanderthals. Estimates of the onset of weaning vary, with different studies suggesting ages of approximately 9 months (T. M. Smith et al. 2018), 7 months (Austin et al. 2013), and 6 months (Nava et al. 2020). In modern humans, the typical age of solid food introduction is around 6 months, with ranges in hunter-gatherer populations being 5.0+/4.0 months (Sellen 2001). Collectively, these studies suggest that while there was variability within species, Neanderthals were weaned at a similar age to modern humans. Even if Neanderthals had a slightly later age at weaning than modern humans (T. M. Smith, Tafforeau, et al. 2010), it appears that a human-like age at weaning either evolved before the divergence of humans and Neanderthals or developed independently in both lineages, with the former scenario being the more likely and parsimonious explanation.

## Reproduction, menopause and other open questions

While some direct evidence exists for the timing of early life history milestones in extinct hominins, much less is known about milestones occurring later in life. Until recently, methods for studying interbirth intervals (IBIs) and post-reproductive lifespan (PRLS) in fossil specimens have been unavailable. Although a minimum IBI can be deduced from the age at weaning, determining the upper limit or typical value remains elusive and may depend on factors like allo-maternal support, especially in cooperatively breeding species such as humans and marmosets (Brügger and Burkart 2021; Hrdy 2009).

This scarcity of data poses challenges for addressing several key questions: I) When did a post-reproductive lifespan first evolve?; II) did the emergence of PRLS align with reduced IBIs, as proposed by the grandmother hypothesis (Hawkes et al. 1998)?; III) or did changes in IBIs coincide with the development of a cooperative breeding system (Burkart et al. 2009), akin to that of callitrichids, where older siblings rather than grandparents provide care?

Currently, evidence on these topics is limited. The earliest signs of older-age individuals (and potentially grandmothers) are found in Upper Paleolithic *Homo sapiens* (Caspari and Lee 2004), with possible reproductive events detected through the analysis of cementum in Neanderthal fossils from Krapina, Croatia (120 kya) (Cerrito, Nava, et al. 2022).

To summarize, certain elements of recent human life history align with a “live slow” strategy, while others suggest a “live fast” approach. A central question in hominin life history research is whether the modern human life history profile evolved as a single, unified framework or through a mosaic process involving staggered shifts in timing across hominin evolution. Among the most derived features of human life history are shortened IBIs and extended PRLSs (Hawkes et al. 1998). However, it remains unclear if these traits evolved simultaneously. Notably, humans are unique among primates in decoupling the age at weaning from the eruption of the first permanent molar (Robson et al. 2006). Some researchers propose that prolonged infant reliance on adult-provided food may be connected to a cooperative breeding system (Hawkes et al. 1998; Hrdy 2009; Kramer 2010; Kramer and Otárola-Castillo 2015; van Schaik and Burkart 2010). To further investigate the relationship between cooperative breeding and grandmothers (as distinct from other forms of alloparenting) (Hawkes et al. 1998), it is crucial to examine the frequency of female reproductive output and the duration of the female post-reproductive phase.

The next section examines the analytical methods that can help infer the frequency of female reproductive events and estimate the age of menopause. These approaches may provide valuable insights into unresolved questions about the evolutionary trajectory of human life history.

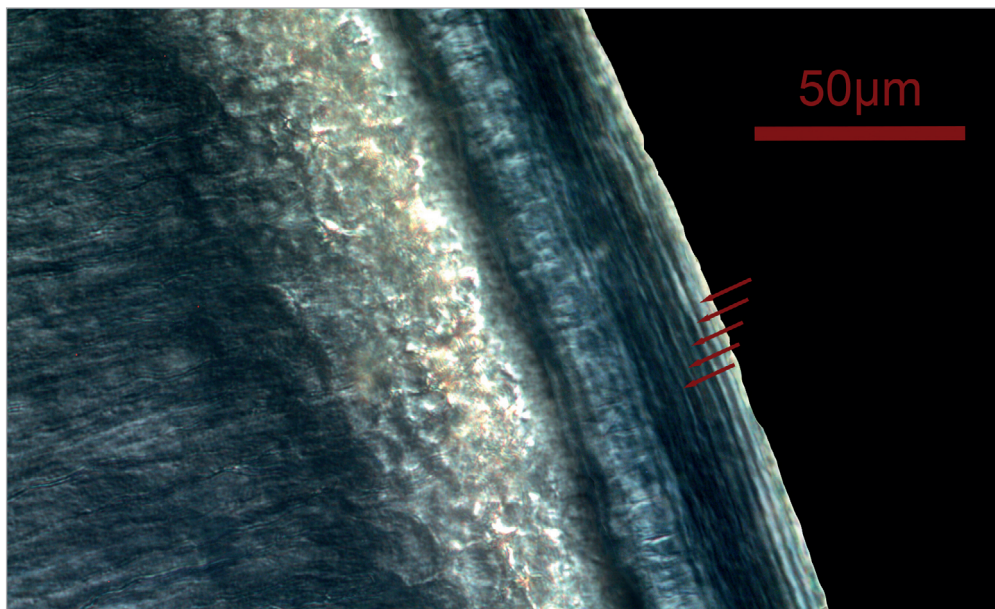
## The skeleton as a dynamic organ

In mammals, skeletal physiology is implicated in energy metabolism, endocrine regulation, and overall mineral homeostasis (DiGirolamo et al. 2012). As a result, it both reflects and influences internal metabolic rhythms (Bromage, Idaghdour, et al. 2016) and responds to environmental cycles (Doherty et al. 2015). Furthermore, skeletal physiology responds to, and plays a role in, various physiologically significant events (Carrel 1994; Dirks et al. 2002; Lemmers et al. 2021)

and adapts to changes in the environment (Bromage et al. 2011; Cipriano 2002; Hamilton et al. 2021). Since the present article addresses the timing of life history events, I will focus on how the skeleton tracks internal metabolic changes, but I will not review how it responds to external (e.g., environmental, climatic) ones.

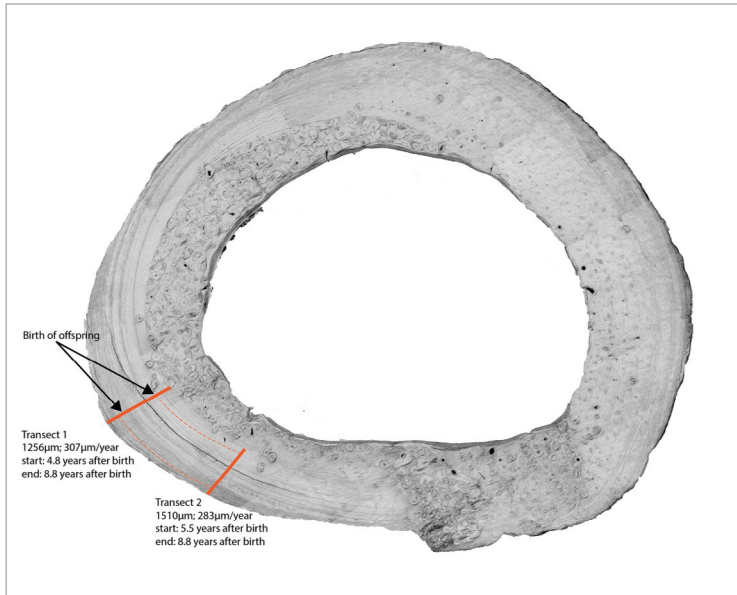
Much of what we know about the timing of life history variables (LHVs) in fossil specimens comes from histomorphological or elemental analyses of teeth, which serve as recording structures. Recording structures (Klevezal 1995) include a variety of animal tissues, such as mollusk shells, scales, otoliths, dental cementum (Fig. 1), bone (Fig. 2), enamel, dentine, claws, nails, horns, and even ear plugs (Trumble et al. 2018). These structures are periodically layered, with each layer being deposited in sequence, and are often referred to as “growth layers.” The layers reflect changes in micromorphology that correspond to shifts in the organism’s physiological state. Different tissues have distinct layer characteristics. For instance, cementum and dentine show bands of varying transparency, while horns exhibit alternating ridges and grooves.

Recording structures can be categorized based on three parameters (Klevezal 1995): sensitivity, which refers to how frequently new layers are added; the period of registration (the time frame



**Fig. 1:** Micrograph obtained in differential interference contrast lighting (DIC) of the cross section of a human lower canine. On the left, the dentine; on the right, the yearly cementum annuli, some of which are indicated with the red arrows.

**Abb. 1:** Mikrofotografie, aufgenommen mit differenziellem Interferenzkontrastlicht (DIC), des Querschnitts eines menschlichen unteren Eckzahns. Links das Dentin; rechts die jährlichen Zementannuli, von denen einige mit den roten Pfeilen markiert sind.



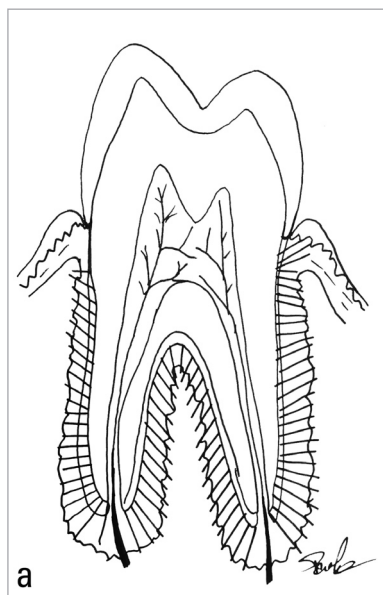
**Fig. 2:** Montaged micrograph of a macaque femur obtained in reflected light. The red lines indicate two transects of primary lamellar bone, where chronology reconstruction is possible. The black arrows and dashed red lines indicate the bone formed during the birth of offspring. For each transect the figure reports the length in micrometers; the yearly growth rate; the age range covered by the transect. For a description of the method used to derive the ages, see the methods section of (Cerrito, Hu, et al. 2022). Figure from Cerrito, Hu, et al. 2022.

**Abb. 2:** Montierte Mikrofotografie eines Makakenfemurs, aufgenommen mit Auflicht. Die roten Linien zeigen zwei Transektabschnitte des primären lamellären Knochens, wo eine Chronologie-Rekonstruktion möglich ist. Die schwarzen Pfeile und gestrichelten roten Linien markieren den Knochen, der während der Geburt von Nachkommen gebildet wurde. Für jeden Transektabschnitt zeigt die Abbildung die Länge in Mikrometern, die jährliche Wachstumsrate und den Altersbereich, der vom Transekt abgedeckt wird. Für eine Beschreibung der Methode, die zur Ableitung der Altersangaben verwendet wurde, siehe den Methodenabschnitt von (Cerrito, Hu, et al. 2022). Abbildung aus Cerrito, Hu, et al. 2022.

during which the structure records); and the persistence of the record (how long the structure retains the recorded layers unchanged). The sensitivity of a structure depends on both its structural complexity (Ryan et al. 2020) and its growth rate. For example, in humans, the recording unit in bone is the lamella, while in enamel, the corresponding unit includes multiple smaller increments known as cross-striations (Hogg 2018). This means that for the same time period, enamel has approximately 8 layers, whereas bone has only one. The mean thickness of a lamella in a human Haversian system is  $9.0 \pm 2.13 \mu\text{m}$  (Pazzaglia et al. 2012), while the thickness of a daily cross-striation in enamel is  $2.7 \pm 0.43 \mu\text{m}$  (Desoutter et al. 2019). As a result, the same time period is recorded in approximately  $9 \mu\text{m}$  of bone and  $20 \mu\text{m}$  of enamel, making enamel

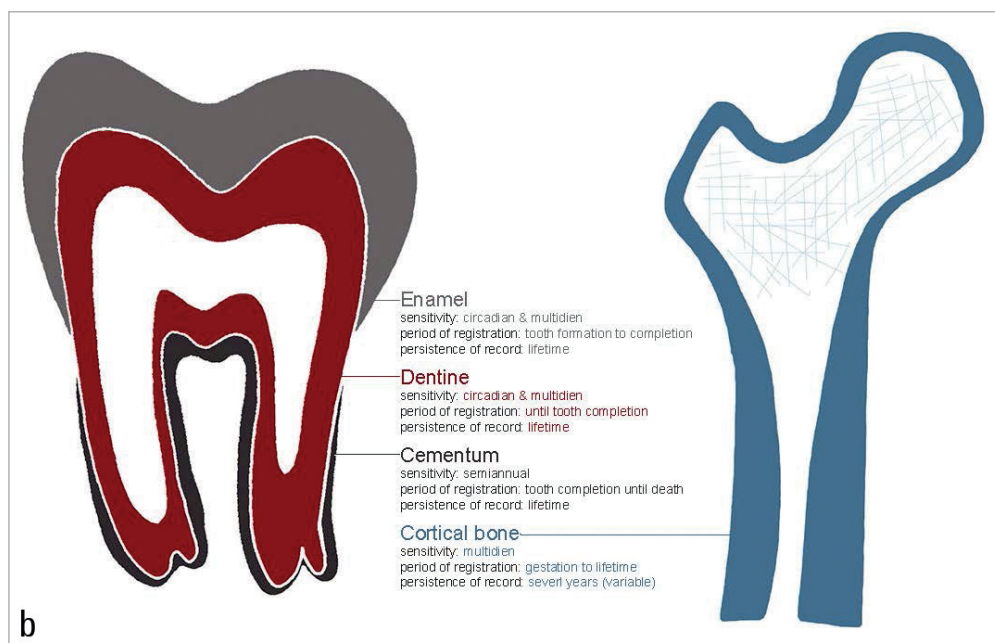
more sensitive than bone. This difference is important when conducting analyses that require high temporal precision, especially when the spatial detection limit of certain instruments (e.g., optical microscopy or laser-ablation mass spectrometry) is considered.

The period of registration refers to the time during which a structure continues to add new layers. In humans, enamel layers stop forming once the tooth crown is fully developed, while bone continues to deposit new layers throughout the individual's life. The persistence of the record is influenced by the turnover rate of the tissue. Enamel does not undergo turnover, while instead bone is resorbed and newly formed in response to both mechanical and physiological demands. This remod-



**Fig. 3a and b:** The three fundamental parameters of the four different “recording structures” present in primates (Klevezal 1995). These parameters determine the suitability of each structure to the different questions in anthropological research.

**Abb. 3a und b:** Die drei grundlegenden Parameter der vier verschiedenen „Aufzeichnungsstrukturen“, die bei Primaten vorkommen (Klevezal 1995). Diese Parameter bestimmen die Eignung jeder Struktur für die verschiedenen Fragestellungen in der anthropologischen Forschung.



eling can cause significant variability in the persistence of the record, even within different bones of the same individual (Fahy et al. 2017). When bone tissue is resorbed, the record contained within it is lost.

In primates, the primary recording structures are bone, dentine, cementum, and enamel. Figure 3 summarizes the temporal characteristics of these four structures. As can be seen in this table, the only two tissues that continue formation throughout an individual's lifetime, and therefore the only two that are capable of recording adult life history events, are cementum and bone. Bone has a higher sensitivity, with a lamella having a period of about eight days in humans (Bromage et al. 2009). However, given its turnover (resorption and new formation) during life, the persistence of the record is limited to some years, making it difficult to derive chronologies for an individual (Fig. 2). On the other hand, cementum has a much lower sensitivity, with a pair of dark and light annuli formed each year (Fig. 1), but it does not undergo remodeling and therefore the record persists unaltered until death.

### Internal environment: metabolism – mediated development

Metabolism in organisms encompasses all chemical processes involved in transforming food into energy (e.g., adenosine triphosphate) and structural molecules (e.g., proteins and nucleic acids), as well as eliminating the waste products generated during these transformations. The rate of metabolic processes, or the “pace of life” (the amount of energy or matter converted per unit of time), is governed by three main periodicities: I) the circadian rhythm, which is highly conserved across species, II) an annual cycle influenced by environmental factors, and III) a multidienn internal rhythm linked to body mass, which nonetheless includes a phylogenetic component. These periodicities regulate the formation of layered structures in hard tissues, forming the basis for estimating age at death and chronologically reconstructing physiologically impactful events, visible as subtle histological changes in these periodic increments.

The circadian rhythm is evident in the daily cross-striations of enamel, resulting from the circadian transcription factors regulating matrix secretion in ameloblasts, the enamel-forming cells (Lacruz et al. 2012).

A much longer cycle, the annual rhythm, also modulates metabolism. This cycle is driven by seasonal variations in sunlight (Gorman et al. 2019) and temperature (Seebacher 2009). These changes manifest as yearly growth lines in hard tissues (Foster and Hujuel 2018). Osteoblasts (bone-forming cells), and likely cementoblasts (cementum-forming cells) due to their similarity, regulate insulin production and adipose tissue metabolism, integrating their high energy demands into the body's overall energy balance, which is affected by thermoregulation (Dirckx et al. 2019; Seebacher 2009).

The multidienn rhythm, known as the Havers-Halberg Oscillation (HHO), modulates metabolic activities that influence variations in the pace of life. This rhythm was first identified in enamel, as accentuated lines with taxon-specific variability. In humans, the HHO cycle averages 8-9 days (Bromage et al. 2009). Research shows that this periodicity correlates with body mass and tissue-specific metabolic rates, with smaller mammals exhibiting faster metabolic rates and

higher HHO frequencies compared to larger mammals (Bromage, Idaghdour, et al. 2016; Karaaslan et al. 2020; MacAvoy et al. 2006). In bone, HHO periodicity influences the density and size of osteocyte lacunae (a small space in the bone containing the osteocyte), with larger individuals displaying increased density and size (Bromage, Juwayeyi, et al. 2016). Furthermore, HHO periodicity governs lamellar increments in hard tissues, with each lamella corresponding to one Retzius periodicity (RP). In dentine and enamel, the number of daily cross-striations between two RPs is used to calculate the RP interval, which reflects the HHO periodicity.

### Adult age estimation

Since the enamel of deciduous teeth begins forming during prenatal development, a Retzius periodicity (RP) increment corresponding to birth is observed. This increment is both histologically accentuated (Weber and Eisenmann 1971) and elementally distinct (reviewed in: Nava et al. 2024). Known as the neonatal line, it provides a clear reference point (birth) from which all subsequent (and prior) increments can be assigned chronological values. Due to the staggered development of different tooth classes, increments in earlier-forming teeth can be matched to those in later-forming teeth, enabling the construction of chronologies that cover the formation times of multiple teeth (e.g., Zollikofer et al. 2024). This approach, which leverages circadian and multidiurnal periodicities, has been applied to estimate the age at death of immature hominin fossil remains (Bromage and Dean 1985; Lacruz et al. 2005; T. M. Smith, Tafforeau, et al. 2010).

For adult individuals, age at death can be estimated using the yearly periodicity of cementum deposition. However, this method is less precise due to the absence of a neonatal line and the need to make assumptions about the age at which cementoblast secretion begins (typically corresponding to gingival emergence). Accurate estimation requires prior knowledge of dental development timelines. Such data is available for many extant primates (AlQahtani et al. 2010; Bolter and Zihlman 2011; Kralick et al. 2017; Liversidge 2008; T. M. Smith 2016; T. M. Smith, Smith, et al. 2010; Trotter et al. 1977; Zihlman et al. 2004) but is more challenging to establish for extinct species.

Despite these challenges, cementum annulations have been widely used to estimate age at death across various mammals (Fig. 1). Examples include rhesus macaques (Kay et al. 1984; Kay and Cant 1988), horses (Prilepskaya et al. 2020), several cervid species (Takken Beijersbergen 2019; Veiberg et al. 2020), bears (Christensen-Dalsgaard et al. 2010), bats (Cool et al. 1994), extinct stem mammals (Newham, Gill, et al. 2020), Jurassic fossil specimen (Panciroli et al. 2024), extinct hominins (Cerrito, Nava, et al. 2022; van Heteren et al. 2023), as well as contemporary (Sultana et al. 2021; Wittwer-Backofen et al. 2004) and archaeological humans (Großkopf 1990; Huffman and Antoine 2010; Le Cabec et al. 2019; Tanner et al. 2021).

### Internal environment: maintenance of homeostasis with changing physiology

During significant physiological events such as birth, weaning, or menopause, organisms must adjust to maintain homeostasis (Gross 1998) while efficiently managing energy availability. Given the systemic complexity of organisms, these homeostatic adaptations involve multiple

systems and organs. Consequently, changes in reproductive physiology and nutrition are closely linked to skeletal alterations.

The skeleton and the endocrine system are interconnected through several proximate mechanisms, to the extent that the skeleton is sometimes described as an endocrine organ (DiGirolamo et al. 2012; Fukumoto and Martin 2009; Guntur and Rosen 2012). Acting as the largest reservoir of calcium and phosphate, bone plays a key role in regulating the balance of these elements. Parathyroid hormone (PTH) and vitamin D elevate serum calcium and phosphate levels by promoting bone resorption and enhancing intestinal absorption, whereas FGF23, a hormone produced by bone, reduces these concentrations (Bergwitz and Jüppner 2010). Bone is also involved in energy and feeding regulation through a hypothalamic-osteoblastic-endocrine loop. In this loop, leptin signals osteoclasts to suppress bone formation and increase resorption (Ducy et al. 2000). Conversely, osteocalcin, a protein specific to bone and cementum and expressed by osteocytes, osteoblasts, and cementocytes (Kagayama et al. 1997), increases insulin secretion (Lee et al. 2007) and stimulates testosterone production (Karsenty and Oury 2014).

Cementum (Silk et al. 2008) and bone (Cauley 2015; Gillies 2017) are both highly responsive to estrogen levels. Estrogen facilitates calcium storage in preparation for reproductive events, while declining estrogen levels—such as during menopause—lead to increased osteoclastic activity and a net loss of bone tissue (Ahlborg et al. 2003). These effects occur across females of various ethnic groups (Finkelstein et al. 2008) and are associated with changes in hydroxyapatite (HA) crystal size and orientation (Burnell et al. 1982; Turunen et al. 2016) as well as cortical bone porosity and mineralization (Sharma et al. 2018).

Other reproductive hormones, such as prolactin (PRL) and oxytocin (OT), also influence the skeleton. PRL receptors are expressed in osteoblasts, and mice lacking these receptors exhibit reduced bone mass due to increased turnover and net bone loss (Clément-Lacroix et al. 1999; Seriwatanachai et al. 2008). OT supports bone (Colaianni et al. 2012) and cementum (Colaianni et al. 2012) by promoting cell proliferation, migration, and differentiation, leading to tissue growth. This aligns with OT's reproductive role and the substantial transfer of calcium and phosphorus from mothers to offspring during lactation, necessitating rapid bone mass recovery post-lactation (Kovacs 2016).

Unsurprisingly, elemental and histological changes in bone and cementum have been associated with life history events like reproduction (Carrel 1994; Cerrito et al. 2020, 2021, 2023; Cerrito, Nava, et al. 2022; Medill et al. 2010; Von Biela et al. 2008; Wittwer-Backofen et al. 2004). Mineral and hormonal fluctuations are recorded in mineralized tissues, preserving these changes during tissue formation.

Zinc concentrations in cementum have been shown to reflect the onset of sexual maturity in walrus (Clark et al. 2020), while declining fertility correlates with increased copper levels in rat teeth (Rahnama 2002). Moreover, lead and cobalt levels in human dentine exhibit sexual dimorphism (Kumagai et al. 2012), as do the relative concentrations of elements in macaque cementum (Cerrito et al. 2023).

Histological changes in cementum linked to reproductive events have been observed in several species, including bears (Carrel 1994; Coy and Garshelis 1992), sea otters (Von Biela et al. 2008), humans (Cerrito et al. 2020; Cerrito, Nava, et al. 2022), and macaques (Cerrito et al. 2021, 2023). Similarly, dentine displays accentuated lines associated with human parturitions (Dean and Elamin 2014). Table 2 summarizes life history variables recoverable from hard tissues, alongside the tissue types, methodologies, and relevant references.

A few studies have demonstrated the potential to recover hormonal concentrations preserved within human dental tissues (Nejad et al. 2016; Quade et al. 2021, 2023) and those of other marine mammals (Hudson et al. 2021).

Life history Variable	Tissue	Method	References
Prenatal growth	Enamel (deciduous teeth)	Histological analysis	(Mahoney 2015; Nava et al. 2017)
Age at weaning	Enamel (deciduous teeth)	Histological + Elemental analysis	(Nava et al. 2024; T. M. Smith et al. 2023)
Age at menarche	Cementum (permanent teeth)	Histological analysis*	(Cerrito, Nava, et al. 2022)
Reproductive events	Dentine (permanent 3rd molar)	Histological analysis*#	(Dean and Elamin 2014)
Reproductive events	Cementum (permanent molars)	Histological + Elemental analysis	(Cerrito et al. 2020, 2023; Wittwer-Backofen et al. 2004)
Menopause	Cementum (permanent molars)	Histological analysis*	(Cerrito et al. 2020; Cerrito, Nava, et al. 2022)
Infant age at death	Enamel (deciduous teeth)	Histological analysis	(Bromage and Dean 1985)
Adult age at death	Cementum (permanent teeth)	Histological analysis	(Le Cabec et al. 2019; Newham et al. 2021; Wittwer-Backofen et al. 2004)

**Table 2:** Summary of the life history variables that can be recovered from hard tissues, together with the type of tissue, the methodologies and some relevant references. \*Additional method development is necessary to determine the elemental signature of the event in order to differentiate its histological signal from that of other physiologically impactful events; #Only captures reproductive events occurring until dentine formation is completed (~19 years of age).

**Tabelle 2:** Zusammenfassung der Lebensgeschichtsvariablen, die aus Hartgeweben gewonnen werden können, zusammen mit dem Gewebetyp, den Methoden und einigen relevanten Referenzen. \*Zusätzliche Methodenentwicklung ist erforderlich, um die Elementarsignatur des Ereignisses zu bestimmen, um sein histologisches Signal von dem anderer physiologisch wirksamer Ereignisse zu unterscheiden; #Erfasst nur reproduktive Ereignisse, die bis zum Abschluss der Dentinbildung stattfinden (~19 Jahre alt).

## Conclusion

The combined literature reviewed here indicates that: 1) cementum reliably records adult physiological stressors in humans and non-human primates; 2) that such information can be recovered non-destructively; and 3) that the method can be applied to the hominin fossil record. Furthermore, recent work on non-human mammals (Cerrito et al. 2023; Clark et al. 2020) provides a methodological framework to overcome a long-standing caveat of histological research applied to life-history studies, by showing that changes in reproductive physiology (onset of menarche, reproduction) can be recovered and timed via the analysis of element concentrations in cementum. Furthermore, the combined evidence of elemental analysis of both cementum (Cerrito et al. 2023) and bone (Cerrito, Hu, et al., 2022) in the same individuals provides evidence for the potential of using a systemic approach when investigating single fossil elements since the same elemental signal is recoverable in different tissues of the same skeleton.

Indeed, there is a rapidly increasing field of research (Dean et al. 2018; Le Cabec et al. 2019; Newham, Corfe, et al. 2020) that identifies dental cementum as a tissue with great potential to expand our current knowledge regarding hominin life history evolution. By constituting a biological archive of the entirety of an individual's life, dental cementum should permit the investigation of our peculiar reproductive strategy.

However, several caveats remain, indicating possible directions for future research. First, while fossils require non-destructive analytical approaches, event identification requires elemental analysis. Nonetheless, several fossil specimens present naturally broken dental roots, thus exposing the cementum in its entire thickness and allowing for its analysis using synchrotron X-ray fluorescence mapping (Dean et al. 2018). This method may be used to recover the reproductive histories, and specifically interbirth intervals, in extinct hominin species for which we have dental specimens with broken roots.

Non-destructive histological methods are limited by their lower resolution (compared to real histology), which increases the error of age estimates. While this problem has limited impact on the study of the evolution of menopause, it is particularly relevant if attempting to investigate the evolution of interbirth-intervals (IBIs). The use of higher-energy beams, allowing for smaller voxel sizes (higher resolutions), could partially resolve this problem.

In addition to exploring the histology and elemental composition of hard tissues to extrapolate physiological information, it is likely that endocrine changes are also recorded in hard tissues and can be used to reconstruct life-history scheduling. Recent research has reported the possibility of recovering hormonal concentrations embedded in the dental tissues of humans (Nejad et al. 2016; Quade et al. 2021, 2023) and other marine mammals (Hudson et al. 2021). The study by Hudson and colleagues is particularly promising for human life history research, because it detects differing concentrations of progesterone and testosterone for individuals of different age classes and reproductive phases. Although their method currently lacks the spatial resolution to detect temporal changes, it effectively identifies variations in progesterone and testosterone levels across individuals of different age groups and reproductive stages. This technique could potentially be applied to determine whether a female has undergone menopause or not.

In sum, several methodological advances of the recent years will likely allow for actual data on when, where and in association with which morphological and environmental conditions a post-reproductive lifespan evolved. A more difficult investigation, because of the high level of resolution necessary, will be the evolution of shortened IBIs – since a difference of as little as one year has profound implications on our understanding of how such an energetically costly adaptation evolved. Advances capable of providing actual data to support or disprove current evolutionary hypotheses are necessary in order to understand the extent to which our cultural adaptations have shaped our physiological and biological ones, with concurrent downstream effect and feedback loops with our cognitive characteristics.

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