1998 Variation in Tooth Formation and Eruption. In: SJ Ulijaszek, FE Johnson and MA Preece (eds.), *Cambridge Encyclopedia of Human Growth*. Cambridge University Press, pp 209-211.

5.10

Variation in time of tooth formation and eruption

Studies of the time of tooth formation and eruption include efforts to develop local standards (**1.16**) and to understand the influence of various genetic and environmental factors on dental developmental timing. Standard development is important for a number of reasons. When birth dates have not been recorded, as is frequently the case in international situations and is nearly always the case in forensic and prehistoric research, dental developmental age is often used as a best proxy for chronological age. Additionally, in some situations dental age is a more appropriate yardstick for determining the time of medical and dental treatment. Last, understanding genetic and environmental influences on dental formation is a fundamental research question. Such studies may provide insights into evolutionary processes and how genes and environment interact during development. The following is a brief summary of recent findings on factors influencing tooth formation and calcification.

Methods and processes

Dental development studies include: 1) the time of emergence of teeth through the alveolar bone and gums, called tooth emergence or eruption studies, and 2) the relative degree of formation of the dental hard tissues. The former type of study is the more common. Such studies include cross-sectional oral examinations of erupted teeth. A few longitudinal studies of dental eruption have also been completed; these involve repeated oral examination of the same individuals. Tooth formation studies are less common because they require either radiographic examination of the developing teeth in their bone crypts or, in a few earlier studies, direct anatomical observation of the developing tooth from dissection of autopsies. A few well-designed longitudinal radiographic studies have been completed since the 1950s. Unfortunately, however, these tend to miss earlier developmental stages.

Although the observations of development are relatively simple, they belie a complex and multifaceted process. Dental formation includes both matrix formation and calcification (**5.6**). Calcification may involve up to four waves. Methods of assessment of degree of formation, most commonly from estimation of opacity of a radiographic image, are based on the relative degrees of calcification that are observable on panoramic or other types of intra-oral radiographs. Factors governing control of the commencement of matrix formation are most likely very different from those controlling the rate of enamel extension and of the timing and completeness of calcification.

The control of eruption is even more multifaceted. Eruption is influenced in part by the degree of dental development. In general, teeth erupt when their roots are about two-thirds to three-quarters developed. However, little is known of what controls the movement of the unerupted tooth through bone (to erupt eventually), and eruption is clearly tied to bone size and the availability of alveolar space to accommodate the erupted tooth. With dental development it appears that the more simple the observation, the more complex the underlying process.

Genetic control of tooth formation

Dental hard-tissue formation, the first stage of development, is considered to be under strong genetic control. It has been suggested that tooth eruption is about one-third as affected by environmental variation as bone ossification. Tooth formation, in comparison, appears to be under even tighter genetic control. Siblings display similarities in timing, whereas endocrinopathologies and nutritional variations do not greatly affect timing. Except for differences between males and females, there is very little evidence to suggest great variation in tooth formation timing among groups or individuals.

Among teeth and dental stages, the least variation occurs in earlier developing teeth of both the deciduous and permanent dentition and earlier developing stages for all teeth. Also, polar teeth, such as first molars, appear to exhibit less variation in developmental timing than non-polar teeth. Polar teeth appear to be more tightly canalized.

Whereas there is little variation in early stages of development, later tooth-formation times do vary significantly among standards. For example, over two years of difference is reported in the mean age of completion of crown formation for canine teeth among standards. These differences could be interpreted as due to genetic and/or environmental factors. However, no clear pattern emerges. The most parsimonious explanation is that the variation is mostly attributable to differences in methodology among studies.

Tooth-formation timing does consistently vary between men and women. Most studies have shown that females tend to be slightly advanced compared to males in both the time of tooth formation stages and eruption.

Dental emergence

The available data suggest that tooth emergence, while being genetically controlled, is moderately affected by environmental and other non-genetic factors. Again, greater variation is seen in later-developing teeth, permanent versus deciduous teeth, and in teeth that are 'non-polar'. Permanent-tooth emergence is generally delayed in European populations, for example, and data suggest associations in emergence time of individuals with shared genetic make-ups.

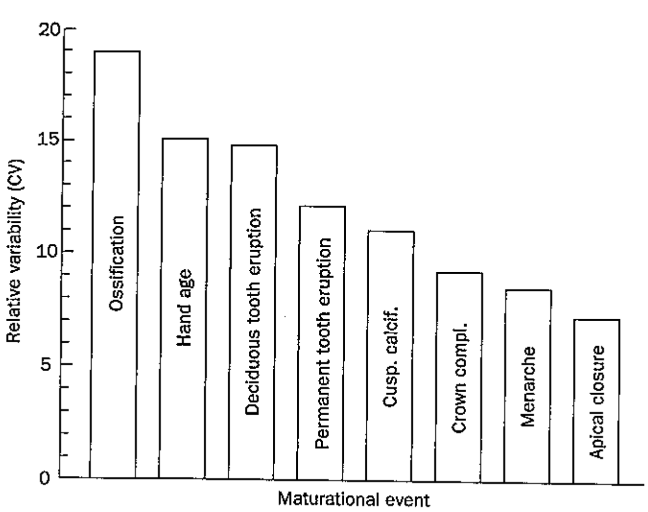


Illustration of the relative amount of variability for various processes of maturation, demonstrating that dental calcification has very low variability compared with other criteria. From Lewis and Garn (1960).

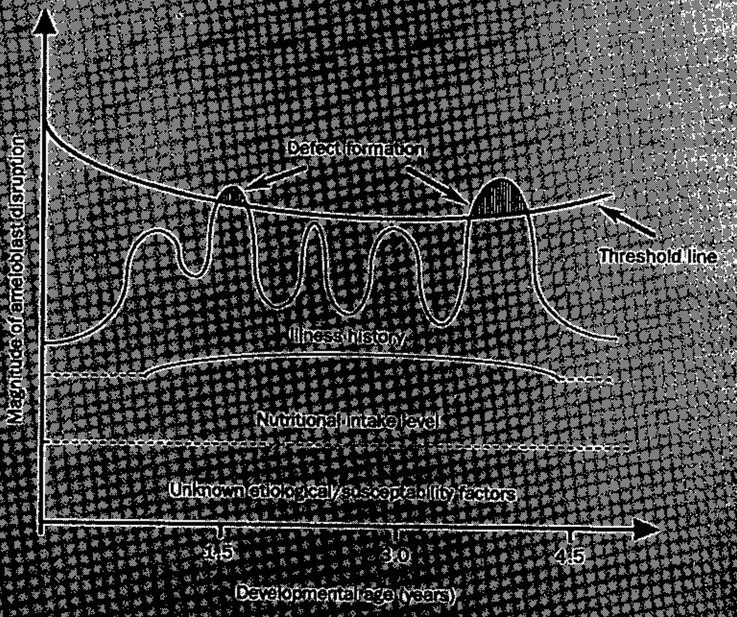
Because many human groups or populations do not record birth dates, tooth emergence has frequently been used as an estimator of chronological age. For this reason, many studies have attempted to better understand how much emergence might be affected by nutritional status and other environmental factors. Most studies have demonstrated that tooth emergence is affected by nutritional status, dietary intake, and economic status. For example, in Guatemala, nutritional supplementation of about 70 kilocalories per day slightly advanced tooth-emergence times, and tooth emergence was earlier in individuals with more adipose tissue. Infants who were small-for-date tend to have delayed dental development. Interestingly, it is not certain how much prenatal as opposed to post-natal factors affect tooth eruption times. Generally, the delays in emergence times with decreased nutritional status are in the order of less than a month or two for the deciduous dentition and only slightly greater for the permanent dentition. Correlations between past or current nutritional status and dental maturation tend

DEVELOPMENTAL DEFECTS OF DENTAL ENAMEL

Tooth-formation timing is under strong genetic control (3.3). Perhaps because of this, the developing tooth is limited in means by which it can respond to environmental perturbations and suboptimal conditions. One frequent method of response is to continue the pace of development while forming thinner or less fully calcified tissues. Thinner or altogether missing enamel is referred to as an enamel hypoplastic defect, and less calcified enamel as a hypocalcification. The most frequent types of hypoplastic defects are somewhat linear (called linear enamel hypoplasia) and transverse in orientation, reflecting the relative development of the tooth crown at the time of disruption. These hypoplastic enamel defects occur because of a disruption during enamel matrix formation (a disruption during the secretory phase of amelogenesis). Decreased calcification, hypocalcification defects, can occur at almost any stage from initial matrix formation to full maturation. Both enamel pathologies are classes of developmental defects of dental enamel.

Enamel hypoplastic defects may be caused by local trauma, hereditary conditions, and systemic stress. Defects due to local trauma affect only one or a few adjacent teeth. Hereditary defects are very severe and tend to involve complete crowns. Defects due to systemic physiological disruption (stress) tend to affect only the teeth developing at the time of stress, and their location on tooth crowns reflects the relative development of the teeth at the time of stress. Over 100 causes of enamel hypoplastic defects have been isolated. For this reason, it is probably more fruitful to consider these defects to be non-specific indicators of stress during development.

The location of enamel defects on tooth crowns reflects the relative completeness of crown formation at the time of the defect-forming event. Thus, the location of enamel defects on different teeth provides a record of the relative development of each tooth at the time of 'stress'. Interestingly, it is common that not all teeth developing at the time of stress stand an equal chance of developing a



Threshold model for the formation of a linear enamel hypoplasia (LEH). Enamel apposition and LEH formation occurs when ameloblasts temporarily cease secretion of enamel matrix. This growth stoppage has been associated with a wide variety of stressors. It is suggested that there is a threshold at which ameloblasts will cease functioning. This threshold may be reached by a combination of unknown etiological factors, chronic or acute undernutrition, and acute morbidity.

to be very low, in the order of r = 0.1–0.2. Thus, when chronological ages are not available, tooth emergence may be used as a somewhat conservative proxy.

Questions concerning the pattern of dental development, that is the order and relative timing of dental events and stages among different teeth, have emerged in the last decade as an important research topic. The pattern of development is a phenotypic characteristic that may be used to distinguish among related taxa. One of the difficulties in such studies, however, is the lack of agreement among standards for the same species. Very little information is available at this time on dental developmental patterns for non-human primates, and great variation exists for humans among standards, due to the aforementioned methodological variations. However, with the possible development of new, low risk methods for detection of hard-tissue development, newer standards, especially for early stages of development, might help to resolve these and other questions.

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See also 'Dental maturation' (1.9) and 'Embryonic development of teeth' (4.4)

hypoplastic defect. Anterior teeth and teeth that are under the strongest genetic control of developmental timing are generally the most susceptible to ameloblastic disruption.

In archaeological and paleontological studies, teeth are often found, and for this reason, enamel hypoplasias have frequently been used as an indicator of relative degrees of stress during tooth crown formation. Studies of populations undergoing the transition from hunting and gathering to agriculture have frequently shown that this transition results in an increase in the rate of enamel hypoplasias. Other studies have shown that enamel hypoplasia rates are very high in poor-house populations and among slaves, thus confirming that these were highly stressed groups. Similarly, studies of contemporary populations have shown that enamel hypoplasias are inversely related to nutritional and socio-economic status.

A number of studies have shown lower rates of enamel hypoplasias in the deciduous dentition compared to the permanent dentition. Apparently this is because of protection to the growing individuals during prenatal and early post-natal times (when the crowns of deciduous teeth are developing). Permanent tooth enamel hypoplasias tend to develop around the second and third years of age. This has been associated with the change to a post-weaning diet and increased infectious disease at this time.

Because enamel hypoplastic defects are easily observed and can provide information on the time of developmental disruption, they may be useful adjunct measures of nutritional status. For example, enamel hypoplasias on deciduous teeth may provide a unique window into the prenatal period, and enamel hypoplasias in permanent teeth may provide a window into early periods of development in adolescents and adults.

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Chronologic enamel hypoplasias (stress-hypoplasias) on right maxillary central incisor and canine (arrows). Both of these shallow hypoplastic bands occurred around 3.5 year developmental age, based on the degree of crown completion (enamel apposition begins at the occlusal tips, which are slightly worn). The common estimated age at formation suggests that these defects were the result of the same systemic physiological perturbation (stress).

1998 Skeletal Growth and Agricultural Intensification. In: SJ Ulijaszek, FE Johnson and MA Preece (eds.), *Cambridge Encyclopedia of Human Growth*. Cambridge University Press, pp. 357-359.

Skeletal growth and time of agricultural intensification

One of the more intensely debated questions in anthropology and archaeology concerns the nutritional and health status of hunters and gatherers versus later agriculturalists. The effect of agricultural development and intensification on human biological well-being occasions more than an isolated academic debate. It strikes at the core of main historical themes, has great popular appeal, and may even have significance for understanding determinants of quality of life for humans in industrial societies. At its core, this question is about progress. Have we, with evolutionary changes from foraging to farming and post-industrial economies, done better or worse?

Over the last 30 years many paleoepidemiological studies have attempted to shed light on this question quantitatively. These studies involve comparisons of the skeletal remains (bones and teeth) of early agriculturalists with those of prior hunter-gatherer groups, and comparisons of variables such as estimated mean ages at death and signs of infectious and other disease processes. Additionally, evidence has been gathered on subadult growth patterns, and lengths and widths of adult long bones. The assumption underlying these studies is that a change in nutritional status would be reflected by a change in growth and adult size.

Methodological issues in anthropometric studies of skeletal populations' growth

Subadults

Studies of growth in prehistoric populations involve the measurement of long bones and, less frequently, of widths and sizes of other bones and dimensions (vertebral canal, skull-base height). These are typically plotted against dental age. From here, the data are managed in much the same way that anthropometric data from contemporary cross-sectional studies are managed. However, the following qualifications and special characteristics of growth studies from skeletal remains should be kept in mind:

- Because archaeological samples are cross sectional 'death assemblage', results can be used to infer periods of peak stress only when conditions are relatively stable over time.
- Cemetery-based studies represent not the healthy or even the 'average' child, but just those who died. This property has great potential for introducing a directional bias in comparison to the growth and size characteristics of the live population. For example, if children who suffered from chronic malnutrition (and were shorter) more often died in childhood, then the death assemblage would be shorter.
- Prehistoric series are frequently limited by small sample-size, particularly after 5 years of age. This is because the probability of death is typically low in late childhood and early adolescence. Thus, most estimations of growth parameters for ages after 5 are based on small numbers.
- There is a technical problem of measuring long bones with and without epiphyses (the unattached growing ends of long bones), which are frequently destroyed or otherwise lost to archaeological recovery. This irregularity has the potential of adding considerable measurement error.
- Dental age is usually used as a best proxy for chronological age. This limits power to find true changes because dental age is also likely to be somewhat affected by environment. (Unfortunately, the differential effects of environment on growth in long bones versus dental age are not precisely known.)

Anterior view of the tibia at various ages showing development of proximal and distal epiphyses.

- Poor ability to distinguish sex of subadult skeletons disallows comparisons between boys and girls.
- There is limited ability to 'standardize' growth of prehistoric long bones to that of contemporary groups. The only sample from which longitudinal growth of long bones is well established is from the Denver Longitudinal Growth Study.

Adults

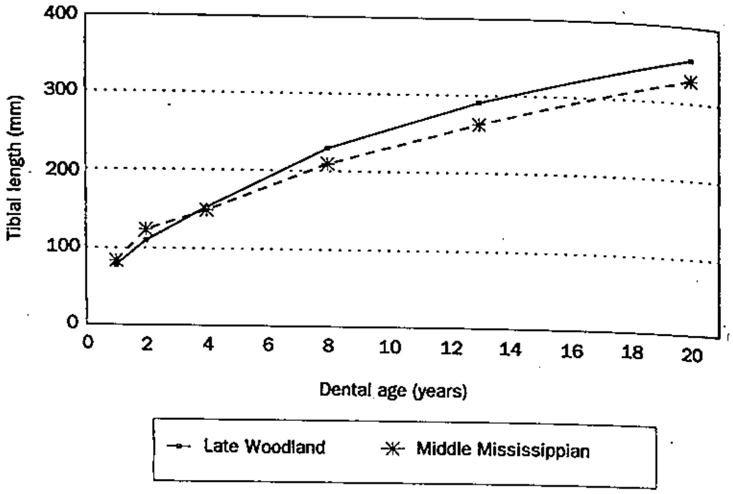
Studies of adults are not constrained to as great a degree by problems of assignment of age and sex, nor are small sample-sizes as frequently a limiting factor. As in studies of adult anthropometry of living populations, the drawbacks to studies in prehistory revolve around the loss of sensitivity for clarifying underlying processes affecting growth and ultimate size at adulthood. The loss of the most stressed segment of the population (subadults) due to death before adulthood, coupled with the ability to catch up in growth, renders adult morphology less sensitive to environmental variation when compared to growth and development of subadults.

Adult anthropometric studies of skeletal remains are most often of lengths of major long bones. A number of equations have been generated to estimate stature based on lengths of one or more long bones. These sometimes include lengths of other bones, such as the talus and calcaneus. Finally, 'robusticity' estimates are often derived as measures of, for example, length versus width of a long bone; and ratios of sexual dimorphism in height have been used as measures of environmental stress.

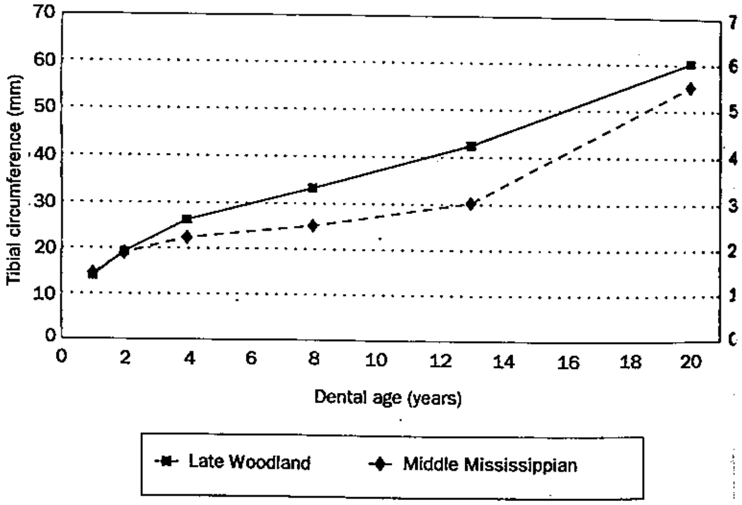
Agriculture and skeletal anthropometry

A handful of paleoepidemiological studies include sufficient sample sizes to compare growth of subadults before and after agricultural development and intensification. Results from North America, where the majority of such studies have been undertaken, show that children of early agricultural groups tend to have shorter and less robust long bones. In a few instances, evidence is available to suggest a reduction in growth velocities around the ages of 2 to 5 years. This decrease in velocity has often been interpreted as being due to the adoption of a weaning diet that is reduced in variety and is low in the availability of key nutrients. Interestingly, shorter children tend to have more evidence of disease on their bones and teeth. Thus, the decrease in growth velocity is consistent with evidence on bones of infectious disease (periosteal inflammations) and porotic hyperostosis (a thickening of bone associated with iron deficiency). For example, in North America the agricultural staple of maize (corn) is low in essential amino acids, and high phytate levels reduce the bioavailability of key nutritional elements such as iron and zinc.

Comparisons of adult stature also suggest a trend of declining nutrition and health with agricultural intensification.



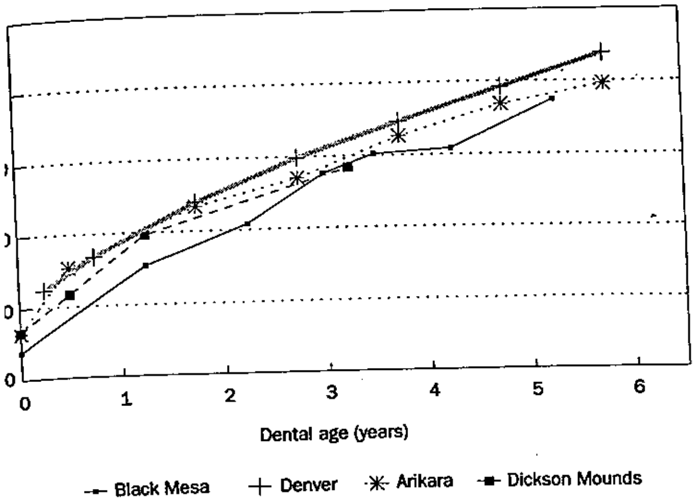
Comparison of the growth in length of the tibia for individuals at Dickson Mounds, Illinois during the late Woodland (circa 950–1100 AD) period of hunting and gathering and Middle Mississippian (circa 1150–1300 AD) period of maize horticulture. Mean growth appears to slow for those who lived during the Middle Mississippian period around the age of 2 years.



Comparison of the growth in circumference of the tibia for individuals at Dickson Mounds, Illinois during the Late Woodland (circa 950–1100 AD) period of hunting and gathering and Middle Mississippian (circa 1150–1300 AD) period of maize horticulture. Mean growth slows dramatically for those who lived during the Middle Mississippian period around the age of 2 years. There is some evidence for 'catch up' growth in the second decade.

ranean show a profound decrease in estimated mean adult stature in males from 177 centimetres during the Paleolithic to 172 centimetres during the Mesolithic and 169 centimetres during the Neolithic periods. The decline in mean female stature is equally profound. Declines in stature are also observed in other parts of Europe and India as well as in the Americas. Conversely, a number of studies have not found a similar pattern.

In summary, there are a number of limitations to the study of growth and size in past populations. None the less, when these studies are applied to the

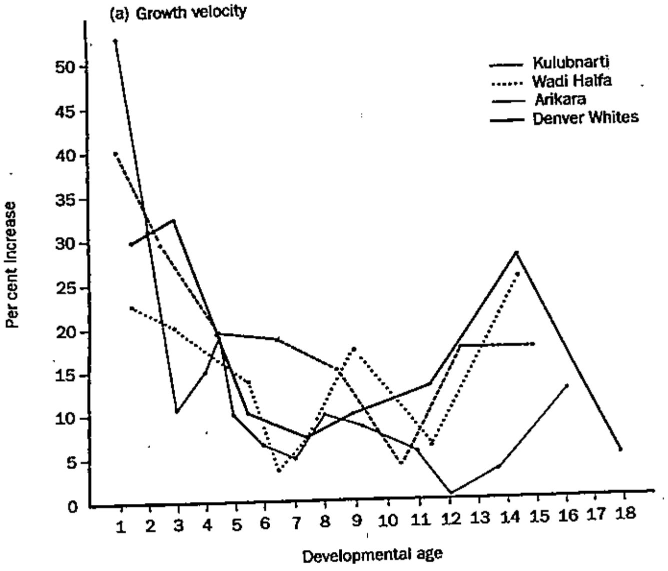


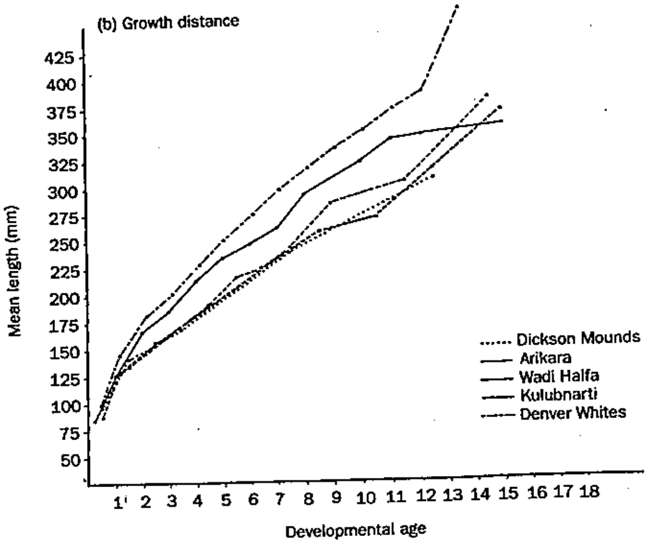
arison of the growth in length of the femur of various archaeological series com- d to radiographic data from the Denver Growth Study (Maresh, 1955).

some intriguing results have been obtained. Although far from invariable, a number of studies point to a decline in growth velocity and adult long-bone lengths with agricultural intensification. Whereas this generalization is of great interest, understanding of the cause of this pattern is far from certain. Changes in dietary quality and quantity are almost certainly involved as proximate causes. The next question concerns whether these dietary changes are due to economic change alone (intensification of agriculture) or are the result of more complex changes between economy, political developments, and local ecologies. Whatever the answer, these data call into question unilinear notions of progress.

Alan H. Goodman

See also 'Dental maturation' (1.9), 'Growth as an indicator of social inequalities' (1.12), 'Creation of growth references' (1.16), 'Morphology' (5.5), 'Skeletal development' (5.6), 'The human growth plate' (5.7), 'Variation in time of tooth formation and eruption' (5.10), 'Adulthood and developmental maturity' (5.17), 'Growth in chronic diseases' (7.8), 'Infant-feeding and growth' (9.1), 'Nutrition' (9.2), 'Infection' (9.3), 'The secular trend' (11.3) and 'Social and economic class' (11.4)


(a) Growth velocity


(b) Growth distance

Comparison of cross-sectional femoral growth curves of modern Europeans with those derived from archaeologicallly recovered skeletons from Dickson Mounds, Illinois, Arikara Indians from North Dakota, and the Mediterranean (Wadi Halfa, Kulubnarti), (a) velocity, (b) distance.