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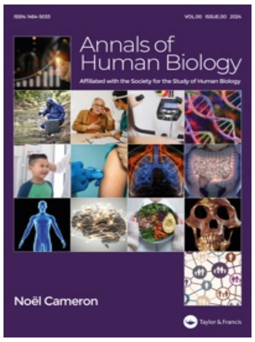

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HUMAN ORIGINS AND SURVIVAL

Palaeoanthropology and the study of pre-adult fossil remains

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ABSTRACT

Context: This review paper captures the topics and discussions during a workshop held in April 2023 in Minden, Nevada, USA regarding the study of pre-adult hominin fossil specimens.

Objective: Perspectives from diverse academic fields were merged to articulate, examine and clarify the many approaches available to interpret fossil remains and reconstruct our hominin ancestors.

Methods: The Wenner-Gren Workshop was organised to address the increasing collection of pre-adult hominin remains. Sixteen scientists from North America, Europe, Australia and Africa participated.

Results: The sizeable sample of immature fossil hominin specimens provided the opportunity to reflect on the state of maturity research, highlight multi-disciplinary advances, and identify future areas for study.

Conclusion: The workshop advanced efforts to understand human evolution, particularly the selective pressures shaping patterns of growth and maturity across a broad range of hominin species.

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The workshop was designed around the integration of multiple research fields, including auxology (human growth studies), biological anthropology, bioarchaeology, comparative anatomy, developmental biology, forensic anthropology, palaeoanthropology, and primatology, to address common language, theory, applications, methods, and goals to support and advance future studies of pre-adult hominins (e.g. Bolter and Zihlman 2003; Cameron 2007, 2015; Pruetz and Bertolani 2009; Berger et al. 2010; Bernstein 2010, 2017; Churchill 2014; Schell 2014; Hawks et al. 2017; Molopyane 2020; Boughner et al. 2021; Stull, Corron, et al. 2021; Stull, Wolfe, et al. 2021; Leece et al. 2022, 2023; Monson et al. 2022; Schell and Rousham 2022; Schroeder et al. 2022; Wolfe 2023; Mahoney et al. 2024; cf. Bolter et al. 2023). Perspectives from each of these cognate areas helped articulate, examine, and clarify the many approaches available to interpret fossil remains and reconstruct our hominin ancestors. As such, the workshop aimed to advance our efforts to understand human evolution, particularly the selective pressures shaping patterns of growth and maturity across a broad range of hominin species.

Despite decades of research, paleoanthropologists and anthropologists continue to debate when the life history signature of the human species evolved (e.g. Mann 1975; Bromage and Dean 1985; Beynon and Dean 1988; Beynon and Wood 1987; Wopoff et al. 1988; Smith 1989, 1991, 1994; Mann et al. 1990a, 1990b; Bogin and Smith 1996; Thompson et al. 2003; Hawkes and Paine 2006; Robson and Wood 2008; Dean and Smith 2009; Schwartz 2012; Ponce de León et al. 2016; Rosas et al. 2017; Miller et al. 2019; Nava et al. 2020; Berghaenel et al. 2023; Henneberg et al. 2023). In other words, what may be uniquely "human" in terms of maturation cadence, or in the timing and development of our species? Is our species unusual in the length of our life stages? Is "childhood" a life history stage special to *Homo sapiens*? Is the adolescent growth spurt uniquely human? How do these human characteristics before adulthood provide us with an adaptive advantage? In any species, altering life history stages can

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result in costly evolutionary trade-offs. This cost is particularly acute if individuals postpone reproduction and must survive a longer period of immaturity before contributing to the species' gene pool (e.g. Smith and Tompkins 1995; Lee 2012). Hypotheses to explain the benefit of extended human stages of life before adulthood include to: divert energy to immune function, thus lowering mortality; increase the period of brain growth, thus extending periods of social and ecological learning; increase the period of body growth, thus mitigating exogenous and endogenous stress events; buffer food supplies, thus weathering periods when resources are unpredictable and inconsistent; extend a period of infertility, thus prolonging adolescent socio-cultural learning; allow older, pre-adolescent children to care for infants after early weaning thereby freeing mothers to stop lactating and reproduce faster; or a combination of these factors (e.g. Leigh and Park 1998; Bogin 2003, 2012; Walker, Burger, et al. 2006; Walker, Hill, et al. 2006; Robson and Wood 2008; Bogin and Varea 2020). Studying the fossil individuals who had not reached adulthood will help test these hypotheses about varying maturity patterns and will help refine our understanding of the evolution of *Homo sapiens*. The larger the sample sizes per hominin species, the more proximate to reality these tests are likely to be.

Pre-adult materials in the fossil record

Life stages are defined by systematic groupings of immature and adult life categories. These stages are assessed in fossils using four main categories of skeletal elements, representing distinct somatic systems. These elements are represented in the fossil record to varying degrees: the cranium, the brain (as represented by the endocranium), the dentition, and the postcrania (cf. Bolter and Cameron 2020). Although other factors are available to integrate into maturity patterns in extant species, such as sexual maturity or change over time (growth) in dimensions such as height and weight (Tanner 1962), the body systems from which to model extinct species are more restricted. Teeth are particularly important in the work of pre-adult fossil remains. Teeth are protected by a hard outer layer of enamel, making them more resistant to the process of decay and decomposition compared to cortical or trabecular bone of the skeleton. This resistance contributes to the high representation of dentition in the fossil record and the use of dental features to define an extinct species (e.g. Kimbel and Delezene 2009; Leece et al. 2022, 2023). Indeed, there are far more deciduous and newly erupted permanent teeth from hominin pre-adults in the fossil record than there are postcranial remains.

Data from multiple somatic systems for each individual are preferred to reconstruct maturation patterns of an extinct species. However, this sampling ideal is elusive: the numbers of immature hominins in the fossil record are less than adults, and typically are *either* cranio-dental remains *or* postcranial remains (cf. Krovitz et al. 2003; Kuykendall 2003). It is rare to find associated immature skeletal elements from one individual (cf. Alemseged et al. 2006; Kelley and Bolter 2013). Table 1 summarises those exceptional Plio-Pleistocene individuals represented by cranio-dental and associated postcranial remains, starting with *Australopithecus* (Figure 1). Immature skeletons increase in frequency with more recent *Homo* species, such as Neanderthals.

Why are immature associated skeletons uncommon in the fossil record? Fossilisation is a rare process; bodies more often decompose and deteriorate rather than fossilise. When fossilisation does occur, the hominin record reflects "discovery bias" in that a majority of remains are adult. This bias towards adult fossils is explained by taphonomic processes and life history. Taphonomic processes unequally destroy immature bones due to their fragility and fragmentary nature (e.g. diaphyses and epiphyses). Life history stages of infancy and juvenility are shorter than the period of adulthood. Related to vulnerability earlier in life, other factors such as predation rates on younger/smaller individuals that would also destroy their remains furthers the unequal preservation against immature individuals. Altogether this results in the majority of fossilised remains disproportionately skewed towards adults, which is why the discovery of pre-adult remains is particularly important, especially when their preservation is more than fragmentary.

It is from the more recently surviving species of *Homo* that the sample of rare immature hominins is most robust. At the Gran Dolina site in the Sierra de Atapuerca cave systems in northern Spain, from the TD-6 stratigraphic level dated to ~720,000–850,000 years, at least eight individuals are represented, of which six are immature (Parés et al. 2013; Arnold et al. 2015; Bermúdez-de-Castro et al. 2017; Grün and Stringer 2023). Also at the Sierra de Atapuerca cave systems, but from a more recent deposit, the Sima de los Huesos site yields an assemblage of *Homo* with several adult and pre-adult dental and postcranial elements (Arsuaga et al. 1997, 2014; Carretero et al. 1997; Bischoff et al. 2007; Grün and Stringer 2023; García-González et al. 2024). In total, the Sima de los Huesos assemblage comprises at least 29 individuals, of which 13 are immature (Bermúdez-de-Castro et al. 2004, 2021).

In Eurasia, several associated immature *Homo neanderthalensis* skeletons have been recovered from multiple localities that date from 130,000 to 40,000 years ago (Heim 1976; Tillier 1983, 1995b; Trinkaus 1983; Rak et al. 1994; Akazawa et al. 1999; Akazawa and Muhesen 2002; Maureille 2002; Tillier et al. 2003; Ponce de León et al. 2008; Martín-González et al. 2012; Weaver et al. 2016; Balzeau et al. 2020; Devièse et al. 2021) (Table 1). Many of these immature skeletons are infants that range from neonates to individuals with all deciduous teeth erupted (Figure 2). The recovered Neanderthal immatures are distinctive in that many have been identified as purposeful burials (cf. Pettitt 2002).

Numerous *Homo naledi* individuals from a single geographic population in South Africa have been recovered (Berger et al. 2015; Dirks et al. 2015; Hawks et al. 2017). Dated between 335,000–241,000 years ago for the Dinaledi Chamber assemblage, the remains have been buffered inside the cave in multiple locations, and have been protected from destructive taphonomic forces including weathering and animal activity (Dirks et al. 2015, 2017; Wiersma et al. 2020). This paleodeme includes individuals across all life stages: infants, early juveniles, late juveniles, sub-adult, young and old adults (Figure 3) (e.g. Bolter et al. 2018; Cofran et al. 2022; Berger et al. 2023; Brophy et al. 2024).

Table 1. Key Plio-Pleistocene hominins with associated cranio-dental and postcranial remains (not intended as a comprehensive inventory; excludes early modern humans/*Homo sapiens*).

Genus	Specimen; locale	Species	Life stage	Material
Australopithecus	Dikika DIK-1-1 "Selam" Hadar, Ethiopia[1]	*afarensis*	Infant	Cranium, mandible with erupted deciduous teeth; elements of the thorax, arm and leg bones
Australopithecus	Malapa MH1 "Karabo" Gauteng, South Africa[2,3]	*sediba*	Juvenile	Cranium, mandible with erupted permanent teeth except third molars; elements of the thorax, pelvis, upper and lower limbs, with combination of unfused and fused elements
Paranthropus	Kromdraai TM1517 assemblage Gauteng, South Africa[4,5]	*robustus*	Sub-adult	Cranium, mandible with erupted permanent teeth, M^3 root ~½ formed; partial elements of arm and one foot bone, with combination of unfused and fused elements
Homo	WT 15000 "Nariokotome Boy" Lake Turkana, Kenya[6,7]	*erectus*	Juvenile	Cranium, mandible with erupted permanent teeth except third molars, with deciduous upper canines; thorax, pelvis, arm and leg bones, with combination of unfused and fused elements
Homo	D2700 assemblage Dmanisi, Georgia[8,9]	*erectus (senso lato)*	Sub-adult	Cranium, mandible with erupted permanent teeth, M^3 partially erupted; elements of the thorax, upper and lower limbs, with combination of fused and unfused elements
Homo	DH 6 Rising Star Cave, South Africa[10]	*naledi*	Infant	Cranium, mandible with partially erupted deciduous teeth; nearly complete skeleton
Homo	DH 7 Rising Star Cave, South Africa[11]	*naledi*	Juvenile	Partial mandible with permanent teeth including second molars, partial skeleton with mixed unfused and fused elements
Homo	Amud 7 Amud Cave, Israel[12]	*neanderthalensis*	Infant	Cranium (fragmented), mandible; partial skeleton
Homo	Mezmaiskaya 1 Mezmaiskaya Cave, Russia[13,14]	*neanderthalensis*	Infant	Cranium, mandible with partially erupted deciduous teeth; nearly complete skeleton
Homo	Kebara 1 Israel[15]	*neanderthalensis*	Infant	Partial cranium, partial mandible with some erupted deciduous teeth; parts of thorax and limb bones
Homo	Roc de Marsal 1 Dordogne, France[16]	*neanderthalensis*	Infant	Cranium, mandible with no erupted permanent teeth; nearly complete skeleton
Homo	Le Moustier 2 (aka La Ferrassie 4), Dordogne, France[17,18]	*neanderthalensis*	Infant	Cranium, mandible with no erupted permanent teeth; nearly complete skeleton
Homo	Shanidar 7 Shanidar Cave, Northern Iraq[19]	*neanderthalensis*	Infant	Cranium, mandible with partially erupted deciduous teeth; parts of thorax and limbs
Homo	La Ferrassie 4 (aka La Ferrassie 4b or 4 *bis*) Dordogne France[18,20,21]	*neanderthalensis*	Infant	Partial skeleton
Homo	La Ferrassie 5 Dordogne, France[20,21]	*neanderthalensis*	Infant	Partial skeleton
Homo	La Ferrassie 6 Dordogne, France[20,21]	*neanderthalensis*	(3–5 yrs)	Partial skeleton
Homo	La Ferrassie 8 Dordogne, France[20,22]	*neanderthalensis*	Infant	Cranium, mandible with no erupted permanent teeth; thorax, pelvis, hand bones
Homo	Dederiyeh 1 Afrin Valley, Syria[23,24]	*neanderthalensis*	Infant	Cranium, mandible with partially erupted deciduous teeth; nearly complete thorax, pelvis, arms, legs, with some hand and foot bones
Homo	Dederiyeh 2 Afrin Valley, Syria[23,24]	*neanderthalensis*	Infant	Partial cranium, mandible with erupted deciduous teeth; partial skeleton
Homo	Teshik-Tash 1 Southeastern Uzbekistan[25]	*neanderthalensis*	Juvenile	Cranium, mandible with mix of erupted deciduous and permanent teeth; elements of thorax, pelvis, upper limb and lower limbs elements
Homo	Sima de los Palomas 97, Murcia, Spain[26]	*neanderthalensis*	Juvenile	Cranium, mandible; elements of upper limbs, thorax, pelvis
Homo	El Sidrón J1 Spain[27]	*neanderthalensis*	Juvenile	Cranium, mandible with mix of erupted deciduous and permanent teeth; thorax, upper and lower limbs with mix of unfused and fused elements
Homo	Le Moustier 1 Dordogne, France[28]	*neanderthalensis*	Juvenile	Cranium, mandible with permanent erupted M2s; fragments and elements of thorax, upper and lower limbs, pelvis; long bones unfused
Homo	Sima de los Palomas 96, Murcia, Spain[26,29]	*neanderthalensis*	Sub-adult	Cranium, mandible, full eruption LM^3; skeleton except feet, with combination of fused and unfused elements

[1]Alemseged et al. (2006); [2]Berger et al. (2010); [3]Cameron et al. (2017); [4]Broom (1942); [5]Cazenave et al. (2020); [6]Brown et al. (1985); [7]Walker and Leakey (1993); [8]Vekua et al. (2002); [9]Lordkipanidze et al. (2007); [10]Cofran et al. in prep; [11]Bolter et al. (2020); [12]Rak et al. (1994); [13]Weaver et al. (2016); [14]Ponce de León et al. (2008); [15]Tillier et al. (2003); [16]Tillier (1983); [17]Maureille (2002); [18]Martín-González et al. (2012); [19]Trinkaus (1983); [20]Tillier (1995b); [21]Heim (1976); [22]Balzeau et al. (2020); [23]Akazawa and Muhesen (2002); [24]Akazawa et al. (1999); [25]Glantz et al. (2009); [26]Walker, López-Martínez, et al. (2011); [27]Rosas et al. (2017); [28]Nelson and Thompson (2005); [29]Walker, Ortega, et al. (2011).

While the increase of pre-adult skeletal remains in the fossil record provides new opportunities to study growth and development of extinct hominins, the workshop participants recognise that the sample is biased by the fact that these individuals died as immatures (cf. Boldsen et al. 2022). Evidence of stress markers in the teeth and bones of some individuals raises the question of whether we are finding these individuals in the assemblage because they were unhealthy (thus the markers denote frailty) or whether they recovered from the stress, but subsequently died at a later age (thus the markers denote resilience: see Wood et al. 1992). Comparative work of modern living and recently deceased *Homo sapiens* individuals suggests no statistical difference in maturational patterns of juveniles who died before reaching adulthood, which supports modelling of an extinct species' developmental patterns based on its deceased immatures (Stull, Wolfe, et al. 2021).

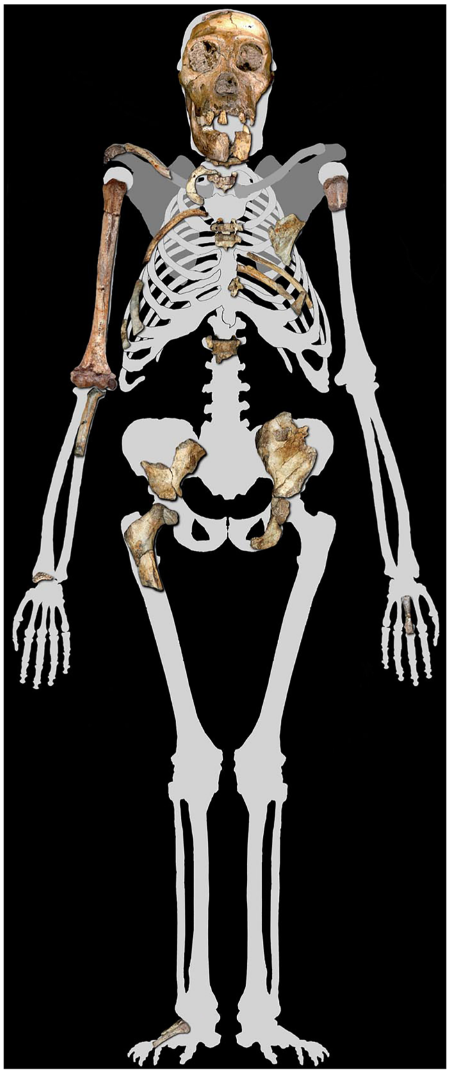


Figure 1. *Australopithecus sediba*, MH 1, juvenile male from Malapa, South Africa circa 2010. CC-BY-SA 3.0 Lee R. Berger. Image by Peter Schmid slightly modified (right tibia was removed from the image as it is no longer associated with MH 1). Note that additional skeletal elements have been recovered for MH 1 and are currently under study.

Life stages in fossil individuals are deduced based on dental and bone patterns of maturation; these patterns may be complicated by undefined physical and/or psychological stressors that disrupt tissue growth and maturation (e.g. Bateson et al. 2014; Macintosh et al. 2018; Ng and Chin 2021). How to refine the interpretation of variations in stressors is another difficult problem to address. For instance, workshop discussants appreciated that growth is eco-sensitive and that paleoecologies for extinct hominins are highly variable and, for this reason and others, it is challenging to parse out stress-inducing factors marked in fossilised tissues (e.g. Lee-Thorp et al. 2010; Cerling et al. 2013; Potts 2013; Blumenthal et al. 2017; Lüdecke et al. 2018). While capturing population-level variation is important for accurate reconstructions of species, natural (i.e. genetically controlled) variability in growth rates such as osteogenesis (e.g. Tillier 1995a) may also confuse interpretations of immature individuals. These specimens may tell us accurate information about life history, survival, and selection, but perhaps in a different way than teased out using growth models from living populations of humans and other primates. Thus, approaching studies of pre-adult fossil specimens may require different theoretical frameworks if not practical methods, which our group of colleagues are working to devise and test using an interdisciplinary approach. We also look for solutions from other scientists studying human evolution by working across fields, as major advances are likely to come from various groups across geographical regions

Figure 2. *Homo neanderthalensis*, Roc-de-Marsal, infant from Dordogne, France. CC-BY-SA 3.0 Leo Fyllnet, photo from display at National Museum of Prehistory, Les Eyzies-de-Tayac, France.

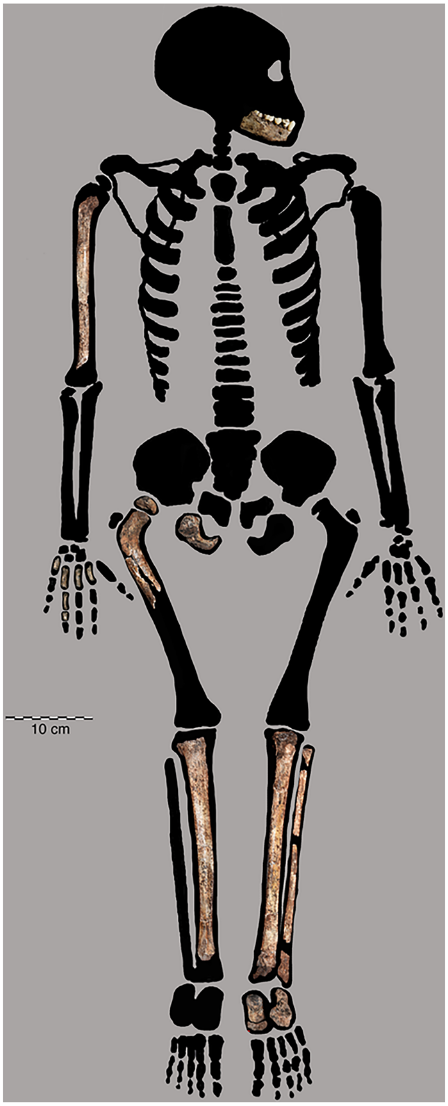


Figure 3. *Homo naledi*, DH 7, juvenile from Rising Star Cave, South Africa. CC-BY-SA 3.0 (Bolter et al. 2020).

and time. But for now, we return to the body tissue used to rigorously define and contrast chronological ages in fossil species: teeth.

Dentition: maturational datasets in the fossil record

The first attempt to score immature fossils for dental ages was Mann's pioneering paleodemographic study on South African materials, building on methodologies developed from radiographs on modern human developing dentitions (Demirjian et al. 1973; Mann 1975; Mann et al. 1990b). The relationship between dental development, life history stages and the development of other somatic systems like the brain furthered research approaches of immature fossil remains (Smith 1989). About 90–95% of brain volume is achieved across primate species with the emergence of the first permanent molars (Ashton and Spence 1958; Smith 1991, 1993). Methods to assess and interpret growth patterns from dental tissues, and to link these chronologies to life history features such as weaning and the end of infancy, and to compare them broadly to ape-like and human-like cadence of maturity, advanced the study of immature fossil hominin remains (e.g. Dean and Wood 1981; Bromage and Dean 1985; Dean 1985, 1987a, 1987b; Beynon and Wood 1987; Bromage 1987; Beynon and Dean 1988, 1991; Conroy and Vannier 1991; Dean et al. 2001). Building on these research methods, new CT scanning technology of unerupted dentition furthered the application of the age-at-death estimate, growth patterns and life history evolution in immature fossil remains (Conroy and Vannier 1987).

The hard mineralised tissues of teeth are information rich, and within a species tend to be less developmentally plastic relative to other body tissues (Liversidge 2003). In particular, the process of dental mineralisation is highly constant, and thus reliable and precise for determining the daily and longer-term periodic history of enamel and dentine formation and of the absolute timing of tooth formation, eruption, and emergence. Using histological techniques developed over the last 40 years, measures and counts of the internal microscopic structures and incremental markings of dental hard tissues provide a replicable way to reliably and precisely determine age-at-death for pre-adult individuals and to identify the timing and duration of stress events (e.g. Bromage and Dean 1985; Schwartz et al. 2006; Dirks et al. 2010; Dean 2012; Birch and Dean 2014; Smith et al. 2018; Austin et al. 2023; Mahoney et al. 2024). The next two sections delve into age-at-death and stress events in more detail, including implications for studies of pre-adult hominins.

Age-at-death as measured from teeth

Primate teeth preserve evidence of growth in the form of incremental markings that can be accessed through physical or virtual thin sections (e.g. Dean et al. 2001; Smith et al. 2015; Mahoney et al. 2021). One of these markings occurs in enamel in response to a circadian 24-hour rhythm that manifests as cross striations (Schour and Poncher 1937; Boyde 1989; Zheng et al. 2013). Counts of cross striations combined with the neonatal line that forms at birth (e.g. Sabel et al. 2008; Mahoney 2011) allow the reconstruction of the timing of tooth formation and relate it to chronological age (Boyde 1964). A real strength of this histological approach is that the estimate of chronological age is based directly on the sampled tooth without need of an external standard, which may not even be available in a fossil specimen. Another key strength is that age can be calculated accurately to within a few days of known age-at-death (Antoine et al. 2009). Indeed, this method has been used to calculate age-at-death in pre-adult fossil hominins, such as the 7.7 year old Neanderthal juvenile skeleton (J1) from El Sidrón in Spain, which provides a starting point from which to assess the cadence of maturation of the associated skeletal elements (Rosas et al. 2017).

Not only enamel and dentine but other dental tissues retain growth markings. Specifically, incremental markings form in cementum, which covers portions of the root and anchors the tooth into the socket. Acellular cementum is deposited incrementally and, unlike enamel, deposition continues throughout life, with pairs of lines relating to an annual cycle. As such, measures and counts of cementum lines have been used to determine age at death beyond the period in which enamel forms (Gustafson and Malmö 1950; Stott et al. 1982). This approach requires knowledge of the period in which the tooth developed prior to formation of the first cementum marking, which is usually obtained either from estimates of tooth emergence age or histologically derived tooth formation times. As powerful as growth lines are for calculating absolute chronological age at death, these lines are also powerful for defining key periods in the individual's life linked to physiological stressors.

Developmental stress as measured in the teeth

Primate teeth can retain evidence of developmental stress in the form of accentuated markings. In enamel, these markings are known as Wilson bands (Rose et al. 1978; Goodman and Rose 1990). The bands can sometimes emerge onto the outer enamel surface as hypoplastic defects (e.g. Mahoney 2008). While the cause of the bands is not well understood it is thought they, like hypoplastic defects, are non-specific markers that form in response to a range of stressors, discussed next (Sarnat and Schour 1941; Sweeney et al. 1971; May et al. 1993; Schwartz et al. 2006; see Guatelli-Steinberg 2001 for a review).

Wilson bands have been related to weaning and other life history events in extant primates (Bowman 1991; Dirks et al. 2002, 2010; Lemmers 2017). Weaning occurs as infants transition from a diet composed of maternal milk to one that includes additional non-milk foods. While weaning can provide additional nutrients that benefit the infant (Kennedy 2005), it can also increase the risk of illness through exposure to new pathogens (Black et al. 1989). Wilson bands have been used to infer the timing of weaning in human archaeological samples (e.g. FitzGerald et al. 2006; Deter et al. 2019; Miszkiewicz et al. 2019). As with age-at-death estimates, reconstructing the timing of these accentuated markings draws upon the circadian cycle of enamel growth (e.g. FitzGerald and Saunders 2005).

The microstructure of other dental tissues can retain evidence of stress. The irregular formation of cementum lines (Lieberman 1993; Cipriano 2002) has been related to periods of physiological stress, coinciding with childbirth for females with a known life history (Cerrito et al. 2020). As with the majority of stress markings in teeth the challenge is to find ways to distinguish between the causes of the markings when applied to fossil material.

Dental studies of enamel defects on Neanderthal individuals record their stressful lives (Rosas et al. 2006; Guatelli-Steinberg et al. 2014). At El Sidrón in Spain, a family of 13 Neanderthals, seven adults and six pre-adults, were excavated out of a cave site dated to 49,000 years ago (De Torres et al. 2010; Lalueza-Fox et al. 2011; Wood et al. 2013; Rosas et al. 2017). The individuals have damage and marks on their bones consistent with cannibalism, and the bodies appeared to have been interred simultaneously in a cave wall collapse (Rosas et al. 2006). The dentition of the El Sidrón individuals exhibit enamel hypoplasia on all tooth types – incisors, canines, premolars, and molars (Rosas et al. 2006). These lines mark an individual's stress, and, in this family group, the lines are most frequent around 4 years of age and again at 12 years of age; the authors suggest these represent potential nutritionally stressful times in Neanderthal life stage transitions (Rosas et al. 2006). In contrast, one well preserved juvenile, the 7.7-year-old El Sidrón J1, only had mild hypoplasia, which occurred around 2–3 years of age (Rosas et al. 2017).

Information about diets can also be gleaned by combining tooth histology with analyses of trace elements (barium/calcium, strontium/calcium) incorporated into enamel and dentine. One such application is to detect age at weaning, i.e. the shift from breast milk to other foods. Barium is restricted by the placenta but is enriched after birth with breast milk in extant macaques (Austin et al. 2013). Strontium calcium ratios of deciduous enamel are altered with the onset of weaning in living humans (Nava et al. 2020). Based upon these types of modern analogues, studies have examined elemental ratios of Neanderthal juveniles to identify the age at which exclusive breastfeeding was supplemented with other foods, estimated to have occurred between 5 and 6 months of age (Austin et al. 2013; Nava et al. 2020). Typically, age is calculated from histological analyses of physical thin sections, and then elemental ratios are determined from laser-ablation inductively coupled plasma mass spectrometry that is applied to the enamel of the same section. Ablation preferentially focuses on the enamel region adjacent to the enamel–dentine junction (Müller et al. 2019). Additional approaches to a young individual's diet combine histology with stable isotope analysis of enamel and dentine (e.g. Lee-Thorp et al. 2010; Beaumont et al. 2013; Wright 2013).

Eruption of teeth

In addition to the microstructure and chemical signatures of dental tissues, patterns of tooth eruption are invaluable for reconstructing growth and maturation in pre-adult hominins. Researchers assign broad life stages from teeth exactly because fossilised dental remains allow at least partial reconstruction of a tooth eruption stage. Molar teeth in particular are used to mark transitions across life stages, for example, pre-M1 eruption is classified as infant; erupted M1 classifies as a young juvenile; and full M3 eruption classifies as an adult (e.g. Smith 1989, 1991; Godfrey et al. 2001; Bermúdez-de-Castro et al. 2004; Kelley and Schwartz 2010; Rosas et al. 2013; Bolter et al. 2018). Eruption status is particularly insightful when combined with age and stressor data gleaned from tooth histology, to more comprehensively characterise an individual's growth story.

Workshop participants spent time discussing variations in dental development. Dental eruptions in *Homo sapiens* are highly variable – within a person and within a population (e.g. Liversidge 2003, 2008; Ramirez Rozzi 2016). For example, modern human children can erupt first molars anywhere from the age of 4.8–7.0 years, and second molars anywhere from 9.9 to 14.5 years (Liversidge 2003; Esan et al. 2018). We recognise from research on living species that there are better estimates of life history stages than from tooth eruption (cf. Bermúdez-de-Castro et al. 2015). However, it may be difficult to standardise alternative methods across the hominin fossil record. Adding in multiple maturity indicators gives a better estimate of life history and pace of maturity, but always keeping in mind the limited dataset that the fossil record affords.

Tooth eruption and reproductive life history

Teeth offer insights into maturity patterns beyond life history markers and age-at-death. For example, the eruption of the first permanent molar in primates corresponds with near completion of adult cranial size, an indirect measure of brain mass (Smith 1989). Recent studies have highlighted the genetic, developmental, and phenotypic relationships between tooth morphology and reproductive life history (e.g. Hlusko et al. 2018; Monson et al. 2019, 2022). In marmoset and tamarin monkeys, for example, the evolutionary loss of the third molar is hypothesised to be linked to reproduction, twinning, and prenatal growth rates (Monson et al. 2019). Because teeth begin developing *in utero*, with sequential development of the molars (e.g. Jernvall and Thesleff 2000), it has been proposed that a slower prenatal growth rate also slows growth of the later developing teeth (e.g. third molars) and may contribute to their absence. Further investigation of this hypothesis across extant primates demonstrated that molar proportions are significantly associated with prenatal growth rates (Monson et al. 2022). Molar proportions are thus an effective proxy for contrasting growth rates among primate taxa. Given this phenotypic correlation in extant primates, it may be possible to use molar proportions to model prenatal growth rates in extinct hominins (see Monson et al. this volume). Research suggests that more rapid foetal growth may have played an essential role in the evolution of the large human brain and body size. While this approach is another valuable use of fossilised tissues to reconstruct a process that cannot fossilise directly, the caveat is of course that the molar row must be sufficiently intact in order to accurately measure crown proportions in fossil individuals.

New approaches: tooth formation prior to eruption

More recent comparative work has explored the process of tooth morphogenesis to document ontogeny variations across species (e.g. Jernvall and Thesleff 2012; Boughner et al. 2015). The development of permanent teeth is perhaps the nearest opportunity to study an embryological process in a post-natal individual. Studying early tooth development in fossil hominin immatures requires the preservation of bone surrounding and housing the developing tooth. Hominin mandibles are composed of dense bone and, like teeth, often survive the rigours of fossilisation. The jaw retains crypts, or holes, in the jaw where teeth will eventually form. The crypt is a proxy for the earliest stages of tooth development, when the tooth organ transitions through bud, cap, and early bell stages, before mineralisation of the cusp(s) begins in the late bell stage (Boughner et al. 2012, 2015; Jernvall and Thesleff 2012; Appelt et al. 2021). This early pre-mineralisation period of tooth development is insulated from environmental perturbations and is comparatively stable in an individual (e.g. Liversidge 2008; Wise 2009; Kjær 2014). High resolution, digital-format scan data can visualise crypt sizes, shapes, and positions of the pre-mineralised tooth organs within the jawbone that are not visible by classic radiographic imaging techniques (e.g. Raj et al. 2014; Gignac et al. 2016). This line of evidence is an added and underused source upon which to compare maturational patterns in fossil hominins.

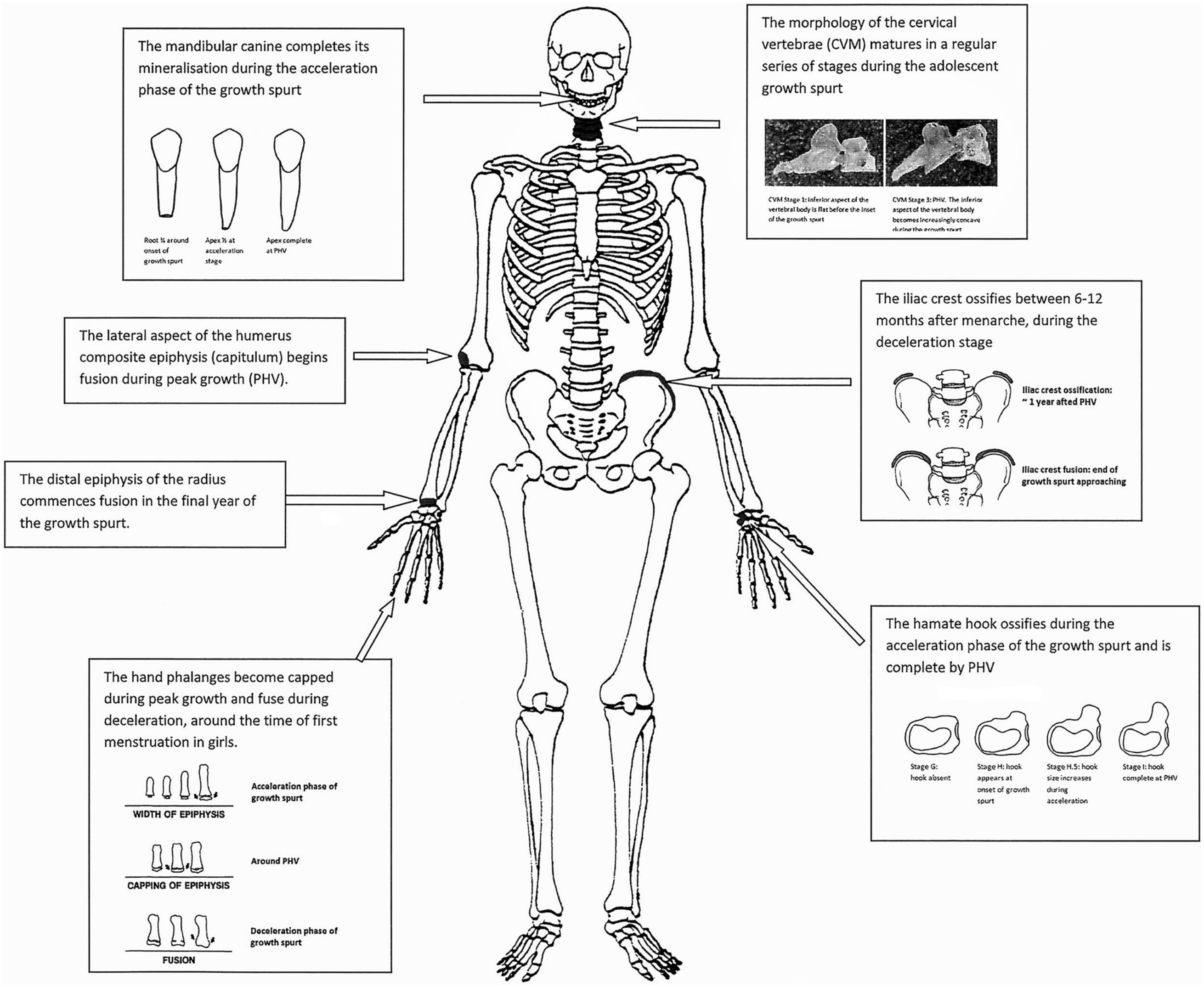
Skeletal datasets for determining age

Skeletal maturity

In contrast to applying aspects of dental development to define, compare, and contrast maturity patterns among contemporary humans, living primates and fossil hominins, assessing maturation across extinct species using skeletal evidence is more difficult. The principal challenge is that, in contrast to static enamel and dentine mineralised tooth tissues, bone tissue remodels (Bolamperti et al. 2022). As such, bone does not encode the continuous life history patterns that are represented in the teeth.

The skeleton does preserve evidence of developmental stages during immature years. The best evidence derives from associations of immature hominin cranial and postcranial materials with dentition, as dental markers allow a chronological ruler with which to compare maturation of other body systems, such as the skeleton and the brain (e.g. Alemseged et al. 2006; Rosas et al. 2017). Fossil immatures can be grouped into life history stages. For example, infant endocranial volume may be estimated from the cranial vault, and then compared by life stage and to an adult average, to characterise the brain growth patterns in an extinct species (e.g. *Australopithecus afarensis*; Gunz et al. 2020). Juvenile hominin skeletons with second but not third molar eruptions can be compared to dental juveniles from modern humans and living apes to ascertain postcranial maturity by assessing open and fused epiphyses, and thereby assess somatic development for an extinct species (e.g. *Australopithecus sediba*; Cameron et al. 2017).

Forensic anthropology and auxology studies document covariance of maturational markers in modern humans. For example, there are skeletal events that correlate with menarche such as iliac crest presence and fusion of the hand phalanges (Shapland and Lewis 2013; Lewis 2022; Dabbs 2024) (Figure 4). Are there evolutionary constraints on body systems maturity, such as the skeleton, due to covariation? In the genus *Pan*, the sequence of fusion of skeletal elements is generally consistent across the two species – *Pan troglodytes* (chimpanzees) and *Pan paniscus* (bonobos, or pygmy chimpanzees). When holding dental emergence as the chronological marker, *Pan* species show differences in the timing of fusion of skeletal elements at a particular stage of dental emergence; environmental conditions (captive versus free ranging) appear to affect the timing of maturity of both dentition and the skeleton in a similar manner (Bolter and Zihlman 2011, 2012). Likewise in modern humans, dental development does not serve as a proxy for skeletal



The mandibular canine completes its mineralisation during the acceleration phase of the growth spurt

The morphology of the cervical vertebrae (CVM) matures in a regular series of stages during the adolescent growth spurt

The lateral aspect of the humerus composite epiphysis (capitulum) begins fusion during peak growth (PHV).

The iliac crest ossifies between 6-12 months after menarche, during the deceleration stage

The distal epiphysis of the radius commences fusion in the final year of the growth spurt.

The hamate hook ossifies during the acceleration phase of the growth spurt and is complete by PHV

The hand phalanges become capped during peak growth and fuse during deceleration, around the time of first menstruation in girls.

Figure 4. Select dental and skeletal maturity markers before, during and after adolescence in female *Homo sapiens*. Physical markers are proxies for pre-puberty, acceleration through a growth spurt, peak height velocity (PHV), deceleration, or post-menarche. CC-BY-4.0 (Lewis 2022).

maturation, although the systems appear to be related (Šešelj 2013). New methods applying statistical techniques of multivariate analyses may further our understanding of the relationships of phenotypes and their integration during development in primates, humans, and hominins (see Wolfe et al. this volume).

Modelling patterns of evolutionary change in skeletal maturity requires robust comparative datasets. While we have significant knowledge of growth and development of living humans in Westernised countries, we have less information about people living in the Global South, and even less archaeologically from that region (Eveleth and Tanner 1991; Šešelj 2013; Lewis 2022). Forensic databases of bone age estimations and identification provide another line of evidence for comparative materials, although as with living referent samples, most specimens are from Westernised populations (e.g. Cole et al. 2015; Stull and Corron 2022). The workshop participants recognised the importance of broad samples for humans, and under multiple conditions, to characterise the *Homo sapiens* pattern and range of skeletal variability in terms of maturity, growth, development, and life history (Eveleth and Tanner 1991). Conclusions drawn without reference to such representative samples must therefore be tentative and open to revision as more data become available.

Compared to our species, we have even less reference material for nonhuman primates (e.g. Nissen and Riesen 1964; Kerley 1966; Gavan 1971; Watts 1971; Conroy and Mahoney 1991; Kuykendall et al. 1992; Winkler et al. 1996; Bolter and Zihlman 2012). We know the least about skeletal and dental maturation from wild-living ape populations (e.g. Pusey 1978; Kimura and Hamada 1996; Zihlman et al. 2007; Brimacombe et al. 2015; Machanda et al. 2015; Galbany et al. 2017; Kralick et al. 2017). Information about these free-ranging populations is valuable because these animals may have subsisted in ways that more closely approximate the lives, including environmental stressors, of extinct hominins. Our workshop discussants identified the need for more robust reference material from ape populations across varied living conditions, including free-lived and institution-housed, to capture the greatest range of maturational data under varied conditions (discussed below). Building these reference materials takes time because not only are many samples rare but also the work of acquiring these samples is highly opportunistic.

Developmental stress and stressors: resiliency and plasticity

Stress is defined as the individual's non-specific response to external stimuli. Stressors are those external stimuli acting on individuals or communities such as specific vitamin deficiency at the individual level or famine at the community or regional level. The effect of stressors is always related to their magnitude, frequency of occurrence, duration, and the age of the organism at the time of exposure (Cameron and Demerath 2022). The recognition of "critical periods" during growth and development when specific stressors have both short-term and long-term impact is well documented (Cameron and Demerath 2022). The early years of infancy and childhood in *Homo sapiens* are particularly sensitive and in auxological studies, it is well documented that there are multiple pathways of resilience to adulthood.

As an example, one such pathway that is most commonly accepted and forms the basis for the measurement of length and weight during infancy and childhood is that stress, nutritional or otherwise, reduces growth rate and thus achieved height and/or weight for age (Tanner 1962; Cameron 2007). However, for such growth patterns to be viewed as an adaptation, rather than an adverse reaction to a stressor, positive outcomes should result. The simple hypothesis that this growth failure takes place without having any deleterious effects – the "small but healthy" hypothesis –was promoted in the early 1980s but is no longer accepted as a reasonable outcome (Martorell 1989; Cameron 1999). It has been demonstrated quite conclusively that nutritional stunting through the first few years of life leads not only to a reduction in adult stature but also cognitive impairment in young adulthood, thus not supporting the "small but healthy" status as an adaptive outcome (Adair et al. 2013; de Onis and Branca 2016). There is an evolutionary trade-off between growth and offspring mortality in that the women who are able to invest more time and energy in their own growth prior to their first birth are reproductively more successful than women who are younger at first birth (Allal et al. 2004). So, in sum, stress experienced in the early years of life is likely to have a long-term impact on adult morphology, cognitive ability, and reproductive success. We anticipate that these three characteristics – morphology, cognition, and reproduction – were affected by stress levels in fossil hominins as they grew into adulthood. In terms of natural selection and fitness, stressors that impacted phenotypes and behaviours during immaturity are critical factors of theory building in pre-adult fossil hominin research.

In addition to body growth, the rate and progression of maturation, and particularly sexual maturation, are also affected by stress and such responses are sex specific. In the research field of the developmental origins of health and wellbeing in *Homo sapiens*, it is accepted that the reproductive and life history strategies of the two sexes are quite distinct (Gluckman and Hanson 2006). Secular trends in the ages at which pubertal events occur, and indeed the rate at which puberty proceeds, are sex-specific, and the response of these pubertal events to stress may also be sex-specific (Stearns and Koella 1986; Steger et al. 2024). It is generally accepted that stress delays sexual maturity in females, but some forms of acute stress, e.g. sexual abuse, have been shown to be associated with earlier menarche, while chronic stress, e.g. severe physical abuse, is associated with both earlier and later menarche (Boynton-Jarrett et al. 2013). Such advances or delays in male maturation are more difficult to assess because of the lack of a clear and unequivocal maturity indicator, but *Homo sapiens* affected by "psycho-social" stress invariably demonstrate delayed maturity.

Usually, stressors do not happen in isolation for modern peoples. Nutritional stressors, behavioural stressors and psycho-social stressors usually cluster in modern human populations and are often related to socio-economic status (Wales et al. 1992; van Minde et al. 2021). The clustering of factors in explaining stress responses is not unexpected when the symphony of factors includes maternal and child health, nutritional quantity and quality, and psychological and social/emotional factors (e.g. Bogin 2023). The scale of the stressor also differentially affects an individual during maturation. If the stressor is regular and predictable, the impacts on the individual will be different than a novel unexpected stressor.

Population level stressors translate into an overall adaptive pressure. The high frequency of Neanderthal hypoplasia across all geographic sites, for example, has been interpreted as a population-level stressor of resource seasonality (Ogilvie et al. 1989). Such nutritional stressors, then, require consideration when interpreting the maturation pattern of an extinct species. However, an individual's stress response in terms of intensity/magnitude, duration, frequency, and age of occurrence provides flexibility for an organism's integrated phenotypes to respond. This overall ability/flexibility allows the organism to survive that impact of the stressor and still guarantee the "normality" of post-stress development. But the stress response may or may not be overall adaptive. Therefore, observable indicators of stress in one immature fossil hominin may not relate to reliable indicators of population-level stressors.

Workshop participants acknowledge that parsing out individual from population-level selective pressures in the fossil record is challenging. Furthermore, can developmental stressors in the skeleton be accurately surveyed for stress responses? Some aspects of ontogenetic signatures remain in bone (e.g. McFarlin et al. 2016). Dental tissues have been the proxy for measuring physiological disruptions during maturity as they do not remodel, and they track disruptions from birth (neonatal line) through dental adulthood. Teeth also survive the process of fossilisation better than bone and are better reflected in hominin assemblages (e.g. Bolter and Zipfel, this volume). Workshop participants discussed the potential of future research in identifying factors during development that affect bone tissue growth and approaches to evaluate stress responses at the individual and population level for extinct species. Workshop participants agree that there is a need for more ontogenetic studies of bone (e.g. McFarlin et al. 2008). One discussion during the workshop highlighted the accelerated maturity of captive colony primates versus wild-living primates, and variation among populations within a species depending on living conditions (e.g. Pusey 1978; Altmann et al. 1981; Phillips-Conroy and Jolly 1988; Kimura and Hamada 1996; Cheverud et al. 1992; Zihlman et al. 2004, 2007; Smith and Boesch 2011; Bolter and Zihlman 2012; Kelley et al. 2020). In free-ranging primates, exposure to adverse environmental conditions and more challenging resource acquisition prolong life history events, like age at first reproduction, and length of interval between births (e.g. Neugebauer 1980; Kano 1992; Kimura and Hamada 1996; Neal Webb and Pruetz in prep). Captive ape colonies, such as those in zoos or research populations, are hypothesised to experience less biological stress than wild-living primates in terms of malnutrition, thermoregulation, parasite load, and locomotion/energy expenditure (Lathouwers and Elsacker 2005; Zihlman et al. 2007; Smith and Boesch 2011). Workshop participants debated the confounding effect of social stress in captive conditions where individuals have no way to avoid each other. Free-living individuals, in contrast, have more flexible space and more ability to escape potentially tense social interactions. In short, biological and social stressors at the population level may have different effects on primate maturity and life history. However, participants noted the limited availability of primate maturational studies across heterogeneous environments upon which to develop ontogeny models to apply to hominin species (cf. Bolter and Cameron 2020).

Research from auxology provides two complimentary models to interpret the disparity of maturity patterns in captive versus free-ranging primates and to aid in building models to apply to extinct species. As discussed previously, in humans, stressful environments during development can lead some children to accelerate maturity; yet other children delay development, particularly under stressful conditions that include malnutrition (Cameron and Demerath 2022). Workshop participants concluded future research is needed to develop the field's understanding of plasticity in ape maturity patterns across multiple environments, periods of growth, and types of stressors. As part of these investigations into stressors and before modelling maturity patterns of extinct species, the effects of varying stressors on growth and development need to be studied across a range of species to clarify how resiliency influences the adaptive potential. These studies presume that all markers of stress are defined, captured, and detectable in body tissues that are also typically fossilised, but this is of course not the case. There is a need to develop or refine markers of stress in non-human primates, including interspecies markers of nutritional and health stress.

In sum, to varying levels of precision dental and skeletal tissues preserve evidence of growth, maturation, stress, diet, reproduction, and lifespan in primates across taxa. As reference samples grow and diversify, there is reasonable optimism that the life histories of fossil hominins can be reconstructed in greater accuracy and detail, with higher confidence.

Prediction models

In humans, one main goal of auxology research is to predict "normal" patterns of growth and identify unhealthy and/or pathological patterns. There are two main ways to predict height in humans: using either a multivariate model including sex, maturity indicators, chronological age, and parental heights or simply using parental heights and the average growth pattern of same sex samples from the same population. Researchers have used regression techniques based on data from modern primates and humans to reconstruct, for example, the estimated brain size at birth for fossil ancestors (DeSilva and Lesnik 2008). Applying auxology models, reconstructions of estimated height have been made based on immature fossil specimens (Ruff and Walker 1993; Ruff 2007; Graves et al. 2010; Cameron et al. 2017). What is the best predictor for modelling growth from teeth and bones, body tissues also present in the fossil record? Can we apply any sort of time-series reconstructions to extinct hominins? Workshop participants noted that developing ways to ascertain "normal" growth in past populations is a goal for future researchers.

Modelling maturity in the fossil record

What has become clear as more immature hominin remains have been recovered, and with a more comprehensive integration of auxology, is that we have moved away from searching for when "the" *Homo sapiens* signature of maturity can be identified in an extinct hominin species. One of the most remarkable immature fossil hominins is the Nariokotome Boy, or WT-15000 from Lake Turkana, Kenya, which represents 80% of the skeleton of a late juvenile *Homo erectus* from about 1.5 million years ago (Brown et al. 1985; Brown and McDougall 1993) (Figure 5). He died before erupting his third molars and permanent upper canines; postcranially his skeleton was mostly unfused. Nariokotome Boy was estimated to be between 154 and 160 cm (~5′1″–5′3″) at death (Ruff and Walker 1993; Ruff 2007; Graves et al. 2010) and with an endocranial volume about 900 cc, over double the size of living chimpanzees (~300–420 cc) but far below that of modern humans (~1200–1600 cc) (Begun and Walker 1993; e.g. Zihlman et al. 2008; Pearce et al. 2013).

Based on a modern human model, his dental eruption age was estimated at 11 years, his skeletal epiphyseal age estimated at 13–13.5 years, and age-for-stature around 15 years (Smith 1993; cf. Graves et al. 2010). A *Homo sapiens* pattern of maturity was not an unreasonable hypothesis for Nariokotome Boy. Variations among age estimates across somatic systems occurs in living and archaeological human populations; Nariokotome Boy was within this range of human variation (e.g. Clegg and Aiello 1999; Smith 2004; Ruff 2007). Although his dental eruption *pattern* aligned him with a human-like model of development (Smith 1993), his dental and skeletal *ages* were more consistent with an ape model, ageing Nariokotome Boy between 7 and 9 years old. Using dental histology, Nariokotome Boy's pace of maturity revealed an absolute timing most similar with free-ranging chimpanzees, and unlike modern humans (Dean et al. 2001; Zihlman et al. 2004; Dean and Smith 2009). Therefore, at 7.6–8.8 years old at death, Nariokotome Boy's somatic maturation neither conformed simply with an ape or a human pattern. Furthermore, his tall stature at that

Figure 5. *Homo erectus*, Nariokotome Boy WT 15000, juvenile male from Lake Turkana, Kenya. CC-BY-NC 2.0 (Dunsworth 2010). Photo by Alan Walker.

age established that the prolonged developmental period characteristic of modern humans did not evolve due to the selective pressures of an overall larger body size or a larger brain (Dean et al. 2014).

Intra- and inter-individual variation is the essential characteristic of growth and development among pre-adults of *Homo sapiens*, and among captive versus free-ranging primates. We recognise that the same is true for extinct hominin species writ large. It is the extent and meaning of this variation which manifest as the ultimate aims of our approach, and to characterise the life histories including growth of pre-adults in the fossil record. Our emphasis redirects from the question, “How did this species get to us?”, towards deliberately considering each species in its own right as a first principal and without defaulting to cross-taxonomic comparisons (see Kuykendall 2003; Thompson et al. 2003) – although of course these comparisons are valuable subsequent steps to contextualise individual finds. The goal is to establish the pressures that each species is under, on its own. We must emphasise variation in these patterns, and consider human and other primates comparatively in size, rates, and timing.

Recent innovative studies

More research on establishing relationships among somatic systems, such as skeletal maturity and dental maturity, as well as the impact of social, ecological, and dietary variables on life history, will further the goals to understand the extent of plasticity across systems. Recognising the role of developmental plasticity and environmental interface on phenotypes will broaden the field of palaeoanthropology and expand methods of interpretation (Lequin et al. 2025). Work on the role of “developmental stress” and how this relates to resilience – in a species, in a population, and in an individual – will further the goals of modelling adaptation in extinct species.

Recent multi-disciplinary research advances the field of pre-adult hominin palaeoanthropology with new immature fossil recoveries, increased comparative data from extant species, and advances in technologies. For example, predictive equations to estimate body mass in immature hominins based on human juvenile reference samples has been developed, generating a body mass at death for *Homo erectus* Nariokotome Boy (WT 15000) at about 50 kg (~110 lbs) (Ruff 2007). The 2008 recovery of the immature partial skeleton of *Australopithecus sediba* (MH1) and its comparison to a recently available wild chimpanzee developmental series supports an ape-like maturity cadence about 2 million years ago in the hominin fossil record (Cameron et al. 2017). Compiling robust captive colony data on infant chimpanzee newborns and their mothers and applying to reconstructions of body mass estimates in fossil hominins establishes that *Australopithecus* species had heavy infants, birthing offspring at least 5% of the mothers’ body mass compared to chimpanzees at ~3.3% (DeSilva 2011). Mountain gorillas of known age and sex under long-term study in the wild were assessed anthropometrically using remote laser photogrammetry, and document that males do not emigrate from their natal groups until reaching full adult body length, while females emigrate before adult body length is achieved (Galbany et al. 2017). Locomotion signatures in the bones of immature primates and humans link skeletal changes to neuromuscular development, with application to interpret life history stages in postcranial elements of immature hominins (Saers et al. 2022). The use of non-invasive laser camera technology to measure wild and captive orang-utan anthropometrics across different developmental ages documents that both ecology and social organisation affects body size in the apes (Knott et al. 2024). The recovery of a partial skeleton of an infant from the Rising Star Cave allows the reconstruction of a ~2-year-old *Homo* *naledi* at a weight of 5 kg (~11 lbs), and a height of 62 cm (~2 feet), considerably smaller than a modern human infant of comparable age (Cofran et al. 2024). Multivariate analyses of epiphyseal fusions across immature hominins compared with modern humans suggests that *Australopithecus sediba* and *Homo erectus* did not share a skeletal maturity cadence with modern humans, but *Homo neanderthalensis* and *Homo naledi* do exhibit higher concordance with the modern human pattern of fusion (Stull and Wolfe 2024). Applying computerised micro-CT and 3D surface scans to reconstruct lower limb and vertebral skeletal elements of Nariokotome Boy (WT 15000) and comparing their developmental status to an immature modern human sample reveals an ontogenetic variation in the axial and appendicular skeleton of *Homo erectus*, with the developmental stage of the spine estimating an earlier age-at-death than one based on the developmental stage of the distal femur (Haeusler et al. 2024).

The workshop participants engaged in discussion over several days across research fields to stimulate ideas about how best to advance this multi-disciplinary approach within palaeoanthropology, addressing the new questions afforded by the significant increase of extinct immature specimens. In anticipation of future, rich discussions in partnership with the wider scientific community, we conclude with several complex questions for further consideration:

- What can we predict based on maturity patterns in fossil species? E.g. stature, gestation length, birth weight.
- Is chronological and/or biological age the appropriate “gold standard” for maturity modelling in fossil species?
- What hard tissue indicators of soft tissue maturity can be detected reliably on fossils?
- What hard tissue indicators of physiological development can be measured on fossils?
- Can these hard tissue indicators facilitate the reintegration of skeletons in the fossil record?
- Does a longer maturational period in fossil species implicate behavioural adaptations more significant to a particular species? What might those behavioural signatures in the fossil record be and how might they manifest in fossilised materials?
- What are the “best” prediction points from the skeleton in humans and non-human primate models for adult biometrics?
- Are there cases of captive primates maturing at a slower pace than wild counterparts? Are there ways to tease out stressors (and lack of) on the pace of maturity in primates from captive data? Can these variables be quantified? Can these populations be used to help model how variation in stressors affects maturity and adult adaptations that can be applied to fossil species?
- Whole-bodied primate skeletal collections with pedigree information may expand our understanding of patterns of maturity in multiple body systems. Can these collections be used to help model how variation in stressors affects maturity and adult adaptations to apply to fossil hominins?
- Is it possible to collaborate and develop an online catalogue that pulls together data across field sites in Africa, Europe, and Asia on available immature hominin fossil materials, and how to access them for study? (see Bolter and Zipfel this volume). What sort of long-term funding would be required to maintain such an online resource?

Conclusion

The Wenner-Gren Workshop “New approaches to studying sub-adult hominins in the fossil record” occurred over three full days. The agenda, while structured by general topics, allowed for a fluid discussion across a wide range of subjects as conversations developed and ideas flowed (cf. Bolter et al. 2023). There were far more subjects than time to discuss. As participants wrapped up the last afternoon session with a summary and an overview of future goals, it was lamented that time had run out. There had yet been an in-depth discussion of some key topics, such as shape changes across ontogeny, including craniofacial morphology and the role of shape in fitness. Other topics mentioned but not discussed included how to tease out morphological evolution by natural selection, versus evolution by chance factors. “Critical genes” and understanding the genetic component in phenotypes also remained unexplored. So did cascading effects and linkage of systems during development. During the American Association of Biological Anthropology (AABA) meetings in Los Angeles, California in March 2024, the workshop conversations continued in the Invited Symposium *The growth and development of sub-adult hominins: multidisciplinary approaches*. Both through the morning presentations, and in a robust discussion at the end of the talks, the conversation broadened as audience members engaged in an extended question and answer session – with symposium presenters, and with each other. The discussions brought up new ideas, and fresh topics to explore.

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