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A B S T R A C T

Childhood and adolescence are two life-history stages that are either unique to humans, or significantly expanded in the human life course relative to other primates. While recent studies have deepened our knowledge of childhood in the Upper Paleolithic, adolescence in this period remains understudied. Here, we use bioarchaeological maturational markers to estimate puberty status of 13 Upper Paleolithic adolescents from sites in Russia, Czechia, and Italy to 1) evaluate the feasibility of the application of bioarchaeological puberty assessment methods to Upper Paleolithic (*Homo sapiens*) skeletal individuals, 2) estimate the timing and tempo of puberty in Upper Paleolithic adolescents compared to other archaeological populations analyzed using the same method, and 3) characterize adolescence in the Upper Paleolithic by contextualizing the results of this puberty assessment with data on individual and population-level health, morbidity and burial practices. Our results revealed that while puberty had begun by 13.5 years of age for the majority of individuals, there was a lot of variability, with the adolescents from Arene Candide (AC1 and AC16), both aged around 16 years when they died, taking several years longer to progress through puberty than their peers. Assessing the age of menarche was challenging due to the paucity of female adolescents, but based on the available evidence, it appears to have occurred between 16 and 17 years of age. For some, full adulthood had been achieved by 17–22 years, similar to the patterns seen in modern wealthy countries and in advance of historic populations living in urbanized environments. The bioarchaeological analysis of puberty among Upper Paleolithic adolescents has important implications for the study of the emergence of adolescence within human-life histories, as well as for understanding the developmental plasticity of sexual maturation across past and present human populations.

1. Introduction

Adolescence is a dynamic life-history stage, during which physical and cognitive development is influenced by individual prenatal and childhood experiences, which can in turn, dictate adult health outcomes (Dorn et al., 2019; Lewis, 2022). Puberty describes both the initial cascade of hormones from the brain, which kick-starts the process of sexual maturation (or fertility), and a longer-term series of physiological changes including the adolescent growth spurt, the development of musculature in males and breasts in females, the appearance of pubic hair, and psychological changes (Goldman, 1981; Bogin et al., 2018). It is the changes of puberty that signal the start and the end of adolescence as a life stage.

Adolescence has recently emerged as a distinct area of enquiry within the field of bioarchaeology. A focus on adolescents in the

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past informs us not only on the experience of those individuals who were undergoing the physiological transition to adulthood but also on the wider health and well-being of the populations to which they belonged (Avery et al., 2021; Avery and Lewis, 2022; French and Nowell, 2022). Much of the recent research into the bioarchaeology of adolescence has been driven by the development of a method by Shapland and Lewis (2013, 2014; Lewis et al., 2016) to estimate the timing of puberty as a proxy for tracing the adolescent growth spurt, using specific dental and skeletal markers. Adapted from clinical observations, this method evaluates the mineralization of the canine, and maturation of the bones of the hand (metacarpals and phalanges), elbow (distal humerus), wrist (distal radius, hamate), neck (cervical vertebrae), and pelvis (ilium), to estimate the stage of puberty reached by the individual at their time of death. This knowledge can then be used to infer the external physical appearance of that individual, an appearance that changes with each stage of sexual maturation.

This 'puberty' method has been used to explore the timing and tempo (pace) of puberty across a range of archaeological contexts, both historic (medieval England: Lewis et al., 2016; DeWitte and Lewis, 2020; Roman England: Arthur et al., 2016; early 20th century Portugal: Henderson and Padez, 2017; medieval Spain: Doe et al., 2019a, 2022; post-medieval Netherlands: Blom et al., 2020; Roman Italy and Gaul: Avery et al., 2023; New Kingdom Egypt: Dabbs, 2023) and prehistoric (Bronze Age Spain: Doe et al., 2019b; pre-Roman Italy: Bareggi et al., 2022) but has yet to be applied to pre-Holocene populations. Here, we present the first direct evidence for the timing of sexual maturation in Pleistocene adolescents by estimating puberty stage in a skeletal sample dated to the European Upper Paleolithic (~54–12 ka; Slimak et al., 2022).

The European Upper Paleolithic is an ideal case study for an investigation of puberty in the Pleistocene. European Upper Paleolithic hunter-gatherers were members of our species, *Homo sapiens*, permitting the application of osteological methods developed on later historical skeletal populations. Current consensus places the emergence of adolescence as a distinct life-history stage in the Middle-Late Pleistocene, as part of the general shift toward the 'slow' life history typical of *H. sapiens* (Robson and Wood, 2008). Hence, the existence of this life stage in the Upper Paleolithic is not in contention, and instead, attention can be directed toward understanding the timing and tempo of the developmental changes of puberty that characterize this life-history stage. For example, when considering the intimate link between physical and psychological development during adolescence, Gluckman and Hanson (2006) had suggested that puberty occurred earlier in mobile Paleolithic hunter-gatherer societies than in sedentary Neolithic farming societies. The developmental delay of the latter, they argued, matched the more 'complex' Neolithic social environment, allowing young people longer to reach the level of psychosocial maturity necessary to function as an adult in a more socially differentiated society. Estimates of puberty status directly applied to the skeletal remains of Upper Paleolithic adolescents allow us to examine the possible links between adolescent development and the wider social environment earlier in our evolution.

The practice of formal burial during the Upper Paleolithic has resulted in a comparatively large and well-preserved (at least in Pleistocene terms) skeletal sample, information on which is increasingly supplemented by the extraction of ancient DNA (aDNA). Adolescence is often a time when individuals are prepared for their future economic and family roles and responsibilities (which vary depending on gender). In recognition of having reached a new life stage, adolescents may be treated differently, in life and death, from both younger children and adults (Schlegel and Barry, 1991; Nowell and French, 2020; French and Nowell, 2022). The rich archaeological record of the period provides a broader contextual framework for interpreting the findings of the puberty-stage assessment, allowing for the exploration of both the biological and sociocultural facets of Upper Paleolithic adolescence.

The aims of this research are as follows: 1) to assess the feasibility of the application of bioarchaeological puberty assessment methods to Upper Paleolithic (*H. sapiens*) skeletal individuals, 2) to estimate the timing and tempo of puberty in Upper Paleolithic adolescents compared with other archaeological populations analyzed using the same method, and 3) to characterize adolescence in the Upper Paleolithic, contextualizing the results of this puberty assessment with data on health, morbidity, and burial practices.

2. Materials and methods

2.1. Skeletal sample

The study sample comprised 13 individuals dated either directly (^{14}C dating) or via their associated archaeology to the European Upper Paleolithic. Permission to examine each skeleton was obtained from the relevant university or museum where they are curated (Table 1; Fig. 1). The individuals were originally drawn from the database of European Upper Palaeolithic adolescents compiled by Nowell and French (2020) and were selected for inclusion based on the availability of a dental age-at-death estimate or adequate preservation to allow such and estimate to be carried out. The presence of a least three of the skeletal elements as described in Lewis et al. 2016 was required for a puberty-stage assessment. We adopted a definition of 'adolescence' that conforms to the World Health Organization's (2024) classification of this life-history stage (10–19 years). Thus, our sample included individuals previously described in the literature as either 'children' or 'adults' rather than adolescents, with age-at-death estimates ranging from ~10 to 20 years. This definition of adolescence both increased the available skeletal sample and acknowledged the variability (from both a biological and social perspective) in the timing and duration of adolescence documented cross-culturally among recent and historical populations. The inclusion of individuals aged up to 20 years also allowed for any variability in sexual maturation to be captured, as the result of genetic or environmental factors, and minimized the erroneous exclusion of still maturing individuals that might result from a narrower definition of adolescence. This approach also maximized the potential of the sample to inform on multiple relevant aspects of puberty in the Upper Paleolithic (e.g., onset, tempo, and completion).

2.2. Biological sex and age-at-death estimation

For the majority of individuals, biological sex was estimated based on the results of aDNA analyses published in the peer-reviewed literature. For Grotta dei Fanciulli 6, the osteological assessment of the male was later confirmed by amelogenin peptide analysis following enamel etching of the right M^3 via a nanoscale liquid chromatography mass spectrometer (nanoLC-MS), following Stewart et al. (2017). This analysis was carried out at the University of Durham, and the School of Pharmacy and Biomolecular Sciences, University of Brighton, England (see Supplementary Online Material [SOM] Table S1 and Fig. S1). Grotta dei Fanciulli 6 is currently the oldest individual to have been assigned a biological sex using this method.

The biological sex of Arene Candide 1 (AC1), Paglicci 25, and Romito 2 was estimated using characteristics of the mandible, ilium, and humerus. Although sex determination using non-adult skeletal remains is problematic due to the complications of morphological changes during growth and the maturation of the

Table 1
Dates and location of the study sample.[a]

Individual	Country	Date (^{14}C, uncal BP)	Chronocultural attribution	Location	Source
Arene Candide 1	Italy	**23,440 ± 190 (OxA-10700)**	Gravettian	Museo di Archeologia Ligure, Genova Pegli	Pettitt et al. (2003)
Arene Candide 16	Italy	**10,820 ± 40 (GrM-16978)**	Epigravettian	Museo Archeologico del Finale, Finale Ligure	Formicola and Toscani (2014); Sparacello et al. (2021)
Barma Grande 3 Barma Grande 4	Italy	None available	Gravettian	Museo Preistorico dei Balzi Rossi	Formicola (1988); Formicola and Holt (2015); Onoratini et al. (2012)
Dolní Věstonice 13 Dolní Věstonice 14 Dolní Věstonice 15	Czechia	**27,040 ± 100 (Aix-12027)** **26,760 ± 100 (Aix-12028)** **26,680 ± 70 (Aix-12029)**	Gravettian	Archeologický ústav, Akademie Věd České Republiky (Dolní Věstonice)	Alt et al. (1997); Fewlass et al. (2019); Formicola et al. (2001); Mittnik et al. (2016); Trinkaus et al. (2001)
Grotta dei Fanciulli (Enfants) 6	Italy	None available	Gravettian	Musée d'Anthropologie Préhistorique de Monaco	Formicola and Holt (2015); Mallegni and Parenti (1972–1973); Ryan et al. (2024); Verneau (1906); de Villeneuve (1906)
Paglicci 12	Italy	**24,600 ± 90 (MAMS-19075, S-EVA 28202)**	Gravettian	Dipartimento di Scienze Fisiche, della Terra e dell'Ambiente-Università degli Studi di Siena	Mezzena and Palma di Cesnola (1972); Ronchitelli et al. (2015); Modi et al. (2021); Posth et al. (2023)
Paglicci 25	Italy	23,470 ± 370 (F-57);	Gravettian	Dipartimento di Scienze Fisiche, della Terra e dell'Ambiente-Università degli Studi di Siena	Mezzena and Palma di Cesnola (1992); Ronchitelli et al. (2015)
Romito 2	Italy	11,150 ± 150 (R-300)	Epigravettian	Museo Archeologico Nazionale di Reggio Calabria	Craig et al. (2010); Fabbri and Mallegni (1988); Frayer et al. (1987, 1988); Mallegni and Fabbri (1995)
Sunghir 2 Sunghir 3	Russia	**30,100 ± 550 (OxX-2395-6)** **30,000 ± 550 (OxX-2395-7)**	Gravettian[b]	Laboratory of Anthropological Reconstruction of the Institute of Anthropology and Ethnology of the Russian Academy of Sciences	Dobrovolskaya et al. (2012); Formicola and Buzhilova (2004); Marom et al. (2012); Sikora et al. (2017); Trinkaus and Buzhilova (2018); Trinkaus et al. (2014)

[a] The ^{14}C dates in boldface represent direct dates on the fossils; dates in lightface are based on associated material.
[b] The burials from Sunghir would not be considered 'Gravettian' sensu stricto (i.e., associated with Gravettian lithics; Reynolds et al., 2017) but would be considered 'Gravettian' as a broad synonym for 'Mid-Upper Paleolithic' (with direct ^{14}C dates (Marom et al., 2012; Nalawade-Chavan et al., 2014), indicating that chronologically they are best described as Early to Mid-Upper Paleolithic).

skull and pelvis (Wilson et al., 2015), differences in the ages at which males and females enter the adolescent growth spurt made this assessment necessary. Several methods based on the ilium have shown improvement in percent accuracy after the age of 10 years, including the following: the sciatic notch angle (72%), sciatic notch depth (81%), and auricular elevation (72–85%; Sutter, 2003; Wilson et al., 2015; Lewis et al., 2016). Pelvic traits have been shown to increase in their accuracy as puberty progresses and peak height velocity (PHV) has been reached (Sanchez and Hoppa, 2023). The shape of the olecranon fossa and angle of the medial epicondyle on the humerus were also assessed, avoiding trochlear asymmetry (Ammer et al., 2019). For the mandible, chin prominence has been shown to have a 78% accuracy rate for determining the sex of non-adults (Sutter, 2003). AC1 was considered to be a male, Paglicci a female, and Romito 2 a possible male as all three of these areas (ilium, humerus, chin) were in agreement (Lewis et al., 2016).

A mean age-at-death was estimated using stages of dental development of the dentition following Šešelj et al. (2019) based on data from 287 females and 303 males recorded in 1940–1982 for the Fels longitudinal study, Ohio. Both radiographs and direct macroscopic assessment of the dental crowns and roots were used to observe the stage of development for the M3, and occasionally the M2 when it was visible on the radiograph or macroscopically and was still developing (Table 2). While the Šešelj et al. (2019) method provides estimates for the mandibular dentition, for some individuals in our sample, only the maxillary teeth were available for an age estimate. Studies comparing the mean ages derived from the upper and lower dentition have shown that for the permanent dentition at least, maxillary and mandibular teeth provide similar age estimations (Cardoso, 2007). As the mandibular canine is used to indicate the stage of puberty, it was excluded from age estimation. Mean dental ages were not available for Barma Grande 3 and Paglicci 25, who were more tentatively aged based on dental eruption (AlQahtani et al., 2010).

2.3. *Puberty-stage estimation*

The extent of epiphyseal fusion and changes in skeletal and dental morphology were used as a proxy for determining different stages of puberty and the adolescent growth spurt in the Upper Paleolithic adolescents. These stages were as follows: 1) prepuberty, 2) the onset of puberty, signaled by growth acceleration, 3) PHV, when most of the final standing height is achieved, and external characteristics such as breast development and a breaking voice become evident, 4) deceleration of growth, when bones begin to fuse and females begin menstruating, 5) maturation, when all but pelvic growth has ceased, and 6) completion, when all bones have fused and sexual maturation has been achieved. Features on the wrist, hand, neck, and pelvis were assessed following the method outlined by Lewis et al. (2016). In the majority of cases, the assessment was carried out directly on the skeletal remains. The estimation of puberty stage at the time of death for Sunghir 2 and 3, and AC1 and Arene Candide 16 (AC16) was done using new detailed photographs and new radiographs provided by Libby Cowgill and by V.S., respectively.

A puberty stage was assigned when three or more features could be observed. Capping of the phalangeal epiphyses and the beginning of fusion at the elbow indicated that the individual had achieved their PHV. In females, the presence of an unfused but ossified superior iliac crest was taken as a sign that PHV had been passed, and that menarche had occurred. When the iliac crest was fully fused, the individual was recorded as reaching completion (that is, post-puberty and an adult). All results of the analysis are presented in this paper. Photographs and radiographs taken by the authors

Figure 1. Location of sites where the individuals included in this study were discovered.

during this research are available from the first author upon request.

3. Results

Table 3 summarizes the results of the biological sex, age-at-death, and puberty-stage estimates for the adolescents in this study. The majority (61.5%, $n = 8/13$) of the individuals in the study sample were estimated to be male. The youngest adolescent was Sunghir 3, who was around 11 years old, and the oldest was Dolní Věstonice 15 (DV15), estimated to have been aged between 19 and 22 years at death.

Details of the maturation stages of the various skeletal elements are presented in Table 4. The distal radius and iliac crest were the most frequently observed features, whereas the hamate either did not survive or was obscured by other bones when individuals were in a museum display. Many of the individuals included in this study were curated for long-term exhibition in museums and consequently had been subject to extensive reconstruction. In some cases, this involved adhering an unfused epiphysis to the diaphysis and molding the bone to make the epiphysis appear fused. These reconstructions hindered the assessment of some skeletal features that needed to be observed when assigning a puberty stage (e.g., the Dolní Věstonice skeletons, and Grotta dei Fanciulli 6; Fig. 2). Radiographs, that would have permitted an assessment of the extent of epiphyseal fusion below the reconstruction were not available.

A puberty stage was only attainable for 11 of the 13 individuals listed in Table 3. Barma Grande 3 and 4, both possible females (Formicola, 2005; Tarsi et al., 2006), had been damaged by a bomb in World War II. The majority of their bones were replicas that lacked detail on the state of fusion of the epiphyses. As only the distal humerus and distal radius were observable (both unfused), a puberty assessment could not be made with confidence for these individuals (at ca.14 and 16.8 years of age, respectively), except that they had likely not entered PHV as their phalangeal epiphyses were not capped and the bones of the elbow were still unfused. The remaining adolescents considered to be females in our sample were Paglicci 12, Paglicci 25, and Arene Candide 16 (AC16). Paglicci 12 had a mean dental age of 13.5 years, was still within the

Table 2
Mean ages estimated using dental development stages following Šešelj et al. (2019).[a]

	Observation method	Dental development	Mean dental age
Arene Candide 1	Radiographic	M_3 = R¾	16.7
Arene Candide 16	Radiographic	M_3 = R¾	16.8
Barma Grande 4	Radiograph	M^3 = R½	16.8
Dolní Věstonice 13	Radiographic	M_3 = Rc	17.1
Dolní Věstonice 14	Radiographic	M_3 = R¾	16.7
Dolní Věstonice 15	Radiographic	M_3 = Ac	19+
Grotta dei Fanciulli 6	Macroscopic	M^3 = Cli	14.3
Paglicci 12	Macroscopic	M_3 = Ri	13.5
Romito 2	Macroscopic	M_3 = R½	16.1
Sunghir 2	Radiographic	M_2 = A½	14.1
Sunghir 3	Radiographic	M_2 = R½; M_3 = Cr½	10.8–11.4

Abbreviations for dental development stages (following Moorrees et al., 1963): Cli = initial cleft formation; C¾ = a third of the crown has developed; Ri = initial root formation; R¾ = a third of the root length is formed; R½ = half the root length has formed, Rc = root length complete; A½ = the apex is half closed; Ac = apex closed—it is not possible to estimate an age once this stage has been reached.

[a] The extent of dental mineralization was not available for Barma Grande 3 and Paglicci 25 and they have not been included in the Table.

Table 3
Estimated biological sex, age-at-death, puberty stage, and physical appearance of the Upper Paleolithic adolescents.

Individual	Biological sex	Biological sex method	Mean age (years)	Puberty stage	Physical appearance
Arene Candide 1	Male	Osteology[a]	16.7	Acceleration	Still child-like, but pubic hair begins to appear, and there is an increase in body mass
Arene Candide 16	Female	aDNA[b]	16.8	PHV	Transitional: increase in height, breast development
Barma Grande 3	Female?	aDNA[c]	ca.14	Not possible to estimate	–
Barma Grande 4	Female?	aDNA[c]	16.8	Not possible to estimate	–
Dolní Věstonice 13	Male	aDNA[d]	17.1	Completion (post-puberty)	Fully adult
Dolní Věstonice 14	Male	aDNA[d]	16.7	Maturation	Adult-like: facial hair appears, muscles increase, height stabilizes
Dolní Věstonice 15	Male	aDNA[d]	19–22[g]	Completion (post-puberty)	Fully adult
Grotta dei Fanciulli 6	Male	Peptides[a]	14.3	PHV	Transitional: increase in height and musculature, voice 'breaks'
Paglicci 12	Female	aDNA[b]	13.5	Acceleration (pre-menarche)	Still child-like, but breast buds and pubic hair appearing, increase in body mass
Paglicci 25	Female	Osteology[e]	ca. 20	Maturation	Adult-like: full height and breast development, post menarche
Romito 2	Male?	Osteology[a]	16.1	Deceleration	Transitional: deeper voice, armpit and pubic hair
Sunghir 2	Male	aDNA[f]	14.1	Acceleration	Still child-like, but pubic hair appearing, increase in body mass
Sunghir 3	Male	aDNA[f]	ca. 11	Pre-Puberty	Child-like

Abbreviation: PHV = peak height velocity.
[a] Current study.
[b] Posth et al. (2023).
[c] Tarsi et al. (2006) these data are not fully published.
[d] Mittnik et al. (2016).
[e] Ronchitelli et al. (2015).
[f] Sikora et al. (2017).
[g] Based on skeletal development.

acceleration phase of her growth spurt, and had not attained menarche. AC16 was older with a mean dental age of 16.8 years, a similar age to AC1, and capping of her phalangeal epiphyses and a fusing distal humerus suggests she had reached PHV, although the epiphysis of the first metacarpal (MC1) was unfused, which was less advanced than the fusing MC1 of Paglicci 12. Again, despite her older age, AC16 had also not achieved menarche when she died. The oldest female in our sample, Paglicci 25, would likely have experience her first menarche but died just short of completing puberty, in the maturation phase (her iliac crest was still fusing) at ca. 20 years.

Small sample sizes make any firm observations about average ages of attainment in the Upper Paleolithic impossible. However, puberty appears to have begun for both males and females between the ages of 11 and 14 years as Sunghir 3 was pre-puberty, and both Sunghir 2 and Paglicci 12 were estimated to be in the acceleration phase by 13.5 and 14.1 years, respectively. Only one individual—Grotta dei Fanciulli 6, with a mean age of 14.3 years, was at PHV at the time of his death, whereas Dolní Věstonice 14 (DV14), the youngest male in the triple burial, estimated to be aged 16.7 years at death, had entered the maturation stage. Dolní Věstonice 13 (DV13) had completed puberty when he died aged 17.1 years. Not all individuals fit within this pattern. AC1, at 16.7 years, had only just achieved acceleration, two-and-half years after another male, Sunghir 2. Romito 2 appeared to have attained deceleration when he died at 16.1 years, somewhat behind the Dolní Věstonice males who had already completed their development by 17 years. Five of the eight males (62.5%) in the study (Grotta dei Fanciulli 6, Romito 2, and DV 13, 14, 15) would have been capable of having children. By contrast, four of the five females in the sample had yet to achieve menarche (if we take a conservative approach to the Barma Grande individuals), and three of them would still have appeared as children, whereas AC16 would likely have started to show some external signs that she was maturing (i.e., breast development), and AC25 would have appeared fully adult.

Finally, to fully appreciate the differences in growth and physicality between these Upper Paleolithic adolescents, their maximum femoral and tibial lengths were compared (Frayer et al., 1988; Mednikova, 2005). These results do not include the Dolní Věstonice males or Paglicci 25, who had finished their growth spurt (i.e., had reached maturation or completion) by the time of their death (Figs. 3 and 4).

These results show a similarity in height among those adolescents (without lower limb deformities), with AC1 already being taller (with greater femur and humerus measurements) than Grotta dei Fanciulli 6, despite the latter being in PHV. AC16's femur on the other hand is slightly shorter than that of the younger Paglicci 12, who had just begun her growth spurt. Humeral lengths were similar for all the females. This pattern corroborates earlier studies that have argued for taller pre-Last Glacial Maximum (LGM) or Gravettian populations compared to smaller post-LGM (Epigravettian/Magdalenian) groups (Formicola and Giannecchini, 1999).

4. Discussion

This study represents the first application of bioarchaeological methods for estimating the stage of puberty, timing of the adolescent growth spurt, and sexual maturation in Upper Paleolithic skeletal remains. From a feasibility perspective, we have demonstrated that multiple Upper Paleolithic individuals are sufficiently complete and well preserved (in terms of the presence of the relevant skeletal and dental features) to undergo a puberty assessment. The re-examination of the Upper Paleolithic individuals in our sample, however, has identified where curatorial practices—particularly reconstruction for museum display—have hindered a full assessment of puberty stage.

Our adolescent sample suffers from further limitations. Firstly, our sample size is small. This small sample size is caused by a combination of the comparatively limited number of Upper

Table 4
Maturation scores used to assign a puberty stage for the Upper Paleolithic adolescents.[a–d]

	AC1	AC16	DV13	DV14	DV15	Grotta dei Fanciulli 6	Paglicci 12	Paglicci 25	Romito 2	Sunghir 2	Sunghir 3
Hamate	I	H5	–	–	I	–	H5	I	I	–	–
Canine	H	H	H	H	H	–	G–F	–	–	G	F
Distal radius	unfused	unfused	fused	fusing	fusing	unfused	unfused	fused	fused	unfused	unfused
Distal ulna	unfused	Unfused	–	–	fused	unfused	unfused	fused	–	unfused	unfused
Capitulum	unfused	fusing	fused	fused	fused	fusing	unfused	fused	–	unfused	unfused
Hand phalanges	equal length	capped	–	fusing	fused	unfused	capped	fused	fused	unfused	unfused
Metacarpal 1	fusing	unfused	fused	–	fused	–	fusing	fused	fused	–	–
Metacarpals 2–5	Unfused	unfused	fused	–	fused	unfused	unfused	fused	fused	–	–
Iliac crest	Unfused	unfused	fused	unfused	fused	unfused	unfused	Fusing	unfused	unfused	unfused
Cervical vertebra morphology	2	2–3	3–4	3–4	–	–	2–3	–	4	2	–
Estimated Puberty Stage	**Acceleration**	**PHV**	**Completion**	**Maturation**	**Completion**	**PHV**	**Acceleration**	**Maturation**	**Deceleration**	**Acceleration**	**Pre-puberty**

PHV = peak height velocity.
[a] The en dash (–) indicates that the feature was unobservable.
[b] Hamate scores: H5—hook half formed, I hook complete.
[c] Canine scores are according to Demirjian et al. (1973) where R¾ (F) indicates the onset of the growth spurt, A½ (G) indicates acceleration, and Ac (H) that PHV has been reached.
[d] Cervical vertebrae scores according to Shapland and Lewis (2014), where 2 is the earliest stage of morphological development and 6 the latest stage of development.

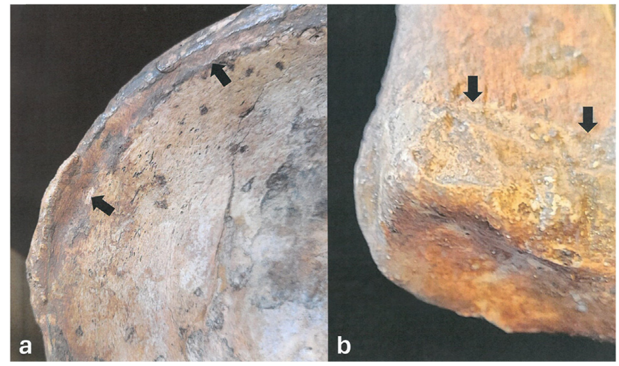

Figure 2. **a**. Glued and molded unfused iliac crest of DV14 (black arrows); **b**. Left distal radius of the Grotta dei Fanciulli adolescent. The epiphysis was glued and molded to the diaphysis, making it appear fused (arrowed). When the right radius was excavated as part of this project, it showed the radial epiphyses were, in fact, unfused and that this individual was in an earlier stage of puberty. (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article.)

Paleolithic skeletal remains relative to later prehistoric and historic periods, perhaps a result of destructive taphonomic processes, small group sizes, high residential mobility (French, 2021:35), and the typical U-shaped distribution of human age-specific mortality risk. Age-specific mortality risk is lowest during the adolescent and young adult years, resulting in fewer individuals of these age classes entering the skeletal record (Lewis, 2007). While such small numbers limit our ability to fully understand the variability of ages at which Upper Paleolithic adolescents from across Europe began their transition to adulthood, some patterns are evident, and at an individual level, a detailed osteobiography can be created (Lewis, 2022; see section 4.3).

Secondly, and in contrast to most other puberty assessment studies, the individuals in our sample do not represent a skeletal 'population' per se (i.e., from the same site and broadly contemporary), but instead derive from multiple sites and dates, to form a pooled subsample of the wider European Upper Paleolithic metapopulation. This subsample exhibits some notable biases. Most of our individuals date to the Mid-Upper Paleolithic (Gravettian; ~35–25 ka), and half derive from sites located in present-day Italy. The majority of individuals for whom a puberty status could be suggested are male. While these biases broadly reflect those of the Upper Palaeolithic skeletal record as a whole (Pettitt, 2011; Riel-Salvatore and Gravel-Miguel, 2013; French and Nowell, 2022; Arenas del Amo et al., 2024), neither this wider skeletal record nor our adolescent sample can be considered wholly representative of the living population from which they derive.

Comparing the age at which an adolescent from an archaeological site achieves a puberty stage with a modern adolescent should be treated with caution, even for skeletal remains of more recent date. Bioarchaeologists can only assess the stage the person was in at their age of death, as opposed to the age at which they attained that stage—a measure used in modern studies. In addition, secular changes in dental and skeletal development are well recognized, meaning archaeological skeletons with a dental age of 17 years, using modern comparisons, may actually be much older at 21 years as they are lagging behind in their development (Liversidge and Marsden, 2010). In fact, it has been reported that the accuracy of the age estimated using dental mineralization of the upper and lower third molars declines during puberty. This is a problem because as one of the last teeth to develop, this tooth is most frequently used as an indicator of age for adolescent skeletons. The dental roots take longer to form in more recent archaeological adolescents, even when compared to modern children

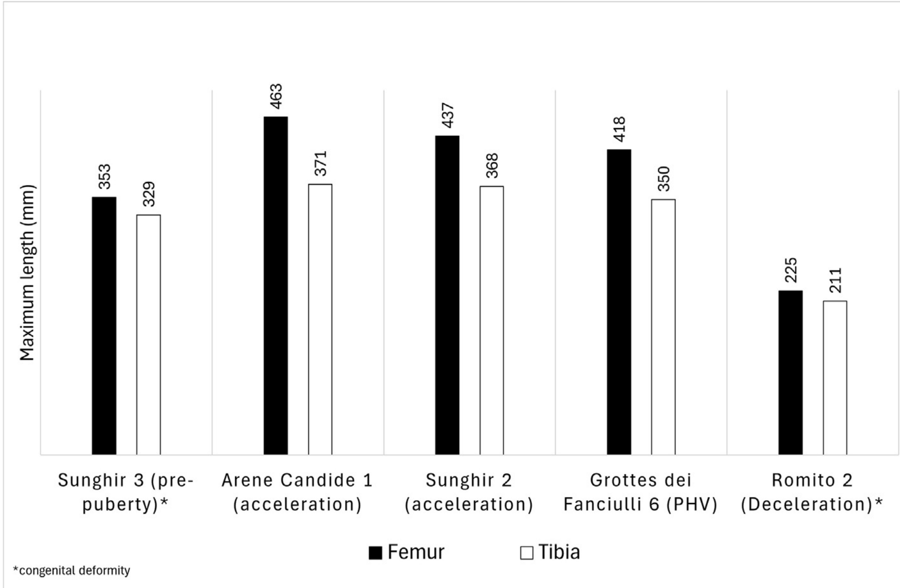

Figure 3. Bar graph comparing femoral and tibial length in the males, ordered by their stage within the growth spurt. Sunghir 3 and Romito 2 had abnormally short limb bones. PHV = peak height velocity. Measurements taken from Frayer et al. (1988) and Mednikova (2005).

from poor environmental conditions (Cardoso et al., 2010, 2018). That said, research into the growth and development of early *H. sapiens* has shown that their teeth (including the upper and lower M3s) actually develop earlier than those of modern reference standards—which are often derived from early industrial populations (Dean and Liversidge, 2015; Šešelj, 2017; Nava et al., 2017; Šešelj and Konigsberg, 2020). The relationship between dental age and skeletal growth—including the adolescent growth spurt—although correlated, is still little understood even in modern humans (Šešelj, 2013). This potentially advanced dental development in our adolescents (perhaps they are a year younger than suggested by the standards we used), may not necessarily be reflected in advanced sexual maturation for age.

Despite these limitations, our results provide the first specific data on puberty in the Upper Paleolithic, which, when integrated with the wider (bio)archaeological record, provide insights into both the biological and sociocultural facets of Upper Paleolithic adolescence.

4.1. Upper Paleolithic adolescence in comparative perspective

Data from the Upper Paleolithic adolescents suggest that puberty began for both males and females between the ages of 11 and 14 years, with completion of sexual maturation reached between 17 and 20 years for the majority of individuals. When trying to gain a picture of the timing and tempo of sexual maturation in the Upper

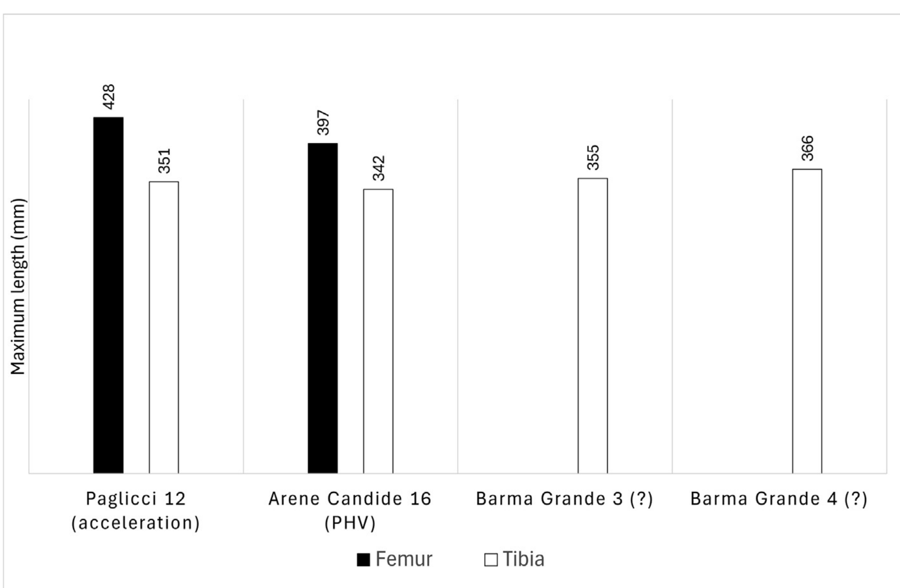

Figure 4. Bar graph comparing femoral and tibial length in the females, ordered by their stage within the growth spurt. The Barma Grande females could not be assigned a puberty stage. PHV = peak height velocity.

Paleolithic, it is important to note that these individuals are intrinsically unusual in that they were specifically selected for burial, perhaps as a means of containing or sanctioning distinctive individuals (Formicola, 2007; Pettitt, 2011). The range of variability noted in the sample, for example, with the later development of AC1 than the other males of a similar age, nonetheless suggests that a normal pattern of adolescent development is being captured, with some individuals being slightly ahead of, or behind their peers, just as with modern adolescents.

While our study is the first to use bioarchaeological puberty assessment methods to directly estimate the timing and tempo of puberty in the Paleolithic, other published estimates exist in the literature. Most notably, Gluckman and Hanson (2006) suggested an age at menarche for Paleolithic *H. sapiens* between the ages of 7 and 13 years. This calculation was based on chimpanzee maturation scales, and the knowledge that humans lag behind them in development by 3–4 years. Data to test this assertion have, however, been limited. One rare insight comes from the Mid-Upper Paleolithic (Gravettian) Ostuni 1 burial, a female who was heavily pregnant at the time of her death at ~20 years age (Nava et al., 2017). If, as in more recent females, a 2- to 5-year anovulatory period after menarche existed (Itriyeva, 2022), and she conceived at around 19 years, her pregnancy suggests a later age at menarche of between 14 and 17 years, although it is possible that this was not her first pregnancy. Our results provide further support for the notion that menarche might indeed have occurred much later in Upper Paleolithic females than suggested by Gluckman and Hanson (2006). Paglicci 25 is estimated to have been at least 20 years of age based on the full eruption of her M3; however, the iliac crest was still fusing placing her in the maturation stage. This suggests menarche had been reached but likely only a few years before she died. Similarly, AC16, with an estimated age of 16.8 years (potentially 15.8 years) had not yet reached deceleration (when menarche occurs). While a clear estimate for the age of menarche is not possible based on current data, it appears to have been no earlier than 16–17 years.

How do our Upper Paleolithic individuals fit within adolescent development seen in other archaeological and modern groups? A comparison based on published data is provided in Table 5. In wealthier countries today, the onset of puberty, indicated through soft tissue changes, is experienced between the ages of 8 and 13 years in females and 9–14 years in males (NICHD, 2024). PHV normally occurs between 11.5 and 12.5 years in females and 13.5 and 14.0 years in males, with sexual maturation complete by 16 and 18 years in females and males, respectively (Lewis, 2022). Among recent hunter-gatherers (foragers)—the present-day populations whose way of life most closely resembles that of the Upper Paleolithic—there is considerable variation in the average age of the start of the adolescent growth spurt (10.0–13.5 years [female]; 11.0–13.0 years [male]) and achievement of PHV (12.5–16.0 years [female]; 13.0–16.0 years [male]; Walker et al., 2006). Substantial variation is also seen in average age at menarche (a proxy for the deceleration stage of puberty) among recent foragers, with an early age reported for the Pumé (mean = 12.9 years; Kramer, 2008) and notably later ages among the Hadza (median = 16.5–16.8 years; Fitzpatrick, 2018; Marlowe, 2010) and Ju'/Hoansi (mean = 16.6 years; Howell, 1979; but see Diekmann et al., 2017; Page and French, 2020, for further consideration of both the accuracy of demographic and developmental data on recent foraging populations, and their relevance to Paleolithic cases).

The largest bioarchaeological study using the same puberty assessment methods as our Upper Paleolithic adolescents was based on 236 males and females from medieval England, encompassing mainly urban and industrial environments (Lewis et al., 2016). The results showed a high degree of variability in ages within each puberty stage, consistent with patterns seen today. Nevertheless, in all samples, the onset of puberty, or the adolescent growth spurt, occurred between the ages of 10 and 13 years, and acceleration (where an increase in height would have been noticeable) occurred at an average age of 12.4 years; PHV, where the changes of puberty would have been the most evident to the community, occurred around 15 years, and a final adult appearance would have been evident by 18–22 years. In females, the age of menarche was estimated to have been between the ages of 12 and 15 years, with the youngest estimates reflecting modern trends of the average age of menarche at 12.5 years.

While there should be caution when comparing a small sample of individuals from across such a long period of time, and from across Europe, these data tentatively suggest that compared to medieval adolescents, puberty was initiated perhaps two years later for the European Upper Paleolithic individuals, at 13–14 years, and it lasted for a shorter period of time, that is, they matured faster. If the length of sexual maturation is calculated using the number of years between the age of onset and the age of completion, Upper Paleolithic adolescents took nine years to go through this process compared to 15 years in medieval Europe and developed at a similar rate to modern adolescents (ca. 10 years for males and females combined), who in most cases are going through this developmental period in optimal environmental circumstances. Male adulthood was achieved between the ages of 17 and 22 years, similar to 18 years for modern males. This estimate may be even younger if dental development was in advance of skeletal development during this time. The medieval data likely reflect the impact of urbanization and industrialization on health—while individuals living in the Upper Paleolithic would have experienced a very different living environment. Overall, the results of our study indicate a pattern of pubertal development in the Upper Paleolithic that is within the range of recorded variation across modern and historical populations, both in terms of the timing and tempo of puberty and in the interindividual variation documented.

4.2. Upper Paleolithic lifestyle, health, and the timing of puberty

Puberty is driven by, and is associated with, a complex interplay of physiological and hormonal processes, which further interact with both the social environment and the overall health condition

Table 5
Mean age ranges (years) related to different stages of puberty in modern, recent archaeological, and the Upper Paleolithic adolescents (male and females combined).[a]

Stage	Modern	Modern foragers	Medieval England	Upper Paleolithic
Acceleration	8.0–14.0	10.0–13.0	10.0–16.5	13.5–16.7 (12.5–15.7)
Peak height velocity	11.5–14.0	12.5–16.0	11.0–19.0	14.3–16.8 (13.3–15.8)
Deceleration	No data	12.9–17.0	12.5–19.5	16.1 (15.1)
Menarche	12.5	12.9–17.0	12.0–17.0	ca. 16.0–17.0
Maturation	No data	No data	22.0	16.7 (15.7)
Completion	16.0–18.0	No data	25.0	17.1–22.0 (16.1–21.0)

[a] Modern deceleration and maturation data are not available, with deceleration marked by the onset of menarche for females. The potential one-year advance in dental development for Upper Pleistocene individuals compared to their modern counterparts is reflected in parentheses (see text for references).

of the individual to influence the timing and tempo of the adolescent growth spurt (Lewis, 2022). For example, among living populations, delays in puberty-stage attainment have been linked to environmental and psychological stressors, such as exposure to violence (Villamor et al., 2009), dietary deficiency, chronic illness (Proos and Gustafsson, 2012; Lewis et al., 2016), and extreme physical exertion (Louis et al., 2008), as well as individual genetic factors. The timing of menarche is equally complex, and in addition to factors noted earlier, represents a biological trade-off between physical growth and sexual maturation—as menarche signals a cessation of linear growth (deceleration). While data can vary, in adverse conditions, a fetus generally will be programmed to reach sexual maturation early in lieu of full skeletal growth, whereas in better conditions, menarche can be delayed until the pelvis is more fully developed and body weight reaches the optimal level to ensure the best possible outcome for the offspring (DeWitte and Lewis, 2020).

It is reasonable to assume that, as members of our species, puberty for adolescents in the Upper Paleolithic was likewise influenced by a range of biological, social, and environmental variables. Given the pooled nature of our sample, it is difficult to interpret these findings in terms of the physical and social environment in which these adolescents lived. Nonetheless, several features of the wider European Upper Paleolithic record (specifically that of the mid-Upper Paleolithic [MUP], or Gravettian, the period to which the majority of our sample dates) provide some relevant context in terms of variables that might have influenced the timing of puberty. Most notable among these are the climatic context of Late Pleistocene Europe and the mobile hunter-gatherer lifestyle of these populations. Climatic conditions during the MUP were variable but typically very cold and dry, falling within the final stages of the cold-temperature Marine Isotope Stage 3 interpleniglacial (Rasmussen et al., 2014). Studies of both upper and lower limb hypertrophy and muscle attachments indicate that the lives of MUP people were characterized by high levels of mobility and physical exertion (Trinkaus et al., 2001; Holt, 2003; Cowgill et al., 2015; Villotte et al., 2017). While life was clearly physically demanding, MUP populations are nonetheless collectively characterized as relatively healthy, at least in comparison with both earlier archaic Neanderthal populations and their Late Upper Paleolithic successors (Formicola and Holt, 2015; Niskanen et al., 2018). The impact of infectious diseases on MUP people is, however, difficult to estimate. Low metapopulation estimates and population densities (Maier and Zimmerman, 2017) might indicate a low population-level infectious disease burden, although high mobility and extended social networks could still have facilitated the spread of these diseases (Houldcroft and Underdown, 2023).

Within this wider context, there is one notable factor specific to the adolescents in our sample of potential relevance to pubertal timing: they exhibit a high rate of skeletal pathology, even by Upper Paleolithic standards (see Trinkaus et al., 2014; Trinkaus, 2018), where it has been proposed that some form of developmental 'difference' might have been a consideration in determining who was given a formal burial (Formicola, 2007). Of the 11 individuals included in our study, for whom a puberty stage could be assessed, eight have some form of pathological condition. These conditions can inform us about the types of activity and childhood experiences of these individuals that may have influenced the ages at which they attained full maturation. The nature and severity of these pathological changes is wide-ranging, encompassing relatively minor conditions such as enamel hypoplasia (e.g., Grotta dei Fanciulli 6) as well as reported examples of developmental abnormalities, for example, in Dolní Věstonice 15 and Sunghir 3 (Alexeeva et al., 2000; Formicola et al., 2001; Mittnik et al., 2016). The overriding pathological condition in the adolescents in our study is trauma, evident in at least five of the individuals, and suggestive of a physically challenging and hazardous lifestyle.

The individuals within our sample who notably lagged behind their counterparts in terms of their development exhibit some form of pathology; AC1 had perimortem trauma to his face and thorax that has been attributed to bear mauling (Mussi et al., 1989); AC16 had a deformity to her wrist, which could be traumatic or congenital in origin (Formicola and Toscani, 2014; Sparacello et al., 2019), and Romito 2 had a congenital condition (chondroplastic dwarfism; Frayer et al., 1987, 1988). Romito 2's condition may account for a delay in the fusion of his iliac crest, but little is known about the impact of skeletal dysplasia on the timing of puberty, especially in males where the common measure, age at menarche, does not apply (Holopainen et al., 2018). Although AC1 did not survive his severe injuries for long, his manner of death may hold indirect implications for his development. This slower tempo may suggest that AC1 was living in a harsher environment than the others in this study, or it may simply reflect the normal extent of individual variation in growth and development that existed at this time. It is possible that the pathological conditions exhibited by our Upper Paleolithic adolescents influenced the timing and tempo of puberty, especially in the absence of the means to control for other potential (genetic, environmental) factors that might also impact puberty. While the estimation of the timing of menarche is tentative in the sample, it appears to have occurred later than in females from modern wealthy countries, but at a similar time to modern foragers (ca. 17 years), perhaps indicating that both in uterine and postnatal conditions were good enough to allow growth to reach optimal levels before fertility was reached. It may also signal, however, that these females were more delayed in their development due to conditions that led to their burial in the first place. Despite such caveats, our results indicate a pattern of onset and progression through puberty in the Upper Paleolithic that was within the range of later historical cases and in the case of final sexual maturation, was earlier.

4.3. Burial evidence: linking social and biological elements of adolescence in the European Upper Paleolithic

The estimation of a puberty stage from the skeleton allows for the physical characteristics of these individuals to be reconstructed, presenting an intimate osteobiography that connects both the biological and sociocultural facets of adolescence. While 'adolescence' encompasses a broad age range, the physical appearance of those within this category can be starkly different, from appearing child-like to appearing to be a full and sexually mature adult. It is possible that this appearance affected an adolescent's relationships with others in their communities. In this section, we consider six individuals, illustrating how combining our puberty assessment with data from the wider burial context can enrich our understanding of the lives of Upper Paleolithic adolescents and the communities in which they lived.

Sunghir 2 and 3 The burial of Sunghir 2 (estimated to be 14 years old at death) and Sunghir 3 (ca. 11 years old at death) provides a compelling example of adolescence as a possible life-history stage of sociocultural importance in Upper Paleolithic communities. Placed head-to-head in a double interment, Sunghir 2 and 3 (initially suggested to be siblings, but now known to be third degree relatives, possibly cousins, Sikora et al., 2017), received a notably elaborate burial within the wider Mid-Upper Paleolithic funerary context. Ochre covers their heads, trunks, and upper arms, and the grave goods include ivory discs and spears, personal ornaments, portable art, and more than 10,000 highly standardized ivory beads (Trinkaus and Buzhilova, 2018). These items are not equally distributed between the two individuals in the burial. While a greater number of the ivory beads are associated with the younger Sunghir 3, it is the unique items associated with Sunghir 2 that hint at a difference in social status, possibly linked to a life-history stage. These items include an isolated femur filled with red ochre (known as 'Sunghir 4'), an animal figure, a decorated belt and pierced arctic fox canines. Ivory discs are distributed throughout the grave, but most are associated with Sunghir 3, as are most of the ivory spears (although the longest of these is placed nearest to Sunghir 2; Trinkaus et al., 2014). Earlier osteological assessments suggested that Sunghir 3 was female and Sunghir 2 male (Formicola and Buzhilova, 2004). Following this, Trinkaus et al. (2014) postulated that the differences in associated grave goods were related to ideas of 'maleness' within the Sunghir community, with the fox canines specifically linking Sunghir 2 with Sunghir 1—an adult male buried nearby (Trinkaus and Buzhilova, 2012)—whose grave also contained these pierced teeth.

This hypothesis of a sex-based distinction reflected in the grave goods was undermined by subsequent aDNA results, which confirmed that both Sunghir 2 and Sunghir 3 were male (Sikora et al., 2017). Instead, French and Nowell (2022) hypothesized that the similar artifacts associated with Sunghir 1 and Sunghir 2 (and not with Sunghir 3) might reflect a social distinction based on age within the Sunghir community, aligning the older Sunghir 2 with the adult men (and their attendant roles and responsibilities) in contrast to the younger Sunghir 3 who was still considered a 'child.' This possible age-based social distinction is further mirrored in buccal dental microwear, which suggests differences in diet between Sunghir 1 and 2 on the one hand and Sunghir 3 on the other (Trinkaus et al., 2014).

Both Sunghir 2 and 3 show developmental skeletal pathology. Sunghir 2 had an asymmetric skull that may have been the result of unilateral craniosynostosis, but which may not have been as obvious to the community (if hidden by hair, for example), whereas Sunghir 3 had bilateral abnormal anteriorly bowed femora (the tibiae appear normal). This condition was suggested to be the result of weight bearing at a young age (Alexeeva et al., 2000), but it may also have been caused by a genetic condition and may have corrected itself had the child lived (Cormier-Daire et al., 2004). The presence of pathology in these individuals may explain their burial in this period, but not necessarily the distinction between the two, as we have no understanding of how rare such conditions were in these communities.

Our puberty assessment provides further support for French and Nowell's (2022) hypothesis of an age-based distinction within the Sunghir community being reflected in the burials and links it specifically with adolescence. Their community might have been aware of the physical distinction at the time of death between the fully child-like appearance of Sunghir 3, who had yet to begin puberty and that of Sunghir 2 whose physical appearance was beginning to change as he reached the acceleration phase of puberty development. Today, this changing physical appearance would be subtle if he had just entered this stage (including an increase in height and initiation of body hair) or more advanced if at the end of it. It is currently unknown, however, how well modern external physical changes would have mapped on to adolescents in the Upper Paleolithic, and this burial treatment might suggest he appeared more mature than a child in acceleration would do today. The life-history data, grave goods, and dietary (microwear) data nonetheless all hint at a possible point of social distinction among the Sunghir community occurring at or near the onset of adolescence and the adolescent growth spurt.

<u>Arene Candide 1</u> This male is notable within our sample of Upper Paleolithic adolescents for his delayed development. At nearly 17 years of age, he had only just achieved the second (acceleration) phase of the adolescent growth spurt. He had yet to achieve PHV, would not have exhibited a significant increase in musculature or height, and his voice would not yet have begun to 'break.' While the reason(s) for his delayed development is unclear, it holds implications for interpretations of his burial.

AC1 is frequently referred to as 'Il Principe' (the Prince) due to the richness of his burial and accompanying grave goods. AC1 lies in a supine and extended position on a bed of red ochre. Further red ochre staining is visible on the skeletal remains, likely from ochre-soaked clothing that has since rotted away. A mass of yellow ochre fills the space between his left clavicle and mandible where both bones are largely missing due to trauma. The grave goods include hundreds of perforated shells and deer canines encircling the head (suggestive of the former presence of a shell cap), four mammoth ivory pendants, four perforated 'batons de commandement' made from elk antler, and a 23-cm long flint blade held in his right hand (Pettitt et al., 2003).

The combination of his elaborate burial and his young age has been interpreted as possible evidence for social stratification and 'ascribed' status within the European Upper Paleolithic (e.g., Hayden, 2020). It is proposed that AC1 was too young when he died to have personally 'earned' preferential treatment in death through his own actions, and therefore may have inherited the high social status reflected in his spectacular burial. Our finding from the puberty assessment, that he was less developed than might be expected for his age, and that he looked more child-like in his physical appearance than previously supposed, strengthens this interpretation by heightening the contrast between his perceived age and his potential status.

Conversely, the developmental delay of AC1 might relate to alternative interpretations of the MUP burial database and AC1's place within this corpus. Recent studies have questioned interpretations linking MUP burials to emergent social hierarchies (d'Errico and Vanhaeren, 2015; Nowell, 2020). Wengrow and Graeber (2015:605), for example, note the frequent co-occurrence of the aforementioned high rate of physical abnormalities and rich burials to suggest that "the ostentatious display of personal wealth was ritually associated with the same kind of 'otherness' seen as inherent in anomalous or exceptional individuals … Such burials were exceptional in every sense and can hardly be interpreted as simple proxies for social structure among the living". AC1's burial is clearly rich, and the manner and circumstances of his death may have represented an exceptional event (although Upper Paleolithic populations as a whole display relatively high rates of trauma; Beier et al., 2018, 2021). However, his delayed development, identified for the first time in this study, could also have marked him out as somehow 'different' from his peers, determining or further heightening the exceptionality of the event.

<u>Paglicci 12 and 25</u> Paglicci 12, a 13- to 14-year-old female adolescent, dated to the Gravettian (Mezzena and Palma di Cesnola, 1972; Modi et al., 2021; Posth et al., 2023), was lying on her back and was covered with red ochre. The left humerus is missing, and the forearm was placed transversally on the abdomen. About 30 pierced red deer 'craches' (fossilized teeth) were found in the area of her head, and one on the left wrist and one near the right ankle. The funeral toolkit consisted of eleven lithic implements and one bone piercer. In addition, two specimens of *Luria lurida* (Cypraeidae) and one small manganese block were discovered among the grave goods. Paglicci 25 was a ca. 20-year-old female buried lying on her back and dates to a slightly more recent phase within the Gravettian (Mezzena and Palma di Cesnola, 1992; Ronchitelli et al., 2015). Ochre was concentrated on her head, pelvis, and feet. She was buried with few grave goods, consisting of only five lithic implements and seven pierced red-deer craches on the forehead; a seashell was also discoveredin this burial, but it is a species of *Pecten* close to her left foot.

These two females would have appeared physically very different, with Paglicci 12 still appearing as a child, and Paglicci 25 a fully grown woman. Unlike their male counterparts for this period, however, there appears to be little distinction made between them in terms of their burial treatment. The two individuals were buried with rituals showing some similarities (ochre, red-deer chraches, and seashells) but with some differences (the distribution of pigments on the bodies, as well as the position and quantity of grave goods). No pathological conditions were found in either individual that distinguished them from the other burials of this period. Basic elements of a similar funerary ritual were also observed, albeit with a greater wealth of grave goods, as at the aforementioned Gravettian site of Grotta di Santa Maria di Agnano (Ostuni 1; Vacca and Coppola, 1993); it is noteworthy that these three individuals belong to a same genetic cluster (Posth et al., 2023).

Romito 2 This adolescent, estimated to be male, represents the earliest known case of chondroplastic dwarfism (Frayer et al., 1987, 1988). Aged around 16 years at death, Romito 2 died during the fourth (deceleration) stage of puberty. The impact of his congenital condition on his development is difficult to determine. In comparative perspective with the other Upper Paleolithic adolescents in our sample, he was behind the Dolní Věstonice males but does not appear to have experienced the greater delay of AC1. Our puberty assessment, however, does generate some further information about Romito 2's likely physical appearance, providing a new perspective on the social role and perception by others of this unique Upper Paleolithic individual.

Romito 2's physical appearance shortly before his death is best described as 'transitional.' He would have likely had the deep voice of an adult male, and would have been physically able to sire children, but may still have appeared youthful with fine facial hair (but not the ability to grow a full beard). When combined with his short stature (his height is estimated to have been between ~1.0 and 1.3 m; Frayer et al., 1988), Romito 2's appearance would have perhaps been more akin to that of a child than an adult man, with implications for how he was perceived by his community. Tilley (2015) has documented how Romito 2's skeletal dysplasia would have limited his engagement in typical Late Upper Paleolithic hunting activities. This physical contrast between Romito 2 and his peers might have taken on added significance as he entered adulthood, and he was unable to assume the roles and responsibilities associated with this phase of life (Tilley, 2015; Nowell, 2021). Along these lines, it is noteworthy that Romito 2 is unique among Upper Paleolithic burials in being buried in the arms of an older woman (Romito 1; often assumed to be his mother; Frayer et al., 1988). We will likely never know why he was buried this way, but it brings to mind a protective or caring gesture perhaps indicating that, despite his changing physical appearance, he might have been still considered more 'child' than 'adult' when he died.

5. Conclusions

Adolescence is an individually experienced and dynamic period of the human life course. The timing and pace at which an individual reaches sexual maturation is the result of a complex relationship between genetic and fetal preconditioning and postnatal life experiences. For Upper Paleolithic individuals, it is clear that this period of development was as variable for them as it is for adolescents today. Some individuals passed through developmental stages at a similar rate to contemporary humans, whereas others, perhaps due to a more demanding environment (evidenced by skeletal trauma) or due to pathological conditions hidden to us, lagged behind. Our study demonstrates the viability of assessing puberty in Upper Paleolithic populations. Despite the shortcomings of a small and temporally and geographically dispersed sample, the adolescents in this study support the expectation that an extended period of development was a feature of human life history in the Upper Paleolithic. Our data further suggest an adolescent growth spurt similar to modern humans and significantly shorter than medieval teens, likely reflecting a healthier living environment.

The physical appearance of Upper Paleolithic teenagers, as they transitioned from child to adult, may have affected the way they were treated in life and finally in death. On average, 20–26% of forager children die before their first birthday (Marlowe, 2001, 2005). Rates of hunter-gatherer juvenile mortality are also high, with 43–49% of forager children (cumulatively) dying before the age of fifteen (Hewlett, 1991; Marlowe, 2001, 2005; Volk and Atkinson, 2013). Those fortunate enough to survive these early years and reach adolescence had a much greater probability of surviving into adulthood. Thus, the loss of adolescents or young adults of the ages of those in our sample would likely have been difficult emotionally for others in their communities and would have impacted the overall survivability of the groups of which they had been a part.

The puberty assessments undertaken here allow for the creation of intimate osteobiographies that can be mapped onto the archaeological record. As adolescence is more widely recognized as a human life-history stage that can be identified in the fossil record, researchers will be better able to explore what it meant to be a 'teen' biologically and culturally in the Upper Paleolithic. To further elucidate the true nature of the adolescent life stage in the Upper Paleolithic, we need to adapt our practices when new adolescents are discovered and displayed—for example, dental radiographs allow for more detailed age assessments, and understanding the importance of leaving unfused epiphyses loose will assist in future attempts to explore puberty in these rare individuals.

CRediT authorship contribution statement

Mary E. Lewis: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Jennifer C. French:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Conceptualization. **Elena Rossoni-Notter:** Writing – review & editing, Resources. **Olivier Notter:** Writing – review & editing. **Abdelkader Moussous:** Writing – review & editing. **Vitale Sparacello:** Writing – review & editing, Investigation. **Francesco Boschin:** Writing – review & editing, Investigation. **Stefano Ricci:** Writing – review & editing. **April Nowell:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no competing interests.

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