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Postnatal Temporal Bone Ontogeny in *Pan*, *Gorilla*, and *Homo*, and the Implications for Temporal Bone Ontogeny in *Australopithecus afarensis*

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ABSTRACT Assessments of temporal bone morphology have played an important role in taxonomic and phylogenetic evaluations of fossil taxa, and recent three-dimensional analyses of this region have supported the utility of the temporal bone for testing taxonomic and phylogenetic hypotheses. But while clinical analyses have examined aspects of temporal bone ontogeny in humans, the ontogeny of the temporal bone in non-human taxa is less well documented. This study examines ontogenetic allometry of the temporal bone in order to address several research questions related to the pattern and trajectory of temporal bone shape change during ontogeny in the African apes and humans. We further apply these data to a preliminary analysis of temporal bone ontogeny in *Australopithecus afarensis*. Three-dimensional landmarks were digitized on an ontogenetic series of specimens of *Homo sapiens, Pan troglodytes*, *Pan paniscus*, and *Gorilla gorilla*. Data were analyzed using geometric morphometric methods, and shape changes throughout ontogeny in relation to size were compared. Results of these analyses indicate that, despite broadly similar patterns, African apes and humans show marked differences in development of the mandibular fossa and tympanic portions of the temporal bone. These findings indicate divergent, rather than parallel, postnatal ontogenetic allometric trajectories for temporal bone shape in these taxa. The pattern of temporal bone shape change with size exhibited by *A. afarensis* showed some affinities to that of humans, but was most similar to extant African apes, particularly *Gorilla*. Am J Phys Anthropol 151:630–642, 2013. © 2013 Wiley Periodicals, Inc.

Temporal bone morphology has played an important role in taxonomic and phylogenetic evaluations of fossil taxa (e.g., Weidenreich, 1943; Tobias, 1967, 1991; Kimbel, 1986; Strait et al., 1997; Martinez and Arsuaga, 1997; Lockwood et al., 2002, 2004; Sherwood et al., 2002; Harvati, 2003; Kimbel et al., 2004; Terhune et al., 2007; Gilbert, 2008). This region of the cranium lends itself to analyses such as these for several reasons. First, the temporal bone is a commonly preserved element of the cranium, and contains a complex set of morphological features related to multiple functional complexes (e.g., auditory, neural, locomotor, masticatory). Second, the temporal bone has been shown to reliably reflect phylogenetic relationships among extant great ape species and subspecies (Lockwood et al., 2004), as well as to reflect population divergence (e.g., molecular relationships) among human populations (Harvati and Weaver, 2006a,b; Smith et al., 2007; Smith, 2009; von Cramon-Taubadel, 2009). This apparent reliability of the cranial base and temporal bone for recovering phylogenetic patterns, at least in great apes and humans, implies that understanding the ontogeny of the temporal bone may help elucidate phylogenetic patterns among living and extinct species of hominids[1], since it is through modifications in ontogeny that differences in adult form are achieved. Evaluating patterns of morphological change throughout ontogeny is of particular importance for the assessment of sub-adult fossil specimens and their inclusion in phylogenetic analyses. To that end, this study examines ontogenetic allometry of the temporal bone in a cross-sectional sample of humans and African apes with the ultimate goal of comparing and contrasting patterns of ontogenetic shape change across taxa.

Temporal bone ontogeny

One reason that temporal bone morphology may hold a phylogenetic signal is due to its unique developmental history. The temporal bone is composed of four separate parts—the petromastoid (which includes the bony

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[1] We use the term hominid here to refer to members of the genera *Homo*, *Pan*, *Gorilla*, and *Pongo*, and all descendants of their last common ancestor. The term hominin includes modern humans and fossil taxa more closely related to humans than to any other extant taxon.

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labyrinth), squamous, tympanic, and the styloid process (e.g., Cartmill et al., 1987; Scheuer and Black, 2000; Baker et al., 2005)—that begin to ossify early in prenatal development via both intramembranous and endochondral ossification from multiple ossification centers (Thomas, 1926; White, 2000; McBratney-Owen et al., 2008). These portions of the temporal bone fuse together in the perinatal period in humans, and by the time of birth or shortly after, the temporal bone is recognizable as a distinct cranial unit (Scheuer and Black, 2000).

In humans, postnatal growth of the articular eminence is rapid and the mature S-shaped outline of the eminence and mandibular fossa are apparent well before eruption of the 2nd molars, although the fossa continues to increase in size (Wright and Moffett, 1974; Dumas et al., 1986; Nickel et al., 1988; Itoh et al., 1995; Katsavrias and Dibbets, 2001, 2002; Katsavrias, 2002). The extent of postnatal shape change in the mandibular fossa is less well documented in the apes. Although Ashton and Zuckerman (1954) examined the great ape articular eminence and demonstrated variation in eminence inclination between apes and humans, they focused primarily on descriptions of adult form and identified few differences in the form of this region in subadult *Pan*, *Gorilla*, or *Pongo*. Further data are necessary to identify whether these taxa follow a similar ontogenetic pattern to that of humans.

The most radical postnatal shape change of the temporal bone occurs in the petromastoid region. Pneumatization of the petromastoid begins prenatally in humans, gorillas, and chimpanzees and extends into the juvenile period in the apes and into adolescence in humans (Sherwood, 1999; Hill, 2011). There are strikingly different patterns of pneumatization in humans in comparison with the great apes, with chimps and gorillas experiencing extensive pneumatization of the squamous temporal bone that is absent in humans (Sherwood, 1999). Human pneumatization is largely limited to the mastoid process, the size and projection of which increases until as late as 15 years in females, and 19 in males (Eby and Nadol, 1986; Scheuer and Black, 2000). Orientation of the petrous and tympanic regions also differs strongly among adult apes and humans [e.g., the coronally oriented petrous in humans when compared to the apes (Dean and Wood, 1981, 1982)], and ontogenetic analyses of this morphology (Dean and Wood, 1984) indicate that these taxonomic differences are established early in ontogeny and follow similar patterns of postnatal change.

Previous analyses of ontogeny in the African apes and humans

Ontogenetic shape change in human and non-human primate cranial form has been a topic of considerable research [see Lieberman (2011) for a review]. Most recently, studies of human and non-human ontogeny have benefited from the use of geometric morphometric methods. These methods allow for the quantification of complex three-dimensional (3D) forms across a range of body sizes and developmental ages. In studies of ontogeny, these methods are particularly useful as they can be used to describe a trajectory of ontogenetic shape change in the sample in question. Typically, shape change in relation to size (e.g., ontogenetic allometry) is examined (e.g., O'Higgins and Collard, 2002; Strand Viðarsdóttir et al., 2002; Mitteroecker et al., 2004, 2005; McNulty et al., 2006; Singleton, 2012). The primary goal of these studies has been to address how postnatal shape changes relate to differences among adults of different hominid species, and to test if trajectories of shape change are statistically different among species or populations.

These studies, primarily of facial growth, have yielded somewhat conflicting results, however. Some researchers (Krovitz, 2000; Ponce de León and Zollikofer, 2001; Ackermann and Krovitz, 2002; Lieberman et al., 2007; Boughner and Dean, 2008) suggest that differences in cranial shape among closely related hominid species arise prenatally, and that postnatal ontogenetic trajectories for these species are parallel (i.e., the slopes of the ontogenetic trajectories are statistically indistinguishable). Others (Strand Viðarsdóttir et al., 2002; Krovitz, 2003; Cobb and O'Higgins, 2004; Mitteroecker et al., 2004, 2005; Strand Viðarsdóttir and Cobb, 2004; McNulty et al., 2006; Bastir et al., 2007) found that divergent postnatal craniofacial shape trajectories (i.e., the shape trajectories have statistically significantly different slopes) also contribute to shape differences between adults of different species, although prenatal shape differences may also be present. The path by which different adult cranial morphologies are achieved during ontogeny therefore remains unclear; analysis of the ontogeny of the temporal bone can contribute to this ongoing debate.

Study goals

Although several of the studies cited above have incorporated aspects of basicranial morphology (e.g., Ponce de León and Zollikofer, 2001; Mitteroecker et al., 2004, 2005; McNulty et al., 2006; Bastir et al., 2007; Lieberman et al., 2007), none of them has specifically employed the temporal bone to examine postnatal ontogenetic trajectories in living or fossil primate species. The goal of our analysis of ontogenetic allometry of the temporal bone is to contribute to this ongoing debate and shed additional light on the extent to which temporal bone form varies across age classes in the African apes and humans.

We address two specific research questions related to temporal bone morphology in the African apes and humans:

1. How does temporal bone shape change during ontogeny in humans and African apes?
2. Are postnatal ontogenetic shape trajectories for the temporal bone divergent or parallel among extant hominid species?

We apply these data to the temporal bone of the early hominin species *Australopithecus afarensis*. Although the ontogenetic series for *A. afarensis* is based on only four specimens, we explore shape variation in this sample to see whether it reveals any clues to patterns of shape change that resulted in its prevailingly generalized (ape-like) adult morphology (Kimbel et al., 2004).

MATERIALS AND METHODS

Extant samples

Twenty-three 3D landmarks (following Lockwood et al., 2002) were digitized on the ectocranial surface of the temporal bone in a cross-sectional ontogenetic sample of *Gorilla gorilla*, *Pan troglodytes*, *Pan paniscus*, and *Homo sapiens* (Fig. 1, Tables 1 and 2). Where possible,

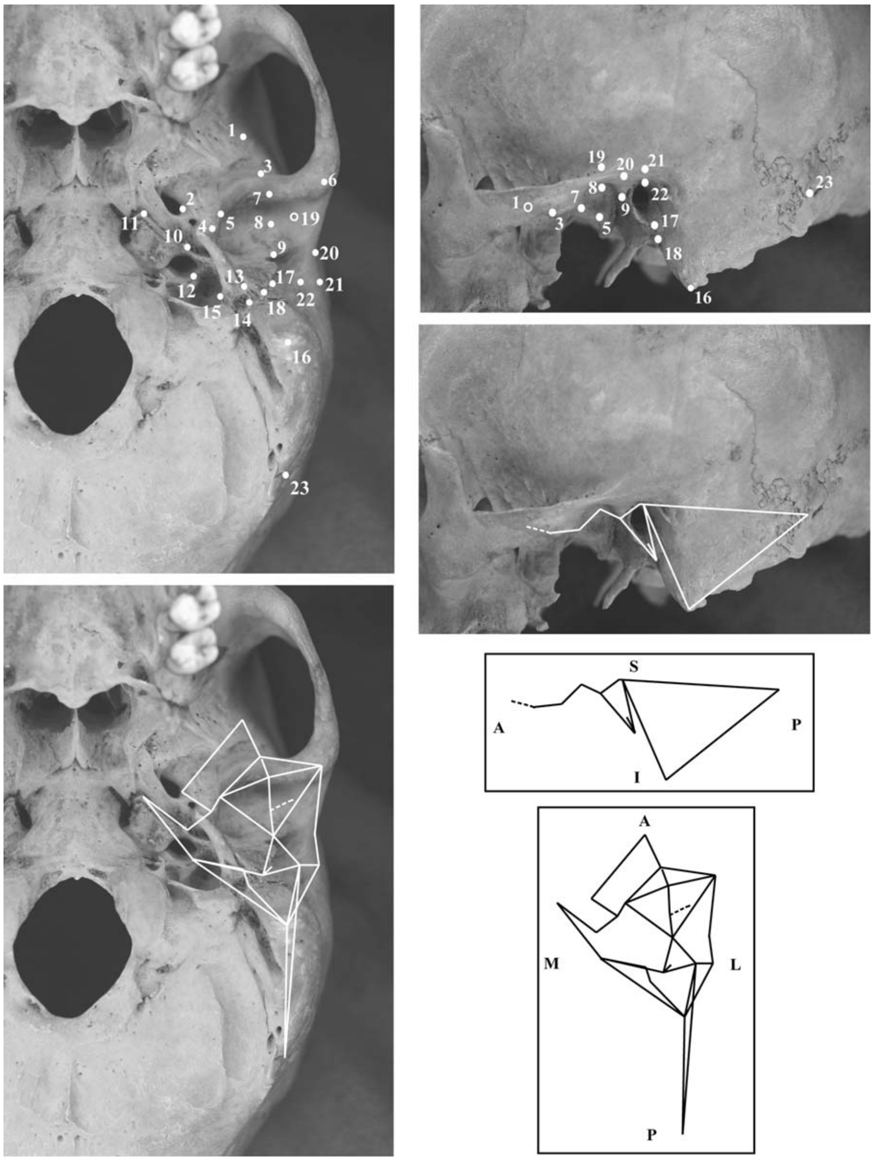

Fig. 1. Inferior (left) and lateral (above right) views of a human cranium showing the landmarks and wireframe diagrams used in this study. Numbers correspond to those listed in Table 2. A: anterior; P: posterior; S: superior; I: inferior; L: lateral; M: medial.

approximately equal numbers of males and females were included in the analysis; subadult specimens are unattributed to sex. The sample for *H. sapiens* was drawn from a single population so that there was no potential for population-level differences (e.g., Strand Viðarsdóttir et al., 2002; Smith et al., in press) to confound the analysis. This population represents an archaeological sample of Nubians housed at Arizona State University. Data were collected using a MicroScribe (Immersion Corp., San Jose, CA) digitizer (either a model 3D or 3DX, depending when data were collected). Landmarks were identified and marked using pencil or artist's putty before digitizing and each specimen was mounted in a stable elevated ring so that all landmarks could be obtained in a single series. Data were collected either by CAL and WHK (extant ape) or by CET (extant humans). Tests for inter- and intraobserver error for this dataset are presented in Terhune et al. (2007) and suggest that these sources of error are minimal.

To ensure even sampling throughout ontogeny, specimens were assigned to growth stage based on dental eruption standards outlined by Schour and Masseler (1941). We identified five separate growth stages: infant (deciduous teeth only), juvenile (M1 erupting or erupted), adolescent (M2 erupting or erupted), young adult (M3 erupting or erupted but spheno-occipital synchondrosis unfused), and adults (M3 erupted and spheno-occipital synchondrosis fused). In humans, these stages correspond roughly to chronological ages 0 to 6 years (infant), 6 to 12 years (juvenile), 12 to 18/20 years (adolescent), 18/20 to <25 years (young adult), and >25 years (adult) (Ubelaker, 1989; White, 2000). In comparison, known eruption times for the permanent molars in the African apes (*P. troglodytes* and *G. gorilla*) are approximately 3 to 3.5 years for M1, 6.5 to 7 years for M2, and 10.25 to 11 years for M3 (summary data presented in Smith et al., 1994); no comparable data are available for *P. paniscus*.

TABLE 1. Extant samples used in this analysis and their subdivision by relative age category

	Infant (deciduous teeth)	Juvenile (M1 erupted)	Adolescent (M2 erupted)	Young adult (M3 erupted)	Adult females/males (SOS fused)	Total
Pan troglodytes[ab]	15	23	13	9	35/35	130
Pan paniscus[c]	12	12	7	5	21/15	72
Gorilla gorilla[ab]	15	12	6	12	34/33	112
Homo sapiens[d]	7	10	8	5	20/20	70

[a] Cleveland Museum of Natural History, Cleveland, OH.
[b] Powell Cotton Museum, Birchington, UK.
[c] Royal Museum for Central Africa, Tervuren, Belgium.
[d] Arizona State University, Tempe, AZ.

TABLE 2. Landmark definitions

No.	Landmark definition
1[a]	Intersection of the infratemporal crest and sphenosquamosal suture
2[a]	Most lateral point on the margin of foramen ovale
3	Most anterior point on the articular surface of the articular eminence
4	Most inferior point on the entoglenoid process
5	Most medial point on the articular surface of the articular eminence
6[a]	Most lateral point on the articular surface of the articular eminence, at the anteroposterior midpoint of the articular eminence
7	Left of the articular eminence
8	Left of the mandibular fossa
9	Most inferior point on the postglenoid process
10	Point on the anterior margin of the tympanic closest to the carotid canal
11[a]	Petrous apex (most anteromedial point on the inferior surface of the temporal bone)
12	Most posterolateral point on the margin of the carotid canal
13	Most lateral point on the vagina of the styloid process (whether process is present or absent)
14	Most lateral point on the margin of the stylomastoid foramen
15	Most lateral point on the jugular fossa
16[a]	Left of the inferior tip of the mastoid process
17	Most inferior point on the external acoustic meatus
18	Most inferolateral point on the tympanic element of the temporal bone.
19	Point of inflection where the braincase curves laterally into the supraglenoid gutter, in coronal plane of mandibular fossa
20[a]	Point on superolateral margin of zygomatic arch at the anteroposterior location of the postglenoid process
21	Auriculare
22	Porion
23[a]	Asterion

[a] Landmark excluded in the fossil analyses.

Although these age categories are unlikely to be exactly homologous across species, the sequence of molar eruption is similar among hominids (Godfrey et al., 2001) and these eruption patterns are important markers of weaning (first molar) and the onset of sexual maturation (third molar) in all of these taxa (Smith, 1991, 1994). Further, given uncertainties in estimating developmental age from dental eruption, we follow previous studies (e.g., O'Higgins and Collard, 2002; Mitteroecker et al., 2004, 2005; McNulty et al., 2006; McNulty, 2012; Singleton, 2012) and assess patterns of ontogenetic allometry (i.e., shape change in relation to size), rather than growth (change in size with age) or development (change in shape with age).

Data analysis

We used geometric morphometric methods (e.g., Bookstein, 1991; Zelditch et al., 2004; Slice, 2005) to examine patterns of temporal bone shape variation and ontogenetic allometry within our sample. Configurations were scaled, translated, and rotated using Generalized Procrustes Analysis (GPA); Principal Component Analyses (PCA) were then performed using these transformed configurations, which facilitated comparison of shape differences among species and age categories. Allometric patterns throughout ontogeny were first examined for each species separately, and shape differences among specimens were visualized using wireframe diagrams. For each species, we performed a multivariate regression of the Procrustes rotated coordinates on the natural log of temporal bone centroid size. A permutation test with 9,999 iterations was performed to assess the significance of the relationships between the independent and dependent variables. Shape variation within the entire sample (i.e., all specimens and species pooled) was then examined using PCA. A multivariate regression with a permutation test (9,999 iterations) was performed for this combined dataset to assess the relationship between shape and size across species. All of these analyses were performed in the programs Morphologika (O'Higgins and Jones, 1998) and MorphoJ (Klingenberg, 2011).

Divergence of the morphological trajectories among species was examined by calculating the angles between the regression coefficients produced by a multivariate regression of shape (i.e., the Procrustes rotated coordinates) onto the natural log of centroid size (McNulty et al., 2006; Collyer and Adams, 2007; Drake and Klingenberg, 2008; Adams and Collyer, 2009; Piras et al., 2010). For this analysis, all taxa were subjected to a single GPA which placed the entire sample into a common morphospace; using these rotated coordinates, we then performed separate multivariate regressions for each species and extracted the regression coefficients as the trajectory vector (Anderson and Ter Braak, 2003; Collyer and Adams, 2007; Adams and Collyer, 2009; Piras et al., 2010). Angles between pairs of taxa were calculated as the arccosine of the dot product of the vectors, and the significance of these angles was assessed by performing a permutation test of the regression residuals with 9,999 iterations, where group membership was randomly shuffled but the sample sizes for each age category were held constant (McNulty et al., 2006). These analyses were conducted in the program *R* (*R* Development Core Team, 2008) using code modified from the package 'geomorph' (Adams and Otárola-Castillo, 2012).

Fossil analyses

Following examination of variation in the extant taxa, fossil temporal bones of *A. afarensis* were incorporated into the analyses. These specimens included A.L. 333-105 (a subadult with an unerupted M1 visible in its crypt), A.L. 333-45 (a presumptive young adult male with cranial vault sutures that are largely unfused, both ecto- and endocranially), A.L. 822-1 (a presumptive adult female), and A.L. 444-2 (a presumptive adult male) (Johanson et al., 1982; Kimbel et al., 1984, 1994, 2003, 2004; Kimbel and Delezene, 2009; Kimbel and Rak, 2010). These specimens are distributed throughout the geological sequence at Hadar, spanning approximately 0.2 myr (A.L. 333 = ∼3.2 Ma; A.L. 822-1 = ∼3.1 Ma; A.L. 444-2 = ∼3.0 Ma) (Kimbel et al., 2004; Kimbel and Rak, 2010). Configurations for A.L. 333-45, A.L. 333-105, and A.L. 444-2 were collected by W.H.K. and C.A.L. directly from the original fossil specimens; A.L. 822-1 was digitized by CET using a reconstruction performed by Kimbel and Rak (2010). Although each of the fossil specimens has undergone some form of postmortem deformation or damage (Kimbel et al., 1984, 1994, 2004; Kimbel and Rak, 2010), plastic deformation of the temporal bones is relatively minimal. We recognize the potential for postmortem deformation to impact the results presented here, and our fossil analyses should be evaluated in light of this possibility.

Along with data from the extant taxa, these fossil specimens were analyzed with PCA, using a reduced landmark dataset of 16 points which was necessary to accommodate the fragmentary fossil specimens (see Table 2). Due to small sample sizes, no statistical analyses of the fossil specimen distribution in morphospace were performed to compare this species to the extant taxa. A discriminant function analysis (DFA) with jackknife cross-validation (Sokal and Rohlf, 1995; Smith et al., 2007) was used to examine how the uncategorized fossil specimens statistically compared with the extant taxa. Two DFAs were conducted: the first examined which taxon each of the fossil specimens was most similar to; the second examined which age group the fossils resembled most. These DFAs were performed using the scores from the first 30 PC axes (representing 95% of the total sample variation), and prior probabilities were set equal to group size. Discriminant function analyses were conducted in the program JMP Pro, version 9 (SAS Institute Inc., 2010).

RESULTS

Extant taxa

Ontogenetic allometric shape change within species. For all species in our sample, the multivariate regression analyses revealed a significant relationship ($P < 0.0001$) between shape and size throughout ontogeny (Fig. 2). These regressions explained between 16% (*H. sapiens*) and 43% (*P. paniscus*) of the shape variation.

Examination of the wireframe diagrams (Fig. 3, Table 3) describing shape change for each species indicates that in all taxa the temporal bone increases in mediolateral (ML) width (i.e., expands laterally relative to the sagittal plane) and superoinferior (SI) height

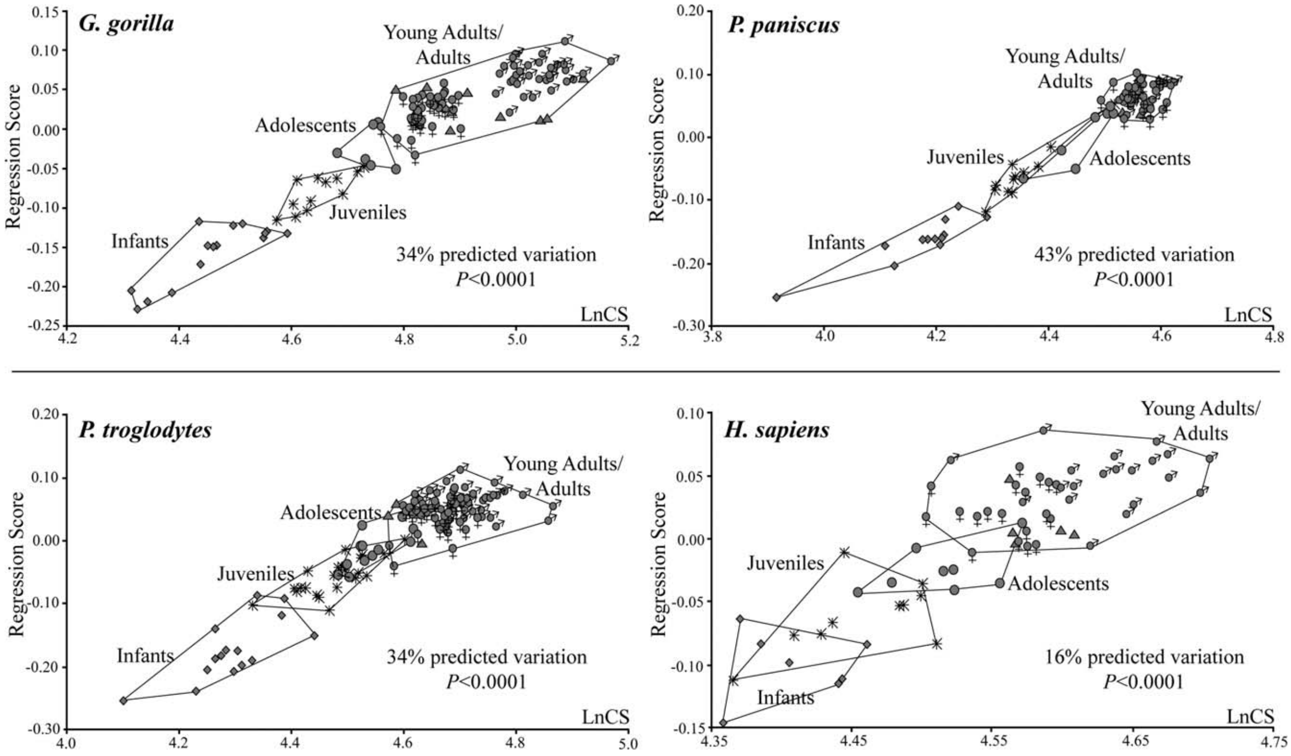

Fig. 2. Bivariate plots of the multivariate regression scores (*y*-axis) versus the natural log of centroid size (LnCS, *x*-axis) for each of the extant species in the analysis. Plots show the distribution of shape in relation to size for each age group. Diamonds = infants; stars = juveniles; circles = adolescents; triangles = young adults; female and male symbols represent adult females and males, respectively. Polygons illustrate the distribution of each of the age groups in morphospace and are not statistically meaningful.

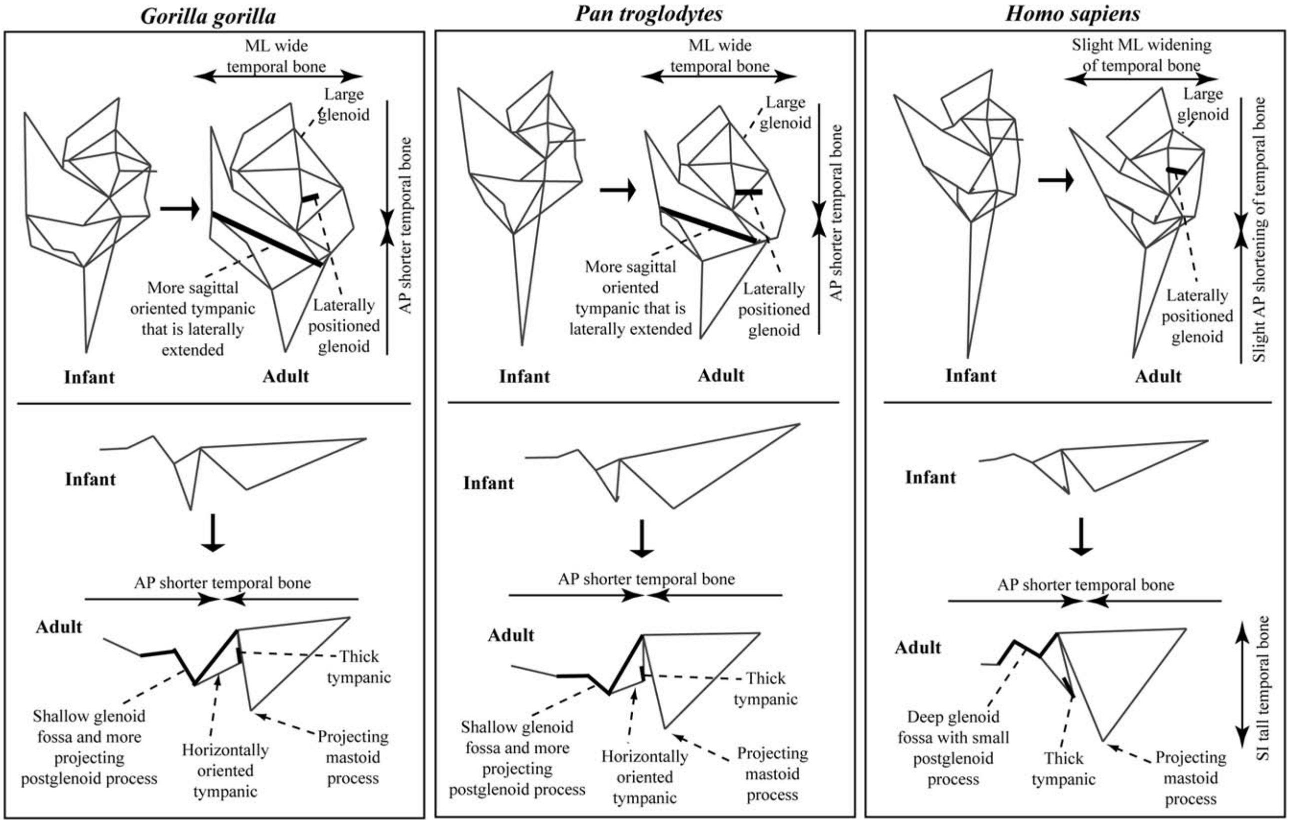

Fig. 3. Wireframe diagrams (top: inferior view; bottom: lateral view) representing temporal bone morphology in infants (left) and adults (right) for *G. gorilla, P. troglodytes*, and *H. sapiens* illustrating major morphological changes during ontogeny in relation to changes in temporal bone size. Data for *P. paniscus* are not shown but are essentially identical to *P. troglodytes*. ML = mediolaterally, AP = anteroposteriorly.

(mostly as a consequence of the enlarged mastoid process). In contrast, relative anteroposterior (AP) length—measured from the infratemporal crest to asterion—decreases in all taxa during ontogeny. The mandibular fossa becomes larger, mediolaterally wider, and more laterally positioned in relation to the braincase; the mastoid process increases in size and inferior projection; and the tympanic element thickens (i.e., the distance from the inferior margin of the external auditory meatus to the inferior margin of the tympanic increases).

These wireframe diagrams also reveal distinct patterns of morphological change in humans versus apes in the region of the mandibular fossa and the tympanic element. During ontogeny in the African apes the articular eminence becomes less inclined relative to the mandibular fossa proper (e.g., the peak of the articular eminence is less inferiorly projecting relative to the roof of the mandibular fossa), while the opposite is the case in *Homo*. Infant apes tend to have a more coronally oriented tympanic that becomes more sagittally oriented and laterally projecting during ontogeny [although the tympanic is still more coronally oriented in adult apes than in humans, as documented by Dean and Wood (1981, 1982)]. Additionally, the tympanic (when viewed in lateral aspect) is vertically oriented in infant apes, gradually tilting posteriorly during ontogeny to become more horizontally oriented (e.g., flat) in adults (Fig. 3). No corresponding changes in the form of the tympanic were observed in humans.

Ontogenetic allometry in the combined extant sample. When all taxa were compared in a single PCA, the species separated well along both PC axes 1 and 2, with distinct trajectories in morphospace observable for each taxon (Fig. 4A). There is considerable overlap of the trajectories for the African apes, however. The individual PC axes show that PC 1 primarily separates apes and humans. The distribution of specimens along this axis also indicates that juvenile apes tend to be more similar in shape to both subadult and adult humans than great ape adults. On PC 2, specimens are distributed primarily on the basis of age group.

Regression of the shape coordinates on centroid size reveals that, in this combined sample, approximately 24% of the shape variation is explained by size. This regression plot (Fig. 4B) illustrates common trajectories for the African apes, with little to no overlap with the human distribution. Notably, the trajectory for *Gorilla* appears considerably extended compared with that of the other taxa. Similarly, the trajectory for *P. troglodytes* is extended past that of *P. paniscus*.

Ontogenetic angles. Examination of the angles describing the ontogenetic allometric trajectories reveals that all trajectories are statistically significantly different (Table 4). The largest angular differences were observed between *H. sapiens* and each of the ape species (58.5–65.5°), whereas the smallest difference was between *P. paniscus* and *P. troglodytes* (20.5°).

TABLE 3. Character state changes along PC 1 for each of the extant species examined

	H. sapiens		*P. troglodytes*		*P. paniscus*		*G. gorilla*	
Character	Infant	Adult	Infant	Adult	Infant	Adult	Infant	Adult
Articular eminence inclination	Shallow	Steep	Steep	Shallow	Steep	Shallow	Steep	Shallow
Asterion position	Posterior	Anterior	Posterosuperior	Anteroinferior	Posterosuperior	Anteroinferior	Posterior	Anterior
Entoglenoid projection	Inferior	Posterior	Posterior	Inferior	–	–	Posterior	Inferior
Entoglenoid size	Small	Large	–	–	–	–	Small	Large
Mandibular fossa depth	Shallow	Deep	Deep	Shallow	Deep	Shallow	Deep	Shallow
Mastoid size/ projection	Small	Large	Small	Large	Small	Large	Small	Large
Petrous orientation	–	–	–	–	–	–	–	–
Postglenoid process size (inferior projection from porion)	Small	Large	Small	Large	Small	Large	Small	Large
Preglenoid plane size	Large	Small	Small	Large	Small	Large	Small	Large
Suprameatal crest size (porion to auriculare)	Large	Small	Large	Small	Large	Small	Large	Small
Temporal bone height (SI)	Short	Tall	Short	Tall	Short	Tall	Short	Tall
Temporal bone length (AP)	Longer	Shorter	Long	Short	Longer	Shorter	Long	Short
Temporal bone width (ML)	Narrow	Wider	Compressed	Wide	Compressed	Wide	Compressed	Wide
Glenoid fossa placement	Medial	Lateral	Medial	Lateral	–	–	Medial	Lateral
Glenoid fossa size	Small	Large	Small	Large	Small	Large	Small	Large
Glenoid fossa width (ML)	Compressed	Wide	Compressed	Wide	Compressed	Wide	Compressed	Wide
Tympanic orientation	–	–	Coronal	Sagittal	Coronal	Sagittal	Coronal	Sagittal
Tympanic inclination	Horizontal	Vertical	Vertical	Horizontal	Vertical	Horizontal	Vertical	Horizontal
Tympanic projection/extension	–	–	Medial	Lateral	Medial	Lateral	Medial	Lateral
Tympanic thickness	Thin	Thick	Thin	Thick	Thin	Thick	Thin	Thick
Zygomatic root size	–	–	Small	Large	Small	Large	Small	Large

Character states are defined as compared between infant and adult specimens and are not intended to be absolute interpretations of morphology among taxa. Note that many of these characters are likely correlated with one another.

–, No change.

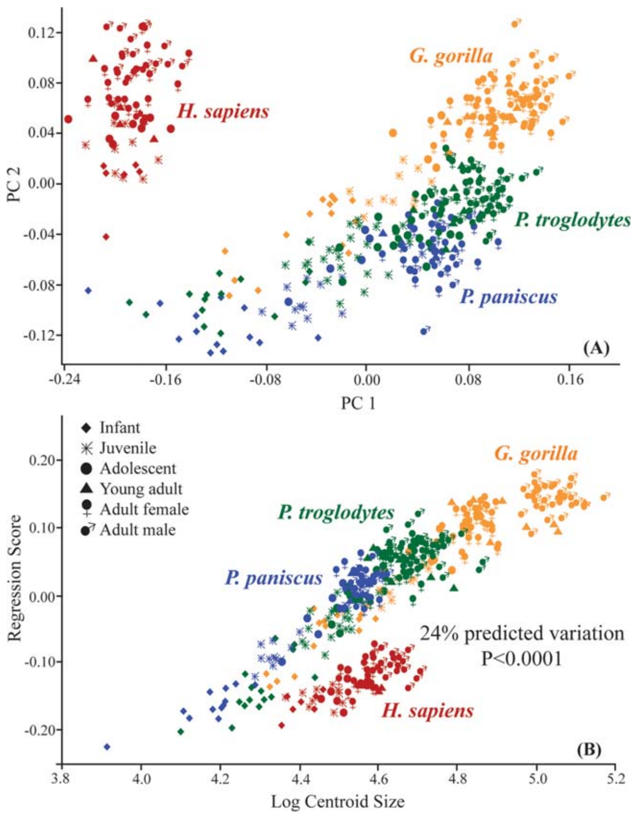

Fig. 4. Principal component and regression plots for the combined extant sample. **A**: PC 2 (y-axis) versus PC 1 (x-axis); **B**: multivariate regression scores (y-axis) versus natural log of centroid size (x-axis). PCs 1 and 2 account for 43% and 13% of the variation in the sample, respectively.

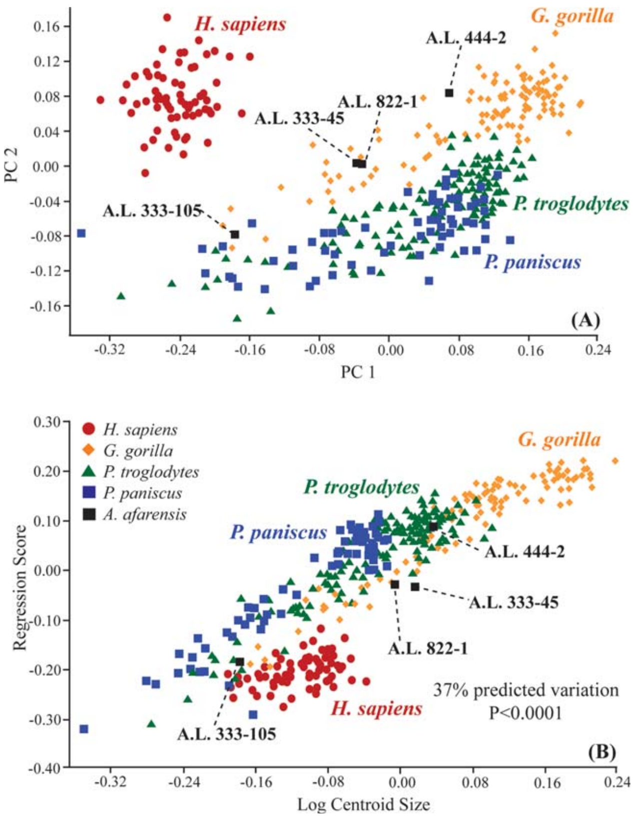

Fig. 5. Principal component and regression plots for the extant and fossil samples. **A**: PC 2 (y-axis) versus PC 1 (x-axis); **B**: multivariate regression scores (y-axis) versus natural log of centroid size (x-axis). PCs 1 and 2 account for 52% and 12.5% of the variation in the sample, respectively.

Fossil analyses

When the fossil specimens were included in the PCA, the distribution of the extant specimens in morphospace was very similar to the analyses in which only they were included (Fig. 5). Thus, despite reduction of the dataset from 23 to 16 landmarks, the pattern of shape variation is maintained. On all axes the fossil specimens fall within the portion of morphospace occupied by the extant taxa. When PC1 and PC2 (which explain ~65% of the sample variation) are plotted against one another (Fig. 5A), the *A. afarensis* specimens largely fall within the same morphospace occupied by the *Gorilla* sample. The A.L. 333-105 subadult falls within the range of infants of the ape species (commonly on the lower end of the *Gorilla* distribution or between the infant and juvenile *Pan* specimens). Both A.L. 333-45 and A.L. 822-1 fall within the middle of the *Gorilla* distribution, appearing most similar to juvenile gorillas, while A.L. 444-2 is most similar to young adult *Gorilla*. The regression plot (Fig. 5B) shows a similar distribution of specimens in morphospace, but indicates some affinity of A.L. 333-105 with infant humans, and A.L. 444-2 falls within the distribution of adult *P. troglodytes*. Results of the discriminant function analysis found that A.L. 333-105 was classified as *P. paniscus,* and was placed in the adolescent age category, A.L. 333-45 and A.L. 822-1 were both classified as *P. troglodytes* and were identified as adults, and A.L. 444-2 was classified as *Gorilla* and was placed in the young adult age group.

TABLE 4. Pairwise differences between ontogenetic trajectories as calculated in the multivariate regression analysis

	G. gorilla	*P. paniscus*	*P. troglodytes*	*H. sapiens*
G. gorilla	–			
P. paniscus	37.1 <0.0001	–		
P. troglodytes	31.5 <0.0001	20.5 0.0059	–	
H. sapiens	65.5 <0.0001	58.5 <0.0001	62.7 <0.0001	–

Values provided for each comparison are the angle (in degrees) and the P-value as indicated by the permutation test. All comparisons are statistically significant.

Ontogenetic allometric shape change in A. afarensis. The wireframes for the fossil specimens (Fig. 6) suggest that, as in the extant taxa, the mandibular fossa becomes larger and more laterally positioned and the size of the postglenoid process increases from the youngest to the oldest *A. afarensis* specimen. However, several features show greater affinity with the human pattern of temporal bone shape change, or are intermediate between apes and humans. In the glenoid region, the mandibular fossa does not deepen appreciably during ontogeny. The tympanic element is the most

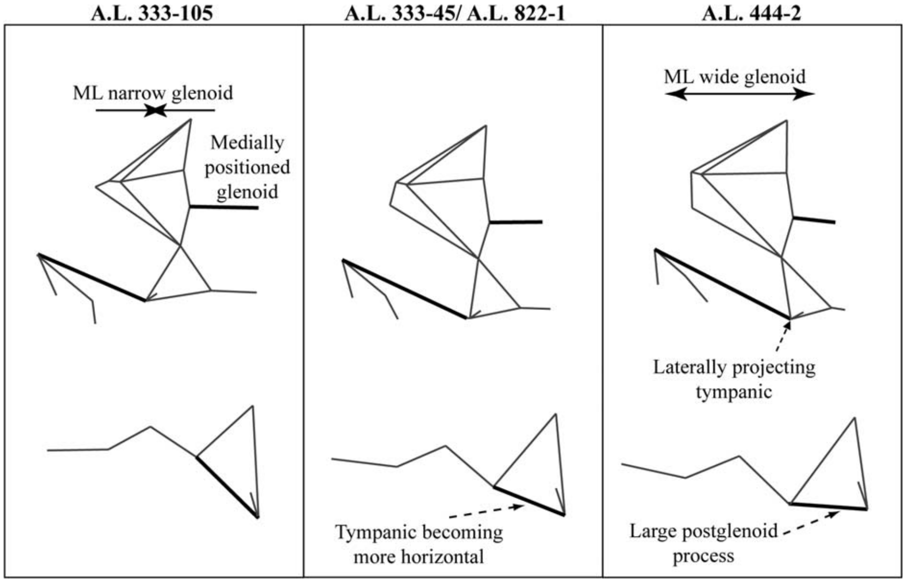

Fig. 6. Wireframe diagrams (inferior view on top, lateral view on bottom) for the fossil specimens with key morphological changes highlighted. A.L. 333-45 and A.L. 822-1 are shown together because of their close proximity in morphospace. ML= mediolaterally.

unique morphologically in contrast to the apes. Unlike the strong change from a coronal to sagittal orientation of the tympanic (in inferior view) during ontogeny in the apes, this feature is relatively stable during ontogeny in *A. afarensis*, as was observed in humans. The tympanic of *A. afarensis* does become more laterally projecting in the adult, but not nearly to the same extent as observed in *Gorilla*.

DISCUSSION

In this study we evaluated temporal bone ontogeny in extant African apes and humans and applied these data to the fossil hominin species *A. afarensis*. We addressed two related questions: first, we assessed how temporal bone shape changes in relation to size during ontogeny in African apes and humans; and second, we examined whether these morphological changes represent parallel or divergent ontogenetic trajectories among taxa.

Temporal bone shape change during ontogeny in humans and African apes

In all extant taxa, temporal bone shape changed considerably across age groups. This study identified consistent patterns of shape change common to all species, mostly associated with changes in relative dimensions of the temporal bone (ML, AP, and SI directions) and that of its components. For example, in all taxa the mandibular fossa shifts laterally in relation to the brain case and increases in size, the mastoid process becomes more projecting, and the tympanic element thickens. These patterns of ontogenetic allometric shape change are broadly consistent with those identified previously for humans (Wright and Moffett, 1974; Dumas et al., 1986; Nickel et al., 1988; Itoh et al., 1995; Katsavrias and Dibbets, 2001, 2002; Katsavrias, 2002). Furthermore, many of the observed shape differences between apes and humans (e.g., differences in the angulation of the tympanic and petrous elements) are consistent with previous work by Dean and Wood (1981, 1982, 1984).

We further identified several differences between the African apes and humans in the tympanic element and mandibular fossa that have not been discussed in detail previously. In apes, as temporal bone size increases, the tympanic element changes position considerably, shifting from a more coronal (in inferior view) and vertical (in lateral view) orientation, to a more sagittal and horizontal orientation (as identified by Dean and Wood, 1984). The tympanic element is also considerably more laterally projecting in adult apes. No such changes occur in the tympanic element in humans; instead, the morphology of this component of the temporal bone appears relatively stable during human ontogeny. Similarly, although previous work has highlighted differences in mandibular fossa form among adult great apes and humans (e.g., Ashton and Zuckerman, 1954), these researchers did not identify any ontogenetic changes in the great ape mandibular fossa. In contrast, the present study suggests considerable differences in mandibular fossa ontogeny between African apes and humans. Our data suggest that in infant apes the fossa is relatively deep (e.g., the articular eminence appears more inclined relative to the mandibular fossa), but during ontogeny the fossa becomes shallower relative to the eminence (e.g., the articular eminence becomes less inclined). In humans, this pattern is reversed: in infant humans, the mandibular fossa is shallow but deepens during ontogeny.

Unsurprisingly, the ontogenetic differences identified here between the African apes and humans are concentrated in regions of the temporal bone that have been considered the most phylogenetically informative for these taxa (Weidenreich, 1943; Ashton and Zuckerman, 1954; Kimbel, 1986; Lockwood et al., 2002; Kimbel et al., 2004). Our data suggest that some of these unique human temporal bone morphologies are present very early in ontogeny (e.g., the more sagittally and vertically oriented tympanic element) and are not acquired as a result of postnatal shape change, whereas other regions (i.e., the mandibular fossa) undergo considerable morphological change postnatally. One possible explanation for these two distinct patterns may be related to the onset of mastication during ontogeny and the concomitant masticatory forces that are experienced in the mandibular fossa, but which are absent or less pronounced in the tympanic element.

Are ontogenetic shape trajectories for the hominid temporal bone divergent or parallel?

The data presented here suggest that the ontogenetic allometric trajectories for the temporal bone are statistically significantly different for all taxa examined. The human trajectory is the most distinct, both when visualized in morphospace and when angles among these trajectories are quantified. Furthermore, although the trajectories for all three species of the African apes appear similar when plotted together, they are also statistically distinct from one another. These results therefore suggest unique patterns of postnatal temporal bone ontogeny even in these closely related ape species. These findings are congruent with analyses by O'Higgins and colleagues (O'Higgins and Collard, 2002; Cobb and O'Higgins, 2004; Strand Viðarsdóttir and Cobb, 2004; Mitteroecker et al., 2004), who have argued that differences in adult craniofacial morphology among hominids and papionins are achieved via divergent, rather than parallel, postnatal shape trajectories. Since the present study did not sample prenatal temporal bone morphology it is impossible to determine whether prenatal trajectories in temporal bone ontogeny are parallel or divergent. However, contrary to previous authors who suggest adult craniofacial differences are a product primarily of shape differences established prenatally (Krovitz, 2000; Ponce de León and Zollikofer, 2001; Ackermann and Krovitz, 2002; Lieberman et al., 2007; Boughner and Dean, 2008), the data presented here for the temporal bone indicate that the observed taxonomic differences in adult shape are likely a combined result of differences in the initial shape of the temporal bone and the direction of postnatal shape change (see Cobb and O'Higgins, 2004). These somewhat conflicting results may be in part due to methodological differences (e.g., Procrustes methods vs. Euclidean distance matrix analysis [EDMA]), and/or may reflect different patterns of ontogenetic shape change in different regions of the cranium (e.g., the face vs. the temporal bone).

When the trajectories for the extant species are examined individually, one particularly striking result is the complete separation between adult male and female gorillas in morphospace (Fig. 2). Much of this shape variation likely reflects differences in adult craniofacial size among sexes, but these data may also be indicative of a continued low level of adult male growth (i.e., bimaturism) in gorillas (e.g., Shea, 1986; Leigh and Shea, 1995; Leigh, 1995). Conversely, the complete overlap between adult male and female bonobos (Fig. 2) suggests a lack of continued growth in adult male bonobos, the consequence of which is decreased levels of sexual dimorphism in adult temporal bone morphology in this taxon (as well as lower levels of sexual dimorphism overall [e.g., Shea, 1983b; Leigh and Shea, 1996; Schaefer et al., 2004]).

The PC plots and the regression analyses both suggest considerable differences in the lengths of these trajectories among species when all extant taxa are included in the same analysis. In particular, the trajectory for *Gorilla* extends well past that of both *P. paniscus* and *P. troglodytes*. The temporal bones of adult gorillas reach absolutely larger sizes than those of any of the other species, although the position of the gorilla infants in morphospace is closest to juvenile or adolescent chimps and bonobos. This extension and displacement of the ontogenetic trajectory in *Gorilla* suggests a contribution of ontogenetic scaling (e.g., Shea, 1983a,b) to temporal bone shape variation among great ape adults. Similarly, the trajectory for *P. troglodytes* extends slightly beyond that of *P. paniscus*, suggesting again that at least some aspects of shape differences among *P. troglodytes* and *P. paniscus* are a result of prolonged growth in chimpanzees (or, alternatively, truncated growth in *P. paniscus*). Although we did not specifically test hypotheses of heterochrony here, this finding is consistent with previous research suggesting that in some aspects of cranial morphology bonobos are paedomorphic in comparison to chimpanzees (e.g., Shea, 1983a,b; Lieberman et al., 2007).

Temporal bone ontogeny in Australopithecus afarensis

Although the sample of *A. afarensis* temporal bones is small, it spans a considerable amount of size and shape variation, allowing us to examine a range of variation in temporal bone morphology in this species. The youngest specimen (A.L. 333-105) is one of the youngest individuals known for this species (Kimbel et al., 1982), and the oldest specimen (A.L. 444-2) has been shown to fall on the high end of the range of size variation in *A. afarensis* (Lockwood et al., 2000; Kimbel et al., 2004). As is true for all fossil analyses, we assume that these specimens represent morphologies typical of their respective age and sex classes, although it is certainly possible that including different specimens in this analysis may yield slightly different results. Furthermore, the temporal bones of *A. afarensis* recovered to date do not sample the period between the eruption of M1 and young adulthood. Although new specimens from this developmental period may alter our interpretation of temporal bone ontogeny in this species, we suggest that the results presented here predict what any such fossils will look like if and when they are found.

Temporal bone shape change from the developmentally youngest to oldest *A. afarensis* specimens is similar to that observed in the African apes, and appears to show few affinities to that of humans. However, *A. afarensis* lacks the marked shallowing of the mandibular fossa and reorientation of the tympanic element observed in the apes. These morphological differences between *A. afarensis* and the African apes foreshadow the differences observed between *H. sapiens* and the African apes. These findings are consistent with previous characterizations of the *A. afarensis* temporal bone as very ape-like (e.g., Kimbel et al., 1984, 2004). On all PC axes in the fossil analyses, *A. afarensis* specimens fall on the edge of the distribution of the African apes, and are most similar in morphospace to the distribution for *Gorilla*. Thus, although the distribution of the *A. afarensis* specimens shares some affinities with the trajectory observed for humans, the pattern of ontogenetic shape change in the temporal bone of *A. afarensis* appears most similar to that of the African apes, particularly *Gorilla*.

Our evaluation of temporal bone shape in *A. afarensis* is relevant to previous research describing ontogenetic shape variation in the skull of *A. africanus* (Ackermann and Krovitz, 2002; Cobb and O'Higgins, 2004; McNulty et al., 2006; McNulty, 2012). Ackermann and Krovitz (2002) previously suggested that morphological differences among extant hominids and *A. africanus* were established early in ontogeny, but that postnatal facial ontogenetic trajectories among these taxa were parallel, whereas Cobb and O'Higgins (2004) identified significantly divergent postnatal ontogenetic trajectories among apes, humans, and *A. africanus*. As identified in the present study of *A. afarensis*, Cobb and O'Higgins (2004) further suggested that *A. africanus* facial ontogeny shared more affinities with that of the African apes than humans. Work by McNulty and colleagues (McNulty et al. 2006; McNulty, 2012) may at least in part explain the conflict between Ackermann and Krovitz (2002) and Cobb and O'Higgins (2004). Using a combination of the techniques employed by these two studies, McNulty et al. (2006) demonstrated that postnatal ontogenetic trajectories in the extant apes and humans were divergent, but that because of the early establishment of shape differences it made very little difference whether developmental simulations utilized ape or human shape trajectories to "grow" the Taung child into an adult *A. africanus*.

CONCLUSIONS

Features of the temporal bone have a long history in taxonomic and phylogenetic analyses of the hominin skull. Because of the utility of this region, evaluating the ontogeny of the temporal bone is important for fully comprehending the range of variation in extant and fossil taxa, and for the inclusion of subadult specimens in phylogenetic and taxonomic analyses. The data presented here describe distinct patterns of ontogenetic and allometric shape change among the extant apes and humans, as well as a small sample of *A. afarensis*. These data indicate that, despite broadly similar patterns, *Pan*, *Gorilla*, and *Homo* show marked differences in development of the mandibular fossa and tympanic portions of the temporal bone. Both of these regions are frequently identified as having unique morphologies in humans in comparison to great apes and other primate taxa (Weidenreich, 1943; Ashton and Zuckerman, 1954; Kimbel, 1986; Lockwood et al., 2002; Kimbel et al., 2004). These findings further indicate divergent, rather than parallel, postnatal ontogenetic trajectories for temporal bone shape among African apes and humans, a finding which is consistent with analyses by O'Higgins and colleagues (O'Higgins and Collard, 2002; Cobb and O'Higgins, 2004; Strand Viðarsdóttir and Cobb, 2004; Mitteroecker et al., 2004) regarding development of the hominid face. Although our analysis did not specifically test hypotheses of heterochrony among the species examined, the results of this study are also consistent with previous suggestions of ontogenetic scaling of the great ape skull (Shea, 1983a,b; Lieberman et al., 2007).

Although we are limited by the number and age distribution of the fossil specimens available for *A. afarensis*, examination of the fossil specimens in the context of the extant data suggests that the pattern of ontogenetic shape change in *A. afarensis* is more similar to that of the African apes, particularly *Gorilla*, than to that of humans. *A. afarensis* temporal bone morphology does, however, display a combination of great ape and human features and patterns of growth and development. These findings are consistent with previous descriptions of the *A. afarensis* temporal bone that describe the morphology of this region as very ape-like (e.g., Kimbel et al., 2004).

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