The ontogeny of *Pan troglodytes* craniofacial architectural relationships and implications for early hominids

Developmental constraints characterize functional growth boundaries of the mammalian face. Enlow and colleagues identified boundary conditions and planes of the midface in humans and other mammal species that are defined on the basis of important growth sites and the developmental disposition of neural and pharyngeal matrices. With few exceptions a conservative mammalian architecture is said to be achieved by the adult stage. Three aspects of this architecture are investigated here for a cross-sectional ontogenetic series of *Pan troglodytes* crania: (1) a line passing from the maxillary tuberosity through the junction of middle and anterior cranial fossae is perpendicular to the neutral horizontal axis of the orbit (PM-NHA angle), (2) an average 45° angle, whose origin is the external auditory meatus, separates the maxillary tuberosity from the midpoint of the orbital opening (meatus angle) and (3) the base of the brain, maxillary tuberosity and prosthion are on or close to the same plane (anterior maxillary hypoplasia).

This investigation considers to what extent samples of chimpanzees and early hominids reflect Enlow's characterization of mammalian craniofacial architecture. Evidence derived from the chimpanzee sample bears out the perpendicularity of the PM-NHA angle and a near 45° meatus angle (though slightly higher overall), but does not conform to the absence of marked anterior maxillary hypoplasia seen in other mammals. *Pan* is instead characterized by considerable ontogenetic variation (noted by Enlow amongst anthropoids) influenced to some extent by sex. Preliminary early hominid data on the meatus angle indicates that *Australopithecus* specimens are similar to the widespread and probably primitive condition, while *Paranthropus* and early *Homo* specimens portray an uncharacteristic mammalian architectural relationship.

*Journal of Human Evolution* (1992) 23, 235–251

Introduction

This study has two objectives: (1) to examine architectural features of the developing chimpanzee skull and (2) to examine these structural relationships among a select collection of Pliocene-Pleistocene hominid skulls. Enlow & Azuma (1975) observed a suite of architectural relationships, based on developmental criteria, for a variety of mature mammals. The ontogeny of these relationships has yet to be investigated for a given species. Should these relationships be maintained over the course of growth and development, then this may be a suitable demonstration of developmental constraints concerning hominoid facial growth. These data may then be employed for the understanding of fossil hominid taxa as well, particularly those for which we have some ontogenetic information (e.g., Bromage, 1989).

Background

Workers over the last half century have identified commonalities of mammalian craniofacial development and architecture that form the structural foundation of the mammalian skull. Thompson (1942) illustrated successive deformations of one form to another with his “Theory of Transformations” (a mathematical treatment of continuous transformations) using DeCartes “Methods of Coordinates”. His transformations of closely related species often illustrated divergent growth properties of their skulls, but Thompson was also able to...
accomplish global transformations of mammalian skulls which led him to state that “... there is something, an essential and indispensable something, which is common to them all, something which is the subject of all our transformations, and remains invariant ...” (1942:1085).

Heintz (1966), operating under another mensurational tradition, similarly noted divergent ontogenetic trajectories of certain craniofacial dimensions amongst primate families and genera. She found, nevertheless, that *Australopithecus*, the apes and humans followed common ontogenetic trajectories of basion–prosthion (BA–PR) against nasion–prosthion (NA–PR) length (her Graphique 55), NA–PR dimensions against upper facial length (BA–NA) (Graphique 57), as well as an angular measure of prognathism (Graphique 91), demonstrating a correspondence between increasing facial projection and height (Heintz, 1966).

Delattre & Fenart (1960) oriented skulls according to the horizontal vestibular axis and likewise showed that the ontogeny of the facial skeleton in the chimpanzee, gorilla and humans followed the same general pattern of down and forward growth. Swindler et al. (1973) illustrate isometry of the upper and lower facial elongation for both *Papio* and *Macaca*, and Sirianni & Newell-Morris (1980) also note a common fetal craniofacial growth pattern and ossification sequence in humans and macaques.

Between the 1960s and the 1980s, Enlow and co-workers explicitly combined histological interpretations of human facial bone growth remodeling with serial radiographic data in order to promote a new cephalometric system. A cephalometric system determined by *actual* sites of growth would, by definition, portray the underlying and developmentally constrained architectural features of the mammalian skull, as observed by the orderliness of skull ontogeny and the overwhelming similarity of facial growth across primates and other mammals. Enlow (1966) noted that “apparent” growth measured using conventional cephalometric methods was apparent simply because the comparison of serial cephalographs was based on registering the skull on fixed points. Although Enlow acknowledged the value of such analyses in providing data on overall growth pattern, he superimposed serial cephalographs in such a way that they would correspond to known growth and remodeling sites, permitting “actual” growth to be visualized as well (1966). Enlow (1968) and Enlow & Hunter (1968) championed this new system and outlined a series of anatomical parts and counterparts which could be evaluated on the basis of growth equivalents and growth compensations between them. Such an analysis, for instance, would assess the correspondence between the horizontal dimensions of an individual's maxillary (part) and mandibular (counterpart) dental arches. Facial growth was characterized by Enlow and colleagues in cephalometric applications which demonstrated a correlation between horizontal equivalents and vertical equivalents responsible for the stability and balance of craniofacial relationships.

Enlarging on this approach, Enlow et al. (1969, 1971a,b), Enlow & Moyers (1971) and Enlow (1974) described a number of points and planes on lateral cephalographs corresponding to architectural units conforming to sites of growth, remodeling and displacement. A procedure was developed to explain *how* a pattern was produced as opposed to systems of cephalometric evaluation which explained *what* craniofacial pattern resulted due to growth. Bhat & Enlow (1985:270–272) subsequently noted that the part–counterpart procedure was more sensitive than traditional cephalometric methods in studies of cranial base relations to craniofacial variability because “an angular value such as basion-sella-nasion is based on midline points, none of which are involved in the actual articular fitting of basicranium,
maxilla, and mandible to each other, or in the anatomic basis of bilateral positioning among the respective parts; nor do they represent growth sites directly participating in this three-part relationship”.

In 1975, Enlow & Azuma investigated the prevalence of certain architectural relationships among a diversity of mammalian skulls. Their comparative sample included lateral radiographs of 116 human subjects of at least 10 years of age and 45 mammal species represented by rodents, lagomorphs, artiodactyls, carnivores and non-human primates. These authors defined several architectural relationships that depend on important growth sites and the developmental disposition of neural and pharyngeal matrices as follows (see Figure 1): (1) a line passing from the maxillary tuberosity (MT) through the junction of middle and anterior cranial fossae is close to perpendicular to the Neutral horizontal axis (NHA) of the orbit, (2) the base of the brain, maxillary tuberosity and prosthion (P) are on or close to the same plane and (3) an average 45° angle, whose origin is the external auditory meatus (EAM), separates the maxillary tuberosity from the midpoint of the orbital opening. These relationships were found to hold for mammals in general. Members of the Anthropoidea, however, were found by Enlow & Azuma (1975) to exhibit a characteristic vertical hypoplasia of the anterior maxilla, meaning that prosthion lay significantly above the inferior brain-to-maxilla plane (IBMP). Thus, while these structural features appear to be developmentally constrained for many mammals, anthropoids were found to depart from a broadly primitive mammalian condition in maxillary development.

An operational definition for developmental constraint is provided by Smith et al. (1985: 265) as “... a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system”. The reference planes and angles investigated by Enlow & Azuma (1975), and investigated here concerning the ontogeny of the chimpanzee craniofacial region, characterize craniofacial relations. These relations between the brain and facial growth vectors determine the size and disposition of the mammalian facial complex and the space available for the pharyngeal contents. Here, developmental constraints over the maintenance of these relations among various mammals are considered homologous—a concept in accordance with De Beer (1937), who emphasized that the issue of homology rested in the preserved morphological “relations” between parts of the skull.

Architectural relations

This study addresses architectural relations in an ontogenetic series, albeit a cross-sectional one. This makes the study particularly relevant to the question of developmental constraint and can add to the empirical foundation established previously on more mature individuals (i.e., Enlow & Azuma, 1975). The brief review (below) of three architectural relationships studied here should serve as a demonstration that concepts of craniofacial growth are well served by methods that include known functional-structural units and key sites of growth in the overall methodological approach. The following investigation of the chimpanzee is based on lateral cephalograms using the development-dependent cephalometric system described by Enlow & Azuma (1975). Figure 1 portrays the architectural relations (landmarks, planes and axes) investigated here.

(1) The posterior maxillary (PM) plane (Figure 1), or boundary, described by Enlow & Azuma (1975), is a natural anatomical interface between the neurocranium and the face and, hence, helps to establish facial growth vectors. (See also descriptions of landmarks, planes and axes below.) Along the top of this boundary, the ethmomaxillary complex and
Figure 1. Orbital midpoint (OM) is between the superior and inferior orbital rims. Orbital apex (OA) is between the superior rims of the superior orbital fissure and the inferior rims of the optic canals. Neutral horizontal axis (NHA) is a plane formed through the OM and the posterior cone-shaped apex of the orbit (OM–OA). Middle-anterior cranial fossae (MACF) is the junction between the middle and anterior cranial fossae. Maxillary tuberosity (MT) is the posterior–inferior point on the MT. Posterior maxillary (PM) plane is formed through the junction between the MACF and the MT. Posterior maxillary plane–neutral horizontal axis angle (PM–NHA) is the angle constructed between the PM and NHA planes. External auditory meatus (EAM) is the central point within the auditory opening. Meatus angle (MA) is formed between the OM, to the EAM, to the MT. Inferior brain (IB) is the inferior-most extent of the brain. Inferior brain-to-maxilla plane (IBMP) is a plane constructed between the IB point and the MT. Prosthion (P) is the most anteroinferior point on alveolar bone between the central incisors. Anterior maxillary hypoplasia (AMH) is the vertical height difference between the IBMP and P.

anterior cranial fossa are separated from the pharyngeal space and the middle cranial fossa. Below, the posterior maxillary boundary intersects the maxillary tuberosity separating the jaws from the pharyngeal space. This boundary relates to important sites of growth and bony remodeling: the expanding neurocranium and anterior remodeling of the pterygoid–maxillary tuberosity region. Thus, the posterior maxillary plane translates anteriorly during growth and is structurally related to the neutral horizontal axis (NHA) of the orbit normally disposed at 90° to each other. This relationship is maintained throughout growth and developmentally constrained among mammals in general.

(2) The alignment of the orbits and the jaws with respect to the external auditory meatus is similarly constrained during growth. The angle originating from the external auditory meatus, to the orbital midpoint (OM) on the one hand, and the maxillary tuberosity on the other, approximates 45° (meatus angle, Figure 1). This suggests that ontogenetic trajectories of the orbit and jaws are isometric and patterned so that the feeding, sight and auditory functions are optimally positioned together. An alternative, or additional, explanation for this relationship may relate to head balance during locomotory behavior (cf. Bramble, 1990).
(3) Enlow & Azuma (1975) also noted that the base of the brain, maxillary tuberosity and prosthion are on or close to the same plane for most mammals (inferior brain-to-maxilla plane, Figure 1). The inferior extent of brain growth marks the inferior limit to which both prosthion and maxillary tuberosity descend during growth. It was noted, however, that anthropoids typically exhibit a vertical hypoplasia of the anterior maxilla so that prosthion is positioned above the inferior brain-to-maxilla plane. Whether this is due to a repositioning of maxillary tuberosity downward or is an actual result of diminished downward remodeling of prosthion, has yet to be determined.

Materials and methods

Chimpanzee specimens
A cross-sectional ontogenetic series of 45 wild-shot *Pan troglodytes* crania, housed at the American Museum of Natural History and the Cleveland Museum of Natural History, were investigated. Specimens were mounted in Frankfurt Horizontal on a Todd Craniostat which rested on a central stage calibrated in degrees. Each specimen was radiographed according to standard cephalometric convention for both lateral (0°) and posterior-anterior (90°) views.

These specimens were divided between three age groups (Table 1) on the basis of the eruption status of the permanent molars. This was done because of the significant contribution to palatal lengthening by the formation and eruption of permanent molars and the resulting translational and transformational movements of landmarks, planes and axes studied here. Group 1 consists of individuals prior to eruption of maxillary first permanent molars and includes as its youngest member an individual with maxillary second deciduous molars still in their crypts. Group 2 consists of juveniles prior to eruption of maxillary second permanent molars. Group 3 consists of older juveniles prior to eruption of maxillary third molars.

The architectural points relevant to the relationships identified by Enlow & Azuma (1975) and investigated here were traced onto acetate sheets and were measured to the nearest millimeter or degree (Figure 1). The superimposition of bilateral features, being less than precise on lateral cephalograms, meant tracing both features and rendering a central tracing between them, herein referred to as “averaged”, from which measures were taken.

Cephalometric landmarks, planes and axes (Figure 1)

**Orbital midpoint (OM).** Superior and inferior orbital rims were traced from the lateral radiograph, they were averaged and the maximum vertical height of the orbital opening was obtained and checked with the posterior–anterior view. This measurement was divided in half and the midpoint registered on the lateral tracing.

**Orbital apex (OA).** The superior rims of the superior orbital fissure and the inferior rims of the optic canals were traced from the lateral radiograph. The distance between the rims was measured along their posterior aspects confluent with the anterior bulge of middle cranial fossa (which is just near the apex), the measurement was halved and the midpoint was registered on the lateral tracing.

**Neutral horizontal axis (NHA).** This plane was formed through the orbital midpoint and the posterior cone-shaped apex of the orbit (OM–OA).
## Table 1  *Pan* craniofacial architecture by dental age categories

<table>
<thead>
<tr>
<th>Specimen no.</th>
<th>Group 1: dm2-M1 in crypts</th>
<th>Group 2: M2 in crypts</th>
<th>Group 3: M3 in crypts</th>
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<tr>
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<td>Meatus angle</td>
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<td>3-38</td>
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<tr>
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<tr>
<td>Grand mean</td>
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<td>46-72</td>
<td>10-73</td>
</tr>
</tbody>
</table>

Listed are specimen numbers, posterior maxillary–neutral horizontal axis (PM–NHA) angle, the meatus angle and the degree of anterior maxillary hypoplasia (AMH) (see text for details). Individual specimens are listed in ascending order of PM–NHA angles within dental age categories. M and F specimen numbers denote male and female individuals, respectively. Students' t-tests were performed to test for significant differences from 90° (PM–NHA column), 45° (meatus column) and no hypoplasia (0-0 mm) (AMH column) within dental age categories.

*P* < 0.05 significance level, **P** < 0.01 significance level; ns, not significant.
Middle-anterior cranial fossae (MACF). The junction between the middle and anterior cranial fossae was defined as the anterior-most extent of the middle cranial fossa determined by the first contact made by a line pivoted on and swung from the maxillary tuberosity. This was basically the same as the anterior-most extent defined in relation to the skull held in the Frankfurt Horizontal.

Maxillary tuberosity (MT). The posterior–inferior point on the MT was defined as a tangent to the tuberosity parallel to a line drawn between the alveolar bone behind the last tooth to erupt and the contact between the tuberosity and the palatine bone.

Posterior maxillary (PM) plane. The PM plane was formed through the junction between the MACF and the MT.

Posterior maxillary plane–neutral horizontal axis angle (PM–NHA). This angle is constructed between the PM and NHA planes and enclosing the facial pocket.

External auditory meatus (EAM). Vertical and horizontal midpoints of the external auditory meati were averaged between left and right sides and the calculated point registered on the lateral tracing.

Meatus angle (MA). The MA was formed from the OM, to the EAM, to the MT.

Inferior brain (IB). The inferior-most extent of the brain was defined by the first contact with the cranial cavity by a line pivoted on and swung from the MT (through the occipital bone).

Inferior brain-to-maxilla plane (IBMP). This plane was defined as a result of defining the IB point from the MT.

Prosthion (P). Prosthion was defined as the most anteroinferior point on alveolar bone between the central incisors.

Anterior maxillary hypoplasia (AMH). The vertical height difference between the IBMP and P, taken parallel to the PM plane, was drawn and measured on the lateral tracing.

Early hominid specimens
Natural size camera lucida lateral tracings were made from casts of crania representing the following Plio–Pleistocene hominid species: the Australopithecus afarensis reconstruction by Kimbel & White (1988), A. africanus represented by Sts 5 and Sts 71, A. aethiopicus represented by KNM-WT 17000, Paranthropus boisei represented by KNM-ER 406, early Homo represented by KNM-ER 1470 and KNM-ER 1813 and African Homo erectus represented by KNM-ER 3733.

These specimens represent the most complete and undistorted adult Plio–Pleistocene hominid crania that preserve the relevant anatomy of interest. KNM-ER 3733 required only slight reconstruction of the MT behind the missing third molar. KNM-ER 1470 required positioning of the face to the braincase as outlined by Bromage (in prep.). The position of the KNM-ER 1470 MT was established according to the architectural relationships outlined by Enlow & Azuma (1975) and examined in this study (the resulting craniofacial architecture—
as regards the hafting of the facial skeleton onto the braincase and the position of P—is similar to other prognathic early hominids). Other South African *Paranthropus* crania were not investigated at this time because of evident distortion. OH 5 is not included here since the specimen lacks any true bony contact between the face and cranium.

The MA was drawn onto the lateral tracing and measured in degrees. The IBMP was approximated and drawn onto the lateral tracing, but no measurement of AMH was attempted, leaving this to qualitative assessment. Determinations of PM–NHA angles were not formally attempted at this time except for KNM-ER 1470 (90°) where this was an integral part of the reconstruction procedure (Bromage, in prep.). (A first order attempt to provide PM–NHA angles for the other early hominid specimens, based upon observations of a large whole-skull comparative chimpanzee series housed at the American Museum of Natural History, resulted in values entirely within the range of values obtained from radiographs of Group 3 chimpanzees described below.)

### Results

Three measurements, PM–NHA angle, MA and AMH distance were tabulated for the chimpanzee sample. Table 1 lists them according to the three major dental age groupings described above. It is evident from these data that mean PM–NHA angles are very near to 90° in all groups, though there are cases 5 or 6° above and below the mean within each group and 9 and 10° below in Group 3 (Table 1; Figure 2). Tests found no significant differences between PH–NHA group means from 90° (Group 1: mean = 89.22°, t = 0.69 N.S.; Group 2: mean = 90.50°, t = 0.65 N.S.; Group 3: mean = 88.20°, t = 2.01 N.S.; see Table 1). Seventy one percent of the study sample is within ±3°.

Mean meatus angles, however, do depart from 45° within dental age groups. The hypothesis that mean MAs do not depart significantly from 45° was rejected for all groups (Group 1: mean = 42.89°, t = 2.56*; Group 2: mean = 46.73°, t = 3.42**; Group 3: mean = 48.60°, t = 6.38**; see Table 1). Sixty seven percent of the study sample is within ±3°. While the Group 1 mean is less than 45°, Groups 2 and 3 are higher, resulting in a grand mean of 46.72°, not significantly different from 45° (t = 1.5187 N.S.). However, tests comparing Group means rejected the hypothesis of equal angles (Groups 1 & 2: t = 4.21**; Groups 1 & 3: t = 4.31**; Groups 2 & 3: t = 4.85**).
Figure 3. Individual specimens are listed in ascending order of PM–NHA angle within dental age categories (see Table 1). Meatus angles (top) are plotted with degree of AMH, illustrating generally higher AMH values in the later age group.

Table 2

<table>
<thead>
<tr>
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<th>PM–NHA angle</th>
<th>Meatus angle</th>
<th>AMH distance</th>
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<td>-</td>
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<tr>
<td>AMH distance</td>
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</table>

Simple correlations (above) are given between craniofacial measurements. Partial correlations are given parenthetically below, controlling for the third variable.

*Significant difference from zero at \( P < 0.05 \).

\( t = 5.68**; \text{Groups 2 \\& 3: } t = 2.37** \) suggesting that there is indeed a small increase in mean MA with age.

Figure 3 graphically portrays the increase in Group 3 AMH values, together with an increased range, above those of Groups 1 and 2 (see also Group 3 statistics, Table 1). Tests found no significant difference of AMH group means from 0.0 mm for Group 1 (Group 1: mean = 2.22 mm, \( t = 1.97 \text{ N.S.} \) but rejected this hypothesis for Groups 2 and 3 (Group 2: mean = 4.31 mm, \( t = 3.69** \); Group 3: mean = 20.45 mm, \( t = 10.47** \); see Table 1).

For any one group of individuals with the same PM–NHA angle there is a range of MA values to the extent that a correlation coefficient of 0.0 exists between these two variables (Table 2). When AMH data are investigated, one also finds low and high values within PM–NHA angle groups, though when assessing the correlation between these variables as PM–NHA angle increases, there is a tendency (however unimpressive) for a reduction in AMH values (Table 2).
An examination of the AMH data in relation to MAs within PM–NHA angle groups reveals that in some cases as MAs rise so also do AMH values, while the reverse is true for other individual cases (see also Figure 3). Overall, the simple correlation between AMH and MA is positive (0.50) and improved slightly by partial correlation between AMH and MA, with the effect of PM–NHA being held constant (0.53) (Table 2).

Table 3 summarizes the architectural data by sex categories. There are 10 specimens in the study sample having field identifications of sex (see Table 1) and it transpires that four of five females have increasing AMH values (≥15 mm) with increasing MAs (>47°) when compared to other individuals with the same PM–NHA angle, while four of five males have relatively low AMH values (<9 mm) with variably low or high MAs (38–53°) when compared to other individuals with the same PM–NHA angle. The hypothesis that male and female mean PM–NHA angles depart from 90° was rejected (male mean = 89.80°, t=0.13 N.S.; female mean = 87.25°, t=0.60 N.S.) as was also the hypothesis that male and female mean MAs depart from 45° (male mean = 43-60°, t=0.24 N.S.; female mean = 50-50°, t=2.18 N.S.—the latter significant only at the 10% level). However, while AMH distance means do not depart significantly from 0.0 mm (male mean = 6.40 mm, t=1.01 N.S.), female AMH distance means are significantly different (female mean = 28.50 mm, t=3.34*). Test comparing male and female group means suggest that PM–NHA angles are not significantly different (t=1.30 N.S.) but reject the hypothesis of equal MAs (t=2.38*) and equal AMH distance (t=4.17**) between the sexes.

Figure 4 portrays distinctive male and female ontogenetic paths for landmarks anterior to the EAM; there is a general ventral placement of female OA, OM, P and MT points relative to those of males. Vertical lines beneath P points on Figure 4 are the amounts of AMH in mm (Table 3).

The results for the early hominid sample—MA and IBMP—are provided together with the lateral tracings in Figure 5. All *Australopithecus* specimens except Sts 71 illustrate MAs well within the range, indeed close to the mean, for chimpanzees (Table 1), humans and other mammals (Enlow & Azuma, 1975). One can question the propriety of accepting a result based on a major reconstruction, as in the case of the *A. afarensis* cranium. However, given compelling morphological evidence for its primitiveness (Kimbel et al., 1984), its architectural similarity to *A. africanus* specimen Sts 5 (Figure 5), as well as its architectural similarity (Figure 5) and numerous primitive features shared with *A. aethiopicus* specimen KNM-WT 17000 (Kimbel et al., 1988), there is every indication that the reconstruction is accurate.

*Australopithecus africanus* specimen Sts 71, *Paranthropus* and early *Homo* specimens have MAs at the extreme high end of the chimpanzee range (Table 1) and beyond the range of modern humans and other mammals (Enlow & Azuma, 1975). *Homo erectus* specimen KNM-ER 3733 has an MA of 66°, which is beyond the known range of any mammal.

**Discussion**

The results of the present study on an ontogenetic series of chimpanzee crania are more or less consistent with those of Enlow & Azuma (1975) concerning humans and a variety of other mammals. Most individuals are within a few degrees (plus or minus) of the perpendicular for PM–NHA angle. Had this angle, for instance, illustrated a tendency to increase with age and, presumably, size, then one could question that this is a structural feature exhibiting developmental constraint. One finds, instead, a similar range of values in each juvenile age
Figure 4. Architectural points for 10 individuals of known sex (see Table 3): male specimens (V) 5, 6, 8, 34 and 35; female specimens (A) 13, 28, 31, 38 and 42. IB point is base of brain for all individuals. Middle-anterior cranial fossae points are represented here as the vertical curvilinear distance of the orbital apex (OA) confluent with the superimposed anterior limit of the middle cranial fossa. The OA would be halfway along this curve and slightly behind. Vertical lines beneath P points are the amounts of AMH in mm. Note the inferiorward placement of female architectural points anterior to EAM (MACF, OM, P and MT points) while registering on base of brain and keeping the PM planes parallel.

Table 3  *Pan* craniofacial architecture by sex categories

<table>
<thead>
<tr>
<th></th>
<th>PM–NHA angle</th>
<th>Meatus angle</th>
<th>AMH distance</th>
<th>PM–NHA angle</th>
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</table>

Listed are specimen numbers, posterior maxillary–neutral horizontal axis (PM–NHA) angle, the meatus angle and the degree of anterior maxillary hypoplasia (AMH) (see text for details). Students t-tests were performed to test for significant differences from 90° (PM–NHA column), 45° (meatus column) and no hypoplasia (0-0 mm) (AMH column) within dental age categories.

*P < 0.05 significance level; ns, not significant.
Figure 5. Early hominid specimens with calculated MAs (in degrees) and an estimated IBMP drawn so as to interpret relative AMH (see text for description). Alternative positions of the KNM-ER 1470 P and MT points have been indicated taking into account the range of chimpanzee PM-NHA angles (see text) in the less prognathic direction only. A chimpanzee at bottom (with a relatively high MA) has been provided for comparison.
46.7° includes 45°). Furthermore, while there is extensive overlap in MAs between age groups, the mean angle does tend to increase with age. The data support the notion that while PM–NHA angles remain relatively stable during growth, increases in posterior facial height (the height of the PM boundary) and hence, the descent of MT, slightly outpace the forward horizontal repositioning of the tuberosity, resulting in greater MAs.

Enlow & Azuma (1975) noted that anthropoids exhibited a characteristic vertical hypoplasia of the anterior maxilla with P lying significantly above the IBMP. This may be due either to a vertical hyperplasia of posterior facial height (cf. Enlow et al., 1971b) or to a true underdevelopment of the anterior maxilla downward. Age Groups 1 and 2 illustrate a low but variable amount of vertical hypoplasia, while Group 3 exhibits an increase in the mean AMH value (Table 1, Figure 3). It was expected that AMH would increase with increasing MAs insofar as MA is a reflection of posterior facial height. Indeed, for most PM–NHA angle groups of 90° and less (except the 88° group), it appears that while MAs increase, AMH values also tend to increase. Indeed, a modest relationship is borne out with the simple correlation (r = 0.50) between AMH and MA (Table 2) (the partial correlation between AMH and MA, controlling for PM–NHA, is 0.53). While the 92, 93 and 95 PM–NHA degree angle groups also suggest the same relationship, there exists a single individual in each group at the highest MA which has a low AMH value.

In an attempt to understand the sex differences in AMH described in the Results (Table 3), radiographs of specimens of known sex were superimposed to compare directly the amount of hypoplasia while simultaneously portraying the generalized down and forward facial growth vector of the face. Evidence from ontogenetic studies of the brain and cranial base indicate that the occipital–cerebellar portions of the cranial base complete more of their growth earlier than other parts of the brain (cf. Dean, 1988) and indeed, registering on IB while keeping PM boundaries of individual specimens parallel resulted in the portrayal of the anteroinferior facial growth vector (Figure 4). Minimal scatter of EAM points, with no apparent directionality, confirmed the precocity of this portion of the cranial base relative to any other registration. This registration had the added advantage of maintaining the parallel growth transgression of the PM boundary.

The most striking feature of Figure 4 is the separation of male and female ontogenetic growth trajectories which are evident prior to eruption of the second permanent molar. Indeed, it appears that these male and female trajectories are already established prior to completion of the deciduous dentition (the smallest inner circle of points representing a male with second deciduous molars still in their crypts: Figure 4, specimen 5). The impression from these lateral tracings is that males have a more steeply inclined posterior cranial base (this remains true even should the upward vertical displacement of all male points be due to a lower base of brain—the architectural point used for registration on Figure 4). This might otherwise constrict the horizontal dimension available for the pharyngeal space which would instead be recompensed by a further anteroinward remodeling shift of MT compared to females. Furthermore, it appears that the PM boundary is indeed longer in Group 3 females compared to their male counterparts (Figure 4), resulting in a net increase in posterior maxillary hyperplasia. This may account for the consistently high AMH values compared to males (represented as vertical lines beneath P points, Figure 4; Table 3). These patterns within sex groups suggest, at least, that some developmentally constrained architectural difference characterizes male and female chimpanzees from an early age.

A discussion of the early hominid material is complicated by a host of unforgiving sources of variation that include individual differences, differences due to sex (as described above),
variation over time within and between lineages, geographic differences as well as the problem of incompleteness and deformation of the material. This is an admission, after all that has been said and observed for the early hominid sample (above), that some architectural constraints such as the MA are not as “constrained”—or constrained in the same way—as thought before. The *A. afarensis* reconstruction, *A. africanus* specimen Sts 5 and *A. aethiopicus* specimen KNM-WT 17000 conform to the architectural principles common to the chimpanzee: MAs in the 46–47° range and pronounced AMH. The *A. africanus* specimen Sts 71, *Paranthropus boisei* specimen KNM-ER 406 and early *Homo* specimens KNM-ER 1470 and KNM-ER 1813 have values at the extreme high end of the chimpanzee range: MAs in the 52–53° range and apparently less pronounced AMH (except perhaps for KNM-ER 1470). As for the African *H. erectus* specimen KNM-ER 3733, unless we are to posit an enormous range of variation or the likelihood of a craniofacial aberration, one is left to hypothesize the existence of increased MAs (e.g., 66° in KNM-ER 3733) in this taxon. Even allowing for some repositioning of the KNM-ER 3733 face and a requisite increased prognathism of the reconstruction, it is not likely that this MA would diminish by more than 5°. We are left with a craniofacial architecture not observed for any other early hominid, modern human or mammal.

Whatever the factors are that control MA variation—and we know that posterior facial height is one of them—it seems that they effected a definite increase for *Paranthropus*, early *Homo* specimens and African *H. erectus* (e.g., KNM-ER 3733) in the study sample (Figure 5). Because of the limited study sample it must be acknowledged that it remains to be seen whether a more comprehensive study and new discoveries of early hominid crania may sustain this accounting of the data. Meanwhile it may be hypothesized that something extraordinary happened with MA temporal variation, something related perhaps to a changing laryngeal and pharyngeal relationship. Presumably, evolutionary forces stabilized this new relationship and the MA returned to the mammalian condition as seen in modern *Homo*.

Should there be any significance to the uniformly high MA values for Sts 71, KNM-ER 406, KNM-ER 1470 and KNM-ER 1813, though 52–53° was close to the mean for their taxa, then it might be to unite features of *Paranthropus* and early *Homo* morphotypes (it is important here to note that Sts 71 is sometimes cited in respect to a *Paranthropus* morphotype—e.g., Clarke, 1988). A persistent theme in paleoanthropology has been the identification of many morphological (e.g., Dean & Wood, 1981, 1982; Kimbel et al., 1984; Dean, 1986; Skelton et al., 1986; Tobias, 1988) and ontogenetic (Bromage, 1989) similarities between *Paranthropus* and *Homo*—most of which have been interpreted as homoplasies. Here we may wish to add an architectural feature—the MA—for these Late Pliocene–Early Pleistocene fossils.

The list of so-called homoplasies that one may draw up from studies of *Paranthropus* and early *Homo* (e.g., Bromage, 1989; Dean, 1986; Dean & Wood, 1981, 1982; Kimbel et al., 1984; Skelton et al., 1986; Tobias, 1988) is long and is provoking reappraisal (e.g., Tobias, 1988). Given the preliminary architectural data presented here it may be relevant to hypothesize that the similarity in architectural relations between *Paranthropus* and early *Homo* is a departure from a primitive architectural program [i.e., like that observed for *A. afarensis* (reconstruction) and *A. africanus* (e.g., Sts 5)] and derived from a common ancestor.

The very high MA of KNM-ER 3733 suggests that the resumption of a near 45° MA in modern *Homo* is relatively recent. If one accepts that this individual was typical of African *H. erectus* and, furthermore, that this specimen is a representative of the lineage leading to modern *Homo*, then either the range of variation has diminished considerably to the present
time or the modern human condition is secondarily derived, returning to the mammalian condition.

The structural relationships (as presented here) and the morphology of some specimens of South African *A. africanus* (here represented by Sts 71) are akin to the *Paranthropus* morphotype and should perhaps take another taxonomic nomen [Clarke's (1988) "Hominid B"). The alternative to taxonomic splitting of Sterkfontein australopithecines is to include the variation between, for instance, Sts 5 and Sts 71 within one quite variable *A. africanus*. Both alternatives admittedly highlight quintessential problems in species recognition.

Another specimen from East Africa, contemporary with the South African australopithecines, *A. aethiopicus* (KNM-WT 17000), clearly has the stamp of early australopithecine structural relationships (*A. afarensis* reconstruction; Sts 5) and craniofacial similarities to both *A. afarensis* and *Paranthropus* (e.g., Walker et al., 1986; Kimbel et al., 1988). It may transpire that whatever we find, wherever we find it, that fossils of this age (c. 2.5 m.y.a.) may show a mixture of *Australopithecus* and *Paranthropus*—primitive and advanced—features. Remembering that *Paranthropus* illustrates some features that also characterize early *Homo*, we have a basis for interpreting or hypothesizing, at least in general, a common ancestral heritage for subsequently distinct *Paranthropus* and *Homo* grades of evolution.

**Summary and conclusions**

Data presented here for *Pan troglodytes* on developmental boundaries and relationships between the face and brain, and between the sensing organs and the jaws, are comparable to those data for humans and other mammals (Enlow & Azuma, 1975). However, the hypoplastic nature of the chimpanzee anterior maxilla clearly emphasizes Enlow & Azuma's (1975) earlier observation that anthropoids exhibit specific deviations from the mammalian architectural condition. While it is likely that with more data one would find much more overlap between the sexes, the data presented here do bear out fundamental architectural differences between the sexes that are evident prior to completion of the deciduous dentition. These deviations and sex differences make the study of the ontogeny and evolution of craniofacial architectural constraints all the more interesting and important for primate evolutionary studies.

Furthermore, the data on modern humans (Enlow & Azuma, 1975) and chimpanzees may not serve as appropriate models on which to assess variation in architectural relationships over human evolutionary time. While modern human and chimpanzee craniofacial architectural relationships are to some extent similar to other mammals studied (cf. Enlow & Azuma, 1975), one of the most interesting transformations of early hominid evolution may have been the increased MA of *Paranthropus* and early *Homo*, both departing from the primitive mammalian architecture.

While the early hominid data presented here are limited by relative incompleteness of the fossil record, their interpretation can be considered as new hypotheses to be tested with the recovery of more relatively complete early hominid craniofacial skeletons. For instance, one intriguing possibility is that the developmental pattern responsible for the architectural modification of *Paranthropus* and early *Homo* craniofacial complexes was shared in a common ancestor. *Australopithecus africanus* specimens, such as Sts 71, and *A. aethiopicus* specimen KNM-WT 17000, that portray a mixture of *Australopithecus* and *Paranthropus* characters, may provide us with glimpses of this heritage.
Acknowledgements

I thank Don Enlow, Fred Szalay, B. Holly Smith and two anonymous reviewers for the depth of their interest and their valuable comments. Don Johanson and Bill Kimbel (then of Cleveland Museum of Natural History) and Guy Musser (American Museum of Natural History) kindly provided the chimpanzee crania for study and Rolph Berhents made it possible to radiograph the specimens. The L.S.B. Leakey Foundation and Foundation for Research into the Origins of Man sponsored the data collection. James Panteleon rendered his artistic talents on the early hominid cranial specimens (Figure 5). I am grateful to Matt Ravosa and Anne Gomez for their invitation to present this paper on behalf of the symposium “Ontogenetic Perspectives on Primate Evolutionary Biology”.

References

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