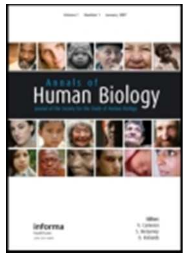

Bone growth, limb proportions and non-specific stress in archaeological populations from Croatia

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Bone growth, limb proportions and non-specific stress in archaeological populations from Croatia

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ABSTRACT

Background: The effect of environmental factors, and in particular non-specific stress, on the growth patterns of limbs and other body dimensions of children from past populations, is not well understood.

Aims: This study assesses whether growth of medieval and post-medieval children aged between 0-11.5 years from Adriatic (coastal) and continental Croatia varies by region, and by the prevalence and type of non-specific stress.

Methods: Dental ages were estimated using the Moorrees, Fanning and Hunt (MFH) scoring method. Growth of long bone diaphyses (femur, tibia, humerus, radius, and ulna) was assessed by using a composite Z-score statistic (CZS). Clavicular length was measured as a proxy for upper trunk width, distal metaphyseal width of the femur was measured as a proxy for body mass, and upper and lower intralimb indices were calculated. Differences between subsets sampled by (a) region and (b) active vs. healed non specific stress indicators, and (c) intralimb indices, were tested by Mann-Whitney U-tests and Analysis of Covariance (ANCOVA).

Results: Adriatic children attained larger dimensions-per-age than continental children. Children with healed stress lesions had larger dimensions-per-age than those with active lesions. No inter-regional difference was found in intralimb indices.

Conclusion: These findings highlight the complexity of growth patterns in past populations and indicate that variation in environmental conditions, such as diet, and differences in the nature of non–specific stress lesions, both exert a significant effect on long bone growth.

INTRODUCTION

Bone growth patterns vary both within and between populations and are affected by a range of environmental and genetic factors. Anthropological studies of growth patterns in past populations are based on cross-sectional analyses of changes in bone dimensions in relation to age (Johnston 1962; Merchant and Ubelaker 1977; Cook 1984; Jantz and Owsley 1984a,b; Mensforth 1985; Owsley and Jantz 1985; Lovejoy et al. 1990; Hoppa 1992; Saunders 1992; Saunders and Hoppa 1993; Hoppa and Gruspier 1996; Steyn and Henneberg 1996; Tanner 1998;Humphrey 1998; Hoppa and Fitzgerald 1999; Jantz and Jantz 1999; Mays 1999; Humphrey 2000; Humphrey 2003; Saunders 2000; Šereikienë and Jankauskas 2004; Floyd and Littletone 2006; Mays et al. 2009). Most studies examined growth of long bone diaphyseal dimensions by plotting each dimension as a function of dental age, based on the assessment of tooth crown and root developmental charts (Moorrees et al. 1963a,b; Buikstra and Ubelaker 1994) and dental formation/eruption charts (see Ubelaker 1989; Buikstra and Ubelaker 1994). These studies indicate inter-population variability in growth of diaphyseal limb dimensions (Sundick 1978; Jantz and Owsley 1984a; Mensforth, 1985; Ribot and Roberts 1996; Humphrey 2000; Lewis 2002a,b; Pinhasi et al. 2005; Pinhasi et al. 2006; Pinhasi et al. 2011). Studies of modern-day populations (Tanner 1986; Wall 1991) have also shown that inter-population differences can increase or decrease in response to the extent to which a process of "catch-up" growth follows recovery from one or more episodes of growth faltering (Tanner 1986).

Growth patterns reflect the overall health of a population (Johnston and Zimmer 1989) and dimensions-per-age from past populations can be compared to modern growth data from various world regions (cf. Ice and James 2011) in order to provide an indicator of the health of past populations. Anthropological studies typically assess the health status of prehistoric populations by recording information about the prevalence type and degree of expression of a series of skeletal markers of stress (c.f.

Goodman et al. 1988). These include markers associated with a specific disease (e.g. leprosy, tuberculosis, etc.), and a range of non-specific stress indicators which do not have specific proximate causes, but their high prevalence in some archaeological skeletal populations is known to be a contributor to poor health (Goodman and Rose 2002).

Only a handful of studies assessed whether there is a significant interaction between skeletal stress indicators and growth in past populations (Lukacs 2001; Sciulli and Oberly 2002; Floyd and Littleton 2006; Pinhasi et al. 2006; Temple 2008; Schillaci et al. 2011). These studies highlighted the complexity of understanding the effects of poor skeletal health on growth and stature trajectories in past population. In the case of some disease markers there is a clear association between a specific stress indicator and lower-than-average diaphyseal long bone dimensions. The "Osteological Paradox" (Wood et al. 1992) asserts that in any population which suffers from disease or nutritional stress the interpretation of "health' is problematic. Any skeletal population will include individuals that never experienced stress and have none of the related skeletal lesions, individuals that experienced moderate stress which lasted long enough to result in some skeletal lesion, and individuals that suffered heavy stress resulting in death soon after the onset of the disease and which may therefore have a few or no skeletal lesions. Wood et al. (1992) further point out that the frequency of pathological lesions that appear to be active at the time of death, without any indication for remodeling (i.e. healing) should be higher in individuals exposed to high levels of stress, in particular during the first five years of life. Therefore, an assessment of stress indicators in skeletal samples should take into consideration both age-specific prevalence rates, and also whether the studied condition was active or inactive at the time of death.

Mixed-longitudinal studies of growth patterns of rural Guatemalan children with suboptimal nutritional intake indicated that body measurements such as head and chest circumferences provide nutritional information which is not evident from the study of body length and weight. Undernourished Guatemalan children have smaller head and chest circumferences compared to the well-nourished Denver children of the same age, but the magnitude of difference between these two groups varied by age and was not correlated with differences in overall limb lengths. Differences between the two groups in chest circumference decreased at the age of 12 - 48 months and increased beyond this age, while head circumference differences were minimal at birth, become established at around 6 months and become progressively greater through 24 months (Malina et al. 1975). This suggests that the assessment of growth in relation to nutritional stress based only on the study of limb dimensions may provide a limited perspective on growth trajectories.

In this study we focus on the analysis of inter-regional variation in growth of long bone diaphyses (femur, tibia, humerus, radius, and ulna) by using a composite Z-score statistic (CZS, see below), the clavicular length (a proxy for upper trunk width), the distal metaphyseal width of the femur (a proxy for body mass), and the upper and lower intralimb indices (brachial and crural indices, respectively). We also assess whether there is a significant difference in long bone diaphyseal dimensions per age between individuals with active versus healed non-specific stress indicators: cribra orbitalia and periostitis. The four archaeological sites analyzed in this study are: Stenjevec (1050–1250 AD) and Nova Rača (1400–1700 AD), located in continental Croatia; and Koprivno (1500–1700 AD) and Dugopolje (1350–1500 AD), which are located in the Adriatic region of Croatia (Figure 1). At present the two regions differ in their ecology as continental Croatia has a central European climate with average winter temperature below 0° C (Goldstein 1999) while Adriatic Croatia has a Mediterranean climate, with short, wet winters during which the temperature rarely falls below 5° C. Estimated temperature variations from the Northern Hemisphere as a whole indicates that during these periods, average temperatures were similar to those in present day, prior to AD 1400 and on average 0.6° C colder during the Little Ice Age, AD 1400-1900 (Mann 2003).

Growth patterns are dependent on both environmental and genetic factors. Historical and archaeological data suggest that the four sites were 'ethnically' heterogeneous. Dugopolje was populated by the descendants of Early Croats and a heterogeneous group of peoples fleeing from Ottoman Turkish military intrusions and/or conquests (Novak and Šlaus 2007). Koprivno was inhabited by the same descendants of the Early Croats and an ethnically heterogeneous group of Turkish subjects known as "Vlachs" (Kužić 2001; Gjurašin 2006). In continental Croatia, Stenjevec was inhabited by heterogeneous Slavs (consisting of Early Croats and their descendants, Slovaks, and Bulgars) and Hungarians (Demo 1996), while Nova Rača (situated as it was on the fortified military border that separated Croatia from the Ottoman Empire during the 16th to 18th centuries) was inhabited by a heterogeneous group of peoples that included Croats, Bosnians and Serbs (Šlaus 2000). Hence, there is no discernible genetic pattern that would imply a consistent or interpretable difference between individuals from continental and coastal regions.

In contrast, historical, archaeological, and dental data suggest there may have been dietary differences between individuals from continental and coastal regions. In continental Croatia the subsistence spectrum was primarily based on agriculture. Historical confirmation is provided by the *urbarii* –legal documents that defined relationships between feudal lords and peasants. One of these, the *urbarium* from the monastery of Streza in continental Croatia dated to 15th century, shows that millet was the staple crop which was a main component of the diet, possibly because it was easily cultivated, had a short period of vegetation, and could be sown in dry and sandy soils (Kolar-Dimitrijevic 2003). Additional crops were wheat, buckwheat, rye, and barley, whilst poultry, pork and fish were rarely consumed (Adamček et al. 1980) .Thus crop failures may have had catastrophic impact on the nutrition and health of these peasants. In the Nova Rača parish Book of the Dead (compiled from 1830–1848 listing the age, sex, and cause of death of its parishioners) the second most common cause of death in children is listed as "*emaceratio*" or "*ex debilitate*" suggesting undernourishment or starvation (Šlaus 2000). A diet based on products rich in carbohydrates also resulted in high frequencies of caries and significant wear on the occlusal surfaces of teeth recorded in individuals from the 11th to the 16th century from continental Croatia (Vodanovic et al. 2005; Novak et al., 2010). In contrast, lack of cultivable soil in the Adriatic hinterland resulted in a livelihood largely dependent on livestock breeding and a diet that was based more on consumption of meat and animal products than in continental Croatia. There is historical information (Šaric 2008) that the primary occupation of the inhabitants of Koprivno was transhumant pastoralism with average flocks consisting of between 200 and 600 sheep, along with some large cattle (Jurin-Starcevic 2008). This dietary difference is further supported by the lower caries frequency in individuals from Koprivno than from continental Croatia (Novak et al. 2007).

MATERIALS

Samples comprised a total of 198 skeletons of children from the following archaeological cemeteries: Dugoplje - excavated from 2004 to 2005 (Gjurašin 2005), Koprivno – excavated from 2001 to 2002 (Gjurašin 2002, 2006), Stenjevec –

excavated from 1983 to 1997 (Simoni 2004), and Nova Rača – excavated from 1986 to 1995 (Jakovljević 1986). The analyzed skeletal material is thus grouped into two composite series; coastal Adriatic, and Continental Croatia (Table I). The pooled cemetery samples encompass fairly extensive time periods – particularly the continental series that covers a time span of potentially 650 years, but can be regarded as a single analytical period on the basis of the historical and archaeological data. The analyzed cemeteries are related to small rural settlements and the analyses of the recovered archaeological artifacts, grave architecture, and available historical sources, suggest that the vast majority of the recovered individuals belonged to lower social categories (Gjurašin 2002, 2005, 2006). Except for six of the adult individuals from the Stenjevec cemetery (three males, and three females), who were buried with jewelry that may be indicative of higher social status (Simoni 2004), there is no evidence of social stratification in any of the analyzed cemeteries. Additionally, during the time period encompassed by the analyzed sites no fundamental technological, scientific, subsistence, or social changes occurred that could significantly affect growth profiles – with one exception, the introduction of syphilis in Croatia in 1500 AD (Gruber 2009). The presence of syphilis is noted in historical documents in both continental Croatia, and on the Adriatic coast and its hinterland (Bazala 1972; Glesinger 1978), and has also been recorded in osteological material (Šlaus and Novak 2007). All skeletons were screened for the presence of congenital syphilis according to criteria outlined in Ortner (2003). No such individuals were detected. Therefore, we believe that that there are no diachronic factors that could significantly affect the growth profiles of the two composite series.

METHODS

Metric measurements

Maximum diaphyseal length dimensions for the humerus, ulna, radius, femur, and tibia were measured directly or using a standard osteometric board following the method described in Buikstra and Ubelaker (1994). Additionally, distal femoral epiphyseal breadth and clavicular length measurements were taken using a standard sliding caliper, following the methods provided in Buikstra and Ubalaker (1994). The left bone was chosen whenever possible but was replaced with the right bone if it was missing or poorly preserved. The brachial index is expressed as a percentage of the relative length of the lower arm to the upper arm, and is calculated as the radius length/humerus length x100 (Aiello and Dean 1990). The crural index expressed as the percentage of the relative length of the lower leg to the upper leg as a percentage, calculated as the tibial length/femoral length x 100 (Aiello and Dean 1990).

Age Assessment

The dental age of all specimens was estimated by applying the Moorrees, Fanning and Hunt (MFH) scoring method for the permanent lower molars, premolars, canines and incisors (Moorrees et al. 1963a) in order to obtain a dental formation rank. Age for each rank was obtained from charts specified in Smith (1991) for each of the analyzed teeth. A chronological age estimate was obtained for all teeth and the mean age for all teeth from each individual was calculated. In cases in which an outlier age estimate was obtained for a given tooth, the radiographs were re-examined by one of the authors (MS) against the dental formation and eruption chart of Schour and Massler (1941) and errors were corrected by re-applying the MFH method, to obtain new age estimates for each of the mandibular teeth. In all cases the final dental age was based on the separate assessment of at least 3 lower teeth, while the mean number of teeth analyzed for the complete sample is 4.6.

Diagnosis of stress indicators

Studies of non-specific stress in children generally involve assessment of the presence of one or more of the following stress indicators: cribra orbitalia, porotic hyperostosis, periostitis, maxillary sinusitis, dental enamel hypoplasia, Harris lines, and endocranial lesions (Lewis 2007). In this study, extensive postmortem tooth loss precluded the assessment of dental enamel hypoplasia. Therefore we considered only cribra orbitalia and non-specific periostitis frequencies reliable enough to be incorporated in this analysis. While the assessment of stress on the basis of only two indicators is not ideal, it does provide the opportunity to directly examine the possible associations between each of the two stress indicators and growth patterns in the analyzed populations.

Cribra orbitalia is a sieve-like expansion in the orbital plates of the frontal bone that is considered to be part of similar bone changes that affect the skull vault (porotic hyperostosis) (Carlson et al. 1974; Cybulski 1977; Stuart-Macadam 1985; Mittler and van Gerven 1994; Fairgrieve and Molto 2000). Various hypotheses have been suggested for the cause of porotic hyperostosis including anemia, metabolic diseases such as scurvy and rickets, syphilis, cancer, and pressure from binding and carrying (Williams 1929; Angel 1966; Mensforth et al. 1978; Stuart-Macadam 1985; Stuart-Macadam 1992; Ortner 2003; Wapler et al. 2004; Papathanasiou 2005; Walker et al. 2009) Porotic hyperostosis and cribra orbitalia are the osseous outcome of marrow hyperplasia (Trancho 1987; Stuart-Macadam 1991; Mittler and van Gerven 1994; Larsen 1997; Fairgrieve and Molto 2000; Walker et al., 2009; but see Ortner et al., 1999, 2001), which can be caused from various disease processes. Possible, although rare, causes include renal osteodystrophy, hereditary spherocytosis, and cyanotic congenital heart disease (Moseley 1966; Ortner 2003; Blom et al. 2005). Other causes include genetically inherited forms of anemia such as thalassemia and sickle–cell anemia, and acquired iron–deficiency anemia (Tayles 1996; Hershkovitz et al. 1997; Larsen 1997; Bocherens et al. 1999; Ortner 2003). Cumulative evidence from numerous bioarchaeological studies worldwide resulted in a general consensus linking porotic hyperostosis in archaeological skeletal populations with acquired iron deficiency anemia (Larsen 1997). However, according to Walker (Walker et al. 2009), hematological research shows that iron deficiency alone cannot sustain the massive red blood cell production that causes marrow expansion responsible for these lesions. He argues that the most likely cause of porotic hyperostosis is rather the accelerated loss and compensatory overproduction of red blood cells seen in hemolytic and megaloblastic anemias, and in addition states that porotic hyperostosis and cribra orbitalia often have different etiologies.

In this study no attempts were made to discern the possible etiologies of cribra orbitalia and the prevalence of this condition was simply assessed as an indicator of stress in all children aged 1–11.5 years (as it was not possible to assess with confidence the prevalence of the condition in newborns). No attempt was made to evaluate the severity of the lesion but a distinction was made between active and nonactive (healed) lesions according to criteria suggested by Mittler and Van Gerven (1994). Because other pathological conditions including metabolic diseases, cancer, and infectious diseases can mimic the osseous changes that result from acquired iron-deficiency anemia, every effort was made to distinguish conditions that resulted in marrow hyperplasia, from those that did not, according to criteria described by Ortner (2003). Additionally, because genetic anemias may have been present– particularly those from the Adriatic hinterland region where malaria was endemic – all skeletons were carefully screened for the presence of thalassemia and sickle-cell anemia, once again according to criteria suggested by Ortner (2003). All cases potentially suspect for genetic anemias, cancer, metabolic and infectious diseases were excluded from this study. The presence of cribra orbitalia was assessed in all individuals with at least one orbital roof preserved. Consequently, the number of individuals that were assessed in regard to the prevalence of cribra orbitalia varied by site (see below). Overall skeletal preservation and recovery of bones were similar at all four cemeteries.

Periostitis is defined as a basic inflammatory response that develops because of non-specific bacterial infections and is macroscopically recognized as osseous plaques with demarcated margins or irregular elevations of bone surfaces. Periostitis can also be caused by trauma and specific infectious diseases such as leprosy, tuberculosis, and treponemal disease (Larsen, 1997; Ortner, 2003). Both leprosy and tuberculosis have been reported in osteological data from Croatia (Šlaus, 2006), and cases of trauma are frequently found in almost all archaeological data. To ensure, therefore, that only cases of non-specific periostitis were included, all skeletons with osteological evidence of leprosy or tuberculosis were excluded from the periostitis sample. Periostitis was not considered present if it was located on the same bone as a fracture or other trauma. Nonspecific periostitis was diagnosed when two or more skeletal elements, excluding the endocranial surfaces of the skull, exhibited active or healed periostitis. Criteria for inclusion in the sample were the presence of least 50% of all long bones (all of the long bones present – including both sides). No attempt was made to evaluate the severity of the lesion but a distinction was made between active and nonactive (healed) lesions according to criteria suggested by Mensforth et al. (1978).

Statistical methods

The raw data included 777 measurements from 7 bone metrics from 198 skeletons.

Since the skeletons were incomplete, the sample sizes for any particular bone metric were small, ranging from n=151 (76%) to n=80 (40%) (Table SI 1). To enable the detection of potential differences with greater sensitivity, we combined different metrics from each individual skeleton. Combining diaphyseal metrics provides two main advantages. Firstly it increased the sample sizes. This was particularly important in this study since we were trying to detect small differences in subsets of an already small dataset, which consisted of measurements from incomplete skeletons. Secondly, it has the minor (but nonetheless useful) effect of reducing the impact of outliers. In order to balance this increased sensitivity against the potential increase in variance from combining different metrics we first assessed the correlation between each pair of metrics. The correlation coefficients (Pearson's R) ranged from 0.931 between the clavicle length and femur breadth, to 0.9943 between the femur length and tibia length (Figure SI 1). However, within this narrow range there appears to be a cluster of five metrics (diaphyseal lengths of the femur, tibia, humerus, radius and ulna) that were particularly strongly correlated, whilst clavicle length, and femoral distal metaphyseal breadth were less so. This difference can be visualized using an un-rooted tree using a distance matrix of the correlation coefficients (Figure SI 2).

We created a single combined metric, or composite Z-score (CZS) (see e.g. Relethford, 2001) for each skeleton by averaging Z-scores or each of the five long bone diaphyseal metrics. This ensured that each CZS was constructed from a minimum of one diaphyseal dimension and a maximum of five. In addition to using the CZS, we also included the distal femoral metaphyseal breadth, clavicle length and both upper and lower intralimb indices.

Considering age as a covariate. Since all bone length dimensions have a strong correlation with age (between age and the combined metric: Pearson's R=0.948, P<2.2e-16), it was essential to adjust for age as a covariate (Pinhasi et al. 2005, 2006). A model selection approach was used to establish a suitable relationship between CZS and age. A cubic model was selected as most appropriate having both the lowest Bayesian information criterion (BIC) (Burnham and Anderson, 2002) and the lowest residual variance of the three tested models (Table SI 2 and Figure SI 3).

To a lesser extent intralimb indices also exhibited a correlation with age, therefore tests were also performed on the residuals from a suitable model. In the case of the crural index, the correlation with age was 0.365 (P<0.001), and a cubic model had the lowest BIC. In the case of the brachial index the correlation with age was 0.275 (P=0.061), and a quadratic model had the lowest BIC.

The residuals were then used in two distinct statistical tests, firstly to test whether or not there is any significant difference between two groups. If a significant difference was found, a second test was applied to estimate the magnitude of that difference.

Testing for a significant difference between groups, and the magnitude of that difference. Firstly, Mann-Whitney U-tests were performed on the residuals to test if there was a significant difference between the Adriatic and continental sets. Secondly, the magnitude of the difference was estimated using Analysis of Covariance (ANCOVA). Specifically, we calculated the sum of the squares of the residuals for region A (SS_A), repeated this procedure for region B (SS_B), and for the total pooled regions (SS_{Total}). The portion of variation attributable to inter-regional differences was estimated by deducting the within-variation portion from the total variation: $SS_{Between} = SS_{Total} - (SS_A + SS_B)$. The proportion of variation attributable to differences between regions was calculated as: $SS_{Between}$ / SS_{Total}. The associated p-value was calculated using a re-sampling with randomization test using 500,000 re-samples. The p-value was calculated as the proportion of re-sampled $SS_{between}$ that were greater or equal to the observed $SS_{between}$ (see Jobling et al. 2004; Pesarin and Salmaso 2010). Both tests were applied using the combined metric, femoral distal breadth and clavicle length.

In addition to testing region as a factor (coastal vs. continental) we repeated the analyses on the two non-specific stress indicators (periostitis, cribra orbitalia) using only the combined metric, as sample sizes for femoral distal breadth and clavicle length were smaller. The independence of these three factors was confirmed using a χ^2 test (Table II).

RESULTS

Table III provides a summary of the results of the statistical tests for (1) regional differences, using the combined metric, femoral distal breadth, and clavicle length, (2) differences between active and healed periostitis, using the combined metric, (3) differences between active and healed cribra orbitalia, using the combined metric, (4) regional differences in the crural index, and (5) regional differences in the brachial index.

Region

A highly significant difference between the two regions was found using CZS (Figure 2) and femoral distal breadth (Figure 3), and to a lesser extent clavicle length (Figure 4), with the Adriatic sub-set exhibiting larger dimensions-per-age (Mann-Whitney U-test P-values are <0.001, <0.001 and 0.053, respectively). The magnitude of the difference between the two regions was estimated at 18.4% for CZS, 14.0% for femoral distal breadth, and 11.6% for the clavicle length (P-values are <0.001, 0.016, and 0.043, respectively).

Stress indicators

Sample sizes for individuals determined to have either active or healed stress indicators were small (cribra orbitalia active N=21, healed N=61, periostitis active N = 63, healed N = 52) compared with the previous regional analysis (continental N = 65, Adriatic N = 133), therefore analysis was only performed using the more sensitive combined metric. Significant differences between active and healed were found for both cribra orbitalia and periostitis, in both cases children with healed lesions exhibited larger dimensions-per-age than those with active lesions (Figures 5 and 6, Mann Whitney U-test P-values = 0.0037 and <0.001 respectively), and the magnitude of the difference was estimated at 15.7% (P = 0.054) and 12.0% (P = 0.026) respectively.

Intralimb indices

Mann-Whitney U-tests of the crural index of Adriatic vs. continental populations revealed no significant differences (Adriatic N = 70, continental N = 24, P = 0.161). Mann-Whitney U tests of the brachial index of Adriatic vs. continental populations also revealed no significant differences (Adriatic N = 45, continental N = 19, P = 0.402).

DISCUSSION

This study reveals significant differences in the growth trajectories of Adriatic vs. continental Croatian children, although p-values above 0.0073 should be treated with caution given the application of multiple tests (Sidak correction using 7 tests). The Adriatic coastal hinterland populations generally attained higher limb length, femoral distal breadth and clavicular length dimensions-per-age than the continental populations. The difference in femoral and distal breadth dimensions implies that body mass of children from continental Croatian was generally lower than that of their peers in the Adriatic hinterland (see Ruff 2007 and references therein for calculation of body size based on femoral distal epiphyseal breadth).

No significant regional differences in the brachial and crural indices were found, suggesting that while the Adriatic children were larger overall, this did not translate into significant differences in their limb proportions, although it should be noted that the sample sizes for this test were small. Cowgill et al. (2012) analysed developmental variation in body proportions in relation to latitudinal and climatic factors in a global set of modern and archaeological subadult samples. They report that both indices are established early in ontogeny in all populations, and that environmental effects on these indices appear to be minimal. Similar results were reported by Temple et al. (2011) in their study of the ontogeny of intralimb indices in relation to ecogoegraphic differences in Jomon period foragers. The results reported here are in accord with these studies as they indicate no significant difference in the ontogeny of these indices between Adriatic and Continental regions. While this study did not assess the potential interaction between growth for a given age category and the wide range of environmentally confounding effects, it suggests genetic conservation of these indices during ontogeny.

In terms of environmental variation, the two regions differ to some extent in their mean annual temperatures and climates, but these differences are not strong enough to exert a significant effect on the growth trajectories of limb dimensions, body mass and intralimb indices (see Katzmarzyk and Leonard 1998). The two regions are located in a similar eco-geographical region with similar elevation. Available historical documents indicate that while living conditions during the medieval and post-medieval periods were harsh in both regions of Croatia, children from the Adriatic hinterland had a better dietary status than those from continental Croatia. The Nova Rača parish Book of the Dead additionally suggests that, at least some children from continental Croatia died as a result of chronic malnutrition and previous studies (Frisancho et al. 1980) have shown that in populations exposed to this type of malnourishment the delay in skeletal growth is most noticeable during childhood. Frisancho et al. (1980) also suggest the influence of environmental factors such as nutrition is greater on younger children.

Ribot and Roberts (1996) assessed the growth of long bone dimensions in Early (Raunds) and Late (Chichester) medieval populations from England with the following non-specific stress indicators: dental enamel hypoplasia, porosity on the ectocranial surface of the skull (both orbital and vault lesions), subperiosteal new bone formation on long bones and the ectocranial surface of the skull, and Harris lines. Individuals were categorized into those with high stress (those exhibiting two or more stress indicators), stressed, or unstressed individuals (those exhibiting just one, or no stress indicators) and the diaphyseal dimensions of their humerii, femora and tibiae were compared. Their results showed no significant differences in growth according to their levels of stress. In contrast, a recent study by Schillaci et al. (2011), reports growth faltering starting soon after birth and continuing until about 5 years of age among Pueblo Indians from the American Southwest, and that children without porotic cranial lesions exhibited a higher degree of stunting than those with lesions. A study by Pinhasi et al. (2006) examined the effects of rickets on long bone growth patterns in medieval and post-medieval populations from Britain and showed no significant differences in long bone growth patterns between individuals with osteological evidence for rickets, and those without the disease. In contrast, Mays et al. (2009) studied the effects of rickets on the growth patterns of long bones in 19^{th} century children from Birmingham, England. They applied multiple regression analyses to long bone dimensions of individuals with active rickets, healed rickets, and no evidence of rickets for the 2–6 years old age cohort, and then compared partial correlation coefficients in order to detect significant associations between growth patterns and rickets. Their results showed that individuals with rickets in the 2–6 year age group had shorter bones for their age than individuals without the disease, however they found no difference between the long bone dimensions.

The apparent incongruities in the results of these various studies might be explained as follows. Firstly, it has been shown that dental age underestimates the chronological age in the case of malnourished children, by 10-12 months on average (Lampl & Johnston 1996). It is therefore possible that the obtained charts undermine the true discrepancies in growth between children with vs. without stress. Secondly, there are at present only a few case studies which assess how bone growth trajectories are interacting with stress and there is no reason to expect that all non specific and specific stress, from a range of diseases and nutritional conditions, would have the same impact on bone growth. This is especially the case when we take into consideration the fact that non-specific stress indicators are associated with either a range of diseases and nutritional conditions, or have unknown etiologies. Thirdly it is expected that the differences between survivors with healed lesions and those with active lesions, can provide insight about the actual correlation (if any) between a given stress indicator and health in past populations.

Future studies which assess a wider range of stress indicators may provide more insight into the effects of stress and to what extent the size and proportions of children with healed stress indicators manage to “catch up”.

CONCLUSION

This study examined differences in the growth patterns using skeletons of children from four medieval and post-medieval cemeteries, comparing differences between those from the Adriatic hinterland, and continental Croatia. Our results indicate that (a) Adriatic children generally have larger bone dimensions per age, (b) children with healed lesions of cribra orbitalia or periostitis attained significantly larger dimensions-per-age than those with active lesions, and (c) no differences in brachial and crural indices of children from the two regions were detected.

Our results indicate that environmental factors play a significant role in in growth trajectories of past populations. Based on the historical documents and the ecological settings we postulate that difference in diet was a substantial contributor to differences in growth patterns of children from the two regions.

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Declaration of Interest

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

LITERATURE CITED

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FIGURE LEGENDS

Figure 1. Geographic location of Croatian samples

Figure 2. A bivariate plot of CZS vs. dental age of (a) Adriatic and (b) continental Croatians

Figure 3. A bivariate plot of femur distal metaphyseal breadth vs. dental age of (a) Adriatic and (b) continental Croatians

Figure 4. A bivariate plot of clavicular length vs. dental age of (a) Adriatic and (b) continental Croatians

Figure 5 A bivariate plot of CZS vs. dental age of chidren with (a) active vs. (b) healed cribra orbitalia

Figure 6. A bivariate plot of CZS vs. dental age of chidren with (a) active vs. (b) healed periostitis

SI Figures

SI Fig 1. Pearson's R correlation coefficients of the long bone and clavicular measurements.

SI Fig 2. An un-rooted tree constructed from a distance matrix of the correlation coefficients

SI Fig 3. Model selection of CZS by age and coresponding residuals

SI Fig. 4. A bivariate plot of the crural index of (a) Adriatic and (b) continental Croatians

SI Fig. 5. A bivariate plot of the brachial index of (a) Adriatic and (b) continental Croatians

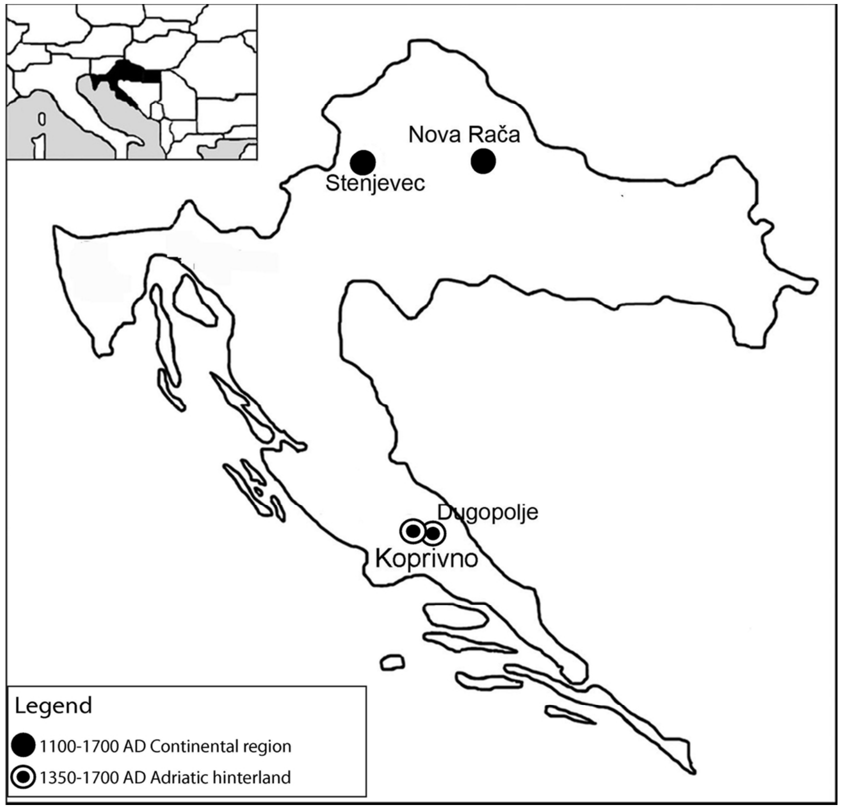

Figure 1. Geographic location of Croatian samples
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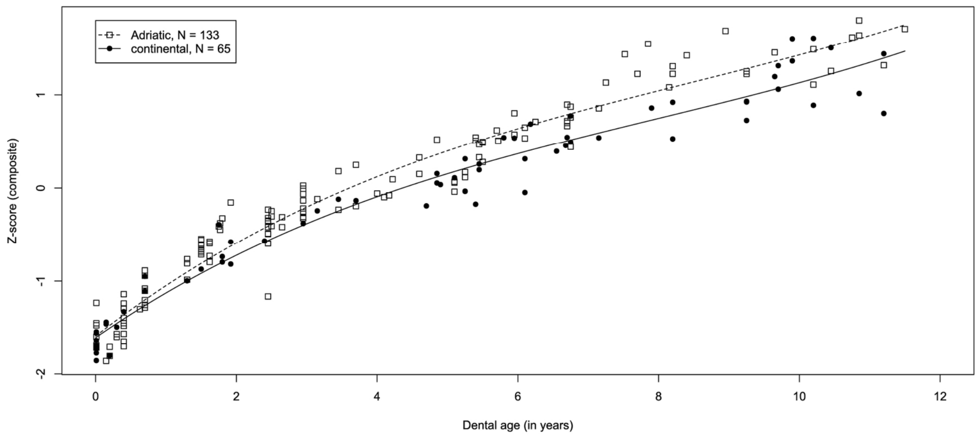

Figure 2. A bivariate plot of CZS vs. dental age of (a) Adriatic and (b) continental Croatians
177x88mm (300 x 300 DPI)

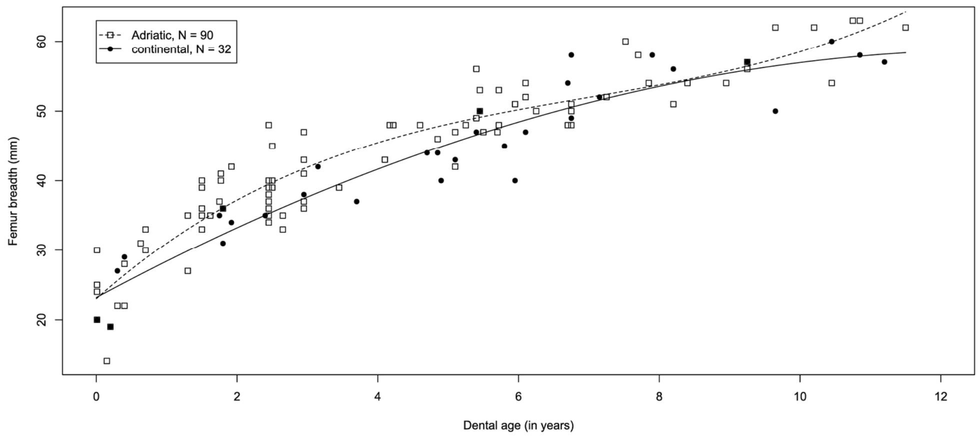

Figure 3. A bivariate plot of femur distal metaphyseal breadth vs. dental age of (a) Adriatic and (b) continental Croatians
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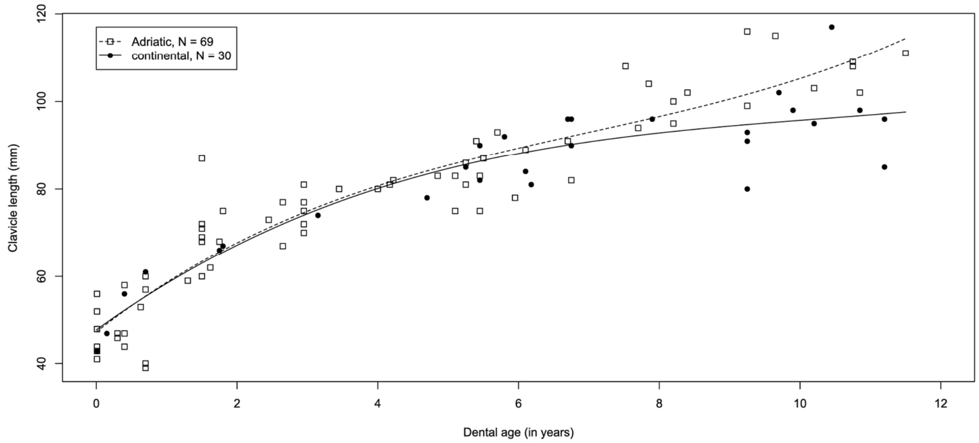

Figure 4. A bivariate plot of clavicular length vs. dental age of (a) Adriatic and (b) continental Croatians
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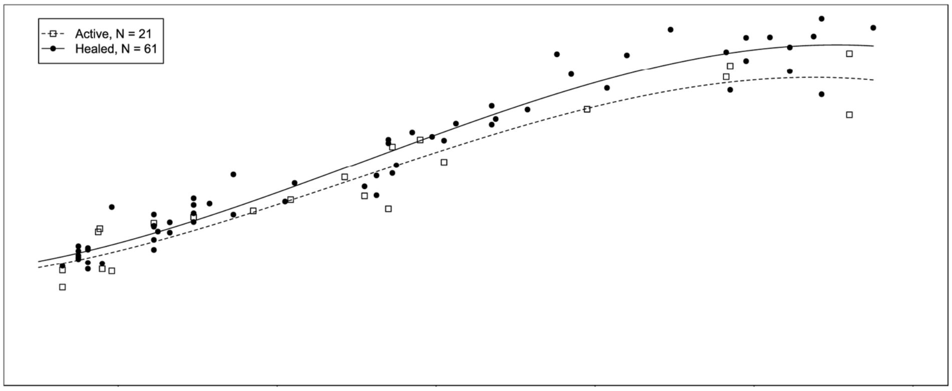

Figure 5 A bivariate plot of CZS vs. dental age of chidren with (a) active vs. (b) healed cribra orbitalia
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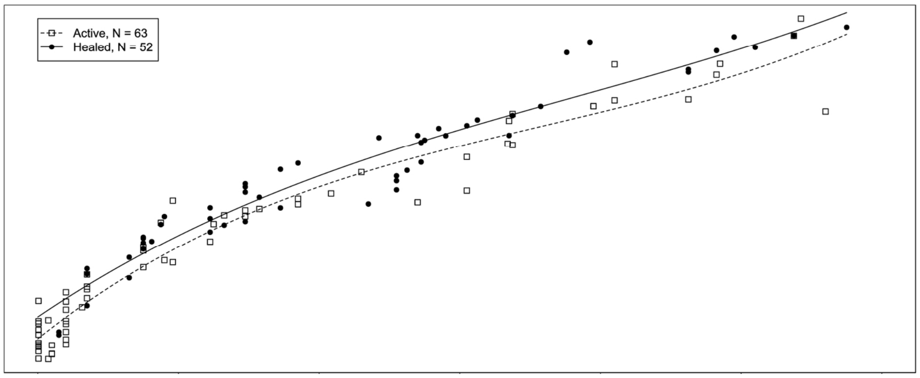


Figure 6. A bivariate plot of CZS vs. dental age of chidren with (a) active vs. (b) healed periostitis
177x88mm (300 x 300 DPI)

Table 1. Contextual details about the skeletal subadult series from Croatia

Site	**N**	**Period**	**Location**
Dugopolje	74	1350-1700 AD	Adriatic
Koprivno	59		hinterland
Stenjevec	40	1100-1700 AD	Continental
Nova Rača	25		Croatia

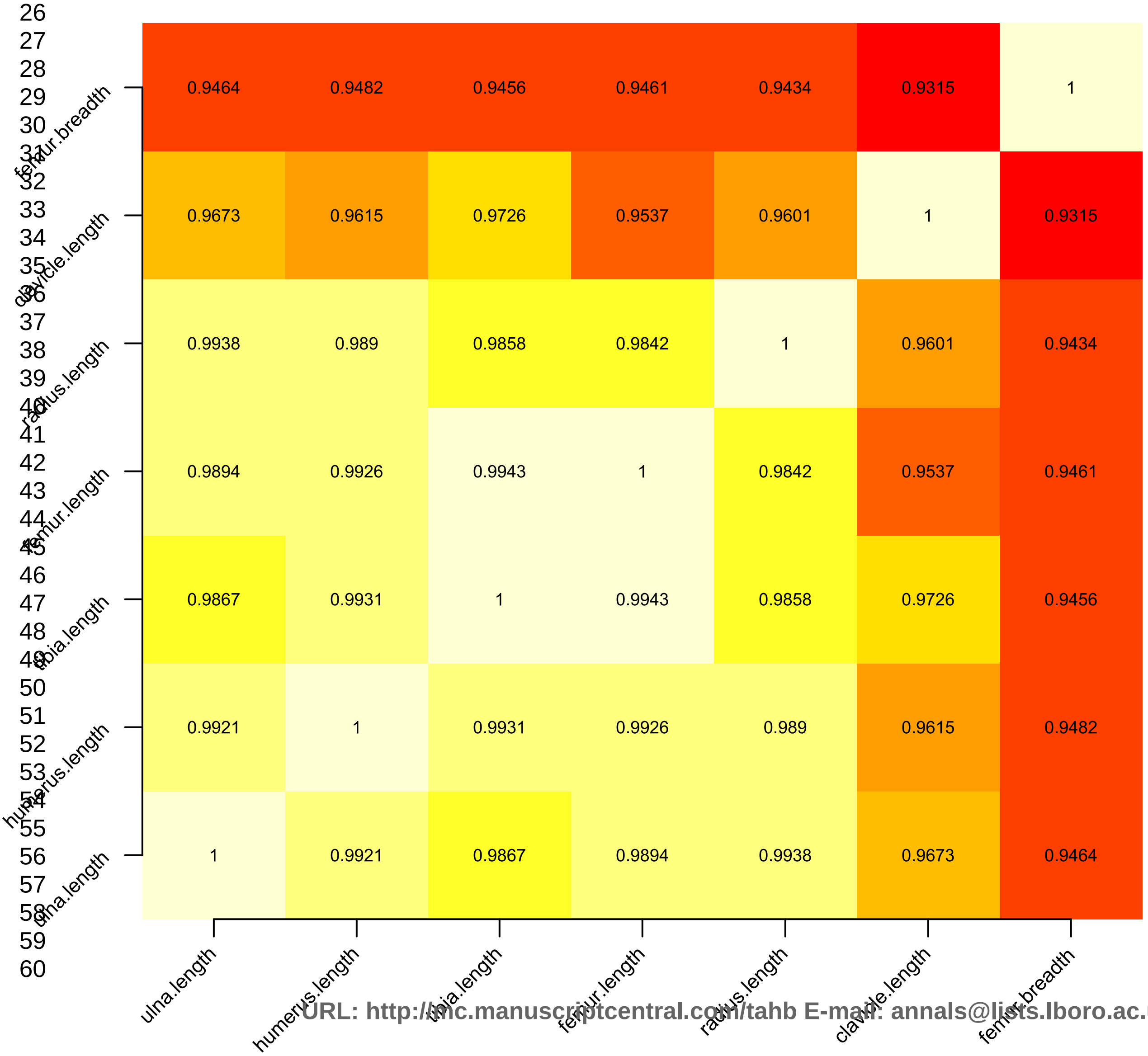
Table 2. Chi-square test results for the three factors.

Factors	**d.f**	**Chi-squared**	**P-value**
Region vs Periostitis	1 d.f.	0.17	0.682
Region vs Cribra Orbitalia	1 d.f.	2.73	0.099
Periostitis vs Cribra Orbitalia	1 d.f.	0.02	0.901

Table 3. Summary of statistical results for test of growth differences by (1) CZS, femoral breadth, clavicle length, (2) limb proportion by region and (3) stress indicators (active vs. healed) for CZS.

Test	Statistic	Variable 1	N	Variable 2	N	MWW p-value	Difference (p-value)
Region	CZS	Adriatic	133	Continental	65	<0.001	18.4% (<0.001)
	Femur breadth	Adriatic	90	Continental	32	<0.001	14.0% (0.016)
	Clavicle length	Adriatic	69	Continental	30	0.053	11.6% (0.043)
Limb proportions	Crural index	Adriatic	70	Continental	24	0.161	
	Brachial index	Adriatic	45	Continental	19	0.402	
Stress indicators	CZS	CO active	21	CO healed	61	0.0037	15.7% (0.054)
	CZS	Per active	63	Per healed	52	<0.001	12.0% (0.026)

CO= Cribra orbitali; Per= Periostitis; MWW- Mann- Whitney Wilcoxon test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0.9464 0.9482 0.9456 0.9461 0.9434 0.9315 1
clavicle.length
0.9673 0.9615 0.9726 0.9537 0.9601 1 0.9315
radius.length
0.9938 0.989 0.9858 0.9842 1 0.9601 0.9434
femur.length
0.9894 0.9926 0.9943 1 0.9842 0.9537 0.9461
tibia.length
0.9867 0.9931 1 0.9943 0.9858 0.9726 0.9456
humerus.length
0.9921 1 0.9931 0.9926 0.989 0.9615 0.9482
ulna.length
1 0.9921 0.9867 0.9894 0.9938 0.9673 0.9464
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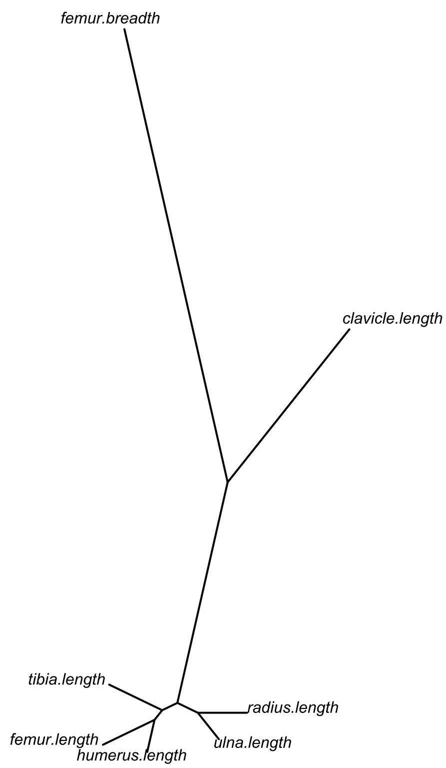
femur.breadth


femur.breadth
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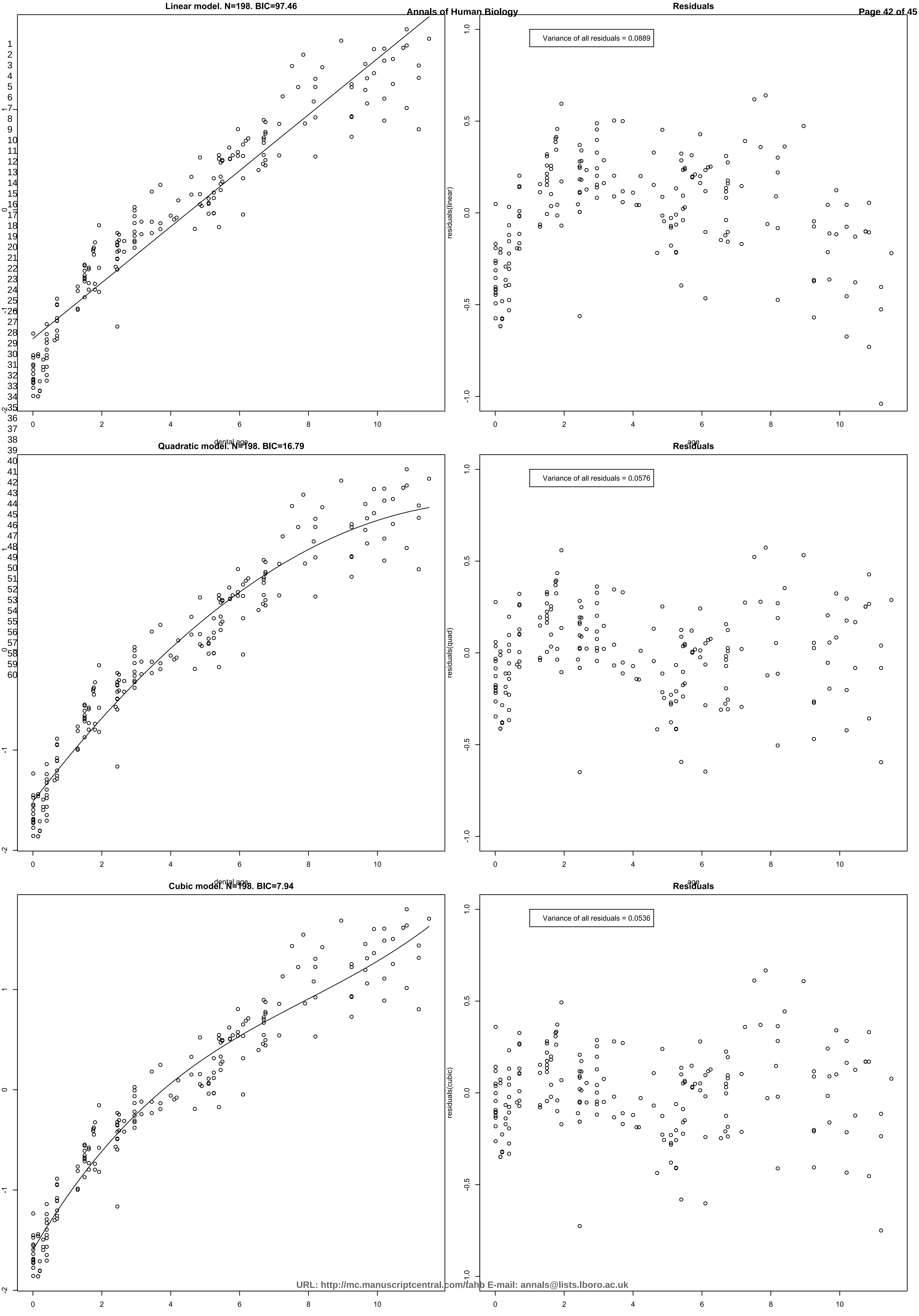
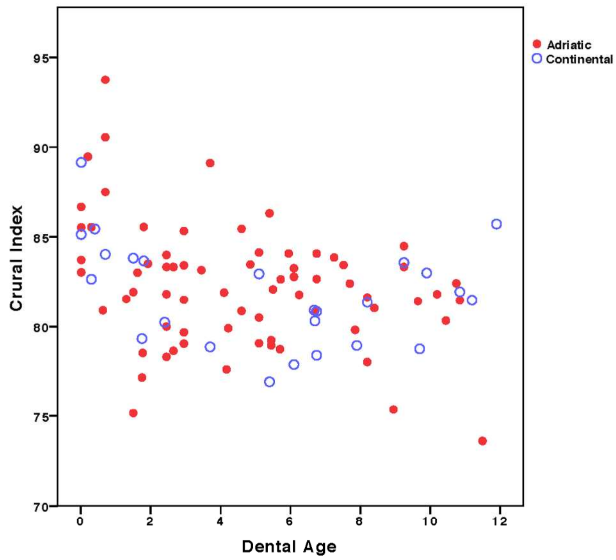
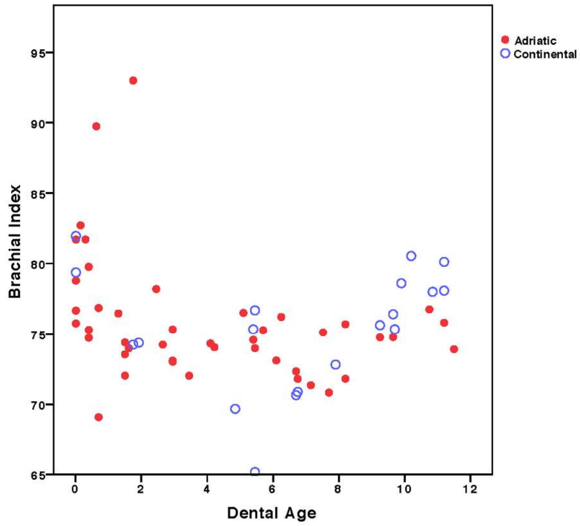

Linear model. N=198. BIC=97.46
dental age
Residuals
Variance of all residuals = 0.0889
residuals(linear)
age
Quadratic model. N=198. BIC=16.79
dental age
Residuals
Variance of all residuals = 0.0576
residuals(quad)
age
Cubic model. N=198. BIC=7.94
Residuals
Variance of all residuals = 0.0536
residuals(cubic)



SI Fig. 4. A bivariate plot of femur length vs. tibia length of (a) Adriatic and (b) continental Croatians
215x279mm (200 x 200 DPI)



Page 1

209x297mm (200 x 200 DPI)

Supplementary Tables

Table SI 1. Number of specimens and percentage of total skeletal sample by measurement.

Measurement	**Sample size**	**% of all 198 skeletons**
Ulna length	87	44
Humerus length	129	65
Tibia length	109	55
Femur length	151	76
Radius length	80	40
Clavicle length	99	50
Femur breadth	122	62

Table SI 2. Model selection based on lowest Bayesian Information Criteria(BIC) and lowest variance of residuals

Model	Variance in residuals	BIC
Linear	0.0106	-337
Quadratic	0.0075	-404
Cubic	0.0067	-424