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A cross-population analysis of the growth of long bones and the os coxae of three Early Medieval Austrian populations

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Running headline: Skeletal growth of Medieval Austrian populations

ABSTRACT

Long-bone and pelvic-bone growth patterns of three Early Medieval Austrian populations from the sites of Gars, Thunau, Zwentendorf and Zwölfaxing are assessed and compared with an Anglo-Saxon population from Raunds, England and with several comparative reference populations. Bone measurements are analysed against dental age estimates in order to assess inter-population differences in growth rates and dimensions. The three Austrian populations are from geographically close locations and share relatively similar archaeological contexts and ecological conditions. The expectation was that the greatest differences in growth patterns would be found between the Anglo-Saxon and the Austrian samples, reflecting variability in their genetic and biocultural background.

Analysis of covariance (ANCOVA) and post-hoc tests were performed for each bone dimension, with dental age as a covariate. Subsequently, Gompertz growth curves were iteratively estimated for each sample in order to inspect variability in growth rates.

The results point to a contrast between inter-population similarities in diaphyseal long bones growth and variability in the distal diaphyseal dimensions of the femur and humerus and the length and breadth dimensions of the ilium. Varying growth patterns are therefore associated with specific morphological structures implying that there is a need to address variation in the growth of each specific morphological structure. The most consistent differences in bone growth and related dimensions are between Gars-Thunau and Zwölfaxing. No significant differences in growth were detected between the Anglo-Saxon and the Austrian populations.

INTRODUCTION

Growth is the product of the continuous and complex interaction of heredity and environment (Tanner, 1989). Traditionally, both longitudinal and cross-sectional studies of skeletal and dental growth were based on living subjects. Such studies could utilise information about the subject's age, sex, weight at birth, genetic makeup, socioeconomic status and the like in order to examine the causes of both individual and population specific differences in growth trends.

In contrast, most studies of growth of past populations rely on skeletal samples from archaeological contexts, for which the relevant information about the individual's age, sex, nutrition, genetic affinities and socioeconomic status is in most cases conjectural. Therefore, the reliability of growth studies of past populations depends to a fair extent on the ability to estimate some of these factors and on the accuracy and reliability of the methods utilised.

A central tenet held of growth studies of skeletal populations is that skeletal growth and dental formation and eruption are three processes which differ in the degree to which they are genetically controlled and capable of buffering some of the environmental factors (Buikstra and Cook, 1980). Thus, differences in growth patterns of these ontogenetic "systems" in relation to specific environmental stressors can provide information about biological variation in past human populations. While growth can be viewed as a function of genetic potential and environmental influences it is often difficult to differentiate between the two. Though inter-population comparisons one can discover population-specific differences, but these can not always be explained in terms of genetic vs. non-genetic factors (Ulijaszek, 1998).

Several studies addressing growth in prehistoric and historic populations dealt with inter-population variability by comparing one or more historic or prehistoric skeletal populations to others from published sources (Hoppa et al. 1992; Miles and Bulman, 1998; Saunders et al. 1993; Saunders et al. 2000; Sundick 1978). However, these studies compare groups that have various temporal, geographic and cultural attributes. Such studies, while informative, cannot explain sufficiently the degree to which variability and similarity in growth patterns of various populations reflect genetic affinities and variability in nutritional and disease stress. Studies which utilised either temporally sequential skeletal populations from a given region (Cook, 1984), or compared populations from the same geographic region (Hummer and Van Gerven, 1983) yielded informative results but the temporal intervals between the populations could not allow for a secure claim of a similar genetic structure. Thus, any interpretation of observed differences as being the outcome of exposure to nutritional stress, different weaning practices, infectious diseases and other environmental factors, could not rule out the probability that much of the observed variation in growth patterns is genetically based.

There are several biases which affect the reliability of any paleodemographically-based analysis of archaeological immature skeletal samples. Subadults are often underrepresented in prehistoric skeletal samples due to differential burial practices and poor bone preservation of young individuals (Ubelaker, 1989). In addition, subadult samples are often hampered by the fact that the number of individuals aged over 5 is small due to low mortality rates in late childhood and adolescence (Goodman, 1998b). Consequently, the assessment of growth from a

paleodemographic perspective requires a careful examination of the degree to which the given skeletal population's mortality profile is a reliable estimator of the profile of the original population.

There is at present no accurate macroscopic method for the determination of sex of subadults and molecular methods are expensive and hindered by problems associated with ancient DNA extraction and contamination (Saunders, 2000). Until more precise sexing methods for subadults are developed, it is preferable to combine the sexes in subadult growth studies (Buikstra and Cook, 1980).

Age estimations are in most cases based on one or more of the following (1) measurements of long bones which are then assessed using standard charts (Scheuer and Black, 2000); (2) timing of the fusion of the various epiphyses (Ubelaker, 1989, El-Najjar and McWilliams, 1978); (3) dental eruption timing (Blanckstein et al. 1990; Eskeli et al. 1999; Darling and Levers, 1975; Dahlberg and Menengaz-Bock, 1958); and (4) dental formation stages (see Demirjian, 1978; Hillson, 1996; and Liversidge et al. 2000 for reviews).

Root and crown formation assessment methods based on the radiographic analysis of the dentition have become the accepted standard for the evaluation of age in large archaeological samples (Saunders et al. 2000). The calcification stages of teeth can be best assessed using a combination of both macroscopic and radiographic techniques.

There are various methods for the estimation of chronological age from the examination of postnatal dental formation. The most commonly applied method

among anthropologists is the one devised by Moorrees, Fanning and Hunt (MFH) (1963a, 1963b). The ageing system is based on comparing each cheek tooth to a series of 14 formation stages, using published plots. The above system was reworked by Smith (1991) in order to accommodate for the fact that MFH's system was based on a longitudinal study while archaeological samples are cross-sectional. Ages for a given growth stage were based on the average age of subjects at a given stage rather than the actual age when that stage was first attained. Consequently, in longitudinal studies in which subjects are examined at specific interval lengths, observation of a growth stage usually postdates the actual onset of attainment by several months or even years. Smith devised new charts for males and females in which a given age for a specific formation stage can be interpreted as the actual average age of attainment of a growth stage. The male and female values can then be averaged to obtain estimates for the age of subadult individuals from archaeological samples.

Until recently, a prevailing assumption among biological anthropologists was that the ontogenetic process of dental root and crown formation is genetically controlled and is thus much less affected by environmental factors (Saunders et al, 2000; Smith, 1991; Demirjan, 1978; Goodman, 1998b). However, this assumption has been questioned by researchers who examined clinical samples of modern American children (Garn et al. 1959) and in more recent comparative studies on past skeletal populations (Tompkins, 1996; Saunders et al. 2000) which yielded varied results.

Tompkins (1996) compared relative dental development in white French-Canadians, black Southern Africans and prehistoric Native Americans. Differences in the frequency distribution of formation stages of mandibular central incisors, canines,

premolars and second and third molars were assessed in relation to first molar (M1) stages. This comparison enables an examination of population-specific differences in relative dental development while avoiding errors associated with the estimation of absolute chronological age. Results indicate differences in the relative dental development of certain permanent teeth among the three populations. The main inter-population difference was the delayed development of the second molar (M2) and other teeth amongst the French-Canadians in comparison with the Africans and the Native American samples.

Saunders et al. carried out a similar comparative study in which the dental formation standards of MFH (1963a, 1963b) were applied to a nineteenth century Canadian skeletal sample and an Imperial Roman sample and then tooth pairs at various stages were plotted. They found no differences between the populations despite considerable evidence for disease-related skeletal stress among the Roman sample.

A large part of inter-population morphological variation among both adults and subadults is attributed to variation of the growth process (Johnston, 1969). It is unclear how much of this variation is caused by genetically based differences and how much should be attributed to environmental factors. Another important point of contention is what specific environmental factor exerts the most notable effects on the skeletal growth process. Some environmental factors, such as high altitude, can affect overall growth rate, while other factors, such as climate have little effect on the process (Tanner, 1989).

It is also known that both nutritional and disease stressors can have a significant impact on the growth process (Larsen, 1997; Cook, 1984). However, it is not always clear how and to what extent each stressor affect the growth at a given period of development.

In this paper we examine the growth pattern of three Early Medieval Austrian populations from the sites of Gars, Thunau, Zwentendorf and Zwölfaxing, and compare these to a reference Anglo-Saxon population from Raunds, England. The growth patterns are compared by examining long-bone and pelvic-bone measurements against obtained dental age estimates. The three Austrian populations are from geographically close locations in Lower Austria. The populations of Gars Thunau and Zwentendorf, are contemporaneous (10th century A.D.), share similar archaeological contexts (Slavonic Period), and ecological conditions. Based on their archaeological background, the expectation is thus that these two populations share a common genetic affinity and that no significant differences in growth rates of any of the studied bones should be noted. Moreover, the assumption is that any differences in growth reflect variability in epidemiological and nutritional factors (currently under study) rather than in the genetic structure of the two populations.

The following aspects are examined:

1. Inter-population variability in bone growth in terms of both (1) absolute dimensions (i.e. differences in growth curves) and (b) relative dimensions of certain bones in relations to other bones (i.e. in which a specific long bone may vary while others are similar to other populations in their growth pattern).

2. Inter-population variability in growth rates—the growth curves for certain bones should differ between samples not only in their absolute average values at a given age, but also in their overall shapes, thus reflecting differences in growth rates at various ages.

SAMPLES AND METHODS

The 10th Century A.D. Slavonic site of Gars Thunau is located north of the Danube (about 80km north-west of Vienna), Lower Austria. The site was excavated starting in 1965 and – with some interruptions – still continuing (Friesinger H. & I., 1991). The 10th Century A.D. Slavonic site of Zwentendorf is located near the south bank of the Danube in Lower Austria (about 50km west of Vienna). Systematic excavations have been carried out by the Österreichisches Archäologisches Institut and the Niederösterreichisches Landesmuseum (see Heinrich, 2001) between 1953 and 1962. The Avar Period site of Zwölfaxing is located south of the Danube, 30km south-east of Vienna. The excavations were carried out by the Department of Prehistory and Anthropology, Natural History Museum Vienna, between 1954 and 1959 (see Szilvássy, 1980).

Additional data consist of raw data from the reference collection of 69 subadults from the Raunds Anglo-Saxon site in England (Hoppa, 1992), and published cohorts of archaeological samples and a modern sample of Caucasian subadults from Denver, Colorado.

The cohort frequencies and overall sample size for the analysed skeletal samples are described in Table 1.

<<Insert Table 1>>

Age distribution frequencies and sample sizes are provided in Figure 1.

<<Insert Fig.1>>

A brief description of the measurements is provided in Table 2. The metric data utilised in this study include diaphyseal length and maximum midshaft diameters of long bones, length and width of the scapula, lengths of ischium and pelvic bones, length and breadth of the Ilium and the breadth measurements of the humerus and femur distal metaphyses. All measurements on subadults from Gars Thunau and Zwölfaxing were taken by RP following the standards specified in Buikstra and Ubelaker (1994). Measurements on subadults from Zwentendorf were taken from the data published by Heinrich (2001). Left side bones were measured and right side was substituted in all cases in which the left bone was either missing or fragmented. Only bones without fused epiphyses were used.

<<Insert Table 2>>

The comparative samples are depicted in Table 3. All samples, with the exception of the modern Caucasian reference sample from Denver, Colorado (Maresh, 1955), are archaeological and therefore there is no information about the chronological age of the individuals. Measurements systems for all other samples were compared and only

variables which were recorded using the same landmarks and procedure as for the present study were included (cf. Bräuer, 1988).

The most accurate means to estimate chronological age for archaeological samples is by the assessment of crown and root calcification stages of the deciduous and permanent dentition. Panoramic x-rays were taken for all subadults from the three Early Medieval Austrian populations. The calcification stages for the deciduous and permanent teeth were assessed from the examination of radiographs except in cases of loose dentition that could be examined macroscopically.

<<insert Table 3>>

Dental age of the primary reference samples was estimated on the basis of the method specified in Smith (1991). The system allows one to obtain a chronological age estimate for each mandibular tooth and is therefore very useful in studies of archaeological samples with high frequencies of missing teeth. In this study, age estimates were obtained for the prevalent posterior dentition—specifically canines, premolars and first and second molars, and were then averaged. In cases in which an outlier age estimate was obtained for a given tooth, the radiographs were re-examined by RP against the dental formation and eruption chart of Schours and Massler (1941) and errors were corrected by re-applying the MFH method, to obtain new age estimates for each of the mandibular teeth of the given individual.

Dental Age estimation for individuals of the reference Anglo-Saxon sample from Raunds was also based on the MFH system. In the case of all of the cohort reference samples, dental age estimation was based on dental formation and thus the published cohorts could be compared.

Analysis of covariance (ANCOVA) was performed on each of the above variables in order to assess whether there is a significant difference between the regression slopes of each of the populations for a given measurement, while controlling for the influence of dental age as a covariate. When using ANCOVA it is necessary to test for the following assumptions (1) linearity of the relationship between the covariate(s), and the dependent variable, and (2) homogeneity of covariate-dependent variable slopes (Stevens, 1996). The first assumption was tested by looking at group scatterplots of the covariate—dental age—plotted against each of the bone variables (see Table 2). The relationship between the covariate and each variable of the subset was linear.

The homogeneity of the regression slopes for each dependent variable (when the independent variable is "dental age") was examined by looking at the interaction between the covariate ("group") and the independent variable ("dental age"). When the significance level for the interaction is less than or equal to 0.05 then the interaction effect is statistically significant and the assumption of homogeneity of slopes is rejected.

Ancova analysis was then performed on all variables with a non-significant level of interaction. Subsequently, Tukey-Kramer post-hoc tests were performed in order to test which pairs of group means were significantly different from each other.

The Gompertz curve is often utilised in growth models (Humphrey, 1998, Seber, 1989). A common modification of the curve is to set its lower asymptote to zero and thus tailoring the curve to fit growth data sets that pass through the origin (equation 1).

$$y=a*(EXP(-EXP(-b*(x-m)))) \quad \text{Equation 1}$$

Where a= upper asymptote, m=point of inflexion (time of maximum growth), b=slope parameter, and x=dental age.

The Levenberg-Marquardt (LM) algorithm is the preferred method for linear and nonlinear regression problems. The algorithm was applied to the Gompertz equation using an iterative method to the initial parameters for solving nonlinear least-squares regressions for each group.

Curve fitting is an iterative process which requires that initial values are specified for each of the given parameters. At the first stage, parameters were estimated for pooled samples. For each variable a mean adult value—taken from the sample of Zwentendorf—was applied for the upper asymptote (a), a value of 0.2 was applied for the slope (b), and a value of 0 for the point of inflexion (m)—following the procedure specified by Humphrey (1998). Subsequently, the estimated parameters obtained from

the estimated curve for the pooled sample were used as initial values for the curve fitting analysis of the separate groups.

In addition, fourth-degree polynomials were used in order to obtain a good curve fit to the data for each dimensions per population. The main advantage of polynomial fits is that the calculations of curves and their significance values are straightforward. These curves, however, are of limited use in the study of growth as they are only applicable for the given data range and the interpolated curve is in appropriate estimator of a growth function. Each polynomial curve was visually compared with the obtained Gompertz curves and a close match between each pair was noted in the case of all variables.

RESULTS

A. PRIMARY SAMPLES

Results of the ANCOVA tests for each of the specified variables are provided in Table 4.

<<insert Table 4>>

Significant differences between the groups were noted for the following variables—length and breadth of the ilium, the diaphyseal length, distal width and midshaft diameter of the femur and humerus, and maximum midshaft width of the ulna, radius and tibia. Two ilium length and breadth dimensions' parameters showed a significant interaction between groups and dental age and were excluded.

Post-Hoc tests results are provided in Figure 2.

The most consistently noticeable differences in bone dimensions are between Gars-Thunau and Zwölfaxing. The populations differ in humerus and femur shaft lengths, distal widths and midshaft diameters, and in tibia and ulna midshaft diameter. Zwölfaxing differs from all three other groups in both femur and humerus distal diameters.

<<Insert Fig. 2>>

Gompertz curves were then fitted for each significant variable per group using the above specified procedure. R-squared values (“pseudo” R-squared, corrected for the lack of intercept) for each group per variable are presented in Table 5. R-squared values indicate a good fit of the Gompertz model with the initial parameters in the

case of most curves (average fit value of 0.84). However, the values for the Gars-Thunau curves are significantly lower than the average for humerus, femur and tibia midshaft diameters.

The curves for the ilium breadth and length dimensions (Fig. 3a-b), when examined against the corresponding scatterplots with linear regression estimates (Fig. 4a-b), show a considerable improvement in data fit. The Gompertz curves display a better, and more realistic, estimation of the actual growth of each bone for the given samples.

Differences between groups in humerus diaphyseal length dimensions (Fig. 5) are pronounced in terms of slopes, and absolute magnitude. Zwölfaxing and Raunds have similar curves which approach their upper asymptotic values at age after the age of 14 and thus differed from the curves of Zwentendorf and Gars Thunau.

A similar trend is apparent in the case of the femur diaphyseal lengths (Fig. 6).

Figure 7 depicts the curves of the humerus distal diaphyseal width dimension. Zwölfaxing, Gars Thunau and Raunds are similar in terms of curvature, with the curve of Zwölfaxing being significantly lower, indicating absolutely smaller diaphyseal dimensions at a given age. The curve of Zwentendorf is more linear, lacking the change in growth rate after the age of 8 years that characterises the other curves. Furthermore, the curves of Raunds and Zwentendorf diverge about the age of 10 years.

A similar trend is noted in the case of the femur distal diaphyseal width (Fig. 8). The only apparent difference is that the Zwölfaxing curve approaches its upper asymptotic value around the age of 12, earlier than in the case of the humerus diaphyseal distal

width. As in the case of the humerus, divergence between the curves of Raunds and Zwentendorf occurs at the age of 10 years.

Inter-population variability in midshaft diameters is apparent in the case of three of the four analysed long bones (Fig. 9a-d). Gars Thunau differ from Zwölfaxing in their femur and tibia midshaft growth curves (Fig. 9, b and d). In the case of both bone dimensions, the curves of Gars Thunau and Zwölfaxing approach their asymptotic values after the age of 14 and differ from the curve of Zwentendorf, which is more linear.

The curves of the ulna and humerus dimensions of Zwölfaxing approach their asymptotic values around the age of 14 and earlier than in the case of the other populations. Post-hoc differences in the case of ulna dimensions were significant between Gars Thunau and Zwölfaxing. This is apparent from the inspection of Figure 9a. In the case of the humerus, the reported difference between Zwentendorf and Zwölfaxing (when their respective linear regressions were compared) is in fact due to difference in slope, inflexion, and upper asymptotic value, and not simply a reflection of mere difference in magnitude (i.e. parallel linear slopes).

B. COMPARATIVE SAMPLES

Comparative data comprise of average long bone diaphyseal lengths for a given age cohort. Mean values for one-year interval cohorts were calculated for Zwölfaxing, Gars Thunau, Zwentendorf and Raunds. Mean data for these samples for each cohort were plotted together with data for the above specified comparative samples.

Two new variables were computed: “Leg length”—the sum of femur and tibia diaphyses dimensions, and “Arm length”—the sum of diaphyseal length of the humerus and radius. These variables were used in order to perform relative comparisons of inter-group differences in growth of upper and lower limbs.

Results indicate that all the sample historic populations differ from the Denver Caucasian sample (Maresh, 1955) in growth rates of both arm length (Fig. 10a) and leg length (Fig. 10b).

Arm length dimensions of the modern Caucasians are larger in absolute size than those of all other prehistoric and historic groups from the age of 2-4 years onwards. Differences are somewhat less pronounced for the long bones of the upper extremities than for the femur and tibia. Moreover, in the case of the latter, there is a difference between the modern sample and the rest not only in size but also in slope—suggesting a faster growth rate in the case of the modern sample. The Leg Length growth curve of the Denver Caucasians is steeper than the corresponding Arm Length curve. A bivariate plot of Arm length against Leg Length (Fig. 11) displays no difference between any of the populations. These results suggest that while significant differences in Arm Length and Leg Length are apparent when comparing the modern Denver sample to all other prehistoric and historic groups, these differences are proportional, highly correlated and nearly constant (cf. Johnston, 1969).

However, the apparent linearity between the two dimensions was not examined as a function of change in age, and therefore does not truly reflect growth as much as static

isometric correlations. In order to assess variability in relation to dental age an arm/leg index was calculated (equation 2):

$$\text{Arm/Leg Index} = ((\text{humerus} + \text{radius}) / (\text{femur} + \text{tibia})) * 100 \quad \text{Equation 2}$$

Group means were then plotted against corresponding mean dental age values (Fig. 12). The scatterplot indicates that the Denver Caucasian group have a lower index than that of any of the other groups. Thus, subadults from the Denver sample have longer leg-relative-to-arm dimensions than in the case of any of the archaeological samples. The lines for the various prehistoric samples in Figure 12 display variability per cohort that does not increase with age. The starting index ratios for all populations are ranging between 80-85; only Zwölfaxing is characterised by a higher index value of 91.58 (based on the index of a single newborn infant). Change in the index rate—reflecting a relative acceleration in the growth of the femur and tibia diaphyses in relation to the growth of the humerus and radius—is similar amongst all populations. The Denver population differ in its absolute index of about 65 after the age of 10 opposed to an index of 73.45 for the Libben group and 70.65 for Mikulčice for the same age cohort.

DISCUSSION

The prevalent assertion among biological anthropologists is that the tempo of bone growth process is mainly under genetic control and that under reasonable environmental conditions this controlling mechanism extends down to many of the details of any studied growth curves (Tanner, 1989; Goodman, 1998a). This assertion can explain the lack of difference between most of the growth curves analysed in this study. Thus, all in all, there are more similarities in growth pattern than differences between the populations.

Lovejoy et al. (1990) compared growth of the Libben skeletal series to the modern Denver series. They report an almost identical growth pattern in the populations except during the postnatal period of the first 3 years of life, during which that prehistoric Libben sample shows a significantly diminished growth velocity. Figure 10a-b illustrate that when mean long bone dimensions for a given cohort were plotted for both sites then the growth line of the Libben sample is similar to the lines of other prehistoric populations and no convergence with the Denver sample is noted.

Similar results were reported by Johnston (1962) in his comparative study of long bones growth of 165 prehistoric Native American subadults from the site of Indian Knoll. Johnston reports that the Indian Knoll sample has overall similar growth curves to the comparative Denver sample of modern Caucasians. However, Johnston reports some discrepancies in estimated growth rates between the two samples. The Indian Knoll subadults have on average shorter long bone dimensions than the modern Caucasians after the age of 2 years. Johnston interpreted the differences as being the

outcome of dissimilar environmental conditions that tend to exert more influence over the growth rate after the age of 2 years.

Miles and Bulman (1994) examined growth curves of a sample of 120 juveniles from a Scottish population from the Ensay Island, dated to 1500-1850 A.D. Diaphyseal measurements of the main six long bones were obtained and corresponding dental ages were estimated based on dental formation stages. Growth curve estimates were fitted to data for each bone by calculating fifth-degree polynomial equations. Subsequently, the Ensay data were combined with data for prehistoric (Indian Knoll, Mikulčice, Altenerding, Prehistoric Nubians, and Aleut) and modern (Denver longitudinal sample reported in Maresh, 1955) and fitted to a total of 24 alternative curve equations.

The authors report little difference in the growth curves of all prehistoric samples. The growth rate of the Denver sample is more pronounced (i.e. steeper slope) for both femur and humerus diaphyseal growth at about 4 months, after which, the curves intersect and diverge with the Ensay curves, thus indicating significant differences between the populations in terms of absolute diaphyseal length dimensions per age cohort. Miles and Bulman interpret the intersection event as being the reflection of the onset of a stunting growth factor among the Ensay population associated with the weaning process.

Results obtained in this study suggest similar growth rates for most long bones among prehistoric populations from disparate geographic locations and time periods. The examination of arm length and leg length of various populations indicated that the

only significant difference is between the modern Denver sample and all other historic and prehistoric populations. However, arm-to-leg ratios were similar among all populations suggesting that inter-population variability is mostly apparent from comparison of certain bone dimensions and mainly in the case of the pelvic bones and is reduced when comparing limb proportions.

Most of the growth graphs in this study indicate a convergence of the curves of 2 or more populations is followed by a divergence occurring during the period of 2-4 years of age. A possible explanation for the divergence of the growth curves at or after the age of 2 is that it is reflect differences in the timing, magnitude and duration of weaning stress—associated with culture-specific weaning practices. In the developing world, breastfeeding usually continues for 1-2 years after birth. Several studies have shown an association between breastfeeding and certain pathological conditions, indicating that breast-milk plays an important role in organ development and growth and in overall reduction of the risk of gastrointestinal and other infections (Binns, 1998).

An examination of Figures 10a and 10b indicates that the Maresh (Denver) line converges with the Mikulčice line during the first postnatal year and then it diverges—reaching larger absolute arm and leg dimensions per age cohort. However, the Denver line does not intersect with the lines of any of the other groups, thus indicating that differences in growth between the modern sample and the rest of the prehistoric samples began from birth onward. This pattern contrasts with the above-mentioned convergence and divergence events noted among the growth curves of the historic samples.

In all four sites examined, the cumulative percentage of mortality is at least 40 percent by the age of 2.5. However, both Gars Thunau and Zwentendorf have high percentages of mortality between the ages of 1.5-2.2 (Gars Thunau—10 cases, 32.3%, Zwentendorf—13 cases, 24.2%) followed by a decline in death frequencies (Fig. 1). Thus while all four distributions have high infant mortality frequencies, Gars Thunau and Zwentendorf clearly differ from Raunds and Zwölfaxing in their age-specific mode. While these mortality distributions are likely affected by the taphonomic and excavation biases that characterise archaeological populations (Saunders, 1992, 2000), we nevertheless cannot reject the possibility that these differences are directly associated with the onset and duration of weaning. In this case, high mortality during the ages of 1.5 to 2.2 years suggests that weaning probably began at or before this age interval and that in many cases stress associated with the weaning process was responsible for the death of many of the infants. The decline in death frequencies in Gars Thunau and Zwentendorf between the ages of 3-5 years suggests that the infants that withstood the nutritional and disease stress associated with weaning survived and probably lived to reach adult age. While such an assumption is speculative, it is substantiated by the fact that out of the four populations examined, Gars Thunau and Zwentendorf are both Slavonic 10th century populations from a proximate geographic location and thus suggests that they are more than likely shared similar cultural practices in regards to the weaning process.

The mortality profile of Gars Thunau and Zwentendorf are in accord with studies that use the concentration of nitrogen, carbon and oxygen stable isotopes in bone or teeth of subadult skeletons (e.g., Katzenberg 1996 for review, Richards et al. 2002, Dupras

et al. 2001, Schwarcz 1998, Moggi-Cecchi et al. 1994) for the determination of timing and duration of weaning periods¹. Such studies indicate a fair amount of cultural variability among prehistoric populations in regards to the timing, duration and method of the weaning process. Nevertheless, in most cases, while weaning began before the age of 2 years the process itself continued for one or more years, suggesting a gradual transition to solid foods and thus a period of high infant mortality associated with lower immunity, unbalanced nutrition, and exposure to new pathogens.

In this study, we detected population-specific variability that is more likely to be environmental rather than genetic. However, results also indicate that inter-population variability differ in magnitude and pattern in the case of specific bones. This observation is in accord with the work of Humphrey, (1998) on cross sectional growth patterns in 18-19th century skeletal sample from London, UK. Humphrey reports different parts of the skeleton vary in their rate of attainment of adult size. These differences are directly related to the developmental basis of sexual dimorphism in a given morphological structure. Sexual dimorphism is caused either by sex differences in growth rate or a combination of sex differences in growth rate and duration. Thus, Humphrey (1998) reports significant differences among post cranial dimensions in regards to the proportion of adult sexual dimorphism caused by growth rate differences and the age at which sexual dimorphism becomes apparent. The analysis reveals that sexual dimorphism in growth rate account for 19-53% in ilium bone diaphyseal growth but for over 60% in the case of corresponding midshaft diameters.

¹ Research currently underway on stable isotope values in bones of juveniles from the three Austrian samples will provide more information about this issue.

Since all analyses were performed on unsexed samples, it is not possible to assess our results against those obtained by Humphrey. Our results indicate that most of the inter-population differences were in that case of various dimensions of specific bones (ilium, humerus and femur) and not with a specific dimension type (i.e. midshaft diameters as opposed to diaphyseal length). It is also possible that the high degree of sexual dimorphism in the growth of some of the bones mask inter-population variability in analysis of unsexed pooled samples. However, we must await the development of a reliable method for the sexing of subadults in order to further investigate this point.

CONCLUSIONS

The following is a summary of the main results:

1. The growth profiles of the subadults of Zwölfaxing differ from the profiles of the other three populations in the case of the distal diaphyseal widths of the femur and humerus and the midshaft diameters of the ulna humerus and tibia. In contrast, the growth curves of the Raunds subadult sample are in most cases not statistically different from the curves of the other three Austrian Medieval populations.
2. The assumption that maximum differences in the above aspects should be noted between the Raunds population and the Austrian samples is rejected. Instead, maximum differences are noted in the case of Zwölfaxing with some additional differences between the two other Austrian populations.
3. Additional differences between the groups are noted in the length and breadth dimensions of the ilium. While no statistical comparison was carried out on

the Gompertz curves (due to mathematical complexities) a visual inspection indicates that the curves differ in absolute magnitude and shape.

4. If one is to accept the assumption that the Slavonic populations of Zwentendorf and Gars-Thunau shared a similar genetic background, then differences in ulna, femur and tibia midshaft diameters (Fig. 9a,b,d) and humerus and femur length after the age of 6 (fig. 5 and fig. 6) may reflect for the most part differences in exposure to environmental stressors. However, as some of the subadult individuals from both sites display pathological conditions such as cribria orbitalia and of enamel hypoplasia—which reflect periods of nutritional stress—caution prevents over-interpretation of these findings prior to a systematic investigation of the health profile of each population.

We conclude that inter-population variability in the rate and duration of growth varies for different parts of the skeleton. The examination of arm and leg length mean growth curves of the studied samples and several reference historic, prehistoric and modern samples indicate that the main difference is between the modern and non-modern samples. However, a comparison of arm length to leg length ratios for all samples indicates no difference between any of the populations, and thus suggests that differences in limb length are proportional and that growth proportions remain similar despite population-specific environmental and genetic variability.

Future studies that will control for variations in some of the genetic and environmental aspects are required in order to shed more light about the growth process of past populations. Moreover, more studies of historic skeletal samples of

known chronological age will provide us with better understanding of absolute inter-population variability not only in bone growth but possibly also in age differences in dental development stages.

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Table 1. Frequencies of individuals per cohort for the four studied sites

Age ¹	Zwentendorf	Zwölfaxing	G. Thunau	Raunds
1	6	4	1	13
2	8	4	5	5
3	10	3	10	7
4	5	3	3	6
5	2	2	4	10
6	3	2	1	2
7	5	2	4	5
8	6	4	3	3
9	1	3		4
10	2			4
11	1	1		1
12	2	1		1
13	1			1
14	2	2		3
15				
16	2			2
17				1
18				1
Total	54	31	31	69

¹ Each number marks the latest age for a given cohort

Table 2. A description of the utilised metric variables

Measurement	Description	Buikstra & Ubelaker, 1994
Clavicle Length, humerus length, ulna length , radius length, femur length, tibia length, fibula length	Maximum length of diaphysis	9a, 14a, 15a, 16a, 17a, 18a, 19a
Clavicle diameter, humerus diameter, ulna diameter , radius diameter, femur diameter, tibia diameter, fibula diameter	Maximum diameter at midshaft	9b, 14c, 15b, 16b, 17c, 18b, 19b
Femur distal width, humerus distal width	Maximum width at the distal end of the diaphysis	17b, 14b
Scapula length	Distance between the medial inferior angles	10a
Scapula width	Distance between the margins of the glenoid fossa and the medial end of the spine	10b
Ilium length	Distance between the anterior superior and posterior superior spines	11a
Ilium width	Distance between the mid-point of the iliac crest and the farthest point on the acetabular extremity	11b

Ischium length	Maximum distance between the acetabular extremity and the most ventral portion of the ischial tuberosity	12a
Pubic length	Greatest distance between the symphyseal end and the acetabular portion	13a

Table 3. Description of the comparative samples

Sample	N	Location	Period	Reference
Libben	152	Ohio	Late Woodland 800-1100 A.D.	Lovejoy et al. 1990
Slavonic Mikulcice	336	Bohemia	7-9 centuries A.D.	Stloukal & Hanakova, 1978
Altenerding	82	South Germany	6th and 7th centuries A.D.	Sundick, 1978
Modern Caucasians	175	Colorado	Modern	Maresh, 1955

Table 4. Results of the analysis of covariance

Variable	N	sites ¹	P Level <0.05	Tukey-Kramer tests ²
Clavicle Length	58	A	—	—
Clavicle Diameter	44	B	—	—
Scapula Length	15	B	—	—
Scapula Width	17	B	—	—
Ilium Length	46	B	0.013224	P*
Ilium Breadth	84	A	0.004542	P*
Ischium Length	32	B	—	—
Pubic Length	21	B	—	—
Humerus Length	91	A	0.023594	P*
Humerus distal width	92	A	0.006702	P*
Humerus Diameter	54	B	0.033361	P*
Ulna Length	60	A	—	—
Ulna Diameter	35	B	0.053809	P*
Radius Length	78	A	—	—
Radius Diameter	40	B	0.039079	—
Femur Length	101	A	0.005198	P*
Femur distal width	93	A	0.000000	P*
Femur Diameter	68	B	0.015255	P*
Tibia Length	59	A	—	—
Tibia Diameter	38	B	0.047531	P*
Fibula Length	38	A	—	—

¹ 'A'-Gars Thunau, Zwentendorf, Zwölfaxing and Raunds, 'B'- Gars Thunau, Zwentendorf, and Zwölfaxing.

² 'P*' indicates significance at P < 0.05 level for at least one pair of sites, see table XX for more detailed results.

Table 5. Adjusted R-squared values for Gompertz curves, by variable.

Variable	Site	R- Squared
Ilium breadth	Zwölfaxing	0.895
	Zwentendorf	0.849
	Gars-Thunau	0.860
	Raunds	0.920
	Combined	0.843
Ilium length	Zwölfaxing	0.892
	Zwentendorf	0.812
	Gars-Thunau	0.890
Humerus length	Combined	0.813
	Zwölfaxing	0.922
	Zwentendorf	0.989
	Gars-Thunau	0.841
	Raunds	0.930
	Combined	0.922
Humerus distal width	Zwölfaxing	0.920
	Zwentendorf	0.891
	Gars-Thunau	0.759
	Raunds	0.776
	Combined	0.772
Humerus midshaft diameter	Zwölfaxing	0.854
	Zwentendorf	0.750
	Gars-Thunau	0.632
	Combined	0.740
Ulna midshaft diameter	Zwölfaxing	0.669
	Zwentendorf	0.926
	Gars-Thunau	0.814
	Combined	0.674
Femur length	Zwölfaxing	0.914
	Zwentendorf	0.983
	Gars-Thunau	0.882
	Raunds	0.940
	Combined	0.918
Femur distal width	Zwölfaxing	0.910
	Zwentendorf	0.952
	Gars-Thunau	0.811
	Raunds	0.894
	Combined	0.827
Femur midshaft diameter	Zwölfaxing	0.851
	Zwentendorf	0.852
	Gars-Thunau	0.545
	Combined	0.781
Tibia midshaft diameter	Zwölfaxing	0.897
	Zwentendorf	0.948
	Gars-Thunau	0.523
	Combined	0.857

Fig. 1.

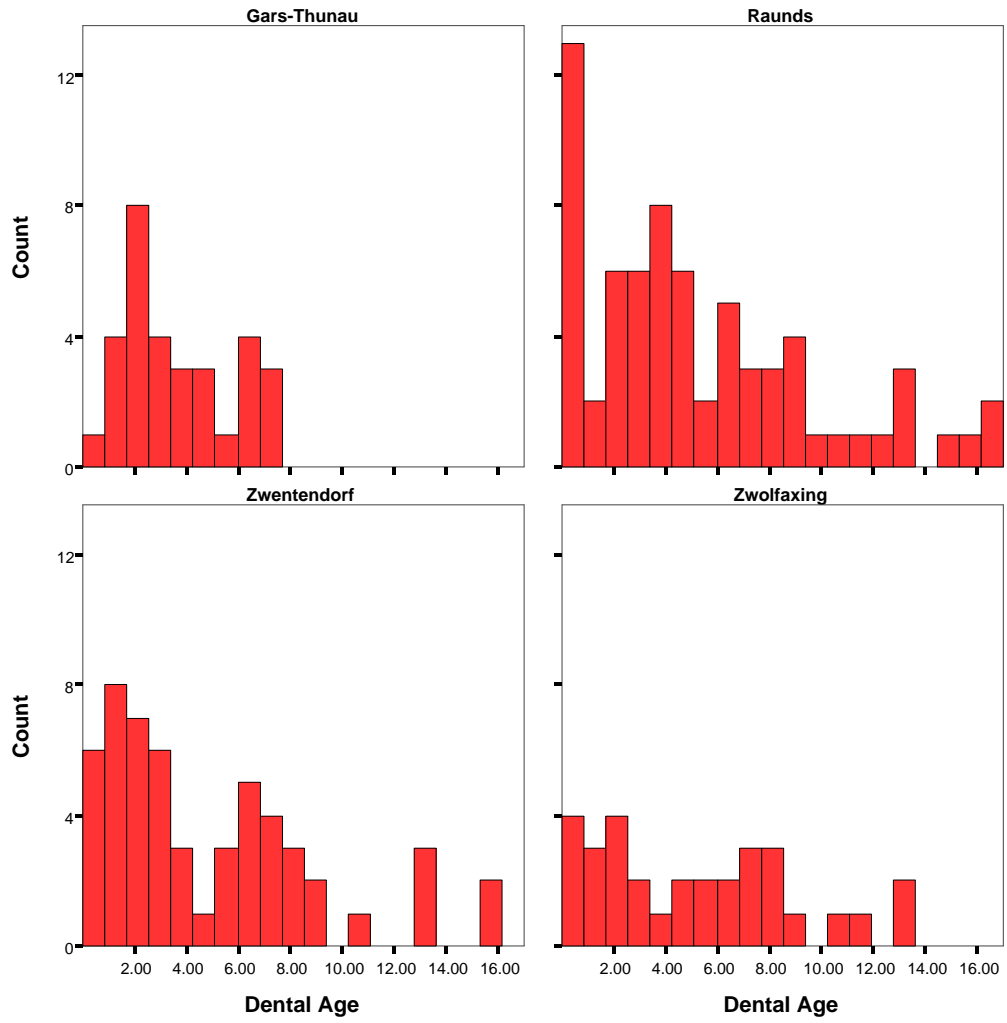
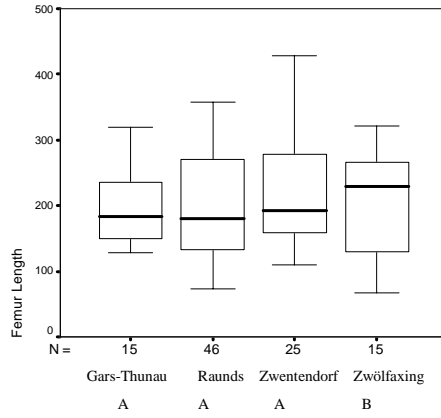
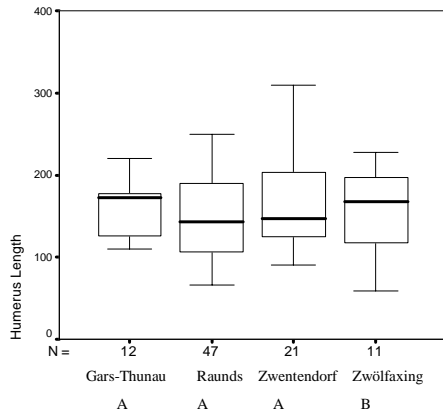
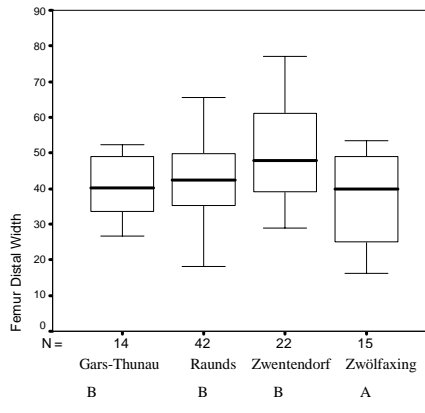
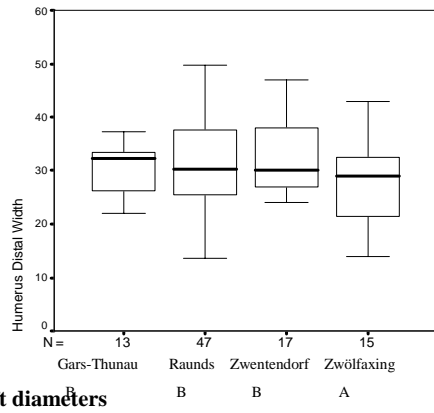


Fig. 2

Diaphysis length



Distal Width diameters



Midshaft diameters

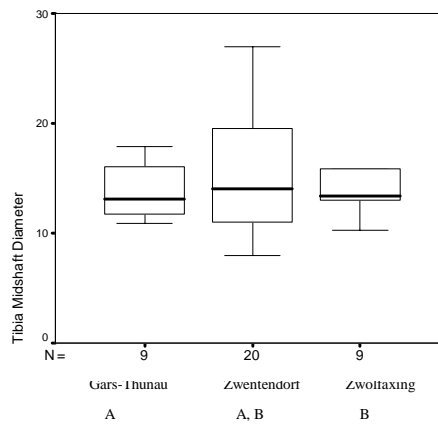
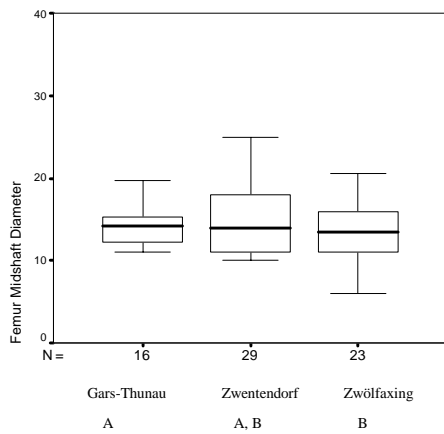
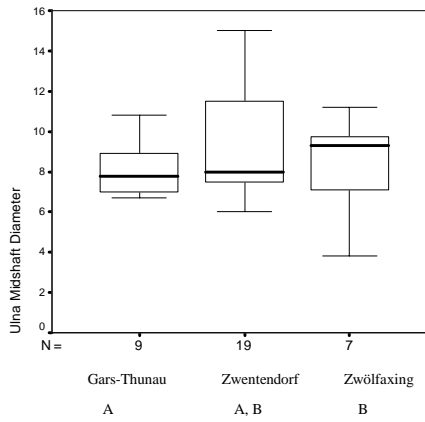
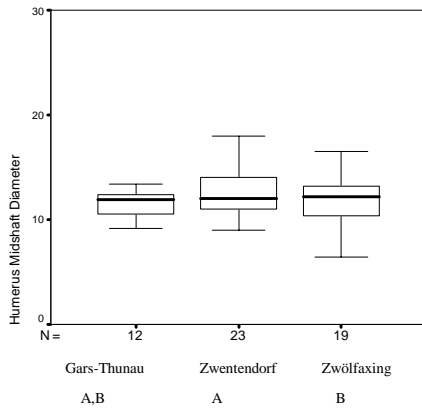


Fig. 3

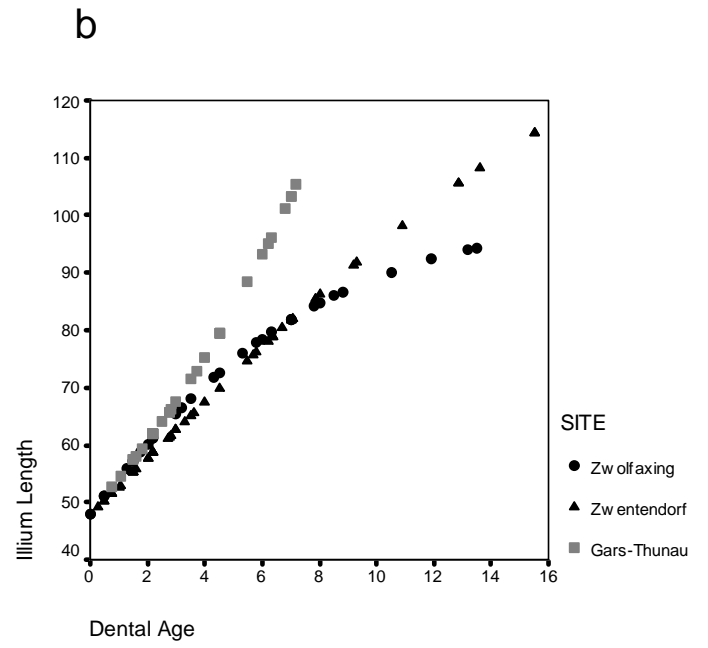
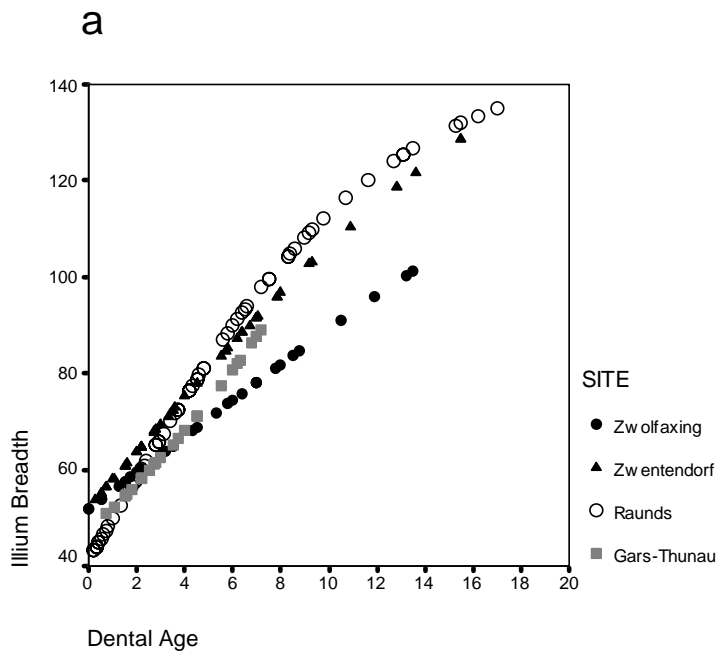


Figure 4

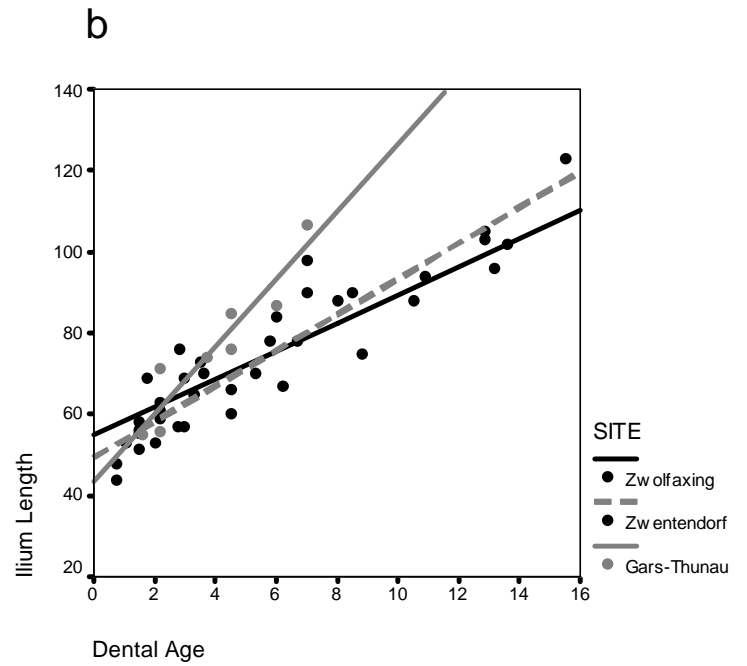
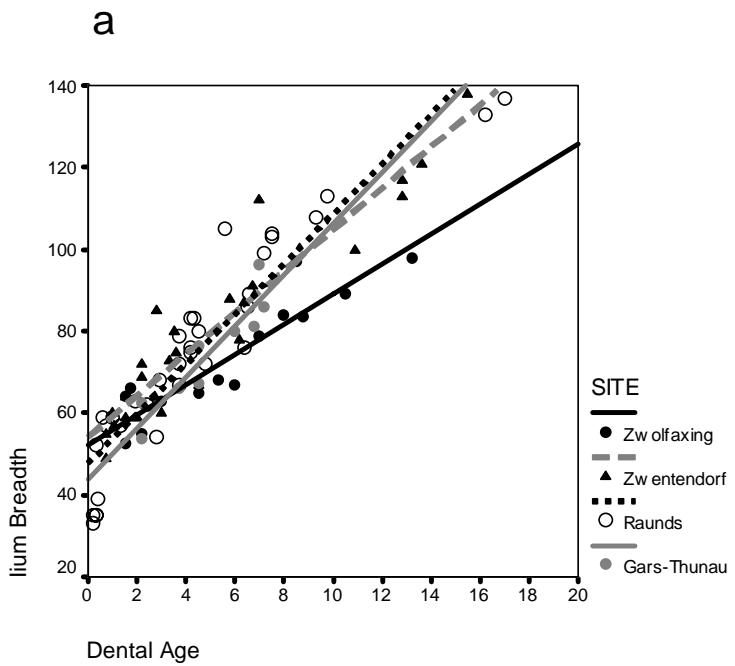


Fig. 5

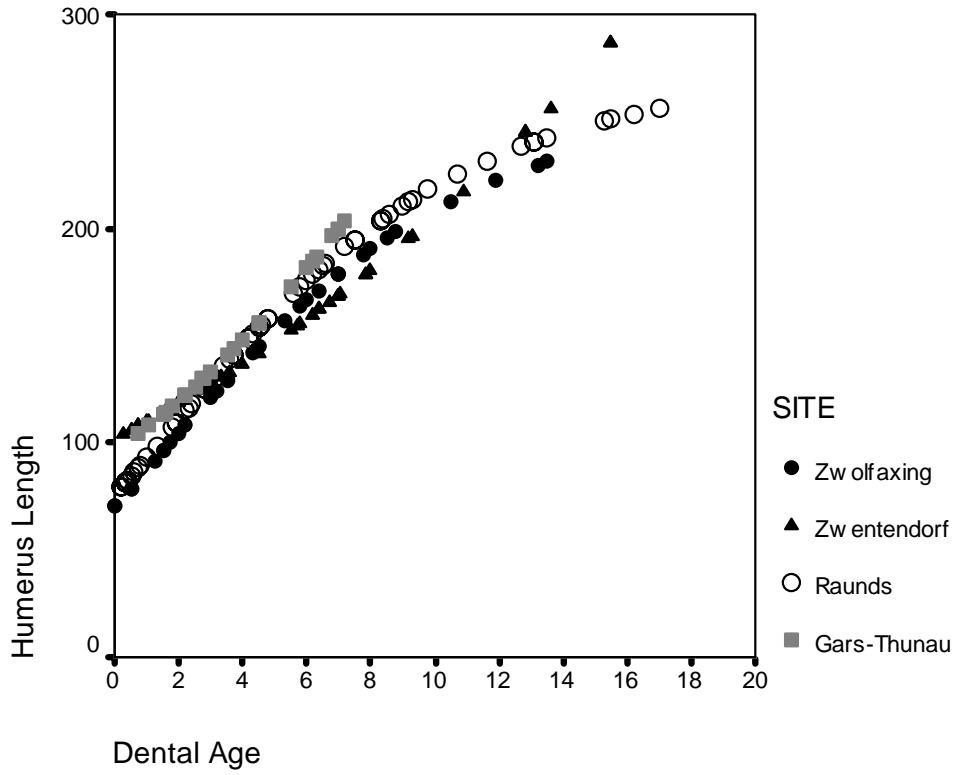


Fig 6

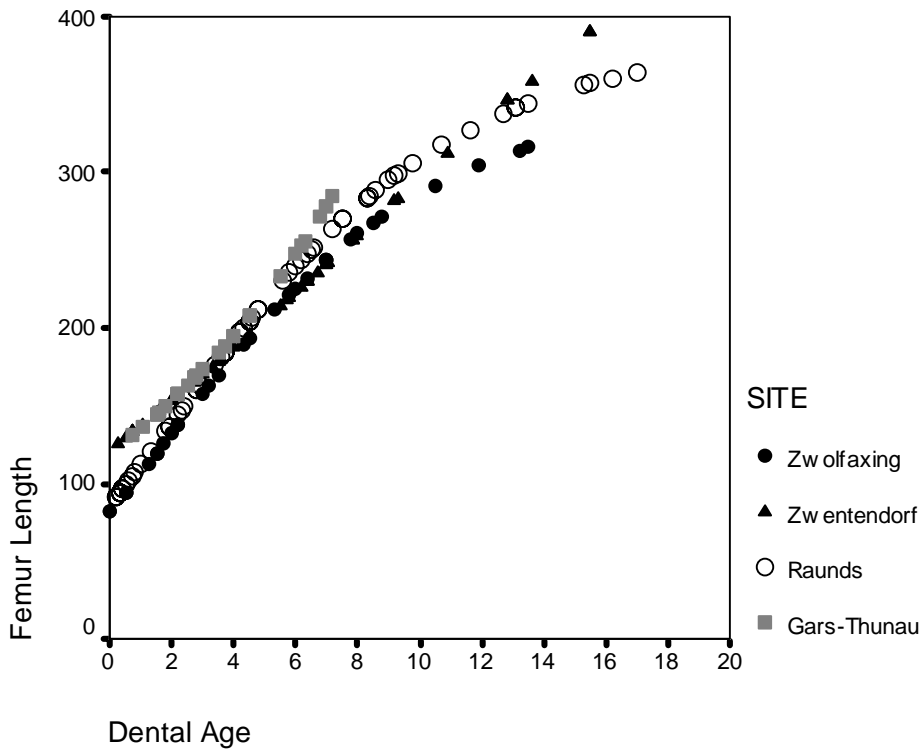


Fig. 7

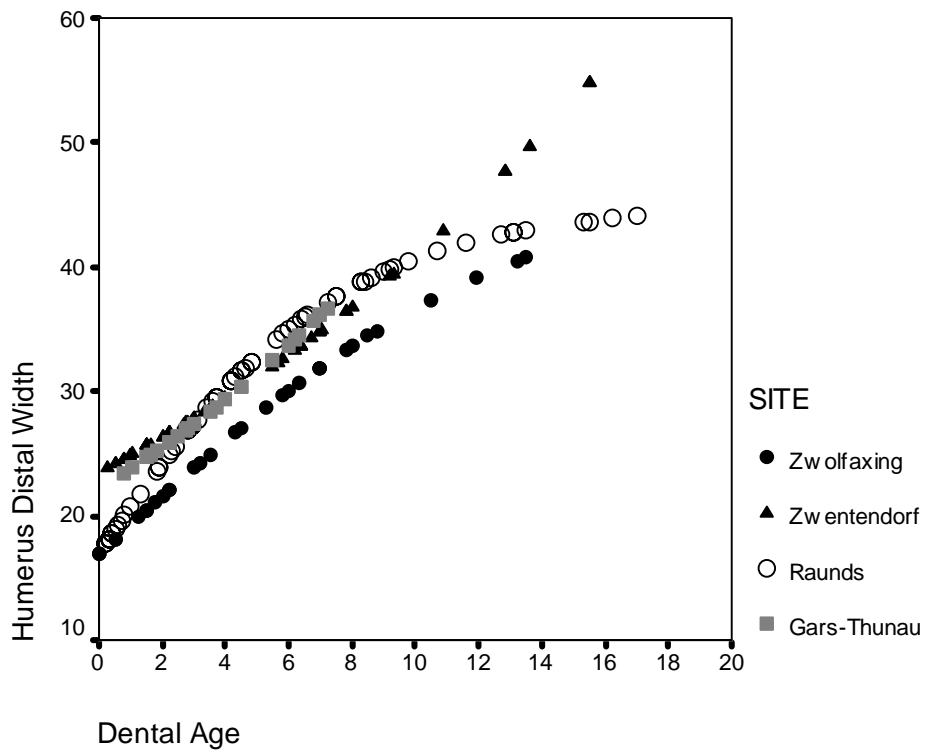


Fig. 8

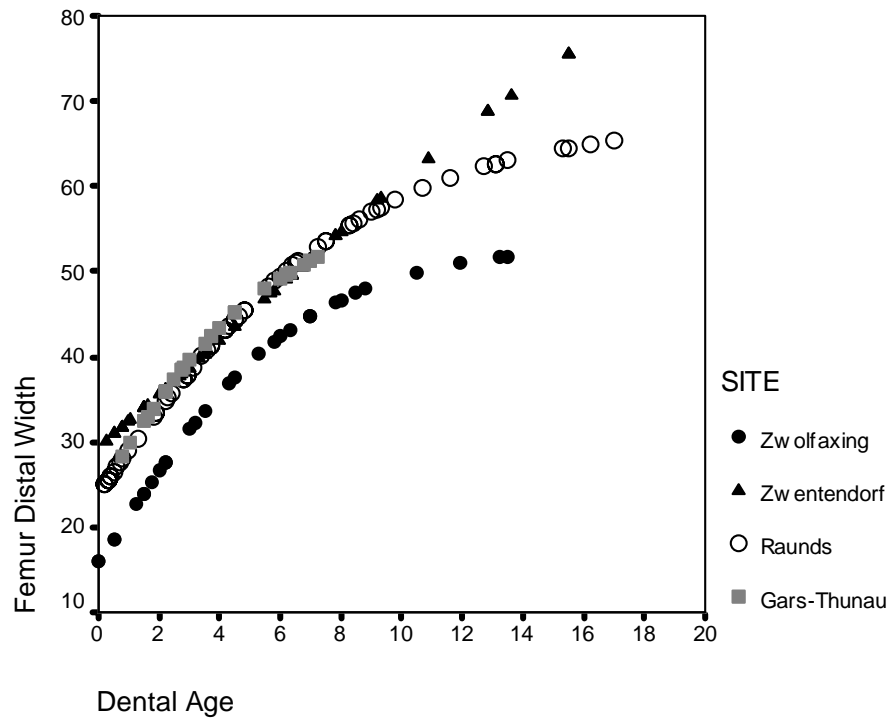


Fig 9

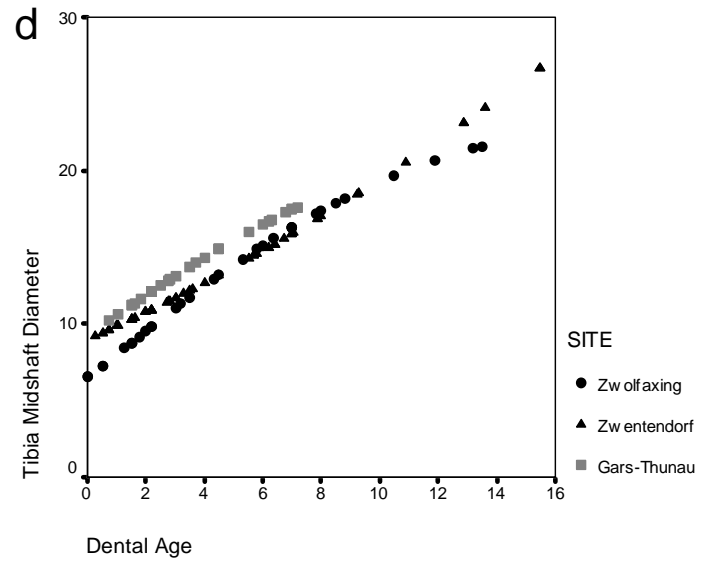
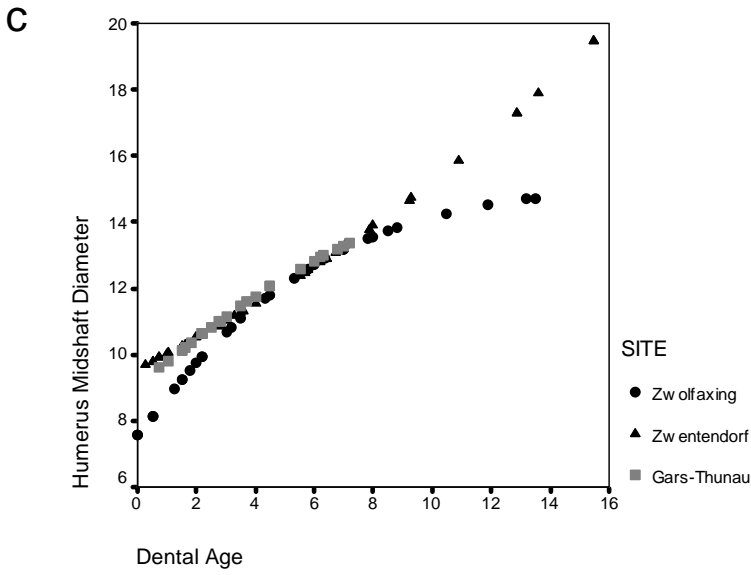
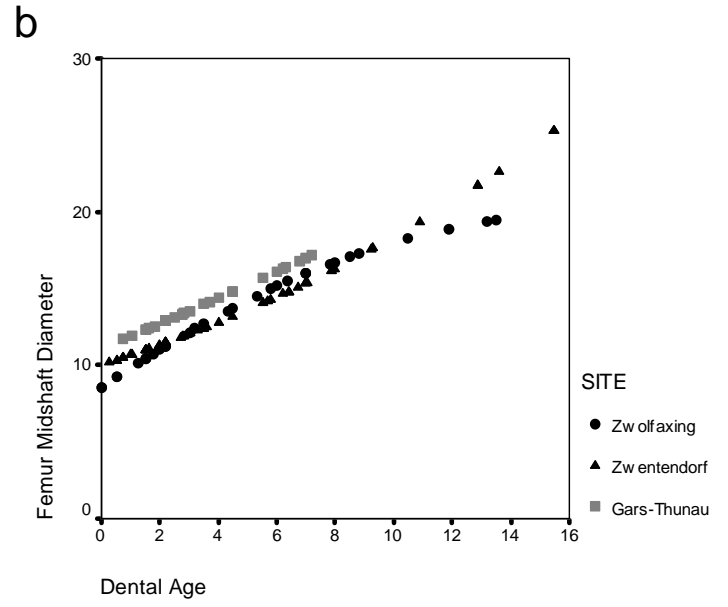
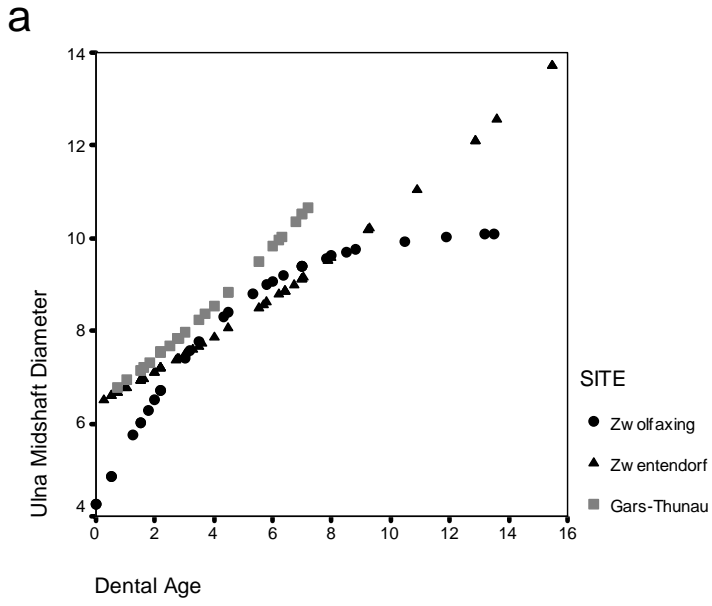


Fig. 10

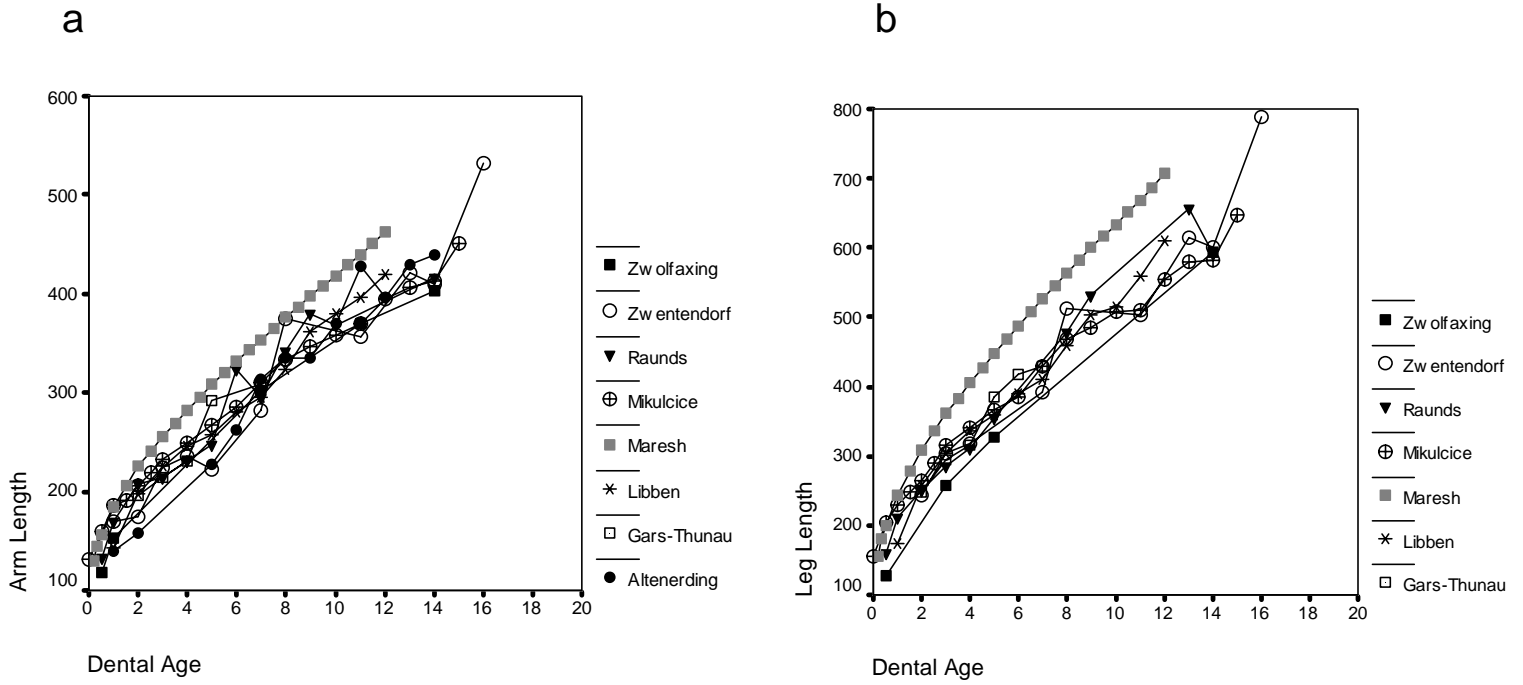


Fig 11.

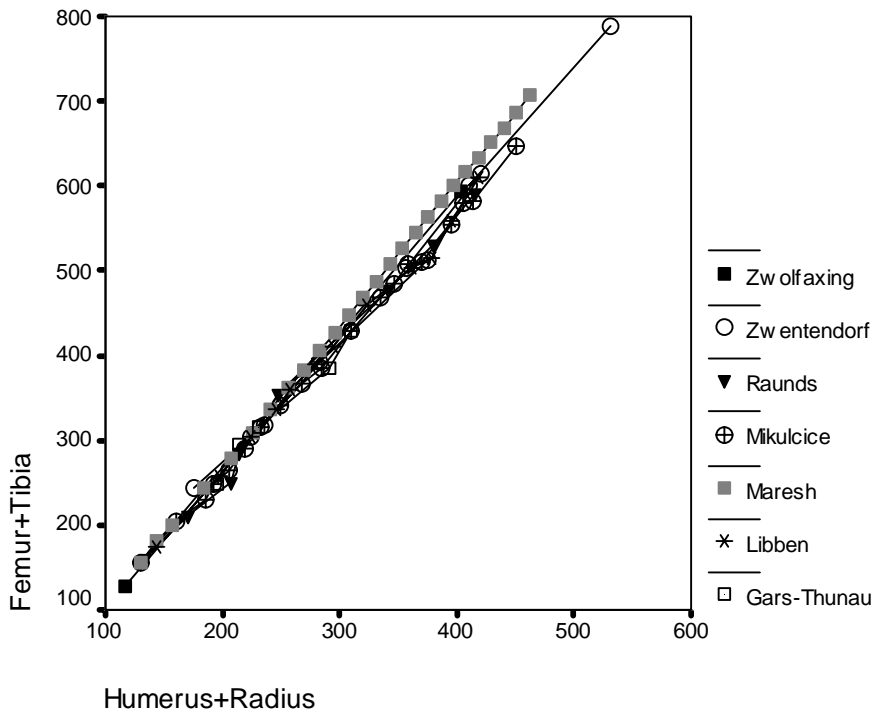


Fig. 12

