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Anthropoid cranial base architecture and scaling relationships

This paper examines how various measures of basicranial length and cranial base angulation affect the relationship between basicranial flexion and relative brain size in anthropoids, including *Homo sapiens*. Most recent studies support the “spatial packing” hypothesis, that basicranial flexion in haplorhines maximizes braincase volume relative to basicranial length. However, a few studies find the basicranium is less flexed in *H. sapiens* than expected for other anthropoids, suggesting that other factors contribute to variation in hominin basicranial flexion. The measure of relative brain size used to test the spatial packing hypothesis, the Index of Relative Encephalization (IRE), is calculated with basicranial length (BL) in its denominator, so that shorter BL and larger brain size potentially inflate *H. sapiens* IREs. To investigate this problem, the lengths of midline cranial floor sections were scaled relative to the cube root of endocranial volume in 157 specimens from 18 anthropoid species. Results indicate that the posterior cranial base and planum sphenoidum are significantly shorter in *H. sapiens* than in other anthropoids, accounting for higher IREs. Including the cribriform plate in BL, advisable in studies using anthropoids, affects whether *H. sapiens* differs from other anthropoids for basicranial flexion vs. IRE. However, despite a shorter BL and elevated IRE, *H. sapiens* does not deviate significantly from the anthropoid relationship between basicranial flexion and relative brain size for two cranial base angles. Because different measures of cranial base angulation change how *H. sapiens* falls along the anthropoid regression line, it remains equivocal whether the basicranium is less flexed in *H. sapiens* than in other anthropoids when compared to relative brain size.


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Introduction

Three recent studies (Ross & Ravosa, 1993; Ross & Henneberg, 1995; Spoor, 1997) support the hypothesis that, in anthropoids, a relatively larger brain is accommodated by a more flexed cranial base.¹ According to this “spatial packing” hypothesis, a flexed basicranium is one way to maximize the volume of the braincase for a given

basicranial length (Moss, 1958; Biegert, 1963; Gould, 1977; Dean, 1988; Strait, 1999). Researchers disagree, however, about the extent to which other factors such as posture or facial orientation influence variations in hominin basicranial flexion (see also Biegert, 1963; Gould, 1977; Dean, 1986, 1988; Strait & Ross, 1999). The most popular alternative to the spatial packing hypothesis is the postural hypothesis that basicranial flexion is an adaptation to reposition the foramen magnum anteriorly (Bolk, 1909; Schultz, 1942, 1955; Ashton & Zuckerman, 1952, 1956; Ashton, 1957; DuBrul, 1977, 1979; Dean & Wood, 1981,

¹In this paper, the terms “flexion” and “flexed” are used specifically to denote the *state* of “a bending or sagittal rotation between (or within) skeletal elements” (Moss & Vilman, 1978:567) and not to indicate *processes* that occur during ontogeny.

1982), and reorient it ventrally (Bolk, 1910; Duckworth, 1915; Moore *et al.*, 1973; Adams & Moore, 1975), in order to place the occipital condyles beneath the center of mass of the head. Using kinematic data, Strait & Ross (1999) recently demonstrated that basicranial flexion is not correlated with posture or neck orientation in interspecific samples of haplorhine and strepsirhine primates, rejecting the postural hypothesis as an explanation for variations in basicranial flexion at this broad taxonomic level. However, the postural hypothesis may still be relevant for understanding hominin basicranial flexion (Wood-Jones, 1917; Weidenreich, 1924, 1941), since several hominin species have more flexed cranial bases than predicted for their relative brain sizes (Ross & Henneberg, 1995; Spoor, 1997).

Several other hypotheses have been proposed for the high degree of basicranial flexion in *Homo sapiens* and other hominins. First, a flexed cranial base can accommodate a more globular brain, which minimizes distances between neurons (Allman & Kaas, 1974; Barlow, 1986; Mitchison, 1991; Cherniak, 1995; Ross & Henneberg, 1995; Van Essen, 1997) and therefore possibly reduces “wiring length”. Second, the combination of a spheroid brain and flexed cranial base serves to reduce stresses in the region of the basicranium rostral to the occipital condyles (Demes, 1985). Lastly, increased flexion of the basicranium may be related to hyolaryngeal descent, either by reorienting the basioccipital and thus the attachments for several suprahyoid muscles and ligaments (Lieberman & Crelin, 1971; Lieberman *et al.*, 1972; but see Falk, 1975; Dean, 1982:50; Houghton, 1993), or else by decreasing significantly the dimensions of the nasopharynx, oropharynx, and oral cavity and thereby restricting room available for the airway, adenoid tissue, tongue and hyolaryngeal apparatus (Bergland, 1963; Laitman & Crelin, 1976; Laitman

et al., 1978, 1979; Laitman & Heimbuch, 1982; Tourne, 1991). The combination of an anteroposteriorly short oral cavity and oropharynx and a low larynx sets up a two-tube supralaryngeal vocal tract with equal horizontal and vertical proportions that permits quantal speech (for details, see Lieberman *et al.*, 1992).

Without discounting postural, bio-mechanical, speech and neural wiring hypotheses as possible adaptive bases for basicranial flexion, this study focuses solely on the spatial packing hypothesis. Two recent studies (Ross & Henneberg, 1995; Spoor, 1997) agree that, in anthropoids, the degree of basicranial flexion is related to the volume of the brain relative to length of the basicranium. However, these studies disagree about how this relationship differs between *H. sapiens* and other anthropoids. According to Ross & Ravosa (1993), there is a significant correlation among haplorhines between basicranial angulation (which they termed CBA²) and the Index of Relative Encephalization (IRE), which they calculated as the cube root of endocranial volume (ECV) divided by basicranial length (BL). Ross & Ravosa measured CBA as the angle between the endocranial surface of the basioccipital and the planum sphenoidale, and IRE as the cube root of ECV divided by a measure of BL that excludes the cribriform plate. Ross & Henneberg (1995) further argued that *H. sapiens* does not fit the haplorhine scaling relationship between CBA and IRE, but instead possesses a basicranium which is much less flexed than expected [see Figure 1(a,b)]. Ross & Henneberg (1995) suggested that there was a limit on basicranial flexion below 90° (see also Enlow, 1990:180) because basicranial flexion influences the position of the basioccipital relative to the anterior cranial base, face and pharynx, and may restrict the

²The measure of basicranial angulation used by Ross & Ravosa (1993) and Ross & Henneberg (1995), “CBA”, is referred to as CBA 4 in this paper.

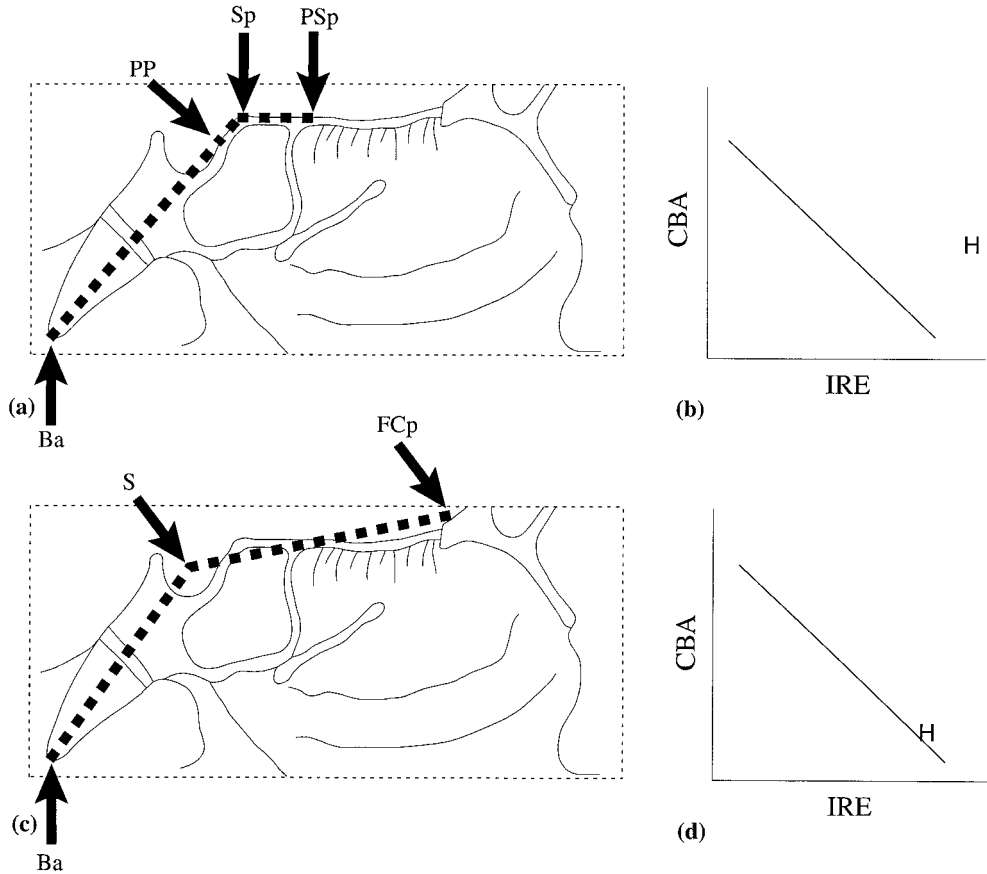


Figure 1. Close-up view of a midsagittal section of an *H. sapiens* infant cranium (see Figure 4) showing the measures of basicranial length (BL) used by Ross & Henneberg (1995) (a) and by Spoor (1997) (c), with results for RMA regressions of basicranial flexion *vs.* relative brain size (calculated as IRE—see text) using Ross & Henneberg's measure of BL (b) and using Spoor's measure of BL (d). (a) and (c) are modified from Enlow (1990). Ba, basion; S, sella; PP, pituitary point; Sp, sphenoidale; PSp, planum sphenoidum point; FCp, foramen caecum point.

room available for the airway, adenoid tissue, tongue and hyolaryngeal complex (see above). Spoor (1997) disputed Ross & Henneberg's argument using a slightly different set of analyses that regressed basicranial flexion, measured as the angle between the posterior cranial base (basion–sella) and the anterior cranial floor (sella–foramen caecum point), against IRE, measured as the cube root of ECV divided by a measure of BL that includes the cribriform plate. Spoor found that the *H. sapiens* basicranium is not less flexed than expected

for a primate of its relative brain size [see Figure 1(c,d)].

The differences between Ross & Henneberg (1995) and Spoor (1997) are of interest to comparative anatomists and paleontologists because they raise the question of whether the unique, highly flexed human cranial base³ is mostly a function of

³*H. sapiens*, and perhaps other hominin species, are unique among primates only. Several other mammals, most notably lagomorphs, possess cranial bases that are highly flexed for reasons other than maximizing the volume of the braincase for a given basicranial length (see, for example, DuBrul, 1950).

large brain size in recent hominids, or is a result of other factors such as bipedal posture or pharyngeal morphology. It is important to first test if the measurements used to quantify basicranial flexion and relative brain size are comparable between *H. sapiens* and other anthropoids. In particular, it is necessary to test how inclusion of the cribriform plate in measures of BL affects the relationship of *H. sapiens* relative to other anthropoids when basicranial flexion is scaled against relative brain size. If *H. sapiens* has a less flexed cranial base compared to other anthropoids, then it is possible that other factors like posture, facial orientation or pharyngeal configuration influence basicranial flexion instead of, or in addition to, spatial packing constraints.

After reviewing the midline anatomy of the cranial floor⁴ in human and nonhuman primates, this study compares scaling relationships of different sections of the cranial floor that reflect anatomical differences among anthropoids. Different measures of basicranial flexion and relative brain size are then compared to determine how cranial floor scaling relationships influence the cranial base architecture of *H. sapiens* relative to other anthropoids.

Midline cranial floor anatomy

This study investigates whether any section of the midline cranial floor (as observed on lateral radiographs) is relatively shorter in *H. sapiens* than in other anthropoids, thereby elevating human IRE values. Fortunately the midline cranial floor upon which the brain rests is divisible into several distinct sections which can be evaluated separately. A quick review of midline cranial base anatomy reveals that the IRE used by [Ross & Henneberg \(1995\)](#) differs from the IRE

used by [Spoor \(1997\)](#) because it excludes the cribriform plate from BL. Anthropoids have cribriform plates which are parallel relative to the planum sphenoidum, or which slope slightly inferoanteriorly or superoanteriorly [[Cartmill, 1970](#); see [Figure 2\(a\)](#)]. Unlike *H. sapiens*, most anthropoids have a cribriform plate which is set within a “deep olfactory pit” ([Cameron, 1930](#); [Aiello & Dean, 1990](#)) which lies within the ethmoidal notch of the frontal bone ([Allen, 1882](#)). This configuration differs from the condition prevalent in many mammals, in which the cribriform plate is close to perpendicular relative to the planum sphenoidum [[Baer & Nanda, 1976](#); [Moss & Vilman, 1978](#); see [Figure 2\(b\)](#)]. If the cribriform plate is parallel or nearly parallel relative to the planum sphenoidum, then it forms a part of the “base” on which the brain rests and should be included in BL.⁵ Therefore it is appropriate to include the cribriform plate in BL, and consequently in IRE, in investigations of anthropoid cranial architecture.

Another factor to consider when comparing scaling relationships between lengths of sections of BL and endocranial volume is the contribution of the midline frontal bone to the anterior cranial floor. In primates, the contribution of the frontal bone to the midline cranial base varies in a manner that is likely to influence BL and ultimately IRE values. In most nonhuman primates, the two “retro-ethmoid processes” of the frontal bone (see [Murphy, 1955](#) for terminology) meet in the midline between the sphenoid body and the cribriform plate of the ethmoid bone [[Wood-Jones, 1929](#); [Ashley-Montagu, 1943](#); see [Figure 3\(d\)](#)]. In hominoids,

⁵Many researchers include the cribriform plate as part of the cranial base (for example, see [Husson, 1950](#); [Scott, 1958](#); [Moore, 1981](#); [Spoor, 1997](#)), but, for embryological reasons, some researchers support a tripartite cranial base, including the ethmoid as part of the face (e.g., [Kummer, 1952](#); [Zuckerman, 1955](#); [Freye, 1959](#); [Hofer, 1965](#); [Ashton et al., 1975](#); [Baer & Nanda, 1976](#); [Moss & Vilman, 1978](#)).

⁴To maintain terminological accuracy, the term “midline cranial floor” will refer to the midline section including the cribriform plate and the term “midline cranial base” will refer to the midline section excluding the cribriform plate.

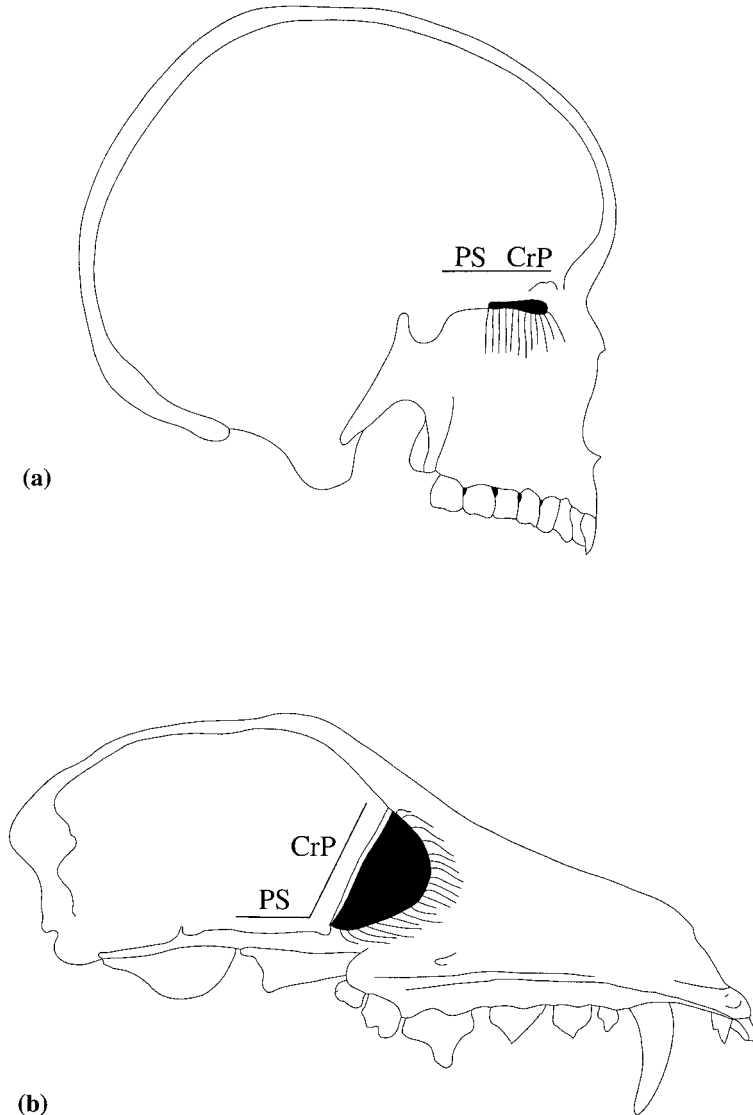


Figure 2. Midsagittal sections of *H. sapiens* (a) and carnivore (b) crania, showing the relative size of the olfactory bulb and the orientation of the cribriform plate (CrP) relative to the planum sphenoidale (PS). *H. sapiens* and other anthropoids have cribriform plates that are fairly parallel relative to the planum sphenoidale, while non-primate mammals and some strepsirhines have cribriform plates that are more nearly perpendicular relative to the planum sphenoidale. Both crania are oriented so that the planum sphenoidale is parallel to the bottom of the page. Modified from Enlow (1990).

however, a retro-ethmoid frontal bone is much more infrequent, an observation reflected in the pattern of sutures in the anterior cranial fossa. A visible sphenothmoid synchondrosis (i.e., one not cov-

ered by midline frontal bone) is common in *H. sapiens* and *Pongo* [Ashley-Montagu, 1943; Wood-Jones, 1948; see Figure 3(a) and (c)], but less so in *Pan* and *Gorilla* (Ashley-Montagu, 1943; Aiello & Dean,

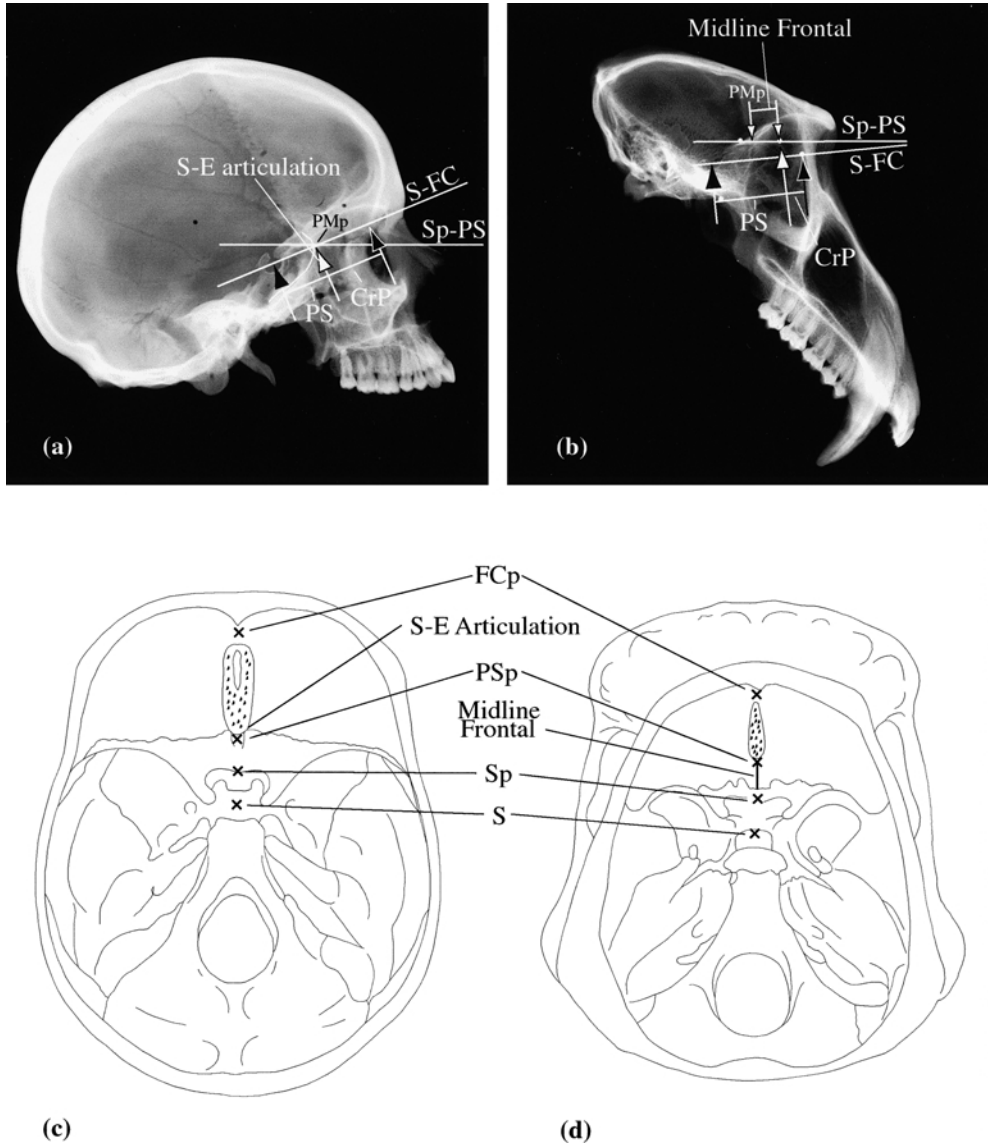


Figure 3. Anterior cranial floor anatomy in: Radiographs of hemisectioned *H. sapiens* (a) and *Papio hamadryas* (b) skulls; supero-inferior views of *H. sapiens* (c) and *Pan troglodytes* (d) skulls with calottes removed. Note that the sphenoid and ethmoid bones articulate in the midline in *H. sapiens* crania but not in the two non-human primate crania. See Table 1 for landmark definitions. The drawings in (c) and (d) are adapted from Aiello & Dean (1990); the crania in (a) and (b) are oriented so that the planum sphenoidaeum (Sp-PSp) is parallel to the bottom of the page.

1990). However, the configuration of bones in the anterior cranial fossa is highly variable intraspecifically; Butler (1949) and Murphy (1955) both found moderate numbers of *H. sapiens* skulls with retro-ethmoid frontal

bones (24% of 25 skulls and 18% of 453 skulls, respectively).

Contact between the sphenoid and ethmoid bones at the brain–cranial base interface is lost early during development in

most primates as the retro-ethmoid processes of the frontal bone invade the midline basicranium (Gregory, 1927, 1951). It is not clear why the frontal bone makes up a much smaller proportion of the anterior cranial fossa in hominoids than in other anthropoids. Wood-Jones (1929) suggested that, in primates with frontal bone in the midline cranial base, the orbits enlarge before the anterior portions of the cerebral hemispheres and thereby necessitate the expansion of the section of frontal bone shared between the cranial base and the orbital roof. Wood-Jones further suggested that the brain develops earlier in *H. sapiens*, so that the orbits become relatively smaller during ontogeny and frontal bone is not “recruited” into the midline cranial base. Ashley-Montagu (1943) proposed an alternative hypothesis that the extent of midline frontal contribution to the anterior cranial fossa is directly related to the degree of prognathism in a species. This hypothesis seems to be contradicted by the observation that *Pan*, *Pongo* and *Gorilla* have very little frontal bone in the midline cranial base in comparison to several more orthognathic species.

A shorter pre-sellar sphenoid body in *H. sapiens* than in other anthropoids may also contribute to IRE elevation in *H. sapiens*. The sphenoid bone is embryologically divided into pre- and post-sellar parts. The post-sellar portion of the sphenoid bone is grouped with the basioccipital as the “posterior cranial base” in this study [Figure 4(a)]. Scaling relationships of the pre-sellar sphenoid body (S-PMp; see Figure 4) are largely unexplored in primates. A recent hypothesis (Lieberman, 1998) suggested that modern and fossil *H. sapiens* have shorter pre-sellar sphenoid bodies than do archaic humans, including Neanderthals (but see Spoor *et al.*, 1999). However, the size of the pre-sellar sphenoid body in *H. sapiens* has not yet been compared to that of other anthropoids.

Variations in posterior cranial base length among anthropoids are also likely to influence BL and thus relative brain size. Following upon the observation that the noncortical brain rests directly atop the midline cranial base, Strait (1999) hypothesized that strong negative allometry of noncortical brain components (medulla, diencephalon and mesencephalon) limits basicranial length, constraining basicranial length to scale also with strong negative allometry relative to body mass. Implicit in this hypothesis is the prediction that the length of the posterior cranial base, the section of the midline cranial base most closely associated with the noncortical brain, scales with strong negative allometry relative to body mass. In other words, large-bodied primates should have relatively short posterior cranial bases. DuBrul & Laskin (1961; see also Dean, 1988) proposed an alternative hypothesis concerning the expected scaling relationship of the posterior cranial base. These researchers suggested that, in hominins, the posterior cranial base may be relatively shorter than in other primates due to architectural constraints related to upright posture.

Finally, it is necessary to consider how differences in cranial base angulation affect interspecific comparisons of the relationship between basicranial flexion and relative brain size. Measures of flexion are summations of angular changes in different sections of the cranial base (Moss & Vilman, 1978). Most traditional measures quantify the orientation of two chords relative to each other at some point near the center of the neurocranium, usually at the center of the sella turcica (sella), the most superior projection of the *tuberculum sellae* as it is superimposed on the midsagittal plane (sphenoidale), or at the point overlying the spheno-ethmoid synchondrosis in the midline (prospension). Basion-sella-nasion, the most commonly used angle, is problematic because nasion is not part of the cranial base, and its location

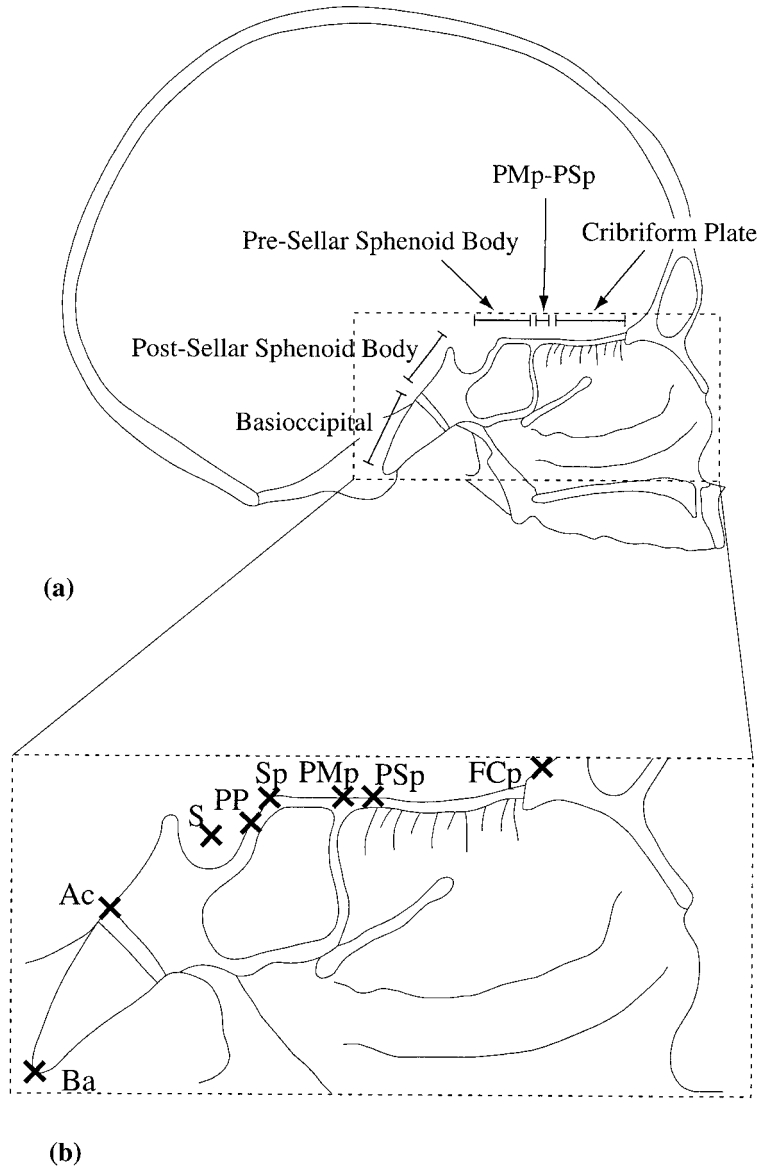


Figure 4. Midsagittal section of a *H. sapiens* infant cranium illustrating portions of the cranial base whose scaling relationships (relative to the cube root of endocranial volume) are investigated in this study. In this study, the basioccipital and post-sellar sphenoid body are combined as the measurement “posterior cranial base”, and the pre-sellar sphenoid body and PMp-PSp are combined as the “planum sphenoidum”. The planum sphenoidum plus the cribriform plate comprises the anterior cranial floor (a). The boxed area is blown up in (b), which illustrates points used to determine BL and measure basicranial flexion in this study. See Table 1 for landmark definitions. Modified from Enlow (1990).

may be affected by facial growth processes independent from cranial base growth. Alternatives to nasion include the foramen caecum (Spoor, 1997; Lieberman & McCarthy, 1999), the intersection of the orbital roof and inner surface of the frontal

bone projected onto the midsagittal plane (frontale) (George, 1978; Sirianni & Van Ness, 1978), or some point in the midline on or before the cribriform plate (Biegert, 1957; Scott, 1958; Cartmill, 1970; Cramer, 1977; George, 1978; Sirianni & Van Ness, 1978; Ross & Ravosa, 1993; Ross & Henneberg, 1995). One such point, the planum sphenoidum point (PSp), helps to delineate the planum sphenoidum, initially defined by Biegert (1957; see also Hofer, 1957, 1960; Hofer & Spatz, 1963; Angst, 1967) as the line drawn from the projection onto the midsagittal plane of the upper rim of the optic canal to the midpoint of the endocranial sphenoid-ethmoid suture. This plane has been modified by Cartmill (1970) and subsequent researchers (Schäfer, 1975; Dmoch, 1975a,b, 1976; Ross & Ravosa, 1993; Ross & Henneberg, 1995; Lieberman & McCarthy, 1999) so that its most anterior point lies on the area of bone directly posterior to the cribriform plate. In anthropoids other than humans, this plane regularly includes parts of the sphenoid and frontal, and perhaps the ethmoid.

Hypotheses

Given disagreement about how to quantify BL in anthropoids, two sets of hypotheses are tested. First, because various sections of the midline basicranium may be shorter in *H. sapiens* than in other anthropoids, scaling relationships of section lengths of BL are investigated relative to brain size. Specifically, logged measurements for lengths of the posterior cranial base (Ba-S), planum sphenoidum (S-PSp) and the cribriform plate (PSp-FCp) are scaled against the natural log of the cube root of endocranial volume [$\ln(\text{cube root ECV})$]. In all cases, a slope of isometry (slope = 1.0) indicates that shape (the ratio of the length of a section of the cranial base relative to ECV) is conserved with increasing size among anthropoids. In addition, it is possible, with only a slight loss of accuracy, to further subdivide

the anterior cranial base using the posterior maxillary (PM) point. Two measurements were derived in this fashion: length of the pre-sellar sphenoid body (S-PMp; see van der Linden & Enlow, 1971; Enlow & Azuma, 1975; Enlow, 1990; Lieberman, 1998), and a "left-over" measurement (PMp-PSp) which may represent parts of one or more of the following three bones: (1) an anterior extension of the sphenoid that crosses the midline, sometimes referred to as the "ethmoidal spine" of the sphenoid [Murphy's (1955) Types I, II III, V], (2) a posterior extension of the horizontal plate of the ethmoid in the midline behind the cribriform plate [Murphy's (1955) Types, V, VI, VII], and (3) frontal bone, present when the right and left retro-ethmoid processes of the frontal bone meet in the midline [Murphy's (1955) Types IV, VII]. Although potentially important for cataloguing variations among anthropoids and especially hominoids, the pattern of sutures and synchondroses in the anterior cranial fossa is not the main focus of this study; therefore, S-PMp is accepted as a rough estimate of the length of the pre-sellar sphenoid body in the midline (see van der Linden & Enlow, 1971). Logged measurements for the pre-sellar sphenoid body (S-PMp) and the section of the midline cranial base between the sphenoid body and the cribriform plate (PMp-PSp) are each scaled against $\ln(\text{cube root ECV})$. In the above scaling analyses, values for *H. sapiens* are compared to values predicted by the anthropoid regression line to determine if *H. sapiens* differs significantly from other anthropoids in terms of lengths of various sections of the cranial base.

Second, to test whether exclusion of the cribriform plate from BL influences the relationship between basicranial flexion and relative brain size, four measures of cranial base angulation were scaled against measures of relative brain size calculated with the cribriform plate (IRE 1) and

without the cribriform plate (IRE 5) (see Table 1). In these two sets of analyses, it is possible to assess the impact of different cranial base chords on the relationship between basicranial flexion and relative brain size, and whether these chords characterize spatial relationships differently in *H. sapiens* than other anthropoids.

Materials and methods

Sample

A sample of 17 extant anthropoid species from the American Museum of Natural History, New York (Table 2) was used for this study. In most cases, six adult crania (three males and three females) from each non-human primate species were radiographed and measured. Specimens were classified as adult if they exhibited complete eruption of the permanent dentition and fusion of the spheno-occipital synchondrosis. In addition, a sample of 60 adult *H. sapiens* crania was radiographed and measured, including 12 specimens (six males and six females) from five geographically diverse populations: Australians, southern Chinese, Europeans (Italy), northern Africans (Egypt), and sub-Saharan Africans (Ashanti) (see Lieberman, 1998; Lieberman *et al.*, 2000 for details). The Italian and Egyptian samples were radiographed at the Peabody Museum, Harvard University using the same protocol that was employed in this study. Strepsirhines are not included in this analysis because basicranial flexion and relative brain size are unrelated in this suborder (Ross & Ravosa, 1993), and because their orbits are not convergent on, nor contiguous with, their cranial bases in the midline (see Dabelow, 1929, 1931; Biegert, 1963).

Measurements

Each cranium was radiographed in lateral view using an ACOMA portable X-ray machine with a 70 mm distance from the

film to the collimator. Care was taken to capture the midsagittal plane for each cranium; slight parallax due to asymmetry or tilting was corrected using standard radiographic averaging procedures (see Merow & Broadbent, 1990). Radiographs with substantial parallax were excluded from this study. Table 1 lists the landmarks used to derive angular and linear measurements. Linear measurements were corrected for radiographic distortion using a correction factor calculated as maximum neurocranial length (Gl-Ops) measured from the cranium divided by maximum neurocranial length measured from the radiograph.

Five sections of the midline cranial base were investigated for their relationship to endocranial volume⁶ and their effect on measures of IRE (see Figure 4). Ba-S is the summed length of the basioccipital and the post-sellar sphenoid body. S-PSp is the planum sphenoidium, which is further subdivided into the pre-sellar sphenoid body (S-PMp) and the section of the midline cranial base (PMp-PSp) anterior to the sphenoid body but posterior to the cribriform plate. These two sections of the planum sphenoidium are delimited by the PM point, which is an approximation of the anterior extent of the greater wings of the sphenoid derived from two parasagittal shadows superimposed onto the midline. Because PMp may represent no more than a crude approximation of the anterior extent of the sphenoid body in the midline cranial base (see van der Linden & Enlow, 1971; Enlow & Azuma, 1975; Lieberman, 1998), results from scaling relationships of the pre-sellar sphenoid body should be treated with more caution than those for the posterior cranial base, planum sphenoidium and cribriform plate. Also, as noted above, the

⁶Endocranial volume (ECV) was used in this study instead of body mass so that the same individuals could be used to calculate ECVs and cranial base dimensions, and so that scaling relationships between the brain and underlying cranial base could be compared directly.

Table 1 Landmarks, chords, angles and formula used

Landmark or relevant anatomy	Abbreviation	Definition
Basion	Ba	The midline point on the anterior margin of the foramen magnum.
Clivus point	Ac	The most posterior point on the clivus before the dorsum sellae curves posteriorly, as projected onto the midsagittal plane.
Dorsum sellae	DS	Plate of bone whose anterior border forms the posterior boundary of the hypophyseal fossa, and whose posterior border forms the superior portion of the clivus.
Foramen caecum point	FCp	The pit on or above the cribriform plate between the crista galli or cribriform plate and the endocranial wall of the frontal bone.
Glabella	Gl	The most anterior point on the frontal bone as projected onto the midsagittal plane when the cranium is oriented in the Frankfurt Horizontal.
Opisthocranion	Ops	The most posterior point on the cranium as projected onto the midsagittal plane that is the farthest chord length from glabella.
Pituitary point	PP	The projection onto the midsagittal plane of the bulging convexity that forms the inferior border of the optic canal.
Planum sphenoidaeum point	PSP	The most superior and anterior midline point on the convexity just posterior to the cribriform plate.
Posterior maxillary point	PMp	The junction of the radiopaque lines representing the greater wings of the sphenoid with the planum sphenoidaeum, as projected onto the midsagittal plane.
Sella	S	The center of the hypophyseal fossa, or sella turcica, as seen on a lateral X-ray.
Sphenoidale	Sp	The most posterior and superior point on the tuberculum sellae, as projected onto the midsagittal plane. This point is the same as the posterior point of the planum sphenoidaeum (pps) used by Ross & Ravosa (1993) .
Chord or angle		
Foramen caecum line segment	FC	Line segment from sella to the foramen caecum point.
Planum sphenoidaeum	PS	Line segment from sphenoidale to the planum sphenoidaeum point.
Clival line segment	CL	Line segment from basion to the clivus point.
Sellar line segment	SL	Line segment from basion to sella.
Cranial base angle 1	CBA 1	Angle between the sellar and foramen caecum line segments (see also Spoor, 1997).
Cranial base angle 2	CBA 2	Angle between the sellar line segment and the planum sphenoidaeum.
Cranial base angle 3	CBA 3	Angle between the clival and foramen caecum line segments.
Cranial base angle 4	CBA 4	Angle between the clival line segment and the planum sphenoidaeum (see also Ross & Ravosa, 1993 ; Ross & Henneberg, 1995).
Formulas		
Basicranial length 1	BL 1	$Ba-PP+PP-Sp+Sp-PSP$ (see also Ross & Ravosa, 1993 ; Ross & Henneberg, 1995).
Basicranial length 2	BL 2	$Ba-S+S-FCp$ (see also Spoor, 1997).
Index of rel. encephalization 1	IRE 1	(Cube root of endocranial volume)/BL 1.
Index of rel. encephalization 5	IRE 5	(Cube root of endocranial volume)/BL 2.

Table 2 List of species with number of specimens and means and standard deviations for section lengths of BL

Species	<i>n</i> (M/F)	Cribriform plate	Planum sphenoid	Sphenoid body	"Left-over"	Posterior cran. base
		(PSP-FCp)	(S-PSp)	(S-PMp)	(PMp-PSp)	(Ba-S)
<i>Alouatta seniculus</i>	6 (3/3)	7.29 ± 1.12	26.70 ± 2.27	11.31 ± 1.31	13.56 ± 2.54	29.79 ± 3.14
<i>Aotus lemurinus</i>	6 (3/3)	5.31 ± 0.65	14.66 ± 1.25	4.49 ± 0.75	9.03 ± 0.72	14.52 ± 0.93
<i>Ateles geoffroyi</i>	6 (3/3)	8.41 ± 1.20	22.88 ± 1.34	10.46 ± 0.58	11.01 ± 0.94	27.22 ± 1.81
<i>Callithrix jacchus</i>	6 (3/3)	3.56 ± 3.56	11.81 ± 0.39	4.50 ± 0.44	6.55 ± 0.26	11.17 ± 0.66
<i>Cebus albifrons</i>	6 (3/3)	5.95 ± 1.23	21.67 ± 0.68	8.57 ± 2.04	11.54 ± 1.32	20.79 ± 2.00
<i>Cercopithecus aethiops</i>	6 (3/3)	7.49 ± 0.57	21.50 ± 2.16	8.87 ± 1.42	10.19 ± 1.28	20.11 ± 1.92
<i>Gorilla gorilla</i>	6 (3/3)	15.78 ± 2.44	24.09 ± 2.35	16.42 ± 3.30	4.12 ± 1.06	46.59 ± 9.09
<i>Homo sapiens</i>	60 (30/30)	22.83 ± 2.45	26.14 ± 2.48	20.50 ± 1.81	3.15 ± 1.10	41.31 ± 3.49
<i>Hylobates syndactylus</i>	6 (3/3)	9.27 ± 2.17	28.36 ± 2.58	11.10 ± 2.53	16.07 ± 1.84	28.85 ± 3.76
<i>Macaca fascicularis</i>	6 (3/3)	6.34 ± 0.81	19.79 ± 1.95	10.16 ± 1.26	9.02 ± 0.70	20.09 ± 2.40
<i>Pan paniscus</i>	1 (0/1)	16.73	22.31	15.43	8.46	29.37
<i>Pan troglodytes</i>	6 (3/3)	15.18 ± 1.70	26.96 ± 2.47	16.55 ± 2.40	10.24 ± 1.21	33.44 ± 2.08
<i>Papio anubis</i>	6 (3/3)	10.36 ± 1.63	26.89 ± 1.96	14.47 ± 1.32	9.22 ± 1.53	30.67 ± 2.24
<i>Pithecia monachus</i>	6 (3/3)	6.41 ± 0.60	18.08 ± 1.36	8.33 ± 0.87	9.36 ± 0.58	20.03 ± 0.87
<i>Pongo pygmaeus</i>	6 (3/3)	12.40 ± 1.75	22.38 ± 2.56	14.61 ± 1.63	8.02 ± 2.56	36.58 ± 5.31
<i>Presbytis melalophos</i>	6 (3/3)	6.37 ± 1.05	22.81 ± 2.39	8.95 ± 1.63	12.14 ± 1.04	19.89 ± 1.94
<i>Procolobus verus</i>	6 (3/3)	7.94 ± 0.80	22.68 ± 2.30	10.22 ± 2.18	10.60 ± 1.36	22.35 ± 1.35
<i>Saguinus fuscicollis</i>	6 (3/3)	3.74 ± 0.18	13.59 ± 0.67	5.77 ± 0.64	6.67 ± 0.79	11.97 ± 0.42

measurement PMp-PSp may represent one or more of the following bones: (1) an anterior extension of the sphenoid, (2) a posterior extension of the ethmoid, or (3) midline frontal bone. Both S-PMp and PMp-PSp are measured perpendicular to the posterior maxillary (PM) plane for standardization. Finally, PSP-FCp approximates the length of the cribriform plate. PSp is near the posterior end of the cribriform plate, and FCp is near the anterior end. Both points border the cribriform plate but do not lie directly on it. In *H. sapiens* FCp may be raised above the level of the cribriform plate and set in the crista galli of the ethmoid bone (Aiello & Dean, 1990). Both S-PSp and PSP-FCp were measured parallel to the foramen caecum line.

Several of the many cranial base angles used in studies that examine the relationship between basicranial flexion and relative brain size were chosen for use in this study. Table 1 lists the angles, measures of basicranial length, and measures of relative brain size, and Figure 5 illustrates the four

measures of flexion used in this study. Angles were measured to the nearest degree using a protractor. ECV was measured by filling each cranium with mustard seed and reading the resulting volume from a graduated cylinder accurate to the nearest 1 ml. In previous studies, relative brain size (termed IRE1) has been calculated in two different ways, each of which employed a different measure of BL. IRE 1, originally defined by Ross & Ravosa (1993), is calculated with BL 1, defined as Ba-PP+PP-Sp+Sp-PSp. IRE 5, equivalent to the IRE used by Spoor (1997), is calculated with BL 2, defined as Ba-S+S-FCp (see Table 1 and Figure 1). To avoid confusion, Spoor's measurement is referred to as IRE 5 in this paper in order to distinguish it from the four other measures of relative brain size used by Ross & Ravosa (1993) and Ross & Henneberg (1995).

Measurement precision was tested by replicating the full set of linear and angular measurements on five radiographs from anthropoids of different sizes (*Pithecia monachus*, *Aotus lemurinus*, *Pan paniscus*,

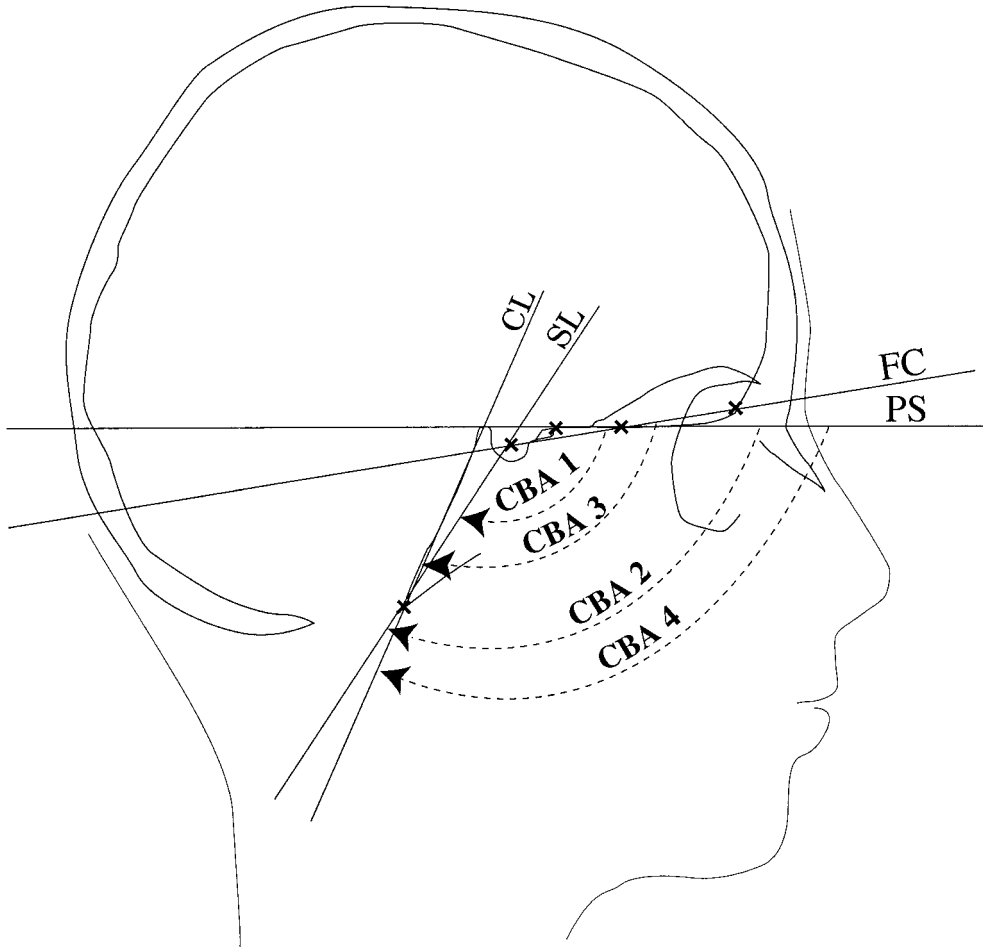


Figure 5. Midsagittal section of a *H. sapiens* cranium showing the cranial base angles used in this study. See Table 1 for measurement definitions.

H. sapiens, *Gorilla gorilla*) on five separate days, for a total of 25 tracings. Average measurement error was 1.30 mm for linear measurements and 1.5° for angular measurements, neither of which constituted a significant difference from zero at the $P < 0.05$ level using single factor ANOVA. Measurement accuracy was tested by radiographing crania of *Papio hamadryas* and *H. sapiens* [these crania are illustrated in Figure 3(a,b)] with and without metal shot on several points (Ac, Ba, FC_L, PMp, PS_L, and Sp); every combination of linear and angular measurements between these points was

then taken on the two radiographs. Average measurement error was 0.78 mm for linear measurements and 1.5° for angular measurements.

Analyses

One ratio, planum sphenoidum (S-PS_L) length divided by total anterior cranial floor length (S-FC_L), was calculated in order to compare the relative contributions of the cribriform plate and the planum sphenoidum to the anterior cranial floor. A single factor ANOVA was used to determine differences between values for platyrrhines,

cercopithecoids, hylobatids, great apes and *H. sapiens* that are statistically significant at the $P < 0.05$ using Fisher's PLSD test. In addition, scaling relationships of section lengths of BL relative to endocranial volume were investigated by reduced major axis (RMA) regression of five logged measurements (Ba-S, S-Psp, S-PMp, PMp-Psp, Psp-FCp) against $\ln(\text{cube root ECV})$. Confidence limits of the slope were calculated following Jolicouer & Mossiman (1968). For $\ln(\text{posterior cranial base})$, $\ln(\text{pre-sellar sphenoid body length})$, and $\ln(\text{cribriform plate length})$, the RMA regression lines were fitted to all anthropoids except *H. sapiens*, and values for deviations of points from the line were calculated as the area of the triangle enclosing the line and both the horizontal and vertical deviations from the line. This calculation is appropriate because RMA regression minimizes these parameters. *T*-tests were used to assess whether deviations for *H. sapiens* were significantly different from deviations for all other anthropoids ($P < 0.05$). For $\ln(\text{PMp-Psp})$ and $\ln(\text{planum sphenoidum length})$, the RMA regression line was fitted to all anthropoids excluding *H. sapiens*, as for the analyses above, and fitted to all anthropoids excluding hominoids.

In order to assess the effects of different cranial base angles and measures of relative brain size on the topology of the regression line, and the placement of *H. sapiens* relative to other anthropoids, four measures of basicranial flexion were regressed against IRE 1 and IRE 5. Different measures of angulation were then compared while holding IRE constant. Cranial base angles 1 and 2 use the same posterior cranial base chord (sellar line segment), so any differences between them are caused by variation in the anterior cranial base chords. Cranial base angles 1 and 3 use the same anterior cranial base chord (foramen caecum line segment), so any differences between them are due to variation in the posterior cranial base

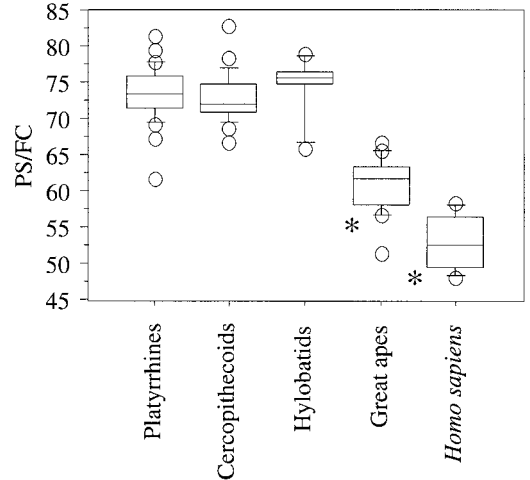


Figure 6. Box plot of the percentage of anterior cranial floor length (FC) constituted by the planum sphenoidum (PS). *indicates that *H. sapiens* and great apes possess relatively longer cribriform plates and shorter planum sphenoida compared to platyrrhines, cercopithecoids and hylobatids.

chords. Finally, cranial base angles 1 and 4 use different anterior and posterior cranial base chords, so differences due to simultaneous variation in both chords are investigated by holding IRE constant. As above, all RMA regression equations were computed excluding *H. sapiens*, and tests of significance were the same as for the above scaling analyses.

Results

Scaling relationships

The relative contribution of the planum sphenoidum to the entire anterior cranial floor is presented in Figure 6. The planum sphenoidum is relatively smaller, and the cribriform plate relatively larger, in hominoids than in other anthropoids. Furthermore, *H. sapiens* possesses a significantly shorter planum sphenoidum and a significantly longer cribriform plate compared to the great apes when anterior cranial floor length is taken into account. Therefore, the relatively short length of the planum

Table 3 RMA regression analysis results for scaling relationships of section lengths of BL relative to the cube root of ECV

Section of BL	Figure no.	Intercept	Slope	Confidence intervals		<i>r</i>
				Lower	Upper	
Cribriform plate	7(a)	0.56	1.04	0.970	1.188	0.971
Planum sphenoidum (w/great apes)	7(b)	2.18	0.60	0.445	0.808	0.835
Planum sphenoidum (w/o great apes)	7(b)	1.94	0.84	0.681	1.026	0.951
Pre-sellar sphenoid body	7(c)	0.79	1.03	0.855	1.241	0.944
PMp–PSP (w/great apes)	7(d)	3.22	−0.70	−0.412	−1.177	0.032
PMp–PSP (w/o great apes)	7(d)	1.32	0.78	0.528	1.152	0.799
Posterior cranial base	7(e)	1.80	0.94	0.806	1.096	0.959

Slope values in bold are not significantly different from isometry.

sphenoidum may contribute to high IRE values in great apes and especially in *H. sapiens*. Table 2 presents means and standard deviations for lengths of sections of BL, and Table 3 presents results for regression analyses of the scaling relationships of these section lengths of BL relative to the cube root of ECV. The length of the cribriform plate scales with isometry relative to ECV across anthropoids, including *H. sapiens* [Table 3, Figure 7(a)]. Planum sphenoidum length [Figure 7(b)] scales with negative allometry relative to ECV whether or not great apes are included in the regression analysis. However, when great apes are excluded from the regression analysis, confidence intervals of the slope include isometry, and the correlation coefficient is higher ($r=0.951$ vs. $r=0.835$ when great apes are included) (see Table 3). The two sections of the planum sphenoidum, the pre-sellar sphenoid body [Figure 7(c)] and the “leftover” section between the sphenoid body and cribriform plate [Figure 7(d)], scale with isometry and negative allometry, respectively, relative to ECV (see Table 3). Although the value for the slope of $\ln(\text{PMp-PSP})$ vs. $\ln(\text{cube root ECV})$ is negatively allometric when hominoids are excluded from the regression analysis, confidence intervals of the slope include isometry because the correlation coefficient

is so low ($r=0.800$; 95% confidence interval=0.528–1.152). When hominoids are included in the analysis, the correlation coefficient is highly insignificant ($r=0.032$). The pre-sellar sphenoid body in *H. sapiens* is slightly shorter than in other anthropoids [Figure 7(c)], but the “leftover” section of the planum sphenoidum is considerably shorter in all hominoids, especially in *H. sapiens* [Figure 7(d)]. The posterior cranial base scales with isometry relative to ECV in anthropoids, although *H. sapiens* is slightly but significantly deviant from this line [Figure 7(e)]. Thus, the posterior cranial base of *H. sapiens* is significantly shorter than predicted for an anthropoid of its endocranial volume.

Relationship between basicranial flexion and relative brain size

Species means and standard deviations for cranial base angles 1–4 and IRE 1 and 5 are given in Table 4. Species means for cranial base angles 3 and 4 are not significantly different from species means for cranial base angles 1 and 2, except in *H. sapiens*.

Figure 8 plots the scaling relationships between different measures of basicranial flexion and IRE 1, which is calculated without including the cribriform plate in BL [see Figure 1(a)]. In all four cases, values for *H. sapiens* are significantly different from

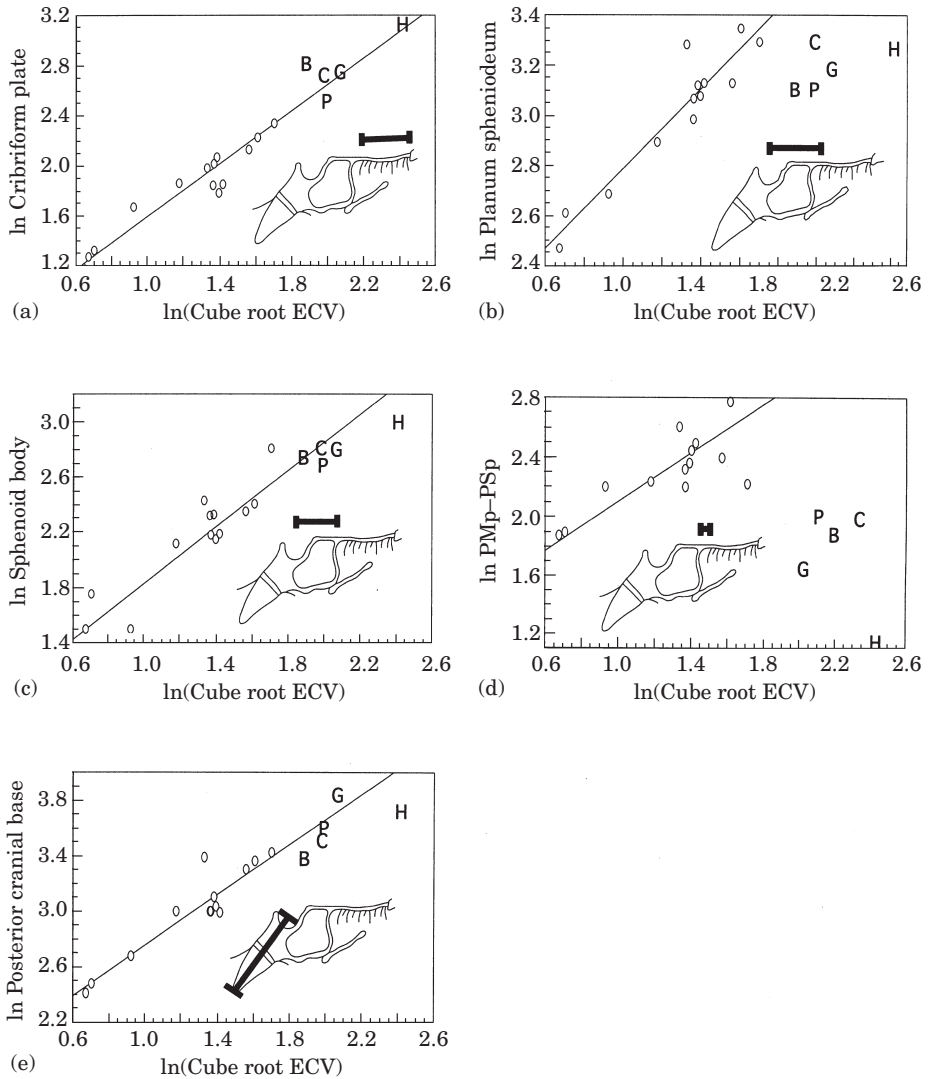


Figure 7. Scaling relationships of portions of the cranial base relative to $\ln(\text{cube root endocranial volume})$: cribriform plate (a), planum sphenodeum (b), pre-sellar sphenoid body (c), PMp-PSp (d), and the posterior cranial base (e). RMA regression lines were calculated excluding *H. sapiens* (H) in each graph. In (b) and (d), the regression line was also calculated excluding *Pan troglodytes* (C), *Pan paniscus* (B), *Pongo pygmaeus* (P) and *Gorilla gorilla* (G). Confidence intervals for slopes of the lines include isometry in each case, except when great apes are included in the regression analyses in (b) and (d) (see Table 3).

values predicted by the anthropoid regression line. These scaling relationships support the contention that IRE values are elevated in *H. sapiens* relative to other anthropoids because of a short planum sphenodeum, which may result from a

truncated midline cranial base segment between the sphenoid body and the cribriform plate [Figure 7(d)], as well as a slightly shorter posterior cranial base compared to other anthropoids [Figure 7(c)]. Figure 8(d) specifically duplicates the

Table 4 Means and standard deviations for cranial base angles 1–4 and IRE 1 and 5 by species

Species	CBA 1	CBA 2	CBA 3	CBA 4	IRE 1	IRE 5
<i>Alouatta seniculus</i>	188 ± 6.83	191 ± 6.01	188 ± 6.83	191 ± 6.01	0.67 ± 0.07	0.59 ± 0.06
<i>Aotus lemurinus</i>	186 ± 4.66	186 ± 4.45	186 ± 4.66	186 ± 4.45	0.85 ± 0.03	0.71 ± 0.02
<i>Ateles geoffroyi</i>	169 ± 3.25	163 ± 4.00	169 ± 3.25	163 ± 4.13	0.93 ± 0.03	0.81 ± 0.02
<i>Callithrix jacchus</i>	171 ± 1.97	164 ± 3.98	171 ± 1.97	164 ± 4.03	0.82 ± 0.03	0.72 ± 0.02
<i>Cebus albifrons</i>	171 ± 4.02	166 ± 5.61	171 ± 4.02	166 ± 5.61	0.93 ± 0.06	0.82 ± 0.05
<i>Ceropithecus aethiops</i>	168 ± 2.70	169 ± 4.02	168 ± 3.40	169 ± 3.80	0.91 ± 0.05	0.79 ± 0.04
<i>Gorilla gorilla</i>	154 ± 4.25	146 ± 4.83	153 ± 5.09	146 ± 4.51	1.10 ± 0.14	0.91 ± 0.08
<i>Homo sapiens</i>	136 ± 5.21	119 ± 7.04	128 ± 5.30	111 ± 6.81	1.63 ± 0.11	1.22 ± 0.06
<i>Hylobates syndactylus</i>	172 ± 5.89	161 ± 7.46	172 ± 6.17	162 ± 7.05	0.87 ± 0.07	0.75 ± 0.05
<i>Macaca fascicularis</i>	165 ± 3.77	166 ± 1.60	165 ± 3.77	166 ± 1.60	0.94 ± 0.03	0.83 ± 0.03
<i>Pan paniscus</i>	148	135	148	135	1.25	0.96
<i>Pan troglodytes</i>	156 ± 6.25	149 ± 5.25	155 ± 6.28	149 ± 5.31	1.19 ± 0.07	0.96 ± 0.07
<i>Papio anubis</i>	151 ± 3.59	151 ± 6.33	151 ± 3.59	151 ± 6.33	0.93 ± 0.04	0.80 ± 0.03
<i>Pithecia monachus</i>	173 ± 2.97	180 ± 4.48	173 ± 2.97	180 ± 4.48	0.84 ± 0.04	0.72 ± 0.03
<i>Pongo pygmaeus</i>	150 ± 4.37	135 ± 2.92	149 ± 5.30	134 ± 2.84	1.17 ± 0.08	1.00 ± 0.04
<i>Presbytis melalophos</i>	159 ± 4.87	151 ± 4.31	159 ± 4.87	151 ± 4.31	0.93 ± 0.05	0.83 ± 0.02
<i>Procolobus verus</i>	166 ± 3.64	149 ± 3.50	166 ± 3.64	149 ± 3.50	0.85 ± 0.03	0.74 ± 0.03
<i>Saguinus fuscicollis</i>	173 ± 3.81	167 ± 5.07	173 ± 3.81	167 ± 5.07	0.77 ± 0.03	0.68 ± 0.02

analysis of Ross & Henneberg (1995), with similar results.

Figure 9 plots the scaling relationships between different measures of basicranial flexion and IRE 5, which is calculated by including the cribriform plate in BL [see Figure 1(b)]. *H. sapiens* is significantly less flexed (or IRE is larger) when the sellar line segment is used to measure the posterior chord of the cranial base [Figure 9(a,b)], but *H. sapiens* is not significantly less flexed (IRE is not larger) when the clival line segment is used to measure the posterior chord of the cranial base [Figure 9(c,d)]. Figure 9(a) conflicts with Spoor's (1997) Figure 2 (see discussion). Figure 9(d) duplicates the analysis of Ross & Henneberg (1995), but with IRE 5 in place of IRE 1. Contrary to Ross & Henneberg (1995), values for *H. sapiens* are not significantly different from values predicted using the RMA regression equation.

A comparison of Figure 9(a) and (b) illustrates that the choice of anterior cranial base chord (foramen caecum line segment *vs.* planum sphenoidum) alters the placement of *H. sapiens* relative to the anthropoid

regression line slightly, but not significantly. In *H. sapiens*, the planum sphenoidum is more highly flexed relative to the posterior cranial base than is the foramen caecum line segment.

A comparison of Figure 9(a) and (c) illustrates that the choice of posterior cranial base chord (sellar *vs.* clival line segments) significantly influences the placement of *H. sapiens* relative to the anthropoid regression line. Humans have a unique cranial base configuration in which the anteroposterior length of the dorsum sellae, along with the extreme flexion of the base, causes an angular difference between the sellar and clival line segments (see Table 4). With the exception of *H. sapiens*, all anthropoids have posterior cranial base lines that are concordant (the sellar and clival line segments are equivalent), so that cranial base angle 1 is largely equivalent to cranial base angle 3 and cranial base angle 2 is largely equivalent to cranial base angle 4 (see Table 4).

A comparison of Figure 9(a) and (d) illustrates that using different methods of quantifying anterior and posterior cranial base line segments simultaneously

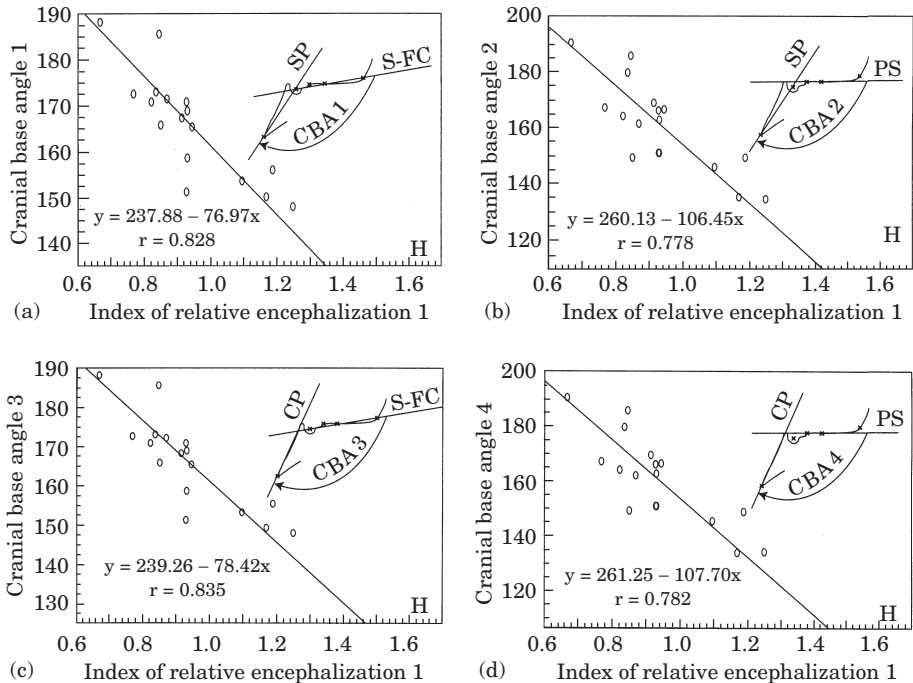


Figure 8. RMA regressions of four measures of basicranial flexion *vs.* IRE 1 (calculated excluding the cribriform plate from BL). Regression lines were calculated excluding *H. sapiens* (H), who deviate significantly from the regression line in all cases.

significantly affects whether *H. sapiens* deviates from the anthropoid regression line. Using cranial base angle 1, *H. sapiens* deviates significantly from the anthropoid regression line, but the *H. sapiens* value for cranial base angle 4 is not significantly different from the value predicted by the regression line.

Discussion

Whether *H. sapiens* deviates from the anthropoid regression line for basicranial flexion *vs.* relative brain size depends largely on the measurements used to characterize these two parameters. It is clear from the contrast between Figures 8 and 9 that different methods of characterizing BL, and therefore IRE, have the greatest effect on the placement of *H. sapiens* relative to the anthropoid regression line. This effect is

illustrated further in Figures 3, 6 and 7, which show that the planum sphenoidum makes up a relatively smaller proportion of anterior cranial floor length in hominoids compared with other anthropoids. This reduction in turn elevates IRE values in these species and especially in *H. sapiens*, since the divisor of the IRE equation (BL) is significantly lower in all hominoids. In contrast, in interspecific regression analyses which employ measures of BL (and thus IRE) that include the length of the cribriform plate, *H. sapiens* may not be significantly different from hominoids and other anthropoids [Spoor, 1997; this study, Figure 9(c) and (d)]. In anthropoids, expansion of the frontal lobes has rotated the frontal lobes and the cribriform plate so that both are oriented more horizontally (parallel) relative to the planum sphenoidum (Biegert, 1957, 1963; Cartmill, 1970;

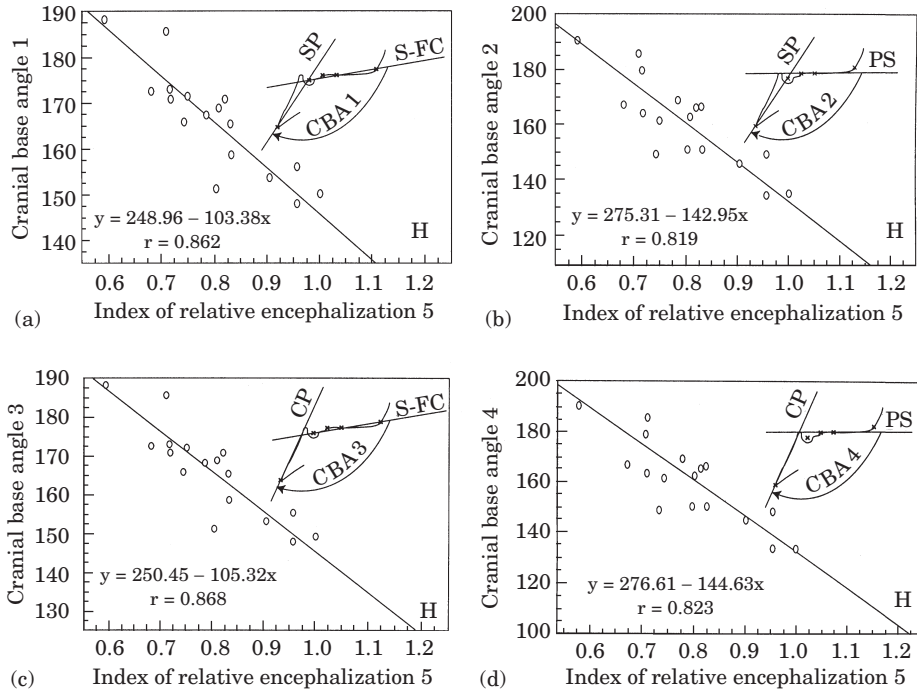


Figure 9. RMA regressions of four measures of basicranial flexion vs. IRE 5 (calculated including the cribriform plate in BL). Regression lines were calculated excluding *H. sapiens* (H), who deviate significantly from the regression line in two out of the four cases [(a) and (b)].

Enlow, 1990). Because of this frontal expansion, the cribriform plate forms part of the cranial floor in anthropoids, and hypotheses which use BL to estimate the influence of the brain on basicranial flexion should therefore include the cribriform plate as part of BL. Inclusion of the cribriform plate in BL may not be suitable for tarsiers because the cribriform plate is angulated drastically anteroinferiorly in this genus (Spatz, 1968; Cartmill, 1970). Similarly, in nonprimate mammals and some species of strepsirhines, the length of the cranial base would more correctly be interpreted as extending to PSp, since the cribriform plate is more vertically oriented (perpendicular) relative to the planum sphenoidum in these taxa, and does not form part of the floor of the cranial cavity (e.g., Baer & Nanda, 1976; Moss & Vilman, 1978). Therefore, interspecific comparisons of anthropoids with

nonprimate mammals or even with some strepsirhine species (e.g., Ross & Ravosa, 1993) are problematic, because different methods of characterizing BL represent different angular and scaling relationships among these taxa.

Different measures of angulation tend to covary, but measures of angulation constructed using a clival line segment [Figures 8(c), (d), 9(c), (d)] tend not to distinguish *H. sapiens* from other anthropoids in terms of the relationship between basicranial flexion and relative brain size. As noted before, humans are unique in that they have an anteroposteriorly long dorsum sellae which creates a divergence between the sellar and clival line segments. In *H. sapiens*, angles that are measured using a clival line segment are always more acute than those measured using a sellar line segment (see also Lieberman & McCarthy,

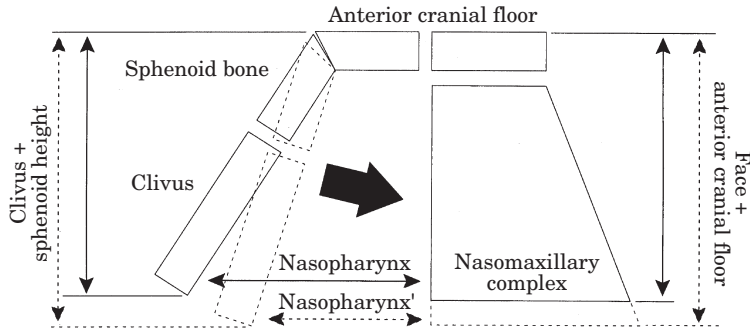
1999). Many Plio-Pleistocene hominins (i.e., Sts 5, OH5) have well-developed dorsum sellae (Aiello & Dean, 1990), so that orientations of the sellar and clival line segments will differ in these fossil hominins, complicating interspecific comparisons of hominins and anthropoids. Unfortunately, there are no stringent criteria for choosing which posterior cranial base chord is more appropriate, although it is probable that values for basicranial flexion calculated using the sellar and clival line segments are not comparable and should be used cautiously, if ever, within the same analysis.

Generally, the choice of which anterior basicranial chord to use must be made based upon the hypothesis being examined. For instance, the entire length of the anterior cranial floor upon which the brain rests is represented in anthropoids by S-FCp or some similar measure (Sp-FCp would also be appropriate), so hypotheses which investigate the relationship of the cortical brain to BL should use this plane. The anterior cranial floor to foramen caecum (S-FCp in this study) also represents the growth counterpart of the nasomaxillary complex (Enlow & Hunter, 1968; Enlow, 1990), so analyses which test hypotheses of integration between the cranial base and the face may prefer this chord.

It is noteworthy that values for *H. sapiens* are not significantly different from values predicted by the regression line when using Ross & Henneberg's (1995) angle CBA with a measure of BL which includes the cribriform plate [Figure 9(d)]. The difference in the placement of *H. sapiens* between the above results and those of Spoor (1997) [see Figure 9(a)] can be explained by the exclusion of strepsirhines from this study. Spoor (1997) includes values for *Propithecus diadema* and *Indri indri* in his RMA regression equation. With these two strepsirhine species included, Spoor's regression equation is $239.9 - 91.0x$, $r = -0.786$. Without these two species, Spoor's regression

equation becomes $249.19 - 102.03x$, $r = -0.720$, which is very close to the regression presented here ($248.96 - 103.38x$, $r = -0.862$) using the same measures of basicranial flexion and relative brain size. The inclusion of *P. diadema* and *I. indri* torques the bottom of the regression line upwards so that it runs closer to the value for *H. sapiens*. However, strepsirhines should not be included in the regression analysis because basicranial flexion does not correlate significantly with relative brain size among strepsirhines (Ross & Ravosa, 1993), and because the hypotheses tested in this paper concern the orientation of the midline cranial base when it is contiguous with, and may be affected by, the orbits. In the analyses presented in this study, *H. sapiens* deviates significantly from the anthropoid regression line for both CBA1 and CBA2 *vs.* relative brain size. How do these results compare to those of previous analyses? Using Ross & Henneberg's (1995) measure CBA (CBA 4) *vs.* a measure of IRE that includes the cribriform plate supports Spoor's (1997) conclusion that *H. sapiens* is not significantly less flexed than other anthropoids. Also, using Spoor's measure of basicranial flexion *vs.* a measure of IRE that includes the cribriform plate supports Ross & Henneberg's (1995) conclusion that *H. sapiens* is significantly less flexed than other anthropoids. Such differences highlight that different measures of basicranial flexion, BL and IRE significantly alter the perceived relationship basicranial flexion has with relative brain size.

Speculations about the degree of basicranial flexion relative to brain size among fossil hominins remain preliminary. For example, of the two specimens of *H. erectus* used in previous analyses, Sangiran 17 (Spoor, 1997) lacks much of the sphenoid (although sella can be estimated with some accuracy; Spoor, personal communication), and OH 9 (Ross & Henneberg, 1995), once heavily covered with matrix, is now largely



$$\text{Face + anterior cranial floor} = \text{Clivus + sphenoid height}$$

Figure 10. Schematic diagram of the cranial base and face. Flexion of the cranial base (represented by the large arrow) increases the vertical height of the posterior cranial base (small vertical arrows on the left) and shortens the anteroposterior length of the nasopharynx (small horizontal arrows). This mechanism may partially explain why both *H. erectus* and *Paranthropus* have such tall faces and flexed cranial bases. Adapted from Enlow & Hunter (1968).

clean but missing the endocranial surface of the sphenoid and basioccipital. Although they used different measures of cranial base angulation and relative brain size, and different hominin specimens, both Ross & Henneberg (1995) and Spoor (1997) agree that several specimens of *H. erectus* and *Paranthropus* are more flexed than predicted by their relative brain size. It is possible that basicranial flexion, in this case, may be explained by bipedal posture and the need to balance the head on an erect spine (Spoor, 1997), but increased flexion may result from more complex interactions between posture and facial architecture. For example, Bromage (1992) found that KNM-ER 3733 (*H. erectus* from East Africa) and specimens of *Paranthropus* have large meatus angles (a measurement that quantifies height of the maxilla in relation to its angulation from the cranial base). Therefore, *H. erectus* and *Paranthropus* have supero-inferiorly tall faces relative to their degree of kyphosis (see also Tobias, 1967; Rak, 1983; Wood, 1991). Enlow & Hunter (1968; see also Enlow, 1990) found that clivus (or posterior cranial base) height matches the height of the maxilla in most

mammalian species, with the exception of some cercopithecines and great apes (Figure 10). However, this relationship is also influenced by angulation of the clivus relative to the maxilla. For a given BL, the more flexed the posterior cranial base, the taller it is vertically (Figure 10). Therefore hominins, who may have short posterior cranial bases due to constraints of bipedal posture [DuBrul & Laskin, 1961; Dean, 1988; see Figure 7(e)], may have flexed posterior cranial bases so that length of the posterior cranial base more nearly matches height of the maxilla. This hypothesis, although preliminary, deserves further testing using interspecific and ontogenetic data not presented here.

It is becoming increasingly clear that basicranial flexion in *H. sapiens* is the result of specialized increases in brain size coupled with specialized decreases in basicranial length during evolution. To date, three different sections of the midline cranial base have been implicated in shortening of BL: (1) the pre-sellar sphenoid body (Lieberman, 1998; this study); (2) the section of the cranial base between the sphenoid body and the cribriform plate (this

study); and (3) the posterior cranial base (DuBrul & Laskin, 1961; Dean, 1988; Strait, 1999; this study). First, as noted above, *H. sapiens* has a slightly shorter pre-sellar sphenoid body than predicted for its brain size [Figure 7(c)]. Results from the present analysis can be used as a baseline with which to assess the length of the pre-sellar sphenoid body in *H. sapiens* and fossil hominins relative to other anthropoids. Again, values for the length of the pre-sellar sphenoid body, which is delimited by the PM point, should be viewed as cautious approximations. Second, although this study did not accurately quantify the effect of the presence or absence of frontal bone in the midline anterior cranial base in anthropoids, it seems probable that this section of the midline cranial base is shorter in *H. sapiens* and other hominoids. Why might this variation exist in the first place? There seems to be no correlation between prognathism and the amount of frontal bone in the midline cranial base (as suggested by Ashley-Montagu, 1943). Wood-Jones' (1929) suggestion that the size of the orbits may constrain the antero-posterior length of the midline frontal bone is interesting and deserves further testing using data on midline frontal bone length and orbital volume. Third, Strait (1999) hypothesized that the strong negative allometry of the noncortical brain in relation to body mass mandates that large-bodied primates will have relatively short basicrania, a point supported by data from this study. However, as noted above, this study indicates that the mechanism of shortening may be different, or may have multiple explanations. An implication of Strait's conclusions is that parts of the base in contact with the noncortical portions of the brain (approximated by the posterior cranial base in this study) would be shorter in larger-bodied primates, a conclusion not entirely concordant with data presented here, in which posterior cranial base length is isometrically maintained in anthropoids

minus *H. sapiens* [see Figure 7(e)]. This result is more congruent with DuBrul & Laskin's (1961) hypothesis that *H. sapiens* has a short posterior cranial base as the result of a constraint on cranial architecture related to bipedal posture.

Finally, the evidence presented here is equivocal concerning whether *H. sapiens* has a cranial base that is less flexed than that of other anthropoids. Since different analyses give different results, the hypothesis that there is a constraint on basicranial flexion necessitated by pharyngeal constriction is neither rejected nor supported.

Conclusions

This study demonstrates the utility of scaling analyses for characterizing species-specific basicranial anatomy in order to address hypotheses about cranial base architecture in anthropoids. Several sections of the midline cranial base are significantly shorter in *H. sapiens* than in other anthropoids. Although *H. sapiens* has the cribriform plate length predicted for an anthropoid of its endocranial volume, it has a shorter posterior cranial base and planum sphenoidum. For the posterior cranial base and pre-sellar sphenoid body, only *H. sapiens* differs from other anthropoids, who scale with isometry relative to ECV for lengths of these sections of the midline cranial base. However, *H. sapiens* shares with other hominoids a truncated midline section of the cranial base between the sphenoid body and the cribriform plate. These results provide preliminary support for several hypotheses concerning the influence of bipedal posture and pharyngeal morphology on cranial base dimensions. Most importantly, results from this study preliminarily support the suggestion of DuBrul & Laskin (1961; see also Dean, 1988) that upright, bipedal posture in *H. sapiens* necessitates shortening of the posterior cranial base; in addition, a short

pre-sellar sphenoid body in *H. sapiens* but not in other anthropoids preliminarily supports Lieberman's (1998) hypothesis that spatial modifications (possibly related to quantal speech) have shortened the pre-sellar sphenoid body in *H. sapiens*. One hypothesis, however, is not supported by this analysis. Strait (1999) hypothesized that negative allometric scaling of the noncortical brain relative to body mass constrains BL, so that the posterior cranial base also scales with negative allometry relative to body mass. However, as noted above, the posterior cranial base scales with isometry relative to endocranial volume in anthropoids, at least for this measurement of the posterior cranial base. It is necessary to further test Strait's (1999) hypothesis using body mass instead of endocranial volume.

Measures of basicranial flexion and relative brain size quantify cranial base architecture differently in *H. sapiens* and other anthropoids. Relative brain size measurements have the greatest influence on this relationship because the lengths of the posterior cranial base and the planum sphenoidale are reduced in *H. sapiens* compared to other anthropoids. Because, in anthropoids, the brain rests on the cribriform plate, which is parallel to the rest of the anterior cranial floor, analyses investigating the relationship between basicranial flexion and relative brain size should include the cribriform plate in BL. When the cribriform plate is included in BL and basicranial flexion is scaled relative to IRE, cranial base angles for *H. sapiens* are not significantly different from those predicted in two out of the four regressions. These equivocal results cannot be used to determine whether spatial constraints related to pharyngeal architecture constrain the degree of basicranial flexion in *H. sapiens*.

Although it is not clear if *H. sapiens* has reached the limit of flexion circumscribed by the architecture of the skull base and pharynx, it is evident that rotations of the

cranial base and face are correlated, and perhaps integrated, both ontogenetically and phylogenetically (see Dmoch, 1975a,b, 1976; Ross & Ravosa, 1993; Ross & Henneberg, 1995; May, 1998; May & Sheffer, 1999). A particularly fruitful line of future research will examine the relationships of facial, basicranial and neural structures to pharyngeal dimensions (see Lieberman & McCarthy, 1999, for a preliminary attempt). Furthermore, these relationships will best be tested using a combination of interspecific, ontogenetic and functional data.

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