

# 1 Why development and why teeth?

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In comparison with other mammals, humans grow up slowly. This is integral to the way we learn the complexities of our language, social organisation and material culture. It is part of what defines us as human. Slow development is also one of the distinctive features of primates as an order of mammals and there is a relationship with size. The larger species within any mammalian order tend to develop more slowly than the smaller species. Humans are among the largest of primates but, even taking that into account, we are still by far the slowest primates to reach full maturity. In any development graph, we are an outlier, in a different category to the rest. One crucial question for archaeologists and palaeoanthropologists is therefore to determine when our slow rate of development evolved. If the earliest stone tools date to 2.6 million years ago, were they made and used by hominins (the subfamily of living and fossil primates to which we belong) for which the pace of development was as slow as ours, or was the pace relatively faster, as in other living primates? This is surely central to understanding the meaning of these tools, the social and behavioural context within which they fitted and the cognitive abilities of their makers.

The evidence to answer this question can only come from the fossil remains of hominins. Most fossils are teeth and jaws, not only for hominins, but for all mammals throughout the geological record. Teeth have evolved for daily wear and tear in the testing conditions of the mouth, so it is not surprising that they survive well in the ground. This means there are more dental fossils which are preserved in a state in which they can be identified and studied than, say, the bones of the limbs. Not only that but, as explained in the following chapters, teeth are the *only* fossils in which growth *rate* can be studied. This is because they have a daily clock built into the layered structure of their tissues against which the growth rate can be measured. That is not to say bones are of no use. Bones of young primates have indeed been found as fossils, frozen at the stage of development reached at death, but on their own they do not have an inbuilt clock to estimate the age at which this stage was reached. For this reason, the debate about the evolution of the human development sequence centres on teeth.

Another special feature of teeth is that, once formed, dental tissues remain little changed throughout life unless they are modified by the effects of tooth wear and dental disease. Bone, by contrast, is constantly being replaced at a slow pace, so all traces of its initial development gradually disappear. This is known as tissue

turnover. The lack of turnover in dental tissues preserves a layered structure that records a detailed chronology of development which is preserved throughout adult life. This makes it possible to determine the ages at which different stages of tooth development were achieved, to reconstruct the sequence in which the teeth were formed and to measure the rate of crown and root growth. If the individual was still growing at the time of death, it is possible to estimate its age on that day. Also preserved in the layered sequence is a record of disruptions to growth caused by fevers, nutritional deficiencies or other factors related to health. On the one hand, the presence or absence of these disruptions might indicate whether or not the individual being studied is a good subject for demonstrating normal development. On the other hand, it leads to other questions. The establishment of a slow pace of development in hominins, similar to that of living humans, might imply cognitive, social and behavioural changes. Could these have led to an increased level of care for the young or greater security of food supply? What was the effect on growing children of increased technological complexity, the adoption of farming or industrialisation? Many studies have attempted to address these questions by examining the record of disruptions to dental development preserved in fossil and archaeological teeth.

The preferential preservation of teeth and jaws is one reason for their importance as fossils. Another is their detailed variation in shape and form. Their morphology has always been a major element in the definition of living mammal species. Traditionally, zoologists collect a skin and a skull with its teeth; the great natural history museums of the world have enormous collections of this kind, including the holotypes or defining examples of each species, against which all other specimens must be compared before they can be identified. Amongst the primates, the order of mammals to which living humans belong, there is considerable variation in the dentition. The prosimians, or lemurs, lorises, bushbabies and the like, show a variety of distinctive dental features related to their diet and behaviour (Swindler, 2002). Overall in the primates, there is a correlation between tooth and body size and the prosimians in general are small on both counts. New World monkeys such as the howler or spider monkey are distinguished from Old World monkeys such as macaques or baboons by the possession of three permanent premolar teeth in each quadrant of the dentition. Old World monkeys, great apes and humans all have just two permanent premolars in each quadrant. The most obvious difference between human and chimpanzee, bonobo, gorilla and orangutan dentitions is in the much larger canine teeth of the non-human primates, which vary considerably between males and females. This changes the whole shape of the dental arcade and the way in which the teeth interlock when the jaw is closed. Canine reduction and the greatly reduced level of so-called sexual dimorphism are additional important questions in human evolution. Further back in the dentition, the pattern of cusps on the molars does not differ greatly between, say, chimpanzees and humans, but the dental enamel which coats the tooth crown surface is substantially thicker in humans. The earliest hominins in the fossil record had much larger post-canine (that is, premolars and molars) teeth than any living hominins, with very thick enamel indeed. Important

trends in the evolution of humans include upright bipedal locomotion, manual dexterity and large brains, but no less important is the evolution of smaller teeth and jaws. Within our own species, *Homo sapiens*, this is the most marked change seen in either the skeleton or the dentition over the past 26 000 years.

Care is needed when using words like hominin, hominine, hominid, hominoid, pongid, pongine or ape. In the past, humans were separated as the family Hominidae, containing just one living genus *Homo* and a number of extinct genera. Chimpanzees, bonobos, gorillas and orangutans were placed in the separate family Pongidae. More recently, genetic evidence has shown how closely related chimpanzees and bonobos are to humans, so it has become common to include them along with gorillas, orangutans, humans and related fossils in the family Hominidae (Appendix A, Tables 1 and 2). To describe a living or fossil species as a ‘hominid’ means it is a member of the family Hominidae. Usage of other names starting in ‘hom-’ depends on the classification system favoured. Hominine means the subfamily Homininae, which most would take to include all the living hominids except orangutans, which are separated off with similar fossil species into the subfamily Ponginae (or family Pongidae). Hominin means a member of the tribe Hominini, a subdivision of the Homininae. Some include living chimpanzees, bonobos and gorillas along with humans and related fossils. Others confine it to the latter, separating chimpanzees, bonobos and gorillas as the tribe Panini. Hominoid means a member of the superfamily Hominoidea, which includes both the hominids and the hylobatids, or gibbons and siamangs. ‘Ape’ is an old English word, originally implying monkeys as well as chimpanzees, gorillas, orangutans and perhaps gibbons too, but never humans. Until recently, most anthropologists confined it to chimpanzees, bonobos, gorillas and orangutans, but now some include humans as well (Robson and Wood, 2008). Not everyone agrees, so the word is avoided in this book which seeks only to be clear and does not deal with issues of taxonomy. Common names are used rather than the binomials, or official names for species, except for fossil taxa which have no common name.

This book therefore aims to address two questions of current interest in palaeo-anthropology and archaeology using the evidence provided by microscope study of the dental tissues; particularly enamel and dentine. The first is the point in the fossil record at which the slow pace of modern human development appeared. The second is whether or not the major biological and cultural transitions shown in the fossil and archaeological record affected the health and well-being of the growing young. The book starts with an examination of the special place of humans in the world of mammalian development. Chapter 2 explores the particular features of the human body size growth curve and contrasts them with other living primates. It is not so much the overall shape of the human curve that is unique, but more the timing and combination of features. Chapter 3 continues with the evidence for a unique pattern of development in the human dentition, based on direct observation or radiographs of living children and other young primates. It is supported by data presented in Appendix A. By far the most straightforward aspect of dental development to observe in the living is the emergence of the teeth through the gums into

the mouth. This, however, is the end of a long chain of developmental stages hidden inside the jaws, for which a variety of evidence has to be drawn together. For these reasons, they are not as well known as might be expected. The core of the book is Chapter 4, introducing the microstructure of enamel and dentine together with the tiny incremental features which are the basis for everything that follows. Techniques for microscopy are outlined in Appendix B. Chapter 5 goes on to describe the ways in which developmental sequences have been built from counts of the incremental structures in dental tissues. There is a tension here between the quality of information provided and the necessity to cut microscope sections from valuable specimens. The few sections which have been made from fossils are an important resource, but fortunately some non-destructive options for microscopy have been made available over the past decade. The resulting sequences make it possible to compare the rate of development in extinct hominins with living species. This comparison fits into a wider debate on primate life history and cognitive development which is outlined in Chapter 6. Disruptions to growth are first described in Chapter 4 along with normal structure, but Chapter 7 returns to the issue of defects and discusses the clinical and experimental evidence for the factors involved in their formation. Finally, Chapter 8 provides a critical review of the theoretical framework within which the defects are interpreted and presents examples from palaeoanthropology and archaeology.

## 2 Development schedule, body size and brain size

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In comparison with other primates, the sequence of human development lasts a long time and has an unusual pattern of peaks in growth rate. But is it unique? Long development might be a function of size and humans are among the largest of primates. Similarly, development patterns vary between primates and it could be that humans form part of a continuum in the sequence of growth stages. Then there is the large human brain. Do humans follow a unique growth trajectory to achieve it?

### How development is studied

Development is studied by measuring growing individuals at different ages. The study may be *cross-sectional*, with just one examination per individual in a group which includes a variety of ages, or *longitudinal*, with several examinations at different ages for each individual. The measurements taken vary. Some relate to general body size. In humans this is usually *stature*, but in young children the equivalent is *supine length*, where the child lies on its back between parallel head and foot boards. There are two alternatives for measuring body size in a foetus or young baby. *Crown-rump length*, from the top of the head to the most prominent part of the buttocks, is approximately equivalent to sitting or trunk height in older children and adults. *Crown-heel length* is measured with the baby lying on its back and one leg stretched out, and is the nearest equivalent to stature. The upright bipedal stance of the human body makes it difficult to find directly comparable stature measurements for non-human primates. For them, crown-rump length (trunk length) is commonly measured, along with lengths of segments of the limbs. Simpler than any of these, however, is to measure *body mass* (or weight in everyday language). This represents all the different systems and tissues of the body and shows different patterns of growth from stature, which reflects largely the size of the skeleton.

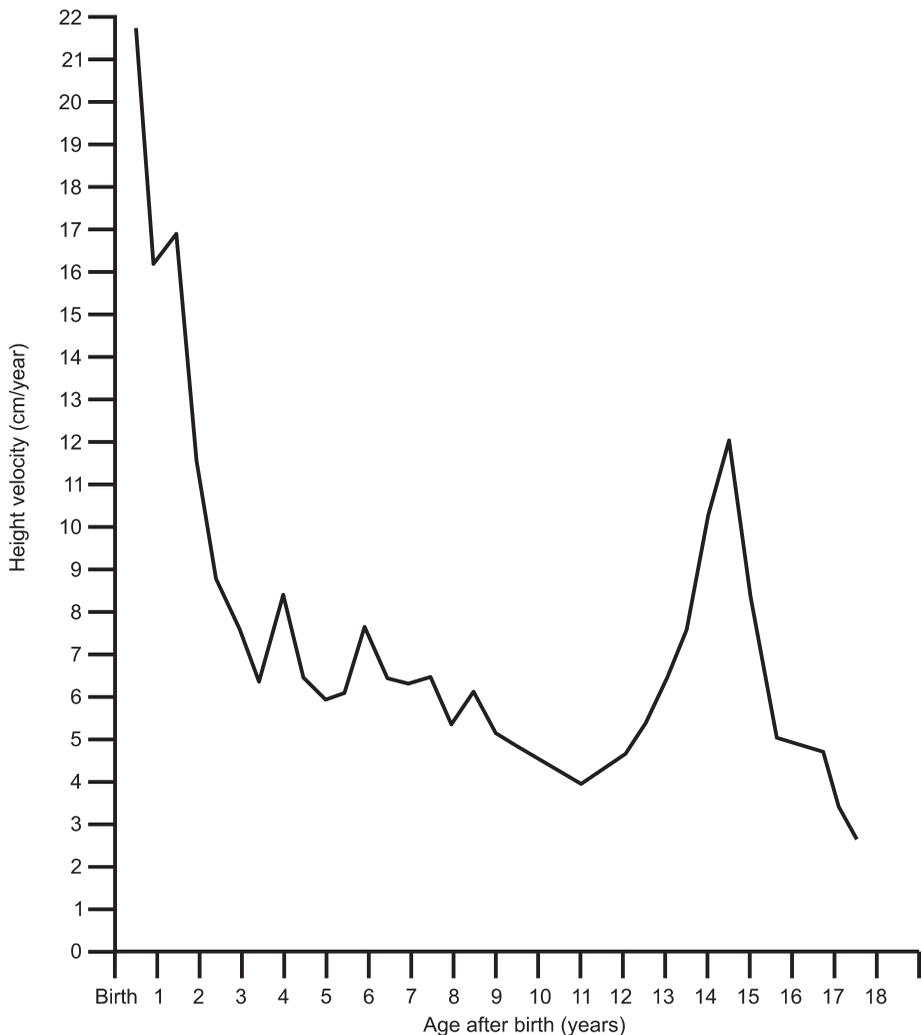
Whilst growth studies can be distinguished as cross-sectional or longitudinal, there are grey areas. For a fully longitudinal study, it is necessary to follow every member of a group of children throughout the range of ages included, but constant effort over many years is needed to maintain this. Some children leave, miss examinations, or join part way through. This situation is known as a *mixed-longitudinal study* and requires statistical manipulation to make sense of the results. A pure

longitudinal study thus tends to include a small group of children but, because it follows individual children over time, it is particularly useful for showing how stature or mass change with increasing age. By contrast, cross-sectional studies are much larger and are more useful for understanding variation in stature or mass for a given age.

### Human growth in body size

Growth rate, or velocity, is the gain in stature, mass or other measurement per year (or per month or week, depending on the animal). A *velocity curve* is the graph showing the change in growth rate from year to year. Each individual child has its own curve and the most famous is that based on the regular measurements made by Philibert Guéneau de Montbeillard between 1759 and 1777 of the height of his son François from birth to 18 years of age. This was done at the request of his friend Georges-Louis Leclerc, Comte de Buffon, who published the measurements in his enormous many volumed *Histoire Naturelle* (de Buffon, 1777, pp. 376–83). de Buffon's table of measurements is still regarded as one of the most detailed individual records (Tanner, 1981) and has been the basis of several published velocity curves (Figure 2.1). To those expecting a smooth curve it looks surprisingly irregular. The jagged line shows considerable variation from one age of measurement to the next, but children grow like that. Short bursts are interspersed by slower periods and de Buffon noted that the boy grew faster in summer than in winter. There is, however, a strong general trend shown in the curve. Growth *in utero* is many times faster than at any time after birth and this is apparent from the near vertical fall in the line during the first three years. François then grew at an irregular rate, fluctuating between 6 and 8 cm per year, until around 7 years of age, after which growth slowed still further, reaching a minimum rate of about 4 cm per year at 11 years of age. After this, there was a sustained rise in rate, slow at first, but increasing to a sharp peak of 12.5 cm per year at 14.3 years. This is the growth spurt accompanying puberty and de Montbeillard's son was not far from the average age in boys today. His growth rate then fell as rapidly as he approached adult size, ending up a rather tall 1.89 m or 6.2 feet. François Guéneau de Montbeillard became a cavalry officer, fathered three children and died at 88 years of age.

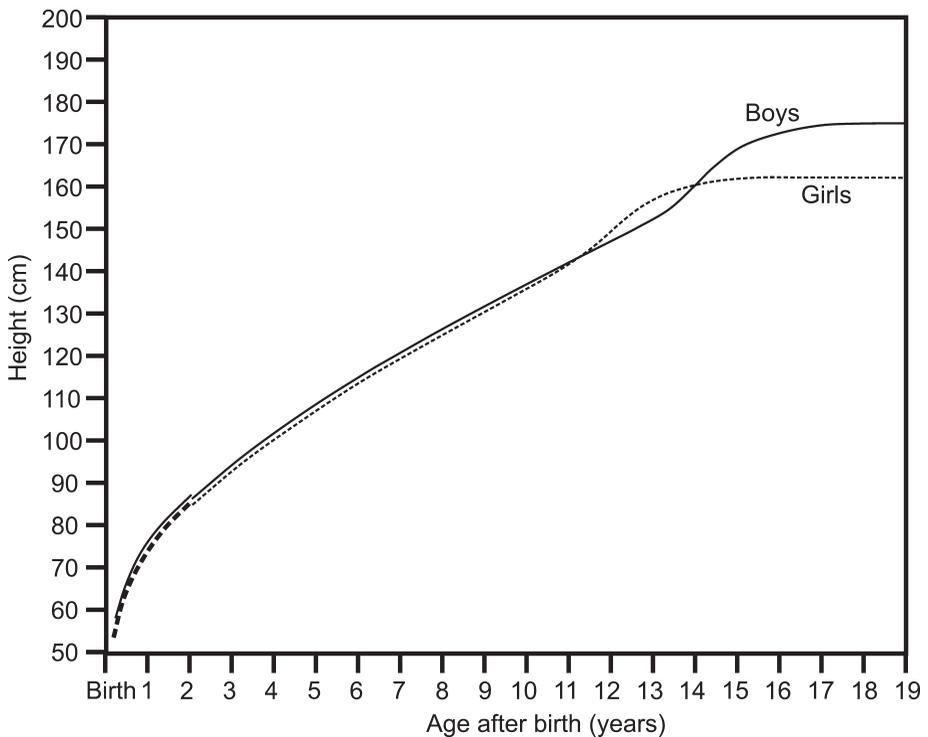
Growth curves are presented (Figures 2.2 to 2.5) for height (supine length from birth to 2 years and stature thereafter) and body mass, both in terms of height or mass attained for age, and growth velocity. They are intended to represent an idealised norm and all the minor variations have been smoothed out. The height velocity curve just after birth is falling rapidly from the overall height velocity peak, which is prenatal (see below). The gradient becomes less steep between 3 and 6 years of age, and the velocity continues to fall to a minimum around 10 years in girls and 12 years in boys. This is followed by the marked peak of the pubertal (adolescent) growth spurt and a final fall in rate as adult size is approached. In some children there is a slight velocity increase at around 6 years of age, the mid-growth spurt, but



**Figure 2.1** Body height growth velocity curve for de Montbeillard's son, plotted from measurements taken between 1759 and 1777. Re-plotted from Tanner (1981), figure 5.3, p. 105.

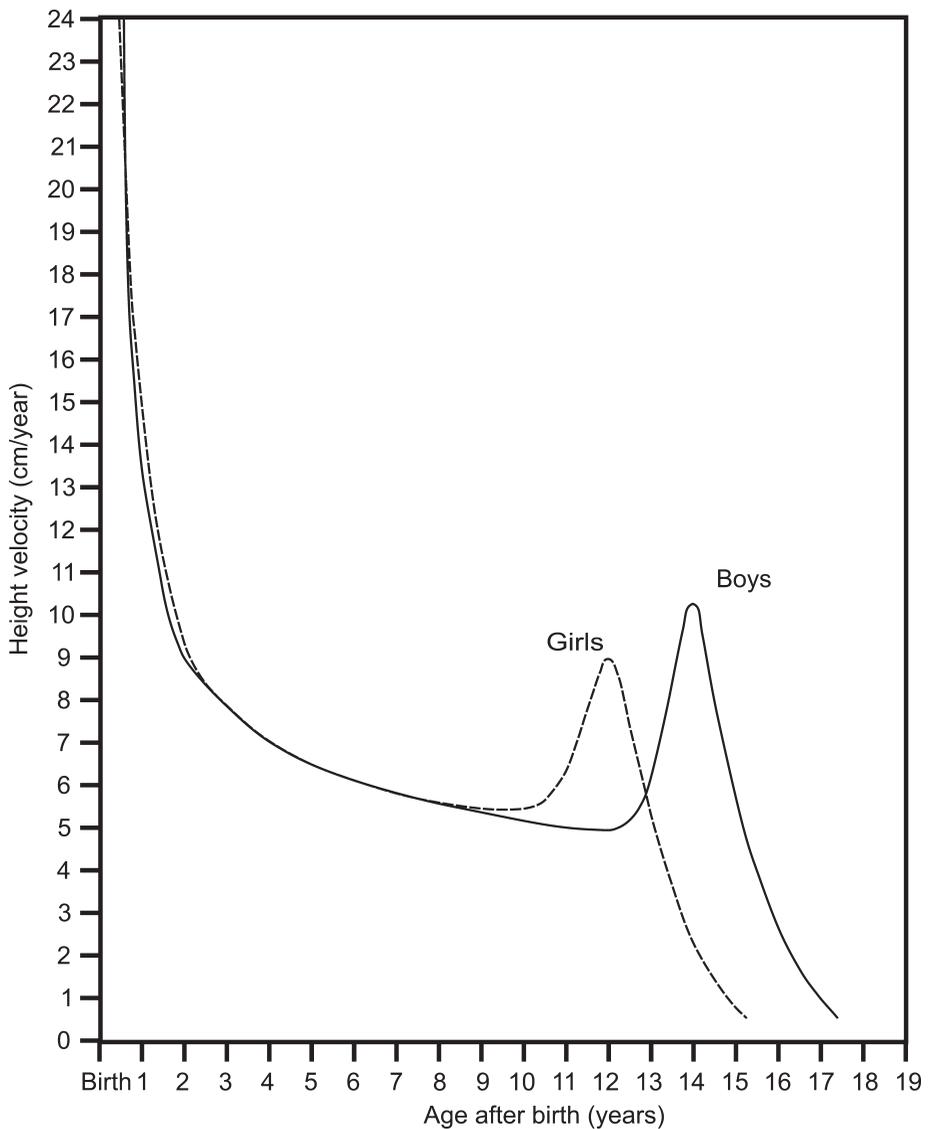
this varies and some studies show it more prominently than others. It is not shown in the norms presented here. The velocity curve for body mass in humans is broadly similar to the curve for stature, particularly in the timing of the adolescent growth spurt. Just after birth, however, body mass velocity rises to a sharp peak (see below) and then falls rapidly to a childhood minimum between 2 and 5 years of age, after which it climbs again gradually.

The timing and height of the main peaks and troughs (particularly the adolescent growth spurt; Figure 2.6) vary between different children, who also show individual patterns of departures from the main trend. This is partly due to a consistent difference between boys and girls, partly to other inherited variations and partly



**Figure 2.2** Body height curve from birth to 19 years of age measured in London boys and girls. Re-plotted from Tanner *et al.* (1966), figure 10, p. 467.

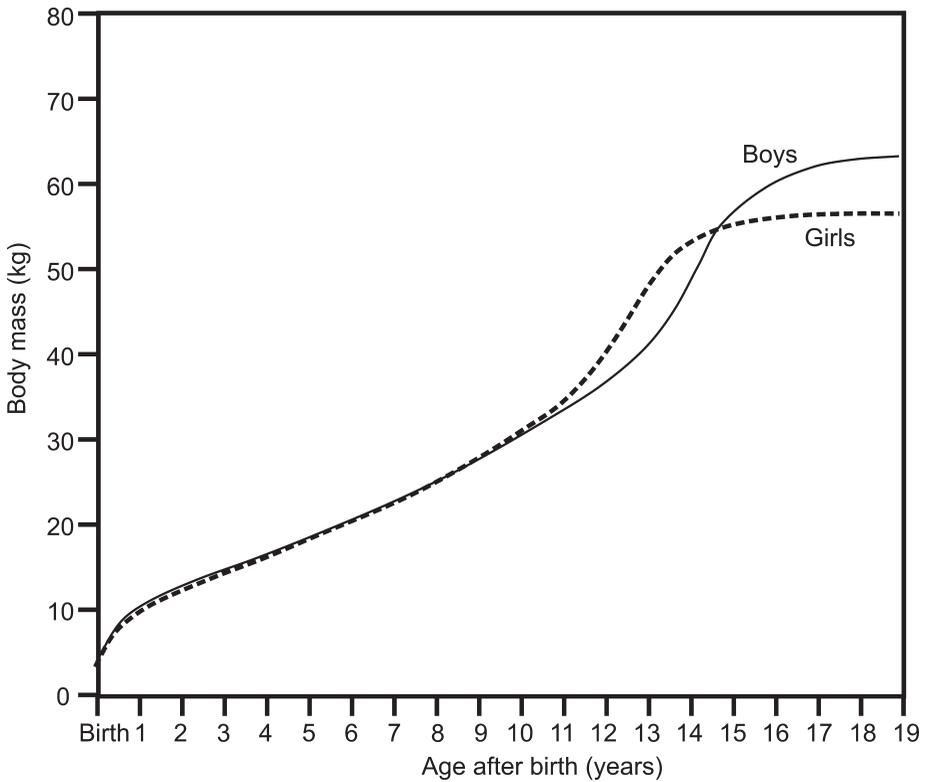
due to variations in the diet, health and social conditions within which the children are growing up. It does, however, need to be taken into account when trying to draw a curve representing the typical pattern of variation in growth velocity for a given group. This is one of the difficulties with cross-sectional studies which, for each year of age, produce a range of (say) statures attained by different children. From this range an average, or some other best estimate value, can be used to represent the stature usually attained by that age. The increase between this value and the mean or estimate for the next year gives the figure for growth rate in centimetres per year. If rates calculated in this way are used to plot a growth velocity curve, the variation included in the rate estimates at each age tends to smooth out the curve so it does not look at all like the curve produced by measurements for any one child. For example, it makes the adolescent growth spurt peak too wide, too low and not pointed enough. In order to draw a curve that represents a typical child (Figures 2.2 to 2.5), it is necessary to use the shapes of curves derived from following individual children in a longitudinal study, combined with values for the start and end of the curve derived from cross-sectional studies (Tanner, 1989). This is a particular difficulty with studies of growth in non-human primates, where most studies are of necessity cross sectional.



**Figure 2.3** Body height velocity curve from birth to 19 years of age measured in London boys and girls. Re-plotted from Tanner *et al.* (1966), figure 8, p. 466.

### Prenatal development

Modern studies of growth *in utero* are mainly based on measurements of the foetus in ultrasound scans of the mother, but older studies employed direct measurements on children born prematurely. The point reached in gestation is expressed as a *gestational age* in weeks (see Definition Box 1). For 5–15 weeks gestational age, the usual measurement is crown-rump length (as discussed earlier), but for 15–22 weeks it is the circumference of the head or femur length. Modern tables to convert these



**Figure 2.4** Body mass curves from birth to 19 years of age for London boys and girls. Re-plotted from Tanner *et al.* (1966), figure 11, p. 467.

measurements to gestational age are available, but are confined to those periods of development (Loughna *et al.*, 2009). Crown-rump length tables covering the full period of prenatal development are found in older textbooks (Arey, 1974; Patten, 1976) and were the basis for gestational age estimation in most studies of deciduous dental development (page 54). It needs to be borne in mind that there is an element of circularity in argument here because one developmental measure (body size) is being used to calibrate another.

**Definition Box 1.** Gestational age, chronological age, embryo, foetus, neonate and infant

Obstetricians count *gestational age* from the first day of the last menstrual period of the mother. This typically pre-dates ovulation by 2 weeks. Fertilisation of the ovum takes place within 24 hours of ovulation and implantation of the embryo in the uterus wall occurs around 1 week later. Variability of these events contributes 4 to 6 days to the overall variation in gestational age at birth (Engle,