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Environmental correlates of growth patterns in Neolithic Liguria (northwestern Italy)

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Abstract

Objective: This study evaluates patterns of human growth in the Neolithic to make inferences about environmental correlates of developmental disturbances.

Materials: 33 children/adolescents from the Neolithic of Liguria (Italy), 29 of which date between 4,800-4,400 cal BCE.

Methods: Neolithic patterns of growth are compared with a modern sample (the Denver Growth Study; DGS). Dental development was used to determine age at death. Proxies for postcranial maturation are femoral length, and proportion of mean adult femoral length attained.

Results: Ligurian children show growth faltering compared to DGS, especially between 4 and 9 years of age. Between 1 and 2 years, and in later childhood and adolescence, values are more similar, or higher than DGS, when using the proportion of adult femoral length attained.

Conclusions: The pattern of growth in Ligurian Neolithic children may reflect a deprived and highly-infectious environment: three individuals show skeletal lesions suggestive of tuberculosis. The relatively faster growth in infancy may result from the buffering provided by maternal milk. Older children and adolescents may exhibit catch-up growth.

Significance: This study contributes to our understanding of Neolithic selective pressures and possible biocultural adaptive strategies.

Limitations: The cross-sectional nature of the data, and the small sample size, make unclear whether the observed pattern is representative of the growth patterns in the living population. The possibility that adults are stunted undermines the interpretation of optimal growth in the first years.

Suggestions for Further Research: Refine age estimates, increase sample size through the study of other bone elements.

Keywords

Growth disturbances; stunting; Neolithic Transition; life history; tuberculosis.

1. Introduction

Developing individuals subjected to high levels of environmental stress, such as poor nutrition (Johnston et al., 1976; Martorell, 1985), infectious disease and parasites (Solomons et al., 1993; Stephensons, 1987), or even psycho-social stress (Powell et al., 1967), may exhibit slower rates of growth, delayed maturation, prolonged growth, and smaller final adult size (Bogin, 1988, 1999; Ulijaszek et al., 1998). Although genetic factors interact with the environment in the expression of body size and rate of growth (e.g. Eveleth and Tanner, 1990; Johnston et al., 1976), studying growth trajectories at a population level provides insights about variation in environmental correlates of growth disturbances, such as warfare, famines, and socioeconomic parameters (Powell et al., 1967; Ulijaszek et al., 1998).

In bioarchaeology, the study of growth trajectories and their interpretation, including comparisons with modern reference samples, faces a number of problems (reviews in Lewis, 2007; Saunders, 2008). Problems related to archaeological assemblages include the differential preservation of juvenile remains (Bello et al., 2006), the cross-sectional rather than longitudinal nature of data (Humphrey, 2003), the representativeness of data due to the osteological paradox (Goodman, 1993; Saunders and Hoppa, 1993; Wood et al., 1992), and the temporal resolution of the data (Albanese, 2002, 2009). Methodological problems mainly relate to age estimation based on dental development (Saunders, 2008). Nevertheless, numerous studies since the early work by Johnston (1962) have explored patterns of growth in prehistoric and more recent skeletal assemblages (reviews in Humphrey, 2000, 2003; Larsen, 2015; Lewis, 2007; Mays, 2018; Saunders, 2008), and made inferences on environmental correlates of developmental disturbances, such as malnutrition and disease, as well as the effect of migration, colonialism, and changing subsistence patterns.

The Neolithic Transition, i.e. is the adoption of a production economy based on the domestication of plants and animals, is *“one of the fundamental structural processes of human history”* (Bocquet-Appel, 2011a, 2011b), and dramatically changed several aspects of the human experience. Various studies suggest that the Neolithic Transition was accompanied by a worsening in health status and well-being, resulting in an increase of osteological markers of stress (e.g. *cribra orbitalia* and enamel hypoplasia; Armelagos et al., 2005; Cohen and Armelagos, 1984; Cohen and Crane-Kramer, 2007; Eshed et al., 2010; Gleń-Haduch et al., 1997; Larsen, 1995; Temple, 2010). Mortality rates increased, especially in infants (Armelagos et al., 2009; Bocquet-Appel 2002, 2009, 2011a, 2011b; Page et al., 2016; Pérez-Losada and Fort, 2010), possibly due to unsanitary and deprived conditions and a more infectious environment (Armelagos et al., 1991, 1996, 2005). In addition, it has been suggested that certain Neolithic infant feeding practices may have had a negative impact on children survivorship (Pearson et al., 2010). Exploring patterns of growth in Neolithic children can integrate data coming from paleopathological and paleodemographic sources, and can contribute to the debate on biocultural Neolithic adaptive strategies.

The prehistoric skeletal series from Liguria (northwestern Italy) represent an important source of information on the past peopling of the northwestern Mediterranean from the Upper Paleolithic to the Metal Ages (Del Lucchese, 1997; Formicola et al., 2005; Maggi, 1997; Sparacello et al., 2018). Evidence of Neolithic occupation comes from several caves and rock shelters opening in the Finalese area, where renowned sites such as Arene Candide have yielded detailed stratigraphic successions (Arobba et al., 2017; Maggi, 1997; Tiné, 1999). About 200 burials and an undefined number of scattered human remains have been reported from these sites (e.g. Del Lucchese, 1997; Delfino, 1981; Issel, 1908; Panelli and Rossi, 2015, 2017; Parenti and Messeri, 1962; Richard, 1942; Sparacello et al., 2018, 2019). However, a large portion of the skeletal series had been excavated since the mid-19th century, and was accompanied by little information about the depositional context (De Pascale, 2007, 2008; Rossi et al., 2014). Only recently, a large-scale campaign of direct dating on Ligurian human remains has been conducted (project BUR.P.P.H., PI VSS and DEN.P.H., PI ID), and allowed for the chronological characterization of most burials and individuals reconstructed from the scattered remains (Sparacello et al., 2018, 2019, and in review).

This study explores patterns of growth in Ligurian Neolithic children through the analysis of femoral length in individuals whose age at death was independently estimated from dental development. The comparison with a reference sample of modern, healthy, and well-nourished children (the Denver Growth Study; Maresh, 1943, 1955, 1970) will allow for an evaluation of well-being among these early agriculturalists, as done in previous studies (e.g. Harrington and Pfeiffer, 2008; Humphrey 2000, 2003; Pfeiffer and Harrington, 2010). Subsistence of Neolithic Ligurian people was based on a variety of domesticated plants (Arobba et al., 2017; Nisbet, 2008), and on livestock breeding, especially sheep (Macphail et al., 1997; Rowley-Conwy, 1992, 1997, 1998), in a highly mountainous environment, resulting in strenuous physical activity and high logistic mobility levels (Marchi et al., 2006, 2011; Sparacello and Marchi, 2008; Sparacello et al., 2011, 2014). Environmental stress and poor health conditions are suggested by a high prevalence of enamel hypoplasia (Formicola, 1987; Orellana-Gonzales et al., in review), and by several cases of osteoarticular tuberculosis (Canci et al., 1996; Formicola et al., 1987; Sparacello et al., 2017; Sparacello et al., 2018, and unpublished data, see below), a highly infectious, debilitating, and growth-impairing disease (Sparacello et al., 2016). We expect that environmental hardships experienced by Neolithic Ligurian people will result in a pattern of development showing growth faltering when compared to a modern industrialized sample.

2. Materials and Methods

The sub-adults included in this study consist of 33 individuals spanning birth to late adolescence, chronologically belonging to the Neolithic of Liguria (c. 5800-3800 cal. BCE). We included only the individuals that were directly dated (Table 1; Sparacello et al., in review), and the vast majority (29/33) chronologically overlap with the Square Mouthed Pottery Culture (SMP; c. 5000-4300 cal. BCE; Binder and Sénépart, 2010; Del Lucchese and Starnini, 2015). Three individuals from Arma dell'Aquila chronologically overlap with the earlier Impresso-Cardial Complex (ICC; Binder et al., 2017; Sparacello et al., 2019), and one from Grotta Pollera with the later Chasséen (4300-3700 BCE; Crepaldi, 2001; Maggi, 1997). All remains were unearthed from six caves (Arene Candide Cave, Arma dell'Aquila, Grotta marina di Bergeggi, Grotta dei Pipistrelli, Grotta Pollera, Arma Strapatente), situated within a radius of 5 km in the Finalese area (Figure 1). Data was collected at the Museo di Archeologia Ligure, Genova, at the Museo Archeologico del Finale, Finale Ligure, and at the Museo di Storia Naturale – Sezione di Antropologia e Etnologia, Università degli Studi di Firenze. All the available remains belonging to the Neolithic of Liguria were surveyed, with the exception of the four subadults housed at the Museo delle Civiltà in Rome.

[Figure 1 about here]

For all children below the age of 12, age at death estimates are based on dental mineralization following AlQahtani et al. (2010). Dental formation shows considerably less populational variation than eruption, and is less influenced by environmental factors (Demirjian, 1986; review in Saunders, 2008). However, the accuracy of age at death determination is influenced by the number of teeth that could be examined. Dental eruption following AlQahtani et al. (2010) was used when mineralization could not be assessed due to impossibility of examining the root (two adolescent individuals). All age estimates and information on tooth development is available in Supplementary Information S1. Due to the small sample size for each age class, we decided to report the results using the midpoint of the age estimate for each individual.

Femoral maximum length was measured following the standards in the field (e.g. Schaefer et al., 2009) using a digital caliper and an osteometric table, as appropriate. Length was measured without epiphyses in children, and with the epiphysis in adolescents above 12 years of age (Ruff, 2007). Unfortunately, in two adolescents (e.g. Pollera 1 PE and Pollera 34 PE) one or both epiphyses were plastered to the metaphysis, and a slight overestimation of the maximum length cannot be excluded (Table 1; Pollera 34 PE was not included in the analysis due to absence of the distal epiphysis, and its measurements are in Supplementary Information S2).

[Table 1 about here]

The growth pattern in our sample was compared with the standards derived from the Denver Growth Study, which consists of longitudinal bone length data from healthy children, deriving from radiographs collected in the United States between 1935-1967 (Maresh, 1943, 1955, 1970), and commonly used in comparisons with prehistoric populations (review in Mays, 2018). The mean of male and female diaphyseal length was used, due to the absence of sex estimation for most of our immature remains.

Following previous research (e.g. Harrington and Pfeiffer, 2008; Humphrey 2000, 2003; Ives and Humphrey, 2017; Pfeiffer and Harrington, 2010), we compared absolute length for age, and relative length as a percentage of the mean adult length (pooled sexes) for the same population (for the Neolithic Ligurian sample: n = 25; males = 13; females: 12; average femur M1 = 410.5 mm; for the Denver Growth Study: n = 68; femur M1 = 489 mm; Harrington and Pfeiffer, 2008).

It should be noted that the values of absolute length for age are biased by radiographic magnification, proportionally to bone size (Feldesman, 1992; Humphrey, 2003). Ruff (2007) proposed two regression equations correcting the radiographic measurements made on the original x-rays of the Denver Growth Study, and applied it to a smaller sample of 20 individuals (10 males and 10 females). The data points obtained for the Ligurian sample were therefore plotted against: 1) the mean and ±1/2 SD absolute length between birth and 12 years of age of the Denver Growth Study (Maresh, 1955, 1970), corrected for radiographic magnification using the formulae proposed by Ruff (Ruff, 2007:702); 2) the mean and ±1/2 SD absolute length between 1 and 17 years of age of the subsample studied by Ruff, based on the data presented in his Table 1 (Ruff, 2007:702).

The proportion of adult age attained at a given age is only minimally influenced by radiographic magnification. Ligurian data were plotted against the mean and ±1/2 SD proportion of adult size attained between birth and 17 years of age of 1) the Denver Growth Study (Maresh, 1955, 1970; see also Humphrey, 2000; Pfeiffer and Harrington, 2010), and 2) the subsample studied by Ruff, based on the data presented in his Table 1 (Ruff, 2007:702), and correcting the adult length of the Denver Growth Study using the regression for bones longer than 217 mm (adjusted = 0.949 × original length +5.63).

In addition, we calculated a residual relative to the proportion of adult femur length achieved, when comparing the Ligurian Neolithic people with the Denver Growth Study (cf. Harrington and Pfeiffer, 2008; Humphrey 2000, 2003; Pfeiffer and Harrington, 2010). The proportion of adult femur length achieved was estimated graphically for the age points of the Ligurian Neolithic children (Supplementary Information S2), and the residuals were plotted on the mean and ±1/2 SD proportion of adult size attained by the Denver sample between birth and 12 years of age, redrawn with the mean as a horizontal line (e.g. Humphrey, 2000, 2003).

3. Results

Figure 2 shows the absolute maximum length of the femur in the Ligurian Neolithic sample, when compared with the data of the Denver Growth Study, corrected for radiographic magnification following Ruff (2007), and the subsample from the Denver Growth Study selected and corrected by Ruff (2007). In both graphs, the Ligurian Neolithic growth pattern tends to fall consistently two standard deviations below the mean.

[Figure 2 about here]

Figure 3 shows the pattern of growth expressed as proportion of mean adult length attained in the Ligurian Neolithic sample, when compared with the data of the Denver Growth Study, and the sample from the Denver Growth Study selected by Ruff (2007). The Ligurian Neolithic sample now falls close to the mean, or above, of the Denver Growth Study up to the age of 2.5, and consistently below between the ages of 4.5 and 9. Most of older children and adolescents fall close or above the mean of the Denver Growth Study, except for one who is more than two standard deviations below the mean. The slight differences observed between the whole Denver sample and the results by Ruff (2007) are mostly due to the greater standard deviations in the latter study, which is based on a smaller sample size (n = 20 compared to n = 70-80 in Maresh, 1970; Humphrey, 2000).

[Figure 3 about here]

The pattern from Figure 3 is visible more clearly in Figure 4, showing the residual relative to the proportion of adult femur length achieved, when comparing the Ligurian Neolithic sample (only measurements without epiphyses) with a) the Denver Growth Study, and b) the sample from the Denver Growth Study selected by Ruff (2007). Neolithic Ligurian individuals tend to fall consistently below the mean of the Denver Growth Study between 4.5 and 8.5 years of age, and in three cases more than two standard deviations below the mean (Figure 4a). Note that Ruff (2007) did not present data for individuals below 1 years of age. Also, the larger standard deviation using data from Ruff’s (2007) study is probably influenced by the smaller sample size (see above).

[Figure 4 about here]

4. Discussion

Through the comparison of dental maturation and skeletal development in a bioarchaeological sample of children and juveniles, this study aimed at the evaluation of Neolithic growth disturbances in Liguria (Italy), and at discerning their possible environmental correlates. This study has the advantage of a very narrow geographical focus, being all sites in a radius of a few kilometers, and most likely belonging to the same agropastoral system (Rowley-Conwy, 1992). In addition, most individuals belong to a precise chronological phase of human occupation, with dates primarily spanning c. 4800-4400 BCE at 2σ, when the Square Mouthed Pottery culture was attested in the region (Maggi et al., 1997). The few individuals belonging to earlier or later chrono-cultural phases do not seem to deviate significantly from the general pattern observed. Although important caveats should be taken into account in any bioarchaeological study, especially when patterns of development are involved (review in Saunders, 2008), the Ligurian sample can be considered representative of a Neolithic population, with presumably a well-defined set of biocultural adaptations to specific environmental challenges.

When compared to the reference sample of the Denver Growth Study, the Ligurian Neolithic people tend to have shorter femora during growth, especially when considering absolute femoral length, and less markedly when length is expressed as a proportion of mean adult size. In addition, using the latter method, a majority of Ligurian individuals falls above the reference sample in early life (between birth and c. 2.5 years), indicating a longer femur for their age compared to Denver, followed by a clear downward deflection between 4.5-9 years. Considering that the Denver sample is composed by healthy and well-nourished modern children, which are assumed to have attained their full growth potential, the pattern observed in the Ligurian Neolithic sample would indicate optimal development in early life, followed by growth faltering.

In previous studies, some prehistoric populations showed a similar pattern: Humphrey (2003) observed that the three Native North American samples included in her review (Knoll, Libben, and San Cristóbal samples; Johnston, 1962; Lovejoy et al., 1990; Ryan, 1976) exhibited relatively longer femoral length than Denver during infancy (until about 1.5 years), followed by a dramatic reversal in the growth trajectory, and discussed the possibility of a genetic component influencing rates of skeletal growth and/or dental maturation. However, the different timing of the growth rate reversal in the three groups suggested that additional environmental factors, such as infant early feeding practices and the weaning process, might have contributed to varying growth trajectories (Humphrey, 2000, 2003).

Maternal milk supplies passive immunity, and weaning increases the pathogen load, requiring a sudden energetic investment into immune defense by the child (McDade, 2003; McDade and Worthmann, 1999). Therefore, various studies have associated the onset of deficits in growth with the cessation of breast feeding (e.g. Mays, 2010; Humphrey, 2000). For example, in the 18th and 19th century London, a widespread practice of early breast feeding cessation was introduced, due to social and cultural factors (Fildes, 1986; 1995; Nitsch et al., 2011), and resulted in growth deficits (beginning around 8 months of age, and becoming marked by 15 months; Humphrey, 2000; Ives and Humphrey, 2017), high prevalence of enamel defects in teeth (King et al., 2002), and high infant mortality (Humphrey et al., 2012). An even earlier onset of growth faltering was attributed to deprived nutritional status of the mother, or poor quality of early supplementary foods (Humphrey, 2003). Mays (2010), noted how the cessation of breast feeding in a medieval sample between 1-2 years of age (estimated via isotopic analysis) "marks the start of a general pattern of deficient growth" (Mays, 2010:69; see also Mays, 2007). Although the link between breast feeding cessation and growth faltering is speculative, given the small sample size, the pattern observed in the Ligurian Neolithic sample, with growth retardation apparent only after c. 2.5 years of age, seems to be compatible with the direct estimation of breast feeding duration in two SMP Neolithic individuals (including the adolescent individual Arene Candide V BB studied here; Goude et al., in review). The isotopic profiles ($\delta^{15}N$ and $\delta^{13}C$) suggest that breast feeding extended into the third year of life, as observed also in other Neolithic groups (Cienkosz-Stepanczak et al., 2017; Fernández-Crespo et al. 2018; Howcroft, 2013; Howcroft et al., 2014; Pearson et al., 2010, 2015; Scharlotta et al., 2018). The presence of a period of metabolic stress around 2.5-3.5 years of age is also supported by a significant increase in linear enamel hypoplasia prevalence in the same Ligurian SMP Neolithic sample (Orellana-Gonzales et al., in review). These multiple signals of developmental disturbances – in correspondence with the estimated end of passive immunity – may be due to poor nutrition and/or increased pathogen load. Although it is difficult to quantitatively assess the caloric intake of SMP Neolithic people, their diet included a significant component of animal protein (Le Bras-Goude et al., 2006; Goude et al., 2014), which was also probably used as a weaning food (Goude et al., *in review*). In this context, the effect of disease may have been relatively more important, as we discuss further below.

It could be argued that higher relative femoral length in early infancy may be influenced by a combination of two factors: relatively low variation in neonatal size (e.g. Leary et al., 2006), and markedly small adult size between the Denver sample and prehistoric populations (mean maximum length of the femur in the pooled sex Ligurian sample is 74 mm smaller). If differences in adult size were not entirely due to genetic differences, but also to stunting due to later metabolic stress, the pattern observed here in children below 2.5 years may not be a reflection of rapid growth, and in general absolute femoral length patterns may be more informative. Although it is difficult to determine the degree to which Ligurian adults attained their full growth potential, body proportions in the European Neolithic were markedly different than in modern times (e.g. Ruff et al., 2006), and Ligurian Neolithic adults do not appear to be significantly smaller than other contemporary Mediterranean Neolithic populations (e.g. Rosenstock et al., 2019). The use of percent of adult size attained is generally advised in these contexts (Hoppa and Fitzgerald, 1999; Humphrey, 2003), but further research is necessary to independently assess the nutritional and developmental status of Ligurian Neolithic infants.

Regardless of the method used to compare Ligurian children with the Denver sample, it is clear that, by the age of 4.5 years, Ligurian Neolithic children are experiencing growth faltering. All individuals fall below the mean of the Denver sample, the majority being between -1 and -2 standard deviations (percent of adult size attained) or well below -2 standard deviations (absolute femoral length). Previous bioarchaeological studies comparing growing individuals from prehistoric groups with the Denver sample almost invariably show a growth deficit in the former (reviews in Humphrey, 2000, 2003; Larsen, 2015; Lewis, 2007; Mays, 2018; Saunders, 2008). However, the variation in the prehistoric patterns can be quite marked, and is assumed to reflect different social and environmental condition, in addition to genetic differences, as happens in contemporary groups (Bogin, 1988; Eveleth and Tanner, 1990). The more apparent growth deficit in agriculturalists when compared to hunter-gatherers has been attributed to their lesser reliance on animal protein (Cook, 1979, 1984; Goodman, 1998; Larsen et al., 2002). Within agriculturalists, the overreliance on staple foods with poor nutritional properties (e.g. maize), seem to coincide with poor growth (Cook, 1984; Goodman et al., 1984). In medieval Croatia, agriculturalist groups from the inland show lower long bone length at the same age than pastoralist communities from the coast (Pinhasi et al., 2014). Archaeological evidence suggests that the subsistence of Ligurian Neolithic people had a strong pastoral component (Macphail et al., 1997; Rowley-Conwy, 1992, 1997, 1998), which led to the consumption of animal protein since early life, as suggested by isotopic studies (Le Bras-Goude et al., 2006; Goude et al., 2014, and in review). The nutritional status of Ligurian Neolithic people may therefore have been relatively good for a prehistoric group, yet the pattern of growth faltering appears to be among the most relevant when compared with other bioarchaeological populations (cf. Humphrey 2003). Few studies on growth patterns have been conducted on Neolithic skeletal series from western Eurasia, probably due to lack of reasonably numerous samples of children. Pinhasi et al. (2011) found similar growth patterns between the lower limbs of the Denver sample and a small sample of Greek Neolithic children. The larger skeletal series from Çatalhöyük (Turkey), which is comparable to the Ligurian one in terms of chronology, diet, and subsistence (e.g. Pearson et al., 2015; Richards, 2003), shows growth patterns during childhood that are in line with the Denver sample (Ruff et al., 2013), and in general appears to have had a good health status (Hillson et al., 2013; Larsen et al., 2019).

In fact, in addition to dietary deprivation, health status and infectious load are considered a major influence on growth patterns in modern and prehistoric populations (Bogin, 1988; Larsen, 2015; Mays, 2018; Stephenson, 1999; Stinson, 2000). In previous bioarchaeological studies, disease burden was inferred based on increased sedentism or contact with European-introduced infectious disease (e.g. Jantz and Owsley, 1984; Lovejoy et al., 1990). In the Neolithic Ligurian sample, several individuals show osteoarticular lesions compatible with tuberculosis, including two children and one adolescent included in this study. Pollera 21, c. 5 years of age, shows multiple cystic lesions and bone erosions in the vertebral column, shoulder joint, and pelvis (Sparacello et al., 2017). At the age of 8.5 years, the most stunted individual (Arene Candide 6730.3+6623.1+6625.2) displays lesions suggestive of tuberculosis in the thoracic and sacral vertebral bodies (Figure 5; Sparacello, unpublished data, forthcoming). Arene Candide V (excavations Bernabò Brea – Cardini), c. 15 years old, suffered from Pott's spine, a collapse of the vertebral column which is considered pathognomonic for TB (Formicola et al., 1987). These individuals add to the growing evidence for this disease in both adults and children in Neolithic Liguria (e.g. Canci et al., 1996; Sparacello et al., 2018, and unpublished data, forthcoming), and mark a sharp contrast with the aforementioned site of Çatalhöyük, where no evidence of skeletal tuberculosis has been found despite the analysis a large skeletal series spanning over a millennium (Larsen et al., 2019).

[Figure 5 about here]

Indeed, evidence of tuberculosis is rare in the bioarchaeological record (Roberts and Buikstra, 2003); finding three individuals with lesions compatible with osteoarticular tuberculosis in our small sample of developing individuals suggests a high prevalence in the Ligurian Neolithic population. This hypothesis is supported by the fact that skeletal lesions manifest only in a small percentage of the affected individuals (estimates ranging from 1% to 3–5%; Turgut, 2001; Vigorita, 1999). In addition, the 5-10 years age class is the one with the lower risk of contracting the disease in modern epidemiological studies (Seddon and Shingadia, 2014). Active tuberculosis is a debilitating disease that impairs skeletal development (Mansukoski and Sparacello, 2018; Sparacello et al., 2016), but also the more common latent and sub-clinical states require a constant investment in immune defenses (Ulrichs et al., 2005;

Lin and Flynn, 2010), possibly diverting energy from growth (Ganmaa et al., 2012; see also McDade et al., 2008). We propose that significant infectious burden due to a high prevalence of tuberculosis in the Neolithic of Liguria may contribute to explain the pattern of growth faltering observed in this study. However, further research is necessary to investigate the paleoepidemiology of tuberculosis among Ligurian Neolithic people, by cross-referencing demographic data with new differential diagnoses.

Although the sample size is small, older children and early adolescents appear to have attained a proportion of the adult femoral length similar or higher than the reference Denver sample, with the exception of the adolescent with tuberculosis. This may indicate growth retardation followed by catch-up growth, resulting from an adaptation or acclimatization to environmental hardships (e.g. Beaton, 1989; Lewis, 2007:67; Stini, 1975). Indeed, during adolescence genetic influence on growth is expressed more strongly than during childhood, and environmental factors are relatively less important (Bogin, 1999). However, when considering absolute femoral length, Ligurian Neolithic adolescents are still well below the Denver sample. As discussed above, the relevance of the two methods to infer optimal growth patterns ultimately depends on whether differences in final stature between the Ligurian and Denver sample are due to genetic factors or failure to attain the full growth potential.

As in all bioarchaeological studies, there are numerous caveats that should be taken into account when interpreting the above results, which are not limited to the small sample size. Growth data from prehistoric populations are cross-sectional instead of longitudinal, and represent a cross-section of non-survivors. Cross-sectional data may not accurately describe the developmental patterns of a population, since growth events are not synchronized between individuals, resulting into a smoothing in the slope of growth curves (Humphrey, 2003). Furthermore, growth of non-survivors may be not representative of the normal development of the living population (which is part of the “osteological paradox”; Wood et al., 1992; Wright and Yoder, 2003), especially if they died of long-term, debilitating diseases (Goodman, 1993; Saunders and Hoppa, 1993; Sundick, 1978). Saunders and Hoppa (1993) noted that the linear growth of survivors is usually greater than that of non-survivors, but they concluded that the effect of this bias is relatively minor. However, given the widespread evidence of tuberculosis, the possibility that non survivors suffered from long-term developmental disturbances may be particularly relevant in the Ligurian sample. The individuals with tuberculous lesions appear stunted, but also most of the individuals between c 4.5 and 8.5 years of age. Ideally, it would be necessary to verify whether children dying of different causes at the same age had similar dimensions, which is problematic given the small sample size of bioarchaeological samples, and especially given the uncertainties in the assessment of causes of death. Luckily, in our small sample, two individuals, Arene Candide VIII (excavations Bernabò Brea – Cardini), age midpoint 4.5 years, and Arene Candide 3 (excavations Tiné), age midpoint 8.5 years, show clear signs of perimortem trauma (Figure 6; Sparacello, unpublished data). Paradoxically, their violent and presumably sudden death makes them more likely to be representative of the population of survivors, although we cannot exclude that they suffered of a long-term disease which did not leave obvious traces in the skeleton. Nevertheless, their proportion of adult femoral length attained falls, like for most individuals between 4.5 and 8.5, between 1 and 2 standard deviation below the mean of the Denver sample. Although the small sample makes any inference tentative at best, this would suggest that growth disturbances during childhood were widespread in the Neolithic of Liguria.

[Figure 6 about here]

5. Conclusions

This study is part of a renewed, multidisciplinary attempt to characterize population health and well-being, subsistence patterns, and biocultural adaptive strategies in a chronologically and spatially well-defined window of European Neolithic variability (e.g. Orellana-Gonzales et al., in review; Goude et al., in review*;* Sparacello et al., 2017, 2018, 2019, in review), adding to the current debate on the competitive advantages and disadvantages of a Neolithic lifestyle.

When considering absolute femoral length, the Ligurian skeletal series is significantly smaller than the modern Denver sample throughout development. However, when considering the proportion of adult size attained at a given age, results suggests optimal development among Ligurian Neolithic people in early infancy, until the age of c. 2.5-3 years. Between 4.5 and 8.5 years, growth faltering is apparent, while later children and adolescents may show catch-up growth.

Although the sample size is small, the onset of growth faltering pattern corresponds with the estimated timing of weaning in the same Neolithic sample, reconstructed via isotopic analysis (Goude et al., in review), and with developmental disturbances observed in enamel mineralization (Orellana-Gonzales, in review). We propose that the growth pattern observed may relate more to disease load than nutritional factors. Early in life, optimal growth may be due to infant feeding practices attempting to favor both growth, via the early introduction of animal protein (Goude et al., in review), and immune protection, by delaying the termination of breast feeding into the third year of life. Evidence of growth faltering between 4.5-8.5 years of age may reflect, among other environmental hardships, the stunting effect of debilitating diseases such as tuberculosis (which is manifest in three individuals) as well as the significant metabolic investment required into the immune system at the expense of growth in areas with significant infectious load.

In addition to small sample size, several methodological and theoretical caveats suggest caution when interpreting these results, and further research is necessary to test the above hypotheses. New differential diagnoses on individuals with suspect tuberculous osteoarticular lesions, coupled with demographic data, will contribute to the assessment of the paleoepidemiology of this disease among Ligurian Neolithic people. Demographic studies on the complete skeletal series of dated Neolithic Ligurian children will evaluate pattern of child mortality in order to verify whether the results observed here may be influenced by differential survivorship and frailty (Goodman, 1993; Saunders and Hoppa, 1993; Wood et al., 1992). The integration of developmental and demographic data will also inform the current debate on the Neolithic Demographic transition and its possible determinants (Bocquet-Appel 2002, 2009, 2011a, 2011b; Page et al., 2016).

The possibility of adaptation/acclimatization to slow growth among Ligurian Neolithic people, followed by catch up growth with adolescence, should be explored with a larger sample of subadults, which can be attained only by expanding the regional focus of the research, or by conducting further excavations in the Finalese area. Additionally, the use of other long bones from this same skeletal series may provide further confirmation of the results found here (e.g. Goode et al., 1993).

Other limitations of this study are the use of the midpoint of the age estimate based on available information about tooth development (Supplementary Information S1). A refined age estimation will be possible with the advancement of non-invasive analyses of tooth microstructure (e.g. Smith et al., 2015). Furthermore, error may be introduced by the lack of sex determination, given the well-known differences in developmental trajectories between sexes (e.g. Schaefer et al., 2009), which may be explored in the future using the amelogenin analysis of the enamel (Stewart et al., 2017).

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Figure 1 – Geographical location of the sites included in this study. Top: the red square indicates the Finalese area within the Liguria region (highlighted in yellow) in northwestern Italy. Bottom: the cave sites analyzed in this study in the municipality of Finale Ligure: 1) Arene Candide Cave; 2) Grotta Pollera; 3) Arma dell'Aquila; 4) Grotta dei Pipistrelli; 5) Arma Strapatente; 6) Grotta marina di Bergeggi. Modified from ArcGIS and Google Maps.

Figure 2 - Absolute maximum length of the femur by age in the Ligurian Neolithic sample, when compared with: Left) the data of the Denver Growth Study, corrected for radiographic magnification using the formulae proposed by Ruff (Ruff, 2007:702), and Right) the sample from the Denver Growth Study selected and corrected by Ruff (2007). The solid lines indicate the mean, the two dotted lines indicate ±1 and ±2 standard deviations. In Ruff (2007) the lengths without epiphyses are reported until the age of 12, and with epiphyses from the age of 11. Solid circles: ICC; empty squares: SMP; stars: Chassean.

Figure 3 – Length of the femur expressed as percentage of mean adult length attained by age in the Ligurian Neolithic sample, when compared with Left) the data of the Denver Growth Study, and Right) the sample from the Denver Growth Study selected and corrected by Ruff (2007). The solid lines indicate the mean, the two dotted lines indicate ±1 and ±2 standard deviations. The lengths without epiphyses are reported until the age of 12, and from the age of 10 (11 in Ruff, 2007) the lengths with epiphyses are reported. Solid circles: ICC; empty squares: SMP; stars: Chassean.

Figure 4 – The residuals of the length of the femur expressed as percentage of mean adult length attained by age in the Ligurian Neolithic sample, with respect to Left) the data of the Denver Growth Study, and Right) the sample from the Denver Growth Study selected and corrected by Ruff (2007). The solid lines indicate the mean, the two dotted lines indicate ±1 and ±2 standard deviations. Solid circles: ICC; empty squares: SMP; stars: Chassean.

Figure 5 – A vertebral body of an individual from Arene Candide (AC 6623.1, catalogue number of the Museo di Storia Naturale – Sezione di Antropologia e Etnologia, Università degli Studi di Firenze; possibly burial n°6 from the excavations Morelli 1884-87) showing an erosion of a thoracic vertebral body compatible with osteoarticular tuberculosis (cf. Sparacello et al., 2017).

Figure 6 – Signs of perimortem trauma in two Neolithic children from Liguria included in this analysis. Left: mandibular fracture in Arene Candide VIII excavations Bernabò Brea 1940-50. Right: fracture of the neural arch of a thoracic vertebra in Arene Candide 3 excavations Tiné 1973-76.


0 km 100


1
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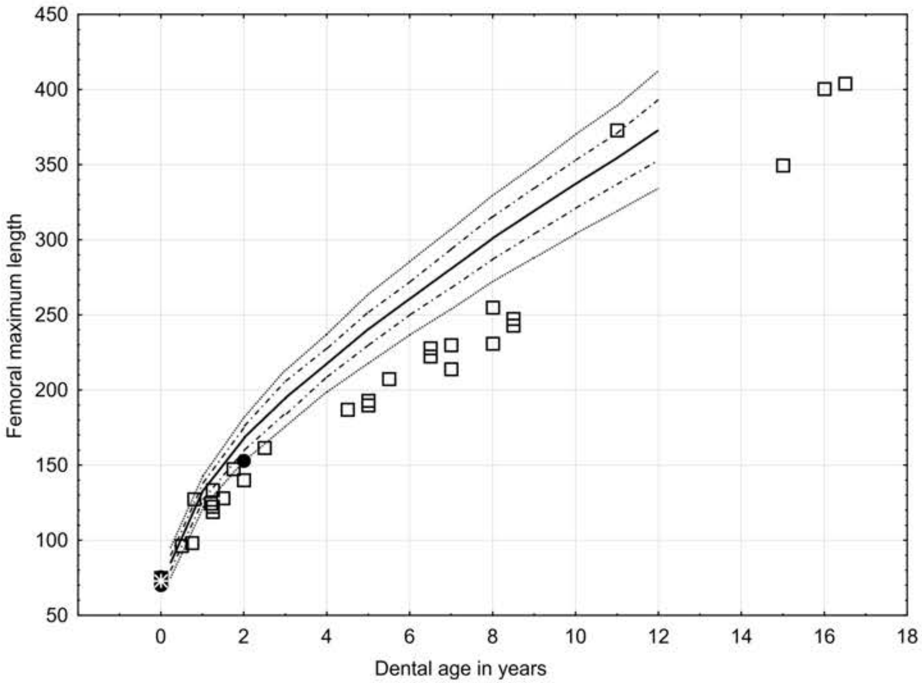
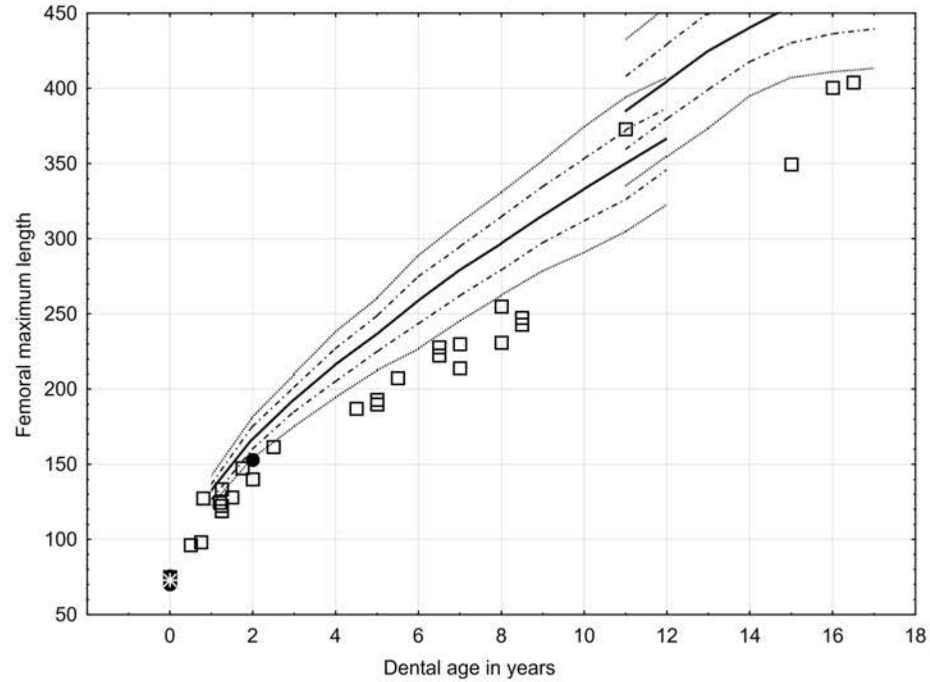
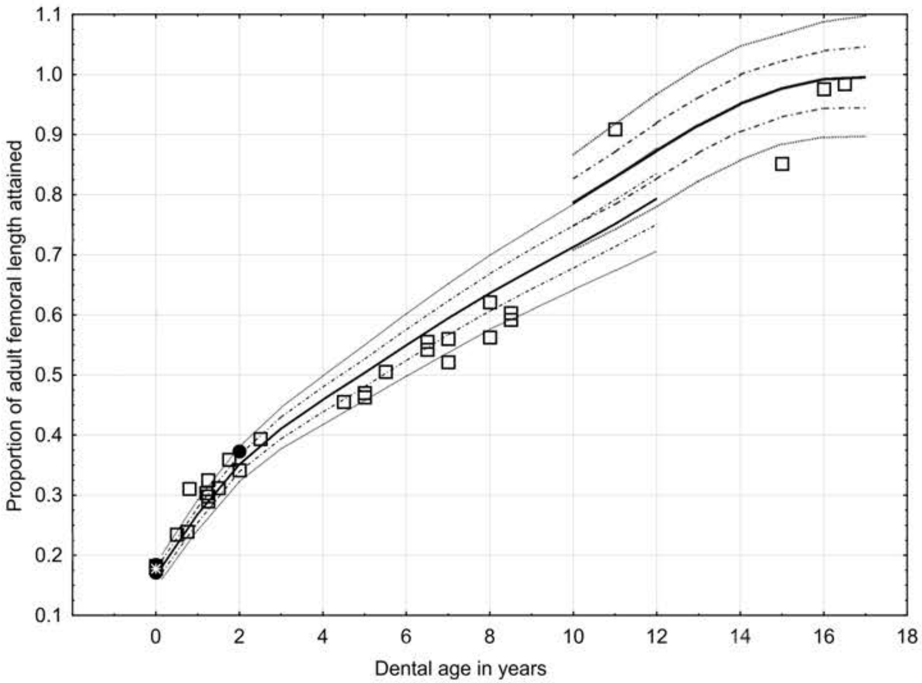
3
4
5
6
FINALE LIGURE
0 Km 1



Femoral maximum length
Dental age in years



Femoral maximum length
Dental age in years


1.1
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Proportion of adult femoral length attained
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4
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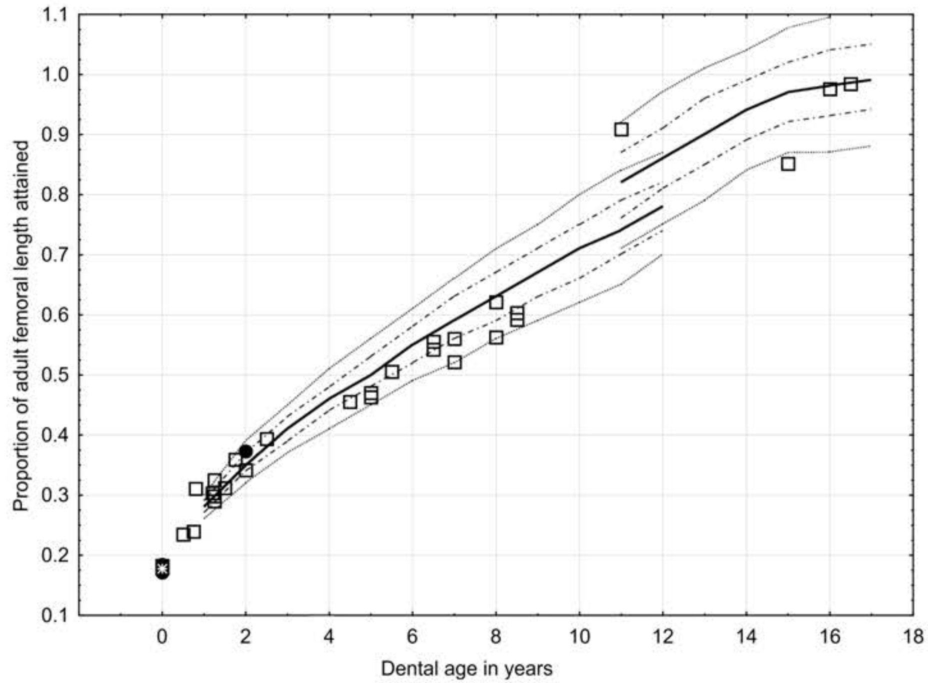
8
10
12
14
16
18
Dental age in years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Proportion of adult femoral length attained
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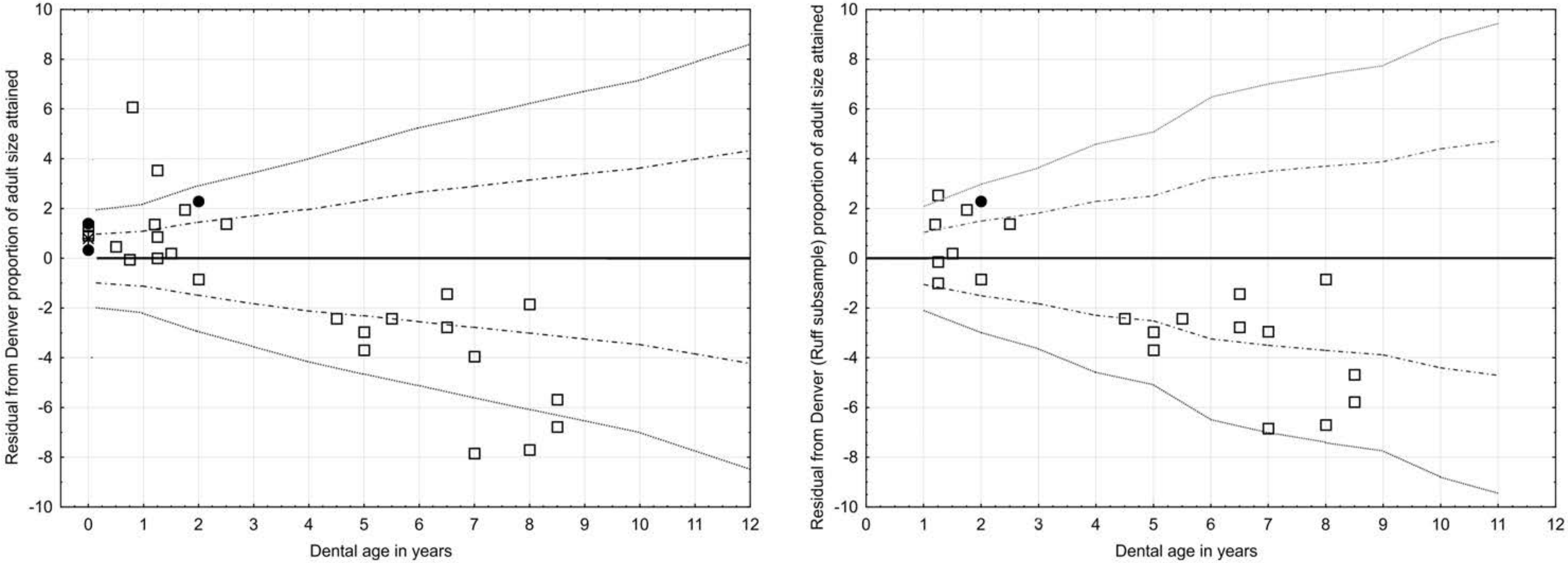
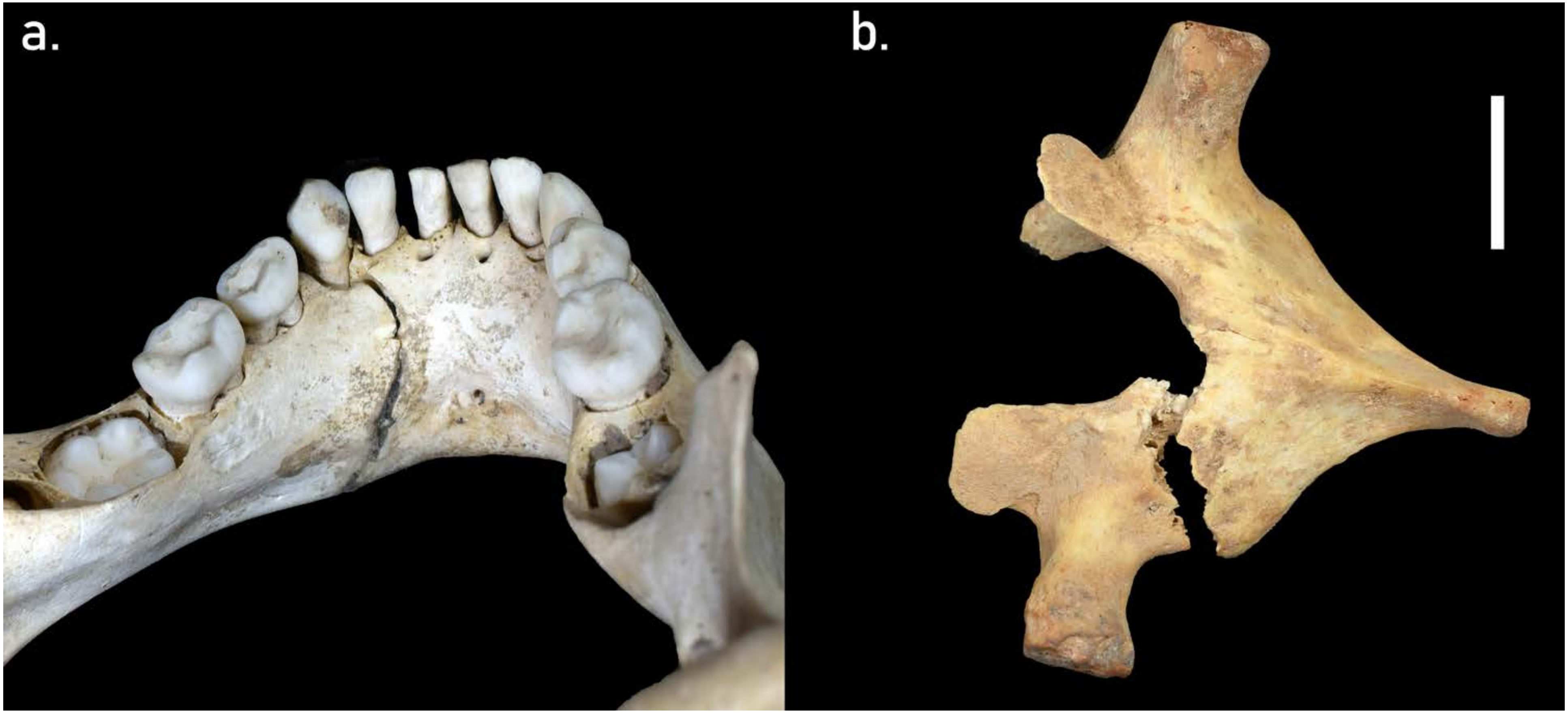
Dental age in years



Residual from Denver proportion of adult size attained
Dental age in years
Residual from Denver (Ruff subsample) proportion of adult size attained
Dental age in years


a.
b.

Individual Id	**Dental Age**	**Age Midpoint**	**Femur R (mm)**	**Femur L (mm)**	**AMS date cal. BCE (95.4%)[1]**	**Chrono-cultural attribution[1]**
Arma dell'Aquila 7 Richard	perinatal	0.0	70.4	70.2	*5657-5533*	ICC
Arma dell'Aquila 8 Richard	perinatal	0.0		75.5	*5646-5527*	ICC
Pollera 6663.1	perinatal	0.0	74	73	*4701-4548*	SMP
Pollera 6664.1	perinatal	0.0		75	*4536-4373*	SMP
Pollera 6665.1+6670.1	perinatal	0.0		73	*3946-3775*	CH
Arene Candide 6633.1	4.5-7.5 months	0.5	96.3		*4726-4557*	SMP
Arene Candide 6629.1	7.5-10.5 months	0.8	98.2	98.3	*4767-4586*	SMP
Pollera 6675.2+6676.1	7.5-12 months	0.8	126	129	*4719-4557*	SMP
Arene Candide 6630.1	10.5-18 months	1.2	124.5	124.7	*4682-4502*	SMP
Arene Candide 6628.1+6625.4	1-1.5	1.3	123	122	*4768-4592*	SMP
Pollera 6666.2	1-1.5	1.3		119	*4712-4556*	SMP
Pollera 6669.1+6671.1	1-1.5	1.3	134	133	*4712-4587*	SMP
Pollera 6680.1	1-2	1.5		128	*4836-4717*	SMP
Pollera 6670.2	1.5-2.5	1.8	147	148	*4682-4502*	SMP
Arene Candide 6631.1	1.5-2.5	2.0	140.4	139.9	*4691-4545*	SMP
Arma dell'Aquila 6 Richard	1.5-2.5	2.0		153	*5657-5538*	ICC
Arene Candide 6632.1+6623.2	2-3	2.5		161.6	*4726-4557*	SMP
Arene Candide VIII BB	3.5-5.5	4.5	184	190	*4800-4619*	SMP
Bergeggi S2 01178PE, 6894-5FI	4.5-5.5	5.0		193	*5047-4857*	SMP
Pollera 21PE	4-6	5.0	190		*4779-4587*	SMP
Pollera 6678.1	5-6	5.5	206	209	*4794-4686*	SMP
Arma dell'Aquila Zambelli JUV B	6-7	6.5	228		*4727-4546*	SMP
Pipistrelli 1_dep. 23.I.2_JUV	6-7	6.5		222.5	*4703-4545*	SMP
Arene Candide 6627.1	6-8	7.0		214	*4690-4544*	SMP
Pollera 20PE	6-8	7.0		230	*4715-4556*	SMP
Pollera 6682.1	7-9	8.0		231	*4707-4555*	SMP
Strapatente I	7.5-8.5	8.0		255	*4531-4369*	SMP
Arene Candide 3 Tinè	7.5-9.5	8.5	246	249	*4782-4502*	SMP
Arene Candide 6730.3+6623.1+6625.2	7-10	8.5		243	*4779-4608*	SMP
Pollera 1PE Issel-Morelli	10-12	11.0		***373**[2]*	*4783-4620*	SMP
Arene Candide V BB	14-16	15.0	348	351	*4720-4557*	SMP
Arene Candide 6621.1	13-19	16.0		400.5	*4726-4557*	SMP
Arene Candide 1 Tinè	15-18	16.5		404	*4704-4374*	SMP

Table 1 – Subadult individuals from the Neolithic of Liguria included in this study. Estimate of age at death based on dental development is in years unless otherwise indicated. ICC: Impresso-Cardial Complex; SMP: Square Mouthed Pottery; CH: Chassean. [1] Details on the direct AMS dates and chrono-cultural attributions are provided in Sparacello et al., in review. [2] Epiphyses were plastered to the diaphysis, the length may be slightly overestimated.

Legend:

- Table legend: upper: upper dentition, lower: lower dentition; n/e: dentition non-erupted, e: dentition partially or fully erupted; R: right, L: left.
- Teeth legend: I, i: incisor; C, c: canine; P: premolar; M, m: molar; U: upper; L: lower; R: right; L: left; d: deciduous; capital letters: indicate the maxilla or mandible tooth and the permanent tooth (e.g. URI1: upper right first incisor), lower case letters: indicate the deciduous tooth (e.g. URdi1: upper right first deciduous incisors). See AlQahtani et al. (2010) for the description used to identify tooth developmental stages of single and multirooted teeth.

Arma dell'Aquila 7 Richard: deciduous dentition not fully mineralized.

		upper																	
R	*n/e*							i2		i1			m1	m2				*n/e*	L
	e																	*e*	
		lower																	
	e																	*e*	
	n/e					m1		i2	i1	i1	i2		m1					*n/e*	

ULdi1: Cr ¾
URdi2: Cr ¾
LRdi1-LLdi1: Cr ¾
LRdi2-LLdi2: Cr ½ - Cr ¾
LRdm1-LLdm1: Coc

- ➢ Age at death: perinatal/new born

Arma dell'Aquila 8 Richard: no teeth present. The estimation of the age at death has been made with the analysis of cranial and post-cranial bones. The skeleton has been compared with the other newborns of the Neolithic Ligurian sample, particularly Arma dell'Aquila 7 Richard.

- ➢ Age at death: perinatal/new born

Pollera 6663.1: deciduous dentition not fully mineralized.

		upper																	
R	*n/e*				m2	m1				i1	i2			m2				*n/e*	L
	e																	*e*	
		lower																	
	e																	*e*	
	n/e				m2	m1			i1	i1	i2		m1	m2				*n/e*	

ULdi1: Crc
ULdi2: Cr ¾
URdm1: Coc
URdm2-ULdm2: Cco - Ci
LRdi1-LLdi1: Crc
LLdi2: Cr ¾
LRdm1-LLdm1: Coc
LRdm2-LLdm1: Cco - Ci

- ➢ Age at death: perinatal/new born

Pollera 6664.1: deciduous dentition not fully mineralized. Maxillary teeth not present.

		upper																	
R	*n/e*												m1					*n/e*	L
	e																	*e*	
		lower																	
	e																	*e*	
	n/e				m2	m1	c					c	m1					*n/e*	

ULdm1: Cr ½
LRdc: Cr ½
LRdm1-LLdm1: Cr 1/2
LRdm2: Coc

- Age: perinatal/new born

Pollera 6665.1+6670.1: deciduous dentition not fully mineralized.

		upper																	
R	*n/e*								i1	i1	i2		m1	m2				*n/e*	L
	e																	*e*	
		lower																	
	e																	*e*	
	n/e				m2	m1		i2			i2							*n/e*	

URdi1-ULdi1: Crc
ULdi2: Cr ¾
ULdm1: Coc
ULdm2: Cco - Ci
LRdi2-LLdi2: Cr ¾
LRdm1: Coc
LRdm2: Cco - Ci

- Age at death: perinatal/new born

Arene Candide 6633.1: deciduous dentition not fully mineralized. Maxillary teeth not present.

		upper																	
R	*n/e*																	*n/e*	L
	e																	*e*	
		lower																	
	e																	*e*	
	n/e										i2		m1	m2				*n/e*	

LLdi2: Crc
LLdm1: Cr ½ - Cr ¾
LLdm2: Cr ½

- Age at death: c. 4.5-7.5 months

Arene Candide 6629.1: deciduous dentition not fully mineralized.

		upper																	
R	*n/e*				m2		c	i2	i1	i1	i2	c	m1					*n/e*	L
	e																	*e*	
		lower																	
	e																	*e*	
	n/e				m2	m1	c	i2	i1	i1	i2	c	m1	m2				*n/e*	

ULdi1: R ¼
URdi2: Ri – R ¼
ULdi2: Ri – R ¼
LLdm1: CrC
ULdm1: Ri
URdm2: Cr ¾

- Age at death: c. 7.5-10.5 months

Pollera 6675.2+6676.1: deciduous dentition not fully mineralized. Partially erupted some deciduous teeth.

		upper																	
R	*n/e*				m2		c					c		m2				*n/e*	L
	e					m1			i1		i2		m1					*e*	
		lower																	
	e					m1				i1			m1					*e*	
	n/e			M1	m2		c	i2			i2	c		m2	M1			*n/e*	

URdm2: R ¼
LLdi2: R ½

- Age at death: c. 7.5 months-1 year (< 1 yr)

Arene Candide 6630.1+CR NNPE Infans: deciduous dentition not fully mineralized. Partially erupted some deciduous teeth.

		upper																	
R	*n/e*						c					c						*n/e*	L
	e							i2	i1	i1	i2							*e*	
		lower																	
	e				m2	m1		i2	i1	i1	i2		m1	m2				*e*	
	n/e			M1			c					c			M1			*n/e*	

ULdi1: R ½ - R ¾
ULdm1: R ½

- Age at death: c. 10.5-18 months

Arene Candide 6628.1+6625.4: two isolated teeth, one deciduous and one permanent, not fully mineralized.

URdi2: R ½ - R ¾
URM1: Cr ½

- Age at death: c. 1-1.5 years

Pollera 6666.2: deciduous dentition not fully mineralized and erupted. It is possible to observe the presence of the lower first mandibular molar. Maxillary teeth not present.

		upper																	
R	*n/e*																	*n/e*	L
	e																	*e*	
		lower																	
	e								i1		i2		m1					*e*	
	n/e						c							m2	M1			*n/e*	

LRdi1: R ½
LLdi2: R ½
LRdc: Ri
LLdm1: R ½

- Age at death: c. 1-1.5 years

Pollera 6669.1+6671.1: deciduous dentition not fully mineralized and erupted. It is possible to observe the presence of the lower first permanent molar.

		upper																	
R	*n/e*				m2		c					c		m2				*n/e*	L
	e					m1		i2	i1	i1	i2		m1					*e*	
		lower																	
	e					m1		i2	i1	i1	i2		m1					*e*	
	n/e			M1	m2		c					c		m2	M1			*n/e*	

URdm2-ULdm2: Ri - R ¼
LRdc: R ¼

- Age at death: c. 1-1.5 years

Pollera 6680.1: deciduous dentition not fully erupted and mineralized. It is possible to observe the presence of the lower first and second permanent incisors. Maxillary teeth not present.

		upper																	
R	*n/e*																	*n/e*	L
	e																	*e*	
		lower																	
	e					m1							m1					*e*	
	n/e				m2		c	I2	I1	I1		c		m2	M1			*n/e*	

LRdm2: Ri
LLM1: Cr ½

- Age at death: c. 1-2 years

Pollera 6670.2: deciduous dentition erupted but not fully mineralized. It is possible to observe the degree of mineralization of upper first permanent molar.

		upper																	
R	*n/e*														M1			*n/e*	L
	e				m2	m1	c	i2		i1		c	m1	m2				*e*	
		lower																	
	e				m2	m1												*e*	
	n/e			M1														*n/e*	

URdc: R ¾

URdm2: R ½
ULM1: Crc

- Age at death: c. 1.5-2.5 years

Arene Candide 6631.1: deciduous teeth erupted, permanent teeth not fully mineralized**.**

		upper																	
R	*n/e*																	*n/e*	L
	e				m2		c								m2			*e*	
		lower																	
	e				m2									m1	m2			*e*	
	n/e			M1							I2	C				M1		*n/e*	

LRM1: Cr ¾ - Crc
LLI2: Cr ¾
LLC: Cr ¾

- Age at death: c. 1.5-2.5 years

Arma dell'Aquila 6 Richard: deciduous dentition erupted but not fully mineralized. It is possible to observe the presence of the first permanent molars of both jaws.

		upper																	
R	*n/e*			M1												M1		*n/e*	L
	e				m2	m1						c	m1	m2				*e*	
		lower																	
	e				m2	m1	c		i1	i1	i2	c	m1	m2				*e*	
	n/e			M1												M1		*n/e*	

LRdc: R ½ - R ¾

- Age at death: c. 1.5-2.5 years

Arene Candide 6632.1+6623.2: deciduous dentition erupted but not fully mineralized. Permanent dentition not fully mineralized.

		upper																	
R	*n/e*			M1				I2										*n/e*	L
	e				m2	m1	c											*e*	
		lower																	
	e					m1							m1					*e*	
	n/e			M1	m2		C	I2	I1	I1	I2	C		m2	M1			*n/e*	

URdm2: R ½ - R ¾
URI2: Cr ¾
URM1: Crc
LLdm2: R ¼ - R ½

- Age at death: c. 2-3 years

Arene Candide VIII BB: deciduous dentition erupted. Permanent dentition not fully mineralized.

		upper																	
R	*n/e*			M1						I1		C	P1	P2	M1	M2		*n/e*	L
	e				m2	m1	c	i2	i1			c						*e*	
		lower																	
	e				m2	m1	c	i2	i1	i1	i2	c	m1	m2				*e*	
	n/e		M2	M1							I2	C			M1	M2		*n/e*	

ULdc: Ac
LLI2: Ri
LLC: Crc

- Age at death: c. 3.5-5.5 years (c. 4-5 yr)

Bergeggi S2 01178 PE, 6894-5-FI: deciduous dentition erupted. Permanent dentition not fully mineralized. For many permanent teeth, it is not possible to determine the degree of mineralization.

		upper																	
R	*n/e*		M2	M1					I1	I1					M1	M2		*n/e*	L
	e				m2	dm1	c	i2	i1	i1	i2	c	m1	m2				*e*	
		lower																	
	e				m2	m1	c			i1	i2	c	m1	m2				*e*	
	n/e			M1									P1		M1	M2		*n/e*	

URM2-ULM2: Cr ½

- Age at death: c. 4.5-5.5 years

Pollera 21PE: deciduous dentition fully erupted. Permanent dentition not fully mineralized.

		upper																	
R	*n/e*			M1											M1			*n/e*	L
	e				m2	m1	c	i2	i1	i1	i2	c	m1	m2				*e*	
		lower																	
	e				m2	m1	c	i2			i2	c	m1	m2				*e*	
	n/e								I1	I1					M1	M2		*n/e*	

LLM1: R ¼
LLM2: Cr ½

- Age at death: c. 4-6 years

Pollera 6678.1: deciduous dentition fully erupted. Permanent dentition not fully mineralized. For many permanent teeth, it is not possible to determine the degree of mineralization.

		upper																	
R	*n/e*			M1											M1			*n/e*	L
	e				m2	m1	c	i2	i1			c	m1	m2				*e*	
		lower																	
	e				m2	m1						c	m1	m2				*e*	
	n/e		M2	M1											M1	M2		*n/e*	

LLM2-LRM2: Coc

- Age at death: c. 3.5-6.5 years

Arma dell'Aquila Zambelli JUV B: three isolated permanent teeth.

URM1-ULM1: R ½
LLM1: R ½

- Age at death: c. 6-7 years

Pipistrelli 1_dep23.I.2_JUV: mixed dentition, deciduous and permanent teeth are erupted. Permanent dentition not fully mineralized.

	upper																		
R	*n/e*							I2			I2							*n/e*	L
	e			M1	m2	m1							m1	m2	M1			*e*	
	lower																		
	e			M1	m2	m1			I1	I1		c	m1	m2	M1			*e*	
	n/e							I2			I2					M2		*n/e*	

URI2-ULI2: R ¼
URM1-ULM1: R ¾
LRI1-LLI1: R ¾
LRI2-LLI2: R ¾
LRM1-LLM1: R ¾
LLM2: Ri

- Age at death: c. 6-7 years

Arene Candide 6627.1: mixed dentition, deciduous and permanent teeth are erupted. Permanent dentition not fully mineralized.

	upper																		
R	*n/e*											C	P1	P2				*n/e*	L
	e								I1	I1				m2	M1			*e*	
	lower																		
	e			M1	m2	m1	c	I2	I1	I1	I2	c	m1	m2	M1			*e*	
	n/e		M2				C					C				M2		*n/e*	

ULdm2: Res ¼
LRdc-LLdc: Res ¼
ULC: R ½
ULP1: R ¼ - R ½
ULP2: R ¼
LLI1: Rc
LRI2-LLI2: Rc - A ½
LLC: R ½
LLM1: R ¾ - Rc

- Age at death: c. 6-8 years

Pollera 20PE: mixed dentition, deciduous and permanent teeth are erupted. Permanent dentition not fully mineralized.

	upper																		
R	*n/e*		M2					I2			I2					M2		*n/e*	L
	e			M1	m2	m1	c		I1	I1		c	m1	m2	M1			*e*	
	lower																		
	e			M1	m2	m1	c	i2	I1	I1	i2	c	m1	m2	M1			*e*	
	n/e		M2													M2		*n/e*	

URM2-ULM2: Crc - Ri
LLM2: Crc

- Age at death: c. 6-8 years

Pollera 6682.1: mixed dentition. All teeth are isolated (no maxilla and/or mandible bones). Permanent dentition not fully mineralized.

		upper																	
R	*n/e*		M2			P1	C											*n/e*	L
	e			M1	m2	m1	c	I2	I1	I1	I2							*e*	
		lower																	
	e					m1	c	I2	I1	I1	I2							*e*	
	n/e											C	P1					*n/e*	

URdm1: Res ½
URdm2: Res ¼
URC: R ½
URP1: R ¼
URM2: R ¼
LLdm1: Res ½
LRI1-LLI1: A ½
LRI2-LLI2: Rc
LLC: R ½
LLP1: R ¼

- Age at death: c. 7-9 years

Strapatente I: mixed dentition, deciduous and permanent teeth are erupted. Permanent dentition not fully mineralized.

		upper																	
R	*n/e*		M2													M2		*n/e*	L
	e			M1	m2	m1	c	I2	I1	I1	I2	c	m1	m2	M1			*e*	
		lower																	
	e			M1	m2	m1	c	i2	I1	I1		c	m1	m2	M1			*e*	
	n/e		M2								I2					M2		*n/e*	

URI1-ULI1: Rc
URI2-ULI2: R ¾
URM1-ULM1: R ¾ - Rc
URM2-ULM2: R ¼

- Age at death: c. 7.5-8.5 years

Arene Candide 3 Tinè: mixed dentition, deciduous and permanent teeth are erupted. Permanent dentition not fully mineralized.

		upper																	
R	*n/e*		M2													M2		*n/e*	L
	e			M1	m2	m1			I1		I2		m1	m2	M1			*e*	
		lower																	
	e			M1	m2	m1	c	I2	I1	I1	I2	c	m1	m2	M1			*e*	
	n/e	M3															M3	*n/e*	

URM2-ULM2: Crc
LRdc: Res ¼
LLI2: A ½

- Age at death: c. 7.5-9.5 years

Arene Candide 6730.3+6623.1+6625.2: permanent teeth not fully mineralized. It is possible to observe in the mandible the presence of the alveoli of deciduous teeth that are not preserved (probably mixed dentition). Maxillary teeth not present.

		upper																	
R	*n/e*																	*n/e*	L
	e																	*e*	
		lower																	
	e														M1			*e*	
	n/e												P1			M2	M3	*n/e*	

LLM3: Coc

- Age at death: c. 7-10 years

Pollera 1PE Issel-Morelli: permanent dentition not fully mineralized and erupetd.

		upper																	
R	*n/e*	M3												P2			M3	*n/e*	L
	e		M2	M1	P2	P1	C	I2	I1	I1	I2	C	P1		M1	M2		*e*	
		lower																	
	e		M2	M1	P2	P1	C	I2	I1	I1	I2	C		P2	M1	M2		*e*	
	n/e	M3															M3	*n/e*	

URM3- ULM3: Crc - Cr ½
LRM3: Cr ½

- Age at death: c. 10-12 years

Arene Candide V BB: permanent dentition erupted. It is not possible to determine the degree of teeth mineralization.

		upper																	
R	*n/e*	M3																*n/e*	L
	e		M2	M1	P2	P1	C	I2	I1	I1	I2	C	P1	P2	M1	M2		*e*	
		lower																	
	e		M2	M1								C						*e*	
	n/e																	*n/e*	

- Age at death: c. 14-16 years

Arene Candide 6621.1: isolated permanent teeth not fully mineralized (no maxilla and/or mandible bones). Mandibular teeth not present.

		upper																	
R	*n/e*																M3	*n/e*	L
	e		M2						I1		I2		P1	P2				*e*	
		lower																	
	e																	*e*	
	n/e																	*n/e*	

ULM3: R ½

- Age at death: c. 13-19 years

Arene Candide 1 Tinè: permanent dentition not fully erupted. It is not possible to determine the degree of teeth mineralization.

		upper																	
R	*n/e*	M3															M3	*n/e*	L
	e		M2	M1	P2	P1	C	I2	I1	I1	I2	C	P1	P2	M1	M2		*e*	
		lower																	
	e		M2	M1	P2	P1	C	I2	I1	I1	I2	C	P1	P2	M1	M2		*e*	
	n/e	M3															M3	*n/e*	

- Age at death: c. 15-18 years