The Primate Cranial Base: Ontogeny, Function, and Integration

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ABSTRACT Understanding the complexities of cranial base development, function, and architecture is important for testing hypotheses about many aspects of craniofacial variation and evolution. We summarize key aspects of cranial base growth and development in primates that are useful for formulating and testing hypotheses about the roles of the chondrocranium and basicranium in cranial growth, integration, and function in primate and human evolution. We review interspecific, experimental, and ontogenetic evidence for interactions between the cranial base and brain, and between the cranial base and the face. These interactions indicate that the cranial base plays a key role in craniofacial growth, helping to integrate, spatially and functionally, different patterns of growth in various adjoining regions of the skull such as components of the brain, the eyes, the nasal cavity, the oral cavity, and the pharynx. Brain size relative to cranial base length appears to be the dominant influence on many aspects of basicranial variation, especially the angle of the cranial base in the midsagittal plane, but other factors such as facial size, facial orientation, and posture may also be important. Major changes in cranial base shape appear to have played crucial roles in the evolution of early primates, the origin of anthropoids, and the origin of Homo sapiens. Yrbk Phys Anthropol 43:117–169, 2000. © 2000 Wiley-Liss, Inc.

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GLOSSARY

Basioccipital clivus: midline “plane” of the posterior cranial base formed by the superior (endocranial) aspects of the basioccipital and the posterior sphenoid.

Brain stem: the ventral parts of the brain, excluding the telencephalon. Specifically, in this paper, the brain stem consists of the medulla oblongata and mesencephalon (= optic tectum and tegmentum) of Stephan et al. (1981; see also Butler and Hodos, 1996).

Chondrocranium: cartilaginous precursors to the basicranium.

Constraint: a limitation or bias on processes and/or patterns of evolution, growth, form, and function.

Cranial base angulation: a series of events by which bone or cartilage deposition in the midline cranial base changes the angle between intersecting prechordal (see below) and postchordal (see below) lines. This causes the inferior cranial base angle to become more acute (flexion) or more obtuse (extension).

Displacement: a series of events by which an osseous region “moves” relative to another osseous region through bone deposition (primary displacement), or through bone deposition in an adjoining bone (secondary displacement).

Drift: a series of events by which an osseous wall “moves” relative to another anatomical region through bone deposition on one surface and bone resorption on its opposing surface.

Ethmomaxillary complex: the upper part of the face, mostly comprising the ethmoid, the nasal capsule, and the maxilla.

Facial projection: degree to which face projects in front of cranial base; measured here by nasion–foramen caecum.

Integration: the genetic, epigenetic, or functional association among elements via “a set causal mechanisms so that change in one element is reflected by change in another” (Smith, 1996). The results of integration are most often recognized as a pattern of significant, hierarchical covariation among the components of a system.

Kyphosis: angle of some aspect of facial orientation relative to the neuro- and/or basicranium, measured here using angle of facial kyphosis (AFK) for the orientation of the palate, and angle of orbit axis orientation (AOA) for orientation of the orbital axis.

Planum sphenoidale: midline “plane” of the anterior cranial base from the sphenoidale (Sp) to the planum sphenoidale (PS) point (see below).
Postchordal cranial base: portion of the cranial base posterior to the sella; frequently called the posterior cranial base.

Prechordal cranial base: portion of the cranial base anterior to sella; frequently called the anterior cranial base.

Telencephalon: forebrain, consisting of paired olfactory lobes, the basal ganglia, and the neocortex.

**LANDMARK DEFINITIONS**

Ba, basion: midsagittal point on anterior margin of foramen magnum.

CP, clival point: midline point on basioccipital clivus inferior to point at which dorsum sellae curves posteriorly.

FC, foramen caecum: pit on cribriform plate between crista galli and endocranial wall of frontal bone.

H, hormion: most posterior midline point on vomer.

OA: supero-inferior midpoint between superior orbital fissures and inferior rims of optic canals; for mammals without completely enclosed orbits, OA is defined as inferior rim of optic foramen.

OM: supero-inferior midpoint between lower and upper orbital rims.

Op, opisthion: most posterior point in foramen magnum.

PMp, PM point: average of projected midline points of most anterior point on lamina of greater wings of sphenoid.

PP, pituitary point: “the anterior edge of the groove for the optic chiasma, just in front of the pituitary fossa” (Zuckerman, 1955).

PS, planum sphenoideum point: most superior midline point on sloping surface in which cribriform plate is set.

Ptm, pterygomaxillare: average of projected midline points of most inferior and posterior points on maxillary tuberosities.

S, sella: center of sella turcica, independent of contours of clinoid processes.

Sb, sphenobasion: midline point on sphenoparietal synchondrosis on external aspect of clivus.

Sp, sphenoidale: most posterior, superior midline point of planum sphenoidale.

**ANGLE, LINE, AND PLANE DEFINITIONS**

AOA: orbital axis orientation relative to CO (Ross and Ravosa, 1993).

BL1: Ba-PP + PP-Sp (Ross and Ravosa, 1993; Ross and Henneberg, 1995).

BL2: Ba-S + S-FC (Spoor, 1997).

CBA1: Ba-S relative to S-FC (Lieberman and McCarthy, 1999).

CBA2: Ba-S relative to Sp-PS (Lieberman and McCarthy, 1999).

CBA3: Ba-CP relative to S-FC (Lieberman and McCarthy, 1999).

CBA4: Ba-CP relative to Sp-PS (Lieberman and McCarthy, 1999).

CO, clivus ossis occipitalis: endocranial line from Ba to sphenoparietal synchondrosis (Ross and Ravosa, 1993).


Forel’s axis: from most antero-inferior point on frontal lobe to most postero-inferior point on occipital lobe (Hofer, 1969).

Head-neck angle: orientation of head relative to neck in locomoting animals, calculated as neck inclination – orbit inclination (Strait and Ross, 1999).

IRE1: cube root of endocranial volume/BL 1 (Ross and Ravosa, 1993).

IRE2: cube root of neocortical volume/BL 1 (Ross and Ravosa, 1993).


IRE4: cube root of neocortical volume/palate length (Ross and Ravosa, 1993).


Meynert’s axis: from ventral edge of junction between pons and medulla to caudal recess of interpeduncular fossa (Hofer, 1969).

Neck inclination: orientation of surface of neck relative to substrate (Strait and Ross, 1999).

NHA: neutral horizontal axis of orbits; from OM to OA (Enlow and Azuma, 1975).

Orbital axis orientation: line from optic foramen through superoinferior midpoint of orbital aperture (Ravosa, 1988).

Orbit inclination: orientation relative to substrate of a line joining superior and in-
The cranial base has important integrative and functional roles in the skull, many of which reflect its phylogenetic history as the oldest component of the vertebrate skull (de Beer, 1937). Architecturally, the cranial base provides the platform upon which the brain grows and around which the face grows. In addition, the cranial base connects the cranium with the rest of the body: it articulates with the vertebral column and the mandible, provides conduits for all the vital neural and circulatory connections between the brain and the face and neck, houses and connects the sense organs in the skull, and forms the roof of the nasopharynx. The shape of the cranial base is therefore a multifactorial product of numerous phylogenetic, developmental, and functional interactions.

The importance of the cranial base is matched by several challenges that make it difficult to study. Because the cranial base is difficult to access surgically, there have been few experimental studies of cranial base growth and function. Also, a large proportion of the cranial base is not only complex anatomically, but is also difficult to measure and/or see externally. In addition, the cranial base in many fossils is missing, damaged, or unobservable without special technology. However, new developmental studies, and new techniques for imaging, have led to a modest renaissance of research on cranial base morphology (reviewed in Spoor et al., 2000). In addition, new analytical techniques which quantitatively compare three-dimensional differences in form have opened up new possibilities for studying growth and variation in complex regions such as the cranial base (Cheverud and Richtsmeier, 1986; Bookstein, 1991; Lele, 1993; O'Higgins, 2000). Ultimately, better information about the relationships between cranial base morphology and the rest of the skull may help to resolve a number of important phylogenetic and behavioral issues throughout primate evolution.

The goals of this review are to provide a background on key aspects of cranial base growth and development necessary to formulate or test hypotheses about the role of the cranial base in cranial growth, integration, and function. Therefore, we review recent research on cranial base variation, development, and evolution in primates, focusing on the major dimensions of the cranial base (especially width, length, and angulation in the sagittal plane). Other, more detailed aspects of cranial base anatomy and morphology, most notably the inner ear, were recently reviewed by Spoor and Zonneveld (1998) and will not be covered in this review (see also Braga et al., 1999). Where relevant, we have made an effort to include data from the few experimental studies on cranial base growth and function. Most experimental research on the mammalian skull has focused on the face and neurocranium; however, some of these studies provide indirect clues on interrelationships among the brain, cranial base, and face (e.g., Sarnat, 1988, 1999). Finally, we conclude with a short discussion of two main issues which we believe require further research to address: what factors determine most of the variation in cranial base shape among primates, and to what extent does variation in cranial base form influence ontogenetic and interspecific patterns of variation in craniofacial morphology?

ANATOMY AND DEVELOPMENT

A detailed understanding of the series of events and underlying mechanisms that generate patterns of morphological variation in the basicranium is vital for developing and testing hypotheses about the cranial base’s role in craniofacial integration.
and function. So we begin with a brief summary of cranial base embryology, fetal growth, and postnatal growth. Most of the information summarized below derives from studies of human basicranial growth and development; the majority of these patterns and processes are generally applicable to all primates, but we tried to distinguish those that are unique to humans or other species. Further information is available in Björk (1955), Ford (1958), Scott (1958), Moore and Lavelle (1974), Starck (1975), Bosma (1976), Moss et al. (1982), Slavkin (1989), Sperber (1989), Enlow (1990), and Jeffery (1999), as well as the many references cited below.

**Development of the chondrocranium**

The human cranial base first appears in the second month of embryonic life as a narrow, irregularly shaped cartilaginous platform, the chondrocranium, ventral to the embryonic brain. The chondrocranium develops between the base of the embryonic brain and foregut about 28 days intra utero (i.u.) as condensations of neural crest cells (highly mobile, pluripotent neurectodermal cells that make up most of the head) and paraxial mesoderm in the ectomeninx (a mesenchyme-derived membrane surrounding the brain) (Sperber, 1989). By the seventh week i.u., the ectomeninx has grown around the base of the brain and differentiated into nine groups of paired cartilaginous precursors (Fig. 1A,B) (Kjaer, 1990).

Fig. 1. Chondrocranium in *Homo sapiens* (after Sperber, 1989). A: Superior view of chondrocranial precursors and ossification centers (after Sperber, 1989). Primordial cartilages are at right, and their cranial base derivatives are on left. Note that the nasal capsule forms the ethmoid, the inferior concha, and the nasal septum; the presphenoid forms the sphenoid body; the orbitosphenoid forms the lesser wing of the sphenoid; the alisphenoid forms the greater wing of the sphenoid; the postphendid forms the sella turcica; the otic capsule forms the petrous temporal; the parachordal forms the basioccipital; and the occipital sclerotomes form the exoccipital. B: Lateral view of chondrocranial precursors in a fetus 8 weeks i.u.

From caudal to rostral these are: 1) four occipital condensations on either side of the future brain stem derived from sclerotomic portions of postotic somites; 2) a pair of parachordal cartilages on either side of the primitive notochord; 3) the otic capsules, lying lateral to the parachordal cartilages; 4) the hypophyseal (polar) cartilages which surround the anterior pituitary gland; 5–6) the orbitosphenoids (ala orbitalis/lesser wing of sphenoid) and alisphenoids (ala temporalis/greater wings of sphenoid) which lie lateral to the hypophyseal cartilages; 7–8) the trabecular cartilages which form the mesethmoid and, more laterally, the nasal capsule cartilages; and 9) the ala hypochiasmatica which, together with parts of the trabecular and orbitosphenoid cartilages, forms the presphenoid.

The chondrocranial precursors anterior to the notochord (groups 5–9) derive solely from segmented neural crest tissue (somitomes), while the posterior precursors (groups 1–4) derive from segmented mesodermal tissue (somites) (Noden, 1991; Couly et al., 1993; Le Douarin et al., 1993). Consequently, the middle of the sphenoid body (the mid-sphenoidal synchondrosis) marks the division between the anterior (prechordal) and posterior (postchordal) portions of the cranial base that are embryologically distinct. Antero-posterior specification of the segmental precursors of the cranial base is complex and still incompletely known, but
appears to mostly involve the expression of the Hox and Dlx gene clusters (Luftin et al., 1992; Robinson and Mahon, 1994; Vielle-Grosjean et al., 1997). For recent summaries of pattern formation and gene expression in the vertebrate cranial base, see Langille and Hall (1993) and Schilling and Thorogood (2000).

At least 41 ossification centers, which begin to appear in the chondrocranium about 8 weeks i.u., are responsible for the transformation of the chondrocranium into the basicranium (Sperber, 1989; Kjaer, 1990). These centers (Fig. 1B) form within a perforated and highly irregularly shaped platform known as the basal plate. In general, ossification begins with the mesodermally derived cartilages toward the caudal end of the chondrocranium, and proceeds rostrally and laterally, eventually forming the four major bones that comprise the primate basicranium: the ethmoid, most of the sphenoid, and parts of the occipital and temporal bones (which also include some intramembranous elements). The sequence in which the four bones of the cranial base ossify from the chondrocranium is complex, and still not entirely resolved (reviewed in Sperber, 1989; Williams et al., 1995; Jeffery, 1999), but we highlight here the major steps, proceeding from caudal to rostral. The occipital comprises four bones surrounding the foramen magnum. The squamous portion is primarily intramembranous bone of the cranial vault, except for the nuchal region, which ossifies endochondrally from two separate centers (Srivastava, 1992) and fuses with the lateral exoccipitals on either side of the foramen magnum that fuse with the basioccipital. The sphenoid body forms from fusion of the presphenoids and basisphenoid around the pituitary, forming the sella turcica (“Turkish saddle”). The greater and lesser wings of the sphenoid develop from the fusion of the alisphenoid and orbitosphenoid cartilages to the body (Kodama, 1976a–c; Sasaki and Kodama, 1976). Later, the medial and lateral pterygoid plates and portions of the greater wings ossify intramembranously. The temporals, which form much of the lateral aspect of the basicranium, develop from approximately 21 ossification centers, several of which are intramembranous, including the squamous, tympanic, and zygomatic regions (Shapiro and Robinson, 1980; Sperber, 1989). The petrous and mastoid parts of the temporal form the inner ear from the otic capsule, and the styloid process of the temporal ossifies from cartilage in the second branchial arch. The ethmoid, which is entirely endochondral in origin, forms the center of the anterior cranial floor, and most of the nasal cavity from three ossification centers in the mesethmoid and nasal capsule cartilages (Hoyte, 1991). An additional cartilaginous ossification center detaches from the ethmoid to form a separate scrolled bone, the inferior nasal concha, inside the nasal cavity.

Patterns and processes of basicranial growth

In order to understand how the basicranium grows and functions during the fetal and postnatal periods, it is useful to keep in mind three important principles of basicranial development. First, the center of the basicranium (an oval-shaped region around the sphenoid body) attains adult size and shape more rapidly than the anterior, posterior, and lateral portions, presumably because almost all the vital cranial nerves and major vessels perforate the cranial base in this region (Figs. 1A, 2) (Sperber, 1989). Second, the prechordal (anterior) and postchordal (posterior) cranial base grow somewhat independently, perhaps reflecting their distinct embryonic origins and their different spatial and functional roles (outlined above). Third, most basicranial growth in the three cranial fossae occurs independently (Fig. 2). The posterior cranial fossa, which houses the occipital lobes and the brain stem (the cerebellum and the medulla oblongata), is bounded laterally by the petrous and mastoid portions of the temporal bone, and anteriorly by the dorsum sellae of the sphenoid. The butterfly-shaped middle cranial fossa, which supports the temporal lobes and the pituitary gland, is bounded posteriorly by the dorsum sellae and the petrous portions of the temporal, and anteriorly by the posterior borders of the lesser wings of the sphenoid, and by the anterior clinoid processes of the sphenoid. The ante-
rior cranial fossa, which houses the frontal lobe and the olfactory bulbs, is bounded posteriorly by the lesser wings of the sphenoid.

Following its initial formation, the cranial base grows in a complex series of events, largely through displacement and drift (see Glossary). Four main types of growth occur within and between the endocranial fossae: antero-posterior growth through displacement and drift; medio-lateral growth through displacement and drift; supero-inferior growth through drift; and angulation (primarily flexion and extension). In order to review how these types of growth occur, we will focus primarily on the sequence of events and patterns of basicranial growth in humans and their major differences from nonhuman primates.

**Antero-posterior growth.** Basicranial elongation during ontogeny occurs in three ways: 1) drift at the anterior and posterior margins of the cranial base; 2) displacement in coronally oriented sutures such as the fronto-sphenoid; and 3) displacement in the midline of the cranial base from growth within the three synchondroses: the mid-sphenoid synchondrosis (MSS), the sphen-ethmoid synchondrosis (SES), and the sphen-occipital synchondrosis (SOS). During the fetal period in both humans and nonhuman primates, the midline anterior cranial base grows in a pattern of positive allometry (mostly through ethmoidal growth) relative to the midline posterior cranial base (Ford, 1956; Sirianni and Newell-Morris, 1980; Sirianni, 1985; Anagnostopolou et al., 1988; Sperber, 1989; Hoyte, 1991; Jeffrey, 1999). During fetal growth, several key differences emerge between humans and other primates in the relative proportioning of the posterior cranial fossa (Fig. 3). In humans, antero-posterior growth in the basioccipital is proportionately less than in the exoccipital and squamous occipital posterior to the foramen magnum, whereas the pattern is apparently reversed in nonhuman primates, with proportionately more growth in the basioccipital (Ford, 1956; Moore and Lavelle, 1974). The nuchal plane rotates downward to become more horizontal in humans, but rotates in the reverse direction to become more vertical in nonhuman primates, apparently because of a growth field reversal (Fig. 3). According to Duterloo and Enlow (1970), the inside and outside of the nuchal plane in humans are resorptive and depository growth fields, respectively; but in nonhuman primates, the inside and outside of the nuchal plane are reported to be depository and resorptive growth fields, respectively. As a result, the foramen magnum lies close to the center of the basicranium in the human neonate and more posteriorly in nonhuman primates (Zuckerman, 1954, 1955; Schultz, 1955; Ford, 1956; Biegert, 1963; Crelin, 1969).

Postnatally, the posterior cranial base primarily elongates in the midline through deposition in the SOS and through posterior drift of the foramen magnum; more laterally, the posterior cranial fossa elongates through deposition in the occipitomastoid suture and through posterior drift. In all primates, the basioccipital lengthens approximately twofold after birth, with rapid
growth during the neural growth period (e.g., up to approximately 6 years in humans) and some additional elongation occurring through the adolescent growth spurt (Ashton and Spence, 1958; Scott, 1958; Riolo et al., 1974; Sirianni and Swindler, 1979; Sirianni, 1985). The SOS contributes to roughly 70% of posterior cranial base elongation in macaques (Sirianni and Van Ness, 1978). The rest of posterior basi-cranial growth in nonhuman primates occurs through posterior drift of the foramen magnum, which has been shown by fluorochrome dye labeling experiments to migrate caudally in nonhuman primates through resorption at its posterior end and deposition at its anterior end (Michejda, 1971; Giles et al., 1981). In contrast, the foramen magnum remains in the center of the human skull base, roughly halfway between the most anterior and posterior points of the skull (Lugoba and Wood, 1990). The posterior cranial base in *H. sapiens* still elongates during postnatal growth, but to a lesser degree than in nonhuman primates.

Postnatal elongation in the anterior cranial base is somewhat more complex because of its multiple roles in neural and facial growth. The anterior cranial base (measured from sella to foramen caecum) elongates in concert with the frontal lobes of the brain, reaching approximately 95% of its adult length by the end of the neural growth period (e.g., 6 years in humans, 3 years in chimpanzees, and 1.2 years in macaques) (Scott, 1958; Sirianni and Newell-Morris, 1978; Sirianni and Van Ness, 1978; Lieberman, 1998). Postnatal anterior cranial base elongation can occur in the SES (in the midline), through displacement in the sphenoid-frontal suture, and through drift of the anterior margin of the frontal bone. In humans, however, the SES remains active and unfused until 6–8 years after birth, when the brain has completed most of its growth, but the SES apparently fuses near birth in nonhuman primates (Michejda and Lamey, 1971). These differences in the timing and sequence of synchondroseal activity and fusion may be related to the different relative contributions of the lesser wings of the sphenoid and the frontal to the anterior cranial floor in humans and nonhuman primates. Although there is some intraspecific variation, the lesser wing of the sphenoid in humans tends to comprise approximately one third of the cranial floor, extending all the way to the cribiform plate; in nonhuman primates, the cribiform usually lies entirely within the ethmoid (Fig. 4), and the...
lesser wing of the sphenoid makes up less than one tenth of the cranial floor (Van der Linden and Enlow, 1971; Aiello and Dean, 1990; McCarthy, 2001). Differences in the sequence of synchondroseal fusion may also be related to differences in the timing and nature of cranial base angulation in human vs. nonhuman primates (Jeffery, 1999; see below).

While the anterior cranial base grows solely during the neural growth phase (it reaches adult size at the same time as the brain), the more inferior portions of the anterior cranial base continue to grow as part of the face after the neural growth phase, forming the ethmomaxillary complex (Enlow, 1990). This complex grows downward and forward mostly through drift and displacement. In addition, the sphenoid sinus drifts anteriorly. Since the ethmoid (with the exception of the cribiform plate) primarily grows as part of the ethmomaxillary complex, its postnatal growth is most properly treated in a review of facial growth.

**Medio-lateral growth.** How the cranial base widens is important because of its various interactions with neurocranial and facial shape (Lieberman et al., 2000; see below). The increases in width of the anterior and posterior cranial fossae occur primarily from drift (in which the external and internal surfaces of the squamae are depository and resorptive, respectively), and from intramembranous bone growth in sutures with some component of lateral orientation, such as the fronto-ethmoid and occipitomastoid sutures (Sperber, 1989). Lateral growth in the middle cranial fossa is slightly more complicated. The sphenoid body does not widen much (Kodama, 1976a,b; Sasaki and Kodama, 1976). Instead, most increases in middle cranial fossa width presumably occur in the sphenotemporal suture and through lateral drift of the squamous portions of the sphenoid.

Increases in cerebellum and brain-stem size have been implicated in changes in the orientation of the petrous pyramids (Fig. 4), which are more coronally oriented externally (but not internally) in humans than in nonhuman primates (Dean, 1988). Spoor (1997) found that petrous pyramid orientation in a broad interspecific sample of pri-
mates was significantly negatively correlated with relative brain size ($r = -0.85, P < 0.001$) but not with the cranial base angle. However, Jeffery (1999) found that petrous pyramid orientation is independent of relative brain size in fetal humans (during the second trimester).

**Supero-inferior growth.** Most brain growth apparently causes the neurocranium and parts of the basicranium to grow superiorly, anteriorly, and laterally (de Beer, 1937). However, the endocranial fossae also become slightly deeper through drift because most of the endocranial floor is resorptive, while the inferior side of the basicranium is depository (Fig. 2) (Duterloo and Enlow, 1970; Enlow, 1990). The endocranial margins between the fossae that separate the different portions of the brain (the petrous portion of the temporal and the lesser wing of the sphenoid) do not drift inferiorly because they remain depository surfaces (Enlow, 1976). Differences in drift most likely reflect variation in the relative size of the components of the brain in conjunction with other spatial relationships among components of the skull. In particular, inferior drift of the anterior cranial fossa is presumably minimal because it would impinge upon the orbits and nasal cavity that lie immediately below. The only exception is the cribiform plate which drifts inferiorly, slightly in humans (Moss, 1963), but sometimes forming a “deep olfactory pit” in many species of nonhuman primates (Cameron, 1930; Aiello and Dean, 1990). Inferior drift of the middle cranial fossa presumably reflects inferiorly directed growth of the temporal lobes, but this hypothesis has not been tested. Likewise, inferior drift in the posterior cranial fossa, which is shallow in most nonhuman primates, is hypothesized to be a function of the size of the occipital lobes, the cerebellum, and the brain stem below the tentorium cerebelli. Note that cranial base flexion during growth, which occurs uniquely in humans (see below), complements inferior drift in the posterior cranial fossa by moving the floor of the posterior cranial fossa more below the middle cranial fossa.

**Angulation.** Angulation of the cranial base occurs when the prechordal and postchordal portions of the basicranium flex or extend relative to each other in the midsagittal plane (technically, flexion and extension describe a series of events in which the angle between the inferior or ventral surfaces of the cranial base decrease or increase, respectively). Angulation has been the subject of much research because flexion and extension of the cranial base affect the relative positions of the three endocranial fossae, thereby influencing a wide range of spatial relationships among the cranial base, brain, face, and pharynx (see below).

Although all measures of cranial base angle are similar in that they attempt to quantify the overall degree of angulation in the midsagittal plane between the prechordal and postchordal portions of the cranial base, there have been at least 17 different measurements used since Huxley (1867) first attempted to quantify the angle (reviewed in Lieberman and McCarthy, 1999, and summarized in Table 1). Many of these angles differ considerably in how they measure the prechordal and postchordal planes and, consequently, the point of intersection between them. Figure 5 illustrates some of these angles. The postchordal plane is most commonly defined using two landmarks, usually basion and sella, or using the line created by the dorsal surface of the basioccipital clivus (the clival line). The prechordal plane has been measured in more diverse ways. Historically, the most common plane is defined by two landmarks, sella and nasion. The sella-nasion line is problematic, however, because nasion is actually part of the face and moves anteriorly and inferiorly relative to the cranial base throughout the period of facial growth (Scott, 1958; Enlow, 1990). Recently, most researchers have defined the prechordal plane either from sella to the foramen caecum (a pit on the anterior end of the cribiform plate between the crista galli between frontal squama), or using the planum sphenoidale which extends from sphenoidale (the most postero-superior point on the tuberculum sellae) to the planum sphenoidale point (defined as the most anterior point on the surface of the midline anterior
cranial base posterior to the cribriform plate).

Since different lines emphasize different aspects of cranial base anatomy, the choice of which cranial base angle to use is largely dependent on the question under study. Both postchordal lines tend to yield roughly similar results (George, 1978; Lieberman and McCarthy, 1999), but the prechordal lines can be substantially different. In particular, S-FC spans the entire length of the anterior cranial base, including the cribiform plate, whereas the planum sphenoidale does not measure the portion of the cranial base that includes the cribiform plate. Because of variation in the growth and position of the cribiform plate, these differences affect comparisons of anthropoids with strepsirrhines, or comparisons of primates with other mammals (McCarthy, in press). In humans and some anthropoids, the cribiform plate lies in approximately the same plane as the planum sphenoidale, but in other anthropoids the cribiform plate lies in a deep olfactory pit within the ethmoidal notch of the frontal bone (Fig. 6) (Aiello and Dean, 1990; Ravosa and Shea, 1994). Moreover, in strepsirrhines and other mammals with more divergent orbits and projecting snouts, the cribiform plate typically lies at a steep angle relative to the planum sphenoidale (Cartmill, 1970).

Variations in cranial base angulation need to be considered in both comparative and ontogenetic studies. For example, it is well known that humans have a much more flexed cranial base than other primates, but it is not well appreciated that the human

<table>
<thead>
<tr>
<th>TABLE 1. Commonly used measures of midsagittal cranial base angle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angle</td>
</tr>
<tr>
<td>External cranial base angle Nasion-sella-basion</td>
</tr>
<tr>
<td>P: basion-sella</td>
</tr>
<tr>
<td>Landzert’s sphenoidal angle Clivus/clival angle</td>
</tr>
<tr>
<td>P: clival plane</td>
</tr>
<tr>
<td>CBA4, planum angle</td>
</tr>
<tr>
<td>P: clival plane</td>
</tr>
<tr>
<td>Ethmoidal angle</td>
</tr>
<tr>
<td>P: basion-sphenoidale</td>
</tr>
<tr>
<td>Internal cranial base angle Sphenoid-ethmoidal angle</td>
</tr>
<tr>
<td>P: basion-ethmoidale</td>
</tr>
<tr>
<td>Clivus angle</td>
</tr>
<tr>
<td>P: clival plane</td>
</tr>
<tr>
<td>Internal cranial base angle</td>
</tr>
<tr>
<td>P: sella-ethmoidale</td>
</tr>
<tr>
<td>Spheno-ethmoidal angle</td>
</tr>
<tr>
<td>P: clival plane</td>
</tr>
<tr>
<td>Cameron’s cranio-facial axis</td>
</tr>
<tr>
<td>P: basion-pituitary point</td>
</tr>
<tr>
<td>Basioccipito-septal angle</td>
</tr>
<tr>
<td>P: basion-pituitary point</td>
</tr>
<tr>
<td>Bolton’s external cranial base angle</td>
</tr>
<tr>
<td>P: Bolton point-sella</td>
</tr>
<tr>
<td>Anterior cranial base angle</td>
</tr>
<tr>
<td>P: clival plane</td>
</tr>
<tr>
<td>Internal cranial base angle, basion-sphenoidale-fronton</td>
</tr>
<tr>
<td>P: basion-sphenoidale</td>
</tr>
<tr>
<td>Internal cranial base angle, basion-sella-fronton</td>
</tr>
<tr>
<td>P: basion-sphenoidale</td>
</tr>
<tr>
<td>Internal cranial base angle, basion-sella-foramen caecum CBA1</td>
</tr>
<tr>
<td>P: basion-sphenoidale</td>
</tr>
<tr>
<td>External cranial base angle, nasion-sphenoidale-basion</td>
</tr>
<tr>
<td>P: basion-sphenoidale</td>
</tr>
<tr>
<td>Orbital angle</td>
</tr>
<tr>
<td>P: clival plane</td>
</tr>
<tr>
<td>Planum angle (PANG)</td>
</tr>
<tr>
<td>P: clival plane</td>
</tr>
<tr>
<td>Orbital angle (OANG)</td>
</tr>
<tr>
<td>P: clival plane</td>
</tr>
</tbody>
</table>
The cranial base flexes postnatally, while the nonhuman primate cranial base extends postnatally, possibly at different locations (Hofer, 1960; Sirianni and Swindler, 1979; Cousin et al., 1981; Lieberman and McCarthy, 1999). These potentially nonhomologous differences exist because changes in the cranial base angle can occur through different growth processes (e.g., drift, displacement) at different locations. The actual cellular processes that result in angulation, however, are not completely understood.

Fig. 5. Major cranial base angles used in this review, illustrated in a human cranium. CBA1 is the angle between the basion-sella (Ba-S) line and the sella- foramen (S-FC) caecum line. CBA4 is the angle between the midline of the postclival plane, and the midline of the planum sphenoidale.

Fig. 6. Lateral radiographs of hemisected baboon cranium (A) and human cranium (B). Note different orientation and position of the cribriform plate (CP) relative to the planum sphenoidale (PS) in the two species.
Some researchers (Scott, 1958; Giles et al., 1981; Enlow, 1990) suggest that changes in cranial base angulation occur interstitially within synchondroses through a hinge-like action. If so, flexion would result from increased chondrogenic activity in the superior vs. inferior aspect of the synchondrosis, while extension would result from increased chondrogenic activity in the inferior vs. superior aspect of the synchondrosis. Experimental growth studies in macaques, which labeled growth using flurochrome dyes, show that angulation also occurs through drift in which depository and resorptive growth fields differ on either side of a synchondrosis, causing rotations around an axis through the synchondrosis (Michejda, 1971, 1972a; Michejda and Lamey, 1971; Giles et al., 1981). All three synchondroses are involved in prenatal angulation (Hofer, 1960; Hofer and Spatz, 1963; Sirianni and Newell-Morris, 1980; Dievert, 1985; Anastagopolou et al., 1988; Sperber, 1989; van den Eynde et al., 1992); however, the extent to which each synchondrosis participates in postnatal flexion and extension is poorly known, and probably differs between humans and nonhuman primates. The SOS, which remains active until after the eruption of the second permanent molars, is probably the most active synchondrosis in generating angulation in primates (Björk, 1955; Scott, 1958; Melsen, 1969). The MSS fuses prior to birth in humans (Ford, 1958), but may also be important in nonhuman primates (Scott, 1958; Hofer and Spatz, 1963; Michejda, 1971, 1972a; but see Lager, 1958; Melsen, 1971; Giles et al., 1981). Finally, the SES fuses near birth in nonhuman primates, and remains active only as a site of cranial base elongation in humans during the neural growth period (Scott, 1958; Michejda and Lamey, 1971). Other ontogenetic changes in the cranial base angle (not necessarily involved in angulation itself) include posterior drift of the foramen magnum (see above), inferior drift of the cribriform plate relative to the anterior cranial base (Moss, 1963), and remodeling of the sella turcica, which causes posterior movement of the sella (Baume, 1957; Shapiro, 1960; Latham, 1972).

A few experimental studies provide evidence for the presence of complex interactions between the brain and cranial base synchondroses that influence variation in the cranial base angle. DuBrul and Laskin (1961), Moss (1976), Bütow (1990), and Reidenberg and Laitman (1991) all inhibited growth in the SOS in various animals (mostly rats), causing a more flexed cranial base, presumably through inhibition of cranial base extension. In most of these studies, experimentally induced kyphosis of the basicranium was also associated with a shorter posterior portion of the cranial base, and a more rounded neurocranium (see below). Artificial deformation of the cranial vault also causes slight but significant increases in cranial base angulation (Antón, 1989; Kohn et al., 1993). However, no controlled experimental studies have yet examined disruptions to the other cranial base synchondroses. In addition, there have been few controlled studies of the effect of increasing brain size on cranial base angulation. In one classic experiment, Young (1959) added sclerosing fluid into the cranial cavity in growing rats, which caused enlargement of the neurocranium with little effect on angular relationships in the cranial base. Additional evidence for some degree of independence between the brain and cranial base during development is provided by microcephaly and hydrocephaly, in which cranial base angles tend to be close to those of humans with normal encephalization (Moore and Lavelle, 1974; Sperber, 1989).

Important differences in cranial base angulation among primates exist in terms of the ontogenetic pattern of flexion and/or extension, which presumably result from differences in the rate, timing, duration, and sequence of the growth processes outlined above. Jeffery (1999) suggested that, prenatally, the basicranium in humans initially flexes rapidly during the period of rapid hindbrain growth in the first trimester, remains fairly stable during the second trimester, and then extends during the third trimester in conjunction with facial extension, even while the brain is rapidly increasing in size relative to the rest of the cranium (see also Björk, 1955; Ford, 1956; Sperber,
Little is known about prenatal cranial base angulation in nonhuman primates; however, major differences between humans and nonhumans appear during the fetal and postnatal periods of growth. As Figure 7 illustrates, the human cranial base flexes rapidly after birth, almost entirely prior to 2 years of age, and well before the brain has ceased to expand appreciably (Lieberman and McCarthy, 1999). In contrast, the nonhuman primate cranial base extends gradually after birth throughout the neural and facial growth periods, culminating in an accelerated phase during the adolescent growth spurt (Hofer, 1960; Heintz, 1966; Sirianni and Swindler, 1979; Cousin et al., 1981; Lieberman and McCarthy, 1999).

The polyphasic and multifactorial nature of cranial base angulation during ontogeny and the ontogenetic contrasts between the relative contribution of underlying factors in humans and nonhumans provide some clues for understanding the complex, multiple interactions between cranial base angulation, encephalization, and facial growth. There is abundant evidence based on interspecific studies (see below) that variation in cranial base angle in primates is associated in part with variation in brain volume relative to the length of the cranial base. However, relative encephalization accounts for only 36% of the variation in cranial base angle among anthropoids, and both interspecific and ontogenetic data suggest that a large proportion of the variation in cranial

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**Fig. 7.** Changes in the angle of the cranial base (CBA1 and CBA4) in *Homo sapiens* (left) and *Pan troglodytes* (right) (after Fig. 6 in Lieberman and McCarthy, 1999). For both species, means (circles) and standard deviations (whiskers) are summarized by the mean chronological age of each dental stage. Note that the human cranial base flexes rapidly during stage I and then remains stable, whereas the chimpanzee cranial base extends gradually through stage V. *P < 0.05.
base angle among primates must also be related to variation in facial growth, orbit orientation, and relative orbit size (Ross and Ravosa, 1993; Ravosa et al., 2000a). As noted above, the ontogenetic pattern of prenatal cranial base angulation in humans is largely unrelated to the rate at which the brain expands (Jeffery, 1999). In addition, the nonhuman primate cranial base angle (regardless of whether the cribriform plate is included in the measurement) mostly extends during the period of facial growth, after the brain has ceased to expand (Lieberman and McCarthy, 1999). Therefore, we will next explore in greater depth the relationship between cranial base angle, brain size, relative orbit size and position, facial orientation, and other factors such as pharyngeal shape and facial projection.

ASSOCIATIONS BETWEEN CRANIAL BASE AND BRAIN

Because of the close relationship between the brain and the cranial base during development (see above), the hypothesis that brain size and shape influence basicranial morphology is an old and persistent one. The bones of the cranial cavity, including the cranial base, are generally known to conform to the shape of the brain, but the specifics of this relationship and any reciprocal effects of cranial base size and shape on brain morphology remain unclear. For example, the human basicranium is flexed when it first appears in weeks 5 and 6 because in the fourth week, the neural tube bends ventrally at the cephalic flexure (O'Rahilly and Müller, 1994). The parachordal condensations caudal to the cephalic flexure are therefore in a different anatomical plane than the more rostral parachordal condensations (which develop by week 7). However, as noted above, it is difficult to attribute many of the subsequent changes in prenatal chondrocranial or basicranial angulation (or other measures of the base) as responses solely to changes in brain morphology.

Here we review several key aspects of the association between brain and cranial base morphology, as derived from interspecific analyses of adult specimens. Structural relationships between the cranial base and the face are discussed below.

Brain size and cranial base angle

Numerous anatomists have posited a relationship between brain size and basicranial angle (e.g., Virchow, 1857; Ranke, 1892; Cameron, 1924; Bolk, 1926; Dabelow, 1929, 1931; Biegert, 1957, 1963; Delattre and Fernart, 1963; Hofer, 1969; Gould, 1977; Ross and Ravosa, 1993; Ross and Henneberg, 1995; Spoor, 1997; Strait, 1999; Strait and Ross, 1999; McCarthy, 2001). The most widely accepted of these hypotheses is that the angle of the midline cranial base in the sagittal plane correlates with the volume of the brain relative to basicranial length (DuBrul and Laskin, 1961; Vogel, 1964; Riesenfeld, 1969; Gould, 1977). This hypothesis is supported by independent analyses of different measures of basicranial flexion across several interspecific samples of primates (Ross and Ravosa, 1993; Spoor, 1997; McCarthy, 2001) (Fig. 8): the adult midline cranial base is significantly and predictably more flexed in species with larger endocranial volumes relative to basicranial length. In particular, the analysis by Ross and Ravosa (1993) of a broad interspecific sample of primates found that the correlation coefficient between relative encephalization (IRE1, see below) and cranial base angle (CBA4, see below) was 0.645 ($P < 0.001$), explaining approximately 40% of the variation in cranial base angle.

Attempts to extend this relationship to hominins have proved controversial. Ross and Henneberg (1995) reported that Homo sapiens have less flexed basicrania than predicted by either haplorhine or primate regressions. They posited that spatial constraints limit the degree of flexion possible, and that humans accommodate further brain expansion relative to cranial base length through means other than flexion, such as superior, posterior, and lateral neurocranial expansion. In contrast, Spoor (1997), using different measures of flexion and relative brain size taken on a different sample, found H. sapiens to have the degree of flexion expected for its relative brain size. Spoor (1997) used the angle basion-sella foramen caecum (CBA1) to quantify basi-
cranial flexion, and the length of these line segments (thereby including cribriform plate length) to quantify basicranial length (BL2), whereas Ross and Henneberg (1995) measured flexion using CBA4 and relative brain size using IRE1 (endocranial volume/BL1).

The two most likely sources of the discrepancy between the results of Spoor (1997) vs. Ross and Henneberg (1995) were the different measures and different samples. McCarthy (2001) has since investigated the influence of different measures, noting that the measure of basicranial length by Ross and Henneberg (1995) excluded the horizontally oriented cribriform plate that contributes to basicranial length in anthropoids more than in strepsirrhines. McCarthy (2001) also demonstrated that the frontal bone contributes less to midline cranial base length in hominoids, especially humans, causing BL1 to underestimate midline basicranial length relative to endocranial volume compared to other anthropoids. However, the data sets of both McCarthy (2000) and Spoor (1997) were small (n = 17 species) in comparison with that of Ross and Henneberg (1995) (n = 64 species). We therefore reanalyzed the relationships between flexion and relative brain size in a large interspecific primate sample, utilizing both CBA1 and CBA4 as measures of flexion and IRE5 as a measure of relative brain size. IRE5 incorporates the more appropriate basicranial length that includes cribriform plate length (see Glossary and Measurement Definitions). The human value for CBA1 falls within the 95% confidence limits of the value predicted for an anthropoid of its relative brain size, but the human value for CBA4 does not. These results corroborate those of McCarthy (2001): the degree of basicranial flexion in humans is not significantly less than expected using CBA1, but is less than expected using CBA4. Thus humans may or may not have the degree of

Fig. 8. Bivariate plot of CBA4 against IRE5. These variables are significantly correlated across Primates (r = -0.621; P < 0.05) and Haplorhini (r = -0.636; P < 0.05).

Measurements were taken on radiographs of nonhuman primates from Ravosa (1991b) and Ross and Ravosa (1993), and on Homo sapiens from Ross and Henneberg (1995). RMA slopes were calculated for nonhominin primates, and the 95% bootstrap confidence limits for the value of y predicted for humans were calculated according to Jolicoeur and Mosiman (1968), using software written by Tim Cole.
flexion expected for their relative brain size, depending on which measures are used.

One problem with the above studies is that they do not consider the potential role of phylogenetic effects on these correlations (Cheverud et al., 1985; Felsenstein, 1985). Accordingly, the above data were reanalyzed using the method of Smith (1994) for adjusting degrees of freedom. Table 2 presents the percentage of total variance distributed at each taxonomic level within the order Primates. Table 3 presents the correlation coefficients for comparisons of CBA and IRE for Primates and Haplorhini, along with sample sizes, degrees of freedom adjusted for phylogeny (df*), and their associated P-values (for which strepsirrhines had no significant correlations). Examination of the variance components in Table 2 shows that the relationship between cranial base angle and relative brain size is subject to significant phylogenetic effects. However, the method of Smith (1994) is conservative and the correlations that survive these corrected degrees of freedom are robust, although of relatively low magnitude. Across primates and haplorhines, both CBA4 and CBA1 are significantly correlated (P<0.05) with IRE5 (Fig. 8; Table 2). These results corroborate the results of Ross and Ravosa (1993), but with a more appropriate measure of basicranial length incorporated into the measure of relative brain size. This confirms that brain size relative to basicranial length is significantly correlated with basicranial flexion, but that the correlations are not particularly strong, indicating that there may be other important influences on the degree of basicranial flexion (see below).

Most hypotheses explaining basicranial flexion have focused on increases in relative brain size as the variable driving flexion. However, as Strait (1999) has noted, it is important to consider the scaling relationships of basicranial length and brain size. Using interspecific data from Ross and Ravosa (1993) in conjunction with other studies, Strait (1999) found that basicranial length scales with negative allometry against body mass and telencephalon volume (results confirmed here using BL2 instead of BL1; see Table 4), and BL2 also

---

**TABLE 2. Variance components for indices of relative brain size and measures of flexion across primates**

<table>
<thead>
<tr>
<th>Level</th>
<th>N</th>
<th>%N eff</th>
<th>%N eff</th>
<th>%N eff</th>
<th>%N eff</th>
<th>%N eff</th>
<th>%N eff</th>
</tr>
</thead>
<tbody>
<tr>
<td>Infraorder</td>
<td>2</td>
<td>12</td>
<td>0.24</td>
<td>48</td>
<td>0.94</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Superfamily</td>
<td>6</td>
<td>22</td>
<td>1.34</td>
<td>10</td>
<td>0.62</td>
<td>34</td>
<td>2.07</td>
</tr>
<tr>
<td>Family</td>
<td>15</td>
<td>54</td>
<td>8.16</td>
<td>16</td>
<td>2.44</td>
<td>44</td>
<td>6.56</td>
</tr>
<tr>
<td>Genus</td>
<td>60</td>
<td>13</td>
<td>7.81</td>
<td>22</td>
<td>12.99</td>
<td>17</td>
<td>10.26</td>
</tr>
<tr>
<td>Species</td>
<td>62</td>
<td>1</td>
<td>0.78</td>
<td>3</td>
<td>2.38</td>
<td>5</td>
<td>3.10</td>
</tr>
<tr>
<td>Total</td>
<td>18.33</td>
<td>17.38</td>
<td>21.99</td>
<td>14.23</td>
<td>12.00</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Maximum likelihood variance components were calculated using mainframe SAS (proc = varcomp). %, percentage of variance at each taxonon 1 mic level; %N eff, effective N at each level; Total %N eff, total effective N for each variable. Bivariate comparisons utilize lowest %N eff of the pair.

**TABLE 3. Correlation coefficients for primates and haplorhini**

<table>
<thead>
<tr>
<th>Variables</th>
<th>CBA4</th>
<th>N (P)</th>
<th>df* (P)</th>
<th>CBA1</th>
<th>N (P)</th>
<th>df* (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primates</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IRE1</td>
<td>-0.783</td>
<td>60 (&lt;0.001)</td>
<td>14 (0.01)</td>
<td>-0.672</td>
<td>60 (&lt;0.001)</td>
<td>10 (0.05)</td>
</tr>
<tr>
<td>IRE5</td>
<td>-0.621</td>
<td>60 (&lt;0.001)</td>
<td>13 (0.05)</td>
<td>-0.790</td>
<td>62 (&lt;0.001)</td>
<td>10 (0.01)</td>
</tr>
<tr>
<td>Haplorhini</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IRE1</td>
<td>-0.813</td>
<td>51 (&lt;0.001)</td>
<td>9 (0.01)</td>
<td>-0.641</td>
<td>51 (&lt;0.001)</td>
<td>9 (0.05)</td>
</tr>
<tr>
<td>IRE5</td>
<td>-0.636</td>
<td>51 (&lt;0.001)</td>
<td>10 (0.05)</td>
<td>-0.548</td>
<td>51 (&lt;0.001)</td>
<td>14 (0.05)</td>
</tr>
</tbody>
</table>

1 N, total N; df* = 2, effective degrees of freedom for each comparison. Bivariate comparisons utilize lowest %N eff of the pair.

---

3Unlike methods such as “independent contrasts” (e.g., Purvis and Rambaut, 1995), Smith’s method uses values for variables in just terminal taxa, therefore avoiding potentially spurious estimates of these values for ancestral nodes. Smith’s method is also more robust when five or fewer taxonomic levels are considered and is less affected by arbitrary taxonomic groupings (Nunn, 1995). We also used the maximum likelihood method for calculating variance components rather than a nested ANOVA method because maximum likelihood does not generate negative variance components.
scales with negative allometry against measures of facial size (Table 4). The only variable that scales close to isometry with basicranial length is brain-stem volume, which is isometric with BL1 and scales close to isometry with BL2 (Table 4). Intuitively this isometry makes sense, because the brain stem rests on the basicranium. However, the posterior basicranium (Ba-S), which predominantly underlies the brain stem, scales with positive allometry to brain-stem volume, whereas the anterior cranial base length scales isometrically with brain-stem volume. Notably, the anterior cranial base always shows lower slopes than the posterior cranial base, suggesting that the strong negative allometry of cranial base length relative to neural variables, and possibly flexion, is disproportionately attributable to relative shortening of the anterior cranial base.

Brain shape and cranial base angle

Given the close anatomical relationship between the brain and basicranium, it seems intuitive that the shapes of the two should be related, but testing this hypothesis in a controlled fashion has been difficult. The best evidence for the presence of interactions between brain shape and the cranial base came from studies of artificial cranial vault deformation and from the effects of closing various cranial vault sutures on the cranial base. The effects of head-binding are difficult to interpret without precise data on the timing and forces used to deform the skull. Nevertheless, antero-posterior head-binding tends to cause lateral expansion of

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Intercept</th>
<th>Slope</th>
<th>95% CI of slope</th>
<th>Scaling</th>
<th>N</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>BL2 vs.</td>
<td>0.908</td>
<td>0.654</td>
<td>0.035</td>
<td>-ve</td>
<td>61</td>
<td>0.978</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.541</td>
<td>0.742</td>
<td>0.091</td>
<td>-ve</td>
<td>33</td>
<td>0.960</td>
</tr>
<tr>
<td>Telencephalon</td>
<td>0.404</td>
<td>1.123</td>
<td>0.100</td>
<td>+ve/Iso</td>
<td>33</td>
<td>0.975</td>
</tr>
<tr>
<td>Neurocranial volume</td>
<td>1.270</td>
<td>0.734</td>
<td>0.056</td>
<td>-ve</td>
<td>62</td>
<td>0.962</td>
</tr>
<tr>
<td>Palate (Pros-PNS)</td>
<td>1.394</td>
<td>0.642</td>
<td>0.032</td>
<td>-ve</td>
<td>58</td>
<td>0.929</td>
</tr>
<tr>
<td>Anterior face (Pros-Nas)</td>
<td>1.623</td>
<td>0.577</td>
<td>0.028</td>
<td>-ve</td>
<td>58</td>
<td>0.933</td>
</tr>
<tr>
<td>Upper tooththrow</td>
<td>1.425</td>
<td>0.666</td>
<td>0.035</td>
<td>-ve</td>
<td>58</td>
<td>0.921</td>
</tr>
<tr>
<td>Geometric mean</td>
<td>0.951</td>
<td>0.750</td>
<td>0.023</td>
<td>-ve</td>
<td>58</td>
<td>0.972</td>
</tr>
<tr>
<td>Ba-S vs.</td>
<td>0.380</td>
<td>0.759</td>
<td>0.056</td>
<td>-ve</td>
<td>62</td>
<td>0.958</td>
</tr>
<tr>
<td>Body mass</td>
<td>-0.226</td>
<td>1.354</td>
<td>0.161</td>
<td>+ve</td>
<td>33</td>
<td>0.946</td>
</tr>
<tr>
<td>Telencephalon</td>
<td>0.313</td>
<td>0.908</td>
<td>0.135</td>
<td>Iso</td>
<td>33</td>
<td>0.924</td>
</tr>
<tr>
<td>Cerebellum</td>
<td>0.105</td>
<td>0.953</td>
<td>0.111</td>
<td>Iso</td>
<td>33</td>
<td>0.948</td>
</tr>
<tr>
<td>Infratentorial brain</td>
<td>-0.064</td>
<td>1.044</td>
<td>0.123</td>
<td>Iso</td>
<td>33</td>
<td>0.947</td>
</tr>
<tr>
<td>Palate (Pros-PNS)</td>
<td>0.595</td>
<td>0.757</td>
<td>0.040</td>
<td>-ve</td>
<td>58</td>
<td>0.917</td>
</tr>
<tr>
<td>Anterior face (Pros-Nas)</td>
<td>0.862</td>
<td>0.681</td>
<td>0.037</td>
<td>-ve</td>
<td>58</td>
<td>0.914</td>
</tr>
<tr>
<td>Upper tooththrow</td>
<td>0.626</td>
<td>0.787</td>
<td>0.043</td>
<td>-ve</td>
<td>58</td>
<td>0.924</td>
</tr>
<tr>
<td>Geometric mean</td>
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<td>0.886</td>
<td>0.034</td>
<td>-ve</td>
<td>58</td>
<td>0.957</td>
</tr>
<tr>
<td>S-FC vs.</td>
<td>0.473</td>
<td>0.759</td>
<td>0.063</td>
<td>-ve</td>
<td>33</td>
<td>0.949</td>
</tr>
<tr>
<td>Body mass</td>
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<td>0.040</td>
<td>-ve</td>
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</tr>
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<td>0.101</td>
<td>Iso</td>
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<td>0.971</td>
</tr>
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<td>Telencephalon</td>
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<td>0.715</td>
<td>0.082</td>
<td>-ve</td>
<td>33</td>
<td>0.963</td>
</tr>
<tr>
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<td>-ve</td>
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<tr>
<td>Infratentorial brain</td>
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<td>0.822</td>
<td>0.085</td>
<td>-ve</td>
<td>33</td>
<td>0.965</td>
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<tr>
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<td>-ve</td>
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<tr>
<td>Anterior face (Pros-Nas)</td>
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<td>-ve</td>
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<tr>
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<td>0.026</td>
<td>-ve</td>
<td>58</td>
<td>0.958</td>
</tr>
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</table>

1 All volumetric and mass variables converted to cube roots. All calculations in log-log space (base 10). Calculations with facial dimensions do not include humans; all other calculations include humans.

2 Geometric mean of the following measures: palate length, palate breadth, anterior face length, maxillary postcanine tooththrow length, outer biorbital breadth, bizygomatic breadth, basicranial length, and lower skull length. Measures of brain volume from Stephan et al. (1981), measures of body mass from Smith and Jungers (1994), and measures of facial size derive from the same skulls from which the radiographs were taken.

Source: 134 YEARBOOK OF PHYSICAL ANTHROPOLOGY [Vol. 43, 2000]
the cranial base along with a slight increase in CBA; conversely, annular head-binding tends to cause medio-lateral narrowing and antero-posterior elongation of the cranial base, also with a slight increase in CBA (Antón, 1989; Cheverud et al., 1992; Kohn et al., 1993). Natural or experimentally induced premature closure of sutures (synostoses) in the cranial vault have similarly predictable effects. For example, bilateral coronal synostoses cause antero-posterior shortening of the cranial base (Babler, 1989; David et al., 1989), and unilateral coronal synostoses (plagiocephaly) cause marked asymmetry in the cranial vault, cranial base, and face.

Interspecific analyses of the relationship between brain shape and cranial base shape in primates are rare. Hofer (1965, 1969) measured the orientation of the cerebral hemispheres relative to the brain stem in primates using two axes: Forel’s axis, from the most antero-inferior point on the frontal lobe to the most postero-inferior point on the occipital lobe, and Meynert’s axis, from the ventral edge of the junction between the pons and medulla to the caudal recess of the interpeduncular fossa. The data of Hofer (1969) measure anterior angles between lines, rather than the inferior angles favored by recent workers (e.g., Ross and Ravosa, 1993). The plotted data therefore represent the complement of Hofer’s angles.

The inferior surface of the cerebral hemispheres; and Meynert’s axis, from the ventral edge of the junction between the pons and medulla to the caudal recess of the interpeduncular fossa, quantifying the orientation of the brain stem. Hofer (1965) also measured the angle of the midline cranial base using a modified version of the angle of Landzert (1866), similar to the CBA4 used by Ross and Ravosa (1993).

Figure 9, a plot of the measure by Hofer of basicranial angle against his measure of brain angle, illustrates that these variables are highly correlated and scale isometrically with each other (i.e., have a slope of 1.0). As the cerebrum flexes on the brain stem, the planum sphenoidale flexes relative to the clivus. The explanation of Hofer (1969) for this phenomenon is that the telencephalon becomes more spherical as it enlarges, to minimize surface area relative to volume. An alternative hypothesis is that increasing the antero-posterior diameter of the head “would be disastrous, making larger animals unusually long-headed, and would pro-
duce serious problems for balancing the skull on the skeleton” (Jerison, 1982, p. 82). In the context of such spatial constraints (i.e., limited cerebral diameter and tendency to sphericity), increased cerebrum size can only be accommodated by expanding the cranial base inferiorly, posteriorly, or anteriorly, thereby necessarily flexing the brain and the basicranium. The hypothesis of Jerison (1982) is refuted by animals such as camels, llamas, and giraffes, which have long heads on relatively orthograde necks; and as discussed below, there is no convincing evidence that head and neck posture are significant influences on basicranial angle in primates (Strait and Ross, 1999).

Biegert (1963) made a claim similar to that of Hofer (1969), in arguing that increases in primate brain size relative to cranial base size, as well as increases in “neopallium” (i.e., neocortex) size relative to other parts of the brain, produced a rounder brain such that “adaptations in the structure of the cranium accompanied these changes in the size and shape of the brain” (Biegert, 1963, p. 120). The predicted changes in skull shape include increased vaulting of the frontal and occipital bones and increased basicranial flexion. Ross and Ravosa (1993) evaluated the hypothesis of Biegert (1963) by calculating correlation coefficients between cranial base angle (CBA4) and the ratio of neocortical volume to basicranial length. Although they found a significant relationship across primates and haplorhines, the correlation coefficients were low (around 0.5). Recalculation of these correlation coefficients using BL2 as a measure of basicranial length produces significant correlations across primates, haplorhines, and strepsirrhines, but only the primate level correlations survive adjusted degrees of freedom (Table 5).

Strait (1999) proposed a hypothesis similar to those of Hofer (1969) and Biegert (1963). Noting that total basicranial length scales close to isometry with noncortical brain volume, Strait (1999) suggested that variation in the midline basicranial angle might be due to increases in the size of the telencephalon relative to the noncortical part of the brain, rather than the size of the brain relative to the cranial base. Analysis of our data set confirms this hypothesis: there are significant correlations between flexion and the size of the telencephalon relative to the brain stem across primates, using CBA4 (Table 5). Moreover, the only significant correlation between cranial base angle and a neural variable among strepsirrhines is the comparison of CBA4 with the ratio of telencephalon to brain-stem volume (Table 5). However, despite relatively high correlation coefficients for haplorhines, these correlations do not remain significant with phylogenetically adjusted degrees of freedom. This suggests that brain size relative to basicranial length may be a better explanation for flexion, because it appears to be more independent of phylogenetic effects.

Whether basicranial flexion accommodates increases in telencephalon volume relative to brain-stem volume, and/or increases in overall endocranial volume relative to cranial base length, the end result is a change in brain shape. The enlarged telencephalon of primates is an outgrowth of the rostral end of the brain stem that communicates with the rest of the brain through the diencephalon at its root.

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4Strait (1999) refers to this as the “noncortical scaling hypothesis”; however, the telencephalon consists of more than cortex: it also includes the white matter and the basal ganglia. Here we evaluate the role of relative telencephalon volume in producing flexion.
Increasing the size of the outer cortex of the telencephalon (the neocortex) while still connecting to the rest of the brain through the diencephalon might be expected to generate a more spheroid shape, regardless of any functional constraints on skull or brain shape. In other words, the telencephalon may be spheroidal because of the geometry of its connections and the way it develops, rather than for any functional or adaptive reason. Alternately, a spheroidal cerebrum may minimize “wiring length” in the brain, a potentially important principle of design in neural architecture (Allman and Kaas, 1974; Barlow, 1986; Mitchison, 1991; Cherniak, 1995; Van Essen, 1997). Accordingly, a spheroid telencephalon may optimize neocortical wiring lengths as well as minimize the distance from all points in the cerebrum to the diencephalon, a structure through which all connections to the rest of the brain must pass (Ross and Henneberg, 1995). Another possible advantage of a flexed basicranium derives from the in vitro experiments of Demes (1985), showing that the angulation of the cranial base in combination with a spherical neurocranium helps distribute applied stresses efficiently over a large area and decreases stresses in the anterior cranial base during loading of the temporomandibular joint. This interesting model, however, requires further testing.

Whether the spheroid shape of the telencephalon is a functional adaptation or a structural consequence of geometry and developmental processes remains to be determined. Nevertheless, the presence of the cerebellum, and ultimately of the brain stem, prevents caudal expansion of the telencephalon, making rostral expansion of the telencephalon the easiest route. This would cause the especially large human brain to develop a kink of the kind measured by Hofer, which in turn may cause flexion of the basicranium. If this hypothesis is correct, then some proportion of the variation in basicranial angle among primates is caused by intrinsic changes in brain shape, and not the relationship between the size of the brain and the base on which it sits.

One caution (noted above) is that ontogenetic data suggest that the interspecific variation in cranial base angle and shape presented above is partially a consequence of variables other than relative encephalization or intrinsic brain shape. Ontogenetic data are useful because they allow one to examine temporal relationships among predicted causal factors. The human ontogenetic data provide mixed support for the hypothesis that cranial base angulation reflects relative encephalization. Jeffery (1999) found no significant relationship between CBA1 and IRE1 during the second fetal trimester in humans, when brain growth is especially rapid; but Lieberman and McCarthy (1999) found that the human cranial base flexes rapidly during the first 2 postnatal years, when most brain growth occurs. Why relative brain size in humans correlates with cranial base angle after birth but not before remains to be explained. In addition, and in contrast to humans, the cranial base in all nonhuman primates so far analyzed extends rather than flexes during the period of postnatal brain growth, and continues to extend throughout the period of facial growth, after brain growth has ceased. In Pan, for example, approximately 88% of cranial base extension (CBA1) occurs after the brain has reached 95% adult size (Lieberman and McCarthy, 1999). Similar results characterize other genera (e.g., Macaca; Sirianni and Swindler, 1985; Schneiderman, 1992).

Ontogenetic data do not disprove the hypothesis that variation in cranial base angle is related to brain size, but instead highlight the likelihood that the processes which generate variation in cranial base angle are polyphasic and multifactorial. Notably, the ontogenetic data suggest that the tight structural relationship between the face and the anterior cranial base (discussed below) is also an important influence on cranial base angle. This suggests that a large proportion of the interspecific variation in CBA, IRE, and other aspects of neural size and shape reported above is explained by interactions between the brain and the cranial base prior to the end of the neural growth phase. Thereafter, other factors (especially those related to the face) influence the shape of the cranial base. One obvious way to test this hypothesis is to compare the
above interspecific analyses of adults with comparable analyses of infants at the period when the brain has ceased growing, but before much of the face has grown.

**Brain volume and posterior cranial fossa shape**

Dean and Wood (1981, 1982) and Aiello and Dean (1990) hypothesized that increases in cerebellum size correlate with increases in the size of the posterior cranial fossa. This correlation is purportedly a result of increases in basicranial flexion; and by lateral and anterior displacement of the lateral aspects of the petrous pyramids, which cause the petrous pyramids to be more coronally oriented in humans than in great apes. However, Ross and Ravosa (1993) found little support for a link between absolute cerebellum volume and CBA4; in addition, Spoor (1997) did not find a correlation between cerebellum volume and petrous orientation. Rather, Spoor (1997) showed that more coronally oriented petrous pyramids in adult primates correlate better with increases in brain volume relative to basicranial length. In addition, the petrous pyramids, when viewed from the internal aspect of the cranial base, are not more coronally oriented in humans vs. other apes (Spoor, 1997).

The probable explanation for these results may be that the posterior cranial base (Ba-S) scales with isometry against both cerebellum volume and CBA4; in addition, Spoor (1997) did not find a correlation between cerebellum volume and petrous orientation. Rather, Spoor (1997) showed that more coronally oriented petrous pyramids in adult primates correlate better with increases in brain volume relative to basicranial length. In addition, the petrous pyramids, when viewed from the internal aspect of the cranial base, are not more coronally oriented in humans vs. other apes (Spoor, 1997).

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**ASSOCIATIONS BETWEEN CRANIAL BASE AND FACE**

It has long been known that the cranial base plays an important role in facial growth, but many details of how these regions interact remain poorly understood. While the face has some influence on cranial base growth (see below), there are two major reasons to believe that the cranial base exerts a greater influence on the face than vice versa during growth by setting up certain key spatial relationships. First, the majority of the cranial base (with the exception of the ethmoidal portions of the ethmomaxillary complex) attains adult size long before the face (Moore and Lavelle, 1974). Second, as noted above, most of the face grows anteriorly, laterally, inferiorly, and around the cranial base. In all mammals, the upper portion of the face (the orbital and upper nasal regions) grows antero inferiorly relative to the anterior cranial base and floor; and the middle face (mostly the nasal region) grows anteriorly relative to the middle cranial fossa. The lower portion of the face (the mandibular and maxillary arches and their supporting structures) interacts only indirectly with the cranial base, since the maxillary arch grows inferiorly from the middle face and anteriorly relative to the pterygoid processes of the sphenoid.

These spatial and developmental associations raise an important question: to what extent does the cranial base influence facial growth and form? In order to address this issue, we first discuss the relationships between two regions of the face and cranial base that are contiguous across functional or developmental boundaries (the so-called growth counterparts of Enlow, 1990): 1) the anterior cranial fossa and the upper, orbital, and nasal portions of the face, and 2) the middle cranial fossa and the middle, ethmomaxillary portion of the face. We conclude with a brief discussion of the possible relationships between cranial base shape and overall facial shape.

**Anterior cranial fossa shape and upper facial growth**

The upper face comprises the orbital cavities, the orbital superstructures, and the upper portion of the nasal cavity. The upper face therefore incorporates elements of the anterior cranial base, including the ethmoid, parts of the sphenoid, and significant portions of the frontal bone. The upper face
grows away from the rest of the cranial base in three ways. Initially, as the eyeballs expand, the orbital cavity expands anteriorly, inferiorly, and laterally through drift and displacement (Moss and Young, 1960; Enlow, 1990). Animals enucleated during the period of eyeball growth consequently have deficient anterior and lateral growth of the upper face (see Sarnat, 1982). In addition, since the roof of the orbit also contributes to the floor of the anterior cranial fossa (i.e., the orbital plates of the frontal bone and lesser wings of the sphenoid), the position, orientation, and shape of the orbital roof must inevitably be affected by growth of the frontal lobes and anterior cranial fossa. Finally, the orbital cavities and superstructures grow anteriorly and laterally away from the anterior cranial base until after the eruption of the second molars (Riolo et al., 1974; Lieberman, 2000). In contrast, the front of the upper face in most nonhuman primates projects anteriorly relative to the front of the anterior cranial fossa prior to the eruption of the first molars (Krogman, 1969; Lieberman, 1998, 2000). Variation in this spatial separation, termed neurocranial-orbital or neuro-orbital disjunction, has been analyzed by various researchers to explain ontogenetic and interspecific patterns of supraorbital torus morphology (Weidenreich, 1941; Moss and Young, 1960; Radinsky, 1968, 1970, 1977, 1979; Shea, 1985a, 1986, 1988; Ravosa, 1988, 1991a,b; Hylander and Ravosa, 1992; Vinyard and Smith, 1997; Shea, 1985a, 1986, 1988; Ravosa, 1988, 1991a,b; Lieberman, 2000).

While the structural boundaries shared by the anterior cranial base and the upper face result in a high degree of integration between these two regions, the extent to which anterior cranial base shape influences other aspects of facial shape is less clear. In an interspecific study of 68 species, Ross and Ravosa (1993) found that both orbit and palate orientation are significantly correlated with anterior cranial base orientation, but that palate orientation accounts for none of the variation in cranial base angle independent of orbital axis orientation. McCarthy and Lieberman (2001) have also shown that the orientation of the orbits and the anterior cranial base are correlated with each other \( r = 0.617, P < 0.05 \) in haplorhines but not in strepsirrhines. These studies suggest that the orientation of the anterior cranial base affects the orientation of the upper face directly, but that it only indirectly influences palate orientation through the integration of palate and orbits (see also Ravosa, 1988; Ravosa and Shea, 1994). Consequently, it seems likely that the anterior cranial base exerts a slight influence on facial orientation as a whole, but that only the orbital region of the face is directly integrated with the anterior cranial base. Higher levels of integration appear to characterize those organisms with greater
encephalization, increased orbital convergence, and relatively large orbits (Ravosa et al., 2000a).

Enlow (1990) proposed several structural relationships between the anterior cranial base and various aspects of facial shape. His general model for the plan of the face is based almost exclusively on analyses of human radiographs, and has not been carefully tested in most respects. However, three hypotheses are of special interest. First, since the floor of the nasal chamber is also the roof of the oral cavity, Enlow (1990) proposed that interorbital breadth should be correlated with prognathism because “the broad nasal base of most other mammals supports a correspondingly much longer snout.” Smith and Josell (1984) tested this hypothesis using a sample of 32 primates, and found a low correlation ($r = 0.46$) between interorbital breadth and mandibular prognathism, and noted that the correlation was even weaker when effects of overall cranial length and body size were taken into account. This is perhaps not surprising, as there is no obvious biomechanical or developmental reason why the length of the face should be correlated with the width of the posterior part of the face. Second, Enlow (1990) proposed that the orientation of the cribiform plate in all mammals, including primates, is perpendicular to the orientation of the nasomaxillary complex (defined as a plane from the most anterior point on the frontal squama to the prosthion). Ravosa and Shea (1994) investigated the angle between the cribiform plane (measured in two ways) and the orientation of the midface (measured from the prosthion tangent to the endocranial contour of the frontal) in a sample of Old World monkeys. They found that when the cribriform plane was defined as the line connecting the anterior-most and posterior-most aspects of the cribiform plate, the mean angle between these planes was $93^\circ$ for cercopithecines and $86^\circ$ for colobines and was independent of face size. However, variability in this angle was relatively high; and when the cribiform angle was measured as the line connecting the anterior-most and posterior-most aspects of the cribiform plate at the ethmoid/nasal cavity junction, the angle was significantly different from $90^\circ$ and correlated with skull size. Thus, there is only limited support for the hypothesis that the cribiform plate and the orientation of the snout are perpendicular. Finally, Enlow (1990) and several others (e.g., Sirianni and Swindler, 1979) have suggested that the palatal plane and the anterior cranial base (S-FC) should be roughly parallel across primates when the cribiform plate is parallel to the planum sphenoidale. However, interspecific analysis of the orientation of the palate relative to both the planum sphenoidale and a line from the sella to the foramen caecum (Table 6) provide little support for the hypothesis of Enlow (1990) across Primates, Haplorhini, and Strepsirhini.

### Middle cranial fossa shape and midfacial growth

The second major region of interaction between the cranial base and the face is along the junction between the middle cranial fossa and the posterior margins of the midface. Whereas the upper face and anterior cranial fossa are tightly integrated because they share many of the same bony walls, the middle portion of the face (the ethmomaxillary complex) and middle cranial fossa are growth counterparts that may interact along their complex boundary, which lies more or less in the coronal plane (Hoyte, 1990).
In particular, the ethmomaxillary complex grows anteriorly, laterally, and inferiorly away from the middle cranial fossa at a number of primary growth sites (e.g., the sphenopalatine suture, the sphenozygomatic suture, and the spheno-ethmoid synchondrosis). Consequently, the shape of the middle cranial fossa, especially the greater wings of the sphenoid (which house the temporal lobes), must also play some role in influencing the orientation of the posterior margin of the ethmomaxillary complex and its position relative to the rest of the cranial base.

Recent research on the integration of the middle cranial fossa and the midface has focused on the role of the posterior maxillary (PM) plane. The PM plane has been defined in several different ways (Enlow and Azuma, 1975; Enlow, 1976, 1990; Enlow and Hans, 1996), but we use here the definition of Enlow and Azuma (1975), as the line connecting two termini: 1) pterygomaxillary (Ptm), the average midline point of the most inferior and posterior points on the maxillary tuberosities; and 2) the PM point (PMp), the average midline point of the anterior-most points on the lamina of the greater wings of the sphenoid (for details, see McCarthy and Lieberman, 2001). These points and their relationship to the cranial base and face are illustrated in Figure 10. Note that because the PM plane is defined using two paired registration points, it is technically not a plane, but is instead an abstract line whose termini do not lie in the same parasagittal plane. Despite its abstract nature, the PM plane is a

Fig. 10. Posterior maxillary (PM) plane and 90° orientation relative to the neutral horizontal axis (NHA) of the orbits; illustrated here in, Homo sapiens. The inferior and superior termini of the PM plane are, respectively, pterygomaxillary (Ptm) and the PM point (PMp). The anterior and posterior termini of the NHA are, respectively, OM and OA (see text for definitions).
potentially useful analytical concept for researchers interested in integration between the cranial base and face because it effectively characterizes both the posterior margin of the face and the boundary between the anterior and middle cranial fossae in lateral radiographs. The inferior terminus, Ptm, is the posterolateral corner of the ethmomaxillary complex and lies just in front of the sphenopalatine suture (Williams et al., 1995). The superior terminus, PMp, is the anterior-most point of the middle cranial fossa, lying close to the midpoint of the sphenethmoid synchondrosis and the midpoint of the sphenofrontal suture on the floor of the cranial base in all primates (Van der Linden and Enlow, 1971; McCarthy, 2001; McCarthy and Lieberman, 2001).

Perhaps the most interesting aspect of the PM plane is its relationship to the orbits and the anterior cranial base. Several researchers have claimed that the PM plane always forms a 90° angle to the neutral horizontal axis (NHA) of the orbits (see Measurement Definitions). In their initial study, Enlow and Azuma (1975) found the PM-NHA angle to average 90° in a combined mammalian sample of 45 species, and 90° in a large sample of adult humans. Ravosa (1991a,b), and Ravosa and Shea (1994) tested the PM-NHA angle in a cross-sectional sample of macaques and two interspecific sample of adult primates, and obtained consistent, but different PM-NHA angles from those of Enlow and Azuma (1975), that ranged between 18° and 5° below 90°. However, these studies measured the PM plane and the NHA (the latter only slightly) differently, and several more recent studies have corroborated the original hypothesis of Enlow and Azuma (1975). In particular, Bromage (1992) found the PM-NHA angle in a cross-sectional sample of 45 Pan troglodytes crania to be 89.2 ± 3.4° SD for dental stage I, 90.5 ± 3.1° SD for dental stage II, and 88.2 ± 4.0° SD for dental stage III. However, these data show some significant variation during growth, and some adult crania have PM-NHA angles somewhat different from 90°, especially those for certain hominids. Lieberman (1998) found the PM-NHA angle to be 89.9 ± 1.7° SD in a longitudinal series of humans (Denver Growth Study; n = 353) aged 1 month through 17 years, 9 months. Also, McCarthy and Lieberman (in press) recently found the PM-NHA angle to average 90.0 ± 0.38° SD in a pooled sample of adults from 18 anthropoid species, and 89.4 ± 0.46° SD in a pooled sample of adults from 15 strepsirrhines species (Fig. 11). Consequently, the PM-NHA does appear to be invariant in primates, with values for the most part near 90°. It should be stressed, however, that the developmental and functional bases (if any) for this purported invariance are still unknown and require further study.

The 90° PM-NHA angle is useful for examining craniofacial integration and variation because, as noted above, the NHA is tightly linked to the orientation of the anterior cranial fossa and the ethmomaxillary complex. The roofs of the orbits (which help
define the NHA) comprise much of the floor of the anterior cranial fossa. Therefore, it follows that the PM plane and the anterior cranial base should also form an approximately 90° angle in primates whose orbits are approximated to the midline. This hypothesis was tested by McCarthy and Lieberman (2001), who found that the angle between the PM plane and the planum sphenoidal averaged 95.2 ± 7.6° SD (n = 18) in anthropoids and 82.8 ± 9.5° SD (n = 14) in strepsirhines. McCarthy and Lieberman (2001) also found that the angle between the PM plane and the midline anterior cranial base (from the sella to the foramen caecum) averages 89.2 ± 9.97° SD (n = 18) in anthropoids, but 70.6 ± 10.5° SD (n = 15) in strepsirhines. The high standard deviations of these angles indicate that the integration between the back of the face and the anterior cranial base is not very strong. Ross and Ravosa (1993) also came to similar conclusions by comparing the orbital axis orientation relative to the posterior cranial base, against the orientation of the planum sphenoideum relative to the posterior cranial base. The differences between anthropoids and strepsirhines in the relationship of the orbits to the cranial base can be explained by the fact that the roof of the orbits does not contribute to the midline cranial base in strepsirhines, and because the cribiform plate tends to be oriented more vertically relative to the planum sphenoideum in strepsirhines than in anthropoids (Cartmill, 1970).

The potential integration of the middle and anterior cranial fossae with the face (as measured via the PM plane) and the anterior cranial base raises several interesting issues. Most importantly, the top and back of the face appear to form an integrated unit, the “facial block” which rotates during ontogeny around an axis through the intersection of the anterior and middle cranial fossae at the front of the greater wings of the sphenoid (McCarthy and Lieberman, 2001). This facial block is characteristic of anthropoids but not strepsirhines, and manifests itself through correlations between cranial base angle and upper facial orientation in primates (Weidenrich, 1941; Moss and Young, 1960; Biegert, 1963; Shea, 1985a, 1986, 1988; Ravosa, 1988, 1991a,b; Ross and Ravosa, 1993; Ross, 1995a,b; May and Sheffer, 1999; Lieberman, 2000; Ravosa et al., 2000a, 2000b). In particular, as the anterior cranial base flexes relative to the posterior cranial base, the PM plane also must flex relative to the posterior cranial base, rotating the posterior and upper portions of the face underneath the anterior cranial fossa (klinorhynchy). In contrast, extension of the anterior cranial base relative to the posterior cranial base will rotate the posterior and upper portions of the face dorsally relative to the posterior cranial base (airorhynchy) (Fig. 12).

The relationship of the orientation of the back of the face (as measured for example by the PM plane) to the anterior cranial base also influences nasopharynx shape. As Figure 12 shows, flexion of the anterior cranial base and/or face relative to the posterior cranial base not only rotates the face under the anterior cranial fossa, but it also shortens (absolutely and relatively) the length of the pharyngeal space between the back of the palate and the front of the vertebral column (Laitman and Heimbuch, 1982; Spoor et al., 1999; McCarthy and Lieberman, 2001). While flexion of the cranial base during ontogeny is completely independent of the descent of the hyoid and larynx (Lieberman and McCarthy, 1999), variation in cranial base angle does influence some aspects of pharyngeal shape (Laitman and Heimbuch, 1982; see below).

Ross and Henneberg (1995) suggested that there must be functional constraints on how far back the hard palate can be positioned without occluding the airway. The integration of the anterior cranial base with the upper and posterior margins of the face means that these constraints on pharynx position might determine the maximum possible degree of basicranial angle, particularly in genera such as Pongo and Alouatta with relatively large pharyngeal structures (Biegert, 1957, 1963). Ross and Henneberg (1995) suggested that hominoids might have found a way to circumvent these “constraints.” Hominoids have more airorhynch (dorsally rotated and less frontated) orbits and palates than nonhominoid primates with comparably flexed basicrania (Shea,
This airorhynchy has yet to be explained developmentally and functionally; however, Ross and Henneberg (1995) suggested that it evolved in hominoids in response to increased flexion of the cranial base producing posterior displacement of the palate.

More research is needed on the integration of the midface and cranial base. In particular, why is the PM plane oriented at 90° relative to the NHA during postnatal ontogeny and thus across taxa? Another question of interest is, what aspects of cranial base and facial shape are responsible for most of the variation in PM plane position, and hence facial orientation? This problem has not been well studied, but the orientation of the PM plane is probably most affected by the size of the middle cranial fossa, especially the length of the temporal lobes, by flexion of the sphenoid, and by the length of the anterior sphenoid in the midline cranial base. Three-dimensional studies of the interface between the PM plane and the cranial base are needed to resolve these and other questions about cranial base-face interrelations and interactions.

Basicranial width and overall facial shape in humans

Although it is clear that the cranial base plays a major role in influencing facial orientation relative to the neurocranium, there is less information about the potential influence of the cranial base on other aspects of facial shape such as height, length, and width. To what extent is overall facial shape independent of the cranial base? It is commonly assumed that the majority of facial growth is independent of cranial base growth, largely because much of the face grows in a skeletal growth trajectory after the end of the neural growth phase. In humans, for example, the face attains 95% adult size by 16–18 years, at least 10 years after the cranial base reaches adult size (Stamrud, 1959; Moore and Lavelle, 1974). In addition, most facial and basicranial dimensions appear to be genetically independent in adults (Cheverud, 1996). However, there is some evidence to suggest that changes in the proportions of the cranial base can influence facial shape. This interaction is predicted to be especially important, and perhaps exclusive to humans, in which the upper face lies almost completely underneath the anterior cranial fossa (Weidenreich, 1941; Howells, 1973; Enlow and Bhatt, 1984; Enlow, 1990; Lieberman et al., 2000).

The most explicit of these hypotheses is that of Enlow (1990), who suggested that humans with absolutely narrow cranial bases (primarily dolichocephalics) tend to
have longer, more flexed cranial bases, and narrower faces than individuals with absolutely wider cranial bases (primarily brachycephalics). If variation in overall facial size is partially independent of cranial base and neurocranial size, then interactions between cranial base width and facial width may have some effects on facial height and length. Enlow (1990) proposed that humans with absolutely narrower cranial bases tend to have proportionately narrower and antero-posteriorly longer faces (leptoproscopy) than humans with wider cranial bases, who tend to have proportionately wider and antero-posteriorly shorter faces (euryproscopy). The hypothesis receives some support from studies of artificial cranial deformation in humans. Antón (1989, 1994), for example, showed that antero-posterior head-binding during the first years of life causes not only a wider neurocranium but also a concomitantly wider face from additional growth in the most lateral regions; conversely, circumferential head-binding results in a narrower neurocranium and face. Lieberman et al. (2000) attempted to test the hypothesis of Enlow (1990) more directly with a partial correlation analysis of a sample of 98 adults from five geographically and craniometrically diverse populations. The study, however, found a low correlation between upper facial breadth and maximum anterior cranial fossa breadth ($r = 0.53, P < 0.001$), and between midfacial breadth and maximum middle cranial fossa breadth ($r = 0.49; P < 0.001$) when differences in overall size were accounted for using partial correlation analysis. In addition, there was only a low tendency ($r = 0.49, P < 0.001$) for individuals with narrow cranial bases to have longer, narrower faces than individuals with wider cranial bases, and the trend may largely be a factor of interpopulation rather than intrapopulation variation. Further studies are needed to better understand these sources of varia-

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$r = 0.40, P < 0.001$ when facial size is held constant (for details, see Lieberman et al., 2000).
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1 Data primarily from Ross and Ravosa (1993).
2 New data collected for this study from same radiographic collection as for Ross and Ravosa (1993).
tion, and also to study potential interactions between cranial base shape and facial shape in primates and other mammals.

THE CRANIAL BASE AND POSTURE

Apart from a few recent studies reviewed here, little is known about the relationship between basicranial morphology, head and neck posture, and other aspects of head morphology related to locomotion. One persistent hypothesis that is especially relevant to hominin evolution is that flexion of the cranial base is an adaptation for orthograde posture in hominins because it causes the foramen magnum to have a relatively more anterior position and ventral orientation (Bolk, 1909, 1910; Duckworth, 1915; Weidenreich, 1941; Schultz, 1942, 1955; Ashton and Zuckerman, 1952, 1956; Ashton, 1952; Moore et al., 1973; Adams and Moore, 1975; DuBrul, 1977, 1979; Dean and Wood, 1981, 1982). Indeed, these features are often invoked in attempts to reconstruct head posture in fossil hominins (e.g., White et al., 1994). All primates have the center of mass of the head located anterior to the occipital condyles, such that more anteriorly positioned occipital condyles relative to head length reduce the lever arm between the center of mass and the atlanto-occipital joint. This balancing, in turn, reduces torque about this joint, thereby reducing the magnitude of the force required from the nuchal muscles to hold up the head (Schultz, 1942).

The occipital condyles can be moved rostrally relative to overall head length by flexing the basicranium and/or shortening the posterior cranial base. In vitro experiments by Demes (1985) demonstrated that the more ventral orientation of rostrally placed occipital condyles orients the articular surfaces closer to perpendicular to the compressive force acting through the center of mass of the head, potentially reducing shearing forces acting across the joint that need to be resisted by muscles or ligaments.

There are some experimental data that rodents forced to walk bipedally (Moss, 1961; Fenart, 1966; Riesenfeld, 1966) develop more flexed cranial bases. However, the hypothesis that variations in cranial base angle are adaptations for head posture, however, is not well supported by comparative data. Among primates, basicranial flexion has been shown to be uncorrelated with either qualitative estimates of body posture (Ross and Ravosa, 1993) or quantitative measures of head and neck orientation (Strait and Ross, 1999). The partial correlation analysis of Strait and Ross (1999) confirmed relative brain size as a more important determinant of variation in basicranial angle, even when facial orientation and head and neck posture were taken into account. Although foramen magnum orientation relative to anterior cranial base orientation (S-FC) has been shown to be related to relative brain size (Biegert, 1963; Spoor, 1997), the relationship between head and neck posture and foramen magnum orientation has not yet been evaluated.

We gathered data on foramen magnum orientation (FM) from the same radiographs used by Ross and Ravosa (1993) and Ravosa (1991b), and combined these data with measures of hominids reported by Spoor (1993) and with measures of head and neck orientation reported by Strait and Ross (1999) (Fig. 13). The head-neck angle is the angle between neck inclination and orbit inclination, both relative to the substrate (Strait and Ross, 1999). The values for FM orientation relative to the clivus (FM < CO) are in Table 7 and are summarized in Figure 14. The values for FM orientation relative to the orbital axis were calculated from measures of the orientation of both these planes relative to the clivus ossis occipitalis (CO) as 180°-AOA-FM, CO. These data show that FM < CO is not significantly correlated with basicranial flexion, orbital axis orientation, the orientation of the head relative to the neck, or the size of the cerebellum relative to the posterior basicranium (Table 8). Nor is foramen magnum orientation relative to the orbital axis (FM < AOA) correlated with any of these variables, except AOA (Table 8). Of particular interest is the lack of correlation between the head-neck angle of Strait and Ross (1999) (Fig. 14), suggesting that foramen magnum orientation is not a good indicator of the orientation of the neck during habitual locomotion. This calls into question attempts to estimate head and neck posture from data on foramen magnum orientation in fossils.
Another widely accepted notion holds that a shift to orthogrady necessitates ventral flexion of the face, particularly the orbits, relative to the rest of the skull so that animals can continue to look rostrally (reviewed in Ross, 1995a; Strait and Ross, 1999). Homo has unusually airorhynch (dorsally rotated) orbits relative to its foramen magnum orientation. Across primates the relationship between these variables is significant ($r = 0.541, P < 0.05$); across nonhuman primates $r = 0.691$ ($P < 0.01$).

These findings suggest that the direction of gaze cannot be reoriented through evolution solely by alterations in neck orientation or head orientation relative to the neck, and that there is a relationship between locomotor behavior and orbit orientation relative to the rest of the skull.

This latter conclusion also explains why the orientation of the lateral semicircular canal (LSC) may correlate with head posture (Fenart and Pellerin, 1988 and references therein). Humans and animals of varying postures habitually hold their heads with the LSCs pitched upwards by several degrees (Sakka et al., 1976; Vidal et al., 1986; Graf et al., 1995). The semicircular canals function as accelerometers, registering changes in head velocity (or changes therein, i.e., acceleration), not head orientation relative to gravity (which is accomplished using the otolith organs). Thus, the intrinsic function of the canals does not explain any relationship between LSC orientation and head posture. An alternative,
more likely answer lies in the role of the semicircular canals in vestibulo-ocular reflexes (VORs). VORs maintain a stable retinal image during head movements by coordinating eye movements with changes in head velocity. To achieve this, each semicircular canal is wired up to two extraocular muscles via a three-neuron reflex arc.6 Because reflex arcs are evolutionarily conservative (Graf, 1988), each semicircular canal must remain roughly parallel with the line of action of the two extraocular muscles to which it provides primary excitatory input during VORs. This functional constraint predicts that evolutionary changes in medial and lateral rectus orientation will be associated with changes in LSC orientation. Because the medial and lateral recti arise from the annulus tendineus around the optic canal and insert on the equator of the eyeball, they lie roughly in the same transverse plane as the orbital axis (see Measurement Definitions). Thus, LSC orientation should be correlated with orbital axis orientation.

As an initial test of this hypothesis, Figure 15 plots AOA (orbital axis orientation relative to clivus (AOA) (Ross and Henneberg, 1995) against lateral semicircular canal (LSC) orientation relative to a line from basion to nasion (Spoor, 1993). The two variables are significantly correlated across all primates ($r = 0.745, P < 0.01$) and nonhuman primates ($r = 0.906, P < 0.0001$). Homo has unusually aiorrhynch (dorsally rotated) orbits for its LSC orientation (see also Ross and Henneberg, 1995; Strait and Ross, 1999).

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6Each posterior semicircular canal is connected to its ipsilateral superior oblique and contralateral inferior rectus, each anterior semicircular canal to its ipsilateral superior rectus and its contralateral inferior oblique, and each LSC to its ipsilateral medial rectus and contralateral lateral rectus (Kandel et al., 1991).
below the orbital axis line). These data therefore lend support to the hypothesis that animals orient their heads at rest (and during locomotion) primarily to orient their eyes towards the horizon rather than to orient their semicircular canals in any particular way. In sum, orbital axis orientation relative to the clivus and foramen magnum orientation relative to the orbital axis are hypothesized to be evolutionary adaptations to head posture during habitual locomotion, and appear necessary because of the limited range of motion at the atlanto-occipital joint (Graf et al., 1995).

**MAJOR UNRESOLVED ISSUES OF CRANIAL BASE VARIATION IN PRIMATE EVOLUTION**

Studies of cranial base variation in fossil primates and hominins have been rare because this region of the skull is usually poorly preserved or destroyed in most fossils, and because it is hard to visualize or measure without radiographs or computed tomography (CT) scans. The coming years, however, are likely to see a renaissance of research on the role of the cranial base in primate cranial evolution as CT scans of fossils become more readily available. Here we review six major topics where future research on the cranial base in both fossil and extant primates promises to provide important insights: 1) the relationship between encephalization, circumorbital form, and the origin of primates; 2) the evolution of the integrated “facial block” in haplorhines; 3) the determinants of basicranial flexion in hominins; 4) the relationship between basicranial flexion and the shape of the vocal tract; 5) the role of the cranial base in facial retraction in *Homo sapiens*; and 6) the reliability of basicranial characters as indicators of primate phylogeny.

**Primate origins, encephalization, and circumorbital form**

The basicranium likely played a key role in the evolution of the unique configuration of the primate skull. Over the past three decades, the visual predation hypothesis (VPH) has become a well-accepted model of primate origins (Martin, 1990; Fleagle, 1999). The VPH argues that the first primates were nocturnal visual predators of small invertebrates and vertebrates, and this required more anteriorly facing and closely approximated orbital apertures (Cartmill, 1970, 1972, 1974, 1992). Increased orbital convergence enlarges the binocular field for greater stereoscopic vision and a clear retinal image for depth perception and prey location (Allman, 1977, 1982). The VPH further posits that relatively larger orbits and grasping appendages with nails are adaptations to being nocturnal in an arboreal, terminal-branch setting (Cartmill, 1970, 1972, 1974, 1992; Kay and Cartmill, 1974, 1977; Dagosto, 1988; Covert and Hamrick, 1993; Hamrick, 1998, 1999; Lemelin, 1999). These adaptations differ significantly from the cranial and locomotor specializations of putative sister taxa such as plesiadapiforms and dermopterans (Cartmill, 1972, 1974, 1992; Kay and Cartmill, 1974, 1977; Beard, 1993; Ravosa et al., 2000a).

According to the VPH, increased orbital convergence moves the orbital apertures out of the plane of the temporal fossa, a condition entailing greater ocular disruption during mastication (Cartmill, 1970, 1972, 1974, 1992). A rigid postorbital bar may function to stiffen the lateral orbital margins and thus counter ocular deformation during biting and chewing to ensure a high level of stereoscopic acuity in an organism that processes food while hunting and foraging (Cartmill, 1970, 1972). This appears to be particularly important, given that strepsirhines with unfused symphyses have been shown to recruit relatively less balancing-side than working-side adductor muscle force during unilateral mastication (Hylander et al., 1998, 2000). This differential muscle recruitment results in a pattern of lower strains along the balancing-side postorbital bar than the working-side postorbital bar (Ravosa et al., 2000a). Thus, an organism with a postorbital ligament and a stepsirhine-like adductor pattern (the latter of which is inferred for basal primates based on the presence of unfused symphyses; Ravosa, 1996, 1999) would experience an asymmetrical circumorbital and, in turn, an ocular loading pattern that is hypothesized
to compromise effective stereoscopic visual acuity.

Analyses of felids (perhaps the best analog for the skull of basal primates), herpes-tids, and pteropodids demonstrate that postorbital bar formation characterizes taxa with increased orbital convergence and/or greater orbital frontation (Noble et al., 2000; Ravosa et al., 2000a). As both orbital characteristics became more developed during early primate evolution (Simons, 1962; Cartmill, 1970, 1972, 1974, 1992; Szalay et al., 1987; Martin, 1990; Fleagle, 1999), it is likely that primate postorbital bar development is correlated with both evolutionary transformations in the orbital complex (Ravosa et al., 2000a).

The role of orbital frontation in postorbital bar formation is especially significant because it apparently reflects interactions among several factors unique to the early evolution of small primates (Ravosa et al., 2000a). First among these factors is enceph-alization. Both early primates and their putative ancestors were tiny, weighing between 100–300 g (Kay and Cartmill, 1977; Dagosto, 1988; Martin, 1990; Beard, 1993; Covert and Hamrick, 1993; Fleagle, 1999). Thus, the greater encephalization of basal primates (Martin, 1990) did not result from phyletic size decreases (Gould, 1975; Shea, 1987). Instead, increased relative brain size and orbital frontation appear linked to nocturnal visual predation (Ravosa et al., 2000a), which is related to increases in the relative size of the visual cortex (Cartmill, 1974, 1992) and greater encephalization (Barton, 1998). This hypothesis complements prior claims that increased encephalization in basal primates is related to the unique combination of arboreality, precoci-ality, and small body size (Shea, 1987).

Apart from being more encephalized than nonprimate archontans, the first primates (and felids) possessed relatively larger eyes and more convergent orbits (Kay and Cart-mill, 1977; Martin, 1990; Covert and Hamrick, 1993; Cartmill, 1992; Ravosa et al., 2000a). This combination of derived features creates a spatial packing problem in which the position of the frontal lobes and anterior cranial fossa have a major influence on orbital aperture orientation, integrating morphological variation in these adjacent cranial regions (see above). Because neural and ocular size scale with negative allometry (Schultz, 1940; Gould, 1975), this structural constraint would be particularly marked in smaller, and thus more fronted, taxa—the morphospace in which basal primates and felids happen to develop postorbital bars.

**Anthropoid origins and cranial base-face interactions**

Another interesting problem is the role of the cranial base in the fundamental rearrangement of the face along the stem lineage leading to haplorhines and anthropoids. These changes include: increased orbital convergence and frontation; increased relative brain size, especially in the frontal and temporal lobes; a more acutely angled (flexed) cranial base; partial retraction of the face below the braincase; reduction of the olfactory apparatus and interorbital region with concomitant approximation of the orbits; relatively smaller orbits associated with diurnality; and the presence of a postorbital septum (Cartmill, 1970, 1980; Radinsky, 1968, 1979; Rosenberger, 1985, 1986; Ravosa, 1991b; Ross and Ravosa, 1993; Ross, 1995a, b). Not surprisingly, changes in cranial base shape have been key features of all the models proposed to explain the order in which these features arose, their putative functions, and their interactions. According to Cartmill (1970), the fundamental difference between haplorhines and strepsirhines centers on whether orbital convergence occurs towards the top of the skull or at the front. If, as in haplorhines, the orbits converge anteriorly (associated with increased orbital frontation), then the orbits not only compress the olfactory region, reducing its dimensions, but also become closely approximated to the midline anterior cranial base. This necessarily reduces the size of the olfactory apparatus and forms an interorbital septum, facilitating a subsequent increase.

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7As phyletic dwarfs are more encephalized than like-sized sister taxa (Gould, 1975; Shea, 1987), presumably they are also more flexed, highlighting the complex relationships between brain evolution and changes in basioccipital and facial form.
in relative encephalization by expansion of the brain forward over the top of the orbits. It has been argued that, as predicted by Dabelow (1931), by bringing the orbits and anterior cranial base into close continuity, they became structurally integrated such that changes in the orientation of one necessarily affect the other (Ross and Ravosa, 1993). Small nocturnal strepsirhines, in contrast, tend to converge their orbits towards the top of their head, not compressing the olfactory apparatus, and preventing brain expansion over the orbits concomitant with a shift to diurnality. The orbits and anterior cranial base in all strepsirhines are not as unified structurally, and thus basicranial flexion and orbit orientation do not covary as greatly.

The evidence that all omomyiforms that are well enough preserved have an interorbital septum below the olfactory tract, like that of *Tarsius* and small anthropoids (Ross, 1994), suggests that this integration of anterior cranial base and upper face may be an early unique derived feature of the haplorhine stem lineage. This integration set the stage for the subsequent evolution of the haplorhine postorbital septum. Increased orbital frontation (klinorhynchy) and convergence in early anthropoids caused the anterior temporal muscles and orbit to come into close proximity, leading to the evolution of a postorbital septum (Ross, 1995b, 1996). Exactly why increased frontation occurred in haplorhines remains unexplained, although it has been argued that increased relative brain size might have caused increased basicranial flexion, producing increased orbital frontation as a consequence of the integration of the anterior cranial base and orbits (Ross, 1996; see also Ravosa et al., 2000a on the effects of small size on skull form in basal primates). This hypothesis remains to be evaluated in fossil stem anthropoids for want of well-preserved specimens, but is not supported by the fact that early anthropoids had a postorbital septum in conjunction with relatively small brains (Ross, 2000). It remains to be determined why the haplorhine stem lineage evolved more frontated orbits, but the findings of Strait and Ross (1999) suggest that the role of posture should be considered.

**Variation in hominin cranial base angle**

How to account for variation in basicranial flexion in hominins has been controversial and remains unresolved. Several recent studies (e.g., Ross and Henneberg, 1995; Spoor, 1997) have shown that the cranial base in *Australopithecus* and *Homo* is generally more flexed than in *Pan* or other non-human primates. This difference raises two questions. First, how much is cranial base flexion among early hominins related to upright posture, facial orientation, or brain size? Second, what factors account for the observed variation in cranial base angle among hominins?

Although cranial base angles vary substantially among hominin species, australopithecines have CBAs generally intermediate between humans and chimpanzees, but with more flexed cranial bases among *A. boisei* and less flexed cranial bases for *A. aethiopicus* (KNM-WT 17000) (F. Spoor, personal communication). Until now, the hypothesis that cranial base flexion in hominins is an adaptation for increased brain size relative to basicranial length (Gould, 1977) has received the most support (Ross and Ravosa, 1993; Ross and Henneberg, 1995; Spoor, 1997; McCarthy, 2001). In particular, if one measures IRE5 vs. CBA1 (thereby including the cribriform plate in measures of both basicranial length and the angle of the cranial base), then *H. sapiens* and other hominin taxa such as *A. africanaus* have exactly the degree of flexion expected by basicranial length.

However, not all of the variation in hominin CBA can be explained by relative brain size. For example, Neanderthals and archaic *Homo* fossils such as Kabwe have considerably more extended CBAs than *H. sapiens* (about 15°), even though they are bipedal and similarly encephalized (Ruff et al., 1997). In addition, other measures of cranial base angle and relative encephalization, which do not include the cribriform plate (CBA4 and IRE5), indicate that *H. sapiens* have less flexed cranial bases than expected for anthropoids of their size (Ross and Henneberg, 1995). This finding highlights the likelihood that no single explanation will account for interspecific differences.
in CBA among hominins. Other factors that have been argued to contribute to variation in CBA, including facial kyphosis and head and neck posture, cannot be shown to be important correlates of basicranial flexion. Most importantly, the comparative study by Strait and Ross (1999) of CBA, head-neck angle, and orbital axis orientation among extant primates found that basicranial flexion is primarily influenced by relative brain size and not head and neck posture. The traditional view that human basicranial flexion is somehow an adaptation for orthograde posture is no longer tenable.

**Cranial base flexion and vocal tract shape in hominins**

Flexion of the cranial base has been argued to be an important correlate of the shape of the vocal tract. In particular, several researchers (Lieberman et al., 1972, 1992; Laitman and Crelin, 1976; Laitman et al., 1978, 1979; Laitman and Heimbuch, 1982) claimed that the degree of flexion of the external cranial base (between the inferior aspect of the basioccipital clivus and the palate) influences the position of the hyo-laryngeal complex. In most mammals, the hyoid and larynx lie close to the soft palate so that the epiglottis and soft palate can engage, permitting simultaneous breathing and swallowing (Laitman and Reidenberg, 1993; German et al., 1996; Larson and Herring, 1996; Crompton et al., 1997). In contrast, humans have a uniquely shaped pharynx in which the hyo-laryngeal complex descends inferiorly relative to the oral cavity, causing the soft palate and epiglottis to become disengaged so that the trachea and esophagus share a common passageway (Negus, 1949; Crelin, 1973). Hyo-laryngeal descent is an important physiological basis for many aspects of human speech. Flexion of the external cranial base in combination with a low position of the larynx relative to the palate divide the human vocal tract (VT) into separate horizontal and vertical “tubes” of approximately equal length, whose cross-sectional areas can be modified independently at least tenfold by the tongue (Stevens and House, 1955; Fant, 1960; Stevens, 1972; Baer et al., 1991). Dynamic filtering in the two-tube human VT functions to produce a wide range of vowels whose formant frequencies are acoustically distinct regardless of vocal tract length (Fant, 1960; Nearey, 1978; Lieberman, 1984; Carre et al., 1994; Beckman et al., 1995).

Although the speech-related acoustical properties of the unique human vocal tract are not in dispute, the role of cranial base flexion in hyo-laryngeal descent is controversial, yet potentially important for reconstructing the anatomy of the vocal tract in fossil hominins. Two questions are of special importance. First, what is the relationship of external cranial base flexion to the descent and/or positioning of the hyoid relative to the oral cavity? Second, how does the angle of the external cranial base change during development, and what is its relationship to internal cranial base angle?

The original hypothesis that flexion of the external cranial base in humans contributes to laryngeal descent, and thus can be used to reconstruct the vocal tract of fossil hominins (Lieberman and Crelin, 1971; Lieberman et al., 1972; Laitman and Crelin, 1976; Laitman and Heimbuch, 1982; Lieberman, 1984), was based on three observations. First, these researchers inferred a relationship between cranial base flexion and laryngeal descent on the basis of comparisons of neonatal and adult humans vs. nonhuman primates. In particular, human neonates, like nonhuman primate adults, have a relatively extended cranial base and a high hyoid, whereas only human adults have both a flexed cranial base and a descended larynx. Second, internal and external basi cranial flexion were believed to covary with the descent of the larynx (George, 1978). Third, external cranial base flexion was believed to reorient the suprahypoid muscles and ligaments more vertically, and to shorten the antero-posterior length of the oropharynx between the palate and the cervical vertebrae, thus requiring the larynx and posterior tongue to be positioned lower relative to the hard palate.

Lieberman and McCarthy (1999) tested the relationship between cranial base flexion and hyo-laryngeal position using a longitudinal series of radiographs in humans (the Denver Growth Study), which pre-
served details of larynx and hyoid position in upright subjects x-rayed during quiet respiration. This study found no statistically significant relationship between either internal or external cranial base flexion and hyo-laryngeal descent. As Figure 16 shows, the cranial base and the position of the larynx must be partially independent in humans because the cranial base flexes rapidly during the first few years after birth, whereas the larynx and hyoid descend gradually until the end of the adolescent growth spurt. Consequently, the flexion of the external cranial base (and presumably its effects on suprahoid muscle orientation) cannot be used to infer vocal tract dimensions in fossil hominins (Lieberman et al., 1998). Similarly, Chan (1991) demonstrated that the correlation between styloid process orientation and laryngeal position is not strong enough to estimate vocal tract dimensions reliably.

Fig. 16. Longitudinal changes in the angle of the external cranial base (CBA5 from basion-sphenobasion-hormion) and the height of the vocal tract (the distance from the vocal folds to the plane of the hard palate, perpendicular to the posterior pharyngeal wall). Data are from a longitudinal study of growth in 15 males and 13 females (for details, see Lieberman and McCarthy, 1999). Note that the height of the vocal tract continues to grow throughout the somatic growth period, whereas the external cranial base angle ceases to change appreciably after approximately 3 postnatal years.

External flexion has been measured in several ways, all of which suggest that external and internal cranial base angles are correlated with each other, but differ in their pattern of growth in humans and non-human primates. Laitman et al. (1976, 1978, 1979, 1982) developed a composite, size-corrected measure of exocranial flexion between the basioccipital and the palate, which they measured on cross-sectional samples of humans, apes, monkeys, and several fossil hominins. More recently, Lieberman and McCarthy (1999) measured external cranial base flexion in a longitudinal sample of humans using two lines, one extending from basion to sphenobasion, and the second from sphenobasion to hormion. May and Sheffer (1999) took essentially the same measurement on cross-sectional samples of humans, chimpanzees, gorillas, and several fossil hominins. These studies all agree that flexion of the internal cranial
base in humans occurs prior to the eruption of the first permanent molars and then remains stable, but that the external cranial base extends gradually in all nonhuman primates throughout the period of facial growth. Moreover, the patterns of external and internal cranial base angulation mirror each other. The internal cranial base (measured using both Ba-S-FC and Landzert’s angle) flexes in humans rapidly prior to 2 postnatal years and then remains stable, but extends in nonhuman primates gradually throughout the period of facial growth (Fig. 7) (Lieberman and McCarthy, 1999).

Cranial base shape and facial projection in Homo

Although the effects of cranial base angulation on the angle of the face relative to the rest of the skull (facial kyphosis) have long been the subject of much research (see above), there has been recent interest in the role of the cranial base on facial projection. Facial projection (which is a more general term for neuro-orbital disjunction) is defined here as the extent to which the nonros- tral portion of the face is positioned ante-riorly relative to the foramen caecum, the most antero-inferior point on the cranial base (note that facial projection and pro- gnathism are different). Variation in facial projection, along with an understanding of their developmental bases, may be important for testing hypotheses about recent hominin evolution. In particular, Lieber- man (1995, 1998, 2000) has argued that variation in facial projection accounts for many of the major differences in overall craniofacial form between *H. sapiens* and other closely-related “archaic” *Homo* taxa, including the Neanderthals. Whereas all nonextant hominins have projecting faces, “anatomically modern” *H. sapiens* is uniquely characterized by a retracted facial profile in which the majority of the face lies beneath the braincase (Weidenreich, 1941; Moss and Young, 1960; Vinyard, 1994; Lieberman, 1995, 1998; Vinyard and Smith, 1997; May and Sheffer, 1999; Ravosa et al., 2000b). As a consequence, *H. sapiens* also has a more vertical frontal profile, less projecting browridges, a rounder overall cranial shape, and a relatively shorter oropharyngeal space between the back of the hard palate and the foramen magnum—virtually all of the supposed autapomorphies of “anatomically modern” *H. sapiens*.

What is the role of the cranial base in facial projection? Lieberman (1998, 2000) proposed that four independent factors account for variation in facial projection: 1) antero-posterior facial length, 2) anterior cranial base length, 3) cranial base angle, and 4) the antero-posterior length of the middle cranial fossa from sella to PM plane. Each of these variables has a different growth pattern, but combine to influence the position of the face relative to the basicranium and neurocranium. For example, facial projection can occur through having a long face relative to a short anterior cranial fossa, a long middle cranial fossa relative to the length of the anterior cranial fossa, and/or a more extended cranial base. Partial correlation analyses of cross-sectional samples of *Homo sapiens* and *Pan troglodytes* indicate that each contributes significantly to the ontogeny of facial projection in humans and apes when the associations between these variables and with overall cranial length and endocranial volume as well as other cranial dimensions are held constant (Lieberman, 2000). In other words, chimpanzees and humans with relatively longer faces, shorter anterior cranial bases, less flexed cranial bases, and/or longer middle cranial fossae tend to have relatively more projecting faces.

In an analysis of radiographs of fossil hominins, Lieberman (1998) argued that the major cause for facial retraction and its resulting effects on modern human cranial shape was a change in the cranial base rather than the face itself. Specifically, middle cranial fossa length (termed ASL) was estimated to be approximately 25% shorter in anatomically modern humans, both re-

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May and Sheffer (1999) did not find evidence for postnatal extension of the cranial base in *Pan*, largely because of insufficient sample sizes that were divided into overly large ontogenetic stages.

This dimension was originally termed anterior sphenoid length (ASL), but it is really a measure of the midline prechordal length of the middle cranial fossa (Lieberman, 2000).
cent and Pleistocene, than in Neanderthals and other taxa of archaic Homo, whereas anterior cranial base length and facial length were not significantly different between these taxa.

Lieberman (1998), however, incorrectly measured ASL in the few archaic humans in which the cranial base is well preserved. As shown by Spoor et al. (1999), ASL is not significantly longer in archaic Homo than in modern humans, but the angle of the cranial base (CBA1) is about 15° more extended in archaic Homo fossils such as Gibraltar, Monte Circeo, and Kabwe than in samples of Pleistocene and recent modern humans ($P < 0.05$). Consequently, Spoor et al. (1999) and Lieberman (2000) concluded that differences in cranial base angle are more likely to account for facial retraction in modern humans, as well as for other differences noted by Lieberman (1998), such as the relatively shorter pharynx behind the palate. This hypothesis needs to be tested carefully, but is explored here in a preliminary fashion with a geometric morphometric analysis comparing the shape of the Kabwe cranium with a large, robust recent *H. sapiens* (a male Australian). Figure 17 shows a thin-plate spline transformation of the Australian into Kabwe (computed using Mor-

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**Fig. 17.** Thin-plate spline analysis of an Australian male (from Queensland) relative to Kabwe 1 (target). Eighteen landmarks from each skull were initially superimposed using a resistant-fit Procrustes analysis. The deformation grid shows that the archaic *Homo* fossil has a relatively more projecting and taller face, a more extended cranial base, a relatively shorter middle cranial fossa, and a relatively longer pharyngeal space between the palate and the foramen magnum.
phometrika, version 0.007, Jeff Walker, Chicago, IL), based on an initial resistant-fit superimposition Procrustes analysis of six cranial base landmarks, seven facial landmarks, and five neurocranial landmarks.10 The thin-plate spline, which is based on a Procrustes analysis that geometrically corrects for most effects of size differences, shows that Kabwe has a considerably more projecting face (i.e., between nasion and the foramen caecum) in conjunction with a relatively more extended cranial base (14o), a dorsally rotated PM plane relative to the posterior cranial base, and a relatively longer pharyngeal space between the maxilla and the foramen magnum. In addition, when one examines specific, size-corrected dimensions (standardized by the geometric mean of all the interlandmark distances), midfacial length (PM-Na) is 19% longer in Kabwe than in the Australian modern individual, but the length of the anterior cranial base (S-FC) is only 4% shorter. In other words, Kabwe exhibits a considerably more projecting face than the \textit{H. sapiens} specimen because it has a more extended cranial base in conjunction with a relatively longer face. Changes in middle cranial fossa shape, therefore, appear to have had major effects on facial retraction in human evolution, but need to be further examined using additional specimens.

Additional, intriguing evidence that the cranial base can play an important role in facial retraction may be come from studies of craniofacial growth abnormalities and from laboratory studies of mice. Mice that are homozygous-recessive for the retrognathic Brachyrrhine (Br) allele are characterized by a primary growth defect in the anterior cranial base (Beechey et al., 1998; Ma and Lozanoff, 1999) that leads to a severely retrognathic midfacial profile but a morphologically normal nasal septum and face (Lozanoff, 1993; Lozanoff et al., 1994; Ma and Lozanoff, 1999). The extent to which the morphological differences between the retrognathic Br mouse and controls is at all similar to the differences evident between \textit{H. sapiens} and archaic \textit{Homo} has yet to be determined. However, these studies, in conjunction with facial growth defects caused by chondrogenic growth disorders such as Crouzon syndrome, Pierre-Robin syndrome, and Down syndrome, highlight the important role the cranial base plays in facial growth and integration (David et al., 1989).

**Cranial base characters in phylogenetic analyses**

One final consideration of interest is whether it might be profitable to focus on characters from the cranial base in taxonomic and phylogenetic analyses of primates. This possibility has been raised by a number of authors (e.g., Olson, 1985; Shea, 1985a, 1988; Lieberman et al., 1996; Lieberman, 1997; Strait et al., 1997; Strait, 1998) for three reasons. First, the cranial base derives from endochondral precursors rather than though intramembranous ossification processes (endochondral bones are thought to have more direct genetic influence in terms of initial shape); second, the cranial base is the first part of the skull to reach adult size and shape (Moore and Lavelle, 1974); and third, the cranial base may play a greater role in influencing facial shape than vice versa (see above). Consequently, one might expect cranial base characters to preserve more phylogenetic signal than facial characters by virtue of being more heritable and less influenced by the epigenetic responses to external influences during postnatal ontogeny rampant in the facial skeleton (Herring, 1993).

Expectations aside, there are currently no data suggesting that the basicranium is actually a better source of characters than other regions of the skull for phylogenetic analyses. In terms of narrow-sense heritability (h²), basicranial, neurocranial, and facial characters have similar levels of heritability among primates (Sjøvold, 1984; Cheverud and Buikstra, 1982; Cheverud, 1995). In addition, basicranial variables appear to be equally well (or poorly) correlated

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10These landmarks are: basion, sella, pituitary point, sphenoidale, PMp (the anterior most point on the greater wings of the sphenoid), foramen caecum, nasion, ANS, PNS, prosthion, maxillary tuberosities, fronton, orbitale, opisthocranion, the superior-most point on the vault, fronton, the inferior-most point on the supratoral sulcus, glabella. Resistant fit superimposition was used in order to minimize effects of the very different shape of the neurocranium in archaic \textit{Homo} vs. modern \textit{H. sapiens}.
with other dimensions or features in hominoids (Strait, 1998), and in the human skull (Lieberman et al., 2000). Finally, those few studies that have focused on cranial base characters do not yield results substantially different from analyses that incorporate other craniodental characters. Lieberman et al. (1996) found that basicranial and vault characters tend to yield similar cladograms that differ only slightly from cladograms based on facial characters. Strait et al. (1997) did not specifically examine characters from the cranial base, but found no major difference between trees based on masticatory characters vs. those that were predominantly neurocranial and basicranial. In their study of primate higher taxonomic relationships, Ross et al. (1998) found the cranial data, consisting primarily of basicranial traits, to yield trees similar to those produced by the dental data, although with better resolution at older nodes. Thus, whether the basicranium is a better source of phylogenetic data remains open to question. The cranial base may be a good place to look for reliable characters if researchers are to focus on characters that describe developmental processes or events (e.g., flexion vs. extension at the sphenoid synchondroses) rather than using characters that solely describe morphological variation (e.g., the angle of the whole cranial base) (Hall, 1994; Lieberman, 1999). This hypothesis, however, has yet to be tested.

The above studies, however, raise another key issue relevant to phylogenetic studies: the problem of independence. Cladistic analyses explicitly require one to use independent characters to avoid problems of convergent and correlated characters incorrectly biasing the outcome of any parsimony analysis. Yet the above studies demonstrate the existence of multiple and complicated interactions between the cranial base and the neurocranium and between the cranial base and the face. For example, variations in orbit size and orientation are linked to variations in the angle of the cranial base, brain size, and the orientation of the face relative to the rest of the skull. Many of these features have been treated as independent characters in recent cladistic analyses (e.g., Strait et al, 1997), but their effect on the results has yet to be determined. Further study of these interactions is needed to improve the reliability of phylogenetic analyses, and again highlight the need to consider morphological characters in terms of their generative processes (e.g., Gould, 1977; Cheverud, 1982; Shea, 1985b; Hall, 1994; Lieberman, 1999).

CONCLUSIONS

Since the last major reviews of cranial base anatomy in primates (Scott, 1958; Moore and Lavelle, 1974; Sirianni and Swindler, 1979), there has been a tremendous increase in our knowledge of chondrocranial embryology, the patterns and processes of basicranial growth, and the nature of basicranial variation across primates. Major advances include details of the morphogenetic independence between the prechordal and postchordal portions of the chondrocranium; comparative data on the relative importance of brain size, orbital orientation, facial orientation, and posture as factors that account for variation in cranial base angulation; and ontogenetic and comparative data on the structural relationships between the anterior cranial base and upper face in haplorhines vs. strepsirhines, and their influences on facial form. Despite these advances, many aspects of cranial base growth, variation, and function remain poorly understood. For example, we do not know what ontogenetic processes govern flexion and extension of the cranial base, or which synchondroses are active in cranial base elongation vs. angulation in humans and other primates. Future research needs to be aimed at studying these processes as they relate to cranial shape, function, and evolution.

To conclude, we highlight two important practical and theoretical issues which we believe merit special consideration, and which promise to further our understanding of craniofacial growth and variation. First, what are the major factors that generate variation in the cranial base among primates? Second, to what extent does the cranial base function to coordinate these factors within the craniofacial complex during growth and development? As noted above, these questions need to be addressed using
two approaches. Ontogenetic studies are crucial for testing hypotheses about the generation of morphological covariation patterns, and comparative studies are important for probing the extent to which interspecific patterns of morphological evolution are epiphenomena of developmental processes.

What major factors generate variation in the cranial base?

The studies summarized above suggest that relative brain size, particularly relative to basicranial length, is an important determinant of the degree of basicranial angulation. However, the effects of (especially prenatal) brain shape on basicranial morphology have yet to be thoroughly investigated. Further experimental and comparative morphological research is needed to relate soft-tissue and bony morphology in the primate head. Despite a long tradition suggesting links between basicranial morphology and head, neck, or body posture, there is currently little empirical support for the hypothesis that these factors are directly related to variation in the cranial base, especially angulation in the midsagittal plane. Better data are also needed on head and neck posture during locomotion before locomotor-related cranial adaptations can be definitively identified. However, connections between facial orientation and basicranial morphology on the one hand and head posture on the other leave open the possibility of an indirect link between basicranial angle and head posture.

What role does the cranial base play in craniofacial integration?

Because many variables influence cranial base shape, it follows that these variables also influence other aspects of cranial shape via the cranial base. Consequently, a key issue that emerges repeatedly in discussions of the role of the basicranium in cranial development, growth, and evolution is integration. Integration, which is defined here as “the association of elements through a set of causal mechanisms so that change in one element is reflected by change in another” (Smith, 1996, p. 70), thereby generating a pattern of significant covariation (see also Olson and Miller, 1958; Cheverud, 1982; Zelditch, 1988), is an important issue because of the many genetic, developmental, and functional interactions that occur between the basicranium and its neighboring anatomical components. As described above, the cranial base is likely to directly interact, developmentally and functionally, with various adjoining skeletal, muscular, and neurosensory complexes, most notably the brain, the orbits, the ethmomaxillary complex, and the neck. These “units,” in turn, have direct and indirect interactions with other putative units such as the oropharynx, nasopharynx, mandible, and maxillary arches.

But does the cranial base play an active or a passive role in integrating cranial shape among these disparate units, and how much integration actually occurs? On an intuitive level, there are several reasons to suggest that the cranial base acts in part as a structural “interface” during growth between the brain and the face, and between the head and the neck. In many regions, the basicranium serves as the actual structural boundary between disparate components of the skull: the floor of the anterior cranial fossa is the roof of the orbits; the back of the midface is the front of the middle cranial fossa; and the posterior cranial base is the posterior roof of the oropharynx. Yet, in spite of these obvious relationships, it is difficult to define or assess quantitative hypotheses about craniofacial integration because we know so little about the extent and nature of the numerous interactions that presumably occur between and among regions of the cranial base and other parts of the skull. What are the actual units in the cranial base and skull that interact, and what regulates their interrelations and, especially, interactions? In other words, the appropriate null hypothesis to be tested is that the cranial base, while associated with variation in other parts of the skull, plays

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11 Note that some researchers (most notably Olson and Miller, 1958) define morphological integration solely as a multivariate pattern of covariation with regard to some a priori biological hypothesis (thus recognizing the importance of generative processes), whereas others (e.g., Cheverud, 1996) define integration more generally as either a pattern or a process that refers to “connections or relationships among morphological elements.”
no more of an integrative role than any other part of the skull (e.g., the mandible, the brain).

In order to explore the basicranium’s role in craniofacial integration, it is first necessary to decide how to test hypotheses about the many different processes through which integration occurs, and the many structural and functional levels at which integration is evident. Readers interested in this huge and complex topic (which is too large to review thoroughly here) should consult the recent review by Chernoff and Magwene (1999). As a first-order analysis, it is useful to test hypotheses about developmental integration by considering the processes by which different components of a system influence one another. Thus, in the context of cranial base growth within the skull, integration can occur through the direct inductive and/or mechanical effects of neighboring tissue-tissue interactions (see Moss, 1997); through secondary effects of growth in one region causing changes in the positional relationships among bones in other regions; and genetically through single genes which have effects on multiple regions, or through the coordinated action of multiple genes via pleiotropy and linkage (Atchley and Hall, 1991; Cheverud, 1982, 1995, 1996; Zelditch and Fink, 1995, Zelditch and Fink, 1996; Chernoff and Magwene, 1999). Of course, the strength of such ontogenetic interactions can vary due to changes in the timing of developmental events, something of great importance for the analysis of heterochrony, as well as due to allometric (size-correlated, size-required) factors. Note that we consider here integration solely in terms of developmental events and processes (e.g., epigenetic responses to mechanical loading, displacement due to cell division), but it is useful to recognize that developmental integration leads to, and is sometimes caused by, structural and functional integration.

Another problem with assessing any integrative role of the cranial base within the skull is the lack of widely accepted criteria for testing hypotheses of integration. Following Olson and Miller (1958) and Chernoff and Magwene (1999), we apply three nonexclusive criteria (correlation, constraint, and ontogenetic sequence) in a preliminary fashion to solely phenotypic variation in the cranial base, using the data presented above.

**Correlation.** Integration is most basically revealed by complex patterns of correlation and covariation which indicate a lack of independence among variables (see Cheverud, 1995, 1996), and which can be recognized a posteriori by comparing theoretically and empirically derived correlation matrices (Cheverud, 1982; Shea, 1985b; Zelditch, 1987, 1988; Cheverud et al., 1989; Wagner, 1989). Such studies have yet to be carried out for models that explicitly focus on the primate cranial base (but see Cheverud, 1995). However, as noted above, a high degree of covariation is frequently evident in interspecific analyses of variation in the cranial base and other parts of the skull. Perhaps the most obvious example of this phenomenon is the percentage of variation in cranial base angle accounted for by factors such as brain volume, basicranial length, facial angle, and posture. IRE1, which appears to be the dominant factor that influences cranial base angle in primates, explains 58% of the variation in CBA1 and 38% of the variation in CBA4 (see Table 5). Furthermore, according to Ross and Ravosa (1993, their Table 2), orbital axis orientation explains 41% of the variation in CBA4 among primates, while facial orientation explains 22% of the variation in CBA4 among primates. The partial correlation analysis of Strait and Ross (1999) (discussed above) found that IRE explained 36% of the variation in CBA1 when the effects of orbital axis and head-neck angle were factored out. Further evidence for this sort of complex pattern of covariation is documented among humans between CBA, cranial base length, cranial base width, and brain volume (Lieberman et al., 2000). These results are indicative (but not proof) of a pattern whereby multiple factors combine to influence CBA in such a way that variation in CBA itself may play some role in modulating the interactions among different, spatially separated components of the cranium. This hypothesis, however, requires further testing with comparative ontogenetic data.
Constraint. Another expected outcome of integration is constraint, which is defined most generally as a restriction or limitation on variation. Regardless of their causes, which can be phylogenetic, functional, developmental, or structural (Alberch, 1985; Maynard Smith et al., 1985), constraints are most basically evident in patterns of invariance. There has not been much work on phenotypic constraint in the cranial base, but several examples suggest it deserves further research. One source of evidence for constraint is revealed by allometry, which measures size-related conservation of shape (keeping in mind that size-correlated patterns due to epigenetic and perhaps genetic factors differ from size-required patterns that have a primarily functional basis). As Table 4 (see also Strait, 1999; McCarthy, 2001) illustrates, there are numerous, strongly correlated ontogenetic scaling relationships across primates between various components of the cranial base, the volume of neural regions, and facial dimensions. Integration between the brain and face via the cranial base is implied by the fact that many scaling relationships between contiguous anatomical units (e.g., the noncortical brain and the posterior cranial base) result in additional strongly correlated scaling relationships between noncontiguous anatomical units, such as those between brain volume and facial size. These scaling relationships require more study.

Another potential source of evidence regarding the presence of a constraint are patterns of angular invariance. One important example is the apparently invariant 90° angle between the PM plane and the NHA, and the limited variability that results from this relationship on the angle between the PM plane and both the planum sphenoi-deum and the anterior cranial base (S-FC) in anthropoids (McCarthy and Lieberman, 2001). Other less secure examples of invariance may include the relationship between cribriform plate orientation and facial orientation (Ravosa and Shea, 1994), and the near 45° angle between the external auditory meatus, the maxillary tuberosities, and the midpoint of the orbital aperture (Bromage, 1992). Further research, however, is needed on the extent to which invariant angles and spatial relationships occur in the skull, and additional research is needed to assess the developmental, structural, and functional bases of these relationships, and whether they reflect constraints that result from integration.

Ontogenetic sequence. Finally, hypotheses of phenotypic integration may sometimes be inferred or tested by examining ontogenetic sequences during normal growth and in the context of controlled experiments. Ontogenetic data allow one to test hypotheses of integration by examining the structural relationships between one variable and another during growth (e.g., heterochrony, heterotopy), and to compare the pattern and timing of developmental events. So far, there have been few attempts to examine hypotheses of integration in the cranial base using ontogenetic data (especially from embryonic stages), but a few examples indicate that the sequence of interactions between the cranial base, the face, and the brain are complex and multiphasic, with the cranial base mediating various interactions between the face and the brain. For example, the prenatal human cranial base initially flexes, then remains stable, and then extends, all during periods of rapid neural growth (Jeffery, 1999). Postnatally, the nonhuman primate cranial base (best studied in Pan and Macaca) appears to extend slightly during the period of neural growth, and subsequently extends more rapidly and for a long time as the face continues to grow. In contrast, the human cranial base flexes rapidly during the first few years of brain growth, and subsequently remains stable. These contrasting sequences imply multiple interactions between the brain and the face via the cranial base, but have yet to be resolved in terms of the actual processes that cause flexion and extension at specific locations during different periods of growth. One hypothesis, which remains to be tested, is that the cranial base functions to accommodate and perhaps coordinate these different aspects of growth. Controlled experimental studies, which can potentially isolate local and regional effects of specific growth stimuli on the cranial base and the rest of the skull, are a promising
avenue for future research on this problem (see Sarnat, 1982; Bütow, 1990; Reidenberg and Laitman, 1991).

Future research

Although the cranial base does appear to play some integrative role in the cranium, we have only a vague, incomplete picture of how this integration occurs, and how much of a role it plays in influencing various aspects of craniofacial form and function, and how these processes relate to evolutionary shifts in the primate cranial base. More research is needed to isolate and define the actual morphogenetic units which interact, to identify and quantify their direct and indirect interactions, and to understand the processes by which they interact. These goals may be accomplished by combining at least four approaches. First, we need to gather more three-dimensional data on cranial base variation in ontogenetic samples at all stages of growth and development (fetal to adult) among different species. The cranial base and the rest of the skull comprise a complex three-dimensional structure whose internal and external structures differ substantially, yet most studies of cranial base variation so far have used external landmarks and/or two-dimensional radiographic analysis of midsagittal landmarks (or nonmidsagittal landmarks projected into the midsagittal plane). Second, more data are needed on the developmental mechanisms which generate variation in the cranial base, and which regulate interactions among components of the skull. Experimental, histological, and other kinds of developmental information will be useful in this regard, because observed morphological patterns are potentially generated by different genetic and epigenetic processes. Third, more data are needed on the genetic bases for variation in cranial base growth and form. Lastly, more detailed interspecific analyses are needed to extend the evolutionary implications of ontogenetic tests of hypotheses about interactions and relationships among morphogenetic units of the skull. Such future research on the cranial base should provide interesting and valuable insights on other aspects of craniofacial growth, function, and evolution in primates and other mammals.

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