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Received 10 June 1998
Revision received
4 November 1998
and accepted
28 November 1998

Keywords: cranial base,
flexion, extension, vocal
tract, pharynx, *Homo*, *Pan*.

The ontogeny of cranial base angulation in humans and chimpanzees and its implications for reconstructing pharyngeal dimensions

This paper examines differences in the processes by which the cranial base flexes in humans and extends in chimpanzees. In addition, we test the extent to which one can use comparisons of cranial base angles in humans and non-human primates to predict vocal tract dimensions. Four internal cranial base angles and one external cranial base angle were measured in a longitudinal sample of *Homo sapiens* and a cross-sectional sample of *Pan troglodytes*. These data show that the processes of cranial base angulation differ substantially in these species. While the human cranial base flexes postnatally in a rapid growth trajectory that is complete by two years, the cranial base in *P. troglodytes* extends postnatally in a more prolonged skeletal growth trajectory. These comparisons also demonstrate that the rate of cranial base angulation is comparable for different measures, but that angles which incorporate different anterior cranial base measurements correlate poorly. We also examined ontogenetic relationships between internal and external cranial base angles and vocal tract growth in humans to test the hypothesis that cranial base angulation influences pharyngeal dimensions and can, therefore, be used to estimate vocal tract proportions in fossil hominids. Our results indicate that internal and external cranial base angles are independent of the horizontal and vertical dimensions of the vocal tract. Instead, a combination of mandibular and palatal landmarks can be used to predict dimensions of the vocal tract in *H. sapiens*. The developmental contrasts in cranial base angulation between humans and non-human primates may have important implications for testing hypotheses about the relationship between cranial base flexion and other craniofacial dimensions in hominid evolution.

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Journal of Human Evolution (1999) **36**, 487–517

Article No. jhev.1998.0287

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Cranial base angulation, in which the ethmoid, sphenoid, and basioccipital bones flex or extend¹ relative to each other in the sagittal plane, is a key process of craniofacial development. Cranial base angulation, which occurs both prenatally and post-

natally, influences the spatial relationships between the three endocranial fossae. A recent study by Ross & Ravosa (1993) supports the hypothesis that, among anthropoids, measures of cranial base angulation correlate with variations in brain volume relative to cranial base length (Moss, 1958; Biegert, 1963; Enlow, 1968; Gould, 1977; Dean, 1988; Spoor, 1997). However, within adult hominids, including *Homo sapiens*, measures of cranial base angulation are highly variable, may not differ significantly

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¹Flexion and extension here are defined in relation to the inferior (ventral) aspect of the intersection of any two basicranial planes, so that they involve a decrease or increase in this angle, respectively.

between species, and may be independent of variations in endocranial volume (Ross & Henneberg, 1995; see, however, Spoor, 1997). Cranial base angulation has also been proposed as an influence on variations in facial prognathism and orientation (e.g., Ashton, 1957; Biegert, 1963; Sirianni & Swindler, 1979; Enlow, 1990) and as a postural adaptation for balancing the head in bipeds (e.g., Weidenreich, 1924, 1941, 1945; Dabelow, 1929; Dmoch, 1975, 1976). In addition, variation in cranial base angulation may affect the angle of the external cranial base, which is proposed to be a determinant of vocal tract dimensions (Lieberman *et al.*, 1972; Laitman & Crelin, 1976; Laitman *et al.*, 1978, 1979; Laitman & Heimbuch, 1982; Lieberman *et al.*, 1992).

Despite widespread interest in and research on cranial base angulation, some major questions remain about the ontogenetic processes by which angulation occurs and which, therefore, generate the wide range of inter- and intraspecific variation in measures of angulation seen in hominids and other primate taxa. This study uses ontogenetic data on cranial base angulation in *H. sapiens* and *Pan troglodytes* to address three interrelated problems. First, the angle of the cranial base has been measured in numerous ways, but it is unclear how alternative methods of characterizing the spatial relationships between the endocranial fossae differ ontogenetically and, hence, affect the ability to test hypotheses about the functional and developmental significance of cranial base angulation. A second problem is the extent to which different processes of cranial base growth affect comparisons of cranial base angulation in humans and other species. Postnatally, the cranial base flexes in humans and extends in most non-human primates, possibly at different locations (Hofer, 1960; Hofer & Spatz, 1963; Heintz, 1966; Sirianni & Swindler, 1979; Cousin *et al.*, 1981). Although different cranial base

angles are directly comparable between humans and other primates, their contrasting ontogenetic processes may lead to possibly misleading comparisons, depending on the hypothesis being tested. Such issues of measurement comparison and homology are particularly important for evaluating a third problem: to what extent does cranial base angulation contribute to growth of the vertical and horizontal dimensions of the pharynx? To study this question, we examined the spatial and ontogenetic relationships between internal and external cranial base angulation, other selected craniofacial dimensions, and the supero-inferior and antero-posterior dimensions of the pharynx in order to examine whether variations in the processes that cause angulation influence the growth of these structures.

Background

Before presenting information on the ontogeny of cranial base angulation in humans and chimpanzees, and any relationships between the cranial base angle and pharyngeal growth, it is useful to review previous research on the mechanisms by which the cranial base flexes or extends, and the potential effects of these movements on measurements of cranial base angulation. Flexion or extension of the cranial base can occur at three possible locations (illustrated in Figure 1): the spheno-ethmoid synchondrosis (SES), the mid-sphenoidal synchondrosis (MSS), and the spheno-occipital synchondrosis (SOS). Flexion and extension can occur through two major processes. First, a pattern of drift in which depository and resorptive growth fields differ on either side of a synchondrosis can cause rotations around an axis through the synchondrosis (Michejda 1971, 1972a, 1972b; Michejda & Lamey, 1971; Giles *et al.*, 1981; see summary in Enlow, 1990: pp. 102–105). Second, the interstitial growth that causes cranial base elongation within the synchondroses

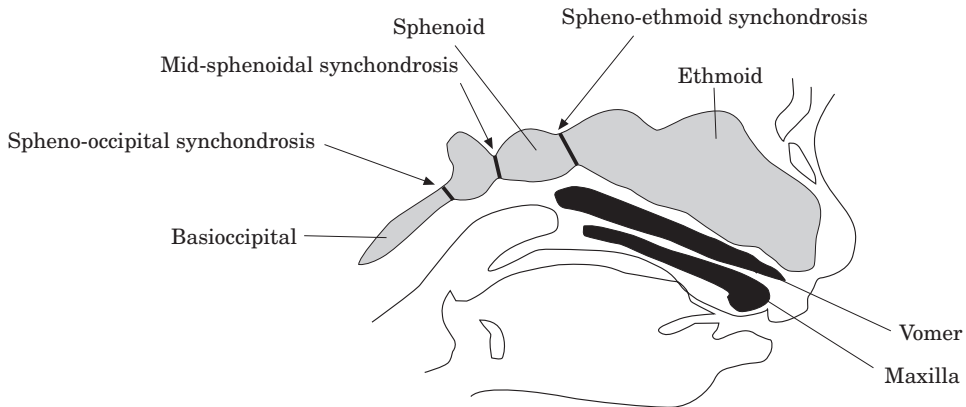


Figure 1. Midsagittal section through the cranial base in a *H. sapiens* fetus, showing the location of the spheno-occipital, mid-sphenoidal and spheno-ethmoid synchondroses (after Sperber, 1989). Cranial base angulation can occur as a result of growth within these synchondroses as well as from differential drift and rotation of the components of the basioccipital, sphenoid and ethmoid relative to each other.

may also generate flexion or extension, like a hinge, through differentially more chondrogenic activity at the superior and inferior margins of the synchondrosis, respectively (Giles *et al.*, 1981).

The timing and nature of activity in the basicranial synchondroses varies considerably between humans and non-human primates, and remains the source of some controversy. The MSS fuses prior to birth in humans (Ford, 1958), and in macaques after the eruption of the second molars (Scott, 1958; Hofer & Spatz, 1963). According to histological studies by Michejda (1971, 1972a, 1972b) the MSS remains active for at least two years postnatally in *Macaca mulatta*, and is the major site of postnatal extension of the cranial base. Other studies (Lager, 1958; Melsen, 1971; Giles *et al.*, 1981), however, indicate that the MSS becomes inactive in *M. mulatta* within a few months of birth, and that the SOS is most likely the major site of postnatal angulation in macaques as it is in humans (Scott, 1958; Schuller, 1976; Williams *et al.*, 1995). Fusion of the SOS occurs after the eruption of the second molars in both humans and non-human primates (Björk, 1955; Scott, 1958; Melsen,

1969). The SES fuses near the time of birth in non-human primates, but remains active for at least six postnatal years in humans (Scott, 1958; Michejda & Lamey, 1971). Although the SES is clearly the primary site of anterior cranial base elongation during the fetal period in all primates and postnatally in humans (Hofer, 1960; Hofer & Spatz, 1963; Diewert, 1985; Aganastopoulou *et al.*, 1988; Hoyte, 1991), there is little evidence that it is a site where much flexion or extension occurs.

Quantification of cranial base angulation

There are numerous possible ways to measure cranial base angulation given that flexion and extension occur at different sites. These angles, reviewed in Table 1 (see also Figure 4), attempt to summarize the overall degree of angulation between various prechordal and postchordal planes. Typically, this intersection is arbitrarily designated as the center of the sella turcica (sella), the superior-most midline point on the *tuberculum sellae* (sphenoidale), or the point overlying the spheno-ethmoid synchondrosis in the midline (prospenion). Unfortunately,

Table 1 Commonly used cranial base angles

Angle	Planes utilized (P=posterior; A=anterior)	References
External cranial base angle, nasion–sella–basion	P: basion–sella A: sella–nasion	Björk, 1951, 1955; Stamrud, 1959; Melsen, 1969; George, 1978; etc.
Landzert's sphenoidal angle, clivus/clival angle*, CBA, planum angle	P: clival plane A: ethmoidal plane (planum sphenoidale (-ale))	Landzert, 1866; Howell, 1951; Biegert, 1957; Moss, 1958; Hofer, 1957, 1960; Hofer & Spatz, 1963; Angst, 1967; Cartmill, 1970; Schäfer, 1975; Dmoch, 1975 ^{a,b} , 1976; Ross & Ravosa, 1993; Ross & Henneberg, 1995 Flügel <i>et al.</i> , 1993
Clivus angle*	P: clival plane A: palate horizontal	George, 1978
Clival angle*	P: clival plane A: sphenoidale–fronton	George, 1978
Ethmoidal angle, internal cranial base angle	P: basion–sella A: sella–ethmoidale	Björk, 1958; Stamrud, 1959
Spheno–ethmoidal angle, cranio–facial axis	P: basion–prospenion A: prospenion–nasion	Huxley, 1867; Topinard, 1890; Duckworth, 1904; Cameron, 1924, 1925; Zuckerman, 1926, 1955; Ford, 1956; Ashton, 1957 Cameron, 1924, 1925, 1927 ^{a,b} , 1930 Ford, 1956
Cameron's cranio–facial axis	P: basion–pituitary point A: pituitary point–nasion	Cameron, 1924, 1925, 1927 ^{a,b} , 1930
Basioccipito–septal angle	P: pituitary point A: pituitary point–septal point	Ford, 1956
Bolton's external cranial base angle	P: Bolton point–sella A: sella–nasion	Broadbent, 1937; Brodie, 1941, 1953; Anderson & Popovich, 1983
Anterior cranial base angle	P: clival plane A: prospenion–anterior cribriform point (ACP)	Scott, 1958; Cramer, 1977
Internal cranial base angle, fronton–sphenoidale–basion	P: basion–sphenoidale A: sphenoidale–fronton	George, 1978
Internal cranial base angle, fronton–sella–basion	P: basion–sella A: sella–fronton	George, 1978
Internal cranial base angle, foramen caecum–sella–basion	P: basion–sella A: sella–foramen caecum	Cousin <i>et al.</i> , 1981 [†] ; Spoor, 1997
External cranial base angle, nasion–sphenoidale–basion	P: basion–sphenoidale A: sphenoidale–nasion	George, 1978
Orbital angle	P: clival plane A: plane of superior orbital roof	Moss, 1958
Planum angle (PANG)	P: basion–sella A: planum sphenoidale	Antón, 1989
Orbital angle (OANG)	P: basion–sella A: plane of superior orbital roof	Antón, 1989

*The term "clivus angle" or "clival angle" has been used to denote a variety of different cranial base angles.

[†]Cousin *et al.*, 1981 differ slightly because they used the anterior-most point on the cribriform plate instead of the foramen caecum.

the most commonly-used angle, basion–sella–nasion, is problematic because nasion is not part of the cranial base and therefore introduces additional sources of variation from facial growth processes (see Schultz, 1955; Scott, 1958; Enlow & Moyers, 1971).

Related, alternative measures of cranial base angulation that help to remedy this problem replace nasion with the foramen caecum or the intersection of the orbital roof and the inner surface of the frontal bone (frontale) (e.g., George, 1978; Sirianni & Van Ness,

1978). All of these measures, however, may introduce variations unrelated to angulation. The position of basion drifts posteriorly during cranial growth along with the foramen magnum, especially in non-human primates (Duterloo & Enlow, 1970); remodeling of the sella turcica after the eruption of the first molar in humans causes sella to move at least 2 mm posteriorly relative to the *tuberculum sellae* (Baume, 1957; Shapiro, 1960; Latham, 1972); the superior margin of the ethmoid, including landmarks such as the foramen caecum, moves relative to the rest of the anterior cranial base through drift of the cribriform plate and deposition along the crista galli (Moss, 1963; Enlow, 1990); and the position of frontale can move anteriorly and superiorly through the process of drift as the anterior cranial fossa elongates in response to expansion of the frontal cortex (George, 1978; Enlow, 1990).

Several measures of cranial base angulation have focused on just the endocranial margins of bones in the anterior cranial fossa. Of special interest, especially in non-human primates, is the anterior cranial base angle that extends from basion to prosphenion and from prosphenion to a point, ACP, formed by the intersection of the near vertical surface of the frontal bone with the cribriform plate (Scott, 1958; Cramer, 1977). Most recently, Ross & Ravosa (1993) have defined an angle between the post-chordal plane along the clivus ossis occipitalis and a prechordal plane along the planum sphenoidale that is similar to Landzert's sphenoidal angle (Landzert, 1886) and to Moss' planum angle (Moss, 1958).

Laitman and colleagues (1976, 1978, 1979, 1982) developed a size-corrected composite measure of exocranial flexion between the basioccipital and the palate. This measure does not quantify solely basicranial angulation but instead summarizes a number of spatial relationships between the posterior cranial base and the midface that have different, possibly inde-

pendent growth trajectories (see below). To date, however, there have been no published studies which directly test the relationship between endocranial and exocranial flexion.² In addition, it is necessary to test the extent to which endocranial and exocranial flexion predict vertical dimensions of the pharynx in a large, ontogenetic sample of humans.

Differences between the above measures of cranial base angulation merit scrutiny because flexion and extension probably occur at different sites and through different processes in humans and other primates. It is therefore possible that not all comparisons of cranial base angles between humans and non-human primates are entirely homologous in a developmental sense (*sensu* Reidl, 1978; Roth, 1984). George's (1978) longitudinal comparison of five angles in humans (Ba-S-Na, Ba-Sp-Na, F-S-B, F-Sp-B, and F-Sp-clival line) partially addressed this problem. George concluded that these angles varied within individuals by as much as 7°, but that their ontogenetic trajectories were quite similar. Her study, however, did not include any non-human primates, and it did not directly relate cranial base angulation to the growth of other craniofacial regions such as the pharynx.

Cranial base angulation and pharyngeal dimensions

Although cranial base angulation differs postnatally in humans and non-human primates, it is unclear to what extent the processes that cause flexion and extension differ from each other developmentally. For example, there is little consensus on the ontogenetic trajectory of angulation in humans. Many authors (e.g., Ortiz & Brodie, 1949; Björk, 1955; Bergland, 1965; Knott, 1969; Lewis & Roche, 1977; George,

²Confusingly, Stamrud (1959) compared basion-sella-ethmoidale with basion-sella-nasion (which he termed external cranial base flexion).

1978) have suggested that cranial base angulation in humans occurs entirely prior to two years of age while others suggest it continues until about six postnatal years or even until the adolescent growth spurt (e.g., Zuckerman, 1955; Cousin *et al.*, 1981). In contrast, there is general agreement that basicranial extension in non-human primates follows an extended (skeletal) growth trajectory that mirrors the rate of growth of the face as a whole (Moore & Lavelle, 1974; Dmoch, 1975a, 1975b, 1976; Flügel *et al.*, 1993).

Such differences are important for evaluating hypotheses about the relationship between internal cranial base angles, external cranial base angles, and pharyngeal growth. Humans have a unique pharyngeal configuration in which the larynx lies well below the oral cavity, so that the trachea and esophagus share a common passageway (Negus, 1949). The low position of the larynx is a physiological basis for many aspects of human speech because it creates a two-tube supralaryngeal vocal tract (SVT), in which the length of the horizontal tube (SVT_H, from the lips to the posterior wall of the pharynx) and the vertical tube (SVT_V, from the vocal folds to the soft palate) have an approximately 1:1 proportion [see Figure 4(a)]. In humans, the cross-sectional areas of SVT_V and SVT_H can be modified independently by roughly ten-fold, forming a dynamic filter that can produce vowels whose formant frequencies are acoustically distinct regardless of vocal tract length (Peterson & Barney, 1952; Stevens & House, 1955; Ladefoged & Broadbent, 1957; Fant, 1960; Nearey, 1978; Lieberman, 1984, 1991). In contrast, non-human primates and human newborns tend to have larynges that are situated higher in the throat, with SVT_H:SVT_V ratios of approximately 2:1 (Lieberman *et al.*, 1972; Crelin, 1973; Laitman & Crelin, 1976). Vocal tract proportions significantly different from 1:1 are less advantageous in terms

of speech because they do not generate vowels whose formant frequencies differ absolutely (Stevens & House, 1955; Fant, 1960).

Lieberman & Crelin (1971), Lieberman *et al.* (1972) and Laitman & Crelin (1976) proposed that flexion of the external cranial base in humans contributes to laryngeal descent, and thus can be used to reconstruct the SVT of fossil hominids. This hypothesis, which has received much criticism (e.g., Carlisle & Siegel, 1974, 1978; Falk, 1975; LeMay, 1975; Burr, 1976; Arensburg *et al.*, 1990; Duchin, 1990; Houghton, 1993; Schepartz, 1993), is based on several lines of indirect evidence. Most importantly, internal as well as external basicranial flexion are believed to occur concurrently with the descent of the larynx (George, 1978; see however Björk, 1955; Schuller, 1976). In addition, flexion of the external cranial base potentially reorients the suprahyoid muscles and ligaments, contributing to a lower position of the larynx in humans than in other primates, and shortening the anteroposterior dimensions of the oropharynx between the back of the tongue and the vertebral column, thus forcing the larynx to descend because of spatial constraints (Lieberman & Crelin, 1971; Laitman & Crelin, 1976; Laitman *et al.*, 1979; Laitman & Heimbuch, 1982; Lieberman, 1984). Although external cranial base angulation and laryngeal position have been compared in adult and neonatal humans and other primates (e.g., Laitman & Crelin, 1976), the relationships between internal cranial base flexion, external cranial base flexion, and pharynx dimensions have never been tested ontogenetically.

Summary of hypotheses to be tested

This study tests three basic interrelated hypotheses by comparing cranial base angles within and between samples of *H. sapiens* and *P. troglodytes* divided into different age

categories. First, we compare four different measures of internal cranial base angulation and one measure of external cranial base angulation intraspecifically in *H. sapiens* and *P. troglodytes* to test the hypothesis that these angles correlate significantly with each other and that they follow similar ontogenetic trajectories. Second, we compare the ontogenetic relationships between internal and external cranial base angles and pharyngeal growth in humans to test the hypothesis that cranial base flexion correlates with pharyngeal dimensions and can, therefore, be used to estimate vocal tract proportions in fossil hominids. Finally, we test whether other craniofacial measurements can be used to estimate pharyngeal dimensions in humans, and potentially in fossil hominids.

Materials and methods

Sample

The human sample, summarized in [Figure 2](#), comes from a longitudinal study of American males ($n=15$) and females ($n=13$) of European descent who were studied between 1931 and 1966 as part of the Denver Growth Study (for details see [Maresh & Washburn, 1938](#); [Maresh, 1948](#); [McCummon, 1970](#)). These individuals were radiographed at a distance of 7.5 feet in lateral and frontal view at the age of 1 month, 3 months, 9 months, and thereafter every 12 months until adulthood. The long distance between the X-ray source and the subjects renders any enlargement factors insignificant and minimizes parallax ([Merow & Broadbent, 1990](#)). From the age of 1 year 9 months, individuals were radiographed from a seated position using a radiographic cephalometer; young infants, however, were hand-held, which may introduce some error (see below). This study used radiographs from each year up to 9 years 9 months, and thereafter radiographs from every other year until the age of 17 years 9 months. Individuals whose radio-

graphic records were very incomplete were not used in this study.

P. troglodytes is used as a comparison to *H. sapiens* because its growth processes are generally similar to those of other non-human primates ([Krogman, 1931, 1969](#); [Sirianni & Swindler, 1979](#); [Bromage, 1992](#)), and because its close phylogenetic relationship and general craniofacial similarities to early hominids makes it an especially useful comparison for testing hypotheses about human evolution. A cross-sectional series of 61 skulls of *P. troglodytes* sp. was studied from collections at the Peabody Museum, Harvard University; the Museum of Comparative Zoology, Harvard University; the American Museum of Natural History, New York, and the Cleveland Museum of Natural History. Radiographs of each cranium were taken using an ACOMA portable X-ray machine on Kodak XTL-2 film at a standard distance of 70 mm. To minimize potential distortion and parallax, each cranium was carefully oriented so that its midsagittal plane was parallel to the X-ray film and collimator. Mid-point averaging procedures, however, were used to correct for any parallax observed (see [Broadbent et al., 1975](#); [Merow & Broadbent, 1990](#)).

Because no precise information on age at death is available for the *P. troglodytes* specimens, each skull was assigned to one of five broad dental stages from visual examination and from radiographs: prior to the eruption of dc (Stage I); after the eruption of dc and prior to the eruption of M^1 (Stage II); after the eruption of M^1 and prior to the eruption of M^2 (Stage III); after the eruption of M^2 and prior to the eruption of M^3 (Stage IV); and after the eruption of M^3 (Stage V). Sample sizes are as follows: Stage I, three individuals (one male, two indeterminate); Stage II, 16 individuals (four females, two males, ten indeterminate); Stage III, 14 individuals (two females, four males, eight indeterminate); Stage IV, 12 individuals (seven females, five indeterminate); Stage V

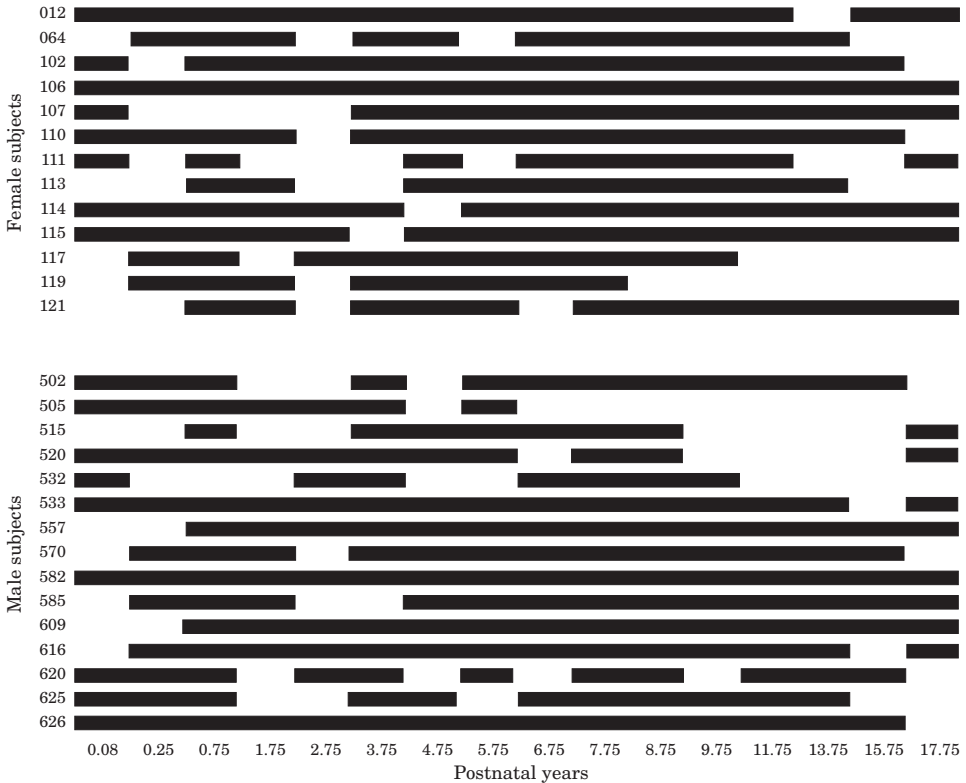


Figure 2. Human longitudinal sample used in this study; spaces indicate missing radiographs.

23 individuals (ten females, 13 males). In order to compare directly the human and chimpanzee data sets, the human sample was assigned to broadly similar dental stages: prior to the eruption of dm^2 (Stage I); after the eruption of dm^2 and prior to the eruption of M^1 (Stage II); after the eruption of M^1 and prior to the eruption of M^2 (Stage III); and after the eruption of M^2 (Stage IV). Although there are some problems with comparing *Pan* and *Homo* using broad dental stages, these divisions are useful for general comparisons because they represent approximately equivalent stages of craniofacial maturity. In both species neural growth is 95% complete by the end of stage II, and facial growth is mostly complete by stage IV (Krogman, 1931; Schultz, 1962; Smith, 1989). The divisions between Stages

I and II were chosen because the eruption of the deciduous upper canine in *P. troglodytes* occurs at about 1.02 years, and the eruption of the second deciduous upper molar in *H. sapiens* occurs by roughly 2.2 years of age (Smith *et al.*, 1994), placing these events approximately one-third of the way through the neural growth trajectory in each species.

Measurements

The high quality of the Denver Growth Study radiographs allows accurate identification of most cranial, vertebral and mandibular landmarks. Moreover, the hyoid body and a number of soft tissue structures in the pharynx including the epiglottis and, often, the vocal folds and arytenoid cartilages are clearly visible in many of the radiographs, as Figure 3 illustrates.

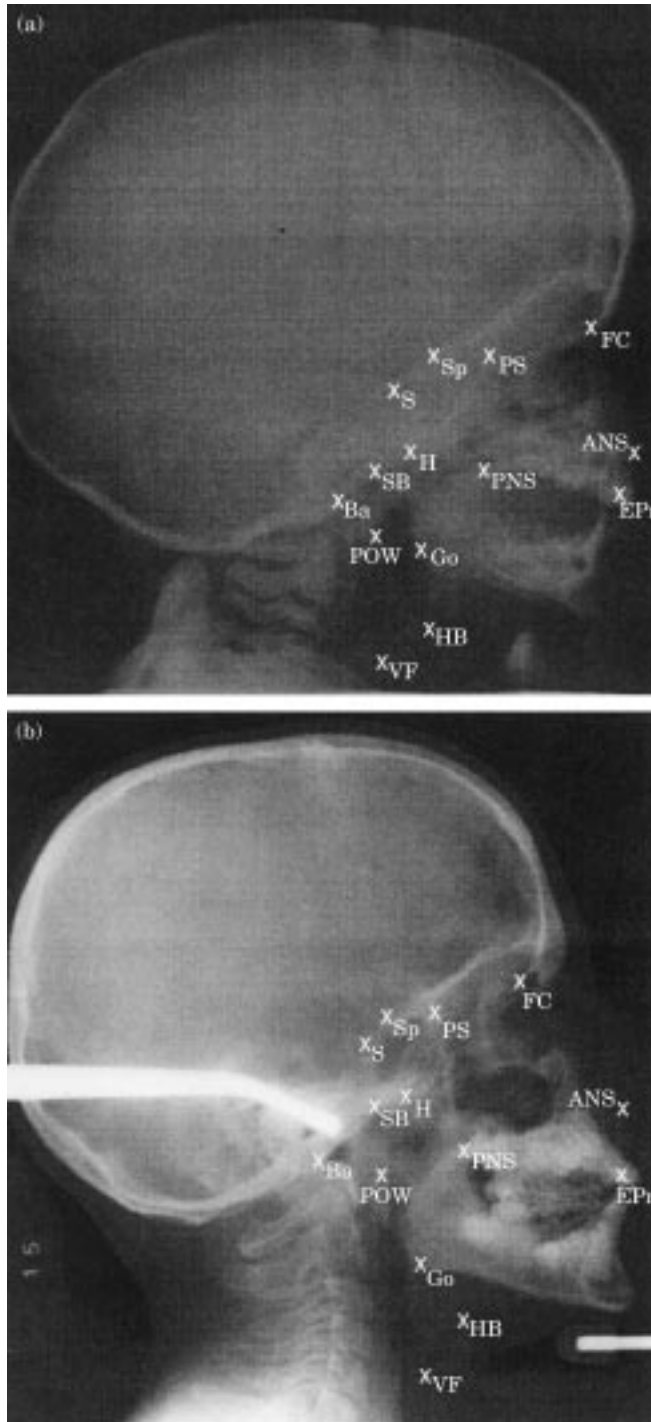


Figure 3. Lateral view radiographs of two individuals from the Denver Growth Study, showing location and visibility of landmarks used in this study. (a) infant, No. 557, aged 9 months; (b) juvenile, No. 515, aged 9 years 9 months. Landmarks are defined in Table 2, and discussed in text.

Radiographs from each individual were traced on acetate, recording the location of the following cranial landmarks, which are defined in Table 2 and illustrated in Figure 4(a): basion, sella, sphenoidale, foramen caecum, hormion, sphenobasion, the anterior nasal spine (ANS), the posterior nasal spine (PNS), the anterior-most point on the planum sphenoidale, and the point on the clivus before the dorsum sellae curves posteriorly. These landmarks are mostly standard points whose utility and reliability have been demonstrated in numerous studies of craniofacial growth in humans (Broadbent *et al.*, 1975; see also King, 1952; Brodie, 1955; Björk, 1955; Stamrud, 1959; Bergland, 1965; Riolo *et al.* 1974; George, 1978; Lugoba & Wood, 1990; Tng *et al.*, 1994) and non-human primates (e.g., Heintz, 1966; Cramer, 1977; Sirianni & Swindler, 1985; Bromage, 1989; Schneiderman, 1992; Ross & Ravosa, 1993). Although the PNS is often registered more anteriorly and inferiorly than is actually the case (Tng *et al.*, 1994), the pterygomaxillary fissure was visible on all radiographs allowing accurate identification of this point.

In order to compare different measurements of internal cranial base angulation, the above-described landmarks were used to define two postchordal planes, one from basion to sella (the sella plane, SP); and another along the dorsal margin of the occipital clivus (the clival plane, CP) following Ross & Ravosa (1993). In addition, we defined two prechordal planes, one from sella to the foramen caecum (the foramen caecum plane, FCP); and a second from sphenoidale to the anterior-most point on the planum sphenoidale (the pre-sphenoid plane, PSP). These four planes are used to define four different measures of internal CBA, illustrated in Figure 4(b), that incorporate major components of important angles used by previous researchers (listed in Table 1):

CBA 1, the angle between the sella plane and the foramen caecum plane;

CBA 2, the angle between the sella plane and the pre-sphenoid plane;

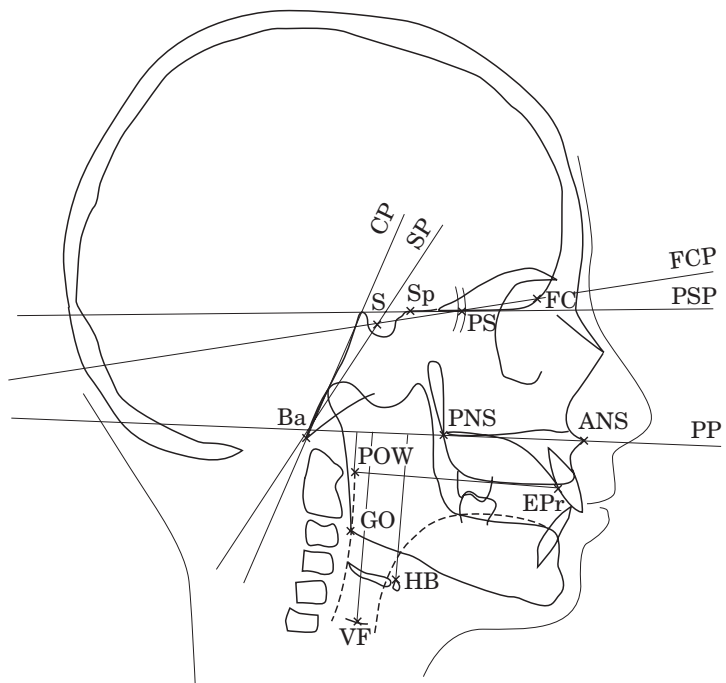
CBA 3, the angle between the clival plane and the foramen caecum plane;

CBA 4, the angle between the clival plane and the pre-sphenoid plane.

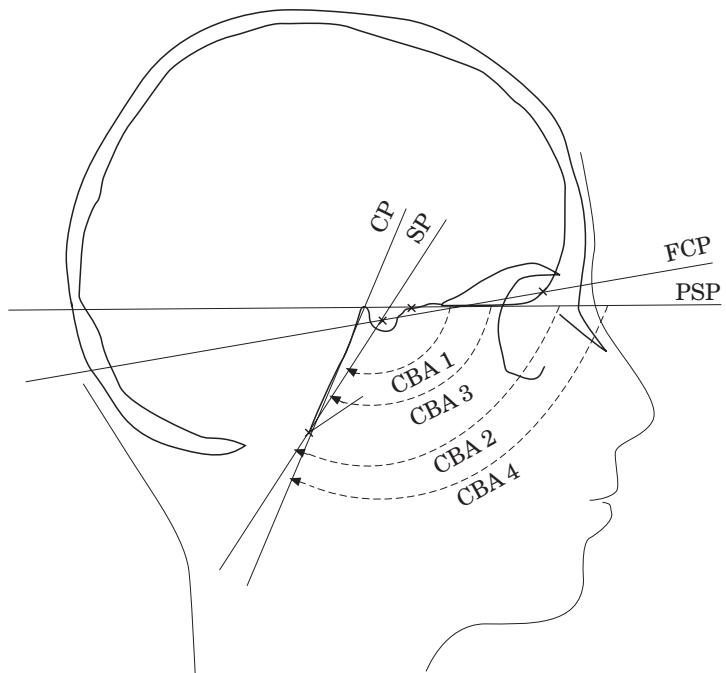
CBA 1–4, therefore, sample a wide range of possible internal cranial base angles, excluding those that incorporate points not actually on the cranial base (for example, the orbital plane of Moss, 1958). All angles were measured to the nearest degree (by RCM) using a hand-held protractor.

One additional measure of external cranial base angulation, CBA 5 (the angle between basion, sphenobasion and hormion), was taken on the human sample. CBA 5 was not measured on the chimpanzee sample, however, because the position of hormion could not be reliably located on radiographs. The ala of the vomer is much smaller and thinner in chimpanzees than in humans, and tends to be bifid, making it difficult to locate its most posterior midline point with precision. CBA 5 describes the flexion of the inferior surface of the basioccipital relative to the inferior surface of the sphenoid body. Note that CBA 5 is just one size-independent component of the composite, size-corrected measure of exocranial shape used by Laitman *et al.* (1978, 1979) and Laitman & Heimbuch (1982). We employ CBA 5 rather than Laitman and colleagues' composite measure of exocranial shape because it is a more direct measure of the angulation of the exocranial base that is not affected by the length, orientation and position of the palate. Future studies, however, are necessary to test more specifically the extent to which overall measurements of external cranial shape which include the cranial base and the palate correlate with pharyngeal dimensions during ontogeny.

To examine the effects of measurement error on the above cranial landmarks we



(a)



(b)

Figure 4. Midsagittal schematic of an adult human, showing landmarks and planes used (a); and different measurements of CBA (b). See [Table 2](#) for explanation and description of landmarks and planes.

Table 2 Landmarks, planes, and angles used

	Abbreviation	Definition
Landmark		
Anterior nasal spine	ANS	The most anterior point on the maxillary body at the level of the nasal floor.
Anterior tubercle of the atlas*	ATA	Anterior-most point on the anterior tubercle of the atlas.
Basion (endobasion)	Ba	The midsagittal point on the anterior margin of the foramen magnum.
Endoprosthion*	EPr	Midline point on the lingual surface of the central incisors, opposite the most anterior, inferior point on the alveolar surface of the premaxilla (Prosthion).
Foramen caecum	FC	Pit on the cribriform plate between the crista galli and the endocranial wall of the frontal bone. In chimpanzees and other non-human primates, this point lies in an olfactory pocket along with the entire cribriform plate.
Gonion*	Go	The point of maximum curvature of the posterior mandibular angle.
Hormion*	H	Posterior-most midline point on the vomer.
Hyoid body*	HB	Point at the superior margin of the hyoid body.
Planum sphenoidum point	PS	Superior-most point on the sloping surface of the pit in which the cribriform plate is set (Ross and Ravosa, 1993).
Posterior nasal spine*	PNS	The most posterior point of the maxillary body at the level of the nasal floor at the articulation of the hard and soft palates (similar to the pterygomaxillare (ptm) point).
Posterior oropharyngeal wall*	POW	Point on the posterior pharyngeal wall opposite the anterior tubercle of the atlas, along the EPr-ATA plane.
Sella	S	The center of the sella turcica (determined independently of the contours of the clinoid processes).
Sphenobasion*	Sb	Point in the middle of the sphenio-occipital suture on the external portion of the clivus, at the junction of the basioccipital and sphenoid bones.
Sphenoidale	Sp	The most posterior and superior midline point on the tuberculum sellae.
Vocal folds*	VF	Taken at level of arytenoid cartilages (only noted when clearly visible).
Planes and angles		
Foramen caecum plane	FCP	Plane from sella to the foramen caecum.
Pre-sphenoid plane	PSP	Plane from sphenoidale to the planum sphenoidum point.
Clival plane	CP	Plane from basion to a point on the clivus before the dorsum sellae curves posteriorly.
Sella plane	SP	Plane extending from basion to sella.
External clival plane*	ECP	Plane extending from basion (endobasion) to sphenobasion.
Hormion plane*	HP	Plane extending from sphenobasion to hormion.
Palatal plane*	PP	Plane from ANS to PNS.
Endoprosthion-posterior oropharyngeal wall*	EPr-POW	Plane from endoprosthion to the posterior wall of the pharynx opposite the anterior tubercle of the atlas. This plane represents the maximum horizontal length of the oral cavity.
Posterior margin of oral cavity*	POC	Plane from PNS to EPr-POW parallel to the posterior wall of the pharynx.
CBA 1	SP-FCP	Angle between the sella and foramen caecum planes.
CBA 2	SP-PSP	Angle between the sella and pre-sphenoid planes.
CBA 3	CP-FCP	Angle between the clival and foramen caecum planes.
CBA 4	CP-PSP	Angle between the clival and pre-sphenoid planes.
CBA 5*	ECP-HP	Angle between the external clival and hormion planes.

*Measured only for the human sample (see text).

used a single factor ANOVA to compare measurements from five separate tracings of one radiograph (taken on different days) to test the null hypothesis that replicate measurements from the same individual were the same ($P < 0.05$). Average measurement error was $\pm 1.15^\circ$ for angles and ± 0.94 mm for distances (Ba-S, Sp-PS, S-FC, Ba-FC, ANS-PNS, Ba-Ho, Ba-Sb, Sb-Ho). In addition, we tested the accuracy of the same measurements by comparing five tracings made from a lateral radiograph of an adult *H. sapiens* skull which was also radiographed with metallic markers glued to basion, foramen caecum, PNS, ANS, hormion, sphenobasion, sphenoidale, and the anterior-most point on the planum sphenoidale. Average measurement error was $\pm 0.80^\circ$ for angles and ± 1.23 mm for distances.

Several additional landmarks (also defined in Table 2 and illustrated in Figures 3 and 4) were recorded from the mandible and pharynx in the human sample: gonion, the inferior plane of the mandible; the anterior-most point on the anterior tubercle of the atlas (ATA); the superior-most point on the hyoid body; the midpoint of the vocal folds at the level of the vocal processes of the arytenoid cartilages; and the point along the posterior wall of the pharynx (POW) which intersects the plane from endoprostion (EPr) to ATA. The posterior pharyngeal wall is a clearly demarcated structure anterior to the vertebral bodies (see Figures 3 and 4). To avoid measurement error as much as possible, the level of the vocal folds was only marked in individuals in which the arytenoid cartilages and the "true" vocal folds were distinctly visible and could be discerned unambiguously from the more superior vestibular ("false") folds. Only one point used in this study, gonion (the most posterior and inferior point on the mandible), does not lie in the midsagittal plane. Gonion is nevertheless a useful landmark for this study because it is easy to locate accu-

rately, it is used in numerous other studies of craniofacial growth (e.g., Riolo *et al.*, 1974), and because it provides a point of reference against which to measure the vertical position of the hyoid and larynx relative to the mandible. It is significant to note that in almost all the Denver Growth Study radiographs, gonion on the left and the right side of the individual line up almost perfectly (within 1 mm), reflecting the long distance between the subjects and the X-ray source, and the fact that most individuals were radiographed with a cephalometer. Nevertheless, standard mid-point averaging procedures (see Broadbent *et al.*, 1975; Merow & Broadbent, 1990) were used to correct for any slight parallax in the position of gonion caused by asymmetry and non-standard position of the head.

Non-cranial base landmarks were measured only in individuals whose mandibles were in resting (closed) position, and who were radiographed while apparently engaged in quiet respiration. While it is impossible to be certain that subjects were not vocalizing when they were radiographed, the following criteria were used to assess quiet respiration and to ensure that they were not swallowing: an extended (upright) epiglottis, a rounded contour of the tongue not in contact with the palate or posterior pharyngeal wall, and non-protrusion of the lips. In addition, it is important to note that there is no resting position of these structures. Vocalization, respiration, administration of anaesthesia, changes in posture, and activities such as locomotion inevitably cause slight vertical movements of the hyoid and larynx relative to the cranial base (Winnberg *et al.*, 1988; Sivarajan & Fink, 1990; Nagai *et al.*, 1989). These variations are inherent, normal aspects of pharyngeal physiology that should not be considered sources of error but instead are important aspects of the variability in the dimensions of the pharynx that need to be measured and incorporated into any analysis.

The above-described non-cranial landmarks were used to measure a number of horizontal and vertical dimensions of the SVT and pharynx. Two horizontal measurements of the SVT were taken: (1) maximum horizontal length of the SVT was measured from the lingual surface of the central incisors (EPr) to the posterior pharyngeal wall opposite the anterior tubercle of the atlas (POW); (2) maximum horizontal length of the oropharyngeal component of the SVT was measured along the EPr-POW plane from the posterior pharyngeal wall to a plane (POC) which runs from PNS perpendicular to the posterior pharyngeal wall, approximating the posterior margin of the oral cavity. Two vertical measurements of the SVT were taken parallel to the posterior wall of the pharynx: (1) from the hyoid body (HB) to the palatal plane (ANS-PNS), and (2) from the level of the vocal folds (VF) to the palatal plane (ANS-PNS). As noted above, the second of these measurements was only recorded in radiographs in which the vocal folds were clearly distinct from the more superior vestibular folds. Finally, the following vertical dimensions of the pharynx were measured parallel to the posterior wall of the pharynx: gonion to the hyoid body, gonion to the palatal plane, gonion to the vocal folds, and the hyoid body to the vocal folds.

It is more difficult to assess the accuracy of the measurements of pharyngeal dimensions of the Denver Growth Study subjects. However, to examine the effects of measurement error we used a single factor ANOVA to compare measurements from five separate tracings of one radiograph (taken on different days) to test the null hypothesis that replicate measurements from the same individual were the same ($P < 0.05$). Average measurement error was ± 0.68 mm. In addition, our measurements of pharyngeal dimensions correspond closely to those of other studies, most notably King (1952), and Goldstein (1980). Potential measure-

ment errors of the infant sample require some additional discussion. There appears to be some variation in the orientation of the skull in relation to the vertebral column among the human infants 9 months old or less, although inspection of the radiographs clearly shows that care was taken to hold the infants so that their heads were neither very flexed nor extended with respect to the atlanto-occipital joint. Beginning at 1 year 9 months of age, the radiographs were taken using a cephalometer which positions the head in a standard orientation. Since F-tests indicate that the range of variation for pharyngeal dimensions is not significantly greater ($P > 0.05$) before and after 1 year 9 months of age, we suspect that this lack of postural control is not a major source of error. Also, King (1952), Falk (1975) and Bibby & Preston (1981) demonstrated that the position of the hyoid body relative to the base of the mandible remains fairly constant in extreme flexion and extension of the head (see discussion below). While variations in head orientation cannot affect the measures of cranial base angulation, measurements of the spatial relationships between the cranium, mandible and pharynx among infants aged 9 months and younger need to be tested with better data.

Hypothesis testing

All measurements were entered into *Statview 4.5*[™] (Abacus Concepts, Berkeley, CA) for analysis. To determine the ontogenetic pattern of each measure of CBA and to evaluate how these measures correlate with each other, we compared means and standard deviations of CBA 1-5 for the longitudinal human sample divided into age groups. A single factor ANOVA was used to compare cranial base angles between age groups to determine intervals at which changes in each measure were statistically significant at the $\alpha = 0.05$ level using Fisher's PLSD test (Sokal & Rohlf, 1981). In order to evaluate differences in the absolute values

among alternative measures of cranial base angulation, least-square and reduced major axis (RMA) regressions were used to compare the slope and intercept of these measures of cranial base angulation. Such comparisons provide information on how the use of different postchordal and prechordal planes influences alternative measures of cranial base angulation. Again, single factor ANOVA was used to test whether measures of CBA differ significantly between males and females. Similar analyses were performed for *P. troglodytes*, with the exception that this sample is more crudely divided into dental stages as described above.

To test whether pharyngeal dimensions correlate with measures of cranial base angulation, a least squares (Model I) regression was used to compare the reliability with which measures of CBA can predict horizontal and vertical dimensions of the pharynx against the null hypothesis that these dimensions are independent. In addition, to determine if there is a reliable means of estimating the vertical dimensions of the vocal tract relative to the cranial base from other skeletal landmarks, the vertical position of the vocal folds and the hyoid body were compared not only relative to each other but also to the position of gonion and to the palatal plane parallel to the posterior wall of the pharynx (see above). Together, these measures may potentially be useful for predicting the height of the vertical tube of the pharynx in humans and possibly in other hominids. Because mandibular and pharyngeal dimensions are known to be sexually dimorphic, these relationships were evaluated separately for males and females.

Results

Internal cranial base angulation

Means, standard deviations and sample sizes of CBA 1–5 in *H. sapiens* and *P. troglodytes* are provided in Tables 3 and 4; these data

are summarized by age for *H. sapiens* in Figure 5, and by dental stage for *H. sapiens* and *P. troglodytes* in Figure 6. Note that average values for CBA 1 and 4 in the human sample at all ages after 12 years are $134.9^\circ \pm 3.00$ and $112.4^\circ \pm 5.28$, respectively, similar to other published values (Schäfer, 1975; George, 1978; Cousin *et al.*, 1981; Ross & Henneberg, 1995; Spoor, 1997). Intervals in which the amount of flexion was statistically significant ($P < 0.05$) as determined by single factor ANOVA are indicated in these figures. In humans, the majority of internal cranial base flexion occurs prior to two years of age, during which time CBA 1–4 decrease between 8.6° and 15.3° (see below). These results agree with several studies based on slightly different measures that have noted that no significant changes occur in cranial base flexion in humans after the second postnatal year (Ortiz & Brodie, 1949; Björk, 1955; Brodie, 1955; Stamrud, 1959; Koski, 1960; George, 1978). Overall, it is clear that for CBA 1–4, humans less than 1 year 9 months old are significantly less flexed than all humans greater than 2 years 9 months old ($P < 0.001$).

A single factor ANOVA finds no statistically significant differences between CBA 1–4 in males and females for all age groups as suggested by Lewis & Roche (1977) and Ursi *et al.* (1993). Table 5 summarizes LSR and RMA regressions between CBA 1–5 in the human sample. There is a tight linear relationship among many but not all of these angles. In general, there is a strong statistical correlation between measures of cranial base angulation that incorporate different postchordal planes (CBA 1 and 3, and CBA 2 and 4); those angles that incorporate the sella plane (CBA 1, 2) are between 3° and 9° more obtuse ($P < 0.001$) than corresponding angles that use the clival plane (CBA 3, 4) because sella is a more anterior point than the point where the dorsum sellae curve away posteriorly, especially in adults.

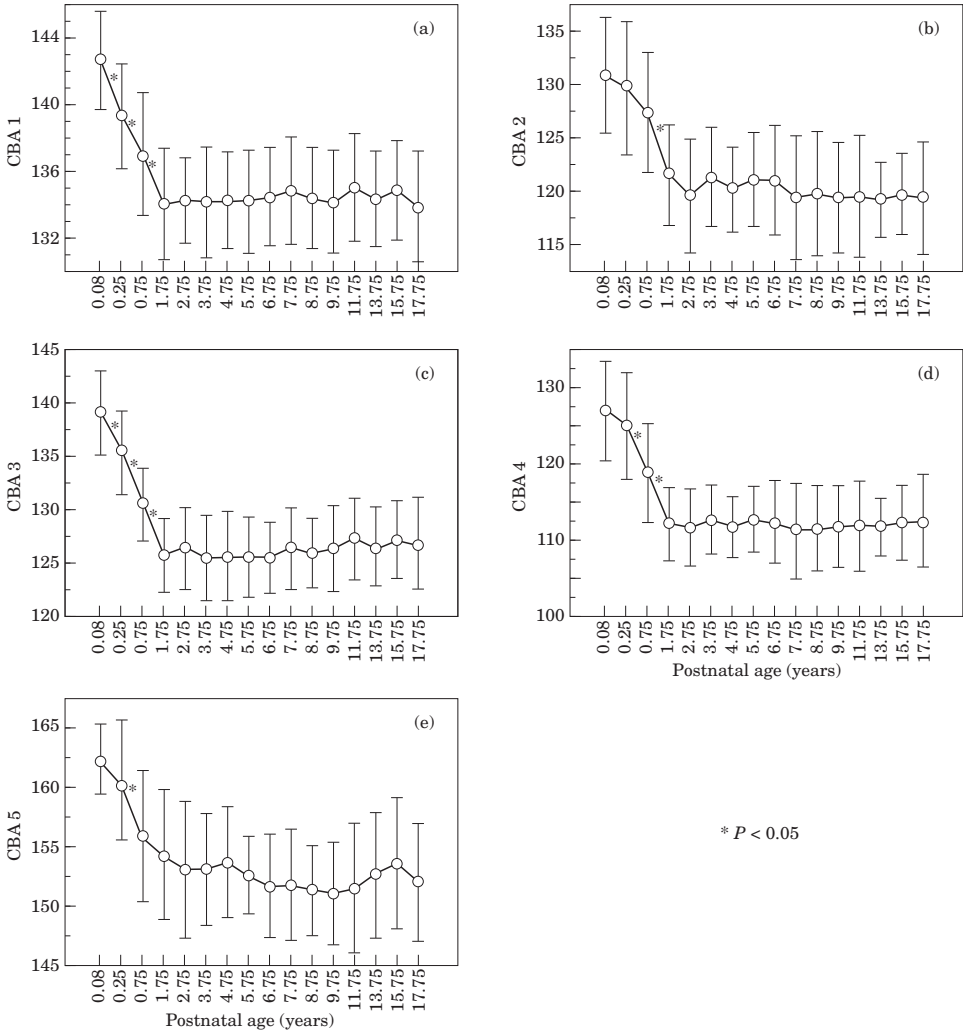


Figure 5. Plot of mean values (circles) and standard deviations (bars) for CBA 1–5 in the human longitudinal sample by age; * indicates a significant ($P < 0.05$) difference in mean CBA between successive intervals as indicated by single factor ANOVA.

Likewise, measures of cranial base angulation that use the foramen–caecum plane (CBA 1 and 3) are more obtuse than those that use the pre-sphenoid plane (CBA 2 and 4) because of the more superior position of the foramen caecum and because sella is always inferior to sphenoidale. However, it is crucial to note that there is a poor correlation between measures of cranial base angulation that incorporate different pre-

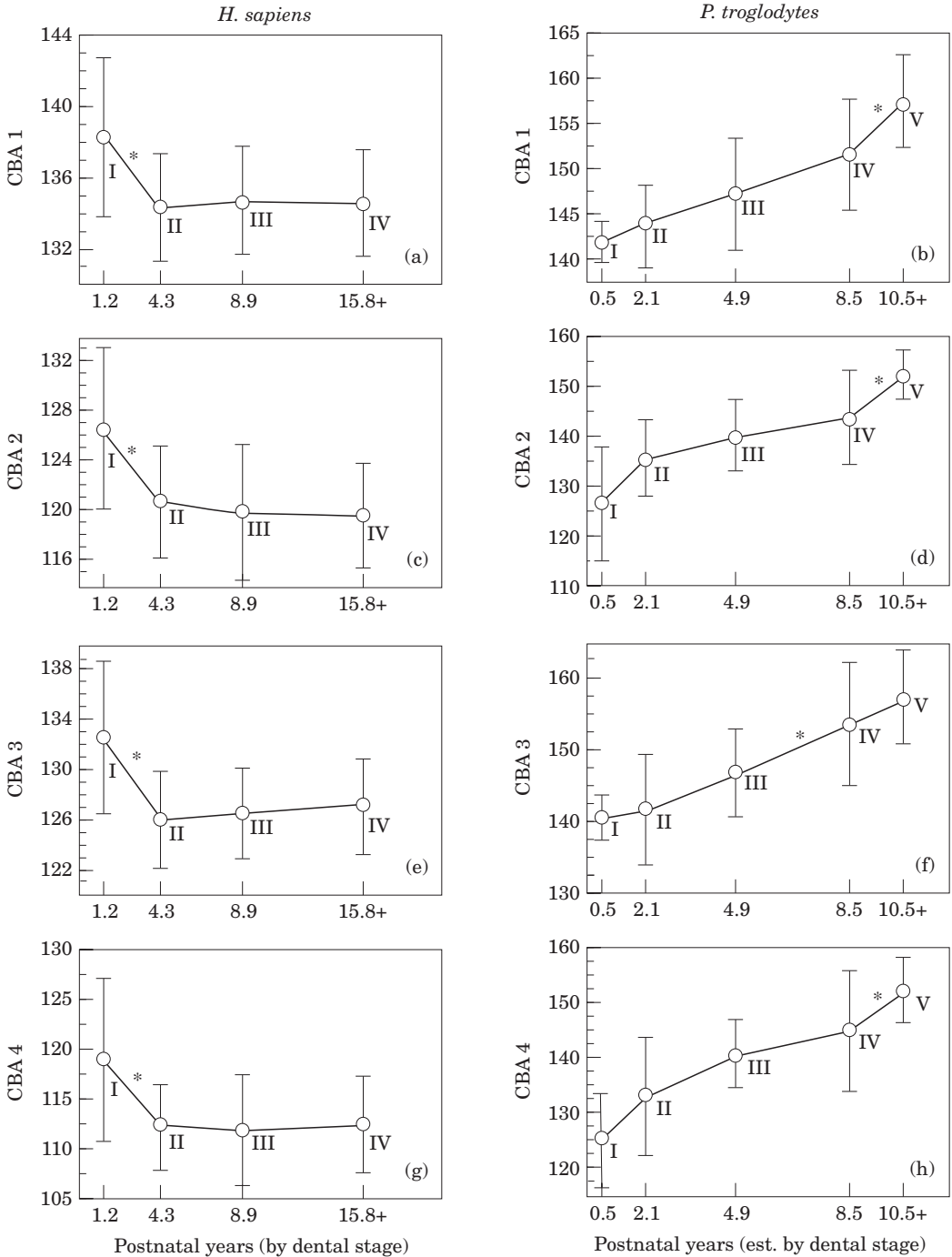
chordal planes. Since the prechordal portions of CBA 1 and 3 all lie on the superior margin of the ethmoid, these angles correlate better with each other than with CBA 2 and 4, both of which lie solely on the superior margin of the sphenoid. In other words, the above angles summarize substantially different spatial relationships between the anterior and posterior portions of the cranial base, highlighting the potential

Table 3 Means, standard deviations and sample number for CBA in *Homo sapiens*

Age (years)	CBA 1			CBA 2			CBA 3			CBA 4			CBA 5		
	<i>n</i>	Mean	Std. dev.	<i>n</i>	Mean	Std. dev.	<i>n</i>	Mean	Std. dev.	<i>n</i>	Mean	Std. dev.	<i>n</i>	Mean	Std. dev.
0·08	19	142·66	2·91	7	130·86	5·48	17	139·09	3·89	7	126·79	6·48	13	162·46	2·86
0·25	18	139·25	3·06	8	129·69	6·30	15	135·60	4·03	7	125·00	7·01	11	160·68	5·02
0·75	24	136·96	3·66	14	127·25	5·59	22	130·84	3·31	15	118·57	6·65	16	156·00	5·60
1·75	18	134·36	3·22	13	122·08	4·74	17	125·82	3·54	14	112·11	4·77	7	154·36	5·41
2·75	17	134·06	2·39	17	119·38	5·26	18	126·50	3·82	16	111·53	4·97	12	153·17	5·80
3·75	24	134·23	3·27	24	121·38	4·71	24	125·58	4·00	24	112·60	4·52	15	153·17	4·75
4·75	22	134·30	2·92	23	120·41	4·17	24	125·56	4·30	23	111·74	4·08	21	153·76	4·69
5·75	23	134·30	3·09	23	121·28	4·51	23	125·83	3·59	23	112·78	4·23	21	152·69	3·28
6·75	25	134·50	2·89	23	121·17	5·07	25	125·58	3·33	23	112·44	5·23	22	151·68	4·42
7·75	27	134·82	2·91	27	119·67	5·78	27	126·61	3·58	27	111·54	4·24	27	151·91	4·73
8·75	27	134·37	2·96	27	119·94	5·77	27	126·26	3·10	27	111·63	5·79	26	151·37	3·86
9·75	25	134·30	2·94	24	119·54	5·10	25	126·56	3·87	24	111·98	5·33	24	151·15	4·37
11·75	26	135·33	3·01	26	119·73	5·76	26	127·52	3·72	26	112·21	6·02	24	151·56	5·42
13·75	20	134·68	3·14	18	119·78	3·78	20	127·23	3·71	18	112·47	4·24	16	152·63	5·28
15·75	21	135·00	2·90	20	120·03	3·59	21	127·41	3·35	20	112·60	4·65	17	153·68	5·59
17·75	16	134·22	3·10	17	119·53	5·44	16	127·03	4·11	17	112·59	6·15	13	152·04	5·02

Table 4 Means, standard deviations and sample number for CBA in *Pan troglodytes*

Dental stage	<i>n</i>	CBA 1		CBA 2		CBA 3		CBA 4	
		Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.
1	3	141.67	2.08	126.00	11.00	140.67	3.06	124.67	8.39
2	13	143.54	4.58	135.00	7.51	141.63	7.49	132.88	10.69
3	9	147.00	5.98	139.67	7.04	146.67	6.02	140.11	6.19
4	11	151.36	5.99	143.05	9.18	153.27	8.55	144.50	10.77
5	19	157.21	4.85	151.79	4.85	157.05	6.48	151.74	5.76



* $P < 0.05$

Figure 6. Plot of mean values (circles) and standard deviations (bars) for CBA 1, 2, 3, and 4, in *H. sapiens* (left) and *P. troglodytes* (right) by dental stage. Dental stages are plotted using mean chronological ages within each stage. These values for *Pan* were calculated from Smith *et al.* (1994). *Indicates a significant difference ($P < 0.05$) in mean CBA between successive intervals as indicated by single factor ANOVA. See text for definitions of dental stages.

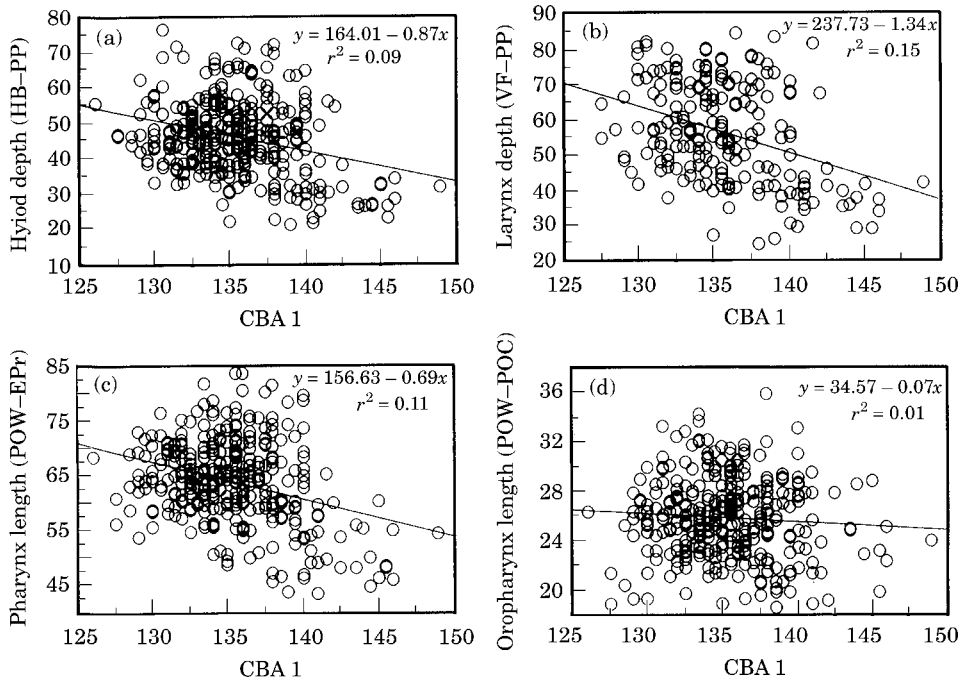


Figure 7. Plot of CBA 1 against vertical and horizontal dimensions of the vocal tract: hyoid depth below the palatal plane (a); larynx depth below the palatal plane (b); maximum horizontal vocal tract length from POW to EPr (c); maximum oropharynx length from POW to POC along the POW-EPr plane (d). See Figure 4 and Table 2 for definitions of measurements.

difficulties that would arise by comparing different measurements of cranial base angulation.

The pattern of CBA in *P. troglodytes*, summarized in Figure 6 and Table 4, differs fundamentally from that of *H. sapiens* in terms of its nature, amount and ontogenetic pattern. The mean values for adult chimpanzees are similar to other published results based on smaller samples (Heintz, 1966; Cousin *et al.*, 1981; Ross & Ravosa, 1993; Spoor, 1997), but provide some new data. Most importantly, Figure 6 demonstrates that the cranial base in this species extends postnatally, confirming earlier observations on *P. troglodytes* and *Pan paniscus* (Ashton, 1957; Heintz, 1966; Angst, 1967; Cramer, 1977; Cousin *et al.*, 1981) and other non-human primates (e.g., Michejda & Lamey, 1971; Dmoch, 1976; Sirianni & Swindler, 1979; Schneiderman,

1992). Note that postnatal cranial base extension in *Pan* ranges between 15.5° and 27.1° , depending on which CBA measure is used. This postnatal extension is more than twice the amount of flexion that occurs postnatally in *H. sapiens*. Another major difference between *P. troglodytes* and *H. sapiens* is that extension in *P. troglodytes* occurs in a gradual, long-term (skeletal) growth trajectory along with the face (see also Angst, 1967; Heintz, 1966; Dmoch, 1976; Cramer, 1977; Flügel *et al.*, 1993). In contrast, there are no significant increases in any measure of cranial base flexion in *H. sapiens* after dental stage II, which is consistent with a neural growth trajectory.³

³Skeletal and neural growth trajectories refer to rates of growth that covary, respectively, with the growth of the skeleton as a whole as opposed to the expansion of the brain. In humans, for example, the skeletal growth trajectory occurs for 18–20 postnatal years, whereas the neural growth trajectory is finished by 6–7 years.

Table 5 Regression comparisons of cranial base angles in *Homo sapiens*

Regression	<i>n</i>	LSR intercept (s.e.)	LSR slope (s.e.)	RMA slope (s.e.)	<i>r</i>
CBA 1 vs. CBA 3	342	- 34.87 (4.39)	1.20 (0.03)	1.33 (0.03)	0.90
CBA 2 vs. CBA 4	308	- 10.11 (2.56)	1.02 (0.02)	1.09 (0.02)	0.94
CBA 1 vs. CBA 2	303	34.45 (12.32)	0.64 (0.09)	1.68 (0.09)	0.38
CBA 1 vs. CBA 4	303	13.50 (13.26)	0.74 (0.10)	1.85 (0.10)	0.40
CBA 2 vs. CBA 3	305	96.00 (5.02)	0.26 (0.04)	0.78 (0.04)	0.33
CBA 3 vs. CBA 4	307	22.65 (8.94)	0.71 (0.07)	1.42 (0.07)	0.50
CBA 1 vs. CBA 5	273	67.79 (11.72)	0.63 (0.09)	1.54 (0.09)	0.41
CBA 2 vs. CBA 5	257	123.46 (7.26)	0.24 (0.06)	0.96 (0.06)	0.25
CBA 3 vs. CBA 5	275	82.20 (7.60)	0.56 (0.06)	1.14 (0.06)	0.49
CBA 4 vs. CBA 5	257	119.08 (6.03)	0.30 (0.05)	0.91 (0.05)	0.33

A single factor ANOVA shows that there are no statistically significant differences between CBA 1–4 in male and female chimpanzees for all dental stages (see also Cramer, 1977).

External cranial base angulation

Data on the ontogeny of external cranial base angulation (CBA 5) in the human sample are summarized in Figure 5 and Table 3. The trajectory of CBA 5 is similar to that of CBA 1–4, with the majority of flexion occurring prior to 2 years of age. However, Table 5 shows that correlations between measures of internal and external cranial base flexion in humans are fairly low (between 0.25 and 0.49), although significant.

As discussed above, this study presents no data on external cranial base angulation in *Pan*, but the ontogeny of CBA 5 is likely to differ in *Pan* and *Homo* in several respects, with extension rather than flexion, and in a skeletal rather than a neural growth trajectory. This hypothesis, however, needs to be tested with data not available from this study.

Relationship of cranial base angulation to vocal tract dimensions

As Figure 7(a) and (b) illustrates for CBA 1 in the human sample, there is no statistically significant, predictive relationship between

internal cranial base angulation and any measure of the vertical height of the vocal tract, including the position of the hyoid body or the vocal folds of the larynx below the palatal plane. The reason for the independence of these dimensions is illustrated in Figure 8, which shows that the hyoid and larynx descend in a typical skeletal growth trajectory up to the end of puberty, long after flexion of the cranial base is complete by the first two years of age (see also Schulter, 1976: 548). These data, therefore, do not support the hypothesis that internal cranial base flexion correlates with laryngeal descent. Figure 7(c) and (d) indicates that flexion of the internal cranial base is also independent of the two most important horizontal lengths of the vocal tract. In particular, CBA 1 is independent of the total horizontal length of the vocal tract as well as the length of the oropharynx behind the oral cavity. These relationships hold true for all measures of internal CBA, providing no support for the hypothesis that internal cranial base flexion itself causes the larynx to descend because of spatial constraints that leave insufficient room behind the tongue (see below). It is true, however, that the maximum length of the oropharynx in the sample aged 17 years 9 months is 26.9 mm (s.d. 4.20, *n*=8) among females and 25.66 mm (s.d. 3.87, *n*=7) among males,

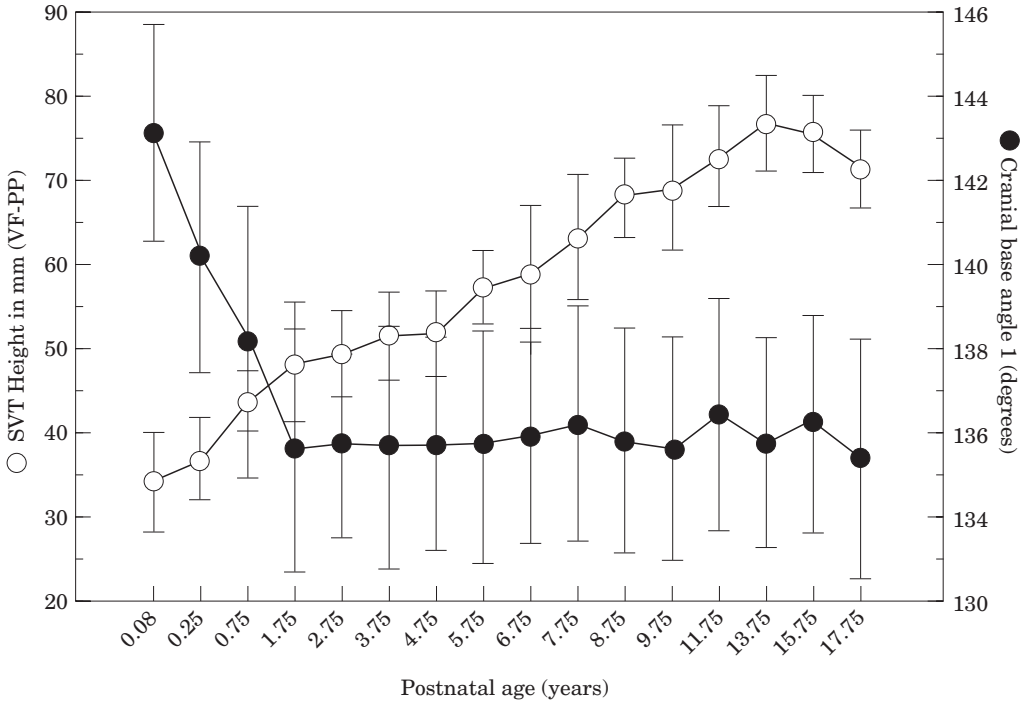


Figure 8. Ontogeny of CBA 1 (right axis) versus SVT height (VF-PP) (left axis) in the human longitudinal sample by age. The vocal tract grows in a typical skeletal growth trajectory, while the cranial base flexes in a neural growth trajectory.

which is too short to fit the average-sized adult human larynx (Eckel *et al.*, 1994).

External cranial base angulation as measured in this study (CBA 5) is also a poor predictor of vocal tract dimensions in humans. As Figure 9 shows, there is no statistically significant, predictive relationship between CBA 5 and the major vertical [Figure 9(a) and (b)] or horizontal [Figure 9(c) and (d)] portions of the vocal tract in the human sample. As is the case for internal cranial base angulation, the external portion of the cranial base ceases to flex prior to 2 years of age, long before the hyoid and larynx attain their adult position relative to the mandible.

The above results, however, do not mean that it is impossible to predict the vertical dimensions of the vocal tract in humans from a combination of several key cranial

and mandibular landmarks. In fact, there are strong linear relationships in the longitudinal human sample among the following five dimensions, all of which we measured parallel to the posterior wall of the pharynx: (1) the distance from the hyoid body to the palatal plane, (2) the distance from the hyoid body to gonion, (3) the distance from gonion to the palatal plane, (4) the distance from the vocal folds to the hyoid body, and (5) the distance from the vocal folds to gonion. These supero-inferior spatial relationships, which are illustrated in Figure 10 and summarized in Table 6 for both sexes, corroborate the findings of Falk (1975) and Haralabakis *et al.* (1993: p. 265) that, ontogenetically, the hyoid remains in a close, predictable relationship with the larynx and the base of the mandible (see also Adamidis & Spyropoulous, 1983). A single

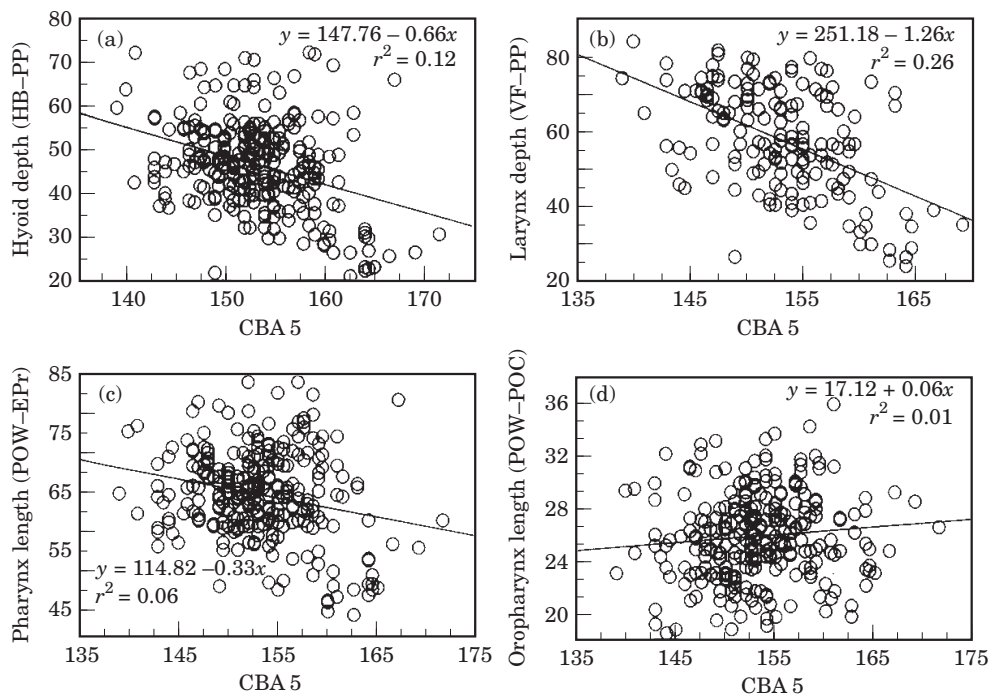


Figure 9. Plot of CBA 5 against vertical and horizontal dimensions of the vocal tract: hyoid depth below the palatal plane (a); larynx depth below the palatal plane (b); maximum horizontal vocal tract length from POW to EPr (c); maximum oropharynx length from POW to POC along the POW-EPr plane (d). See Figures 3 and 4 and Table 2 for measurement definitions.

factor ANOVA indicates that both gonion and the hyoid body are significantly lower relative to the palatal plane in males than in females ($P < 0.05$); males do not have significantly lower vocal folds than females, which is explained by the fact that there is a larger distance from the hyoid body to the vocal folds of the larynx in females ($P < 0.05$).

Discussion

Processes of cranial base angulation

The results of this study support the hypothesis that the cranial base in *H. sapiens* flexes in a rapid trajectory that is mostly complete by roughly 2 years of age, in contrast to the cranial base in *P. troglodytes* and other non-human primates, which extends gradually in a skeletal growth trajectory along with the face and pharynx. The results reported here

for *P. troglodytes* are therefore in close agreement with other ontogenetic studies of cranial base angulation in apes. Most notably, Angst (1967) found comparable degrees and rates of cranial base extension in *P. troglodytes*, *P. paniscus*, *Pongo pygmaeus* and *Gorilla gorilla*, but based on very small sample sizes divided into three very broad dental categories (infant, juvenile and adult). Cousin *et al.* (1981) also found the cranial base in *P. troglodytes* and *P. paniscus* to extend in the same growth trajectory as the face, with significant differences occurring between males and females in *P. paniscus* during the adolescent growth spurt. In addition, the human results reported here differ in only a few respects from other ontogenetic studies of cranial base angulation in humans. In particular, Cousin *et al.* (1981) suggested that humans have a

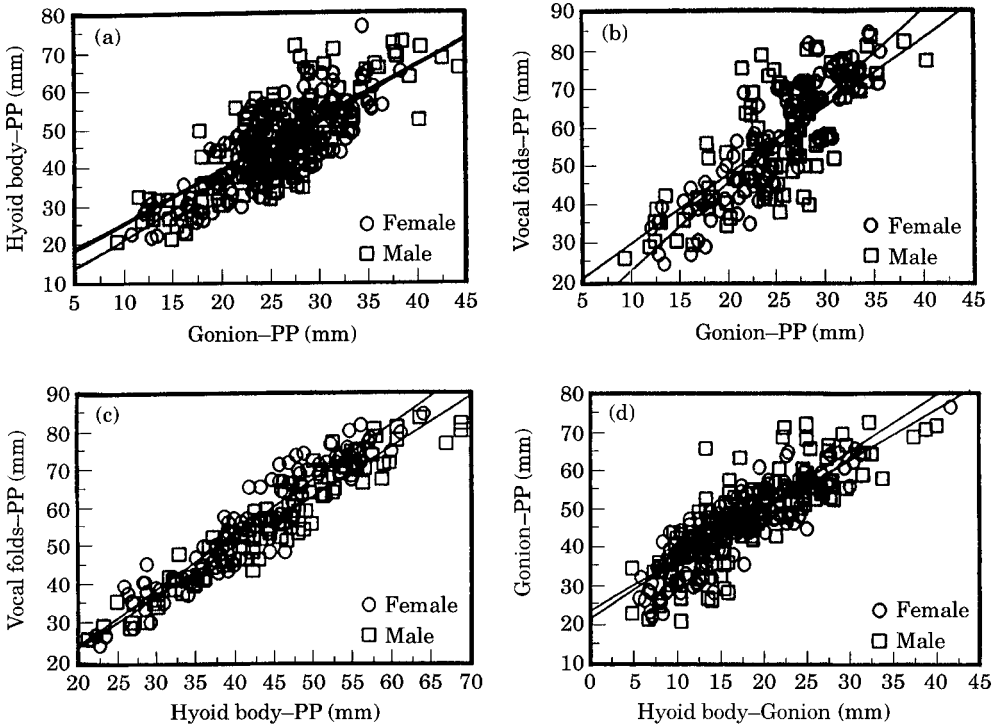


Figure 10. Plots of the depth of the hyoid body (HB) (a) and vocal folds (VF) (b) below the palatal plane (PP) relative to the position of gonion (Go) below the PP; the depth of the vocal folds (c) and gonion (d) below the PP relative to the position of the hyoid body below the PP. All measurements are parallel to the posterior wall of the pharynx. See Figure 4 and Table 2 for definitions of measurements.

Table 6 LSR comparisons of pharyngeal dimensions (parallel to the posterior pharyngeal wall) in *H. sapiens*

Regression	Sex	<i>n</i>	Intercept (s.e.)	Slope (s.e.)	<i>r</i>
Go-PP vs. HB-PP	F	179	6.52 (2.09)	1.49 (0.08)	0.81
	M	164	11.79 (2.52)	1.36 (0.09)	0.75
Go-PP vs. VF-PP	F	105	0.28 (3.25)	2.25 (0.13)	0.87
	M	102	11.86 (4.22)	1.78 (0.16)	0.74
HB-PP vs. VF-PP	F	104	-4.75 (2.17)	1.44 (0.05)	0.94
	M	102	-2.01 (1.81)	1.30 (0.04)	0.96
HB-PP vs. HB-Go	F	173	21.49 (1.06)	1.45 (0.06)	0.87
	M	154	23.76 (1.50)	1.30 (0.08)	0.81

slightly more prolonged trajectory of cranial base angulation, with approximately 3° of flexion occurring until the period between 4 and 8 postnatal years. Differences between these two studies may be attributable to the use of cross-sectional versus longitudinal

samples. Cousin *et al.* (1981) used a cross-sectional sample with smaller sample sizes divided into fairly broad dental stages that may be less precise than the longitudinal sample used here for detecting slight shifts in the timing of cranial base movements.

The hypothesis that human cranial base flexion occurs almost entirely within 2 years of birth is also supported by George (1978) using the same Denver Growth Study data, as well as by several other independent studies (Ortiz & Brodie, 1949; Björk, 1955; Brodie, 1955; Stamrud, 1959; Koski, 1960).

Developmental studies of the processes of cranial base angulation in humans and other primates are relevant to several important issues about the nature and significance of cranial base flexion during human evolution. One major question raised by the above-described contrasts between humans and chimpanzees is how different cranial base flexion in humans is from extension in non-human primates. Although the morphological consequences of cranial base flexion and extension are obviously comparable in a quantitative sense between taxa such as chimpanzees and humans whose cranial bases grow differently after birth, it is worth considering whether flexion and extension are sufficiently different *processes* to allow meaningful comparisons between the two in terms of development. At least three inter-related criteria can be used to evaluate whether flexion in humans and extension in non-human primates constitute a reasonable developmental (or biological) homology (Wagner, 1989): (1) do the components of the cranial base maintain the same spatial relationships in flexion and extension? (2) are flexion and extension generated by the same developmental stimuli and subject to the same developmental constraints? and (3) do flexion and extension share a similar sequence and/or pattern of growth?

This study provides insufficient information to test the first two criteria, but the third criterion suggests that there is some reason to be cautious when comparing cranial base angulation in humans and non-human primates. It is not clear to what extent the processes of flexion and extension occur at different synchondroses and are caused by

different stimuli. For example, most postnatal flexion in humans probably occurs at the spheno-occipital synchondrosis, but postnatal extension in non-human primates may also occur at the spheno-ethmoid and mid-sphenoidal synchondroses (Ford, 1958; Lager, 1958; Scott, 1958; Melsen, 1971; Michejda, 1971, 1972a, 1972b; Michejda & Lamey, 1971; Dmoch, 1975a, 1975b; Schulter, 1976; Giles *et al.*, 1981). In addition, both humans and non-human primates experience cranial base flexion prior to birth, presumably from the effects of increases in brain size (De Beer, 1937; Sperber, 1989), but it is unknown if, or to what extent, different stimuli induce postnatal extension in non-human primates and postnatal flexion in humans. More research is needed on the specific developmental processes that cause as well as constrain both cranial base flexion and extension. Such differences may explain why postnatal remodeling of the hypophyseal fossa moves sella posteriorly in humans, but anteriorly in non-human primates (Latham, 1972).

Although comparisons of CBA 1–4 in humans and non-human primates provide useful quantitative information on the spatial relationships between the endocranial fossae, cranial base flexion in humans clearly differs from cranial base extension in non-human primates in terms of pattern and timing, and therefore perhaps in terms of causation. In *H. sapiens*, the cranial base flexes postnatally by about 8–16° in an extremely rapid growth trajectory that occurs almost entirely during the first two years after birth. In contrast, the cranial base in *P. troglodytes* extends by about 15–28° (depending on the measurement used), possibly at a different location, and in a much more prolonged skeletal growth trajectory. The dramatic differences in timing of these processes is illustrated by the fact that cranial base flexion in humans is complete soon after the first deciduous teeth erupt, but cranial base extension in chim-

panzees continues until the eruption of the third permanent molars. Basicranial flexion as a postnatal growth process appears to be unique to humans among extant primates.

Given these contrasts, can we say that the processes which cause cranial base flexion in humans are the same as those which cause cranial base extension in non-human primates? In humans, it seems reasonable to assume that expansion of the brain is a major stimulus of postnatal cranial base flexion. However, the fact that the majority of cranial base extension in chimpanzees occurs *after* the brain has ceased to grow suggests that, in these primates, the processes of postnatal cranial base extension may be influenced more by facial than neural stimuli (Dmoch, 1976). This possibility, however, does not negate any adaptive relationship between cranial base angulation and brain size relative to basicranial length (Ross & Ravosa, 1993), but does indicate that facial growth processes may contribute to much of the variation in cranial base extension in non-human primates but not in humans. This hypothesis merits further study.

An additional consideration is how best to measure cranial base angles. Because flexion and extension are complex and varied developmental processes, they are difficult to characterize satisfactorily using any single measure. As we have shown above, the four internal cranial base angles used in this study provide more or less comparable results within *P. troglodytes* and *H. sapiens*. There is no best or most useful measure of the angle of the cranial base. In terms of their growth trajectories, CBA 1–4 all flex or extend at roughly the same rate relative to each other (see Figure 5). Also, for humans, the growth trajectory of CBA 5 is similar to those of CBA 1–4. However, the contrasts in how these angles quantify spatial relationships between the endocranial fossae sometimes result in low correlations between different measures (Table 5). Since the

amount of movement for various cranial base angles may differ substantially, the choice of which cranial base angle to use depends to a large extent on the taxa and research questions under consideration. For example, studies of interactions between the face and basicranium should use CBA 1 or 3, because the anterior cranial floor (from sphenoidale–foramen caecum) is a growth counterpart of the face (Enlow, 1990; Spoor, 1997). In contrast, studies (such as this) which examine the relationship between the cranial base and shape of the vocal tract should probably focus on CBA 5, since this angle most directly measures the orientations of the clivus and the inferior surface of the body of the sphenoid that forms the superior margin of the pharynx.

Cranial base angulation and vocal tract dimensions

The above data on postnatal cranial base flexion in humans also has implications for evaluating attempts to predict vocal tract dimensions in extant humans, and to reconstruct vocal tract dimensions in fossil hominids. In particular, it is evident that both internal and external cranial base flexion have no direct relationship with the vertical growth of the pharynx in humans. Consequently, measurements of cranial base angulation cannot be used to make inferences about the dimensions of the human vocal tract. There are several reasons to suggest that no such relationship should exist. First, cranial base angulation and vocal tract growth occur at different rates and at different times. Second, the position of the hyoid and larynx relative to the palate appears to be highly correlated and possibly dependent on certain dimensions of the mandible and maxilla that grow independently of cranial base flexion. With the possible exception of the unique configuration of neonates (Crelin, 1973), the hyoid body must lie inferior to the origins of its various muscular insertions on the mandible; as the mandible

and oropharynx grow inferiorly, the position of the hyoid and larynx must also move along with the mandible to maintain proper pharyngeal function.⁴ As Falk (1975) noted, such an inferior position of the hyoid with respect to the mandible is especially necessary in an orthograde biped with an upright cervical vertebral column in which the infrahyoid muscles position the hyoid below the mandible. In a less orthograde quadruped, the infrahyoid muscles can and do pull the hyoid more posteriorly relative to the mandible. As we have shown, hyoid position relative to the palate is strongly dependent on the position of the mandible but independent of CBA 1–5 because the maxilla and mandible grow through processes that correlate weakly with rotation of the posterior portion of the cranial base. In particular, the maxilla elongates mostly through primary displacement along its posterior margin, and grows inferiorly through drift and displacement at various other locations (see Enlow, 1990). In turn, the mandible grows inferiorly and anteriorly along with the maxilla, which explains the independence of the antero–posterior and supero–inferior dimensions of the vocal tract from CBA 1–5. Instead, these dimensions relate to the growth of the midface and lower face relative to the middle cranial fossa.

Consequently, the spatial relationships between the larynx, hyoid body, mandible, and palate in humans (summarized in Table 6) allow prediction of the vertical height of the vocal tract from a human skull with a mandible. To what extent these relationships can be used to assess vocal tract dimensions in fossil hominids from their

⁴Young infants, in which the distance between the top of the pharynx and the larynx is small, can raise the hyoid and larynx sufficiently to form a seal with the soft palate (Negus, 1949; Laitman & Crelin, 1976; see also Larson & Herring, 1996). During skull growth in humans, this degree of elevation becomes impossible because of the greater vertical distance involved (Crelin, 1977; Sasaki *et al.*, 1977) and perhaps because there is insufficient space behind the soft palate to accommodate the larynx.

skulls is difficult, perhaps impossible to assess. Further, the above results indicate that if there is any correlation between exocranial flexion and pharynx dimensions as predicted by Laitman *et al.* (1978, 1979) and Laitman & Heimbuch (1982), then these effects are likely to be the consequence of mostly facial rather than basicranial growth processes (Dean, 1982: 50). Such predictions need to be tested ontogenetically using samples such as the Denver Growth Study described here. In addition, the major contrasts in the processes of cranial base flexion in humans and extension in non-human primates suggest that any correlations between neonatal human and adult non-human primate cranial base morphology and pharyngeal anatomy may have no developmental basis. The fairly obtuse external cranial base of adult non-human primates such as chimpanzees, although somewhat comparable to human neonates, has a markedly different ontogeny.

Finally, these results highlight the advantage of studying complex anatomical relationships such as the cranial base angle from an explicitly developmental perspective. The processes that cause postnatal flexion in the human cranial base are possibly unique to hominids, and differ in several important respects from those that cause cranial base extension in extant non-human primates. Comparative studies of cranial base angulation between solely adult human and non-human primates risk conflating the consequences of different developmental processes, complicating the ability to test hypotheses about the evolutionary basis for morphological similarities and differences among primates.

Acknowledgements

This research was made possible in part by funding from Rutgers University (to DEL) and by a grant from the Bigel Fellowship (to RCM). We are especially grateful to Dr

A. Moore for access to copies of the radiographs from the Denver Growth Study. We thank A. W. Crompton and M. Rutzmoser (Museum of Comparative Zoology, Harvard), B. Latimer and L. Jellema (Cleveland Museum of Natural History), R. McPhee, B. Mader, and the late W. Fuchs (American Museum of Natural History, New York), and D. Pilbeam (Peabody Museum, Harvard) for permission to study and radiograph the primate collections in their care. We would also like to thank K. Mowbray, who helped take the radiographs, and R. Bernstein, who helped take some measurements. Finally, we are extremely grateful to C. Dean, C. Ross, F. Spoor, D. Strait, D. Pilbeam, B. Wood, and two anonymous reviewers for their comments and suggestions on previous drafts of this paper.

References

- Adamadis, P. I. & Spyropoulos, N. M. (1983). The effects of lymphadenoid hypertrophy on the position of the tongue, the mandible and the hyoid bone. *Eur. J. Orthodont.* **5**, 287–294.
- Aganastopoulou, S., Karamaliki, D. D. & Spyropoulos, M. N. (1988). Observations on the growth and orientation of the anterior cranial base in the human foetus. *Eur. J. Orthodont.* **10**, 143–148.
- Anderson, D. & Popovich, F. (1983). Relation of cranial base flexure to cranial form and mandibular position. *Am. J. phys. Anthropol.* **61**, 181–187.
- Angst, R. (1967). Beitrag zum formwandel des craniums der ponginen. *Z. Morph. Anthropol.* **58**, 109–151.
- Antón, S. C. (1989). Intentional cranial vault deformation and induced changes in the cranial base and face. *Am. J. phys. Anthropol.* **79**, 253–267.
- Arensburg, B., Schepartz, L. A., Tillier, A.-M., Vandermeersch, B. & Rak, Y. (1990). A reappraisal of the anatomical basis for speech in Middle Paleolithic hominids. *Am. J. phys. Anthropol.* **83**, 137–146.
- Ashton, E. H. (1957). Age changes in the basicranial axis of the Anthropoidea. *Proc. Zool. Soc. Lond.* **129**, 61–74.
- Baume, J. L. (1957). A biologist looks at the sella point. *Europ. Orthodont. Soc. Trans.* **33**, 150–159.
- Bergland, O. (1965). The bony nasopharynx. *Acta Odont. Scand.* **21**, 7–135.
- Biegert, J. (1957). Der formandel des primateschindels und seine beziehungen zur ontogenetischen entwickelung und den phylogenetischen spezialisationen der kopforgane. *Morph. Jahrbuch.* **98**, 77–199.
- Biegert, J. (1963). The evaluation of characters of the skull, hands and feet for primate taxonomy. In (S. L. Washburn, Ed.) *Classification and Human Evolution*, pp. 116–145. Chicago: Aldine de Gruyter.
- Björk, A. (1951). The significance of growth changes in facial pattern and their relationship to changes in occlusion. *Dent. Rec.* **71**, 197–208.
- Björk, A. (1955). Cranial base development. *Am. J. Orthod.* **41**, 198–225.
- Blechschild, M. (1976). Biokinetics of the developing basicranium. In (J. F. Bosma, Ed.) *Development of the Basicranium*, pp. 44–53. Bethesda, Maryland: U.S. Department of Health, Education, and Welfare.
- Broadbent, B. H. (1931). A new X-ray technique and its application to orthodontia. *Angle Orthodont.* **1**, 45–66.
- Broadbent, B. H. Sr, Broadbent, B. H., Jr & Golden, W. H. (1975). *Bolton Standards of Dentofacial Developmental Growth*. St Louis: C.V. Mosby.
- Brodie, A. G. (1941). On the growth pattern of the human head from the third month to the eighth year of life. *Am. J. Anat.* **68**, 208–262.
- Brodie, A. G. (1953). Late growth changes in the human face. *Angle Orthodont.* **23**, 146–157.
- Brodie, A. G. (1955). The behaviour of the cranial base and its components as revealed by serial cephalometric roentgenograms. *Angle Orthodont.* **25**, 148–160.
- Bromage, T. G. (1992). The ontogeny of *Pan troglodytes* craniofacial architectural relationships and implications for early hominids. *J. hum. Evol.* **23**, 235–251.
- Burr, D. B. (1976). Neandertal vocal tract reconstructions: A critical appraisal. *J. hum. Evol.* **5**, 285–290.
- Cameron, J. (1924). The cranio-facial axis of Huxley. Part I. Embryological considerations. *Trans. Roy. Soc. Can.* **18**, 115–123.
- Cameron, J. (1925). The cranio-facial axis of Huxley. Part II. Comparative anatomy. *Trans. Roy. Soc. Can.* **19**, 129–136.
- Cameron, J. (1927a). The main angle of cranial flexion (the nasion-pituitary-basion angle). *Am. J. phys. Anthropol.* **10**, 275–279.
- Cameron, J. (1927b). The pituitary-nasion-basion angle. A new cranial angle: its significance in man, the anthropoids, and lower mammals. *Am. J. phys. Anthropol.* **10**, 280–286.
- Cameron, J. (1930). Craniometric memoirs. No. II. The human and comparative anatomy of Cameron's craniofacial axis. *J. Anat. Lond.* **64**, 324–336.
- Carlisle, R. C. & Siegel, M. I. (1974). Some problems in the interpretation of Neandertal speech capabilities: a reply to Lieberman. *Am. Anthropol.* **76**, 319–322.
- Carlisle, R. C. & Siegel, M. I. (1978). Additional comments on problems in the interpretation of Neandertal speech capabilities. *Am. Anthropol.* **80**, 367–372.
- Cartmill, M. (1970). The orbits of arboreal mammals. Unpublished Ph.D. Dissertation, The University of Chicago.
- Cousin, R. P., Fenart, R. & Deblock, R. (1981). Variations ontogenetiques des angles basicraniens et faciaux. *Bull. Mem. Soc. Anthropol. Paris* **8**, 189–212.

- Cramer, D. L. (1977). Craniofacial morphology of *Pan paniscus*: a morphometric and evolutionary appraisal. *Contrib. Primatol.* **10**, 1–64.
- Crelin, E. S. (1973). *Functional Anatomy of the Newborn: An atlas*. New Haven: Yale University Press.
- Crelin, E. S. (1977). *The Human Vocal Tract*. New York: Vanguard Press.
- D'Aloisio, D. & Pangrazio-Kulbersh, V. (1992). A comparative and correlational study of the cranial base in North American blacks. *Am. J. Dentofac. Orthopol.* **102**, 449–455.
- Dabelow, A. (1929). Über korrelationen in der phylogenetischen Entwicklung der Schädelform. I. *Morph. Jahrb.* **63**, 1–49.
- Dean, M. C. (1982). The comparative anatomy of the hominoid cranial base. Unpublished Ph.D. Dissertation, University of London.
- Dean, M. C. (1988). Growth processes in the cranial base of hominoids and their bearing on morphological similarities that exist in the cranial base of *Homo* and *Paranthropus*. In (F. E. Grine, Ed.) *Evolutionary History of the Robust Australopithecines*, pp. 107–112. New York: Aldine de Gruyter.
- Diewert, V. M. (1985). Development of human craniofacial morphology during the late embryonic and early fetal periods. *Am. J. Orthodontol.* **88**, 64–76.
- Dmoch, R. (1975a). Beiträge zum formenwandel des primatencraniums mit bemerkungen zu den sagittalen knickungsverhältnissen. II Streckenanalyse, I, Neurocranium. *Geg. Morph. Jb.* **121**, 521–601.
- Dmoch, R. (1975b). Beiträge zum formenwandel des primatencraniums mit bemerkungen zu den sagittalen knickungsverhältnissen. IV. Komplexueberbrückende merkmale und winkelanalyse. *Geg. Morph. Jb.* **121**, 625–668.
- Dmoch, R. (1976). Beiträge zum formenwandel des primatencraniums mit bemerkungen zu den sagittalen knickungsverhältnissen. V. Schlussbetrachtung, zussammenfassung, literatur und tabellenanhang. *Geg. Morph. Jb.* **122**, 1–81.
- Duchin, L. (1990). The evolution of articulate speech: comparative anatomy of the oral cavity in *Pan* and *Homo*. *J. hum. Evol.* **19**, 687–697.
- Duckworth, W. L. H. (1904). *Studies from the Anthropological Laboratory*. Cambridge: Cambridge University Press.
- Duterloo, H. S. & Enlow, D. H. (1970). A comparative study of cranial growth in *Homo* and *Macaca*. *Am. J. Anat.* **127**, 357–368.
- Eckel, H. E., Sittel, C., Zorowka, P. & Jerke, A. (1994). Dimensions of the laryngeal framework in adults. *Surg. Radiol. Anat.* **16**, 31–36.
- Enlow, D. H. (1968). *The Human Face*. New York: Harper and Row.
- Enlow, D. H. (1990). *Facial Growth, 3rd Edn*. Philadelphia: Saunders.
- Enlow, D. H. & Moyers, R. E. (1971). Growth and architecture of the face. *J. Am. Dent. Assoc.* **82**, 763–774.
- Falk, D. (1975). Comparative anatomy of the larynx in man and the chimpanzee: implications for language in Neanderthal. *Am. J. phys. Anthrop.* **43**, 123–132.
- Fant, G. (1960). *Acoustic Theory of Speech Production*. The Hague: Mouton.
- Flügel, C., Schram, K. & Rohen, J. W. (1993). Postnatal development of the skull base, neuro- and viscerocranium in man and monkey: morphometric evaluation of CT scans and radiograms. *Acta Anat.* **146**, 71–80.
- Ford, E. H. R. (1956). The growth of the foetal skull. *J. Anat.* **90**, 63–72.
- Ford, E. H. R. (1958). Growth of the human cranial base. *Am. J. Orthodont.* **44**, 498–506.
- George, S. L. (1978). A longitudinal and cross-sectional analysis of the growth of the postnatal cranial base angle. *Am. J. phys. Anthrop.* **49**, 171–178.
- Giles, W. B., Philips, C. L. & Joondeph, D. R. (1981). Growth in the basicranial synchondroses of adolescent *Macaca macaca*. *Anat. Rec.* **199**, 259–266.
- Gould, S. J. (1977). *Ontogeny and Phylogeny*. Cambridge, MA: Belknap Press.
- Haralabakis, N. B., Toutountzakis, N. M. & Yiagtzis, S. C. (1993). The hyoid bone position in adult individuals with open bite and normal occlusion. *Eur. J. Orthodont.* **15**, 265–271.
- Heintz, N. (1966). Le crâne des anthropomorphes: croissance relative, variabilité, évolution. *Musée Royal de L'Afrique Centrale—Tervuren, Annales Science Zoologiques (n.s.)* **6**, 1–122.
- Hofer, H. (1957). Zur kenntnis der kyphosen des primatenschädels. *Verh. Anat. Ges.* **54**, 54–76.
- Hofer, H. (1960). Studien zum problem des gestaltwandels des schädels der säugetiere, insbesondere der primaten. I. Die medianen krüemmungen des schädels und ihr ehfassung nach Landzert. *Z. Morph. Anthrop.* **50**, 299–316.
- Hofer, H. & Spatz, Wb. (1963). Studien zum problem des gestaltwandels des schädels der säugetiere, insbesondere der primaten. II. Über die kyphosen fetaler und neonater primatenschädel. *Z. Morph. Anthrop.* **53**, 29–52.
- Houghton, P. (1993). Neandertal supralaryngeal vocal tract. *Am. J. phys. Anthrop.* **90**, 139–146.
- Hoyle, D. A. (1991). The cranial base in normal and abnormal growth. *Neurosurg. Clin. N. Am.* **2**, 515–537.
- Huxley, T. H. (1867). On two widely contrasted forms of the human cranium. *J. Anat. Physiol.* **1**, 60–77.
- King, E. W. (1952). A roentgenographic study of pharyngeal growth. *Angle Orthod.* **22**, 23–37.
- Knott, V. B. (1969). Ontogenetic change of four cranial base segments in girls. *Growth* **33**, 123–142.
- Koski, K. (1960). Some aspects of the growth of the cranial base and the upper face. *Sart. Odontol.* **68**, 344–358.
- Krogman, W. M. (1931). Studies in growth changes in the skull and face of anthropoids. IV. Growth changes in the skull and face of the chimpanzee. *Am. J. Anat.* **47**, 325–342.
- Krogman, W. M. (1969). Growth changes in the skull, face, jaws and teeth of the chimpanzee. In (G. H. Bourne, Ed.) *The Chimpanzee*, Vol 1, pp. 104–164. Basel: Karger.

- Ladefoged, P. & Broadbent, D. E. (1957). Information conveyed by vowels. *J. Acoust. Soc. Am.* **29**, 98–104.
- Lager, H. (1958). A histological description of the cranial base in *Macaca rhesus*. *Europ. Odont. Soc. Trans.* **34**, 147–156.
- Laitman, J. T. & Crelin, E. S. (1976). Postnatal development of the basicranium and vocal tract region in man. In (J. F. Bosma, Ed.) *Development of the Basicranium*, pp. 206–219. Bethesda, Maryland: U.S. Department of Health, Education, and Welfare.
- Laitman, J. T., Heimbuch, R. C. & Crelin, E. S. (1978). Developmental change in a basicranial line and its relationship to the upper respiratory system in living primates. *Am. J. Anat.* **152**, 467–483.
- Laitman, J. T., Heimbuch, R. C. & Crelin, E. S. (1979). The basicranium of fossil hominids as an indicator of their upper respiratory systems. *Am. J. phys. Anthropol.* **51**, 15–34.
- Laitman, J. T. & Heimbuch, R. C. (1982). The basicranium of Plio-Pleistocene hominids as an indicator of their upper respiratory systems. *Am. J. phys. Anthropol.* **59**, 323–343.
- Landzert, T. (1866). Der Sattelwinkel und sein Verhältnis zur Pro- und Orthognathie. *Abhandl. Senckenb. naturf. G.* **6**, 19–165.
- Larson, J. E. & Herring, S. W. (1996). Movement of the epiglottis in mammals. *Am. J. phys. Anthropol.* **100**, 71–82.
- Latham, R. A. (1972). The sella point and postnatal growth of the human cranial base. *Am. J. Orthod.* **61**, 156–162.
- Le May, M. (1975). The language capability of Neanderthal man. *Am. J. phys. Anthropol.* **42**, 9–14.
- Lewis, A. B. & Roche, A. F. (1977). The saddle angle: constancy or change? *Angle Orthodont.* **47**, 46–54.
- Lieberman, P. & Crelin, E. S. (1971). On the speech of Neanderthal man. *Ling. Inq.* **1**, 203–223.
- Lieberman, P., Crelin, E. S. & Klatt, D. H. (1972). Phonetic ability and related anatomy of the newborn and adult human, Neanderthal man, and the chimpanzee. *Am. Anthropol.* **74**, 287–307.
- Lieberman, P. (1984). *The Biology and Evolution of Language*. Cambridge: Harvard University Press.
- Lieberman, P. (1991). *Uniquely Human*. Cambridge: Harvard University Press.
- Lieberman, P., Laitman, J. T., Reidenberg, J. S. & Gannon, P. J. (1992). The anatomy, physiology, acoustics and perception of speech: essential elements in analysis of the evolution of human speech. *J. hum. Evol.* **23**, 447–467.
- Lugoba, S. A. & Wood, B. A. (1990). Position and orientation of the foramen magnum in higher primates. *Am. J. phys. Anthropol.* **81**, 67–76.
- Magriples, U. & Laitman, J. T. (1987). Developmental change in the position of the fetal human larynx. *Am. J. phys. Anthropol.* **72**, 463–472.
- Maresh, M. M. (1948). Growth of the heart related to bodily growth during childhood and adolescence. *Pediatrics* **2**, 382–402.
- Maresh, M. M. & Washburn, A. H. (1938). Size of the heart in healthy children. *Am. J. Dis. Child* **56**, 33–60.
- McCammon, R. (1970). *Human Growth and Development*. Springfield: C.C. Thomas.
- Melsen, B. (1969). Time of closure of the sphenoccipital synchondrosis determined on dry skulls. A radiographic craniometric study. *Acta Odontol. Scand.* **27**, 73–90.
- Melsen, B. (1971). The postnatal growth of the cranial base in *Macaca rhesus* analyzed by the implant method. *Tandlaegebladet* **75**, 1320–1329.
- Merow, W. M. & Broadbent, B. H. (1990). Cephalometrics. In (D. H. Enlow, Ed.) *Facial Growth*, pp. 346–395. Philadelphia: W.B. Saunders.
- Michejda, M. (1971). Ontogenetic changes of the cranial base in *Macaca mulatta*. *Proc. Third Int. Congr. Primatol. Zurich 1970* **1**, 215–225.
- Michejda, M. (1972a). The role of basicranial synchondroses in flexure processes and ontogenetic development of the skull base. *Am. J. phys. Anthropol.* **37**, 143–150.
- Michejda, M. (1972b). Significance of basicranial synchondroses in nonhuman primates and man. *Proc. Third Conf. Exp. Med. Surg. Primates, Lyon* **1**, 372–378.
- Michejda, M. & Lamey, D. (1971). Flexion and metric age changes of the cranial base in the *Macaca mulatta*. Infants and juveniles. *Folia Primatol.* **34**, 133–141.
- Moore, W. J. & Lavelle, C. J. B. (1974). *Growth of the Facial Skeleton in the Hominoidea*. London: Academic Press.
- Moss, M. L. (1958). The pathogenesis of artificial cranial deformation. *Am. J. phys. Anthropol.* **16**, 269–286.
- Moss, M. L. (1963). Morphological variations of the crista galli and medial orbital margin. *Am. J. phys. Anthropol.* **21**, 259–264.
- Nagai, M., Kudo, A., Matsuo, I., Yokoyama, M., Manabe, J., Hasegawa, S. & Nakamura, S. (1989). Hyoid bone position and airway accompanied with influence of head posture. *J. Jap. Orthod. Soc.* **48**, 214–225.
- Nearey, T. (1978). *Phonetic Features for Vowels*. Bloomington: Indiana University Linguistics Club.
- Negus, V. (1949). *The Comparative Anatomy and Physiology of the Larynx*. New York: Hafner.
- Ortiz, M. H. & Brodie, A. G. (1949). On the growth of the human head from birth to the third month of life. *Anat. Rec.* **103**, 319–348.
- Peterson, G. E. & Barney, H. L. (1952). Control methods used in a study of the vowels. *J. Acoust. Soc. Am.* **30**, 175–184.
- Riedl, R. J. (1978). *Order in Living Organisms*. New York: Wiley.
- Ross, C. & Henneberg, M. (1995). Basicranial flexion, relative brain size, and facial kyphosis in *Homo sapiens* and some fossil hominids. *Am. J. phys. Anthropol.* **98**, 575–593.
- Ross, C. & Ravosa, M. J. (1993). Basicranial flexion, relative brain size, and facial kyphosis in non-human primates. *Am. J. phys. Anthropol.* **91**, 305–324.
- Roth, V. L. (1984). On homology. *Biol. J. Linn. Soc.* **22**, 13–29.

- Sasaki, C. T., Levine, P. A., Laitman, J. T. & Crelin, E. S. (1977). Postnatal descent of the epiglottis in man. *Acta Otolaryngol.* **103**, 169–171.
- Schäfer, W. (1975). Messungen zur stufung der menschlichen schädelbasis und winkelbestimmungen. *Geg. Morph. Jb.* **121**, 1–25.
- Schepartz, L. A. (1993). Language and modern human origins. *Yearb. Phys. Anthropol.* **36**, 91–126.
- Schneiderman, E. D. (1992). *Facial Growth in the Rhesus Monkey: a longitudinal and cephalometric study*. Princeton: Princeton University Press.
- Schulter, F. P. (1976). Studies of the basicranial axis: A brief review. *Am. J. phys. Anthropol.* **45**, 545–552.
- Schultz, A. H. (1955). The position of the occipital condyles and of the face relative to the skull base in primates. *Am. J. phys. Anthropol.* **13**, 97–120.
- Schultz, A. H. (1962). Metric age changes and sex differences in primate skulls. *Yearb. Phys. Anthropol.* **10**, 129–154.
- Scott, J. H. (1958). The cranial base. *Am. J. phys. Anthropol.* **16**, 319–348.
- Shapiro, R. (1960). *The Normal Skull: A roentgen study*. New York: Hoeber.
- Sirianni, J. E. & Swindler, D. R. (1979). A review of postnatal craniofacial growth in Old World monkeys and apes. *Yearb. Phys. Anthropol.* **22**, 80–104.
- Sirianni, J. E. & Van Ness, A. L. (1978). Postnatal growth of the cranial base in *Macaca nemestrina*. *Am. J. phys. Anthropol.* **49**, 329–340.
- Sivarajan, M. & Fink, B. R. (1990). The position and state of the larynx during general anesthesia and muscle paralysis. *Anesthesiology* **72**, 439–442.
- Smith, B. H. (1989). Dental development as a measure of life history in primates. *Evolution* **43**, 683–688.
- Smith, B. H., Crummett, T. L. & Brandt, K. L. (1994). Ages of eruption of primate teeth: A compendium for aging individuals and comparing life histories. *Yearb. Phys. Anthropol.* **37**, 177–231.
- Sokal, R. F. & Rohlf, F. H. (1981). *Biometry*. New York: W.H. Freeman.
- Sperber, G. H. (1989). *Craniofacial Embryology, Fourth Edition*. London: Wright.
- Spoor, C. F. (1997). Basicranial architecture and relative brain size of Sts 5 (*Australopithecus africanus*) and other Plio-Pleistocene hominids. *S. Afr. J. Sci.* **93**, 182–186.
- Stamrud, L. (1959). External and internal cranial base. *Acta Odontol. Scand.* **17**, 239–266.
- Stevens, K. N. & House, A. S. (1955). Development of a quantitative description of vowel articulation. *J. Acoust. Soc. Am.* **27**, 484–493.
- Tng, T. T. H., Chan, T. C. K., Hagg, U. & Cooke, M. S. (1994). Validity of cephalometric landmarks: An experimental study on human skulls. *Eur. J. Orthodont.* **16**, 110–120.
- Topinard, P. (1890). *Anthropology*. London: Chapman and Hall.
- Ursi, W. J. S., Trotman, C.-A., McNamara, J. A. & Behrents, R. G. (1993). Sexual dimorphism in normal craniofacial growth. *Angle Orthodont.* **63**, 47–56.
- Wagner, G. P. (1989). The biological homology concept. *Ann. Rev. Ecol. Syst.* **20**, 51–69.
- Weidenreich, F. (1924). The special form of the human skull in adaptation to the upright gait. *Z. Morph. Anthropol.* **24**, 157–189.
- Weidenreich, F. (1941). The brain and its rôle in the phylogenetic transformation of the human skull. *Trans. Am. phil. Soc.* **31**, 328–442.
- Weidenreich, F. (1945). The brachycephalization of modern mankind. *Swest. J. Anthropol.* **1**, 1–54.
- Williams, P. L., Bannister, L. H., Berry, M. M., Collins, P., Dyson, M., Dussek, J. E. & Ferguson, M. W. J. (1995). *Gray's Anatomy, 38th Edn*. Edinburgh: Churchill Livingstone.
- Winnberg, A., Panherz, H. & Westesson, P. L. (1988). Head posture and hyo-mandibular function in man: A synchronized electromyographic and videofluorographic study of the open-close-clench cycle. *Am. J. Orthod. Dentofac. Orthoped.* **94**, 393–404.
- Zuckerman, S. (1926). Growth changes in the skull of the baboon, *Papio porcarius*. *Proc. Zool. Soc. Lond.* **2**, 843–873.
- Zuckerman, S. (1955). Age changes in the basicranial axis of the human skull. *Am. J. phys. Anthropol.* **13**, 521–539.