

# Functional Morphology of the First Cervical Vertebra in Humans and Nonhuman Primates

EVELYN MANFREDA, PHILIPP MITTEROECKER,\* FRED L. BOOKSTEIN, AND KATRIN SCHAEFER

The cervical vertebral column bears or balances the weight of the head supported by the nuchal muscles that partly originate from the cervical vertebrae. The position of the head relative to the vertebral column, and consequently locomotion and posture behavior, could thus be associated with the form of the cervical vertebrae. In spite of this assumption and some empirical indications along these lines, primate vertebral morphologies have been reported to be very similar and not clearly related to locomotion. We therefore study the relationship between the morphology of the first cervical vertebra, the atlas, and the locomotion pattern within primates using a geometric morphometric approach. Our analysis is based on a total of 116 vertebrae of adult *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, *Pongo pygmaeus*, *Hylobates lar*, *Macaca mulatta*, *Papio hamadryas*, *Ateles geoffroyi*, and *Alouatta palliata*. On each atlas, 56 landmarks were digitized and superimposed by Procrustes registration. The resulting shape variables were analyzed by principal component analysis, multivariate regression, and partial least-squares analysis. We found that the nine primate species differ clearly in their atlas morphology and that allometric shape change is distinct between the nonhuman primates and *Homo sapiens*. We could further identify morphological features that relate to the species' locomotion pattern. Human atlas shape, however, cannot be predicted by an extrapolation of the nonhuman primate model. This implies that either the primate atlas is generalized enough to allow bipedal locomotion or else the human atlas morphology is a unique adaptation different from that in the more orthograde nonhuman primates. *Anat Rec (Part B: New Anat)* 289B:184–194, 2006. © 2006 Wiley-Liss, Inc.

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## INTRODUCTION

A major interest in primate evolutionary morphology is the relationship between locomotion and bony morphology in recent primates. Frequently, models of functional morphology have been used to infer positional behavior in extinct taxa. Skeletal ele-

ments that are typically correlated with locomotion patterns are, for example, the hip bones, the limbs, and the vertebral column (Baba, 1985; Hildebrand et al., 1985; Tuttle and Watts, 1985; Fleagle and Meldrum, 1988; Gebo, 1993; Aiello and Dean, 2002). Our understanding of vertebral

morphology is largely influenced by qualitative anatomical descriptions such as the classic studies of Schultz et al. (1961) and Ankel (1967, 1970, 1972). Recent and quantitative studies that focus on specific vertebrae deal with the lumbar vertebrae only, so that relatively little is known about the functional morphology of the cervical vertebrae.

The cervical spine bears less weight than other parts of the body, but it still bears or balances the weight of the head. The nuchal muscles connect the cervical vertebrae with the occipital part of the cranium to enable the active movement of the head. The mass and force of the nuchal muscles depend on the position of the head relative to the vertebral column as well as on the weight of the head (Schulz, 1942). Allometry, the effect of (body) size on shape, is therefore also expected to account for some morphological variation observed in cervical vertebrae. Additionally, specific phy-

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logenet histories might contribute to the atlas morphology in a way that is unrelated to any functional causes. However, Oxnard (1998, 2000) elaborated that while phylogenetic relationships can be more reliably read from the overall morphology of organisms, species differences of single isolated structures often reflect adaptations to the functional and behavioral milieu.

These considerations are in contrast to previous findings that locomotor specialization is not clearly reflected in vertebral morphology (Ankel, 1967, 1970, 1972; Ankel-Simmons, 2000). Largely based on qualitative descriptions, she stated that vertebral morphology of Old and New World monkeys is nearly uniform and that the assignment of single vertebral elements to taxa at the family level is difficult and taxonomic identification at the generic level nearly impossible. In other words, the primate vertebral column must be considered as relatively unspecialized among primates. "Therefore, animals can do more functionally than may be indicated by structure; and not all morphological features have a functional explanation. From many attempts to correlate function and morphology in primates, we learn that it is not possible to deduce function from morphology alone" (Ankel, 1972: p. 236). Ankel also argued in 1967 that human vertebral morphology is not specialized enough to allow major deductions about locomotion from hominin fossil material. She concluded that the vertebral column of primates is both morphologically and functionally generalized so that, even without large morphological changes in the construction of the basic anatomical plan, there is the possibility of walking erect. If the functional potency of a morphological feature is high, this structure is not likely to undergo morphological specialization during evolution. The erect human vertebral column, she argues, is more a functional than a morphological specialization.

Recent quantitative analyses do not seem to support Ankel's line of argument. Several authors studying lumbar vertebral morphology of primates report significant species differences and partly relate them to locomotion and postural behavior (Rose, 1974; Swindler and Wood, 1982; Shapiro,

1993, 1995; Ward, 1993; Johnson and Shapiro, 1998; Sanders, 1998; Shapiro and Simons, 2002; Martelli and Schmid, 2003; Nakatsukasa and Hirose, 2003; Shapiro et al., 2005). These studies are in agreement with results obtained from broader comparisons of vertebral morphology among mammalian taxa (Giffin, 1995; Boszczyk et al., 2001; Sargis, 2001; Argot, 2003; Chen et al., 2005).

Fewer studies have specifically addressed the functional morphology of the atlas, which is, like the axis, an atypical cervical vertebra (Aiello and Dean, 2002). The atlas is ring-shaped, lacking a vertebral body and a dorsal spine. There are two relatively large concave superior facets articulating with the occipital condyles of the head. Aiello and Dean (2002) pointed out that these superior articular facets are more concave in apes than in modern humans and conclude that this may be an adaptation for extending the head further back. Similarly, Olivier (1964) and Gommery (1996, 1997) described the dorsal part of the facies articularis superior (the retroglenoid tubercle) as being the most variable part of the atlas among primates and related its form to locomotion behavior. Olivier (1964) mentioned that a concave and craniodorsally extended cavity with its pronounced tubercle, as seen, e.g., in strepsirrhines, permits a good articulation with the occipital condyles during flexion or extension of the head. The apes, in contrast, exhibit a strongly dorsolaterally projected tubercle with a less concave cavity. In humans, the facets are more flat and the retroglenoid tubercle least prominent and dorsolaterally projected instead of cranially. Gommery (1996) further argued that the morphology of the atlanto-occipital articulation is specific to the angulation of the cranial base and the location of the foramen magnum, allowing large angular movements of the head in Strepsirrhini and reduced movements in humans.

As Aiello and Dean (2002) noted, the midline anterior tubercle on the atlas is very prominent in large apes and points downward rather than forward as it does in humans. Swindler and Wood (1982) reported that the transverse foramen perforating the trans-

verse process is large in chimpanzees and humans as compared to baboons. Le Minor (1997) and Le Minor and Trost (2004) found species-specific distributions for the retrotransverse foramen and for bony ponticles in the primate atlas. Huggare (1992) and Sandikcioglu et al. (1994) correlated modern human atlas morphology with head and neck posture.

In this article, we specifically address the relationship between locomotion pattern and gross morphology of the first cervical vertebra, the atlas, in nonhuman primates and in humans. We test the two general assertions of Ankel (1967, 1972) about the primate vertebral column for the first cervical vertebra: that the atlas morphology is not distinguishable among different primate taxa, and that locomotion behavior has no influence on atlas morphology.

We further assess whether human atlas morphology can be explained as an adaptation to our unique style of locomotion. For this purpose, we model the influence of locomotion pattern on atlas shape for several nonhuman primate species and explore how this model accommodates human atlas. Given the well-known allometric effects on the primate locomotor skeleton (Corruccini, 1978; Shea, 1983; Jungers, 1984, 1985) and on the axial skeleton (Majoral et al., 1997; Nakatsukasa and Hirose, 2003), we additionally explore the influence of (body) size on atlas morphology. We specifically expect allometric shape changes at the posterior arcus and the transverse processes where the nuchal muscles attach.

## MATERIALS AND METHODS

Our sample consists of 116 vertebrae from in vivo sexed adult specimens of nine extant primate taxa: *Homo sapiens*, *Gorilla gorilla*, *Pan troglodytes*, *Pongo pygmaeus*, *Hylobates lar*, *Maca mulatta*, *Papio hamadryas*, *Ateles geoffroyi*, and *Alouatta palliata*. The number of specimens and the sex distribution for each taxon are presented in Table 1. Most of the atlas vertebrae belong to the Schultz Collection at the Institute and Museum of Anthropology, University of Zurich, in Zurich, Switzerland. The remainder are from the Department of Zoology and De-

**TABLE 1. Sample of specimens by sex and species, locomotor bouts after Gebo (1996), and average angles describing the convexity of the superior articular facets**

Taxon	Males	Females	Total	Brachiation	Vert. climbing	Bipedal.	Quadrup.	Facet angle
<i>Homo sapiens</i>	10	7	17	0	0	100	0	145.0°
<i>Gorilla gorilla</i>	10	7	17	1	1	0	99	136.0°
<i>Pan troglodytes</i>	7	10	17	1	5	6	89	129.7°
<i>Pongo pygmaeus</i>	4	6	10	10	25	0	12	130.9°
<i>Hylobates lar</i>	8	7	15	50	17	5	0	133.3°
<i>Macaca mulatta</i>	10	8	18	0	7	0	69	127.2°
<i>Papio hamadryas</i>	7	5	12	0	1	0	99	108.7°
<i>Ateles geoffroyi</i>	2	3	5	25	7	6	46	109.1°
<i>Alouatta palliata</i>	3	2	5	0	6	0	47	115.9°
	61	55	116					

partment of Archaeological Biology and Anthropology, Natural History Museum, in Vienna, Austria.

For each specimen, the 3D coordinates of 56 landmarks covering the complete atlas gross morphology were recorded by one of the authors (E.M.) using a MicroScribe-3D digitizer (Table 2). The vertebrae were fixed either with plasticine mass or with glue so that they could be digitized in one session. All of these landmarks are of type II or type III after Bookstein (1991) and Bookstein et al. (2004) due to the lack of juxtapositions of tissues such as bony sutures. Out of a concern for the great digitizing noise for landmarks of that type, we measured one human atlas eight times and found that the largest Procrustes distance among the remeasurements was approximately one-third of the smallest distance among all other atlas shapes. Furthermore, we repeated the analyses skipping the 10 landmarks with the largest measurement error and arrived at the same results as with the full set of landmarks.

The 116 sets of 56 landmarks were superimposed by generalized Procrustes analysis (Rohlf and Slice, 1990; O'Higgins, 2000), resulting in 168 shape variables, called Procrustes coordinates, with 161 degrees of freedom (as the other 7 standardize for position, size, and orientation from the raw coordinates). Information about overall size of the vertebrae is preserved in a variable called centroid size: the associated measure of scale that is approximately uncorrelated with shape in the presence of identical

isotropic Gaussian noise around a fixed mean form (Bookstein, 1991; Dryden and Mardia, 1998). Centroid size is calculated as the square root of the sum of squared distances of a set of landmarks from their centroid. Procrustes distance, the measure of shape difference between two forms, is the square root of the summed squared distances between the positions of the corresponding landmarks after all forms are superimposed. In order to analyze the patterns of differences in this high-dimensional shape space, the Procrustes shape coordinates were subjected to principal component analysis (PCA).

As is customary, linear multivariate regressions of the Procrustes shape coordinates on centroid size of the atlas vertebrae (shape regressions) were used to examine the effects of size on shape. The vector of regression slopes (one slope for each coordinate) was then visualized as an actual shape change.

To assess the influence of locomotion on atlas morphology, we relate the Procrustes shape coordinates to a set of four variables that provide estimates of species-specific locomotion patterns: brachiation, vertical climbing, bipedalism, and quadrupedalism. The values of these four variables for the nine species used in our study are drawn from Gebo (1996), who summarized data reported by several other authors (Fleagle, 1976, 1980; Mendel, 1976; Susman, 1984; Tuttle and Watts, 1985; Cant, 1986, 1987, 1988; Mittermeier, 1978; Hunt, 1991; Gebo, 1992; Doran, 1993). Some of these authors provide locomotion fre-

quencies for traveling and feeding separately, while others supply only totals. The separate locomotor assessments were averaged together for a total locomotion profile (Table 1) as suggested by Gebo (1989).

Instead of relating shape to the four locomotion variables separately or to an arbitrary combination of them, we use a two-block partial least-squares (PLS) analysis (Bookstein et al., 1990, 2003; Rohlf and Corti, 2000) between the shape coordinates and all four of these locomotion variables. When PLS is applied to Procrustes coordinates, this procedure is often called singular warp analysis. PLS describes the multivariate relationship between locomotion and atlas shape in terms of a pair of latent variables (one for shape and one for locomotion) that together have the highest possible covariance or predictive power. The weightings for these two linear combinations are contained in the two respective singular vectors, and the corresponding singular value is the covariance between the two variables so defined. The actual values of the new variables are called latent variable scores (nonshape) or singular warp scores (shape). The word "singular" comes from an ancient algebraic maneuver (see the references cited above).

There further exists a second pair of variables that is (geometrically) orthogonal to the first pair, such that the corresponding scores, the second pair of singular warp scores, exhibit the highest covariance of any vectors so defined (which covariance equals the second singular value). Subsequent

TABLE 2. Landmark descriptions

Number	Type <sup>1</sup>	Description
1	3	The most superior point on the anterior arcus in the midsagittal plane
2	3	The most superior point on the fovea dentis
3	3	The most right point on the fovea dentis
4	3	The most inferior point on the fovea dentis
5	3	The most left point on the fovea dentis
6	3	The most inferior point on the anterior arcus in the midsagittal plane
7L, R	2	Maximum of curvature on the anterior end of the facies articularis superior (FAS); left and right side
8L, R	3	The most lateral extension of FAS
9L, R	3	The most anterior extension of FAS
10L, R	3	The most medial extension of FAS
11L, R	3	Most lateral point of the curvature on the upper superior rim
12L, R	2	Point where the medial end of the sulcus (canalis arteriae vertebralis) meets the upper rim of the foramen vertebrale
13	2	The most posterior point on the superior rim of the arcus in the midsagittal plane
14	2	Most posterior point on the posterior tubercle
15L, R	2	Point where the lateral end of the sulcus (canalis arteriae vertebralis) meets the upper rim of the outline of the arcus posterior
16L, R	3	Most inner point of the curvature where the transverse process meets the arcus posterior
17L, R	2	Most laterally extended tip of the processus transversus
18L, R	2	Junction where the transverse process join in the arcus anterior
19	2	Most anterior point on the arcus anterior in the midsagittal plane
20	2	Most posterior point on the inferior rim of the foramen vertebrale in the midsagittal plane
21L, R	3	Point in the middle of landmark 20 and 22L, R
22L, R	3	Most posterior inferior extension of the foramen transversarium (FT)
23L, R	3	Most lateral inferior extension of FT
24L, R	3	Most anterior inferior extension of FT
25L, R	3	Most medial inferior extension of FT
26L, R	3	Most lateral extension of the facies articularis inferior (FAI)
27L, R	3	Most anterior extension of FAI
28L, R	3	Most medial extension of FAI
29L, R	3	Most posterior extension of FAI
30L, R	3	Most anterior superior extension of FT
31L, R	3	Most lateral superior extension of FT
32L, R	3	Most posterior superior extension of FT
33L, R	3	Most medial superior extension of FT

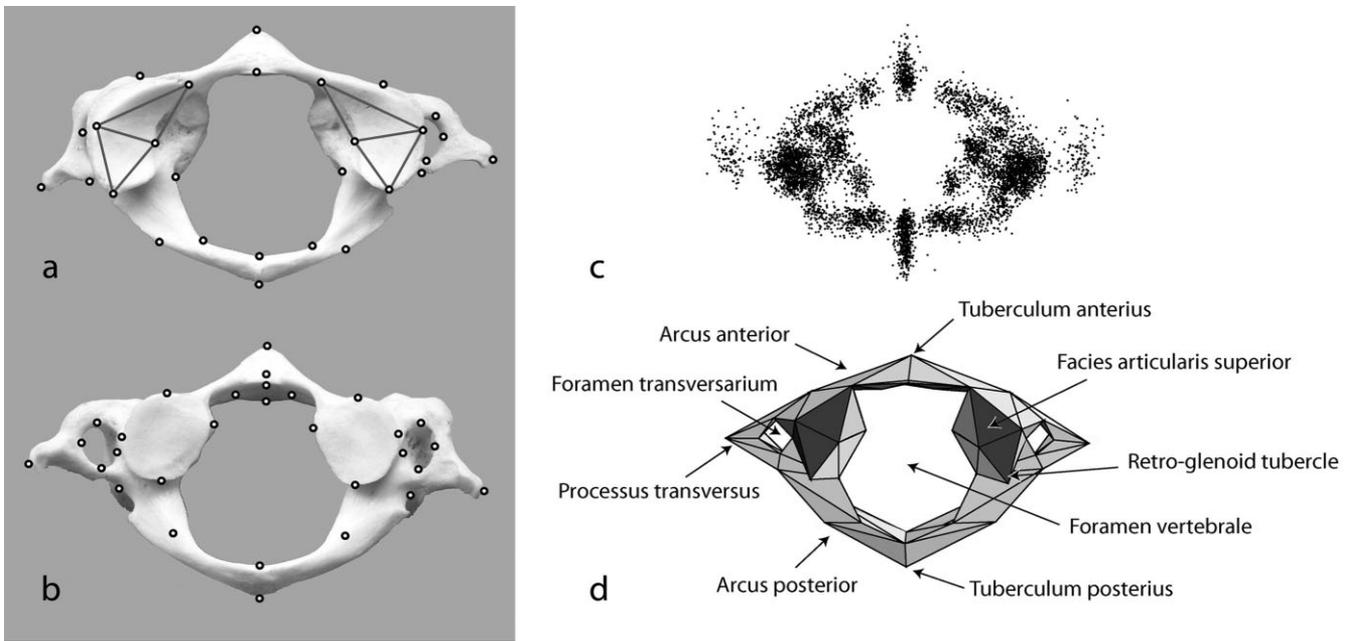
<sup>1</sup>After Bookstein (1991).

pairs of variables are defined analogously. For two blocks of variables (the shape variables and the locomotion variables), the calculation of the singular vectors is based on a singular value decomposition of the cross-block covariance matrix containing all covariances among the two blocks. The maximum number of vectors that can be extracted is the smallest number of variables in either block (in our case, four).

The singular warp scores can be plotted against each other in the spirit of a principal component analysis, and the singular vectors containing the weightings of the Procrustes coor-

dinates can be visualized as shape deformations. Such visualizations are typically conveyed via thin-plate spline deformation grids or by landmark displacement vectors. For the complex three-dimensional structure of an atlas, we used another visualization technique based on surface representations. The configuration of landmarks was triangulated by hand, enabling visualizations as exemplified in Figure 1. To visualize actual shape changes, we show several of these surfaces as they deform along a specific vector in shape space. All analyses and visualizations in this study were performed with Mathematica 5.0.

PLS extracts linear combinations of the four locomotion variables that explain most of the net covariance with atlas shape. The corresponding scores for the shape variables are the scores along those shape changes that covary most with locomotion; it is natural to interpret these as "most responsive" in a functional or developmental sense. In order to test whether a nonhuman model of functional atlas morphology can explain human morphology, we used only the eight nonhuman primate species to calculate the singular vectors. The scores along these vectors were then computed for all species, including humans, to assess whether the human



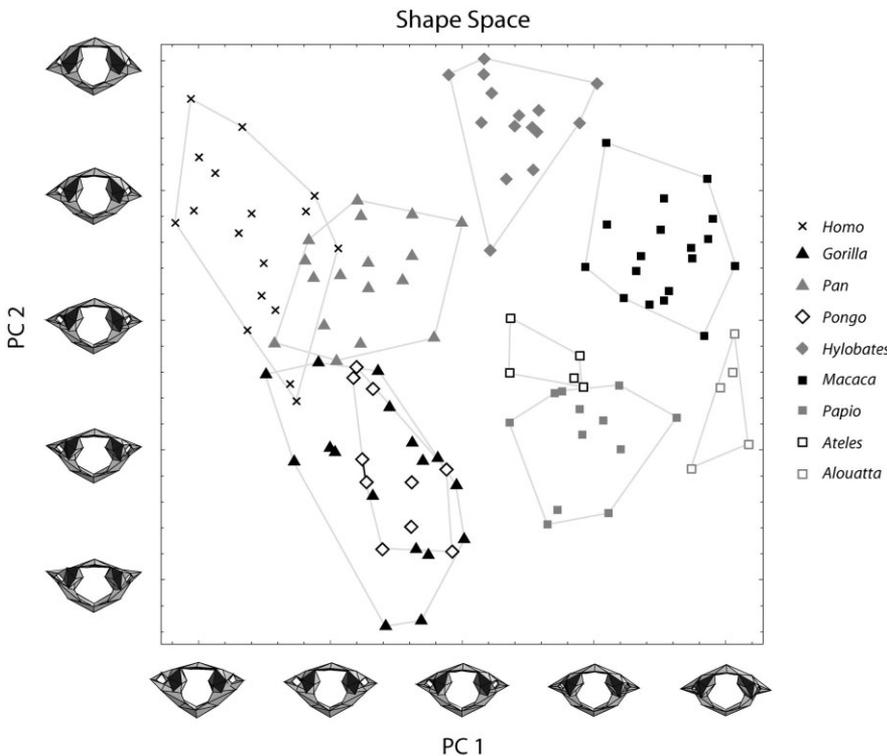
**Figure 1.** Cranial (a) and caudal (b) views of a human atlas. c: All 116 superimposed landmark configurations. d: Surface visualization of the average atlas shape in our sample, showing the major anatomical structures that are visible in a cranial view. The two atlantocranial articular surfaces are drawn in dark gray.

atlas shape is similar to, or is an extrapolation of, the more erect primate taxa along these dimensions.

As several previous studies on atlas

morphology focused on the shape of the superior articular facets, specifically their convexity, we measure the angle in space between the two trian-

gles of landmarks covering the facets (see the gray lines in Fig. 1). We average the angles for the left and right facets on each atlas and subsequently average those for each species.

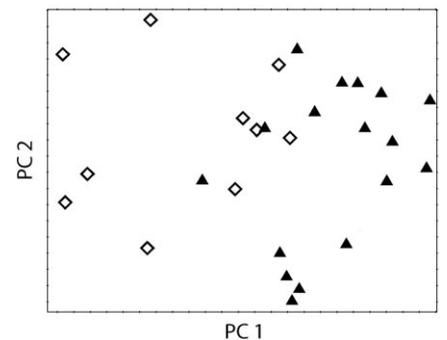


**Figure 2.** PC scores of the Procrustes shape coordinates. The two series of atlas surface representations are deformations of the average shape (the two middle shapes) along the first and second PC, respectively. The shapes correspond to their positions along the axes at which they are drawn.

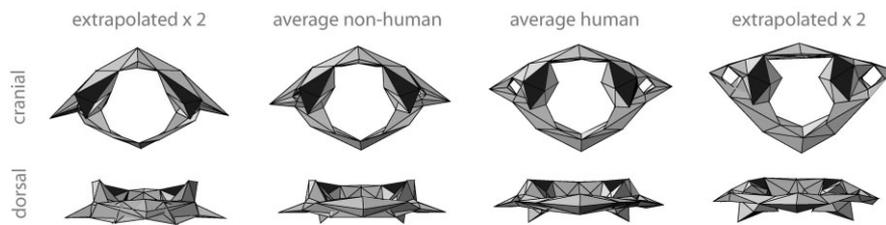
## RESULTS

### Species Differences

Figure 2 presents the results of the principal component (PC) analysis of the Procrustes shape coordinates (relative warps). The first PC explains approximately 16% of total shape variation and the second 13%. Apparently, the species form distinct clusters that (except for *Pongo* and *Gorilla*) only marginally overlap in the first two



**Figure 3.** Separate principal component analysis of *Gorilla* and *Pongo*. The legends for this and the subsequent figures are as in Figure 2.



**Figure 4.** Difference between the average nonhuman and the average human atlas shape (second and third columns, respectively). The first and the last columns are extrapolations of this difference by a factor of two in either direction. Top row: cranial views with the ventral part at the top. Bottom row: dorsal views with the cranial surface at the top.

PCs. Figure 3 specifically addresses the differences between *Gorilla* and *Pongo* by restricting the PCA to those two species. The two scatters clearly differ along the horizontal axis.

Whereas the surface representations along the two axes in Figure 2 illustrate the shape changes that correspond to the first two PCs, Figure 4 is a visualization of the differences between the human and the average nonhuman atlas morphology. Compared to the average nonhuman primate, the atlas of *Homo sapiens* is characterized by a more ventrally inclined processus transversus, a less rounded facies articularis superior, a more robust arcus posterior, and a relatively larger foramen transversarium and thus a differently shaped processus transversus.

To quantify the average shape differences among the nine species, the average configuration of the Procrustes coordinates was computed for each species and the 36 pairwise Procrustes distances (for shape only) computed among these means. Table 3 lists the Procrustes distances among the species together with the species' average centroid size. Confirming the PCA of Figure 2, *Gorilla* and *Pongo* have the lowest Procrustes distance and are thus most similar in this metric. *Homo* is most similar to *Pan* and generally more similar to the great apes than to the other primates. *Alouatta* generally exhibits the largest distances to all other species, including *Homo*. *Gorilla* and *Homo* have the largest atlas vertebrae and *Alouatta* the smallest.

For all 36 Procrustes distances, we carried out a permutation test (10,000 permutations) to assess the significance of the group differences. Except for the pair *Alouatta/Ateles*, all other 35 tests resulted in a  $P$  value less than

0.0004, so that even after a Bonferroni correction the differences remain significant at  $P = 0.014$  or better. The shape distance between *Alouatta* and *Ateles* is significant separately at  $P \sim 0.007$ , in spite of the small samples of both.

In addition to these general shape comparisons, we specifically compared the convexity of the superior articular facets by the angle between the two triangles spanned by the landmarks 7, 8, 9, 10 (Fig. 1, Table 2). The last column in Table 1 presents averages of them by species. Humans possess the flattest facets, followed by the apes, while in *Papio* and *Ateles* the facet is most concave. The average angle in humans differs significantly from each of the others ( $P < 0.002$  by permutation test, with 5,000 permutations each).

### Allometry

To explore the influence of evolutionary and static allometry on atlas shape, we performed multivariate regressions of the Procrustes shape coordinates on centroid size of the atlas vertebra (Fig. 5). The upper part of Figure 5 is a visualization of evolutionary allometry, i.e., the regression pooling all nine species (Cheverud, 1982; Klingenberg, 1998). On the left side are shown cranial and dorsal views of the atlas shape predicted at two standard deviations less than average size. Similarly, the shapes at the right correspond to a larger vertebra. Apparently, the whole atlas, particularly the arcus posterior and its tuberculum, becomes more robust (that is, thicker) when size increases. A permutation test for the linear dependence of shape on size rejects the null hypothesis of no association at  $P <$

0.001; explained shape variance, in units of squared Procrustes distance, is 13.9%.

The two lower parts of Figure 5 visualize static allometry, the (adult) dependence of shape on size within single species. As the eight nonhuman allometries are quite similar in their main features, we contrasted the allometric trend within humans to a pooled estimate of nonhuman allometry. The allometry within *Homo* seems very distinct from the pooled nonhuman estimate. In nonhuman primates, the atlas becomes more robust with increasing size, especially the arcus anterior and the arcus posterior, and the processus transversus becomes longer and more cranially oriented. In humans, however, robusticity of the atlas is decreasing with increasing size, while changes of the lateral extension and angulation of the processus transversus are comparable to the nonhuman allometry.

For most specimens, we also measured the femur head diameter, which is often regarded as a reliable estimate of body size (Ruff, 1988). We therefore additionally performed all calculations of allometry with femur head diameter instead of centroid size. Also, we calculated evolutionary allometry with species-specific estimates of average body weight from Smith and Jungers (1997). All these results (available on request) were virtually identical to the ones using centroid size and are thus not shown here.

### Atlas Shape and Locomotion

To assess the influence of locomotion on atlas shape, we performed a PLS analysis of the Procrustes shape coordinates against the four locomotion variables (brachiation, vertical climbing, bipedalism, and quadrupedalism) in the eight nonhuman primate species. The singular values (the covariances between the four extracted pairs or latent variables) are 1.534, 0.335, 0.098, and 0.047. The first singular warp (the first dimension of the PLS analysis) thus explains 76.2% of the total squared covariance between the shape coordinates and the locomotion variables. The first two singular warps

**TABLE 3. Procrustes distances between the species' average landmark configurations and average centroid size**

	<i>Homo</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>	<i>Hylobates</i>	<i>Macaca</i>	<i>Papio</i>	<i>Ateles</i>	Centroid Size
<i>Homo</i>									5.154
<i>Gorilla</i>	0.1403								5.159
<i>Pan</i>	0.1129	0.1206							4.903
<i>Pongo</i>	0.1319	0.0914	0.1326						4.997
<i>Hylobates</i>	0.1580	0.1715	0.1275	0.1777					4.307
<i>Macaca</i>	0.1650	0.1602	0.1560	0.1598	0.1430				4.309
<i>Papio</i>	0.1795	0.1315	0.1289	0.1407	0.1724	0.1374			4.545
<i>Ateles</i>	0.1730	0.1316	0.1326	0.1430	0.1362	0.1414	0.1244		4.316
<i>Alouatta</i>	0.2243	0.1820	0.2095	0.1835	0.1929	0.1564	0.1767	0.1698	4.251

span 92.8% of the total squared covariance pattern and account for 21.6% of total Procrustes shape variation. The correlation between the

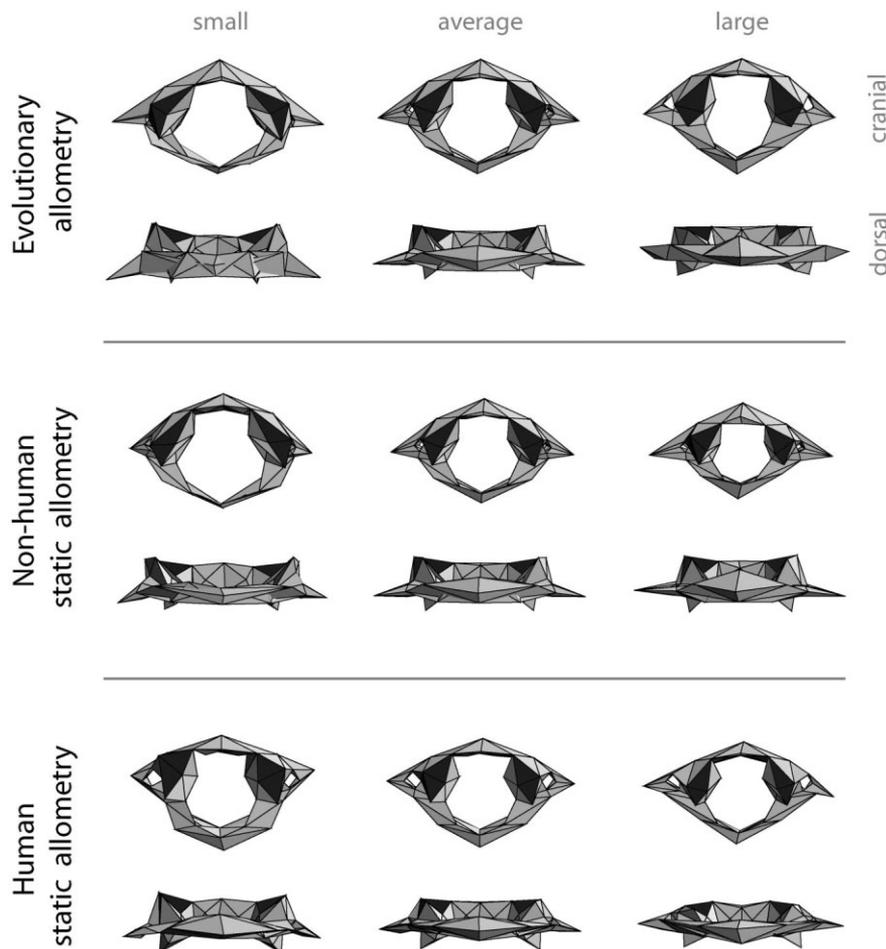
first pair of PLS scores (shape vs. locomotion) is 0.79; between the second pair 0.71. The customary permutation test yields a significance

level for the first two singular warps of  $P < 0.001$  on 5,000 permutations.

Table 4 gives the loadings of the first two singular vectors for the locomotion variables, and Figure 6 shows the scores along these two vectors. As the values for the locomotion variables are identical for all specimens of one species, there is only a single symbol for each species in that figure. The first singular warp seems to estimate erectness versus the extent of quadrupedal posture. High scores are exhibited by the quadrupedal species such as *Gorilla* and *Papio*, while the more upright species such as *Hylobates* and *Pongo* have low scores. The second dimension loads highly on brachiation (Table 4) and is thus differentiating *Hylobates* from *Pongo*, which climbs more frequently than it brachiates.

Because the shape scores in Figure 7 were computed to maximize covariance with the locomotion scores of Figure 6, the patterns must be similar to some extent. *Pongo* exhibits higher scores along component one than expected from its locomotion scores. *Hylobates*, the most frequently brachiating species, has low scores along singular warp one (note its location in the left upper corner of Fig. 7). The quadrupedal species such as *Papio* and *Gorilla* are on the right end of this graph, while the more frequent climbers (*Pongo*, *Macaca*, *Alouatta*) are separated from the others along the second component. When the human vertebral shapes are projected into this space, they fall in an intermediate position on both singular warp axes (the crosses in Fig. 7).

As is apparent from Table 4 and Figure 6, the first singular warp represents



**Figure 5.** Allometric shape change. Top: Evolutionary allometry (regression of shape on size through all nine species). The images in the middle column represent the overall mean shape while the left and right columns illustrate small and large vertebrae, respectively (two standard deviations below or above the mean centroid size). Middle: A pooled estimate of static allometry (regression of shape on size within one species) for the eight nonhuman species. The middle shape is the nonhuman average configuration, and the left and right shapes are morphs toward a smaller and a larger atlas size. Bottom: Static allometry in humans. The human average shape in the middle and shapes corresponding to small versus large human atlases on the left and the right side, respectively.

TABLE 4. Loadings of the first two singular vectors for the locomotion variables

Variables	Singular vector 1	Singular vector 2
Brachiation	-0.450	0.857
Vertical climbing	-0.127	-0.151
Quadruped locomotion	0.883	0.426
Biped locomotion	-0.041	0.249

the difference between more upright and more quadruped moving nonhuman primate species. Figure 8 visualizes the corresponding shape differences as predicted by the loadings of the first singular vector for the shape variables. The middle column of that figure shows the average atlas shape from a cranial (top) and a dorsal view (bottom). The left shape corresponds to an atlas of a more erect primate, while the right atlas is representing a quadruped species. (We scale these differences over three standard deviations to ease the visual interpretation.) Within nonhuman primates, the shape features that are associated with high scores along the first singular warp, and that thus correspond to a more quadruped locomotion, include increased robustness of the atlas, a pronounced tuberculum posterius, and a relatively smaller foramen vertebrale. The processus transversus is inclined more dorsally and cranially, and the facies articularis superior is less curved and more transversally oriented.

## DISCUSSION

In her extensive work on comparative vertebral anatomy, Ankel concluded that, in general, vertebral morphology is relatively similar among primates

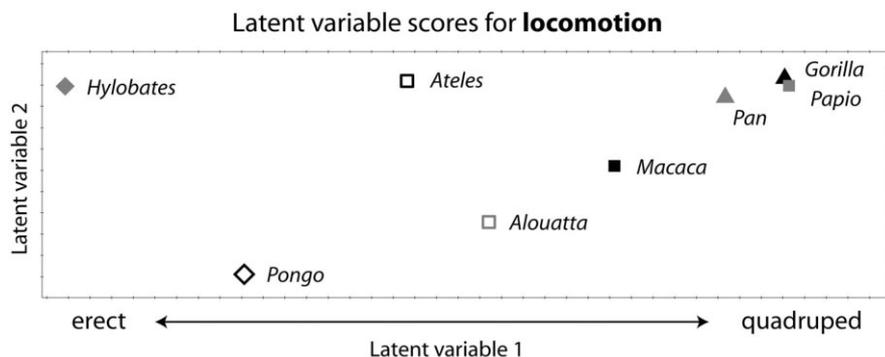
and not clearly related to locomotion. Our geometric morphometric analysis finds that Ankel's statements do not hold for the primate atlas. The PCAs in Figures 2 and 3 unequivocally demonstrate that the atlas shapes of each species form distinct, mainly nonoverlapping, clusters. For nonhuman primates, we could also identify shape deformations that relate to locomotion. We found that the locomotion pattern that most strongly covaries with atlas shape is the gradient from quadrupedalism to a more erect locomotion (Figs. 6–8). For more orthograde species, the associated shape features are a relatively thinner anterior and posterior arcus, a more ventrally and caudally oriented processus transversus, and a more inclined and laterally rounded facies articularis superior. It is noteworthy that both these sets of patterns, that for locomotion variables and that for shape variables, were not a priori selected but are those that exhibit the highest mutual predictive power; they are the latent variables as calculated by the PLS algorithm. It is thus a finding, not an assumption, that it is the gradient between more erect and more quadrupedal locomotion that best covaries with atlas shape. This result stays stable even when using slightly different sets

of locomotion variables or landmarks in the PLS analysis (results not shown). It might change if postural variables are included (Dagosto and Gebo, 1998), but these are not at present available from the literature.

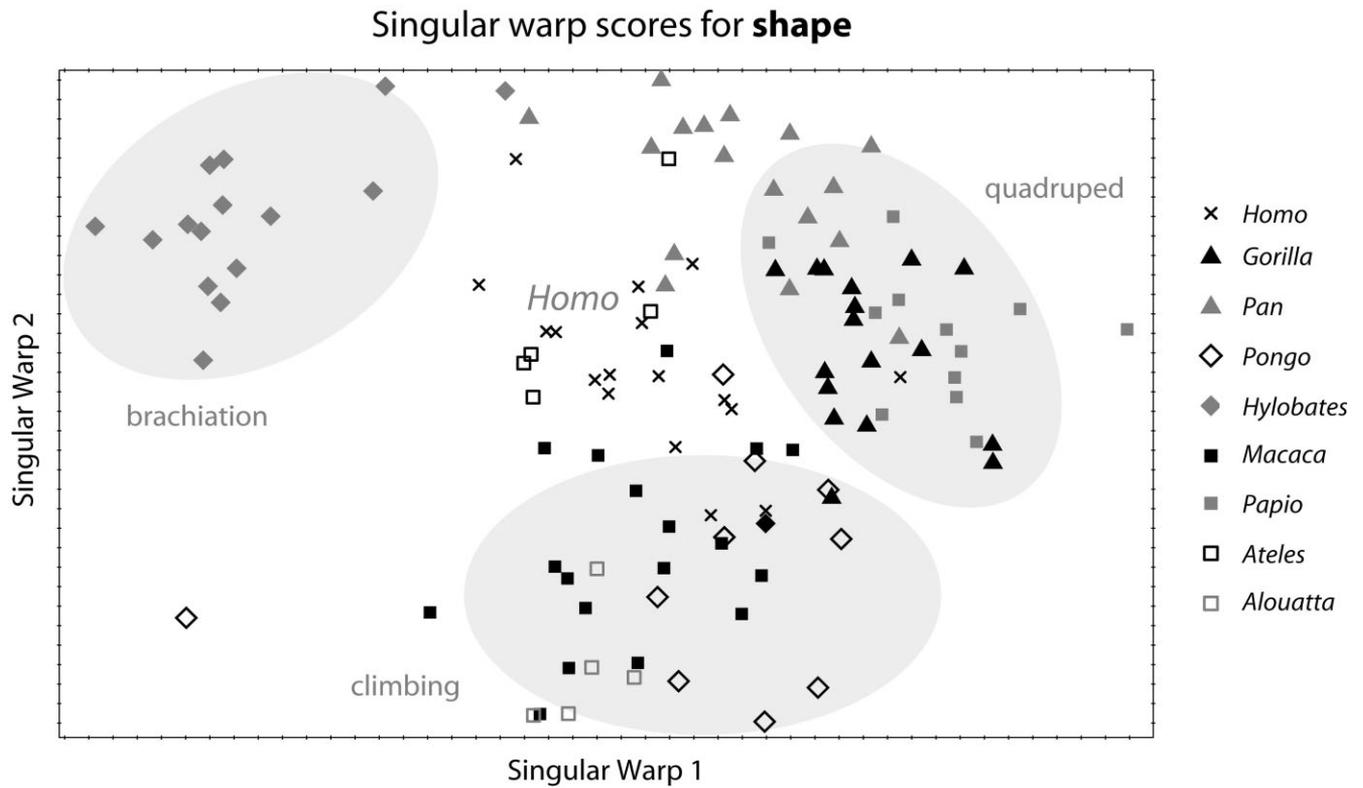
Our findings on atlas morphology and locomotion concur with the more recent literature on the functional morphology of lumbar vertebrae (Rose, 1974; Swindler and Wood, 1982; Shapiro, 1993, 1995; Ward, 1993; Johnson and Shapiro, 1998; Sanders, 1998; Shapiro and Simons, 2002; Martelli and Schmid, 2003; Nakatsukasa and Hirose, 2003; Shapiro et al., 2005). These authors could identify shape differences in the vertebrae among several primate species and explain some of them as responsive to locomotion. Also, and in spite of her contradictory generalization, Ankel (1967) described differences in the angulation of the dens and the superior articular facets of the axis among humans and other primates.

As observed by other authors (Olivier, 1964; Gommery, 1996, 1997; Aiello and Dean, 2002), we also find species differences in the concavity of the superior articular facets (Table 1). Humans exhibit flatter (less concave) facets than apes or baboons. But it is unclear from our data whether the concavity of the facets directly relates to locomotion. *Gorilla* and *Pan*, both mainly quadrupedal, also possess relatively flat facets, while *Ateles*, a frequently brachiating species, has strongly concave articular facets.

Figure 5 displayed the overall atlas shape differences that owe to evolutionary (cross-taxon) and static (within-taxon) allometry. In either, the atlas, especially its arcus posterior, becomes more robust with size and the processus transversus more cranially inclined. Nonhuman static allometry also involves an elongation of the lateral processus. Additionally, we performed these shape regressions on



**Figure 6.** The first two latent variable (LV) scores for the locomotion variables. LV 1 distinguishes between more erect (left side) and more quadrupedal (right side) locomotion, whereas LV 2 approximately contrasts brachiation and vertical climbing.



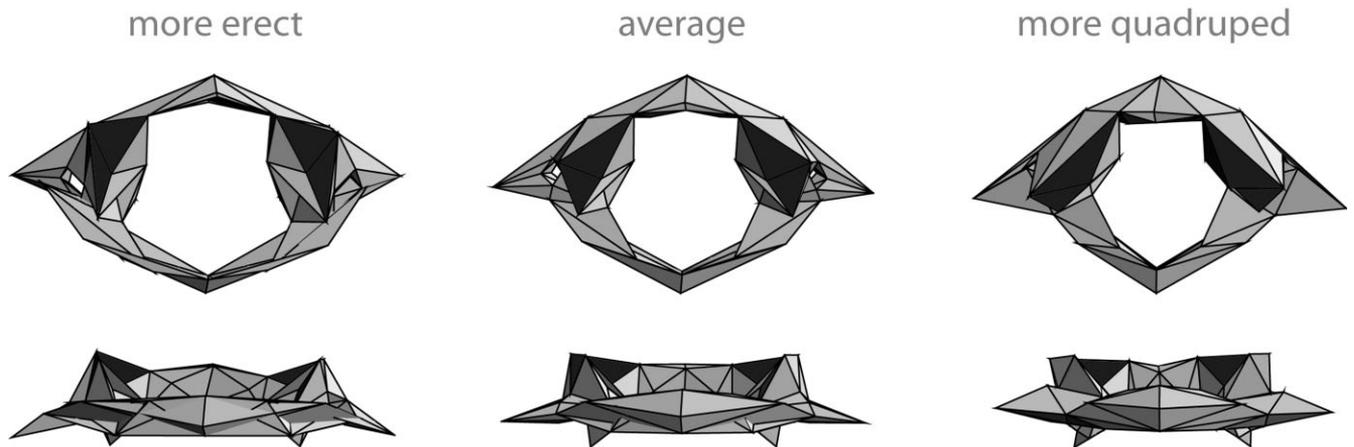
**Figure 7.** The first two singular warp scores for the shape coordinates. The first and the second dimensions here correspond to the first and the second dimensions in Figure 6. The gray ellipses approximately mark three different locomotion patterns. Specimens of *Homo sapiens* were not used in the computation of these axes; locations of these points were produced using the formulas for the singular warp scores of the nonhuman primates only. Note that the human atlas shapes then score intermediate along both components.

femur head diameter and body size estimates instead of atlas centroid size. The three computations yielded very similar results so that the shape deformations shown in Figure 5 are not only related to atlas size but also to body size. As the cervical vertebrae bear the weight of the head, these allometric shape changes can be construed straightforwardly as adaptations

to, or effects of, a heavier head and the resulting more massive nuchal muscles. The muscles connecting the atlas with the head arise at the arcus posterior and the processus transversus of the atlas, so that these structures are mostly affected by allometric increase in robusticity. Whether body size influences locomotion behavior itself, and thus might additionally influence atlas mor-

phology, is still debated (Fleagle and Mittermeier, 1980; Doran, 1993; Gebo and Chapman, 1995; McGraw, 1998).

As in nonhuman primates, the processus transversus in the human atlas becomes somewhat enlarged and more cranially oriented with increasing size. But while evolutionary allometry and nonhuman static allometry both indicate an allometric increase of robustic-



**Figure 8.** Visualization of the first singular warp represents the difference of the atlas shape between more erect and more quadrupedal moving species. Upper row: cranial views; bottom row: dorsal views.

ity, human atlas vertebrae seem to become less robust with increasing overall size. This might itself be a result of locomotion: *Homo sapiens*, as the sole completely upright walking primate, balances the head on the vertebral column instead of bearing it in front of the cervical vertebrae. As Schultz (1942: p. 490) wrote: "very much less force is required to balance the head in adult man than in adults of other primates. The heads of the primates when posed in the ear-eye horizon, are always heavier in front of the occipital condyles than behind them." A quadrupedal primate would thus need to strengthen its nuchal muscles and related bony structures much more than humans would in order to bear a heavier head. The human atlas can thus increase in size without significantly thickening its bony structures. As a consequence, it would appear relatively less robust.

### Human Atlas Morphology

As Figures 2 and 4 show, humans exhibit a distinctive atlas morphology. It is not clear whether this distinction is a consequence of our exceptional locomotion pattern or is due to evolutionary processes unrelated to such functional effects. Ankel (1967, 2000) argued that the vertebral column of primates is so morphologically and functionally generalized as to permit erectness without major morphological changes in the basic anatomical plan. The erect human column, she argues, is more a functional than a morphological specialization.

For nonhuman primates, we have presented shape differences that are associated with erect vs. quadruped locomotion (Fig. 7). Figure 6 shows the scores along the two shape components that exhibit the highest covariation with locomotion. If the human atlas morphology was an adaptation to its locomotion strategy, then when human specimens are projected onto the figures we would expect the human shape scores to be an extrapolation of the quadrupede vs. erect trend. Contrary to that expectation, we find *Homo* scores to be intermediate along both components of Figure 6. This finding suggests that perhaps the specific human atlas morphology is not related to locomotion and that the primate atlas already em-

braces the possibility of bipedalism. Alternatively, human atlas morphology might simply not be predictable from a nonhuman primate sample. It could instead be a unique adaptation not comparable to those for brachiation or vertical climbing.

This discrepancy can also be seen in Figures 4 and 8. While in more erect nonhuman primates the atlas is less robust than in quadruped species, humans exhibit a relatively robust atlas shape, especially at the arcus posterior. Also, the shape and orientation of the facies articularis superior in humans is not as expected from Figure 8. However, both in humans and in the typical erect atlas shape, the processus transversus is oriented more ventrally. Yet we recommend caution in pursuing any adaptationist explanation for this similarity until more functional or experimental data are available (Gould and Lewontin, 1979). Also, it is not clear to what degree the differences in atlas shape are inherited and reflect evolutionary adaptations or are instead epigenetic results of different locomotion patterns. Preuschoft et al. (1988), for example, report that Japanese macaques trained to walk bipedally acquire a pronounced lordosis of the lumbar spine due to a relative increase of the ventral lengths of the vertebral bodies.

In summary, there are clear differences in atlas morphology among the nine primate taxa, along with allometric effects that differ between nonhuman primates and humans. While some of these shape differences relate to locomotion, human atlas morphology still cannot be explained by the nonhuman model. Human atlas shape could thus be an adaptation different from that in the brachiating or vertically climbing orthograde primates, or it might be an adaptation unrelated to locomotion behavior.

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