

Line of Sight in Hominoids

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Objectives: It remains unclear how the realignments of the face and basicranium that characterize humans were acquired, both phylogenetically and ontogenetically. The developmentally constrained nature of the skull has been previously demonstrated in other primates using Donald H. Enlow's mammalian craniofacial architectural relationships. Here, we compare crania of our closest relatives to gain greater understanding of how and why the relationship of the face and cranial base is developmentally constrained in order to inform instances of abnormal growth and clinical intervention. **Study design:** A method for evaluating these fundamental architectural relationships using 3D landmark data was developed, thereby taking overall size and the geometric relationships among points into account. A sample of cone-beam computed tomography scans derived from humans and extant apes were analyzed ($n=10$ and $n=6$, respectively), as well as fossil hominid crania ($n=7$). Landmarks for 23 craniofacial architectural points were identified and recorded. **Results and Conclusions:** Principal components analyses reveal that despite the similarities in craniofacial architecture between humans, extant apes and fossil hominids, appreciable trends in variation between the extant species suggest that the repositioning of the foramen magnum was only one of a constellation of traits that realigned the basicranium and face during the transition to bipedalism.

Key words: craniofacial architecture, geometric morphometrics, hominoids, line of sight

INTRODUCTION

A fundamental shift in the organization of the craniofacial complex has occurred during hominin evolution, including flexion of the basicranium, anterior movement of the occipital condyles, reorientation of the orbits, and the reduction of the anterior midface (see, for example¹). However, these shifts are often studied as isolated variables in a dimensionally limited perspective, and we are still attempting to understand how these characteristics were assembled as a mosaic, both phylogenetically and ontogenetically. Therefore, 3D landmark-based data examining the spatial and geometric relationships of the craniofacial region across related taxa will help shed light on the evolution of this area's morphology, ultimately aiding in the implementation of better clinical intervention and practice.

In comparison to extant apes, flexion of the hominin basicranium, combined with the reduction of the maxilla and mandible results in the mid- and lower face being positioned "under" the orbits in humans such that the face is situated below the frontal lobes of the brain². However, despite these realignments in the hominin lineage, some mammalian characteristics are developmentally constrained and thus conserved in humans. These include the ca. 90° relationship of the posterior maxillary (PM) plane to the neutral horizontal axis (NHA) and the 45° relationship of the meatus angle (MA; the angle formed between the mid-orbit, external auditory meatus and the maxillary tuberosity)³. Enlow and Azuma were specifically interested in the study of these landmarks and the planar and angular relationships between them because they represent key sites of growth in the human cranium³.

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In an investigation of these landmarks in two-dimensional projections of *Pan troglodytes* crania acquired from lateral cephalograms, Bromage⁴ found that the PM-NHA and MA angles reflected the values determined by Enlow's characterization of mammalian craniofacial architecture, and that the magnitude of these angles remained relatively stable throughout ontogeny, indicating their developmentally constrained nature. Subsequent studies have corroborated the ca. 90° relationship of the PM-NHA angle in humans⁵, as well as the interspecific and ontogenetic consistency of the angular relationship between a modified version of the PM plane and the orbital plane, the latter of which runs from the superior to inferior orbital margin⁶⁻⁸. Therefore, since the basicranium flexes through hominin evolution, but the Enlowian craniofacial relationships remain stable, these represent key sites and spatial relationships for understanding the reorganization of craniofacial architecture along our lineage. Furthermore, because these sites are conserved across mammals, they represent appropriate and fruitful areas for gaining understanding of human biology via the study of experimental animal models, such as mice.

The basicranium

Because the basicranium is responsible for supporting the brain, and it acts as the scaffold off of which the face is arranged, it is important to understand its architecture, as well as its relationship to the facial skeleton^{1, 9-17}. It is well recognized that a fundamental shift in the organization of craniofacial architecture has occurred along the hominin line, including an increasing angle of basicranial flexion, which has been extensively studied in both humans, extinct hominins, and extant non-human primates^{1, 11-12, 18-26}. Gould's spatial packing hypothesis²⁷, in which increasing brain size and relative shortening of the basicranium contributes to greater degree of basicranial flexion, has been supported by numerous subsequent studies^{1, 12-13, 15, 20, 22-23}.

As for the bony articular connections between head and neck, an early hypothesis for explaining the changing location of the occipital condyles and foramen magnum was that the shift to bipedalism necessitated a better balancing of the head atop the cervical spine in orthograde animals^{28, 29}. Subsequently, the balancing hypothesis had lost traction due to the observation that many animals, like giraffes, that hold their torso and/or neck in an orthograde posture, but are not bipedal, and have not reorganized their crania, especially not in relation to the anteroposterior position of the occipital condyles⁹. Recent work has suggested that foramen magnum position *is* influenced by locomotion and posture, as recently demonstrated across three diverse clades of mammals, including marsupials, rodents and primates²⁶. Bipedal locomotion, and to a lesser extent, orthograde posture even in the absence of bipedality, both result in more anteriorly positioned occipital condyles within these groups, supporting the basicranium as a viable area from which to assess locomotor patterns in hominin fossil material^{26, 30, 31}.

The viscerocranium

Neurocranial and facial dimensions are developmentally integrated^{4-5, 16-17}, and facial size itself is also positively correlated with basicranial flexion^{1, 13-15, 24}. Therefore, the spatial architecture of the viscerocranium constitutes an important consideration, and for the purposes of this paper, we will focus on orbital orientation.

The reorientation of the orbits can be measured in terms of

“frontation,” or the vertical direction of the orbital plane in relation to a chord from nasion to inion³². In terms of orbital orientation, orthograde primates do not consistently display more frontated orbits than pronograde ones³². Simiiformes have highly frontated orbits, which could be the result of frontal lobe expansion or increased basicranial flexion; however, no significant relationship was found between orbit frontation and basicranial flexion in hominoids, likely due to *Pongo*'s airorhynch³². It should also be noted that it is difficult to separate posture from allometric influences, since hypertrophic frontal lobes are closely related to an overall increase in the brain, which in turn contributes to basicranial flexion according to the spatial-packing hypothesis^{27, 32}. Furthermore, questions dealing with orbital reorientation are often posed in functional terms, *i.e.*, the reorientation occurring in response to the animals' behaviors.

Posture, locomotion, and mobility

Dabelow's postural hypothesis¹⁸ maintains that orthograde posture and bipedal locomotion contribute to reorganization of the basicranium and face, particularly causing the flexion of the basicranium in order to maintain the anteriorly-facing orientation of the orbits in hominids. Ross and Ravosa's findings¹² corroborate Dabelow's postural hypothesis¹⁸ in that they found a plausible relationship between basicranial flexion and orbital reorientation; however, the authors reject its likelihood because the flexible mammalian cervical spine may render the effect of orthograde posture on basicranial flexion insignificant. Further, correlations corroborate the spatial packing hypothesis²⁷, where relative brain size is the main driver of basicranial flexion¹ and wherein orbital reorientation occurs mainly to adjust primates' line of sight in relation to their head and neck posture, regardless of brain size²⁰.

Empirically examining the postural head-neck relationship, especially during locomotion, then becomes important for testing assumptions about correlations between craniofacial morphology, postural behaviors and locomotion^{20, 23}. In fact, diverse groups of catarrhine primates, including humans, all hold the orbital plane—made by the superior- and inferior-most margins of the orbits—in a fairly consistent orientation during locomotion, pointing generally anteriorly and slightly inferiorly, regardless of posture or craniofacial morphology²³. However, transverse (anterior-inferior) range of motion at the atlanto-occipital joint is severely limited by bony morphology in humans, as well as Old World and New World monkeys, when compared to other quadruped mammals³³. This morphological constraint is possibly due to the disadvantages of controlling excessive amounts of mobility in the cervical spine during orthograde locomotion, both during terrestrial bipedalism and brachiation³³.

Furthermore, habitual posture and the relationship of the head and neck correspond to differences in adult facial morphological differences in humans¹⁰. Individuals who hold their necks habitually extended tended to have a longer lower facial height, an obtuse gonial angle, decreased vertical dental development and mandibular retrognathism; whereas, the opposite of these characteristics occurred in individuals who habitually held their head/neck in flexion¹⁰. Therefore, differing posture may affect the degree of orbital kyphosis in humans, indicating that the angulation of the orbits is a developmentally plastic trait, and that clinical intervention at an early enough point during growth and development may change outcomes for patients diagnosed with postural abnormalities.

Issues of spinal mobility, and particularly that of the cervical spine, inherently impact Dabelow's argument¹⁸ for orbital and basicranial reorganization based on orthograde posture and/or bipedal locomotion because of the flexible and variable nature of these craniofacial proportions^{10, 33}. There is a significant correlation between the head-neck angle of catarrhine primates during locomotion and orbital kyphosis²⁰. Orbital kyphosis refers to the anteroinferior repositioning of the orbits relative to the rest of the skull, akin to the 'downward rotation of the orbits' referenced by Enlow and Hans², and may relate to maintaining the anteriorly (horizontally) directed visual field¹⁸. Instead of the line of sight (NHA) being parallel to the ground, they argue that the functional proxy for cranial orientation during life is the plane of the anterior orbital margin being perpendicular to the ground, and therefore disregarding historical registration planes, such as Frankfort horizontal, as useful for orienting hominid fossil crania²⁰. Fortunately, geometric morphometrics negates the need for a traditional reference plane, as an integral step in the analysis is rotating each specimen's data points so that the distances between homologous landmarks is reduced and the entire sample is optimally aligned³⁴. Furthermore, especially utilizing a 3-dimensional approach allows for the visualization of the spatial and architectural relationships between different parts of the cranium.

Despite a large body of pertinent literature, it still remains unclear how and by what mechanisms the reorganization of craniofacial architecture occurred, especially phylogenetically along the hominin lineage. Relative brain size and basicranial flexion seem to be correlated, to the exclusion of postural variables¹; however, recent studies have demonstrated that both orthograde posture and bipedal locomotion do limitedly contribute to reorganizing the basicranium, particularly the anteroposterior position of the occipital condyles²⁶. On the other hand, orbital orientation appears to be intimately linked to postural and other behavioral considerations, yet these shifts occur more or less concomitantly in our lineage, while still maintaining developmentally constrained architectural relationships in the craniofacial skeleton^{2, 20}. In the present study, we develop the method for evaluating Enlow's craniofacial architectural relationships using 3D landmark data and geometric morphometrics in order to investigate the relationship of the line of sight (Neutral Horizontal Axis) to the brain base. Enlow himself understood that the relationships between these developmentally distinct areas of the craniofacial skeleton are important for investigating the functional significance of line of site in respect to dietary and locomotor niche adaptations of extant primate taxa and fossil hominins, and perhaps even more importantly, for investigation and implementation within clinical practice³⁵.

MATERIALS AND METHOD

The study sample is composed of cone beam computed tomography (CBCT) scans of modern human, chimpanzee and orangutan skulls, as well as of physical casts of fossil hominid crania (Table 1). The sample consists of a wide range of species, of both males and females when available.

Twenty-three (23) landmarks on the cranium were captured, consisting of seven midline points and eight paired, bilateral points that were measured twice—once on the right and left sides of each individual (see Table 2). These points were selected for analysis

Table 1. Sample size and method of data collection (total n=23)

Species	Data Collection Method	n
<i>P. boisei</i>	MicroScribe of cast ¹	1
<i>A. africanus</i>	MicroScribe of cast ¹	1
<i>H. habilis</i>	MicroScribe of cast ¹	1
<i>H. erectus</i>	MicroScribe of cast ¹	1
<i>H. ergaster</i>	MicroScribe of cast ¹	1
<i>H. heidelbergensis</i>	MicroScribe of cast ¹	2
<i>H. sapiens</i>	MicroScribe of skeletal material ² ; Analyze 11.0 of CBCT ³	4 6
<i>P. troglodytes</i>	Analyze 11.0 of CBCT ⁴	5
<i>P. pygmaeus</i>	Analyze 11.0 of CBCT ⁴	1
Total		23

¹Hominid casts housed at the University of Florida Department of Anthropology.

²Modern sample of adult human donated anatomical specimens curated at the University of Florida.

³Adult human CBCT scans originate from Dr. Ari Masters' NoBrace Center in Melbourne, Australia, and retain only sex and age information. Only scans of dentally mature individuals (erupted third molars) were included.

⁴Adult chimpanzee and orangutan specimens originating from the American Museum of Natural History were scanned at the NYU College of Dentistry

based on Enlow's work with Azuma on functional growth boundaries in the face, because these are sites of growth that are developmentally and, to some extent, phylogenetically, constrained³. Indeed, Bromage⁴ found that some functional boundaries are conserved in *P. troglodytes* through ontogeny, namely the perpendicular relationship of the posterior maxillary (PM) plane to the neutral horizontal axis (NHA) and the 45° relationship of the meatus angle (MA), or the angle between the mid-orbit, external auditory meatus and the maxillary tuberosity³.

Three-dimensional data were collected for geometric morphometric analyses, instead of the angles, planes, and linear distances used by Enlow & Azuma³ and others^{4, 5, 8, 16}. Using this method, we can take overall size and the geometric relationships among points into account and build images to visually illustrate the changes in shape^{17, 36}.

However, since the points selected are based on Enlow's studies of craniofacial architecture that were performed on 2D lateral radiographs, 3D landmarks from CBCT scans had to be chosen, and the selection of some surrogate points became necessary (Table 3). Surrogate points were often necessary because some 2D points, such as Inferior brain or Middle-anterior cranial fossa, relied on the vagaries of 2D radiography, and were influenced by the positioning of the specimen and foreshortening. Since we used 3D CBCT scans or physical casts to capture the specimens' "images", these specific points typically required surrogates based on the conditions of the new study (Table 3). Additionally, some points that may be clearly visible and measurable in a lateral radiograph, such as maxillary tuberosity, are more difficult to accurately and precisely measure in three dimensions (Table 3). Furthermore, in addition to directly substituting points, some of the original points were substituted

Table 2. Point Definitions

Unpaired (Midline) Points		
Point	Point number ¹	Definition
Nasion	1	Midline point of the frontonasal suture, where the frontal and nasal bones meet ²
Basion	2	Midline point at the posterior-most projecting point on the foramen magnum's anterior margin ²
Hormion	3	Posterior-most point at the midline of the vomer ²
Incisive foramen	12	Center of the incisive foramen at the inferior-most point of the incisive canal
Rhinion	21	Midline point at the inferior end of the internasal suture ²
Anterior Nasal Spine	22	Midline point at the anterior-most projecting point of the anterior nasal spine
Posterior Nasal Spine	23	Midline point at the posterior-most projecting point of the posterior nasal spine
Paired (Lateral) Points – left and right sides measured for each point		
Point	Point numbers ¹ (R-L)	Definition
Stylomastoid foramen	4 - 5	Center of the lateral exit of Cranial Nerve VII from the petrous portion of the temporal
Foramen rotundum	6 - 7	Center of the foramen rotundum canal at the anterior-most point where the canal is complete
Inferior orbital foramen	8 - 9	Central point of the inferior orbital foramen of the maxilla
Greater palatine foramen	10 - 11	Center of the foramen at its inferior-most point where the canal exits the maxilla and palatine
Lateral orbit	13, 17	Lateral orbital point at the center of the frontozygomatic suture (essentially a midpoint between frontomale orbitale and frontomalare temporale ²)
Medial orbit	14, 18	Point on the lateral ethmoid traced directly medially from lateral orbit indicating the medial extent of the orbit
Superior orbit	15, 19	Superior-most point on the orbital margin
Inferior orbit	16, 20	Inferior-most point on the orbital margin (<i>i.e.</i> , orbitale ²)

¹Landmarks assigned numbers based on order in which their position was measured and entered into MorphoJ (Klingenberg, 2011) for analysis

²After White et al. 3rd Ed. Human Osteology

Table 3. Surrogate Points with Former Points' Definitions

Surrogate Point	Former Point ³	Definition ³
Greater palatine foramen	Maxillary tuberosity	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.
Foramen rotundum	Middle- anterior cranial fossa	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 Frankfort Horizontal.
Basion & Hormion	Inferior brain	The inferior-most extent of the brain was defined by the first contact with the cranial cavity by a line pivoted and from the MT (maxillary tuberosity) through the occipital bone.
Semi-circular canal (SC)	External auditory meatus	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.

³All points and their definitions from Bromage (1992) after Enlow & Azuma (1975)

for surrounding structures; for example, it becomes redundant to calculate an orbital midpoint when the superior, lateral, inferior and medial points of the orbit can all be conserved for analysis using geometric morphometrics. Points other than those adopted from Enlow & Azuma³ and Bromage⁴ were selected for their homologous nature, developmental stability, as well as their ability to “complete the picture” of the architecture of the viscerocranium. Lastly, data collected from casts consisted of the same set of landmarks as those gathered from the CBCT scans, except where postdepositional breakage has resulted in missing points, and where endocranial landmarks were inaccessible.

Data collection from CBCT scans using Analyze 11.0

CBCT scans were obtained in DICOM format (0.4 x 0.4 x 0.4 voxels/mm) and visualized in Analyze 11.0³⁷ to facilitate analysis. Analyze 11.0 is Mayo Clinic software for “multi-dimensional display, processing, segmentation, registration and measurement of ... biomedical images”³⁷.

In Analyze 11.0³⁷, cross hairs on the *x*-, *y*- and *z*-planes pinpoint the voxel coordinates for each measured landmark. For points that are taken in the middle of a structure or foramen, such as Hormion or Foramen Rotundum, the cross hairs were placed so that they most accurately intersected the center of the area in question. For points that constitute an endpoint or the directionally-most placed point on a structure, such as the Anterior Nasal Spine or Mastoidale, the cross hairs were placed so that the corner abuts but does not overlap the structure being measured.

Data collection from casts and skulls using a MicroScribe

Fossil hominid casts and modern human crania were mounted on a cork ring support. Using a MicroScribe G2X and MicroScribe Utility software, data was collected by placing the stylus on the structure in question and clicking a button to capture the 3-dimensional placement of the tip of the stylus. Because of the inaccessibility of endocranial points (such as the Semicircular Canals), or missing areas of the fossil crania due to taphonomic processes, some points were not measured, and therefore these landmarks were not included for certain specimens. However, several missing points did not impede the creation of shape variables, or the specimens' inclusion in this study.

Data analysis

After collecting the 3D coordinates of the craniometric points, the data were loaded into geometric morphometric software, MorphoJ³⁸, for analysis. Geometric morphometrics is the statistical study of shape variation and its covariation with other variables. Shape refers to the geometry of an object that is invariant to changes in scale, rotation and translation; therefore to analyze shape the factors of size, orientation and position must be removed³⁹.

The full data set was firstly partitioned into subsets of extant non-human species, fossil hominids, and humans. All non-shape related variation was removed using Generalized Procrustes Analysis (GPA), where landmark points are iteratively scaled, translated and rotated such that the sum of squared distances to all landmarks once they are superimposed is minimized^{34, 36, 38}. After this process is complete, the data consist of shape variables, which can then be subjected to any number of standard uni- or multivariate statistical

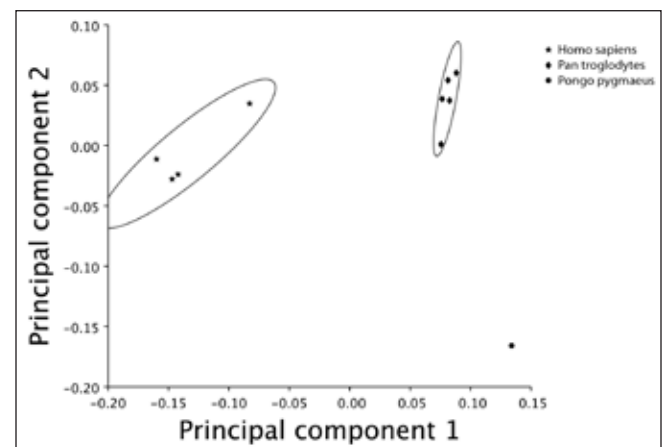
methods. Firstly, we computed a covariance matrix, from which a Principal Components Analysis (PCA) could then be generated. In the PCA each species received a unique identifying symbol as a *post hoc* illustration of group membership, although the initial analysis is exploratory and has no *a priori* ‘knowledge’ of group assignment. Additionally wireframe models were constructed to illustrate the shape differences along the PC axes, facilitating visualization of the complex shape changes occurring along the axes of reduced dimensionality in the Principal Components Analyses.

RESULTS

Analysis of extant species

Principal components 1 and 2 together account for 82.2% of the variance in the sample. The principal components graph below illustrates this exploratory analysis of shape differences within the sample, including equal frequency ellipses in order to more easily visualize the shape of the data's scatter. In PC1 vs. PC2, it is clear that the data do not overlap, and are in fact widely separated in morphospace (Fig. 1).

Figure 1. Plot of Principal Components 1 vs. 2 with equal frequency ellipses. *H. sapiens* represented by stars, *P. troglodytes* by diamonds, and *P. pygmaeus* by a circle.



The wireframes model shape changes along a given principal components axis (Figs. 2 & 3); the lighter wireframe illustrates the mean shape of the sample, whereas the darker wireframe shows the shape resulting from moving positive .01 units of Procrustes distance along the given PC axis away from the mean shape. Figure 2 shows the lateral view of shape changes along PC1, and Fig. 3 shows the frontal view of the shape changes along PC1's axis.

The wireframes along PC 1 reveal some interesting information about the patterns of variation in this sample. The shape change positively along PC1 seems to correspond to a reorientation of the basicranium and orbits (Fig. 2). The inferior orbital border remains relatively stable, and the midline basicranium, represented by a line connecting basion and hormion (Points 2 & 3, respectively) orients further anteroinferiorly while keeping its center point close to the same position. At the same time, the position of the superior orbits is rotating posteriorly and the palate moves anteriorly and slightly inferiorly (Fig. 2). The combination of these ‘movements’ results in an overall shape change of an anteroposteriorly longer face when moving positively along PC 1.

In Figure 3, increasing the Procrustes distance 0.1 units positively along PC2 away from the sample's mean shape results in relatively smaller orbits, as well as a general inferior displacement of the structures of the midface (Fig. 3, Points 8-12). Given that PC 1 accounts for over 60% of the variance in this sample, and PC 2 accounts for less than 20%, it is unsurprising that the shape changes along PC 1 are much more visible and pronounced in the wireframes.

Figure 2. Darker lateral wireframe showing the shape change along PC1. Lighter wireframe represents mean shape of the total sample after GPA. Anterior is to the right, superior is at top in this image. Numbers indicate individual landmarks.

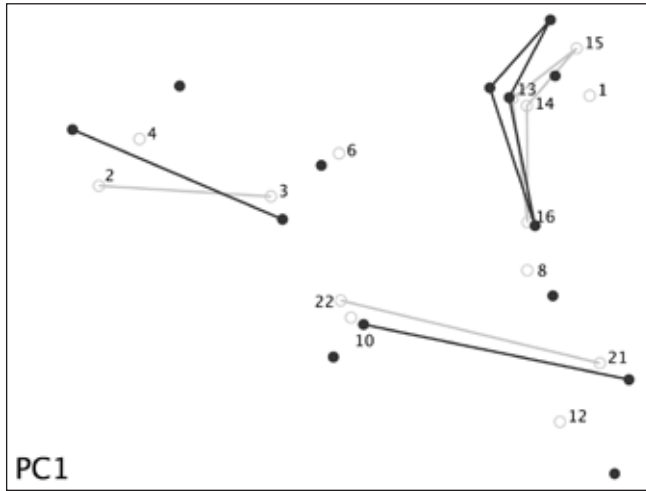
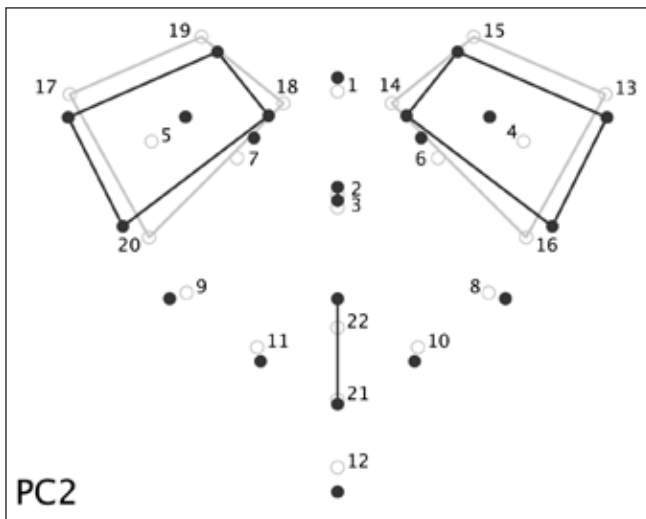


Figure 3. Darker frontal wireframe showing the shape change along PC2. Lighter wireframe represents mean shape of the total sample after GPA. Numbers indicate individual landmarks.

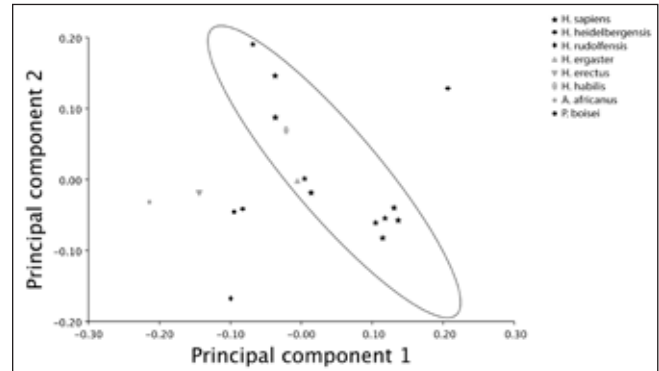


Analysis of hominids

Principal components 1, 2 and 3 together account for 59.4% of the variance in the sample. The principal components graph in Figure 4 illustrates this exploratory analysis of shape differences within the sample, including an equal frequency ellipsis around the *H. sapiens* sample in order to more easily visualize the shape of that subset of data's distribution. In a plot of PC1 vs. PC2, it is clear that

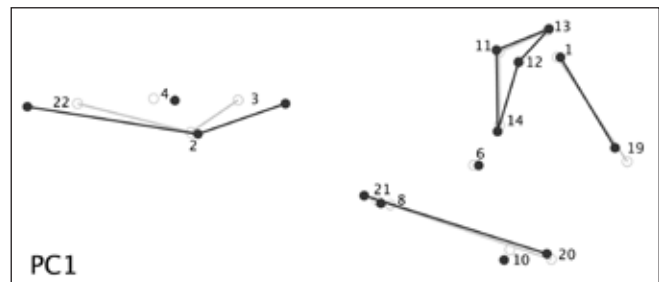
several of the fossil taxa overlap with the range of human variation, namely *H. ergaster* and *H. habilis* individuals (Fig. 4). All of the remaining fossil hominids, except for the Steinheim *H. heidelbergensis* specimen, lie toward the lower ends of both PCs 1 and 2.

Figure 4. Plot of Principal Components 1 vs. 2 with equal frequency ellipses, species represented by different symbols.



Once again, wireframes were used to model shape changes along a given principal components axis (Fig. 5), where the lighter wireframe illustrates the mean shape of the sample, whereas the darker wireframe shows the shape resulting from moving .01 units of Procrustes distance positively along PC 1's axis from the mean shape. In Figure 5, which shows the lateral view of shape changes along PC1, it is clear that the majority of shape differences are being manifest in the basicranium, while the facial skeleton is essentially stable.

Figure 5. Darker lateral wireframe showing the shape change along PC1. Lighter wireframe represents mean shape of the total sample after GPA. Anterior is to the right, superior is at top in this image. Numbers indicate individual landmarks.



DISCUSSION

Analysis of extant species

The overall cranial shape differences between *H. sapiens*, *P. troglodytes* and *P. pygmaeus* can be readily appreciated as occurring along PC 1 since the species cluster distinctly and do not overlap along this principal component axis, and therefore changes along PC 1 can be interpreted as relating primarily to interspecific differences (Fig. 1). Given their phylogenetic relationships it is unsurprising that *P. troglodytes* falls between *H. sapiens* and *P. pygmaeus* along PC 1.

PC 2, on the other hand, shows considerable overlap between humans and chimpanzees, but seems to isolate the single *P. pygmaeus* individual (Fig. 1). From the wireframe in Figure 3, it seems as though orangutans' relatively larger and more medially placed orbits are driving this separation along PC 2, especially since these differences do not coincide with much, if any, variation in the palate or basicranium along this PC axis.

In Enlowian terms, then, we can interpret the results seen in the analysis of extant apes as indicating that in order to keep the line of sight parallel to the substrate (Enlow's NHA: measured in this study using foramen rotundum and points around the orbital margin), some rearrangement of the relationship between the viscerocranium and basicranium must have occurred. Of course, the foramen magnum is repositioned anteriorly in humans, and the angle at which it opens to the cervical spine is necessarily changed by its shifted placement. However, in this study the changes to the basicranium and upper face all occur atop a relatively stable hard palate (see Fig. 2). Thus, if the hard palate and greater palatine foramen (as a surrogate for maxillary tuberosity) and foramen rotundum (as a surrogate for middle-anterior cranial fossa) remain in the same position, the basicranium and orbits rotate opposite to one another—*i.e.*, not merely rotating as a unit about a fixed point. In other words, if instead of the hard palate we consider orbital orientation as being fixed, a repositioning of the midfacial viscerocranium can be readily appreciated and the differences in foramen magnum position and angulation are even more pronounced. Therefore we may not expect the mammalian angular relationships (such as MA) to persist with such regularity in the evolving lineages of hominoids as opposed to *Pan troglodytes*, as discussed by Bromage⁴. Furthermore, the posterior rotation of the orbits along PC1 may represent a compensation for the forwardly-inclined middle basicranial floor, basicranial floor, aiding in the developmental and phylogenetic maintenance of forward-facing eyes that are relatively parallel to the substrate, implying that the imperative for maintaining visual awareness in the horizontal field of gaze was a coincident phylogenetic pressure with the energy exigencies of efficient stance and locomotion consequent during the evolutionary assumption of orthograde, obligate bipedalism. Hence, features such as foramen magnum orientation and occipital condyle migration co-occurred in the context of strong selective pressure to maintain the center of mass of the head and trunk over the feet during erect standing and locomotion while maintaining a near horizontal visual field. The posterior rotation of the orbits referenced above also increases the area of the anterior cranial fossa and frontal lobes of the brain. These findings may help explain why extant hominoids conserve the PM-NHA and MA angular relationships, but do not follow some of the other strict mammalian craniofacial architectural constraints observed in other primates and mammals, for instance the presence of anterior maxillary hypoplasia^{3,4}.

Analysis of hominoids

The distribution of specimens along PC1 is fairly continuous, however the human sample occupies the positive quadrant of PC1 and, as would be expected, humans demonstrate a more tightly flexed basicranium than all hominid fossil taxa (Figs. 4 & 5). It is interesting to note that one specimen, *H. heidelbergensis* from Steinheim, occupies the PC 1 vs. 2 plot far removed from the rest of the data, as well as on the opposite side of the humans' frequency

ellipse from the rest of the fossil hominids. Although not statistically an outlier in this sample, this specimen's uncharacteristic position in morphospace may be due to the taphonomic damage to the left side of the face and the basicranium, which prohibited the gathering of several data points on this specimen. Additionally, a majority of the fossil hominids inhabit approximately the same range (around -.02) along PC2, including *A. africanus*, *H. ergaster*, *H. erectus*, *P. boisei*, and the other *H. heidelbergensis* individual, Kabwe 1. Interestingly, the two *H. sapiens* individuals clustering near the square-shaped *H. ergaster* specimen are both archaic fossil crania from Skhul and Hotsu Cave (Fig. 4).

Furthermore, as the lateral wireframe in Figure 5 demonstrates, the majority of shape differences are manifest in the basicranium, while the facial skeleton and particularly the orbits remain essentially stable. If the Steinheim *H. heidelbergensis* specimen's PC scores are indeed due to noise generated from missing points on this taphonomically distorted cranium, humans represent virtually the entirety of the positive area of PC1, and the geologically oldest species, *A. africanus*, has the lowest score on PC1 (Fig. 4). Therefore, moving positively along PC1 can loosely be interpreted as moving through evolutionary time.

Line of sight among hominoids and along the hominid lineage

Interesting patterns have emerged when considering the relationship of the line of sight (NHA) to the craniofacial complex among extant hominoids and along the hominid lineage. In contrast with extant hominoids, it seems that humans maintain the line of sight relatively parallel to the substrate through the anterior shift of foramen magnum along with anteroposterior reduction in the midface, as evidenced in this study by the retraction of the hard palate relative to the orbits and basicranium. When examining fossil hominid individuals in order to possibly elucidate changes since our divergence from a non-human ape ancestor, the vast majority of shape changes occur in basicranial area, specifically with regard to basicranial flexion, indicating that this may be the main compensatory mechanism to maintain line of sight (NHA) during major locomotory and ecological shifts in hominid evolution.

CONCLUSION

Shape differences between the crania of extant hominoids are readily apparent, the three taxa clustering distinctly and separately in dimensionally-reduced morphospace (Fig. 1, PC1 & PC2). Our sample followed the expected pattern of an anteriorly shifted foramen magnum, more tightly flexed basicranium, and superiorly rotated orbits atop a relatively stable palate in humans as compared to *P. troglodytes* and *P. pygmaeus*. Conversely, humans and fossil hominids showed more overlap in their craniofacial architecture, but patterns in the changes along PCs 1 & 2 were appreciable and indicated trends of interest for future research. Maintenance of the line of sight (NHA) relatively parallel to the substrate is achieved in the hominid lineage mainly by modification of basicranial flexion. Furthermore, comparing human morphology to that of extant hominoids, along with basicranial differences, pronounced shape changes are also apparent in the position of foramen magnum and rotation of the hard palate relative to the orbits, as well as in the anteroposteriorly reduced midface in humans.

It must be acknowledged that morphometric analyses, especially geometrically based, require caution when being applied to paleoanthropological fossil specimens, due to issues such as taphonomic damage and warping. Further limitations include a relatively small sample size in this study, and the issues of small sample size and statistical power become even more pronounced when seeking to gather many landmarks from a wide range of species when (mostly) complete crania are only available from single individuals of each taxon.

In the future, reconstructing crania from CT scans of fossils, rather than using casts, will aid in not only locating and measuring potential endocranial points, but will also allow a better appreciation of the organisms' true morphology, especially by employing Enlow's developmentally constrained craniofacial relationships for said reconstructions (e.g., Zollikofer and colleagues' study²⁵). Furthermore, increasing the sample size, particularly of extant species, will not only increase the robusticity of such studies, but will also aid in representing the range of variation within each species. Moving forward, questions about the reorganization of craniofacial architecture along the hominin lineage will also benefit from further investigation into the ontogenetic origins of basi- and viscerocranial morphology using geometric morphometric analyses. For example, Mitteroecker et al.⁴⁰ found that human cranial shape and size is clearly distinct from other great apes from birth, the taxa then separated even further during postnatal ontogeny. This combination of results indicates that pure heterochrony cannot fully explain the resultant adult human craniofacial morphology, or the differences among African apes' cranial morphology, and opens the door for further research on this topic^{14, 40}.

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