

Posterior Maxillary (PM) Plane and Anterior Cranial Architecture in Primates

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ABSTRACT

This study tests several hypotheses of integration between the cranial base and face in primates. After reviewing the definition and anatomical basis for the posterior maxillary (PM) plane, which demarcates the back of the midface at its junction with the sphenoid, we demonstrate how the PM plane can be identified accurately on radiographs, and confirm that it maintains a 90° angle relative to the Neutral Horizontal Axis of the orbits in all primates. In addition, we use the PM plane to test Dabelow's (1929) hypothesis that the orbits and anterior cranial base are more highly integrated in anthropoids than in strepsirrhines, and we test the hypothesis that the midline anterior cranial base (planum sphenoidum) and anterior cranial floor (planum sphenoidum plus cribriform plate) in primates are highly correlated with each other relative to the PM plane. The mean angle between the anterior cranial base and the PM plane does not differ significantly from 90° in anthropoids, but differs significantly in strepsirrhines. The anterior cranial base and anterior cranial floor, however, correlate well with each other relative to the PM plane in both suborders of primates, independent of orbital orientation and configuration. The PM plane, anterior cranial base, and anterior cranial floor, therefore, form an integrated structural complex, a "facial block," whose orientation relative to the posterior cranial base influences craniofacial shape among anthropoids in which orbital orientation influences the orientation of the anterior cranial base. One such effect is that increases in cranial base flexion shorten the antero-posterior length of the nasopharynx. *Anat Rec* 264:247–260, 2001.

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Key words: posterior maxillary (PM) plane; neutral horizontal axis; integration; "facial block"

The posterior maxillary (PM) plane¹ is defined as the line connecting two radiographically determined termini projected onto the midsagittal plane: (1) the average most posteroinferior point on the maxillary tuberosities, and (2) the average point on the anterior-most extent of the greater wings of the sphenoid (Fig. 1). Although the PM

plane was developed for, and has principally been used in, radiographic studies of cranial growth in humans (Enlow et al., 1971; Enlow and Moyers, 1971; Enlow and McNamara, 1973; Enlow and Azuma, 1975; Enlow, 1990), it may have a wider utility for comparative studies of primate and hominin craniofacial growth and architecture

¹Technically, the PM plane is not a plane (which is defined by three points), but is really a line defined by the average of two points inferiorly and two points superiorly. We use the term "plane" because it is established in the literature.

Grant sponsor: National Science Foundation.

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Received 30 June 1999; Accepted 15 July 2001

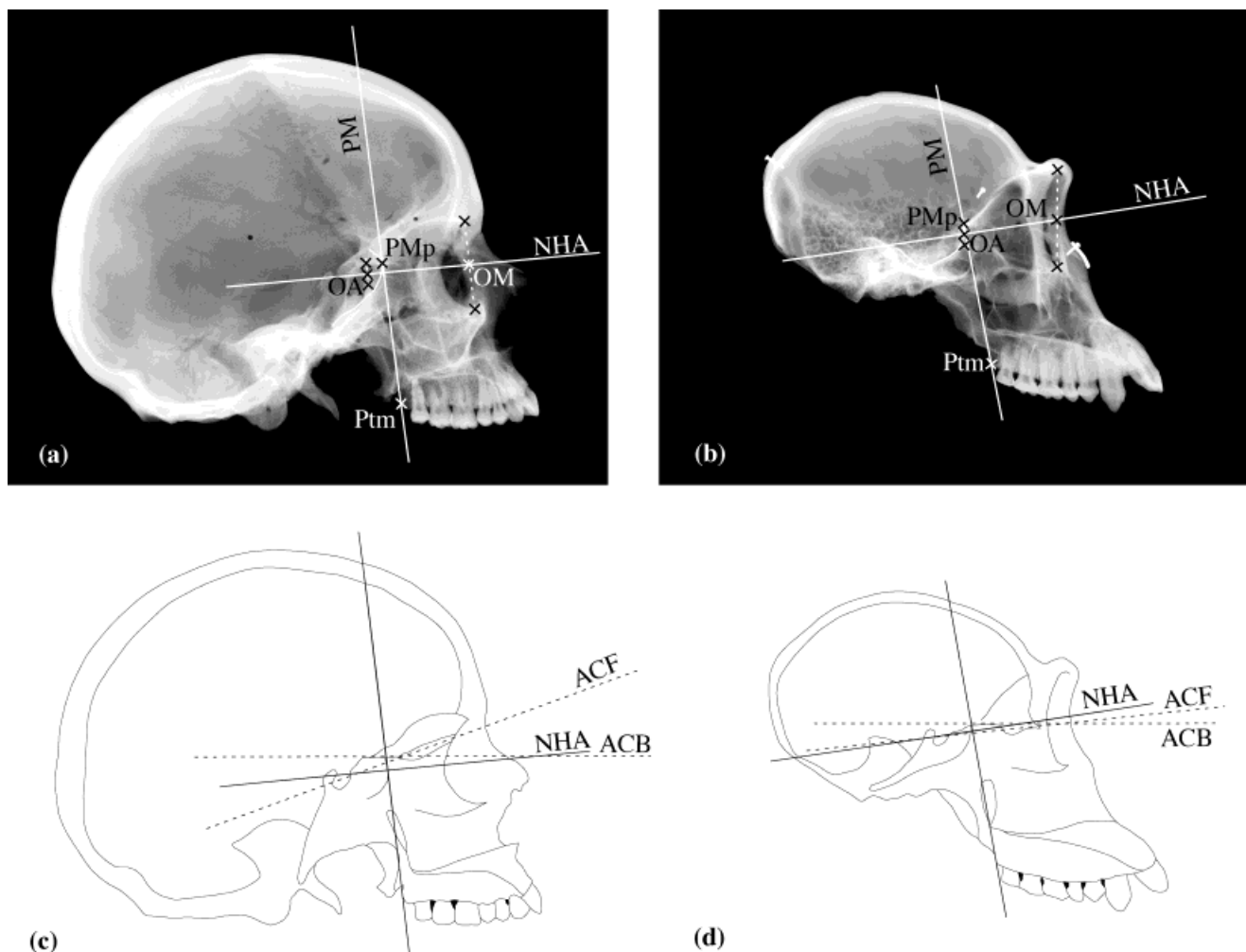


Fig. 1. Lateral radiographs of *Homo sapiens* (a) and *Pan troglodytes* (b) illustrating termini used to define the PM plane and NHA. Line drawings of the above human (c) and chimpanzee (d) crania are presented below, which illustrate the planes used to characterize the ante-

rior cranial floor (ACF) and anterior cranial base (ACB) in this study. In both specimens, the cranium is oriented so that the planum sphenoidum lies parallel to the bottom of the page.

(Bromage, 1992; Lieberman, 1998). According to Enlow (1990:171), the PM plane is “one of the most basic and important planes in the whole head” for several architectural and developmental reasons. Spatially, the PM plane is an attempt to characterize the posterior margin of the ethmomaxillary complex (the ethmoid, maxilla, and palatine) where it articulates with the boundary between the anterior and middle cranial fossae superiorly, and with the boundary between the oral cavity and the nasopharynx inferiorly. The PM plane is also claimed to separate the postero-inferior borders of the frontal lobes from the anterior margins of the temporal lobes (van der Linden and Enlow, 1971; Enlow, 1990:171). In addition, previous studies have argued that the PM plane maintains throughout ontogeny a nearly 90° orientation relative to the Neutral Horizontal Axis (NHA, defined below) of the orbits in all mammals, including chimpanzees and humans (Enlow et al., 1971; Enlow and Moyers, 1971; Enlow and McNamara, 1973; Enlow and Azuma, 1975; Enlow, 1990; Bromage, 1992; Lieberman, 1998). According to En-

low (1990:184), this constant 90° angle suggests that the PM plane is a “natural anatomic and morphogenetic plane” that maintains key relationships between growth counterparts in the face, the cranial fossae, and pharynx throughout the growth process.

Because of the potential importance of the PM plane, this study focuses on several issues related to its definition and to its use in comparative studies of primate cranial morphology. First, we discuss methodological problems with identifying the PM plane accurately in humans and other primates from radiographs, and test the hypothesis that the PM plane and the Neutral Horizontal Axis of the orbits can be reliably measured. Second, we test the hypothesis that the PM plane and NHA form a 90° angle not only in anthropoids with convergent orbits but also in strepsirrhines with divergent orbits. Third, we test the hypothesis that the orientation of the PM plane relative to the posterior cranial base correlates with the orientations of other important anatomical line segments in the anterior cranial base and the face previously used by other

researchers (Dabelow, 1929; Björk, 1955; Biegert, 1957, 1963; Enlow, 1990; Ross and Ravosa, 1993). In haplorhines, convergence of the orbits and their approximation toward the midline (Cartmill, 1970, 1972) results in a configuration in which the roof of the orbits forms most of the floor of the anterior cranial fossa. If the PM plane forms a 90° angle with the NHA, and if, in anthropoids, the anterior cranial base and anterior cranial floor are also constrained to a near-90° relationship with the PM plane, then angulation of the cranial base will have a major influence on the position of the orbits and the whole facial composite because of midline orbital approximation (Dabelow, 1929; see Fig. 6). In addition, the relationship between the PM plane and the posterior cranial base is expected to be related to the antero-posterior length of the nasopharynx (Enlow, 1990; McCarthy, 2001), antero-posterior ramus length (Enlow, 1976; Smith and Josell, 1985), and other part-counterpart relationships in the cranium (see below).

BACKGROUND

Definition and Radiographic Assessment of the PM Plane

Some confusion exists over the exact definition of the PM plane, in part because it has been defined in several different ways by Enlow (see, for example, Enlow and Azuma, 1975:223; Enlow, 1976:37; Enlow, 1990:183, 394; Enlow and Hans, 1996:159, 263). We use here the definition of Enlow and Azuma (1975), which is designed to characterize both the posterior margin of the ethmomaxillary complex and the boundary between the anterior and middle cranial fossae using lateral radiographs. According to this definition (see Fig. 1), the inferior terminus of the PM plane is pterygomaxillare (Ptm), the average midline point of the inferior, posterior-most point on each maxillary tuberosity. The superior terminus, which we denote the PM point (PMp)², is the average midline point of the anterior-most point on the lamina of each greater wing of the sphenoid. The laminae of the greater wings of the sphenoid are visible in radiographs as a pair of curved radio-opaque lines that run from their junction with the basioccipital at the sphenoccipital synchondrosis to approximately the level of the planum sphenoidale. In almost all primates, and in most humans, PMp is coincident with the intersection of the laminae of the greater wings of the sphenoid with the planum sphenoidale (sometimes called the ethmoid plane) of the anterior cranial base. In some cases, especially in large-brained primates such as humans, the greater sphenoid wings curve superiorly and/or posteriorly above the planum sphenoidale (see below).

Note that both Ptm and PMp are paired registration points that do not lie in the midsagittal plane. It is therefore necessary to average the left and right points in order to minimize as much as possible any distortion due to

asymmetry or parallax (see below). Because the points used to define it are not in the midsagittal plane, the PM plane is an abstract line that does not correspond to any midline anatomical landmarks and whose termini do not lie in the same parasagittal plane.

Although the PM plane is really an abstract line, it may be anatomically useful because it approximates several important growth boundaries of the back of the face and the middle and anterior cranial fossae, and because it can be located on radiographs with a reasonable degree of precision and accuracy. The primary sites of bone deposition between the sphenoid and the ethmomaxillary complex are the sphenoclinoid synchondrosis and the sphenozygomatic suture superiorly, and the sphenopalatine suture inferiorly (Williams et al., 1995). Growth in the sphenofrontal and frontoethmoid sutures is an important correlate of anterior cranial base elongation, but presumably does not contribute much to the growth of the ethmomaxillary complex, which enlarges through (1) displacement resulting from growth in the midline cranial base synchondroses (van Limborgh, 1970; Enlow, 1990), (2) drift resulting from bony deposition and resorption on opposite sides of the upper, middle, and lower portions of the face (Enlow, 1990), and (3) growth in the facial sutures. The inferior terminus of the PM plane, Ptm, marks the posterolateral corner of the ethmomaxillary complex and lies slightly antero-inferior to the sphenopalatine suture. The superior terminus of the PM plane, PMp, marks the anterior-most location of the temporal lobes and the middle cranial fossa. This point also lies slightly posteromedial to the midpoint of the sphenozygomatic suture, and is not only lateral but also slightly anterior to the midpoint of the sphenoclinoid synchondrosis on the floor of the cranial base in modern humans. In other words, PMp may be a reasonable midline approximation of the postero-superior corners of the ethmomaxillary complex because it not only coincides with the anterior-most point on the middle cranial fossa, but also lies roughly in between the sphenoclinoid synchondrosis (or sphenofrontal suture in many non-human primates) and the average midline representation of the sphenozygomatic suture. In most primates, including 80% of adult humans, PMp is coincident with the point at which the laminae of the greater wings of the sphenoid bone intersect the planum sphenoidale (van der Linden and Enlow, 1971). In humans, the PMp lies inferior or superior relative to the planum sphenoidale in 15 and 5% of adults, respectively (van der Linden and Enlow, 1971). It is important to note, however, that PMp is not coincident with the sphenoclinoid synchondrosis in all primates with the exceptions of *Homo sapiens*, *Pongo*, and possibly some individuals of *Pan* and *Gorilla*, since in these taxa the sphenofrontal suture is often obliterated by the articulation between the sphenoid and ethmoid bones on the midline endocranial floor (Wood-Jones, 1929; Ashley-Montagu, 1943; Butler, 1949; Murphy, 1955; van der Linden and Enlow, 1971; McCarthy, 2001).

Several additional features about the PM plane, which are illustrated in Figure 1, merit discussion, in part because they help to ensure its accurate identification on radiographs. First, the PM plane runs through or sometimes slightly anterior to the pterygomaxillary fissure. In fact, in some definitions of the PM plane (e.g., Enlow and Hans, 1996) the inferior-most point of the pterygomaxillary fissure is defined as the PM plane's inferior terminus.

²The PM point (PMp) is sometimes referred to as the sphenoclinoid (SE) point (Enlow et al., 1969), a misnomer because PMp does not always demarcate the junction of the sphenoid and ethmoid bones endocranially (see below); or as point W (Knott, 1969), which is defined as the midline registration point between the averaged lines of the greater wings of the sphenoid at the level of the planum sphenoidale.

In addition, the PM plane always intersects the planum sphenoidum anterior to the lesser wings of the sphenoid and to the superior orbital fissure, which separates the lesser and greater wings of the sphenoid. Consequently, care must be taken not to confuse the laminae of the greater wings with the anterior wall of the sphenoid sinus or the posterior root of the lesser wings, both of which can appear similar to the laminae of the greater wings but which lie more posteriorly. Finally, in most primates, the PM plane passes anterior to the sphenoid sinus. However, in some humans and great apes, the PM plane can lie posterior to the most anterior point of the sphenoid sinus. The PM plane, therefore, does not necessarily coincide with the anterior-most point of the sphenoid in the mid-sagittal plane.

PM Plane and Facial Orientation

One of the most intriguing and potentially useful aspects of the PM plane is its proposed relationship to the orientation of the face. According to Enlow, the PM plane maintains a constant 90° angle with the Neutral Horizontal Axis of the orbits, a line through the skull that describes the orientation of the orbital framework in lateral view on a radiograph³ (see Fig. 1). The anterior terminus of the NHA, OM (Orbital Margin point), is defined as the supero-inferior midpoint between the lower and upper orbital rims; the posterior terminus of the NHA, OA (Orbital Axis point), is defined as the supero-inferior midpoint between the superior orbital fissures and the inferior rims of the optic canals (Enlow and Azuma, 1975; Enlow, 1990; Bromage, 1992). For mammals without completely enclosed orbits, the inferior rim of the optic foramen is substituted for OA (Enlow and Azuma, 1975).

Despite its potential significance for testing hypotheses about cranial base-face relationships, the hypothesis that the PM plane maintains a 90° relationship to the NHA has not been thoroughly tested among a wide range of taxa, with a few exceptions that yield disparate results. Initially, Enlow and Azuma (1975) examined the PM-NHA angle in a large sample of humans 10 years of age and older and 45 mammalian species (rodents, lagomorphs, artiodactyls, carnivores, and non-human primates). Although many sample details are not provided, Enlow and Azuma (1975) found that, within *Homo sapiens*, the PM-NHA angle was within ±1° of 90° in 65 individuals, ±2° in 33 individuals, and ±3° in 18 individuals. For the combined mammalian sample, they found that 24 individuals were within ±1° of 90°, 8 individuals were within ±2°, 7 individuals were within ±3°, and 6 individuals were within ±4°. Bromage (1992) measured the PM-NHA angle in a cross-sectional sample of 45 *Pan troglodytes* crania. Bromage found mean values for each of three groups (representing ascending ages) of 89.22±3.38° (n = 9), 90.50±3.08° (n = 16), and 88.20±3.99° (n = 20), but with

some fluctuation during growth, and some individuals with extremely divergent values (e.g., 77° in one adult). Most recently, Lieberman (1998) found that the PM-NHA angle was 89.9±1.7° in a longitudinal series of humans (Denver Growth Study; n = 353) aged 1 month through 17 years 9 months.

Not all studies have found the PM-NHA angle to be 90°. Ravosa tested the PM-NHA relationship ontogenetically in macaques (Ravosa, 1991a), interspecifically among primates (Ravosa, 1991b) and interspecifically among Old World monkeys (Ravosa and Shea, 1994), and obtained slightly different results from Enlow and Azuma (1975). In these studies, the PM plane was defined in a different manner as “a line from the maxillary tuberosity to the anterior aperture of the optic canal” (Ravosa, 1991b:376). Ravosa compared his modified PM plane to the neutral orbital axis (NOA) rather than the NHA, defining the NOA as “a perpendicular line running from the OP [orbital plane, which runs from the superior to the inferior orbital contours] to the optic canal which bisects the OP and two-dimensionally represents the orbit as an isosceles triangle with the optic canal as the unequal bisected vertex” (Ravosa, 1988:541). Ravosa’s line segments differ from those proposed by Enlow, but he demonstrated that his modified PM-NOA angle averaged 80° in an ontogenetic cross-sectional sample of *Macaca fascicularis* (n = 44; 12 adults, 32 juveniles); 78° in an adult interspecific sample of 64 anthropoid species; 73° in an adult interspecific sample of 27 prosimian species; 79° in cercopithecoids (n = 37); 80° in cercopithecines (n = 23); and 78° in colobines (n = 14). No standard deviations were reported for these means. In a more detailed analysis of several hypotheses of angular invariance among Old World monkeys, Ravosa and Shea (1994) tested their modified PM-NOA angle in a sample of 79 adults from 24 cercopithecine and 14 colobine species. Values for PM-NOA, which averaged 84±6.33 in the combined sample, were significantly more variable as judged by coefficients of variation than were four other angles, including the highly-variable basicranial flexion. Although values for cercopithecines (85±6.99) were not significantly different from values for colobines (82±5.14), PM-NOA values overlapped with 90° in the former subfamily but not in the latter. Another set of analyses used least-squares regression and correlation to test the effect of skull size on angular invariance. Slopes and correlation coefficients for PM-NOA vs. palate length (measured from the posterior nasal spine [PNS] to prosthion [Pr]) were not significantly different from zero for the entire sample (slope = -0.029±0.024 [s.e.], r = -0.129), and for each of the two subfamilies (Cercopithecinae slope = -0.038±0.028 [s.e.], r = -0.208; Colobinae slope = -0.139±0.082 [s.e.], r = -0.307), indicating that PM-NOA values are not influenced by overall skull size.⁴ Although Ravosa’s modified PM-NOA angle was not 90° in any one of these analyses, his angular measure remained relatively consistent ontogenetically and interspecifically.

³Unlike other measurements [e.g., Ross and Ravosa’s (1993) “AOA”], NHA does not rely solely on the position of the optic canal, so that it describes the orientation of the bony framework of the orbit and not the orientation of the eyeball. This is an important distinction, because eyeball position and orientation may be partially independent of orbital orientation in larger-bodied primate species in which the orbit is much larger than necessary to contain the eyeball (Schultz, 1940).

⁴Ravosa and Shea (1994) used the number of individuals, and not the number of species or higher taxa, to estimate effective sample size. This methodological decision may have the effect of overestimating degrees of freedom and inflating Type I error rates.

Further study of the PM-NHA angle is useful for testing hypotheses about the relationship between the anterior cranial base and the orientation of the orbits. Dabelow (1929, 1931) suggested that the orientations of the anterior cranial base and orbits should be highly correlated in haplorhines since approximation of the orbits toward the midline results in a high degree of integration between the anterior cranial base and the upper face in this suborder. Support for this hypothesis was provided by Ross and Ravosa (1993), who found significant correlations between the orientations of the orbits (measured as in Ravosa, 1988), the planum sphenoidale (anterior cranial base), and the palate relative to the orientation of the posterior cranial base in haplorhines. However, Dabelow's (1929, 1931) hypothesis has never been tested without reference to the posterior cranial base, which flexes or extends markedly relative to the anterior cranial base during ontogeny in primates (Michejda and Lamey, 1971; Moore and Lavelle, 1974; Cousin et al., 1981; Flügel et al., 1993; Lieberman and McCarthy, 1999). Because the posterior cranial base, the anterior cranial base, and the orbits do not move independently of one another, this study reexamines Dabelow's hypothesis using the PM plane as a reference line. In this paper, we test if there is a strong correlation and a consistent angular relationship (near 90°) between the anterior cranial base (from sphenoidale to the anterior-most point on the planum sphenoidale), the anterior cranial floor (from sella to the foramen caecum), and the PM plane. A well-correlated and/or consistent relationship among these line segments may be evidence for structural integration. If these three line segments are integrated with the PM plane and with each other among primate species, then the orientation of the PM plane relative to the posterior cranial base may influence the position of the anterior cranial floor and the ethmomaxillary complex, or vice versa, as suggested by Enlow and Hunter (1968).

Hypotheses to Be Tested

Three hypotheses about the PM plane are tested in this paper. First, we test the accuracy and reliability of identification of the PM plane against the null hypothesis that the PM plane and other craniofacial line segments cannot be measured with a statistically significant degree of accuracy and precision. Second, the hypothesis that the PM plane is consistently oriented 90° relative to the NHA is tested among and between anthropoids (who have convergent orbits) and strepsirrhines (who have divergent orbits) against the null hypothesis that the PM-NHA angle is not 90°. Third, the orientation of the PM plane was measured relative to the anterior cranial base (ACB) and the anterior cranial floor (ACF) in order to test Dabelow's (1929, 1931) observation that anthropoids have cranial bases and orbits that covary with one another, whereas strepsirrhines have a less integrated relationship between anterior craniofacial and orbital lines. If the anterior cranial floor, anterior cranial base, and orbits covary with one another in anthropoids, and if the PM-NHA angle is consistently 90° across primates, then the relationship between the PM plane and the orbital framework may constrain the orientations of the anterior cranial floor and anterior cranial base in anthropoids but not in strepsirrhines. Finally, values for the orientation of the orbital framework, anterior cranial floor, and anterior cranial base were regressed against palate length to determine

whether variation in these angular variables is significantly correlated with overall size. Angular invariance predicts a non-significant slope and correlation coefficient with increasing size, both in the sample as a whole and when analyzed separately by suborder.

MATERIALS AND METHODS

Sample

In order to test the precision of locating the PM plane and other anterior cranial line segments, a test sample of one adult from each of five species that represent a wide range of cranial size and shape (*Pithecia monachus*, *Aotus lemurinus*, *Pan paniscus*, *Homo sapiens*, and *Gorilla gorilla*) was measured. These crania comprise a subsample of the interspecific sample, which includes 18 anthropoid and 15 strepsirrhine species (see Table 2). The non-human primate species come from collections of the American Museum of Natural History (AMNH) and the Peabody Museum, Harvard University (PMH). The human crania include 12 adults (six males and six females) from Australia (AMNH), southern China (AMNH), West Africa (AMNH), Italy (PMH), and Egypt (PMH) (see Lieberman, 1998; Lieberman et al., 2000 for details). When possible, six adult crania were radiographed for each species, for a total of 237 crania. All crania possessed completely erupted permanent dentition and a fused sphenoccipital synchondrosis.

Each cranium was radiographed in lateral view with Kodak XTL film at a distance of 70 mm from the film to the collimator. Care was taken to align each cranium so that its midsagittal plane was parallel to the film. Crania from the AMNH and the PMH were radiographed using an ACOMA portable X-ray machine; crania from the NMNH were radiographed using a Picker X-ray machine.

Measurements

Linear and angular measurements were taken from tracings of the radiographs; linear measurements were corrected for distortion using a correction factor computed as maximum neurocranial length taken on the skull divided by the same measurement taken on the radiograph. To test the precision with which the landmarks that comprise the PM plane can be identified, PMp, Ptm, OA, and OM were located on one radiograph from each of the five species in the "test sample" (1) by one observer (RCM) on five separate days, for a total of 25 tracings; and (2) by two different observers (the two authors), for a total of 10 tracings. Linear measurements between each pair of points were taken using Mitutoya™ digital calipers to the nearest 0.01 mm, and coefficients of variation (CV) corrected for small sample size (see Sokal and Braumann, 1980) were calculated for each measurement. The precision with which landmarks comprising the anterior cranial base and anterior cranial floor (Sp, S, FC, PSp; see definitions below) can be identified was tested previously by McCarthy (2001) using identical anthropoid samples, and measurement error was not significantly different from zero as indicated by single factor ANOVA ($P < 0.05$).

The orientations of four line segments were measured with respect to one another in the interspecific sample. The PM plane was defined using two termini: PMp and Ptm (defined above). The Neutral Horizontal Axis of the orbits, NHA, was defined using two termini: OM and OA (defined above). The anterior cranial base (ACB) was de-

TABLE 1. Coefficients of variation for single-observer precision measurements*

Species	Ptm-PMp	OA-OM	Ptm-OM	Ptm-OA	PMp-OA	PMp-OM
<i>Aotus lemurinus</i>	2.507	4.828	3.126	4.080	6.820	4.031
<i>Gorilla gorilla</i>	0.423	1.469	0.632	0.559	3.289	3.945
<i>Homo sapiens</i>	0.572	0.967	1.258	0.377	1.180	1.275
<i>Pan paniscus</i>	1.647	3.369	2.941	1.445	3.279	3.493
<i>Pithecia monachus</i>	1.478	4.846	1.960	3.249	9.920	3.709
Grand mean \pm s.d.	1.325 \pm 0.852	3.096 \pm 1.825	1.983 \pm 1.070	1.942 \pm 1.650	4.898 \pm 3.462	3.291 \pm 1.146

*The majority of measurements are within 5% of one another.

defined as the line segment from sphenoidale (Sp, the most posterior and superior midline point on the tuberculum sellae) to the planum sphenoidale point (PSP, the most superior and anterior midline point on the convexity just posterior to the cribriform plate). The anterior cranial floor (ACF) was defined as the line segment extending from sella (S, the center of the hypophyseal fossa as viewed on a lateral radiograph) to 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, as projected onto the midsagittal plane) (see also Lieberman and McCarthy, 1999; McCarthy, 2001). These line segments allow the following angles to be measured using a protractor to the nearest 1° (see Fig. 1):

PM-NHA°, orientation of the Neutral Horizontal Axis relative to the PM plane

PM-ACF°, orientation of the anterior cranial floor relative to the PM plane

PM-ACB°, orientation of the anterior cranial base relative to the PM plane.

The foramen caecum could not be identified with accuracy in *Loris tardigradus* and, therefore, statistics for PM-ACF° are not presented for this species.

Palate length, a measure of overall size comparable between anthropoids and strepsirrhines, was measured as the linear distance from the posterior nasal spine (PNS, the most posterior and inferior midline point on the palatine bones) to prosthion (Pr, the most anterior and inferior point on the premaxilla/maxilla, as projected onto the midsagittal plane) (see Ravosa and Shea, 1994).

Analyses

Coefficients of variation (CV) were calculated for each of the six measurements (Ptm-PMp, OA-OM, Ptm-OM, Ptm-OA, PMp-OA, PMp-OM) for the single-observer precision analysis (5 species * 5 days = 25 tracings). The difference between the values for each of the six measurements taken by the two observers was calculated by subtracting the smaller value from the larger value.

Means and standard deviations for PM-NHA° were calculated for all species, and significant deviations from 90° were assessed by means of unpaired *t*-tests ($P < 0.05$) by suborder and by species.

Two hypotheses of integration were tested in this paper. First, to determine if the orientation of the PM plane affects the orientations of the anterior cranial base and anterior cranial floor in anthropoids, values for orientations of these two planes were recorded relative to the PM plane (see Fig. 1). Means and standard deviations for

orientations of the anterior cranial base and anterior cranial floor relative to the PM plane were calculated for individual species and for anthropoids and strepsirrhines; significant deviations of the PM-ACB° and PM-ACF° from the PM-NHA° were assessed using Student's *t*-tests. Differences in variances between anthropoids and strepsirrhines for these two orientations were assessed using *F*-tests. Next, we regressed values for the orientations of the orbital framework (PM-NHA°), the anterior cranial floor (PM-ACF°), and the anterior cranial base (PM-ACB°) against palate length, to test whether variations in overall size allometrically affect angular values. Degrees of freedom for the regression analyses were calculated using the number of species instead of the number of individuals (see footnote 4), and using least squares regression so that results would be comparable to results from Ravosa and Shea (1994). Finally, correlation analyses were used to determine the strength of the relationship between species means for PM-NHA° vs. PM-ACB° and PM-ACF°, for both anthropoids and strepsirrhines.

The second hypothesis of integration concerns whether the anterior cranial base and anterior cranial floor are highly correlated in strepsirrhines and anthropoids. Specifically, we test whether the orientation of the cribriform plate, which contributes to the anterior cranial floor, correlates with variations in the orientation of the anterior cranial base, which comprises just the planum sphenoidale. Integration of the anterior cranial base (PM-ACB°) and anterior cranial floor (PM-ACF°) was assessed using reduced major axis (RMA) regression of species means for these two angles in anthropoids and strepsirrhines. RMA is employed here because error is expected to occur in both measurements; also, there is no clear distinction between independent and dependent variables. Confidence intervals for the RMA slope were calculated following Jolicouer and Mossiman (1968). Student's *t*-tests were used to assess if PM-ACB° and PM-ACF° are parallel (with values not significantly different from each other) within species of anthropoids and strepsirrhines.

RESULTS

In order to assess the precision with which points demarcating the PM plane and NHA can be measured by a single observer, Table 1 presents CVs for each of six measurements taken on 25 tracings from five specimens. Only two, PMp-OA in *Aotus lemurinus* and *Pithecia monachus*, have values above 5%. These variations presumably result from a moderate standard deviation in conjunction with the small size of this dimension for these two species (PMp-OA mean = 4.160, s.d. = 0.270 for *A. lemurinus*; PMp-OA mean = 4.140, s.d. = 0.391 for *P. monachus*), and do not signify that the PM plane and NHA cannot be

TABLE 2. Sample sizes for anthropoids and strepsirrhines with means and standard deviations for PM-NHA°

Taxonomic group	n	PM-NHA°
Anthropoids		
<i>Alouatta seniculus</i>	6	88.7 ± 1.16
<i>Aotus lemurinus</i>	6	89.9 ± 0.22
<i>Ateles geoffroyi</i>	6	90.2 ± 0.41
<i>Callithrix jacchus</i>	6	89.7 ± 0.41
<i>Cebus albifrons</i>	6	90.4 ± 0.25
<i>Cercopithecus aethiops</i>	6	90.1 ± 0.22
<i>Gorilla gorilla</i>	6	89.9 ± 0.42
<i>Homo sapiens</i>	60	89.8 ± 2.30
<i>Hylobates syndactylus</i>	6	90.4 ± 0.35
<i>Macaca fascicularis</i>	6	90.3 ± 0.29
<i>Pan paniscus</i>	1	90.0
<i>Pan troglodytes</i>	6	90.3 ± 0.42
<i>Papio anubis</i>	6	90.1 ± 0.25
<i>Pithecia monachus</i>	6	90.0 ± 0.32
<i>Pongo pygmaeus</i>	6	90.2 ± 0.82
<i>Presbytis melalophus</i>	6	90.2 ± 0.45
<i>Procolobus verus</i>	6	89.9 ± 0.25
<i>Saguinus fuscicollis</i>	6	89.7 ± 0.41
Anthropoid pooled mean		90.0 ± 0.38
Strepsirrhines		
<i>Arctocebus calabarensis</i>	3	88.7 ± 0.58
<i>Avahi laniger</i>	4	89.8 ± 0.29
<i>Cheirogaleus major</i>	1	89.5
<i>Daubentonia madagascarensis</i>	6	89.3 ± 0.67
<i>Eulemur fulvus</i>	6	89.4 ± 1.20
<i>Euoticus elegantulus</i>	6	89.5 ± 0.45
<i>Hapalemur griseus</i>	6	90.1 ± 0.55
<i>Indri indri</i>	6	88.3 ± 0.93
<i>Lepilemur mustelinus</i>	6	89.7 ± 0.52
<i>Loris tardigradus</i>	6	89.3 ± 0.91
<i>Nycticebus coucang</i>	6	89.6 ± 0.92
<i>Otolemur crassicaudatus</i>	6	89.5 ± 0.45
<i>Perodicticus potto</i>	6	89.4 ± 0.49
<i>Propithecus verreauxi</i>	6	90.1 ± 0.42
<i>Varecia variegata</i>	6	89.0 ± 0.71
Strepsirrhine pooled mean		89.4 ± 0.46

measured with precision in primates. All other measurements have small ranges of variation. For the multiple-observer precision analysis, Ptm-PMp differed between the two observers by 2.1 mm, OA-OM by 1.5 mm, Ptm-OM by 1.8 mm, Ptm-OA by 2.0 mm, and PMp-OM by 2.3 mm.

Table 2 summarizes means and standard deviations for the orientation of the orbits (NHA) relative to the PM plane (PM-NHA°) in order to test the null hypothesis that this angle does not differ significantly from 90° in all primates. Mean PM-NHA° is 90.0° ± 0.38 for anthropoids (range for individual specimens = 85.5°–92.5°) and 89.4° ± 0.46 for strepsirrhines (range for individual specimens = 87.0°–91.0°). None of the anthropoid or strepsirrhine species studied was found to have mean values for PM-NHA° significantly different from 90°. Among anthropoids, *Alouatta seniculus* has the most deviant PM-NHA° (mean = 88.7°), and among strepsirrhines, *Indri indri* has the most deviant PM-NHA° (mean = 88.3°).

Hypothesis of Integration 1

In order to test the hypothesis that the orientations of the anterior cranial base and floor are closely related to the PM-NHA°, mean species values for PM-ACF° and

PM-ACB° are presented in Table 3 along with the Student's *t*-test probabilities that they differ from PM-NHA°. Table 3 indicates that PM-ACF° and PM-ACB° values are substantially more variable than PM-NHA° values. Both anthropoids and strepsirrhines have PM-ACF°s that are variably above and below 90°, although anthropoids have distributions for PM-ACF° that tend to be somewhat closer to 90° than do strepsirrhines (see Fig. 2). In contrast, anthropoids have PM-ACB° values that tend to be close to PM-NHA°, whereas strepsirrhines have PM-ACB° values that are significantly less than 90° and are, therefore, flexed relative to the NHA° (see Fig. 3). The range for PM-ACF° is 75.0°–110.0° in anthropoids, which is less than the range of PM-ACF° among strepsirrhines (59.5°–107.0°) but does not reach significance ($F = 0.782$; $P = 0.284$). Ranges for PM-ACB° are 55.0°–111.0° in anthropoids and 51.0°–92.0° in strepsirrhines; these levels of variation are not significantly different from each other ($F = 1.01$; $P = 0.966$). Table 3 also presents results of Student's *t*-tests for suborder and species mean differences from PM-NHA° for PM-ACF° and PM-ACB°. The pooled means of PM-ACF° in anthropoids, and PM-ACF° and PM-ACB° in strepsirrhines, differ significantly from mean values for PM-NHA° ($P < 0.001$). However, the mean value for PM-ACB° in anthropoids does not differ significantly from the mean value for PM-NHA° (mean deviation = 0.76°), despite the fact that in several species PM-ACB° differs significantly from 90°. In particular, *Aotus lemurinus*, *Cebus albifrons*, and *Macaca fascicularis* have PM-ACB° means significantly greater than 90°, indicating that the anterior cranial base is extended relative to the NHA. *Gorilla gorilla*, *Pongo pygmaeus*, and *Procolobus verus* have PM-ACB° means that are significantly less than 90°, indicating that the anterior cranial base is flexed relative to the NHA. Anthropoids have a similar pattern for angulation of PM-ACF° in which only *G. gorilla* and *P. pygmaeus* have values significantly less than 90°, whereas all other anthropoid species have high values for PM-ACF°, indicating that the anterior cranial floor is extended relative to the NHA. Eight of the strepsirrhine species studied here have PM-ACF° values significantly less than 90° (flexed relative to the NHA), while four species have PM-ACF° values significantly greater than 90° (extended relative to the NHA). In addition, all strepsirrhines have PM-ACB° means less than 90° ($P < 0.05$ in all but two species).

Table 4 presents least-squares correlation coefficients, slopes, and standard errors of the slopes testing the hypothesis that the orientations of the orbital framework (PM-NHA°), anterior cranial floor (PM-ACF°), and anterior cranial base (PM-ACB°) remain invariant with increasing size. The majority of these line segments, measured relative to the PM plane, do not covary with palate size as predicted by the hypothesis of angular invariance. However, PM-ACB° covaries significantly with palate length in anthropoids.

Correlations of PM-NHA° vs. PM-ACF° and PM-ACB° for anthropoids and strepsirrhines, presented in Figure 4, indicate that these planes correlate poorly with each other. PM-NHA° vs. PM-ACB° is significant among strepsirrhines ($r = 0.535$, $P < 0.05$), but this result should be viewed with caution because of the presence of outliers in a relatively homogenous distribution (see Fig. 4d).

TABLE 3. Means, standard deviations, and t-values for differences from PM-NHA° for orientations of the anterior cranial floor (PM-ACF°) and anterior cranial base (PM-ACB°)

Taxonomic group	PM-ACF°	t-Val. (p-Val.)	PM-ACB°	t-Val. (p-Val.)
Anthropoids				
<i>A. seniculus</i>	82.5 ± 8.68	1.408	84.8 ± 9.02	0.821
<i>A. lemurinus</i>	100.1 ± 3.04	-9.057***	100.3 ± 3.40	-6.187**
<i>A. geoffroyi</i>	89.8 ± 5.29	0.155	82.4 ± 7.65	2.449
<i>C. jacchus</i>	94.4 ± 1.72	-6.862***	88.7 ± 3.27	0.609
<i>C. albifrons</i>	103.6 ± 4.84	-10.967***	102.1 ± 6.87	-2.909*
<i>C. aethiops</i>	100.9 ± 3.84	-5.802**	103.0 ± 4.29	-6.581**
<i>G. gorilla</i>	84.8 ± 3.48	3.003*	75.4 ± 10.44	3.065*
<i>H. sapiens</i>	106.0 ± 4.30	-7.981***	89.7 ± 5.07	0.497
<i>H. syndactylus</i>	97.8 ± 6.28	-2.068	87.9 ± 9.38	1.610
<i>M. fascicularis</i>	103.0 ± 4.28	-10.339***	102.3 ± 2.90	-8.232***
<i>P. paniscus</i>	89.5	—	76.5	—
<i>P. troglodytes</i>	91.0 ± 1.30	-1.772	84.4 ± 6.56	2.208
<i>P. anubis</i>	98.8 ± 7.24	-2.450	97.6 ± 6.26	-2.494
<i>P. monachus</i>	89.1 ± 6.45	0.350	95.8 ± 7.24	-1.975
<i>P. pygmaeus</i>	80.9 ± 3.47	6.985***	67.8 ± 7.98	6.683**
<i>P. melalophus</i>	97.5 ± 2.69	-5.495**	89.8 ± 2.28	0.343
<i>P. verus</i>	102.0 ± 1.00	-16.747***	79.8 ± 3.25	5.283**
<i>S. fuscicollis</i>	101.2 ± 3.42	-7.874***	95.6 ± 5.25	-2.676*
Pooled mean	95.2 ± 7.63	-6.888***	89.2 ± 9.97	0.755
Strepsirrhines				
<i>A. calabarensis</i>	75.2 ± 8.08	2.700*.*.*.*	64.8 ± 7.10	5.405*.*.*.*
<i>A. laniger</i>	93.6 ± 1.49	-5.007**	87.4 ± 3.20	1.536
<i>C. major</i>	88.5	—	75.0	—
<i>D. madagascarensis</i>	72.3 ± 2.47	9.430***	61.7 ± 2.26	18.676***
<i>E. fulvus</i>	81.7 ± 4.88	4.490**	68.2 ± 6.10	9.967***
<i>E. elegantulus</i>	79.6 ± 3.07	7.864***	73.3 ± 4.82	8.192***
<i>H. griseus</i>	94.4 ± 1.67	-6.143**	87.3 ± 2.59	3.011*
<i>I. indri</i>	94.0 ± 3.23	-5.222***	68.8 ± 2.75	22.029***
<i>L. mustelinus</i>	85.1 ± 8.29	1.430	81.6 ± 8.49	2.465
<i>L. tardigradus</i>	—	—	53.5 ± 1.78	46.355***
<i>N. coucang</i>	75.1 ± 5.02	7.696***	58.2 ± 6.85	12.269***
<i>O. crassicaudatus</i>	81.6 ± 6.80	2.722*	76.2 ± 4.41	7.116***
<i>P. potto</i>	74.4 ± 4.61	10.607***	57.8 ± 4.02	19.535***
<i>P. verreauxi</i>	99.9 ± 6.13	-5.553**	81.7 ± 4.19	4.532**
<i>V. variegata</i>	81.2 ± 1.86	8.237***	64.4 ± 2.33	24.955***
Pooled mean	82.8 ± 9.50	6.726***	70.6 ± 10.50	17.348***

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

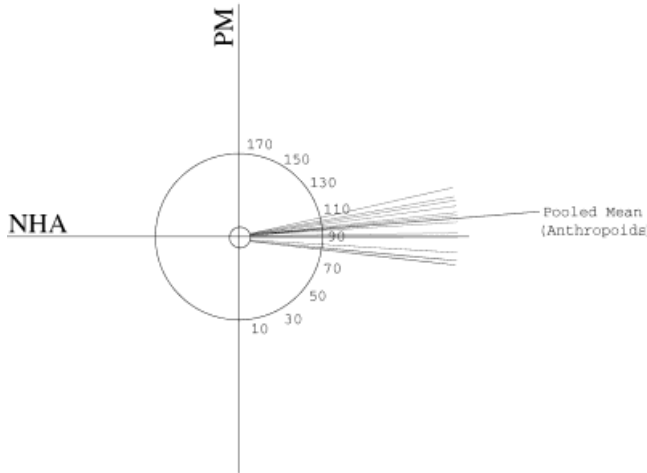
****Highest level of significance obtainable for small sample size.

Hypothesis of Integration 2

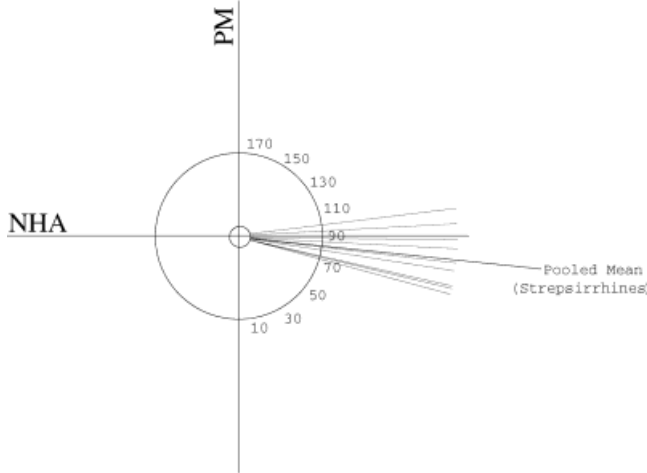
Figure 5 presents regressions of PM-ACB° vs. PM-ACF° for anthropoids (Fig. 5a) and strepsirrhines (Fig. 5b). The orientations of the anterior cranial floor and anterior cranial base are moderately correlated (Fig. 3, $r = 0.69$ for anthropoids and $r = 0.79$ for strepsirrhines) and, therefore, appear to be integrated to some extent in both suborders. Both anthropoids and strepsirrhines scale with negative allometry for PM-ACB° vs. PM-ACF°, although confidence intervals for the slopes of the line include isometry in both cases because the moderate correlation coefficients produce wide confidence intervals (anthropoids, slope = 0.77, confidence interval = 0.529–1.12; strepsirrhines, slope = 0.90, confidence interval = 0.646–1.255). Student's t -tests indicate that PM-ACB° and PM-ACF° differ significantly in all strepsirrhines. In anthropoids as a whole, PM-ACB° differs significantly from PM-ACF°, but regression residuals for *A. seniculus*, *A. lemurinus*, *C. albifrons*, *C. aethiops*, *G. gorilla*, *M. fascicularis*, and *P. anubis* are not significantly different than the predicted values.

DISCUSSION

The above results appear to confirm the utility and importance of the PM plane for studies of craniofacial shape. The PM plane (as well as the NHA) can be located with considerable precision and accuracy. In addition, this study confirms that the PM plane and the NHA form a 90° angle in all primates, including strepsirrhines with divergent orbits. These data agree with the conclusions of Enlow and Azuma (1975), Bromage (1992), and Lieberman (1998), and contrast with results obtained by Ravosa (1991a,b; Ravosa and Shea, 1994). The perpendicularity of the PM-NHA° may be one of the few invariate postnatal spatial relationships in the cranium (see also Enlow, 1990: 171–172; Bromage, 1992). Further research is needed to establish when, how and why this perpendicularity develops (see below). It is worth noting that data from Enlow and Azuma (1975) suggest that this perpendicular angle is common to all mammal species. This hypothesis remains to be tested thoroughly, but preliminary data from goats (*Capra hircus*), bats (*Vampyrum spectrum*), naked mole rats (*Talpa europaea*), and dogs (*Canis familiaris*) have

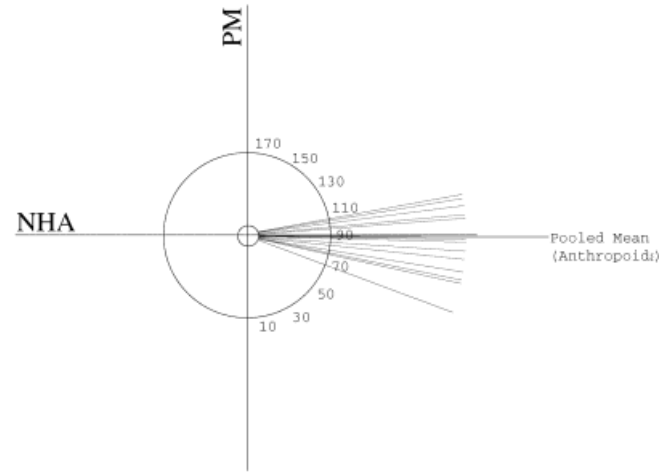


(a)

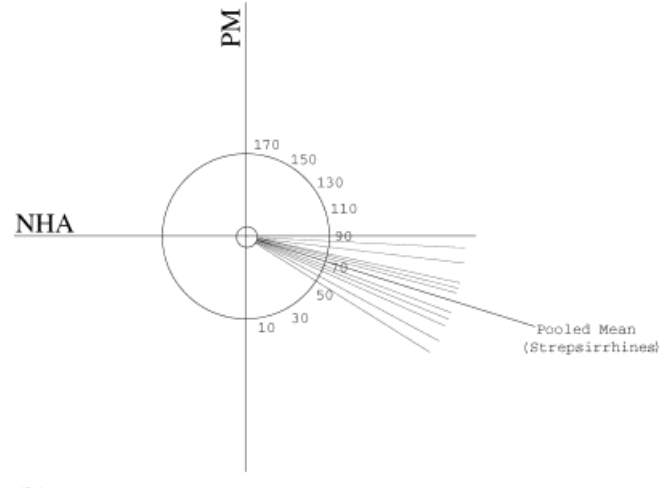


(b)

Fig. 2. Mean species and pooled values for PM-ACF° in anthropoids (a) and in strepsirrhines (b). Note that several species have near-identical means and are, therefore, represented with one line.



(a)



(b)

Fig. 3. Mean species and pooled values for PM-ACB° in anthropoids (a) and strepsirrhines (b). Note that several species have near-identical means and are, therefore, represented with one line.

failed to reveal any exceptions (McCarthy and Lieberman, unpublished data).

The right angle formed by the PM and NHA planes is potentially useful for a number of reasons. In combination with other conservative spatial relationships in the cranium (see, for example, Enlow and Azuma, 1975; Smith and Josell, 1985; Enlow, 1990; Bromage, 1992; Ravosa and Shea, 1994), this fairly invariable relationship may help paleontologists reconstruct certain aspects of fossil cranial morphology, especially the position of the face relative to the cranial base and neurocranium. For example, Bromage (1993) used the PM-NHA° to reconstruct facial position in KNM-ER 1470 (see, however, Grine et al., 1996), and Lieberman (1998) used the 90° PM-NHA angle to reconstruct the orientation of the PM plane from the NHA in several fossil hominins. Obviously, more work in this area is needed before fossil hominin reconstructions can be based on, or evaluated in the light of, the PM-NHA°.

The apparently invariable 90° angle between the PM and NHA planes highlights the utility of the PM plane as a

TABLE 4. Correlation and regression analyses testing the effect of overall skull size on the orientations of anterior cranial planes

Angle (vs. palate length)	r	Slope	SE (slope)
PM-NHA° (combined)	0.197	0.009	0.004
PM-NHA° (anthropoids)	0.176	0.006	0.004
PM-NHA° (strepsirrhines)	-0.185	-0.015	0.010
PM-ACF° (combined)	0.113	0.066	0.049
PM-ACF° (anthropoids)	-0.291	-0.112	0.042
PM-ACF° (strepsirrhines)	0.214	0.207	0.123
PM-ACB° (combined)	0.043	0.035	0.069
PM-ACB° (anthropoids)	-0.466*	-0.244	0.053
PM-ACB° (strepsirrhines)	-0.004	-0.005	0.156

*Slope and correlation coefficient significantly different from zero at the $P < 0.05$ level.

reference line with which to compare other lines of the face and cranium (Enlow and Azuma, 1975; Bromage, 1992; Lieberman, 1998). This relationship may be useful for examining a variety of hypotheses about craniofacial or-

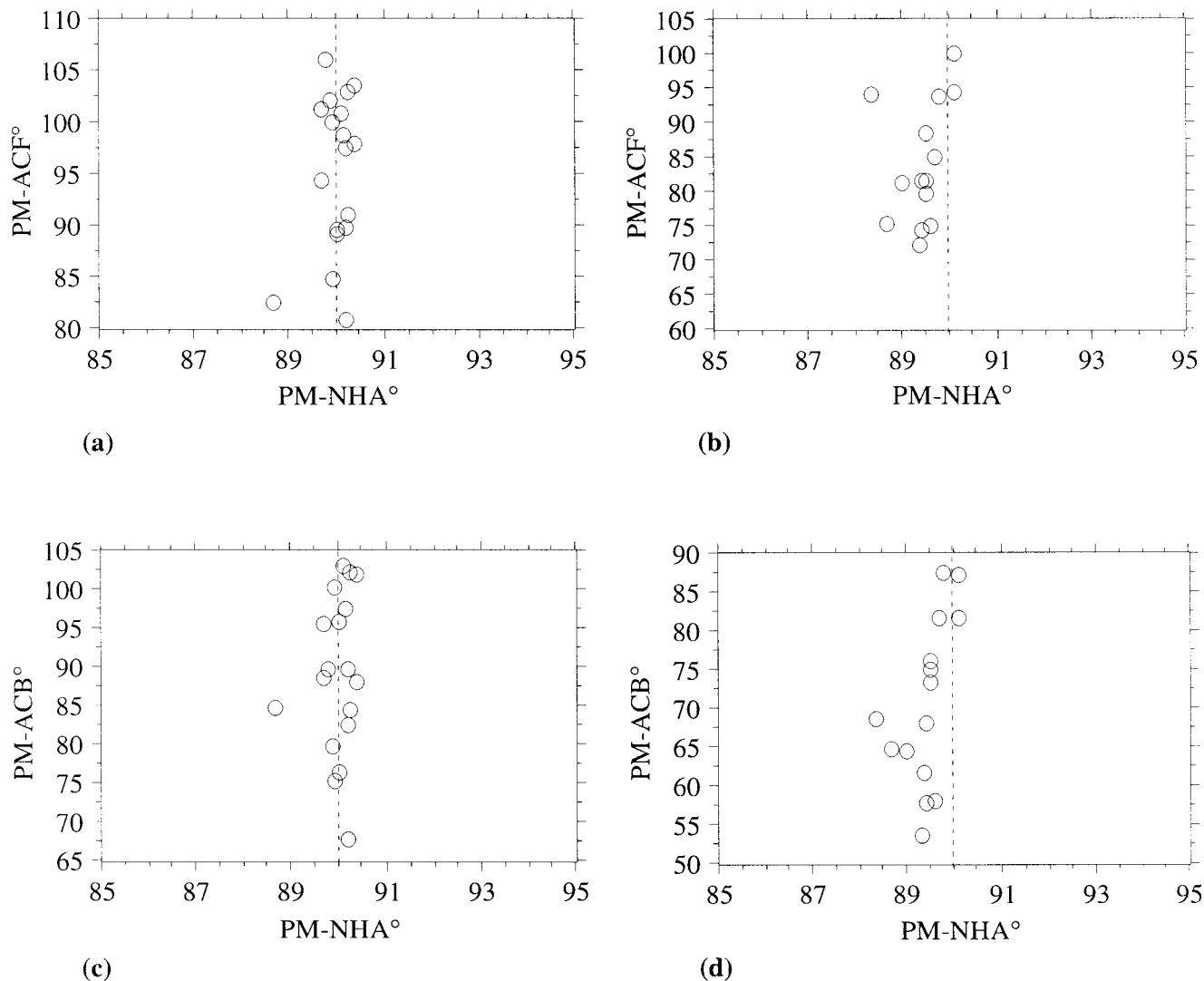


Fig. 4. Scatterplots of correlations of PM-NHA° vs. PM-ACF° for anthropoids (a) and strepsirrhines (b), and correlations of PM-NHA° vs. PM-ACB° for anthropoids (c) and strepsirrhines (d). The dotted line represents a 90° PM-NHA°.

ganization including Dabelow's (1929, 1931) observation that the orbits and anterior cranial base are more integrated in anthropoids than in mammals with divergent orbits. This hypothesis receives some support from the observation that, in anthropoids, the mean value for the orientation of the orbits relative to the PM plane is not significantly different from the mean value for the orientation of the anterior cranial base relative to the PM plane. However, the orientation of the midline anterior cranial floor relative to the PM plane does differ significantly from 90° in anthropoids. There are four possible explanations for this difference. First, the cribriform plate slopes slightly anteroinferiorly or anterosuperiorly relative to the planum sphenoidum among anthropoids (Cartmill, 1970). Second, the point sella is slightly inferior relative to the anterior cranial floor in most anthropoids, which elevates values of PM-ACF° above 90°. The inferior

position of sella relative to the planum sphenoidum is likely to affect anterior cranial floor orientation; thirteen anthropoids have mean values for PM-ACF° above 90° (seven of which are significant). Third, many anthropoids have cribriform plates and foramina caecae that lie in a deep olfactory pit (see Cameron, 1930; Aiello and Dean, 1990) within the body of the ethmoid bone, which may account for depressed values of PM-ACF° (such as in *A. seniculus*, *G. gorilla*, *P. paniscus*, and *P. pygmaeus*). Note, however, that values of PM-ACF° do not differ significantly from values of PM-NHA° in *A. seniculus*, since PM-NHA° also tends to be lower (albeit not significantly) than 90° in this species. Fourth, *H. sapiens* crania often have foramina caecae that are elevated above the level of the cribriform plate because of growth of the crista galli (see Moss, 1963). This phenomenon might account in part for the high values of PM-ACF° in humans.

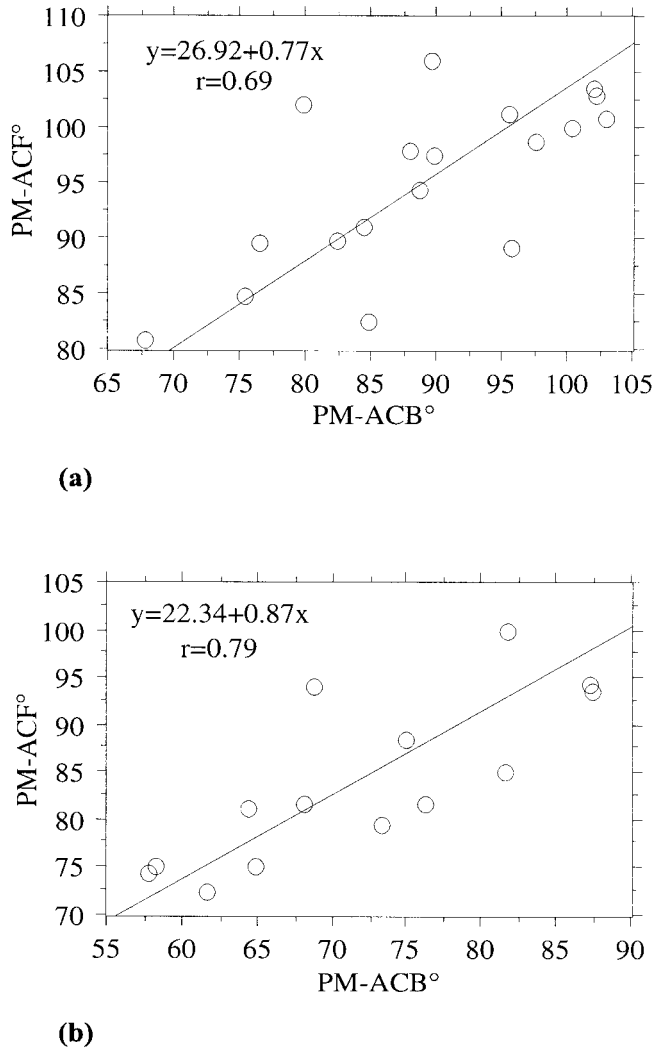


Fig. 5. Reduced major axis (RMA) regressions of PM-ACB° vs. PM-ACF° for anthropoids (a) and strepsirrhines (b). Confidence intervals for the slopes of the regression lines are 0.53–1.12 for anthropoids and 0.65–1.26 for strepsirrhines.

Strepsirrhines, in contrast, have mean values for PM-ACF° and PM-ACB° that differ significantly from mean values for PM-NHA°. The lesser degree of integration among these planes corroborates Dabelow's (1929, 1931) hypothesis in which strepsirrhines are not predicted to exhibit highly correlated orbital and anterior cranial base orientations because their divergent orbits are not contiguous with the midline cranial base. As the above results indicate, the orientation of the midline anterior cranial floor in strepsirrhines is quite variable with respect to the PM plane, with values of PM-ACF° both above and below 90°. Moreover, all strepsirrhines have mean PM-ACB° values below 90°, which may be related to kyphosis of the anterior cranial base, perhaps because of greater prognathism. This hypothesis requires further testing with data on degrees of prognathism and facial orientation. A preliminary evaluation of data from this study lends some support to this idea, since *G. gorilla*, *A. seniculus*, and *P.*

pygmaeus, all highly prognathic anthropoids, also have anterior cranial bases and floors that are kyphosed relative to the orientation of the orbits. However, it must be noted that the orientations of the anterior cranial base and the anterior cranial floor do not correlate significantly with palate length in strepsirrhines (see Table 4).

Use of the PM plane in this study supports the results of Ross and Ravosa's (1993) recent analysis of Dabelow's (1929) hypothesis. Ross and Ravosa (1993) correlated the orientation of the orbits relative to the posterior cranial base (AOA) against the orientation of the planum sphenoidium relative to the posterior cranial base (CBA). They concluded that the orbital axis (the "OA" of "AOA") and planum sphenoidium were integrated in haplorhines but not in strepsirrhines on the basis of a moderately strong but significant correlation between the two variables in the former ($r = 0.617$; $P < 0.001$) but not the latter ($r = 0.379$; not significant). In a later analysis, Ross and Henneberg (1995) used a different measure of orbital orientation to test Dabelow's hypothesis, thereby partially addressing the problem of autocorrelation. By holding the PM plane constant, this study confirms Ross and Ravosa's (1993) findings in a manner that avoids any potential conflation between non-independent movements of the posterior and anterior chords of the cranial base. In fact, Figure 4, which plots orientations of the anterior cranial floor and anterior cranial base relative to the PM-NHA° for anthropoids and strepsirrhines, illustrates some problems inherent in using bivariate regression or correlation to test hypotheses of integration between cranial base and facial planes. Although the mean values for PM-ACF° (Fig. 4a) and PM-ACB° (Fig. 4c) are generally closer to 90° in anthropoids than in strepsirrhines, strepsirrhines with more flexed cranial floors and bases tend to have lower PM-NHA°s (by about 0.5°–1°) than anthropoids, giving them slightly higher correlation coefficients. Since posterior cranial base orientation relative to the PM plane varies more than PM-ACB° or PM-ACF°, then the orientation of ACB and ACF relative to the posterior cranial base is auto-correlated as an artifact of the choice of the reference plane. The use of the PM plane in this study therefore provides an independent test of Dabelow's (1929, 1931) hypothesis of integration. It should be noted, however, that the correlation between the anterior cranial line segments and the PM plane in anthropoids is perhaps less strong than we might expect given Biegert's (1958, 1963) and Dabelow's (1929, 1931) predictions, but actually accords well with Ross and Ravosa's results (outlined above). Because there is a significant, negatively allometric correlation between PM-ACB° and palate length in anthropoids (see Table 4), larger anthropoids may have more flexed anterior cranial bases. This result supports other studies that find that basicranial flexion increases with increasing endocranial volume relative to basicranial length, and might explain why orbital orientation varies independently of anterior cranial base orientation in individual anthropoid species, even though the mean values for these two angles are not significantly different for anthropoids as a whole. Although these results, in combination with those of Ross and Ravosa (1993) and Ross and Henneberg (1995), generally support Dabelow's (1929) model for non-independence of the orbits and the anterior cranial base in anthropoids, they question the stringency of this relationship given the considerable variability among anthropoids.

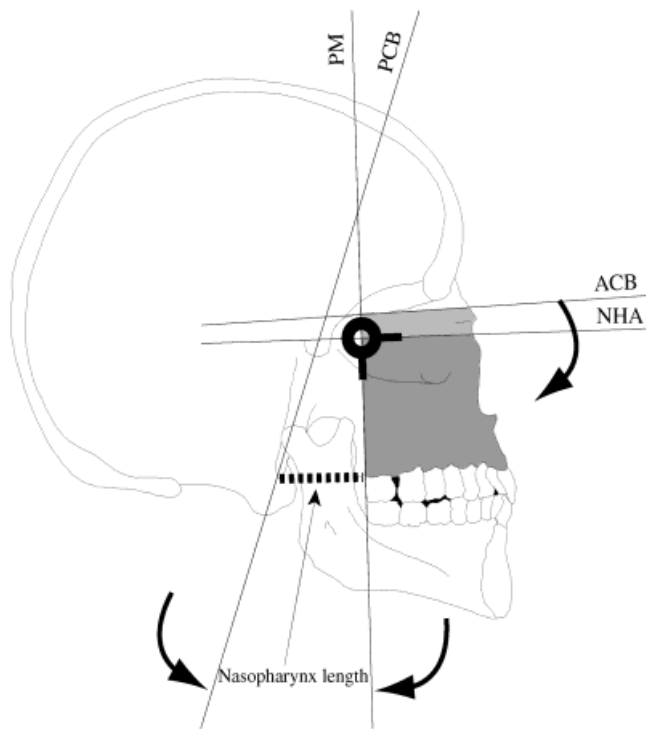


Fig. 6. Proposed anthropoid "facial block" hypothesis. The invariant 90° relationship of the PM plane and NHA ensures that flexion of the anterior cranial base or floor relative to the posterior cranial base rotates the orbits (which are integrated with the anterior cranial base in anthropoids) and the back of the midface as a block. Flexion of the PM plane relative to the posterior cranial base in turn constricts the antero-posterior length of the nasopharynx and the antero-posterior length of the mandibular ramus, the counterpart to the nasopharynx.

In contrast, both this study and previous studies agree that the orientation of the orbits and anterior cranial line segments is unrelated in strepsirrhines. The fact that some strepsirrhines have PM-ACF $^\circ$ s that are not significantly different from PM-NHA $^\circ$ s is somewhat misleading, since the S-FC line segment does not correspond to the bodies of any bones in the strepsirrhine anterior cranial fossa due to this suborder's characteristic vertically oriented cribriform plate (see Cartmill, 1970; McCarthy, 2001). Anthropoids have cribriform plates that are more nearly parallel relative to their anterior cranial bases, and therefore the measurement PM-ACF $^\circ$ is more relevant for anthropoids than for strepsirrhines.

The invariant 90° relationship between the PM plane and the NHA may have even broader implications for understanding variations in craniofacial shape among anthropoids. If the PM plane always forms a right angle with the orbits, and to a lesser extent with the anterior cranial base, then it follows that upward or downward rotation of the orbits must entail concomitant rotation of the PM plane, which approximates the back of the midface. In other words, the top and back of the midface along with the anterior cranial base form a "facial block" whose imaginary axis of rotation lies somewhere near the junction of the middle cranial fossa and the ethmomaxillary complex at the PM point (Fig. 6). Flexion of the cranial base in anthropoids, whose convergent orbits necessarily inte-

grate the anterior cranial base with the orbits, therefore, results in downward rotation (kyphosis) not only of the orbits but also of the facial block as a whole. Flexion of the anterior cranial base along with rotation of the PM plane and kyphosis of the orbits thus rotates the back of the midface closer to the posterior cranial base. Such movements may shorten the antero-posterior length of the nasopharynx (see also Enlow, 1990; Ross and Henneberg, 1995; Lieberman, 2000; McCarthy, 2001), which in turn has effects on other growth counterparts such as the antero-posterior length of the mandibular ramus (Smith and Josell, 1985). In contrast, strepsirrhines and other mammals may be less constrained in this respect because they lack convergent orbits. The anthropoid facial block, if it exists, potentially explains why brain volume apparently influences so many aspects of craniofacial shape. In anthropoids, the degree of flexion of the cranial base has been shown to be dependent on brain volume relative to basicranial length (Gould, 1977; Ross and Ravosa, 1993; Ross and Henneberg, 1995; Spoor, 1997; Strait, 1999; McCarthy, 2001). It follows that variations in both orbital orientation and the antero-posterior length of the nasopharynx—features that are highly derived in humans and some fossil hominins—may be influenced by variations in cranial base flexion that are ultimately driven by changes in the size of the brain and length of the cranial base. These hypotheses require further analyses that integrate developmental and comparative data on the relationships among these craniofacial regions.

A final question is, why does the PM plane maintain a nearly 90° angle relative to the orbital framework in all primates and perhaps all mammals? So far, there has been little speculation about this problem, despite the likelihood that the PM-NHA $^\circ$ is a basic structural constraint in the mammalian cranium. The problem requires further, concerted study. One possibility is that a constant 90° PM-NHA angle may be a structural adaptation to maintain a constant shape of the airway during growth. A 90° PM-NHA angle aligns the nasal and oral cavities, which lie anterior to the PM plane, in a constant orientation relative to the nasopharynx and oropharynx, which lie posterior to the PM plane, thereby preserving spatial relationships between the nasal, oral and pharyngeal parts of the airway. Shape constancy in the relationships between these different parts of the airway may allow muscle pattern generators involved during deglutition to remain constant during growth (see Lieberman et al., 2001 for a similar example involving ontogenetic conservation of hyolaryngeal proportionality). Another possibility is that the 90° PM-NHA relationship functions to integrate 3-D positional information from sense organs in the face (especially the eyes) with the vestibular system (located in the posterior cranial fossa) in a constant way during growth.

CONCLUSIONS

The PM plane is an important anatomic and morphogenetic line segment within the cranium that demarcates the boundary between the cranial base posteriorly and the midface anteriorly. This study used an interspecific sample of primates to verify previous claims by Enlow and others that the PM plane maintains a constant 90° angle with the Neutral Horizontal Axis of the orbits. Other parts of the skull are affected by the invariant PM-NHA $^\circ$. In particular, in anthropoids the structural integration of the orbits and anterior

cranial base (Dabelow, 1929, 1931) appears to constrain the anterior cranial base to a near-90° relationship with the PM plane, although this relationship is not as invariant as the relationship between the PM plane and the NHA. The orientations of the anterior cranial base (planum sphenoidum) and the anterior cranial floor (planum sphenoidum plus cribriform plate) also correlate well with each other among anthropoids and strepsirrhines independent of the orientation or position of the orbits themselves. Only in anthropoids with closely approximated and convergent orbits do movements of the anterior cranial base significantly affect movements of the orbits.

The 90° PM-NHA relationship may constrain the range of variation of certain aspects of craniofacial architecture in mammals. In particular, the 90° PM-NHA angle appears to cause the ethmomaxillary complex and the anterior cranial base to rotate as a “facial block” relative to the posterior cranial base. Flexion of the cranial base in modern humans swings the entire face under the frontal lobes of the brain, which may have secondary effects on the antero-posterior length of the nasopharynx (see Enlow, 1990; Ross and Henneberg, 1995; Spoor et al., 1999; Lieberman, 2000; McCarthy, 2001) and the antero-posterior length of the mandibular ramus (Smith and Josell, 1985). Further elucidation of these and other architectural relationships in the skull may lead to more accurate reconstructions of hominin crania as well as a greater understanding of the processes that underlie and generate many craniofacial variations.

ACKNOWLEDGMENTS

We thank K. Mowbray and O. Pearson for help with taking some of the radiographs, G. Sawyer and F. Brady (American Museum of Natural History) and R. Thorington, L. Gordon, and J. Jacobs (National Museum of Natural History) for providing access to specimens, and the Robert Wood Johnson Radiology Department for providing X-ray developing facilities. We also to thank R. Smith, C. Dean, D. Strait, and three anonymous reviewers for providing comments on the manuscript, and M. Ravosa for useful advice about hypothesis testing. This research was supported by a National Science Foundation Graduate Fellowship and Smithsonian Institution Predoctoral Fellowship to R.C.M.

LITERATURE CITED

- Aiello L, Dean C. 1990. An introduction to human evolutionary anatomy. London: Academic Press.
- Ashley-Montagu MF. 1943. The mesethmoid-presphenoid relationships in primates. *Am J Phys Anthropol* 1:129–141.
- Biegert J. 1957. Der Formwandel des Primatenschädels und seine Beziehungen zur ontogenetischen (Entwicklung und den phylogenetischen Spezialisations der Kopforgane). *Gegenbaurs Morphol Jahrb* 98:77–199.
- Biegert J. 1963. The evaluation of characters of the skull, hands and feet for primate taxonomy. In: Washburn SL, editor. *Classification and human evolution*. Chicago: Aldine de Gruyter. p 116–145.
- Björk A. 1955. Cranial base development. *Am J Orthod* 41:198–225.
- Bromage TG. 1992. The ontogeny of *Pan troglodytes* craniofacial architectural relationships and implications for early hominids. *J Hum Evol* 23:235–251.
- Bromage TG. 1993. Developmental criteria for an empirically based reconstruction of KNM-ER 1470. *Am J Phys Anthropol (Suppl)* 16:63.
- Butler H. 1949. A rare suture in the anterior cranial fossa of the human skull. *Man* 49:25–27.
- Cameron J. 1930. Craniometric memoirs. No. II. The human and comparative anatomy of Cameron's craniofacial axis. *J Anat Lond* 64:324–336.
- Cartmill M. 1970. The orbits of arboreal mammals. Unpublished Ph.D. Dissertation. University of Chicago.
- Cartmill M. 1972. Arboreal adaptations and the origin of the order Primates. In: Tuttle R, editor. *The functional and evolutionary biology of primates*. New York: Aldine de Gruyter. p 97–122.
- Cousin RP, Fenart R, Deblock R. 1981. Variations ontogenetiques des angles basicraniens et faciaux. *Bull Mem Soc Anthropol Paris* 8:189–212.
- Dabelow A. 1929. Über korrelationen in der phylogenetischen Entwicklung der Schädelform. I. *Morph Jahrb* 63:1–49.
- Dabelow A. 1931. Über korrelationen in der phylogenetischen Entwicklung der Schädelform. II. *Morph Jahrb* 67:84–133.
- Enlow DH. 1976. Postnatal growth and development of the face and cranium. In: Cohen B, Kramer IRV, editors. *Scientific foundations of dentistry*. London: Heinemann. p 29–46.
- Enlow DH. 1990. *Facial growth*. 3rd ed. Philadelphia: Saunders.
- Enlow DH, Azuma M. 1975. Functional growth boundaries in the human and mammalian face. In: Bergsma D, editor. *Morphogenesis and malformation of face and brain*. New York: Alan R Liss. p 217–230.
- Enlow DH, Hans MG. 1996. *Essentials of facial growth*. Philadelphia: WB Saunders.
- Enlow DH, Hunter WS. 1968. The growth of the face in relation to the cranial base. Report of the Forty-Fourth Congress of the European Orthodontic Society. p 321–345.
- Enlow DH, McNamara JA. 1973. The neurocranial basis for cranial form and pattern. *Angle Orthodont* 43:256–270.
- Enlow DH, Moyers RE. 1971. Growth and architecture of the face. *J Am Dent Assoc* 82:763–774.
- Enlow DH, Moyers RE, Hunter WS, McNamara JA Jr. 1969. A procedure for the analysis of intrinsic facial form and growth. *Am J Orthodont* 56:123–142.
- Enlow DH, Kuroda T, Lewis AB. 1971. The morphological and morphogenetic basis for craniofacial form and pattern. *Angle Orthodont* 41:161–188.
- Flügel C, Schram K, Rohen JW. 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.
- Gould SJ. 1977. *Ontogeny and phylogeny*. Cambridge, MA: Belknap Press.
- Grine FE, Jungers WL, Schultz J. 1996. Phenetic affinities among early *Homo* crania from East and South Africa. *J Hum Evol* 30: 189–225.
- Jolicouer P, Mossiman J. 1968. Intervalles de confiance pour la peute de l'axe majeur d'une distribution normale bidimensionnelle. *Biométrie Praximétrie* 9:121–140.
- Knott V. 1969. Orthogenetic change of four cranial base segments in girls. *Growth* 33:123–142.
- Lieberman DE. 1998. Sphenoid shortening and the evolution of modern human cranial shape. *Nature* 393:158–162.
- Lieberman DE. 2000. Ontogeny, homology and phylogeny in the hominid craniofacial skeleton: the problem of the browridge. In: O'Higgins P, Cohn M, editors. *Development, growth and evolution*. London: Academic Press.
- Lieberman DE, McCarthy RC. 1999. The ontogeny of cranial base angulation in humans and chimpanzees and its implications for reconstructing pharyngeal dimensions. *J Hum Evol* 36:487–517.
- Lieberman DE, Mowbray KM, Pearson O. 2000. Basicranial influence on overall cranial shape. *J Hum Evol* 38:291–315.
- Lieberman DE, McCarthy RC, Hiemae KM, Palmer JB. 2001. Ontogeny of hyoid and larynx descent in humans. *Arch Oral Biol* 46:117–128.
- McCarthy RC. 2001. Anthropoid cranial base architecture and scaling relationships. *J Hum Evol* 40:41–66.

- 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 WJ, Lavelle CJB. 1974. Growth of the facial skeleton in the Hominoidea. London: Academic Press.
- Moss ML. 1963. Morphological variations of the crista galli and medial orbital margin. *Am J Phys Anthropol* 21:259–264.
- Murphy T. 1955. The sphenothmoidal articulation in the anterior cranial fossa of the Australian aborigine. *Am J Phys Anthropol* 13:285–300.
- Ravosa MJ. 1988. Browridge development in Cercopithecidae: A test of two models. *Am J Phys Anthropol* 76:535–555.
- Ravosa MJ. 1991a. Ontogenetic perspective on mechanical and non-mechanical models of primate circumorbital morphology. *Am J Phys Anthropol* 85:95–112.
- Ravosa MJ. 1991b. Interspecific perspective on mechanical and non-mechanical models of primate circumorbital morphology. *Am J Phys Anthropol* 86:369–396.
- Ravosa MJ, Shea BT. 1994. Pattern in craniofacial biology: evidence from the Old World monkeys (Cercopithecidae). *Int J Primatol* 15: 801–822.
- Ross CF, 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 CF, Ravosa MJ. 1993. Basicranial flexion, relative brain size, and facial kyphosis in nonhuman primates. *Am J Phys Anthropol* 91:305–324.
- Schultz AH. 1940. The size of the orbit and of the eye in primates. *Am J Phys Anthropol* 26:389–408.
- Smith RJ, Josell SD. 1985. The plan of the human face: a test of three general concepts. *Am J Orthod* 85:103–108.
- Sokal RR, Braumann CA. 1980. Significance tests for coefficients of variation and variability profiles. *Syst Zool* 29:50–66.
- Spoor F. 1997. Basicranial architecture and relative brain size of *Sts5 (Australopithecus africanus)* and other Plio-Pleistocene hominids. *S Afr J Sci* 93:182–186.
- Strait DS. 1999. The scaling of basicranial flexion and length. *J Hum Evol* 37:701–719.
- van der Linden FPGM, Enlow DH. 1971. A study of the anterior cranial base. *Angle Orthod* 41:119–124.
- van Limborgh J. 1970. A new view on the control of the morphogenesis of the skull. *Acta Morphol Neerl Scand* 8:143–160.
- Williams PL, Bannister LH, Berry MM, Collins P, Dyson M, Dussek JE, Ferguson MWJ. 1995. *Gray's anatomy*. 38th ed. Edinburgh: Churchill Livingstone.
- Wood-Jones F. 1929. *Man's place among the mammals*. London: Arnold.