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Basicranial influence on overall cranial shape

This study examines the extent to which the major dimensions of the cranial base (maximum length, maximum breadth, and flexion) interact with brain volume to influence major proportions of the neurocranium and face. A model is presented for developmental interactions that occur during ontogeny between the brain and the cranial base and neurocranium, and between the neurobasicranial complex (NBC) and the face. The model is tested using exocranial and radiographic measurements of adult crania sampled from five geographically and craniometrically diverse populations. The results indicate that while variations in the breadth, length and flexion of the cranial base are mutually independent, only the maximum breadth of the cranial base (POB) has significant effects on overall cranial proportions, largely through its interactions with brain volume which influence NBC breadth. These interactions also have a slight influence on facial shape because NBC width constrains facial width, and because narrow-faced individuals tend to have antero-posteriorly longer faces relative to facial breadth than wide-faced individuals. Finally, the model highlights how integration between the cranial base and the brain may help to account for the developmental basis of some morphological variations such as occipital bunning. Among modern humans, the degree of posterior projection of the occipital bone appears to be a consequence of having a large brain on a relatively narrow cranial base. Occipital buns in Neanderthals, who have wide cranial bases relative to endocranial volume, may not be entirely homologous with the morphology occasionally evident in *Homo sapiens*.

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Introduction

It has long been known that the cranial base, vault and face derive from embryologically distinct regions (the basicranium, neurocranium and splanchnocranium) but that these regions grow in a morphologically integrated manner through numerous developmental and functional interactions (de Beer, 1937; Moss & Young, 1960; Enlow, 1968, 1990; Cheverud, 1982; Sperber, 1989). Although these interactions occur as the result of many morphogenetic (e.g., neural) and functional (e.g., masticatory, respiratory)

stimuli, the role of the cranial base in influencing overall cranial shape merits special consideration. Developmentally, the basicranium differs from the neurocranium and splanchnocranium in several important respects. Unlike the rest of the skull, which develops intramembranously from neural crest-derived tissue, the basicranium mostly grows from endochondral ossification processes in which mesodermally-derived cartilaginous precursors (the chondrocranium) develop *in utero* and are gradually replaced by bone after birth (Sperber, 1989). The basicranium is also the first region of the

skull to reach adult size (Moore & Lavelle, 1974), and it is the structural foundation of many aspects of craniofacial architecture. The cranial base forms the platform upon which the rest of the skull grows and attaches (see Biegert, 1963), and it provides and protects the crucial foramina through which the brain connects to the face and the rest of the body. These aspects of cranial base growth and function may account for its apparent morphological and developmental conservatism in mammals compared to other regions of the skull (de Beer, 1937; Bosma, 1976 and references therein; Sperber, 1989: 117). Consequently, a number of recent phylogenetic studies of hominids (e.g., Olson, 1981; Lieberman, 1995; Lieberman *et al.*, 1996; Strait *et al.*, 1997; Strait, 1998) have proposed that variations in cranial base morphology may be better indicators of taxonomy and phylogeny than neurocranial or facial characters. Some studies (e.g., Skelton & McHenry, 1992; Lieberman *et al.*, 1996; Strait *et al.*, 1997) have specifically examined cladograms that emphasize the importance of basicranial traits by grouping neurocranial and facial characters into functional complexes. However, it must be stressed that whether or not the basicranium is a better source of phylogenetic data remains open to question. Basicranial, neurocranial, and facial dimension show similar levels of heritability within the primate skull (e.g., Sjøvold, 1984; Cheverud & Buikstra, 1982; Cheverud, 1995) and appear to be equally well (or poorly) integrated with other dimensions or features in primate phylogeny (Strait, 1998).

This study tests the extent to which variations in the major dimensions of the cranial base (length, breadth and flexion) may influence several aspects of the shape of the face and cranial vault in humans. After presenting a model for interactions between the basicranium, neurocranium and face during growth, we test two sets of hypotheses. First,

it is predicted that variations in the shape of the human neurocranium are influenced by interactions between two factors: (1) variations in the shape of the basicranium upon which the neurocranium grows, and (2) endocranial expansion driven by brain growth. Because the face is displaced in a forward and downward trajectory from the basicranium and neurocranium, we also test the related hypothesis that variations in basicranial and neurocranial breadth constrain upper- and mid-facial breadth, and hence influence other aspects of facial morphology, especially facial depth and height (Weidenreich, 1941; Enlow & Bhatt, 1984; Enlow, 1990). These hypotheses are examined using a pooled-sex sample of adult anatomically modern *Homo sapiens* from five geographically and craniometrically diverse populations in order to examine as wide a range of cranial variation as possible. This study does not examine inter-population or intra-population variability. A future goal is to test the model within populations and between sexes, but larger samples sizes are required than presently available (see below).

The results of these analyses are also used to examine variation in occipital "bunning" among Upper Pleistocene hominids and recent human populations. Occipital buns, which have been suggested to be important for testing phylogenetic hypotheses about recent human evolution, are defined as posteriorly-directed projections of the occipital beyond the nuchal plane that result in a distinctive swollen morphology when viewed in norma lateralis (Ducros, 1967; Trinkaus & LeMay, 1982). Bunning has been suggested to be a derived Neanderthal character the presence of which in some early modern humans from Europe indicates regional continuity (Smith, 1984; Frayer, 1992a, 1992b; Frayer *et al.*, 1993; Wolpoff, 1996). However, Trinkaus & LeMay (1982) and Lieberman (1995) have suggested that bunning may be a developmental consequence of posteriorly-directed cranial

vault expansion that occurs in very large-brained hominids, such as Neanderthals or Upper Pleistocene modern humans, in which a relatively narrow cranial base constrains lateral vault expansion. If this hypothesis is correct, then the degree of occipital projection among adult recent humans as well as Pleistocene hominids should be correlated with the ratio of endocranial volume relative to cranial base breadth.

Background

In order to investigate the relationship between basicranial dimensions and overall skull shape, it is useful to review several aspects of craniofacial development, focusing on [Enlow's \(1990\)](#) model of the ontogenetic interactions between the basicranium, neurocranium, and splanchnocranium (illustrated in [Figure 1](#)). The basicranium is defined here as the portion of the skull which derives from the chondrocranium and which grows through endochondral ossification. As the basicranium grows, it elongates and flexes in the sphenothmoid, mid-sphenoid, and sphenoccipital synchondroses ([Scott, 1958](#)). Increases in basicranial breadth and length also occur in sutures (e.g., the occipito-mastoid), and the endocranial fossae of the basicranium deepen through drift in which the resorption and deposition occur along the superior and inferior surfaces, respectively ([Enlow, 1990](#)). In contrast, the neurocranium grows entirely from intramembranous ossification processes without any cartilaginous precursors. Intramembranous osteogenesis of the neurocranium occurs within the outer portion of ectomeninx membrane that differentiates from the dural meninges ([Friede, 1981](#)).¹ During normal growth in humans, the upper half of the neurocranium enlarges

mainly from deposition within the cranial sutures, although some resorption does take place; its lower half also expands through drift in which the external (ectocranial) surface is depository and the internal (endocranial) surface is resorptive ([Duterloo & Enlow, 1970](#)). Therefore, as [Figure 1](#) illustrates, the basicranium and neurocranium grow in tandem in a rapid neural growth trajectory, forming a highly integrated morphological unit, the neuro-basicranial complex (NBC).

This model of cranial growth assumes that overall shape of the NBC has two primary influences: the shape of the brain, and the shape of the basicranium. This integrated growth occurs through many processes, the most important of which are sutural expansion, synchondroseal deposition, drift, and flexion. As the brain expands, it generates tension along the endocranial surface of the neurocranial cavity, activating osteoblast deposition within intra-sutural periosteum throughout the upper portion of the vault, drift in the lower portions of the vault and cranial base ([Duterloo & Enlow, 1970](#); [Lieberman, 1996](#)), and endochondral growth within certain synchondroses ([Figure 1](#)). Antero-posterior and lateral NBC growth occur through coronally-oriented and sagittally-oriented sutures and synchondroses, respectively. The role of basicranial flexion is an additionally important, but complex component of NBC expansion that requires consideration. [Ross & Ravosa \(1993\)](#) demonstrated that among anthropoid non-human primates variations in basicranial flexion are most probably adaptations to accommodate increases in brain size relative to cranial base length ([Biegert, 1963](#); [Gould, 1977](#)). Basicranial flexion, however, remains constant (albeit variable) and independent of endocranial volume and cranial base length among the Hominidae, suggesting that other processes such as those listed above account for the additional increases in cranial volume

¹In cases of anencephaly, the neurocranium fails to develop due to the absence of cerebral tissue and its meningeal coverings (see [Sperber, 1989](#)).

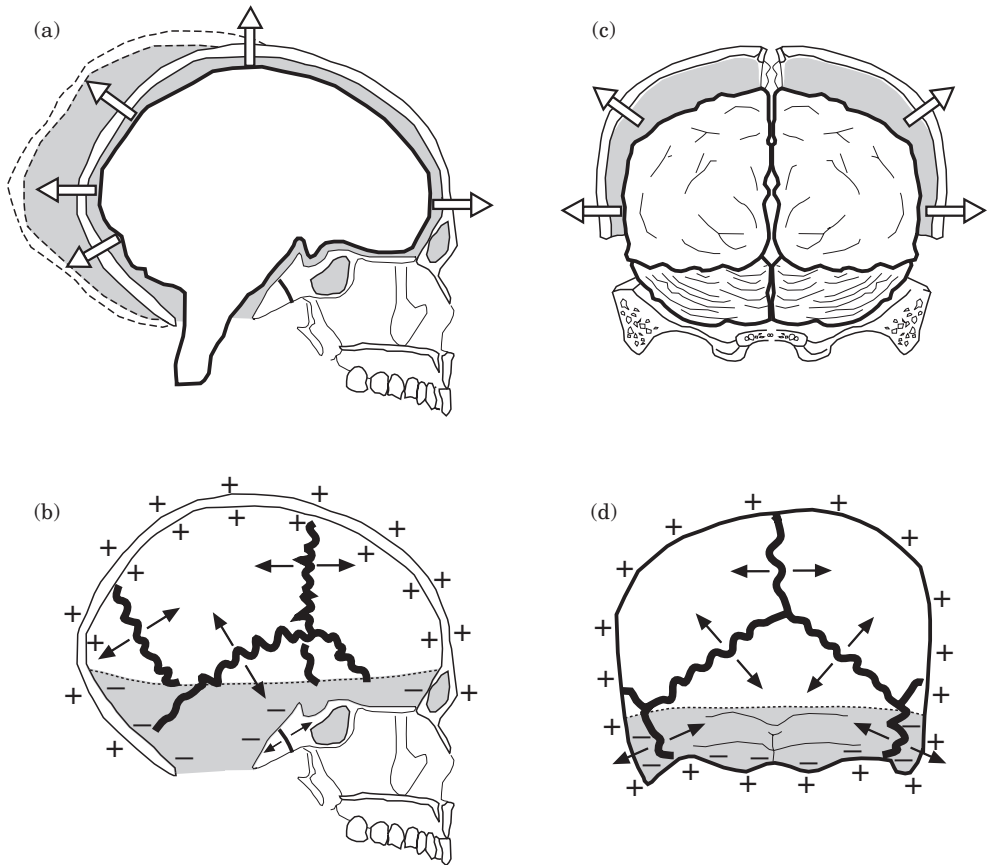


Figure 1. Model of integrated growth in the neurobasiscranial (NBC) complex (derived from [Enlow, 1990](#)). (a) Brain expansion in midsagittal plane; (b) neurocranial and basicranial growth sites in composite lateral and midsagittal view; (c) brain expansion in coronal plane; (d) neurocranial and basicranial growth sites in posterior view. Open arrows indicate directions of neural expansion; closed arrows indicate sutural and synchondroseal growth directions; + indicates sites of pericranial and endocranial bone deposition; - indicates sites of pericranial and endocranial bone resorption. Expansion of the brain induces posterior- and superior-, and to a lesser extent inferior- and anterior-directed tension in the neurocranium and basicranium (a and c). The NBC expands in response to tension through intra-sutural and synchondroseal growth (arrows in b and d), and through drift below the circumcranial reverse line (dark-shaded areas).

that characterize the genus *Homo* ([Ross & Henneberg, 1995](#)).

The model presented here proposes that variations in human NBC shape should, therefore, arise primarily from elongation and widening of the cranial base combined with neurocranial growth in the lateral, posterior and superior directions. These processes are not independent because it is likely that the cranial base and vault influence each other's growth, particularly in

early development. Studies of artificial vault deformation clearly demonstrate some effects of neurocranial growth on cranial base shape: anterior-posterior head-binding increases the breadth of the lateral portion of the cranial base, circumferential head-binding elongates the foramen magnum, and both practices inhibit basicranial flexion and alter the timing of synchondroseal fusion ([Antón, 1989](#); see also [Moss, 1958](#); [McNeil & Newton, 1965](#); [Plourde & Antón,](#)

1992). However, there are several reasons to hypothesize that the basicranium exerts more constraints on neurocranial growth than *vice versa*. First, the initial morphologies of endochondral bones, which derive from segmented paraxial mesoderm, may be less subject to epigenetic effects from interactions with other tissues than those of neural crest-derived intramembranous bones (Hall, 1978; Jacobsen, 1993; Thorogood, 1993). In addition, abnormalities of cerebral shape and/or size such as microcephaly and hydrocephaly tend to influence the shape of the neurocranium more than the basicranium (de Beer, 1937; Weidenreich, 1941; Babineau & Kronman, 1969; David *et al.*, 1990). An early onset of hydrocephaly, for example, results in a wide array of changes in neurocranial shape, but mostly causes basicranial widening (Richards & Antón, 1991). Moreover, Howells (1969, 1973) has shown that variations in basicranial breadth are the greatest non-facial source of cranial variation among modern human populations. Finally, it is important to note that studies of the effects of artificial cranial deformation demonstrate that some alterations of the cranial vault such as cradle-boarding among the Hopi tend to have less pronounced effects on the endochondrally-derived portions of the basicranium (e.g., Kohn *et al.*, 1995), while other forms of artificial deformation such as annular and anteroposterior deformations produce similar magnitudes of shape change in the vault, face, and basicranium (Cheverud *et al.*, 1992; Kohn *et al.*, 1993; Antón 1989, 1994). However, perturbations of basicranial growth sometimes have profound effects on neurocranial shape (Bütow, 1990). As noted above, anterior-posterior head-binding can cause lateral expansion of the cranial base (Antón, 1989; Cheverud *et al.*, 1992), primarily by widening the most lateral portions of the cranial base around the temporo-mandibular joint (Antón, 1989). In cases of artificial deformation,

however, the timing of the application of external stresses to the growing cranium may play a crucial role in whether the deformation produces compensatory growth in the face and basicranium as well as the vault. Deformations applied during the first year of life—when the neurocranium, basicranium, and face are all growing at a rapid rate—influence the growth of all of these regions; deformations that begin later (after 2 to 4 years) have less potential to influence the growth of the basicranium. Artificial deformation, therefore, acts as a natural experiment which alters the growth of some or all of the components of the skull, depending on its timing in ontogeny and the specific portions of the skull that are developmentally constrained due to the type of deformation.²

With regard to the development of certain aspects of cranial form, Green & Smith (Green, 1990; Green & Smith, 1991; Smith & Green, 1991) have proposed an alternative, ontogenetically-based model for the development of occipital buns and many of the other cranial traits that distinguish Neanderthals from modern humans. Green & Smith (1991) hypothesize that the overall cranial form of Neanderthals, including an occipital bun, midfacial prognathism and a strongly projecting supraorbital torus, all result from accelerated growth of the components of the basicranium. A test of Green & Smith's (1991) model would require an examination of the growth rates

²Although Cheverud *et al.* (1992) and Kohn *et al.* (1993) report that annular vault and fronto-occipital vault deformation cause specific growth changes in either the cranial base or vault, it is difficult to discern whether these changes are directly responsible for "primary evolutionary changes" in the vault, base, and/or face (Cheverud *et al.* 1992: 343). This uncertainty stems from the fact that application of cranial deformation techniques involve apparatuses that apply strain to both the neurocranium and basicranium simultaneously. Therefore, at least in regard to annular vault and fronto-occipital vault deformation techniques, it is still unclear whether changes in the cranial base or vault are responsible for the changes seen in the rest of the skull.

of the components of the basicranium in juvenile Neanderthals and several ontogenetic series of modern humans drawn from populations that differ in their adult morphology. The focus of the present study is upon patterns of correlations among dimensions in the adult cranium (which serve as a record of total attained growth throughout ontogeny), and thus does not address Green & Smith's (1991) hypothesis.

Another prediction of the model tested in the present study is that the major dimensions of the basicranium and neurocranium exert an influence on facial growth. Like the neurocranium, the face grows through intramembranous ossification of neural crest-derived tissue (facial prominences and branchial arches) (Couly *et al.*, 1993; Le Douarin *et al.*, 1993; Selleck *et al.*, 1993). It is widely appreciated that facial growth is partially independent of the NBC, to a large extent because much of it occurs in a skeletal growth trajectory after the completion of neural expansion (Moss & Young, 1960; Moore & Lavelle, 1974; Sirianni & Swindler, 1979; Sirianni, 1985; Watts, 1985; Moyers, 1988). In humans, facial growth is about 95% complete by 16–18 years, at least 10 years after the majority of the neuro-basiscranial complex has reached adult size (Stamrud, 1959; Farkas *et al.*, 1992). Indeed, the genetic basis for later-occurring facial growth appears to be different from that for the earlier expansion of the neurocranium and basicranium (Cheverud, 1996). The basicranium and neurocranium, however, may have some influence on the growth of certain facial dimensions because the upper face articulates with the anterior cranial base and the anterior cranial fossa and the mid-face articulates with the middle cranial fossa. In particular, the upper and middle portions of the face in humans grow primarily from lateral drift and anterior displacement around the ethmoid and in front of the sphenoid (Sperber, 1989; Enlow, 1990). The upper face grows anteriorly and

inferiorly from the anterior cranial fossa through drift, the middle face grows anteriorly from the middle cranial fossa through displacement; and the lower face drifts inferiorly from the middle face and displaces anteriorly from the back of the maxilla. As Weidenreich (1941) suggested, the absolute breadth of the neuro-basiscranial complex therefore probably constrains facial breadth. This hypothesis receives some support from studies of artificial cranial deformation. Antón (1989, 1994), for example, has shown 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. In addition, cranial base flexion may have some additional influences on facial orientation such as the degree of klinorhynchity (Enlow, 1968; Shea, 1985; Ravosa, 1991; Ross & Ravosa, 1993; Antón, 1994; Ross & Henneberg, 1995), but is not expected to influence other facial dimensions.

Hypotheses to be tested

The above described developmental and spatial interactions between the cranial base, vault and face suggest that in adults, as a final result of growth processes, the shape of the cranial base may be correlated with the shape of the neurocranium in several basic ways. In particular, we propose several inter-related hypotheses about predicted correlations between selected basicranial, neurocranial, and facial dimensions of adult crania. Our first hypothesis regarding these relationships concerns the relationship between endocranial volume (ECV) and basicranial form, under conditions in which the major dimensions of the basicranium (maximum breadth, maximum length, and flexion) vary independently among adults (an assumption which we test). The model

proposes that the basicranium acts as a platform upon which the brain expands, and that when the basicranium ceases to grow, its dimensions constrain the directions in which the expanding brain and cranial vault can grow. The model predicts that basicranial width constrains the breadth of the cranial vault, but that basicranial length (the distance from basion to foramen caecum) does not act as a strong constraint on the growth of the brain posteriorly and any associated elongation of the cranial vault. If these relationships are true, we hypothesize that breadth of the neurocranium correlates positively with basicranial breadth and endocranial volume, but is independent of the length and degree of flexion of the cranial base. In addition, the model predicts fewer constraints on the length of the neurocranium in adults, especially in the posterior cranial fossa, than on its breadth.

Our second hypothesis, which follows from the above model, is that variations in the length of the neurocranium have a low correlation with or are independent of basicranial length and flexion, but correlate positively with endocranial volume and negatively with basicranial breadth. Third, we hypothesize that variations in endocranial volume relative to basicranial breadth correlate positively with the height of the neurocranium and with the degree of posterior extension of the neurocranium in the posterior cranial fossa. Another way of stating this hypothesis is that given a large brain and a narrow cranial base, the cranial vault is likely to grow backward and upward to accommodate the brain. As a result, the degree of occipital bunning among recent and fossil humans is predicted to be a function of endocranial volume relative to basicranial breadth, and is therefore expected to occur more frequently in large-brained, narrow-skulled individuals.

A second, related set of hypotheses concerns the influence of the NBC on facial growth as suggested by [Weidenreich \(1941\)](#),

[Enlow & Bhatt \(1984\)](#), [Enlow \(1990\)](#) and others. Because the face grows downward and forward from the cranial base, we hypothesize that maximum upper facial breadth in adult humans is constrained by the breadth of the anterior cranial fossa and that midfacial breadth is constrained by the breadth of the middle cranial fossa. [Enlow \(1990\)](#), [Howells \(1973\)](#), and a number of researchers who have studied artificial vault deformation (e.g., [Cheverud *et al.*, 1992](#); [Kohn *et al.*, 1993](#); [Antón, 1994](#)) have also suggested that NBC proportions influence certain facial proportions. The basis for the first hypothesis regarding facial dimensions stems from the observation that growth of the NBC, hence growth in midfacial breadth, is complete long before the majority of facial growth occurs. Therefore, increases in facial size after the cessation of the neural growth trajectory occur mostly as anteriorly and inferiorly directed growth ([Moss & Young, 1960](#); [Moore & Lavelle, 1974](#); [Moyers, 1988](#); [Farkas *et al.*, 1992](#)). Enlow has specifically proposed that a relationship exists between cranial form and the prevalence of certain malocclusions (illustrated in [Figure 2](#)). According to [Enlow \(1990: 196–198\)](#), individuals with absolutely narrow NBCs (primarily dolichocephalics) tend to have more flexed cranial bases, longer anterior cranial bases, and narrower faces than individuals with absolutely wider NBCs (primarily brachycephalics). As a result, a second hypothesis derives from [Enlow's \(1990: 222–228\)](#) prediction that individuals with absolutely narrower NBCs have proportionately narrower and antero-posteriorly longer faces (leptoprosopy) than individuals with wider NBCs who have proportionately wider and antero-posteriorly shorter faces (euryprosopy).

Hypothesis testing

The above hypotheses can be tested using comparisons of adult skulls or ontogenetic

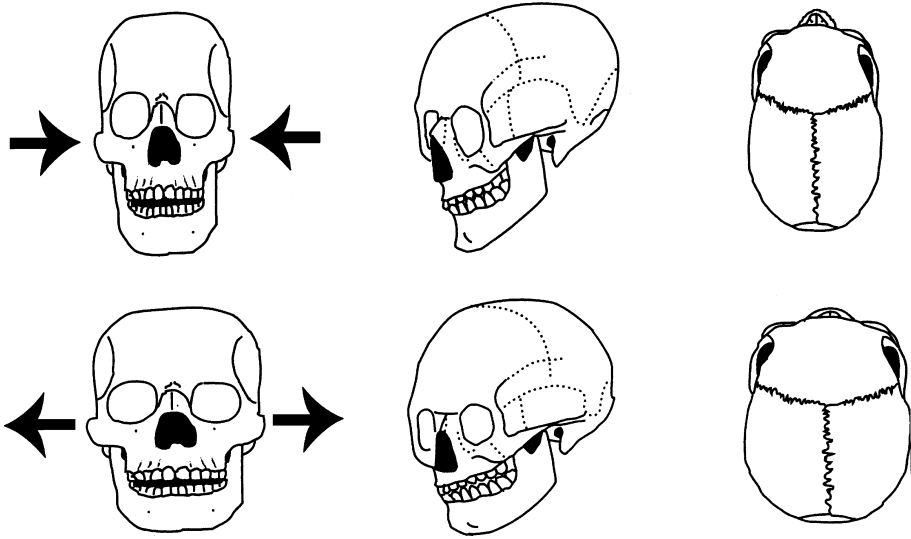


Figure 2. Enlow's (1990) model of differences in facial form between dolichocephalic and brachycephalic individuals. According to this model, individuals with narrower NBCs will have proportionately narrower and antero-posteriorly longer faces than individuals with broader NBCs. See text for details.

samples of skulls with different overall cranial shapes. This paper employs the former because of the difficulties of using available ontogenetic data to distinguish among the effects of the many diverse components of the skulls that grow concurrently in a similar trajectory. During the first 6 years of growth, the basicranium flexes and the dimensions of the neurocranium and basicranium all increase dramatically in size in a common neural growth trajectory, largely driven by the capsular functional growth matrix of the expanding brain (Moore & Lavelle, 1974; Ranly, 1988). Differences in attained growth in adult crania are relatively small compared to the disparity in size between adults and neonates. As a result, ontogenetic series of skulls inevitably produce high correlations between endocranial volume and all the components of the NBC, making it difficult to factor out autocorrelations that result from the tremendous collinear growth that occurs in all cranial dimensions in infancy and childhood (for a discussion of these statistical problems, see Sokal & Rohlf, 1995: 583–586).

Rather than focusing upon the correlations between cranial dimensions during growth, future studies may address these problems by studying the timing of growth differences, the correlations between growth rates, and the relative timing of growth cessation events between individuals (or populations) that ultimately develop differently-shaped crania. Relationships between elements of the cranial base and neurocranial and facial dimensions during ontogeny could be tested using longitudinal data from many individuals who differ in adult cranial shape, or by comparing ontogenetic cross-sectional samples from populations that differ in adult cranial shape. In either case, the processes of growth would not be expected to differ fundamentally except perhaps in terms of the slope and/or intercept values of selected basicranial, neurocranial and facial proportions throughout ontogeny. Investigation of the relative timing of onset and cessation of specific growth centers would complete the picture of how differences in adult morphology are achieved through growth. Unfortunately, such longitudinal

and cross-sectional data are not available currently, but hold much promise for future study.

The hypotheses presented above concerning the influence of basicranial growth on overall cranial shape can also be tested using adult skulls from diverse populations that sample a wide range of overall cranial shapes. The adult skull is the final product of ontogeny and represents the cumulative product of the particular growth processes of interest. In particular, this study uses a pooled sample of males and females from five craniometrically and geographically diverse populations in order to examine as wide a range of craniofacial forms as possible. Although the inclusion of several populations raises the possibility that some proportion of the variation results from inter-population differences (see below), we emphasize that the hypotheses tested here derive from a general model of craniofacial growth that is not population or sex specific and must apply to all craniofacial types. The hypotheses we have proposed do not constitute a test of the ontogenetic model itself, but rather they serve as a test of the pattern of correlations between the sizes of adult structures expected from the model of cranial ontogeny. For the ontogenetic model to have any general validity, it must be able to explain differences among as diverse an array of cranial types as possible. As other researchers (e.g., Howells, 1973; Lahr 1996) have shown, this kind of pooled sample is necessary to examine a wider range of craniofacial variation than is present within single populations.

Materials and methods

Sample

The sample of recent *Homo sapiens* used in this study comes from five geographically and craniometrically diverse populations from Australia, East Asia, Europe, North Africa and sub-Saharan Africa (Table 1).

Roughly 20 adults whose M³s had fully erupted were measured from each population. An attempt was made to select equal proportions of males and females from each population by estimating sex using standard sexually dimorphic characteristics (Bass, 1987: 81). As Figure 3 illustrates, these skulls encompass a broad range of overall cranial shapes: the Ashanti and Australian individuals tend to be dolichocephalic, the Chinese and Egyptian individuals tend to be mesocephalic, and the Italian individuals tend to be brachycephalic. Although the pooled cranial sample is skewed towards dolichocephalic individuals, this bias reflects the prevalence of dolichocephaly among human populations (Weidenreich, 1945; Martin & Saller, 1956). A sample of Pleistocene human skulls (archaic and anatomically modern) which are substantially complete and for which lateral radiographs were available were also studied.

Measurements

A series of measurements (listed in Table 2) were taken on each cranium from external landmarks and from radiographs. Summary statistics for these measurements are provided in Table 3. Exocranial linear dimensions to the nearest 0.1 mm were taken using Mitutuyo[™] digital sliding or spreading calipers. Lateral and superior-inferior radiographs were taken of all specimens using an ACOMA[™] portable X-ray machine on Kodak XTL-2 film. To minimize potential distortion and parallax, care was taken to orient the midsagittal plane of each cranium parallel to the X-ray film and collimator for the lateral radiographs and in the Frankfurt horizontal for the supero-inferior radiographs. Linear measurements of the radiographs were taken to the nearest 0.1 mm from tracings using Mitutuyo[™] digital sliding calipers. All linear radiograph measurements were adjusted for size distortion using a correction factor calculated as the ratio of maximum cranial length

Table 1 Samples used

Sample	Taxon	<i>n</i> (m/f)	Modern samples (S.D.s in parentheses)				Location
			ECV	POB	CI	BI	
Ashanti	Recent <i>Homo sapiens</i>	18 (9/9)	1404·4 (145·5)	107·7 (4·5)	0·73 (0·04)	2·17 (0·4)	AMNH
Australians	Recent <i>H. sapiens</i>	21 (12/19)	1287·8 (125·8)	111·3 (5·3)	0·71 (0·03)	1·93 (0·67)	AMNH
Chinese	Recent <i>H. sapiens</i>	19 (10/9)	1496·7 (92·3)	116·7 (5·0)	0·79 (0·04)	1·66 (0·47)	AMNH
Egyptians	Recent <i>H. sapiens</i>	20 (10/10)	1342·4 (119·1)	108·7 (4·9)	0·75 (0·03)	2·10 (0·64)	PM
Italians	Recent <i>H. sapiens</i>	20 (11/9)	1350·3 (151·8)	118·0 (4·9)	0·82 (0·03)	1·53 (0·60)	PM

Skull	Taxon	Fossils			Source of radiograph
		ECV*	POB	CI*	
Abri Pataud	<i>H. sapiens</i>	1380	104	75·4	D. Lieberman (this study)
Skhul 4	<i>H. sapiens</i>	1554	117	71·8	B. Arensburg (personal communication)
Skhul 5	<i>H. sapiens</i>	1518	116	74·5	D. Lieberman (this study)
Cro Magnon 1	<i>H. sapiens</i>	1600	115	74·0	D. Lieberman (this study)
Obercassel 1	<i>H. sapiens</i>	1500	129	74·2	J. Weiner (NHM)
Obercassel 2	<i>H. sapiens</i>	1279	114	71·3	J. Weiner (NHM)
La Chapelle	<i>Homo neanderthalensis</i>	1626	119	75·0	D. Lieberman (this study)
Monte Circeo	<i>H. neanderthalensis</i>	1330	129	75·9	J. Weiner (NHM)
La Ferrassie 1	<i>H. neanderthalensis</i>	1681	128	76·1	D. Lieberman (this study)
La Quina 5	<i>H. neanderthalensis</i>	1350	119	—	J. Weiner (NHM)

*From Vandermeersch, 1981: 140–143.

Abbreviations in Table 1: ECV, endocranial volume; POB, bi-porionic breadth; CI, cranial index; BI, bunning index. Locations of the cranial collections: AMNH, American Museum of Natural History; PM, Peabody Museum (Harvard University); NHM, Natural History Museum archives (courtesy of T. Molleson).

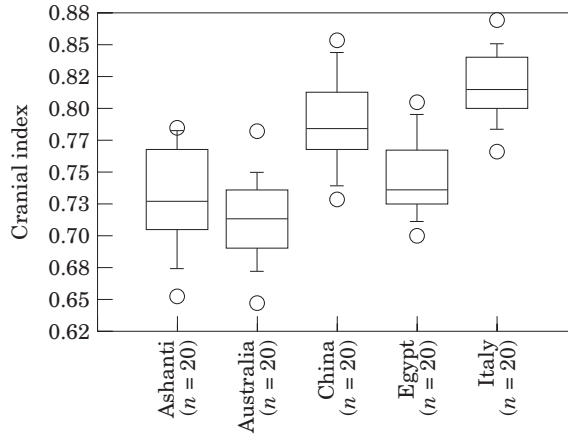


Figure 3. Summary of variation in cranial index (XCB/GOL × 100) of recent human populations used in this study.

Table 2 Linear and angular measurements used

Measurement	ABBR.	Definition
Neurocranial length	GOL	Chord distance from glabella to opisthocranium (Howells, 1973)
Max. cranial breadth	XCB	Maximum cranial breadth perpendicular to sagittal plane (Howells, 1973)
Max. basicranial breadth	POB	Bi-porionic breadth (Wood, 1991)
Upper facial breadth	FMB	Bi-frontomolare temporale breadth (Wood, 1991)
Mid-facial breadth	JUB	External malar breadth at jugale (Howells, 1973)
Lower facial breadth	EPB	External palate breadth at M ¹ (Wood, 1991)
Mid-facial breath	MFB	Bi-maxilofrontale breadth (Wood, 1991)
Neurocranial height	BBH	Chord distance from basion to bregma (Howells, 1973)
Facial height	NPH	Chord distance from nasion to prosthion (Howells, 1973)
Orbital height, left	OBH	Chord distance between upper and lower borders of orbit, perpendicular to the long axis of orbit (Howells, 1973)
Cranial base length ^L	BCL	Chord distance from basion-sella plus sella-foramen caecum
Cranial base angle ^L	CBA	Angle between basion-sella and sella-foramen caecum
Ant. cranial base length ^L	ACL	Chord distance from sella-foramen caecum
Mid-facial length ^L	MFL	Minimum chord from PM plane* to nasion (Lieberman, in press)
Lower facial length ^L	LFL	Chord distance from anterior to posterior nasal spines
Ant. cranial fossa breadth ^S	ACB	Maximum anterior cranial fossa breadth anterior to clinoid processes
Mid. cranial fossa breadth ^S	MCB	Middle cranial fossa breadth at sella

^LFrom lateral radiograph.

^SFrom supero-inferior radiograph.

*The posterior maxillary (PM) plane, from the maxillary tuberosities to the anterior-most point where the greater wings of the sphenoid intersect the planum sphenoidaleum (the junction of the anterior and middle cranial fossa), is the boundary between the ethmomaxillary facial complex and the middle cranial fossa (Enlow, 1990).

measured exocranially and maximum cranial length measured from the radiograph. Angular measurements of cranial base flexion were made from tracings with a protractor to the nearest degree. ECV was

measured in each cranium by filling the neurocranial cavity with lentils through the foramen magnum while shaking and tapping the skull gently until no more lentils could fit below the level of the

Table 3 Descriptive statistics of modern human sample (in mm, standard deviations in parentheses)

Population	<i>n</i>	CBA	XCB	GOL	BBH	LFL	MFL	NPH	OBH	FMB	JUB	EPB	ACB	MCB	FI
Ashanti	18	131.6 (4.7)	129.3 (6.9)	177.4 (7.1)	132.7 (5.9)	43.1 (2.8)	42.8 (3.0)	66.2 (4.9)	34.0 (2.5)	101.7 (4.4)	112.2 (4.5)	60.9 (3.8)	103.3 (5.5)	116.2 (5.9)	2.64 (0.19)
Australians	21	132.4 (4.5)	125.4 (6.0)	176.0 (8.4)	129.8 (4.9)	45.0 (3.4)	43.6 (2.1)	63.8 (4.3)	33.3 (1.8)	106.0 (4.2)	114.2 (4.7)	61.2 (3.5)	103.1 (4.5)	116.0 (4.6)	2.63 (0.16)
Chinese	19	132.8 (6.7)	137.3 (4.2)	175.5 (8.7)	132.8 (6.6)	42.8 (3.9)	39.7 (2.7)	70.5 (5.2)	34.5 (2.2)	103.7 (3.4)	114.3 (3.9)	60.5 (3.9)	109.3 (4.5)	125.5 (5.2)	2.90 (0.21)
Egyptians	20	136.3 (3.0)	134.8 (5.9)	181.0 (6.3)	128.9 (5.6)	41.6 (4.5)	37.6 (2.5)	64.0 (4.6)	35.3 (4.7)	97.7 (3.8)	105.6 (3.8)	54.9 (3.1)	101.3 (3.2)	112.3 (5.0)	2.83 (0.18)
Italians	20	135.7 (2.8)	142.3 (6.2)	174.2 (8.2)	130.3 (6.5)	43.6 (4.2)	39.0 (3.7)	62.3 (4.6)	34.3 (5.1)	102.1 (5.6)	112.8 (7.8)	55.5 (5.5)	107.4 (7.2)	119.6 (7.4)	2.93 (0.24)
Combined	98	133.8 (4.8)	133.7 (8.4)	176.8 (7.7)	130.8 (5.9)	43.3 (3.9)	40.5 (3.6)	65.2 (5.4)	34.3 (3.5)	102.3 (5.1)	111.7 (6.1)	58.5 (4.9)	104.8 (5.8)	117.8 (7.0)	2.79 (0.23)

See Table 2 for measurement details and abbreviations; FI, facial index (JUB/MFL × 100).

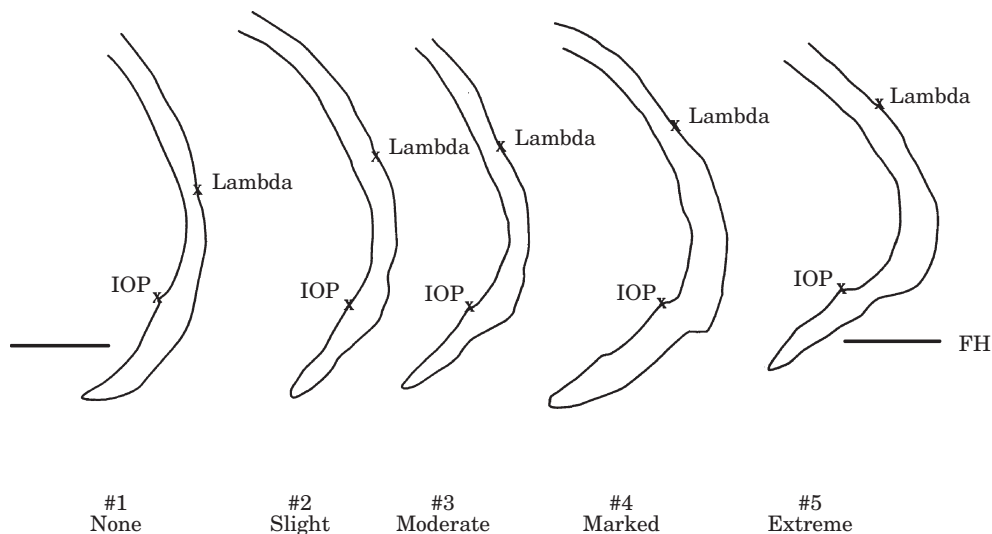


Figure 4. Grades used to evaluate degree of occipital bunning in individuals from lateral radiographs. See text for details. Occipital projection is evaluated primarily from the internal occipital table relative to the internal occipital protuberance (IOP) and to lambda (L). Note that grades 3 and 4 differ solely in terms of the morphology of the outer table. Most previous appraisals of bun development have generally been made upon the external morphology of the occipital rather than the internal contour, as used here.

foramen magnum. The lentils were then emptied via a funnel into a graduated cylinder which was shaken until they had subsided completely, and the volume read to the nearest milliliter. In order to make the volumetric measurements similar in scale to the linear dimensions of the cranium, the measurement of ECV used in the analysis is calculated as the cube root of the measured cranial capacity.

Although widely considered to be a continuously variable feature, occipital bunning is difficult to quantify because it combines projection of both the internal and outer tables of the occipital inferior to lambda and superior to the internal occipital protuberance (IOP), the attachment site of the tentorium cerebelli (Ducros, 1967; Trinkaus & LeMay, 1982; Lieberman, 1995). Appraisals of occipital bunning probably often rely upon subjective, visual examination of the amount of external projection of the occiput. Our definition, based on Trinkaus & LeMay (1982), primarily emphasizes the

internal curvature of the occipital bone, which more closely reflects the shape of the brain. Following Lahr's (1994, 1996) approach of dividing continuously varying aspects of cranial morphology into discrete categories, the degree of occipital bunning was quantified in each individual from lateral radiographs using a system of grades, reflecting examples of minimum, intermediate and maximum degrees of development selected from the total sample studied (including Neanderthals). Five grades (illustrated in Figure 4) were defined using the contours of both internal and outer tables of the occipital from lateral radiographs as follows: 1, no bunning, with very little posterior projection of the occipital tables above the IOP and below lambda; 2, minor bunning, with slight posterior projection of the internal table of the occipital above the IOP and below lambda; 3, moderate bunning, with a significantly more concave internal occipital table above the IOP and below lambda; 4, marked bunning, with a

similar degree of internal occipital concavity to grade 3, but in which the external table is also substantially more developed above the IOP and below lambda; 5, extreme bunning, with a highly concave internal occipital table above the IOP and below lambda, combined with a thick and highly convex outer table. Note that grades 3 and 4 differ solely in terms of the morphology of the outer table.

An important detail with respect to occipital bunning concerns the fossil specimens that could be included in the analysis. Most of the early modern humans that have pronounced occipital buns come from central European Aurignacian or Gravettian sites such as Mladec, Zlatý Kun, Stetten, Předmostí, Brno, Dolní Věstonice, and Pavlov (Jelínek, 1969; Smith, 1982, 1984; Vlček, 1991). The crania from Předmostí were destroyed in World War II, and other specimens lack a cranial base, limiting their value for this study. Similarly, we were unable to obtain radiographs of some of the more complete Central European specimens, and the western European early modern specimen that has the most pronounced occipital protuberance, Cro-Magnon 3, was not included because its cranial base is not preserved. Thus our sample of early modern humans does not include many of the specimens in which external bunning is most pronounced and it does not include the Mladec specimens, which play a crucial role in discussions of possible continuity from Neanderthals to modern humans in Central Europe (e.g., Jelínek, 1969; Smith, 1984; Frayer, 1986; Wolpoff, 1996). Thus the sample of measurements and radiographs of early modern humans we obtained can only serve as a preliminary test of the hypothesis that early modern humans and Neanderthals developed occipital buns in different ways.

Statistical analysis

All measurements were entered and analyzed using *Statview 4.5*[™] (Abacus Con-

cepts, Berkeley, CA, U.S.A.) and *Systat 5.2* (Systat Inc., Evanston, IL, U.S.A.). The accuracy of the linear, angular and volumetric measurements were tested by taking each measurement five times on the same skull. Average measurement error was 1.4%. The cube-root of ECV was used in order to compare linear and volumetric measurements. Normality was tested for each variable using the Lilliefors test (Lilliefors, 1967). In order to examine the effects of overall cranial size, a geometric mean (GGM) of ten diverse craniofacial dimensions was computed as the tenth root of the product of the following measurements: ECV, maximum cranial breadth (XCB), upper facial breadth (FMB), mid-facial breadth (JUB), neurocranial length (GOL), facial height (NPH), orbital height (OBH), lower facial length (LFL), maximum basicranial (bi-porionic) breadth (POB), and basion-bregma height (BBH); a geometric mean of overall facial size (FGM) was calculated as the fifth root of the product of facial height (NPH), orbital height (OBH), midfacial breadth (MFB), lower facial breadth (EPB), and lower facial length (LFL).

Because the majority of the variables examined in this study are normally distributed (see below), predicted relationships among craniofacial dimensions were examined in the pooled modern human sample primarily using Pearson correlation coefficients, and using partial correlation analysis in order to hold certain variables (which serve as a proxy for overall cranial size) constant. Linear regression and stepwise multiple regression analyses are also used to estimate the proportion of variance explained by specific variables. The strengths of the correlations among categorical data (e.g., occipital bunning) and any non-normally distributed variables are examined with Spearman rank correlation analysis. Significance testing of Pearson correlation coefficients was determined

Table 4 Correlation (top) and partial correlation (bottom) analysis of major basicranial and neurocranial dimensions

	POB	BCL	CBA	ECV	GGM
POB	—	0.437‡	0.005	0.409‡	0.644
BCL	-0.026	—	-0.031	0.453‡	0.697‡
CBA	-0.041	-0.096	—	0.025	0.053
ECV	-0.041	-0.027	-0.018	—	0.670‡
GGM	0.476*	0.538*	0.104	0.505‡	—

* $P < 0.05$; † $P < 0.01$; ‡ $P < 0.001$.

using Fisher $r-z$ test; significance of partial correlations was determined using the significance of partial regression coefficients.

Results

Basicranial–neurocranial interactions

The first hypothesis regarding relationships between the basicranium and neurocranium predicts that the length and breadth of the cranial base should be independent, and that the interaction of endocranial volume with these two basicranial dimensions potentially influences the major dimensions of the neurocranium. Correlation and partial correlations in Table 4 indicate that there is a moderate, significant correlation between cranial base length (BCL) and POB, but that these two dimensions are entirely independent ($r=0.026$) when one holds CBA, ECV and GGM constant using partial correlation analysis. These results also indicate that variations in ECV do not correlate with variation in BCL and POB when one holds overall cranial size constant, and confirms the hypothesis that variation in CBA among adult humans is independent of ECV, overall cranial size, and other cranial base dimensions (Ross & Henneberg, 1995). These data, therefore, clearly support the hypothesis that attained growth in the breadth, length and flexion of the cranial base result from independent processes in the sense that they do not appear to affect each other's size.

A second hypothesis is that both POB and ECV influence the maximum breadth of the neurocranium, but that maximum neurocranial breadth is expected to be independent of cranial base length and flexion. The pairwise correlations show that there is a weak but highly significant ($r=0.283$, $P < 0.001$) association between basicranial length and maximum neurocranial breadth, while the correlation between maximum cranial breadth and cranial base flexion is both low and non-significant (Table 5). If considered in isolation, the significant correlation between XCB and BCL might falsify the first hypothesis. However, the hypothesis is supported more strongly by partial correlation analysis (Table 5), which shows that XCB correlates moderately and significantly with POB ($r=0.440$, $P < 0.05$) and ECV ($r=0.358$, $P < 0.05$), and that these correlations remain moderate when one holds BCL, CBA and GGM constant. In addition, BCL, CBA and the GGM measurements all have extremely low partial correlations with XCB. In other words, basicranial breadth and endocranial volume appear to be major influences on neurocranial breadth, holding overall cranial size constant. According to a stepwise multiple regression, POB and ECV together account for approximately 56% of the variation in XCB ($P < 0.001$) in the recent human sample studied here.

Given the independence between cranial base breadth and length and the observation that POB and ECV remain associated with

Table 5 Correlation (top) and partial correlation (bottom) analysis basicranial and neurocranial breadth with endocranial volume, basicranial flexion, and overall cranial size

	XCB	POB	ECV	BCL	CBA	GGM
XCB	—	0.592‡	0.541‡	0.283‡	0.139	0.516‡
POB	0.440*	—	0.409	0.427‡	0.005	0.644‡
ECV	0.358*	-0.192	—	0.453‡	0.025	0.670‡
BCL	-0.111	0.025	0.014	—	-0.031	0.697‡
CBA	0.165	-0.109	-0.076	-0.076	—	0.053
GGM	0.030	0.414*	0.461*	0.538*	0.097	—

* $P < 0.05$; † $P < 0.01$; ‡ $P < 0.001$.**Table 6** Correlation (top) and partial correlation (bottom) analysis of neurocranial length with basicranial length, basicranial flexion, endocranial volume, and overall cranial size

	GOL	BCL	CBA	ECV	GGM
GOL	—	0.397‡	0.137	0.605‡	0.520‡
BCL	0.090	—	-0.031	0.453*	0.697‡
CBA	0.154	-0.107	—	0.025	0.053
ECV	0.414*	-0.061	-0.079	—	0.670‡
GGM	0.100	0.583‡	0.079	0.459‡	—

* $P < 0.05$; † $P < 0.01$; ‡ $P < 0.001$.

variation in XCB when other factors (e.g., GGM as a measure of overall cranial size) are held constant, the developmental model tested here predicts that there should be fewer constraints on neurocranial length and height, especially in the posterior cranial fossa. In particular, the second hypothesis predicts that GOL should be independent with or have a low correlation with BCL and CBA, but should be highly correlated with ECV, holding overall cranial size and the other variables constant. This hypothesis is tested using correlation and partial correlation analysis in Table 6. As these analyses indicate, GOL is moderately and significantly ($P < 0.001$) correlated with BCL, ECV and GGM, which would seem to disprove the hypothesis. However, when the interactions among these variables are removed using partial correlation, GOL is independent of CBA, BCL and GGM, and has a moderate but significant (partial $r = 0.414$; $P < 0.05$) partial correlations with

ECV. In other words, the second hypothesis is supported because neither cranial base length nor flexion has much influence on total neurocranial length independent of other factors.

Since cranial base breadth apparently constrains neurocranial breadth, cranial base length is independent of neurocranial length, and ECV significantly affects both neurocranial dimensions, then it follows that the developmental interactions between brain volume and cranial base *breadth* should influence the length and height of the neurocranium more than its breadth. This hypothesis is tested in Table 7 using correlation and partial correlation analysis. While the Pearson correlation coefficients between the ratio of ECV/POB and GOL, XCB, CBA and BBH are all quite low, there is a moderate but significant partial correlation between the ratio of ECV/POB and GOL (partial $r = 0.400$), holding the other dimensions including GGM constant. In other

Table 7 Correlation (top) and partial correlation (bottom) analysis of the ratio of endocranial volume to basicranial breadth with major neurocranial dimensions

	ECV/POB	GOL	XCB	BBH	CBA	GGM
ECV/POB	—	0.225*	-0.254	0.075	0.004	-0.233
GOL	0.400*	—	0.247*	0.432‡	0.137	0.520‡
XCB	-0.124	0.025	—	0.240*	0.139	0.516‡
BBH	0.268*	0.005	-0.106	—	0.012	0.657‡
CBA	-0.012	0.129	0.127	-0.024	—	0.053
GGM	-0.408‡	0.432‡	0.375‡	0.603‡	-0.053	—

* $P < 0.05$; † $P < 0.01$; ‡ $P < 0.001$.

words, individuals with larger brains relative to basicranial breadth tend to have slightly longer cranial vaults, controlling for other factors. It is important to note, however, that in a multiple stepwise regression, variations in ECV and POB explain only 35% of the variation in GOL ($P < 0.001$) and 38% of the variation in BBH ($P < 0.001$), indicating that other factors probably related to brain shape and overall cranial size (e.g., the dural bands) have more dominant influences on these dimensions. The Pearson and partial correlations reveal that individuals with a high ratio of ECV/POB also tend to have a cranium with a relatively small GGM.

These results support the hypothesis that the cranial vault tends to expand vertically and especially posteriorly to a greater extent in individuals with a large brain relative to cranial base breadth. The interactions between brain volume and cranial base breadth that apparently influence neurocranial length may, therefore, explain some of the variation in occipital projection or “bunning” in recent and Pleistocene humans. Among the recent human sample studied here, posterior projection of the occipital is generally modest: 87% were scored as having no bunning (type I) or only slight bunning (type II), and only 13% were scored as having moderate bunning (type III). However, the Spearman rank correlation between the degree of occipital projection and the ratio of ECV/POB is moderate and highly significant ($\rho = 0.600$;

$P < 0.001$), and thus supports the hypothesis that posterior projection of the occipital is partially a function of having a large brain relative to cranial base area. As predicted by Lieberman (1995), the degree of bunning also has a moderate negative Spearman rank correlation ($\rho = -0.428$, $P < 0.001$) with the cranial index, indicating that dolichocephalic individuals are more likely to have posteriorly-projecting occipitals than brachycephalic individuals. As noted by Trinkaus & LeMay (1982), posterior projection of the occipital in these humans was always above the tentorium cerebelli, suggesting that the expansion was probably a result of local growth effects exerted by the occipital lobe on the occipital squama.

When the Pleistocene sample of recent modern humans, who tend to have large brains and narrow cranial bases, is added to the analysis, the relationship between occipital bunning and between brain size is strengthened (Figure 5). However, it is clear from Figure 5 that Neanderthals do not fit the early modern human pattern, primarily because they have somewhat wider cranial bases relative to endocranial volume [which, with the small sample size used, does not reach significance ($P = 0.16$)], and marked occipital buns (Grade 5). Other differences in bunning are also evident from Figure 6, which compares lateral radiographs of the occipital in several Neanderthals and Pleistocene modern humans. As Figure 6 shows, while some early modern humans

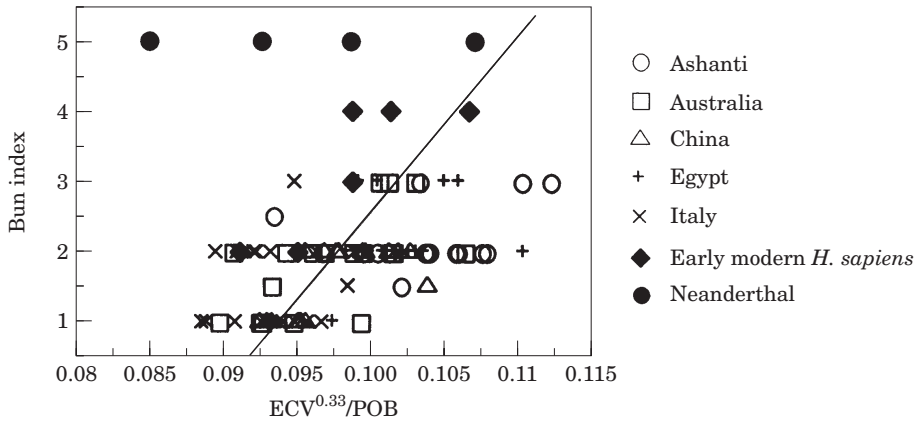


Figure 5. Variation in occipital bunning plotted against endocranial volume (cube root) divided by bi-porionic breadth. *H. sapiens*, but not Neanderthals with larger endocranial volumes relative to POB, tend to have significantly more posterior projection of the occipital.

have posteriorly projecting occipitals relative to the IOP and to lambda, none have the degree of internal table concavity that is typical of Neanderthals. Viewed externally, however, many of these early modern human fossils have marked “buns” because of the thickness of the cranial vault in this region (Lieberman, 1996). It is worth reiterating that, for developmental reasons, the definition of occipital buns used here places the greatest emphasis upon the curvature of the *internal table* of the occipital. The results support Trinkaus & LeMay’s (1982) hypothesis that other developmental factors—possibly related to differences in the timing of posterior cerebral growth relative to the growth of the cranial vault bones—apparently account for the extreme degree of posterior projection of the occipital in the Neanderthals. Therefore, it appears that the externally visible similarities in occipital form between large-brained dolichocephalic humans and Neanderthals may not be entirely homologous in a developmental sense. Indeed, Smith (1984) has noted that the form of occipital buns differs in Neanderthals and robust early modern humans, leading him to describe the occipital protuberances of the early moderns as

“hemi-buns.” If these morphologically divergent structures are not developmentally homologous, then the presence of occipital buns in Neanderthals and post-Neanderthal Europeans does not necessarily indicate genetic continuity.

The above results regarding the relationship between bunning and brain size relative to cranial base width must be interpreted with some caution, however, given problems with the sample studied here. Our sample of early modern humans does not include Eastern European specimens such as the Mladec, Předmostí, Dolní Věstonice, and Pavlov which have some of the largest occipital protuberances of early modern crania. In addition, the early modern sample does not include Cro-Magnon 3, the western European early modern cranium with the greatest degree of bun development, because the specimen lacks its cranial base. Furthermore, although bi-porionic breadths (POB) have not been published for the Mladec crania, Frayer (1986) reports measurements for bi-auricular breadth (which is usually a few millimeters larger than POB) for Mladec 1, 2, and 5 (128·8, 130·4, and 150·0 mm, respectively). These bi-auricular dimensions are remarkably

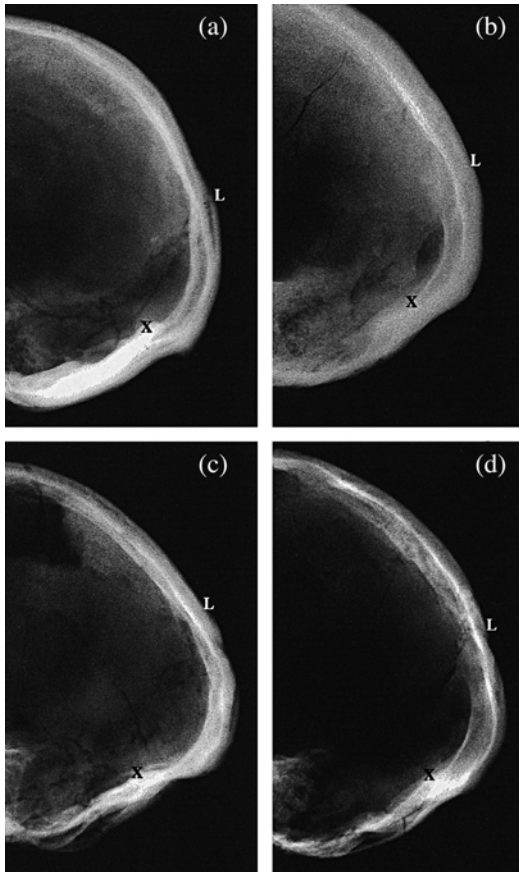


Figure 6. Lateral radiographs of posterior cranium in Abri Pataud (a), Cro-Magnon I (b), La Chapelle aux Saints (c) and La Ferrassie I (d). Internal occipital protuberance, X; Lambda, L.

large, comparable with, or even larger than, the corresponding POB measurements in the Neanderthals sampled here. Therefore, the argument that early modern humans developed buns upon narrow cranial bases, while Neanderthals developed their buns upon wide cranial bases probably cannot be extended to the early modern crania from Mladec.

Neuro-basiscranial-facial interactions

The second set of hypotheses tested here attempts to relate the potential developmental influence of neuro-basiscranial complex (NBC) breadth on certain facial dimensions

as predicted by Weidenreich (1941) and Enlow (1990). According to the above model, the breadth of the upper face is predicted to be constrained by the breadth of the upper cranial fossa, and the breadth of the midface is predicted to be constrained by the breadth of the middle cranial fossa. Correlation analyses provide some support for this hypothesis. Among the recent human sample, Pearson correlation coefficients between upper facial breadth and anterior cranial fossa breadth ($r=0.532$, $P<0.001$) and between midfacial breadth and middle cranial fossa breadth ($r=0.490$, $P<0.001$) are moderate in strength and highly significant. However, Enlow's (1990) hypothesis that NBC dimensions influence facial proportions receives only partial support. Among the sample studied here, there is no significant correlation between XCB or the cranial index (CI) with either CBA or anterior cranial base length (ACL), as the model predicts. Nevertheless, there is a moderate and significant correlation ($r=0.491$, $P<0.001$) between XCB and the facial index (FI)—the ratio of facial breadth (JUB) to facial length (MFL)—which yields a partial correlation coefficient of $r=0.397$ when overall facial size (FGM) is held constant. Moreover, there is also a significant, moderate correlation between the cranial and facial indices ($r=0.492$, $P<0.001$), which yields a partial correlation of $r=0.499$ when FGM is held constant. In other words, Enlow's observation that individuals with absolutely and relatively narrower neuro-basiscranial complexes (NBCs) tend to have proportionately longer (antero-posteriorly) and narrower faces than individuals with wider NBCs is partially supported, but the trend is weak and is largely the result of variation between populations rather than within them (see Figure 7). In particular, Italian and Chinese individuals tend to have relatively high values for the facial index and a broad neurocranium, while Australian and, to a lesser extent, Ashanti individuals

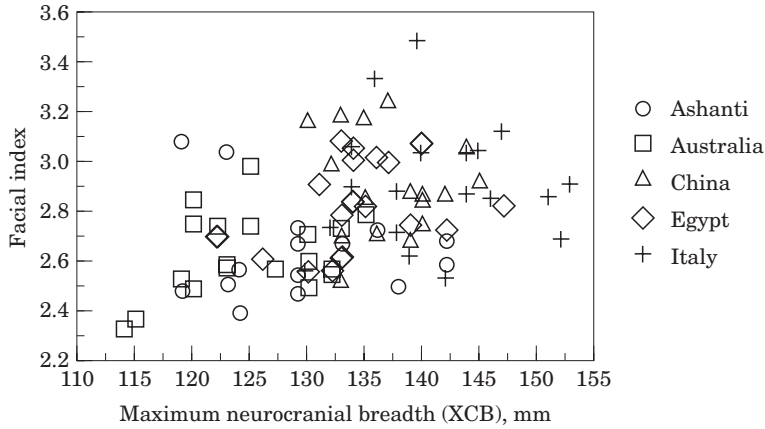


Figure 7. Bivariate scattergram of facial index (JUB/MFL) versus maximum NBC breadth (XCB) in recent modern human sample.

tend to have a low facial index and a narrow neurocranium. Variations in overall NBC shape (as expressed by the cranial index) account for approximately only 25% of the variation in the facial index, highlighting the high degree of variability of facial form in relation to cranial form between and, to a lesser extent, within, recent human populations that must be explained by other factors unrelated to the NBC.

Discussion

The above results support the hypothesis that certain dimensions of the cranial base, mostly bi-porionic breadth, do have some influence on the shape of the NBC, as noted by Howells (1969, 1973). In the adult cranium, variations in the breadth, length and flexion of the cranial base are independent of each other, and POB affects overall NBC shape to some extent by influencing the breadth of the neurocranium. However, the effects of POB on neurocranial shape mostly occur as the result of interactions with brain size, and the correlations between POB and most NBC dimensions (e.g., cranial vault length and height) are only moderate, indicating that other factors such as overall cranial size have substantial effects. In

addition, it is important to stress that variations in basicranial length and flexion appear to have no significant influence on most aspects of craniofacial shape independent of other factors. These results do not necessarily mean that CBA and CBL do not affect NBC shape, but their effects are apparently more regional. Lieberman (1998), for example, has shown that in ontogenetic samples of humans and chimpanzees the length of the sphenoid body affects the degree of facial projection relative to the anterior cranial fossa, which in turn affects on other aspects of cranial shape.

In addition, Weidenreich's (1941) and Enlow's (1990) hypotheses that facial shape is influenced by cranial base and neurocranial dimensions are only weakly supported. As the above results indicate, narrow-skulled individuals tend to have narrower faces than wider skulled individuals. In addition, narrow-faced (leptoprosopic) individuals tend to have antero-posteriorly longer faces relative to facial breadth than wide-faced (euryprosopic) individuals, but these correlations account for only about 25% of the variation in the facial index among adults. In other words, Enlow's (1990) prediction that individuals with absolutely and relatively narrower NBCs

should have proportionately longer (anteroposteriorly) and narrower faces than individuals with wider NBCs is only a tendency and not a strong relationship. These results, which suggest that most aspects of variation in facial shape are independent of NBC dimensions, should not be surprising given the very different ontogenetic trajectories of facial and NBC growth, and their contrasting modes of growth.

These results need to be tested further using ontogenetic samples from different populations, and using large samples from single populations. However, they confirm the tremendous amount of integration that occurs between the cranial base, the neurocranium and the face during growth (see also, Cheverud, 1982, 1996; Kohn *et al.*, 1993). Although it is tempting to consider the neurocranium and basicranium to be separate regions by virtue of their distinct embryological origins, their dimensions exhibit considerable intercorrelation in the adult skull largely because of the unifying capsular functional growth matrix of the brain. One consequence of these integrative processes is that there are few aspects of neurocranial shape which are independent of brain size and basicranial dimensions such as POB. The phylogenetic implications of these results are sobering because independence is one of the major criteria for characters in both phenetic and cladistic analyses (Sokal & Sneath, 1963; Shaffer *et al.*, 1991; Lieberman, 1999). Characters add phylogenetic information to an analysis only to the extent that they are independent of other characters; moreover, intercorrelated characters will tend to bias phylogenetic inferences incorrectly if they are homoplastic or otherwise poor indicators of ancestry and descent. Consequently, measurements of overall cranial shape and size are unlikely to be good characters for either cladistic or phenetic analyses because they result from processes of integration that are likely to obscure independent, heritable

units of information (Bookstein, 1994; Lieberman, 1999). For example, the above results indicate that variations in overall neurocranial form (dolichocephaly *vs.* brachycephaly) result in part from variations in basicranial breadth, but also derive from interactions with brain size and other factors that influence overall cranial size such as long-term adaptations to climate (Guglielmino-Matessi *et al.*, 1979; Beals *et al.*, 1984).

Following Cheverud (1996), it may be more sensible to identify characters for phylogenetic analysis that comprise several highly intercorrelated dimensions that may evolve together as integrated morphometric units. It is also possible that other basicranial characters may prove to be more useful for phylogenetic analysis, but most of these characters are likely to be local, specific features whose growth and morphology are largely independent of the effects of brain growth and other dominant functional matrices in the skull. As Cheverud (1982, 1996) has shown, the independence of such characters needs to be tested using techniques such as cluster analysis in order to examine the intensity of statistical associations among characters from functionally and developmentally interdependent sets. Defining and recognizing such characters is a challenge, however, given the prevalence of epigenetic influences on cranial growth. Consider, for example, just a few of the epigenetic stimuli that affect facial growth and integration. Intramembranous bone growth around the oropharynx and nasopharynx, which comprise much of the middle and lower portions of the face, are induced to a large extent by air-flow resistance (Linder-Aronson, 1979; Principato & Wolff, 1985; Franciscus & Trinkaus, 1988; Cooper, 1989; Warren *et al.*, 1992; Franciscus, 1995). In addition, mechanical strains from generating and resisting masticatory force influence lower and midfacial growth along a complex strain

gradient, with more dominant effects occurring in the mandible and zygomatic arches, and lesser effects occurring further away from the teeth or muscle attachment sites (e.g., Carlson & Van Gerven, 1977; Corruccini & Beecher, 1982; Kiliaridis *et al.*, 1986; Hylander, 1988; Hylander & Johnson, 1992; Herring, 1993; Bouvier & Hylander, 1997). Moreover, much of the early growth of the orbital cavity (which comprises parts of seven bones) is stimulated by expansion of the eyeballs, but the subsequent infero-lateral expansion of the orbital cavities is a consequence of other processes of facial growth (Enlow, 1990; Denis *et al.*, 1993).

Although this study does not directly test the hypothesis that cranial base dimensions, by virtue of their growth, are likely to be better sources of phylogenetic information than facial or neurocranial dimensions, these results do highlight the utility of considering how the pattern of correlations between the cranial base and the brain contribute to other important morphological variations. In particular, these data clearly indicate that the degree of posterior projection of the occipital bone (bunning) may to some extent be influenced by having a large brain on a relatively narrow cranial base. Posterior projection of the occipital lobe relative to the internal occipital protuberance and to lambda is more marked in large-brained, dolichocephalic individuals, as predicted by Trinkaus & LeMay (1982) and Lieberman (1995). However, these interactions do not explain the thickening of outer table that results in Grade 4 occipital buns among some robust early modern humans and the extreme Grade 5 buns in Neanderthals. These aspects of cranial vault thickness, common to all Pleistocene populations, have a different etiology, most probably a function of systemic cranial and/or skeletal bone growth (Lieberman, 1996). In addition, the above results tentatively indicate that occipital bunning in Neanderthals, who have wide

cranial bases relative to endocranial volume, must be accounted for by other factors perhaps related to the timing of brain growth relative to basicranial growth, and thus may not be entirely homologous with the morphology occasionally evident in anatomically modern *H. sapiens*. Caution on this last point is required, however, because the sample of early modern human analyzed herein does not include many of the specimens with the largest occipital buns (at least as viewed externally). Further testing of this hypothesis needs to include the early modern crania from the early Aurignacian site of Mladec, which resemble Neanderthals in having distinct occipital protuberances and wide cranial bases.

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