RESEARCH ARTICLE

Comparative ontogeny of functional aspects of human cervical vertebrae

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Abstract

Objectives: Differences between adult humans and great apes in cervical vertebral morphology are well documented, but the ontogeny of this variation is still largely unexplored. This study examines patterns of growth in functionally relevant features of C1, C2, C4, and C6 in extant humans and apes to understand the development of their disparate morphologies.

Materials and Methods: Linear and angular measurements were taken from 530 cervical vertebrae representing 146 individual humans, chimpanzees, gorillas, and orangutans. Specimens were divided into three age-categories based on dental eruption: juvenile, adolescent, and adult. Inter- and intraspecific comparisons were evaluated using resampling methods.

Results: Of the eighteen variables examined here, seven distinguish humans from apes at the adult stage. Human-ape differences in features related to atlantoaxial joint function tend to be established by the juvenile stage, whereas differences in features related to the nuchal musculature and movement of the subaxial elements do not fully emerge until adolescence or later. The orientation of the odontoid process—often cited as a feature that distinguishes humans from apes—is similar in adult humans and adult chimpanzees, but the developmental patterns are distinct, with human adultlike morphology being achieved much earlier.

Discussion: The biomechanical consequences of the variation observed here is poorly understood. Whether the differences in growth patterns represent functional links to cranial development or postural changes, or both, requires additional investigation. Determining when humanlike ontogenetic patterns evolved in hominins may provide insight into the functional basis driving the morphological divergence between extant humans and apes.

KEYWORDS
development, functional morphology, hominoids, vertebral column

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1 | INTRODUCTION

Variation in the vertebral column of extant hominoids is well documented and acts as a broad foundation for inferences about positional behavior in fossil taxa (Been et al., 2012; Haeusler et al., 2002; Nakatsukasa et al., 2007; Robinson, 1972; Shapiro, 1993a, 2007; Shapiro et al., 2005; Ward, 1993; Whitcome et al., 2007; Williams et al., 2019). Much of this research has focused on the morphology of the thoracolumbar region because of its relevance for understanding the evolution of bipedal locomotion in hominins. The cervical region has attracted less attention, but interest in the comparative anatomy and the functional consequences of variation in this part of the vertebral column has increased in recent years (Arlegi et al., 2017, 2018, 2022; Manfreda et al., 2006; Meyer, 2015; Meyer et al., 2018; Nalley & Grider-Potter, 2015, 2017; Nalley et al., 2019a; Vander Linden et al., 2019; Villamil, 2018). Researchers have expanded phylogenetic sampling, incorporated new methodologies, explored patterns of developmental integration, and examined cervical variation in the context of more refined, quantified measures of head and neck postures and locomotor behaviors. Researchers have also begun to test the functional hypotheses developed from bony patterns of variation by examining soft tissues and *in vivo* and *in silico* relationships (Grider-Potter, 2019; Grider-Potter et al., 2020; McGechie, 2021; McGechie et al., 2019, 2020). One area that requires further investigation is the developmental basis of the differences between humans and apes established by this body of work.

The mammalian cervical spine can be functionally and morphologically divided into upper (C1 and C2), middle (C3–C5), and lower (C6–C7) regions (Arnold, 2021; Arnold et al., 2016; Buchholtz, 2012; Graf, De Waele, & Vidal, 1995; Graf, De Waele, Vidal, Wang, et al., 1995; Kessel & Gruss, 1991; Kessel et al., 1990; Randau & Goswami, 2017a, 2017b; Vidal et al., 1986; Villamil, 2018). The elements of the upper cervical region differ from each other and from C3–C7 and are anatomically specialized for head movement and shifts in gaze orientation (e.g., Graf, De Waele, & Vidal, 1995; Graf, De Waele, Vidal, Wang, et al., 1995; Vidal et al., 1986; Villamil, 2018). The vertebrae of the middle cervical region are generally more uniform in shape and are primarily limited to movements of axial rotation (e.g., Arnold et al., 2016; Graf, De Waele, & Vidal, 1995; Graf, De Waele, Vidal, Wang, et al., 1995; Villamil, 2018). The morphology of the lower cervical vertebrae, though also exhibiting classic vertebral features (i.e., centrum, neural arch, transverse, and spinous processes) do mark distinct changes in shape at C6 (e.g., the carotid tubercle) and C7 and are functionally linked with the pectoral girdle via forelimb muscle attachments (Arnold et al., 2016; Randau & Goswami, 2017a). The developmental constraint of seven cervical vertebrae and consistency of their regionalization across mammals facilitates morphological specializations along functional axes (Arnold, 2021; Williams & Meyer, 2019) that may also be useful for phylogenetic analysis.

1.1 | Atlantoaxial complex

Features of the first (atlas, C1) and second (axis, C2) cervical vertebrae have been the most widely examined across extant primates.

Manfreda et al. (2006) explored the relationship between locomotor pattern and the overall bony morphology of the C1 in nine primate taxa, including five hominoid species. They found that primates differ in atlas shape along a locomotor gradient, ranging from terrestrial quadrupedalism to arboreal orthogrady. The C1 of the more quadrupedal species exhibits dorsoventrally expanded anterior and posterior arches and more dorsally and cranially oriented transverse processes. A notable result of Manfreda et al.'s analysis was the distinctiveness of extant human morphology, demonstrating an overall increased robusticity, with an especially robust posterior arch. Nalley and Grider-Potter (2017) identified associations between direct measures of primate head and neck posture and two C1 features across 20 primate taxa: relative craniocaudal height of the posterior arch and the curvature of the superior articular facet. Primate taxa with more horizontal neck postures exhibit atlases with craniocaudally taller posterior arches and superior articular facets with greater curvature in the transverse plane.

At C2, several researchers have observed that the angulations of the odontoid process and the superior articular facets differ between hominoids and other primates (Ankel, 1970, 1972; Ankel-Simons, 2007; Gommery, 1997; Meyer, 2015). These studies found that extant humans have odontoid processes that are more vertically oriented than in other primates, and superior articular facets that are not as steeply sloped in the coronal plane relative to the odontoid process. Apes display facets that are generally intermediate between those of humans and other primates. Nalley and Grider-Potter (2017) also observed these bony patterns and found a correlation with quantitative measures of neck posture: species with more vertical neck postures tend to have more vertical odontoid processes and less sloped superior facets.

1.2 | Subaxial vertebrae

The spinous and transverse processes of the subaxial cervical vertebrae (C3–C7) have attracted the attention of primate functional morphologists because they are sites of muscle attachment. Their shape and size relative to the axis of motion are therefore related to muscle function. Variation in these features, especially the spinous process, has been observed in the cervical vertebral column for over half a century. Slijper (1946) and Toerien (1961) reported that monkeys and humans generally have relatively short spinous processes in comparison to apes (see also Schultz, 1961). Since then, other researchers have replicated this result using larger samples of hominoids and 3D geometric morphometric methods (Arlegi et al., 2017; Meyer, 2015). Nalley and Grider-Potter (2015) observed this pattern and established correlations with quantified measures of head and neck posture in a sample that included hominoids, monkeys, and strepsirrhines. Orientation of the spinous process has also been used to distinguish extant humans from other hominoids. The subaxial cervical vertebrae of extant humans have spinous processes that are more caudally angled in comparison to other primates, including fossil hominins (Ankel-Simons, 2007; Arlegi et al., 2017; Arsuaga et al., 2015; Carretero

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et al., 1999; Gómez-Olivencia et al., 2013; Gómez-Olivencia & Been, 2019; Meyer, 2015; Meyer & Williams, 2019b; Schultz, 1961; Williams & Meyer, 2019).

The transverse processes of the subaxial vertebrae are quite variable in size and shape across primates (e.g., Ankel, 1972; Toerien, 1961), but a few morphological patterns are evident. First, the transverse processes of great apes are relatively short when compared to most other primates, including humans (Schultz, 1961; Tominaga et al., 1995). Second, Grider-Potter et al. (2020) found a correlation between the transverse process angle in the coronal plane and the range of motion at the C4/C5 spinal level in a broad sample of primate taxa: species with more caudally oriented transverse processes have a greater range of lateral flexion.

Differences in the dimensions of the vertebral bodies (centra) have also been reported. Humans have centra that are mediolaterally wide, dorsoventrally short, and craniocaudally short when compared to other hominoids (Arlegi et al., 2017; Meyer, 2015; Nalley & Grider-Potter, 2015; Schultz, 1961). Nalley and Grider-Potter (2015) noted that primates with more horizontal head and neck postures have vertebrae with increased craniocaudal dimensions, including longer centra and laminae in C3–C6 and craniocaudally longer anterior and posterior arches in C1.

The orientations of the articular facets of the C4 and C7 vertebrae are also correlated with head and neck postures. Nalley and Grider-Potter (2015) observed that species with more horizontal neck postures have more coronally oriented (or vertical) facets. Meyer (2015) and Arlegi et al. (2017) also observed differences between humans and African apes in the orientation of the articular facets, with apes exhibiting more vertically oriented facets. Additionally, Arlegi et al. (2017) noted that African apes have superior articular facets that are more sagittally oriented than those of extant humans.

1.3 | Research objectives

The patterns of variation in primate cervical vertebrae summarized above are based on adult morphology. Most research investigating cervical development in primates has been limited to extant humans (e.g., Been, Shefi, & Soudack, 2017; Cunningham et al., 2016; Dias, 2007; Dickson & Deacon, 1987; Johnson et al., 2016). Ontogenetic data from other primates, especially the great apes, are critical for understanding the evolutionary changes that occurred in the neck as hominins adapted to bipedal locomotion, one of the most interesting and perplexing transitions in positional behavior in primate evolutionary history. The developmental patterns that produce differences in adult form between humans and great apes have important implications for identifying the mechanisms that structure morphological variation among the extant Hominidae and potentially inform how shape differences influence function during growth. Such patterns are also useful for interpreting subadult morphology in the fossil record and linking it to evolutionary trends in the hominin lineage. Applying a developmental perspective to the paleoanthropological record has the potential to provide novel insights into the biology of the earliest

bipeds (e.g., DeSilva et al., 2018; Green & Alemseged, 2012; Nalley et al., 2019; Ward et al., 2017).

The goals of the present study are to quantify and compare the ontogenetic changes in cervical vertebral features that have been previously identified as either functionally or phylogenetically relevant in extant humans and great apes. We focus on how humans differ from other members of Hominidae because we are interested in building a framework for interpreting the hominin fossil record. Thus, we ask two interrelated questions: First, how are the morphologies that distinguish adult humans from great apes expressed in subadults? Second, within each taxon, how does the morphology vary among age-groups and at what stage is adultlike morphology achieved?

2 | METHODS AND MATERIALS

2.1 | Sample

The extant sample consisted of individual vertebral series from 146 individuals, representing species from all four hominid genera: *Homo sapiens, Pan troglodytes, Pongo pygmaeus, and Gorilla gorilla*, and *Gorilla beringei* (Table 1). The single individual of *G. beringei* included here was combined with the *G. gorilla* sample to increase sample size for this genus. Specimens come from comparative osteological collections held at the American Museum of Natural History (New York, NY, USA), the Cleveland Natural History Museum (Cleveland, OH, USA), the National Museum of Natural History (Washington, DC,

TABLE 1 Species and sample sizes for each vertebral level.

	C1	C2	C4	C6
Pongo pygmaeus				
Juvenile	4–7	5–7	3–7	5–7
Adolescent	14–17	14	15	10–15
Adult	13	13	13	12–13
Gorilla				
Juvenile	1–6	4–10	5–9	7–9
Adolescent	7–9	7–10	9–10	10
Adult	8–9	10	9–10	10–11
Pan troglodytes				
Juvenile	6–9	9–10	7–10	7–9
Adolescent	10	10	11	10–11
Adult	12–14	14	14	13–14
Homo sapiens				
Juvenile	4–7	7–8	7–9	8–9
Adolescent	6–11	13	11–12	11–13
Adult	16	12–14	14	13–14

Note: A range is reported when sample sizes vary for different variables at that vertebral level. The juvenile *Gorilla* sample contains one individual of *G. beringei*; all other gorilla individuals are *G. gorilla*. Refer to Tables S1 and S2 in the Supporting Information for the raw data and summary statistics, respectively, for each variable.

USA), and the Powell-Cotton Museum (Birchington, UK). Pathological and damaged vertebrae were excluded, except in a few cases where minimal damage did not impede data collection. Although sexual dimorphism is a potential concern, our samples are small, and we did not observe evidence of sexual differences in the variables examined here. We therefore combined males and females in our analyses. Note that sample sizes vary across vertebral levels owing to the completeness of specimens. Sample sizes across variables for the youngest age-group also differ due to the lack of fusion of the vertebral centrum to the neural arch, which prevented accurate measurement of certain variables using the methods employed here.

Each individual was assigned to an age-category based on the state of dental eruption, using the criteria developed by Shea (1985; Table 2). This scheme is meant to facilitate comparisons among individuals of comparable developmental stages, rather than implying a direct correspondence between dental-eruption stage and chronological age (Cobb & O'Higgins, 2007; Green & Alemseged, 2012; Nalley et al., 2019; Simons & Frost, 2016; Taylor, 1997). Maxillary teeth were prioritized for aging, as crania were better represented in the sample than mandibles. Categories were combined into broader groups to ensure adequate sample sizes for statistical testing as follows: juveniles, dental stages 0–2 (no teeth or only deciduous teeth); adolescents, stages 3–4 (mix of deciduous and permanent teeth); adults, stages 5–7 (only permanent teeth). Dental developmental stages have been shown to correlate with life-history variables (Harvey & Clutton-Brock, 1985; Smith, 1989), allowing for comparisons among major developmental events. This categorical approach, necessitated by the constraints imposed by available samples, will discard important information about developmental trajectories, but it should capture major differences between humans and great apes.

2.2 | Data acquisition and trait definitions

Measurements from C1, C2, C4, and C6 vertebrae were collected to capture functionally and phylogenetically relevant vertebral shapes at the upper, middle, and lower regions of the neck. Measurements were collected from landmarks placed on photographs and stills of CT scans in cranial, ventral, lateral, and dorsal views. Photographs of vertebrae were captured with a high-resolution digital single-lens reflex camera (Canon EOS Rebel T3 SLR), using a flat macro to avoid issues of parallax and image distortion. To further minimize measurement error from perspective distortion, procedures recommended by Spencer and Spencer (1995) were followed, including using a calibration grid to establish the minimum distance between the camera and specimen (approximately 10× the length of the largest specimen) and centering vertebrae within the image frame. A millimeter scale bar was placed in the same plane as either the vertebral body surface or the neural arch when the vertebral body was not present, as in the case of C1 or individuals too young to exhibit neurocentral fusion.

In addition to photographs, stills were taken from CT images generated from microCT scans of cervical vertebrae for $n = 37$ individuals. MicroCT scans of cervical vertebrae were generated at the University of Chicago using a custom-built dual tube General Electric Phoenix v|tome|x Microfocus CT scanner (PaleoCT). Vertebrae were scanned at the highest resolution available, ranging between 25 and 70 μ^3 depending on the specimen. Image stacks of specimens were then imported into Avizo Lite v2020.2 (Thermo Fisher Scientific, Waltham, MA, USA) for visualization. Vertebrae were first segmented and rendered using the threshold tool in Avizo, before being smoothed using the .smooth labels function in Avizo and then exported as .ply files. After surfaces were rendered, they were imported into Geomagic Studio v14 (3D Systems, Rock Hill, SC, USA), where all holes were filled before being resaved as .ply files. Next, the same individual vertebrae (C1, C2, C4, and C6) were imported into Checkpoint software v2022.12 (Stratovan Corporation, Davis, CA) where a scale bar was set to the width of the joint surface or length of the spinous process before a still was taken.

Landmarks, distances, and angles were measured from photographs and stills using ImageJ (Schneider et al., 2012). Linear measurements were size-adjusted by dividing each by the geometric mean of two centrum dimensions: bilateral width and dorsoventral height. Because C1 does not have a vertebral body, the geometric mean was calculated from the centrum measurements for C2, C4, and C6 of the same individual. We used the size of the vertebral body to size-adjust the features of interest rather than a geometric mean of all measurements because the vertebral bodies are the primary weight-bearing structures of the bony neck and should therefore provide a good approximation of the overall size of the head and neck (see reviews by Oxland, 2016; White & Panjabi, 1990). Moreover, because the features of interest are likely to have functional significance, including them in the denominator would complicate interpretations of differences between genera and between age-groups (Vinyard, 2008). Table 3 describes the vertebral landmarks used to calculate distances and angles of interest; the distances and angles are described in Table 4 and illustrated in Figure 1. All specimens were measured by the first author. The raw data are available in Table S1 of the Supporting Information. Summary statistics for each measurement are presented in Table S2.

TABLE 2 Dental stages (Shea, 1985).

Stage	Dental eruption and suture fusion
0	No deciduous teeth erupted
1	Deciduous teeth not fully erupted
2	All deciduous teeth fully erupted
3	Deciduous dentition with partially or fully erupted M1
4	M2 partially or fully erupted
5	Erupted canine and/or M3
6	Full permanent dentition, basioccipital suture open or slightly open, light tooth wear
7	Full permanent dentition, basioccipital suture closed, moderate/heavy tooth wear

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TABLE 3 Vertebral landmark definitions.

No.	Landmark	Definition
Atlas vertebra (C1)		
1	Ventral arch, caudal	Midpoint of ventral arch along caudal surface
2	Ventral arch, cranial	Midpoint of ventral arch along cranial surface
3	Lateral extent of transverse process, coronal plane	Most lateral extent of the transverse process in coronal plane
4	Dorsal arch, cranial	Midpoint of posterior arch along cranial surface
5	Dorsal arch, caudal	Midpoint of posterior arch along caudal surface
6	Vertebral neural arch, ventral	Most ventral point on cranial surface of the vertebral neural arch in midline
7	Vertebral neural arch, dorsal	Most dorsal point on cranial surface of the vertebral neural arch in midline
8	Lateral extent of transverse process, transverse plane	Most lateral extent of the transverse process in transverse plane
Axis vertebra (C2)		
1	Vertebral body, caudal	Most caudal point on ventral surface of vertebral body in the midline (in ventral view)
2	Vertebral body, cranial	Most cranial point on ventral surface of vertebral body (junction of the vertebral body and neck of the dens) in the midline
3	Superior articular facet, medial	Most medial point of the superior articular facet
4	Superior articular facet, lateral	Most lateral point of the superior articular facet
5	Vertebral body, lateral caudoventral	Most caudal point on ventral surface of vertebral body (in lateral view)
6	Odontoid process, caudal	Most caudal point on dens articular facet (in lateral view)
7	Odontoid process, cranial	Most cranial point on dens articular facet (in lateral view)
8	Vertebral neural arch, dorsal	Most dorsal point on cranial surface of vertebral neural arch in midline
9	Dorsal extent of spinous process	Most dorsal point on cranial surface in midline
10	Vertebral body, caudoventral	Most ventral point on caudal surface of vertebral body (in caudal view)
11	Vertebral body, caudodorsal	Most dorsal point on caudal surface of vertebral body (in caudal view)
12	Vertebral body, caudolateral left	Most lateral point on left side of caudal surface of vertebral body (in caudal view)
13	Vertebral body, caudolateral right	Most lateral point on right side of caudal surface of vertebral body (in caudal view)
Subaxial vertebrae (C4, C6)		
1	Vertebral body, caudal	Most caudal point on ventral surface of vertebral body in the midline (in ventral view)
2	Vertebral body, cranial	Most cranial point on ventral surface of vertebral body in the midline
3	Vertebral body, left	Most lateral point on cranial surface of ventral body on left side (at junction with uncinate process). Replicated on right when left side was unavailable.
4	Lateral extent of transverse process, coronal	Most lateral extent of the transverse process in coronal plane
5	Vertebral body, caudoventral	Most caudal point on ventral surface of vertebral body (in lateral view)
6	Vertebral body, craniodorsal	Most cranial point on ventral surface of vertebral body (in lateral view)
7	Inferior articular facet, ventral	Most ventral point of the inferior articular facet
8	Inferior articular facet, dorsal	Most dorsal point of the inferior articular facet
9	Vertebral neural arch, dorsal	Most dorsal point on cranial surface of vertebral neural arch
10	Dorsal extent of spinous process	Most dorsal point on cranial surface
11	Vertebral body, cranioventral	Most ventral point on cranial surface of vertebral body in the midline
12	Vertebral body, craniodorsal	Most dorsal point on cranial surface of vertebral body in the midline
13	Lateral extent of transverse process, transverse plane	Most lateral extent of the transverse process in transverse plane
14	Vertebral body, caudoventral	Most ventral point on caudal surface of vertebral body (in caudal view)
15	Vertebral body, caudodorsal	Most dorsal point on caudal surface of vertebral body (in caudal view)
16	Vertebral body, caudolateral left	Most lateral point on left side of caudal surface of vertebral body (in caudal view)
17	Vertebral body, caudolateral right	Most lateral point on right side of caudal surface of vertebral body (in caudal view)

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2.3 | Analytical procedures

Two types of comparisons were conducted for each vertebral feature. The first type of comparison is interspecific and examines how humans

TABLE 4 Vertebral variables and definition.

Measurement	Definition
Atlas vertebra (C1)	
Transverse process angle in coronal plane (TPAco)	Angle created by the neural arch line (landmarks 1, 2) and the transverse process line (landmarks 2, 3)
Dorsal arch craniocaudal height (DAH)	Distance between landmarks 4 and 5
Transverse process angle, transverse plane (TPAtr)	Angle created by the neural arch line (landmarks 6, 7) and the transverse process line (landmarks 6, 8)
Axis vertebra (C2)	
Superior articular facet angle (SFA)	Angle created by the vertebral body line (landmarks 1, 2) and the facet line (landmarks 3, 4)
Odontoid process angle (OPA)	Angle created by the vertebral body line (landmarks 5, 6) and the dens facet line (landmarks 6, 7)
Spinous process length (SPL)	Distance between landmarks 8 and 9
Dorsoventral height	Distance between landmarks 10 and 11. Included in the C1 and C2 geometric means.
Bilateral width	Distance between landmarks 12 and 13. Included in the C1 and C2 geometric means.
Subaxial vertebra (C4, C6)	
Vertebral body craniocaudal height (VBH)	Distance between landmarks 1 and 2
Transverse process angle—coronal plane (TPAco)	Angle created by the vertebral body line (landmarks 1, 2) and the transverse process line (landmarks 3, 4)
Inferior articular facet angle—sagittal (IFA)	Angle created by the vertebral body line (landmarks 5, 6) and the inferior articular facet line (landmarks 7, 8)
Spinous process length (SPL)	Distance between landmarks 9 and 10
Spinous process angle (SPA)	Angle created by the vertebral body line (landmarks 5, 6) and the spinous process line (landmarks 9, 10)
Transverse process angle—transverse plane (TPAtr)	Angle created by the vertebral body line (landmarks 11, 12) and the transverse process line (landmarks 12, 13)
Dorsoventral height	Distance between landmarks 14 and 15. Included in the C1, C4, and C6 geometric means.
Bilateral width	Distance between landmarks 16 and 17. Included in the C1, C4, and C6 geometric means.

differ from great apes at each developmental stage. Since our goal is to identify developmental patterns that distinguish humans from great apes, we did not test for differences among the apes. The advantage of restricting statistical testing in this way is that it limits the penalties for conducting multiple comparisons. In adopting this approach, we are not assuming that the great apes are homogeneous. Rather, we are identifying traits in which humans differ from the ape genera in consistent ways and maximizing statistical power to detect those differences at subadult stages, where variation may be less salient.

The second type of comparison is intraspecific and examines how age-groups within each species differ from each other. For this part of the analysis, we only compared juveniles and adolescents to adults. Juveniles and adolescents were not directly compared to avoid reductions in statistical power. Thus, these tests are structured to detect when adultlike morphology is achieved, on average, within each genus.

The statistical significance of each comparison was evaluated using the bootstrap. Each species-age sample was resampled with replacement 2000 times, at a sample size equal to that of the original sample, to generate standard errors and 95% confidence intervals. Pairwise comparisons between groups were carried out by randomly pairing the bootstrapped samples for the different species-age groups (e.g., adult chimpanzee with adult human) to generate 95% confidence intervals for the observed differences between the groups for each variable. The resulting distributions were used to compute p-values, with the alpha level adjusted for multiple comparisons using the sequential Bonferroni method (Rice, 1989). Resampling was conducted using an Excel macro.

3 | RESULTS

3.1 | Overview

Of the eighteen variables examined here, seven distinguish adult humans from the adults of all three ape genera: relative lengths of the spinous processes (SPL) at C2, C4, and C6; angles of the spinous processes (SPA) at C4 and C6; angle of the C2 superior articular facet (SFA); and relative craniocaudal height of the vertebral body (VBH) at C6 (Table 5). There is variation in when humans become distinct from apes in these features: by the juvenile stage in the case of C2 SFA, C2 SPL, and C6 SPA; by the adolescent stage in the case of C4 SPA, C4 SPL, and C6 SPL; and by the adult stage in the case of C6 VBH. Humans achieve adultlike form prior to adulthood in three of these traits: C6 SPA at the juvenile stage, and C4 SPA and C6 SPL at the adolescent stage (Table 6). For the remaining variables, humans do not differ significantly from at least one of the apes at the adult stage. This group of variables is not discussed further (see Tables S3 and S4 in the Supporting Information for statistical comparisons, and Figure S1 for representative images of C1), with one important exception—angle of the odontoid process (OPA), which has been identified in previous studies as a feature that distinguishes humans from apes and a possible indicator of bipedality in the fossil record (Gommery, 1997, 2006).

FIGURE 1 Linear and angular measurements used in this study demonstrated on human vertebrae: C1 (left column), C2 (middle), and the subaxial vertebrae (right). Row A shows the measurements taken in ventral view. Row B shows the measurements taken in posterior view on C1 and in lateral view on C2 and the subaxial vertebrae. Row C shows the measurements taken in cranial view. All measurements and the landmarks they were derived from are described in Tables 3 and 4.
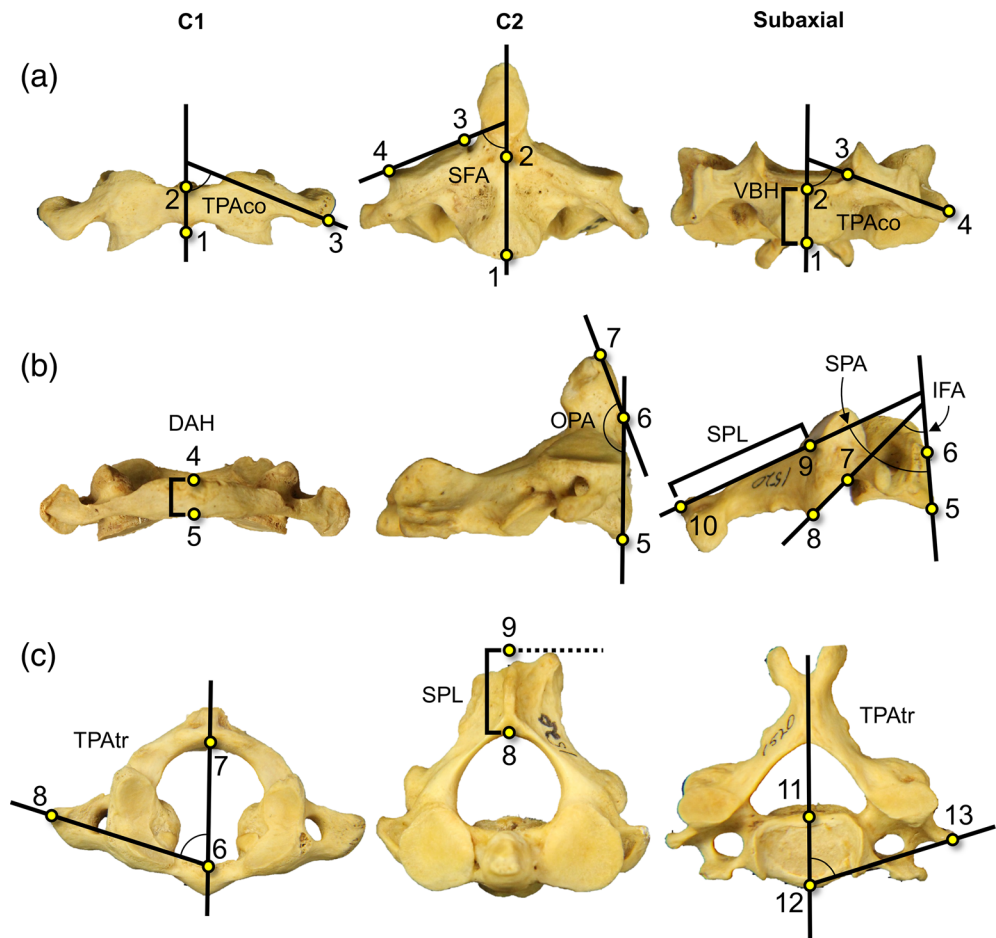
3.2 | Angles of the odontoid process and superior articular facet of C2

Adult humans are not clearly distinct from all apes in OPA (Figures 2 and 3). Adult humans have more vertically oriented odontoid processes than adult gorillas and orangutans, but human and chimpanzee adults cannot be statistically distinguished at this developmental stage. However, at the juvenile and adolescent stages, human odontoid processes are significantly more vertical than those of all of the apes. OPA increases—that is, the process becomes more vertical—during development in all four species. Humans achieve adultlike form by the adolescent stage; in apes, OPA continues to increase, with adult chimpanzees converging on the adult human morphology.

Adult humans have a significantly higher SFA in comparison to adult apes, indicating that the slope of the facet of adult humans is not as steep in the coronal plane as in apes (Figures 2 and 4). This difference is established early in development: the SFAs of juvenile and adolescent humans are significantly greater (i.e., the facets are more horizontally oriented in the coronal plane) than those of apes at the same developmental stage. Apes exhibit little change in SFA over the course of development, whereas adult humans have significantly greater SFAs than adolescents and juveniles. Thus, the adult human morphology emerges much later in development in comparison to the apes.

3.3 | Lengths and angles of the spinous processes of C2, C4, and C6

Adult humans have significantly shorter spinous processes relative to vertebral body size than do apes at all levels examined here. For C2, this pattern is present early in development, with juvenile and adolescent humans having relatively shorter SPLs than all other taxa (Figure 5). For C4 and C6, differentiation between humans and apes does not fully emerge until adolescence: juvenile humans are not statistically distinguishable from chimpanzees at C4 or C6, or from juvenile orangutans at C6, but the SPLs of human adolescents are relatively shorter than those of all of the apes (Figures 6–8; Figure S2 in the Supporting Information). All hominids show a pattern of increasing relative SPL as they age, with adult form being significantly different from that of juveniles and adolescents. The one exception to this generalization is the human C6, where adolescent and adult humans are not significantly different from each other, indicating that humans achieve adultlike SPL morphology earlier than apes do at this level.

The C4 and C6 spinous processes of adult humans are significantly more caudally angled than those of apes (Figures 6–8; Figure S2 in the Supporting Information). In the case of C6, humans are statistically distinguishable from the apes at all developmental

TABLE 5 The *p* values for interspecific comparisons discussed in the results section (see Table S3 in the Supporting Information for other interspecific comparisons).

| Variable	Age group	*Homo* vs. *Pan*	*Gorilla*	*Pongo*
C2 OPA	Juvenile	**0.0005**	**0.0015**	**0.0250**
	Adolescent	**0.0005**	**0.0005**	**0.0005**
	Adult	0.0700	**0.0030**	**0.0005**
C2 SFA	Juvenile	**0.0005**	**0.0020**	**0.0005**
	Adolescent	**0.0005**	**0.0005**	**0.0005**
	Adult	**0.0005**	**0.0005**	**0.0005**
C2 SPL/GM	Juvenile	**0.0005**	**0.0005**	**0.0005**
	Adolescent	**0.0005**	**0.0005**	**0.0005**
	Adult	**0.0005**	**0.0005**	**0.0005**
C4 SPA	Juvenile	0.1614	**0.0005**	**0.0215**
	Adolescent	**0.0005**	**0.0005**	**0.0005**
	Adult	**0.0005**	**0.0005**	**0.0005**
C4 SPL/GM	Juvenile	0.0700	**0.0005**	**0.0005**
	Adolescent	**0.0025**	**0.0005**	**0.0005**
	Adult	**0.0005**	**0.0005**	**0.0005**
C6 SPA	Juvenile	**0.0275**	**0.0030**	**0.0205**
	Adolescent	**0.0005**	**0.0005**	**0.0005**
	Adult	**0.0005**	**0.0005**	**0.0005**
C6 SPL/GM	Juvenile	0.4438	**0.0035**	0.0380
	Adolescent	**0.0005**	**0.0005**	**0.0005**
	Adult	**0.0005**	**0.0005**	**0.0005**
C6 VBH/GM	Juvenile	0.0835	0.0585	0.1384
	Adolescent	0.0495	0.4858	0.2554
	Adult	**0.0005**	**0.0005**	**0.0010**

Note: Bolded values are significant after adjustment for multiple comparisons (applied within row).
Abbreviations: GM, geometric mean; OPA, odontoid process angle; SFA, superior facet angle; SPA, spinous process angle; SPL, spinous process length; VBH, vertebral body craniocaudal height.

TABLE 6 The *p* values for intraspecific comparisons discussed in the results section (see Table S4 in the Supporting Information for other intraspecific comparisons).

Variable	Taxon	Adult vs. Juvenile	Adolescent
C2 OPA	*Homo*	**0.0205**	0.2229
	Pan	**0.0005**	**0.0160**
	Gorilla	**0.0005**	**0.0070**
	Pongo	**0.0285**	**0.0025**
C2 SFA	*Homo*	**0.0250**	**0.0005**
	Pan	0.6592	0.4618
	Gorilla	0.3598	0.7056
	Pongo	0.0505	0.2129
C2 SPL/GM	*Homo*	**0.0005**	**0.0015**
	Pan	**0.0005**	**0.0005**
	Gorilla	**0.0010**	**0.0080**
	Pongo	**0.0005**	**0.0005**
C4 SPA	*Homo*	**0.0005**	0.1944
	Pan	0.0805	0.8316
	Gorilla	0.6527	**0.0180**
	Pongo	0.5652	0.0670
C4 SPL/GM	*Homo*	**0.0005**	**0.0020**
	Pan	**0.0005**	**0.0005**
	Gorilla	**0.0005**	**0.0005**
	Pongo	**0.0005**	**0.0005**
C6 SPA	*Homo*	0.0640	0.3248
	Pan	0.6212	0.1589
	Gorilla	0.1674	0.2429
	Pongo	0.1579	0.3758
C6 SPL/GM	*Homo*	**0.0005**	0.1384
	Pan	**0.0005**	**0.0005**
	Gorilla	**0.0005**	**0.0005**
	Pongo	**0.0005**	**0.0005**
C6 VBH/GM	*Homo*	**0.0005**	**0.0400**
	Pan	**0.0005**	**0.0005**
	Gorilla	**0.0005**	**0.0005**
	Pongo	**0.0005**	**0.0005**

Note: Bolded values are significant after adjustment for multiple comparisons (applied within row).
Abbreviations: GM, geometric mean; OPA, odontoid process angle; SFA, superior facet angle; SPA, spinous process angle; SPL, spinous process length; VBH, vertebral body craniocaudal height.

stages; for C4, humans are distinct from the apes at the adolescent stage but are similar to chimpanzees at the juvenile stage. Changes in SPA during development are not always directional in hominoids. Human C4 SPAs show a simple pattern of decrease with age (i.e., becoming more caudally angled), with juveniles, but not adolescents, having significantly larger angles (i.e., more horizontally oriented) than adults. Gorillas present a contrasting pattern in which C4 SPA increases from juveniles to adolescents and then decreases from adolescents to adults, such that only adolescents are significantly different from adults, whereas adults and juveniles are not distinguishable. Chimpanzees and orangutans do not exhibit clear evidence of developmental change in C4 SPA. With regard to the C6 SPA, adults of all species are statistically similar to conspecific juveniles and adolescents, indicating that adult morphology appears early in development.

3.4 | Craniocaudal height of the vertebral body of C6

Adult humans have relatively shorter VBHs at C6 than do adult apes (Figure 9). Juvenile and adolescent humans do not differ from the corresponding age-groups of any of the great apes in this feature, indicating that this is a late-emerging difference. VBH increases during

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FIGURE 2 Bootstrap distributions for C2 odontoid process angle (OPA; left) and superior articular facet orientation (SFA; right) by species and age group. The middle 95% of each distribution is equivalent to a 95% confidence interval.
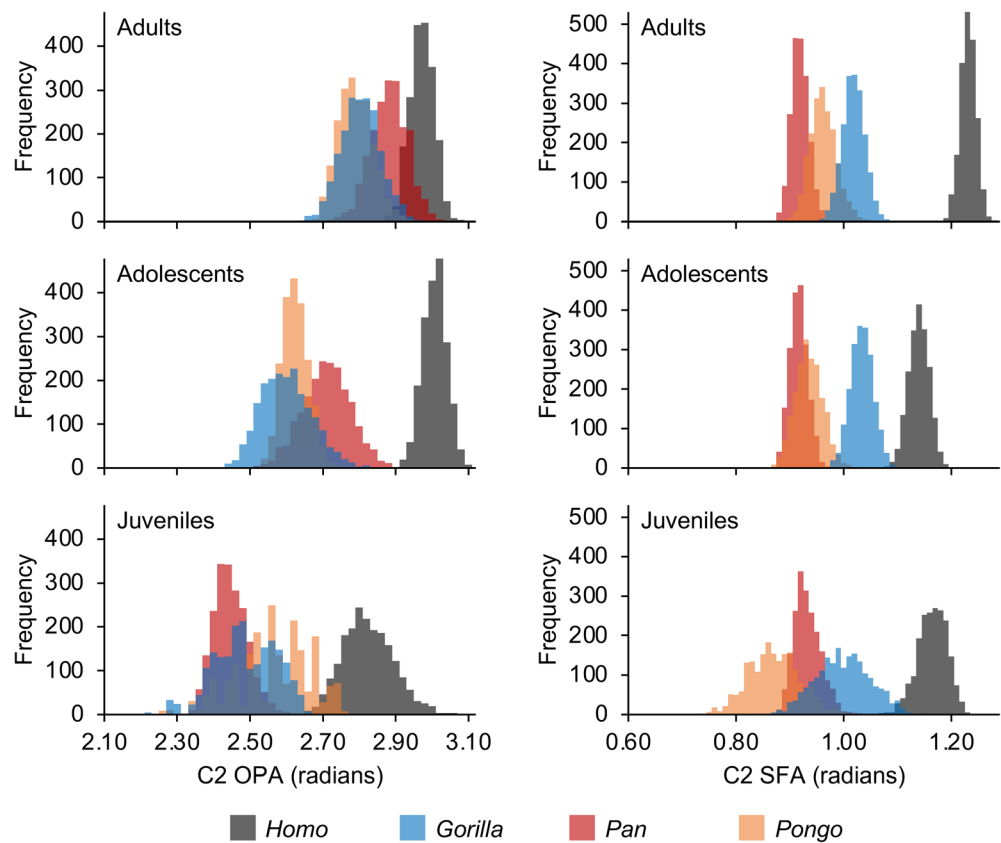
development, with all hominoid genera achieving adult morphology after adolescence.

4 | DISCUSSION

4.1 | Comparative ontogeny of the cervical vertebrae of extant humans

The results of this study show that many of the features of the cervical vertebral column that are characteristic of extant human adults appear early in development. Morphological differences in three of the seven features in our analysis that distinguish adult humans from great apes are established by the juvenile stage, and differences in three other features emerge by adolescence (Table 7). Notably, for the traits in the latter group, juvenile humans are similar to juvenile chimpanzees in all three cases, significantly different from juvenile gorillas in all three cases, and significantly different from juvenile orangutans in two cases. Thus, there is some evidence for phylogenetic signal in that humans share more developmental starting points for these traits with chimpanzees than with the more distantly related gorillas and orangutans. Note, however, that we cannot establish character polarity with confidence, given our limited phylogenetic sampling. Expanding the comparative framework to include other anthropoids, including fossil hominoids, should clarify the evolutionary trajectories of the developmental patterns documented here.

Humans maintain or achieve their distinctiveness in a variety of ways. For traits that distinguish humans from apes at the juvenile stage, there are three patterns: (1) humans and apes exhibit little or no developmental change subsequent to the juvenile stage, with the differences established by the juvenile stage being maintained (angle of C6 spinous process); (2) humans and apes exhibit developmental changes that are similar in direction and magnitude, with differences established by the juvenile stage being maintained or accentuated (relative length of C2 spinous process); and (3) humans exhibit developmental change but apes do not, with humans becoming more different from the apes as development proceeds (angle of C2 superior articular facet). There are also three patterns for traits in which humans become differentiated from the apes only after the juvenile stage: (1) humans diverge from their juvenile morphology whereas the other apes show little or no developmental change (angle of C4 spinous process); (2) humans and apes diverge from their juvenile morphologies in the same direction, but humans achieve adultlike morphology at the adolescent stage while apes continue to diverge (relative length of C6 spinous process); and (3) humans and apes diverge from their juvenile morphologies in the same direction and all four genera continue to change until they reach the adult stage, but humans begin to lag behind the apes (relative length of C4 spinous process; relative height of C6 vertebral body).

Comparison of the developmental trajectories of functionally related traits reveals some interesting differences. The relative lengths of the human C2, C4, and C6 spinous processes all increase over the course of development but humans become differentiated from great
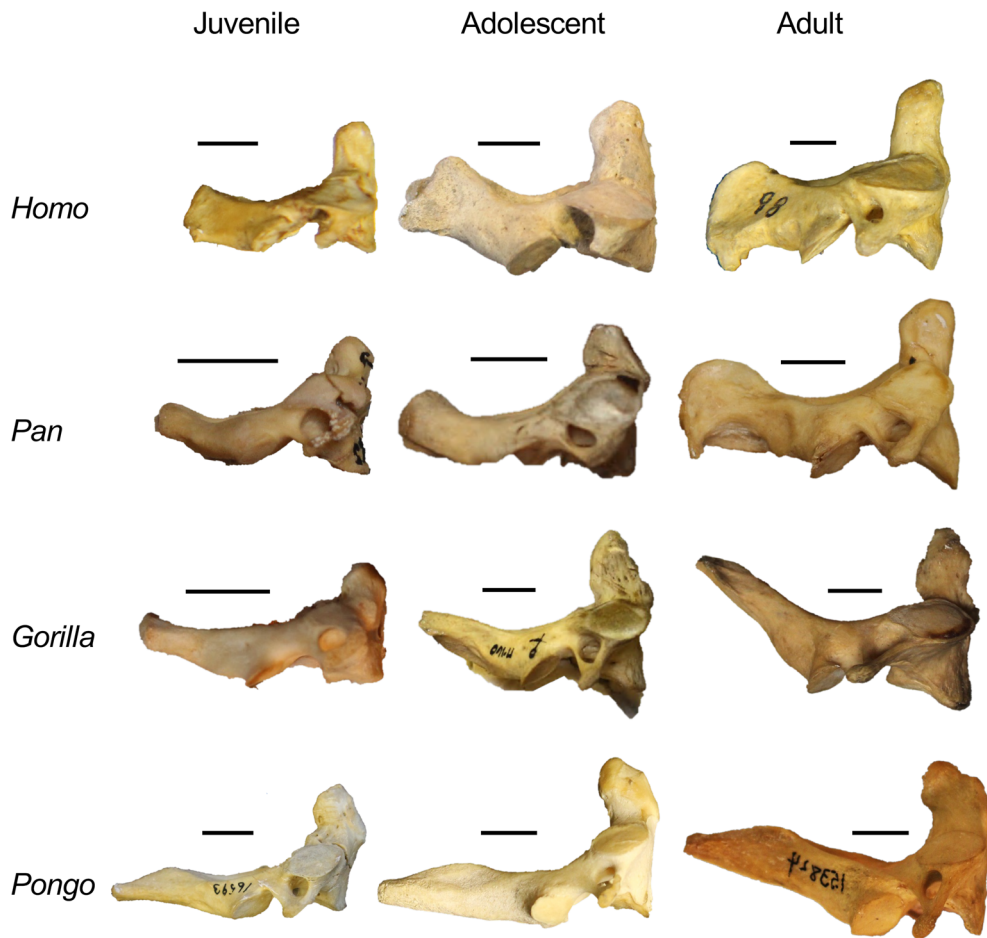
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FIGURE 3 Second cervical vertebrae in lateral view from individuals of *Homo*, *Pan*, *Gorilla*, and *Pongo* from each age group. Note the differences among the genera in the angle of odontoid process and in the length of the spinous process. Scale bars = 1 cm.

apes earlier for C2 (juvenile stage) than for C4 and C6 (adolescent stage), and the human C6 achieves its adultlike morphology earlier (adolescent stage) than is the case for the other two levels (adult stage). With regard to the angles of the C4 and C6 spinous processes, the human C6 is differentiated from those of great apes and has achieved its adultlike morphology by the juvenile stage, whereas differentiation and adultlike morphology (i.e., caudal orientation) are not reached until the adolescent stage in the human C4. Finally, the angle of the C2 superior articular facet and the angle of the odontoid process, both part of the atlantoaxial joint complex, exhibit contrasting developmental trajectories. Humans are differentiated from great apes at the juvenile stage for both traits, but the human odontoid process does not maintain this differentiation into adulthood, when chimpanzees achieve a degree of verticality that is similar to that of humans. In contrast, humans have C2 superior articular facets that are more horizontally oriented than those of apes at all stages, and this difference becomes amplified as the facets of humans become more horizontal with age, whereas apes show little or no change from the juvenile condition. These two traits also differ in when adultlike morphology is reached in humans: the odontoid process at the adolescent stage and the C2 superior articular facets at the adult stage.

An important question is how the use of crude developmental categories impacts interpretation of our results. The use of dental-

eruption stages is common in studies of skeletal development (Cobb & O'Higgins, 2007; Green & Alemseged, 2012; Nalley et al., 2019; Shea, 1985; Simons & Frost, 2016; Taylor, 1997), but there are differences among hominids in the relative timing of dental and skeletal maturity. Brimacombe et al. (2015, 2018) showed that postcranial skeletal maturity tends to occur earlier relative to dental maturity in humans than it does in chimpanzees and bonobos. Our finding that humans achieve adultlike morphology earlier than chimpanzees in some features (angle of odontoid process, length of C6 spinous process) is consistent with Brimacombe et al.'s observations, but in other cases, humans achieve adultlike morphology later than chimpanzees (angle of C2 articular facets, angle of C4 spinous process). In our view, the most important developmental baselines for the features examined here are the ontogenetic trajectories of their functional environments, which are poorly understood. Comparative developmental data on head and neck postures, range of motion in the cervical vertebral column, and nuchal musculature—all of which are currently unavailable—will be critical for understanding the developmental patterns documented here. In any event, these patterns should be useful for generating and testing functional hypotheses, and for interpreting the morphology of subadult fossil hominins. In the discussion that follows, we focus on how our results inform previous ideas about the functional morphology of hominid cervical vertebrae.

FIGURE 4 Second cervical vertebra in ventral view from individuals of *Homo*, *Pan*, *Gorilla*, and *Pongo* from each age group. Note the differences among the genera in the angle of superior articular facet. Scale bars = 1 cm.
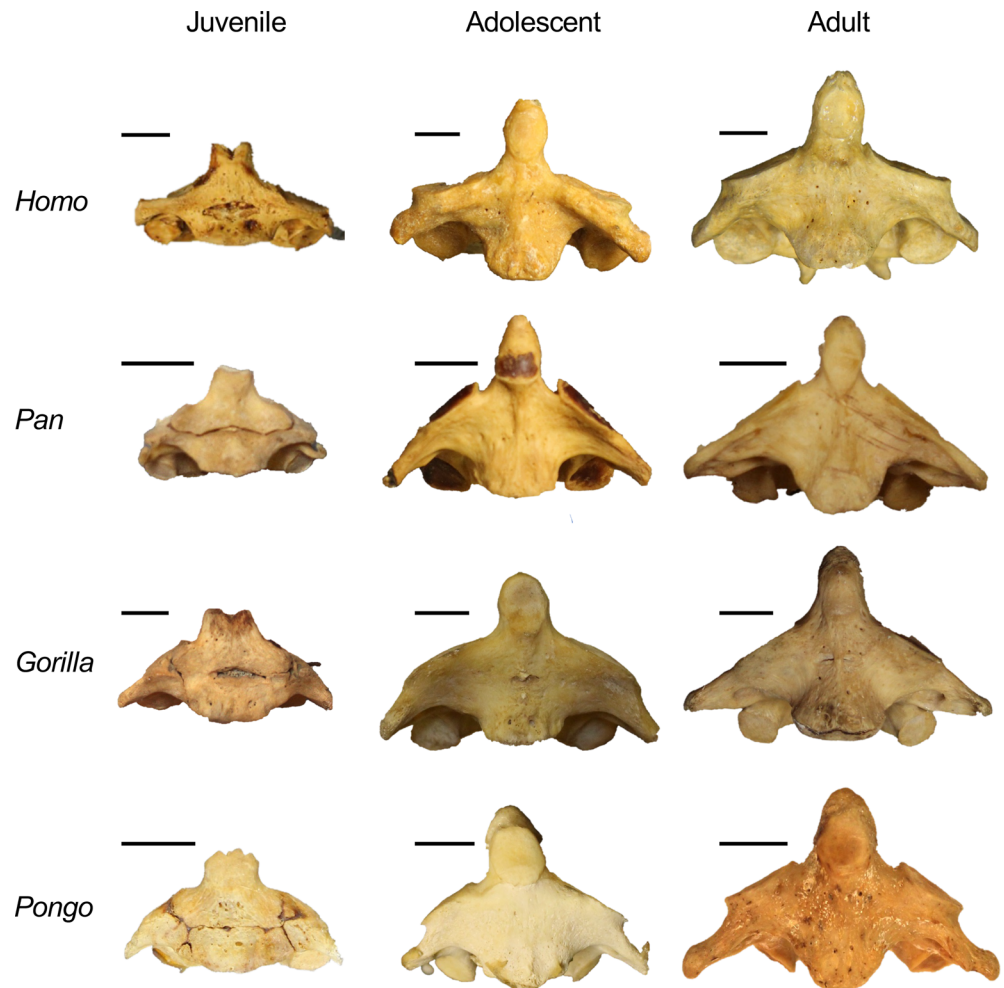
4.2 | Form, function, and development of the atlantoaxial joint complex

The atlantoaxial joint complex comprises three articulations between the C1 and C2, including a single median joint between the dorsal surface of the C1 anterior arch and the ventral surface of the C2 odontoid process, and two lateral joints between the C1 inferior articular facets and the C2 superior articular facets. Although it is widely considered a primary component in mammalian head and neck kinematics (e.g., Anderst et al., 2017; Bogduk & Mercer, 2000; Kapandji, 2008; Schikowski et al., 2021; Westworth & Sturges, 2010; White & Panjabi, 1990; Zhou et al., 2020), there are major gaps in our understanding of normal *in vivo* joint kinematics and physiology in extant humans (Anderst et al., 2017; Zhou et al., 2020) and other mammals (Schikowski et al., 2021), making biomechanical interpretations of the skeletal variation found in hominids somewhat tenuous.

Differences between humans and other primates in odontoid process angle (OPA) and superior articular facet orientation (SFA) have been reported previously, where humans have been described as having more vertical odontoid processes and less sloped facets (or more horizontal) than other taxa (Ankel, 1970, 1972; Ankel-Simons, 2007; Gommery, 2006; Meyer & Williams, 2019a; Meyer & Williams, 2019b). In general,

these two variables have been observed to correlate with each other across phylogenetically broad samples of primates, and this relationship has been linked to the shared biomechanical environment of the basicranium, atlas, and axis (Meyer & Williams, 2019a; Meyer & Williams, 2019b; Nalley & Grider-Potter, 2017). Some authors have discussed these features as possible indicators of bipedality in fossil hominin taxa (Gommery, 1997, 2006), but others have noted similarly vertical odontoid processes in gibbons and chimpanzees (Ankel-Simons, 2007) and more dorsally angled (i.e., retroflexed) odontoid processes in fossil hominins that have clear indicators of bipedality in other postcranial elements (Meyer & Williams, 2019a, Meyer & Williams, 2019b).

The results of our study confirm that adult humans and great apes differ in SFA and support the observation that OPA does not consistently distinguish adult humans from adult chimpanzees. This pattern indicates some degree of functional independence between the two features. This conclusion is also suggested by the different developmental trajectories of OPA and SFA in humans, in which adult OPA morphology is achieved earlier than adult SFA morphology. OPA does separate humans from chimpanzees (and other apes) prior to adulthood: at the juvenile and adolescent stages, humans have more vertical odontoid processes. Another notable difference between humans
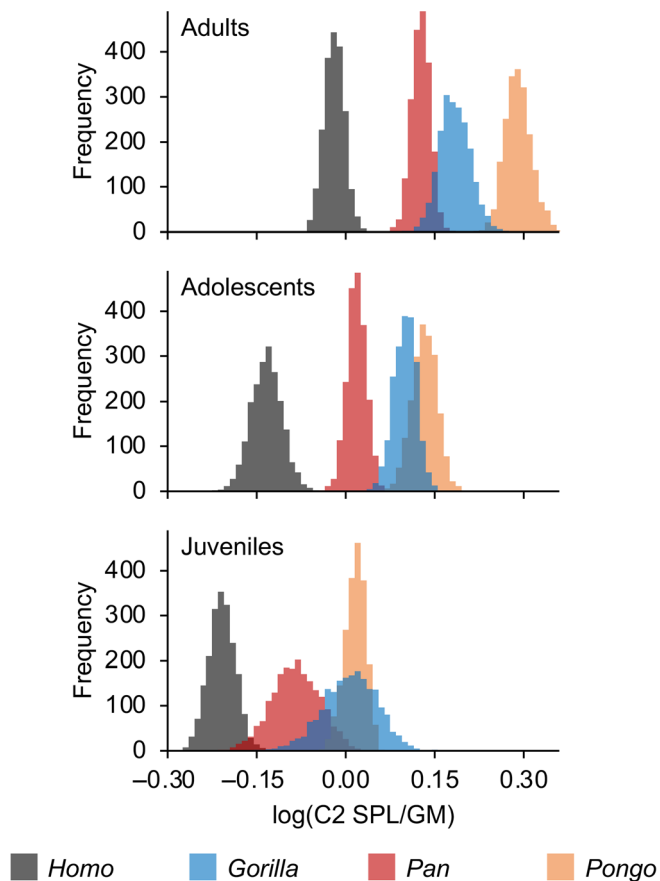
FIGURE 5 Bootstrap distributions for C2 relative spinous process length (SPL divided the geometric mean, GM) by species and age group. The middle 95% of each distribution is equivalent to a 95% confidence interval.

vertebral column. The vertical odontoid process and less sloped C2 superior articular facets of humans have been linked to cervical lordosis and the need to resist increased compressive forces in taxa with more vertical positional behaviors (Gommery, 2006). Conversely, the dorsally oriented odontoid processes and steeply sloped C2 superior articular facets found in species with more horizontal neck postures may lower energetic requirements of the nuchal musculature by shifting the head dorsally relative to the neck, positioning the weight of the head to be better supported by the vertebral column (Nalley & Grider-Potter, 2017). Alternatively, the orientation of the odontoid process may be linked with the orientation of the foramen magnum rather than with differences in positional behavior (Meyer & Williams, 2019a, Meyer & Williams, 2019b). According to this argument, a more dorsally oriented foramen magnum would require a more dorsally oriented odontoid process to avoid impingement of the spinal cord as it exits the skull (Meyer & Williams, 2019a, Meyer & Williams, 2019b). This proposed functional relationship deserves further investigation across primates, but we note that our finding of similar OPA values for adult humans and chimpanzees (contra Meyer & Williams, 2019a, Meyer & Williams, 2019b) suggests that the orientation of the foramen magnum is unlikely to explain variation in OPA among hominoids.

In sum, the results of this study, in agreement with previous work (Ankel-Simons, 2007; Meyer & Williams, 2019a; Meyer & Williams, 2019b), do not support a strong link between locomotor behavior and OPA. The contrasting patterns of development documented here provide the basis for future work examining covariation between OPA and SFA and the relationship between those features and the ontogeny of the skull, brain, and vertebral column.

4.3 | Nuchal musculature, neck mobility, and the cervical spinous processes

It is well established that, among adults, the cervical vertebrae of apes have relatively long spinous processes when compared to humans (Arlegi et al., 2017; Meyer, 2015; Nalley & Grider-Potter, 2015; Schultz, 1961; Slijper, 1946). Our results agree with previous observations, but we can also now consider how this variation manifests in subadults. At the C2 level, humans have relatively shorter spinous processes in comparison to all of the great apes beginning at the earliest developmental stage. In the subaxial spine, humans have shorter spinous processes than gorillas and orangutans at all developmental stages but are not distinct from chimpanzees until the adolescent stage. The similarity of juvenile humans and chimpanzees and their common difference from gorillas and orangutans identifies this age-group as an important comparison for testing the relationship between spinous process length (SPL) and previous functional hypotheses.

The long cervical spinous processes of apes are thought to reflect nuchal musculature that is relatively larger and more powerful (i.e., greater physiological cross-sectional area) (Dean, 1982; Larson, 1995; Stern & Susman, 1983; Swindler & Wood, 1982).

and chimpanzees is that humans achieve adultlike form by their adolescent stage, whereas chimpanzees do not do so until the adult stage. This difference in developmental patterns is unlikely to be a consequence of differences in ossification or fusion rates, as humans and chimpanzees are generally considered similar in when the odontoid process begins to ossify and subsequently fuse to the C2 centrum (Martelli, 2019). It is also unlikely to be related to the adoption of adult positional behaviors, as adolescent and adult chimpanzees have similar frequencies of climbing and suspension (Doran, 1997). The fact that the OPA of *Pan* converges on that of *Homo* later in development implies a greater degree of change from juveniles to adults in *Pan* relative to *Homo* and perhaps the other great apes (Figure 2). Comparisons of bootstrapped differences between adult OPA and juvenile OPA within taxa reveals that *Pan* has a significantly greater magnitude of developmental change than *Homo* ($p = 0.0085$) but not *Gorilla* ($p = 0.3053$) or *Pongo* ($p = 0.1164$). Understanding the contrasting developmental trajectories of humans and chimpanzees is challenging in the absence of a well-grounded biomechanical framework for atlantoaxial function.

Discussion of the functional significance of variation in OPA and SFA has focused on neck posture and the configuration of the cervical

FIGURE 6 Bootstrap distributions for C4 spinous process angle (SPA; left) and relative spinous process length (SPL divided by the geometric mean, GM; right) by species and age group. The middle 95% of each distribution is equivalent to a 95% confidence interval.
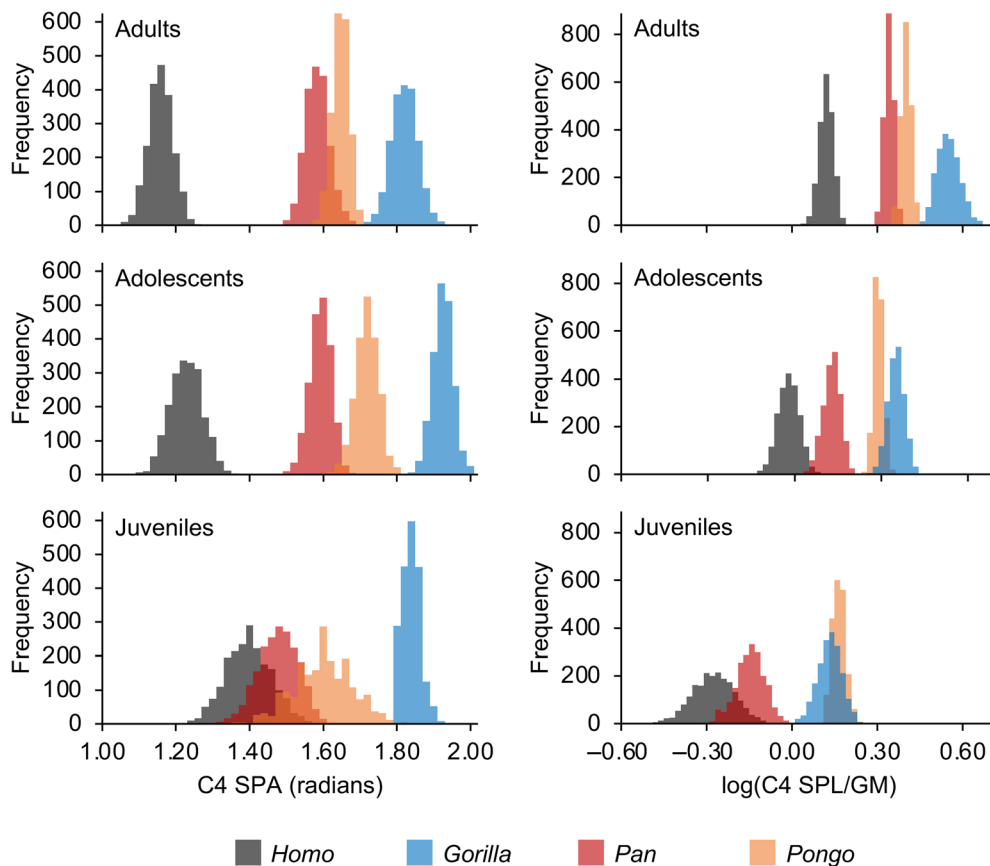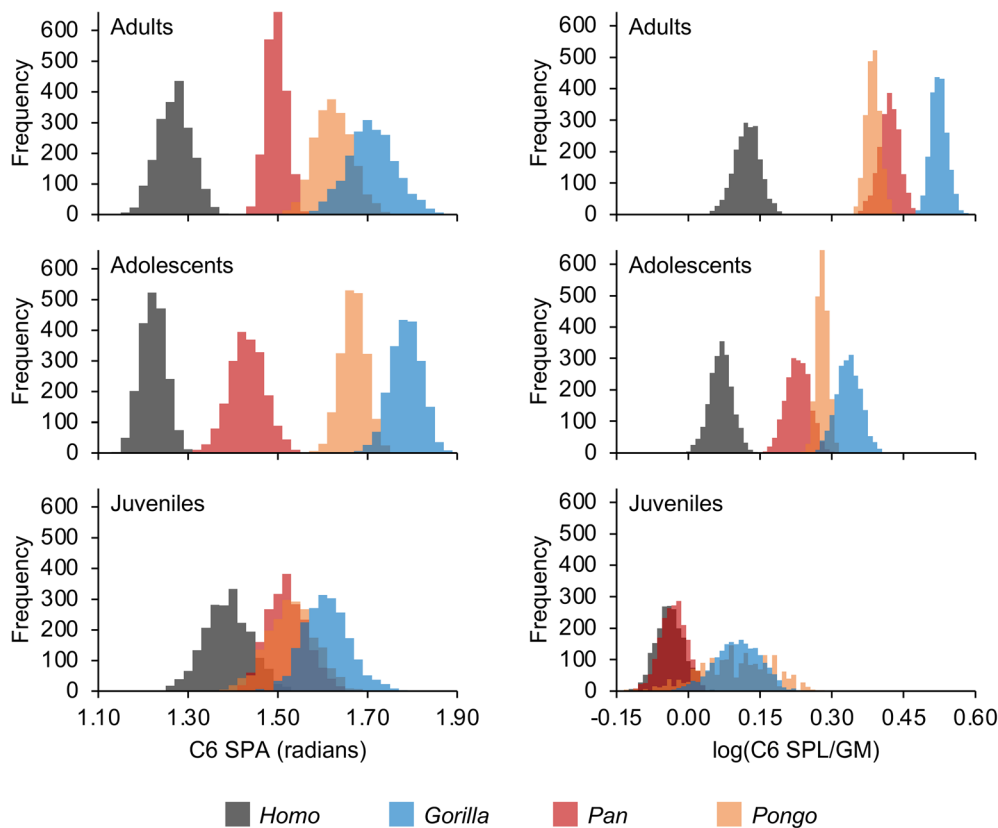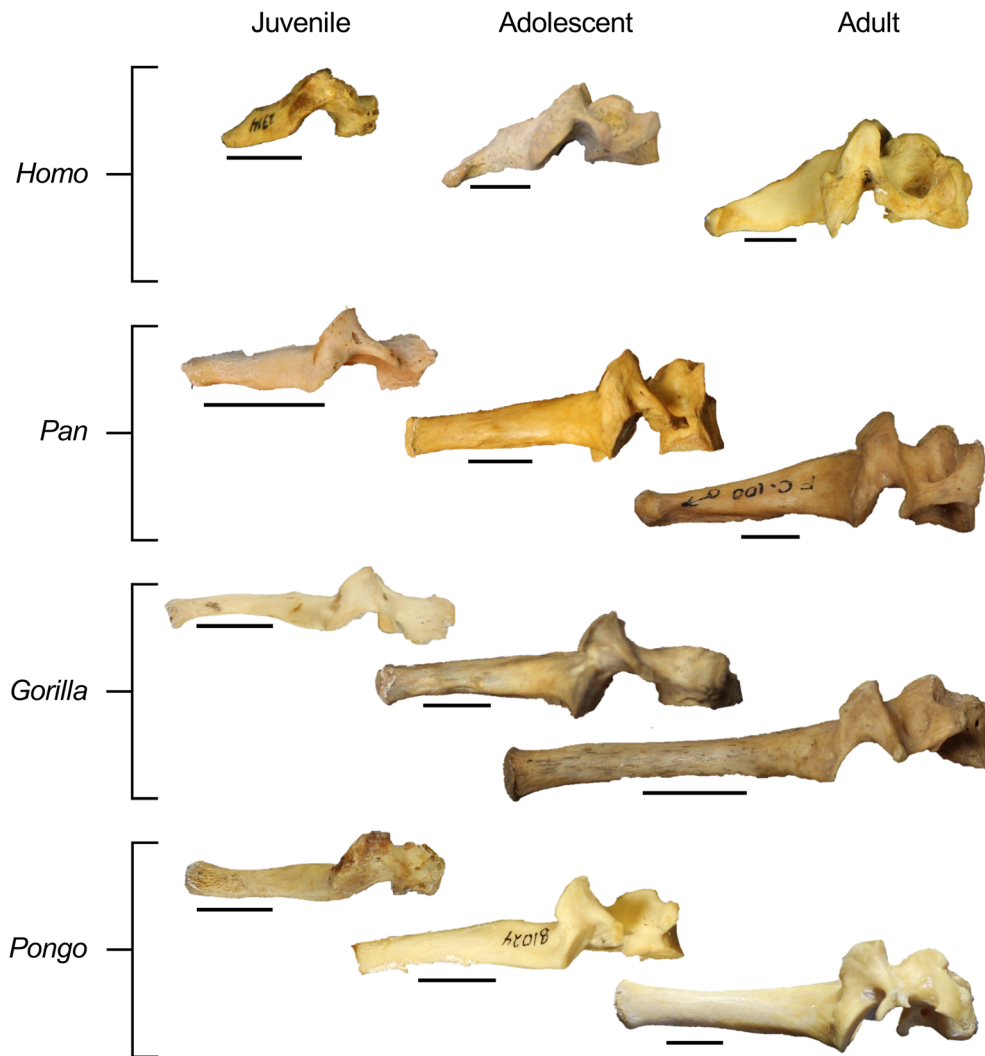

FIGURE 7 Bootstrap distributions for C6 spinous process angle (SPA; left) and relative spinous process length (SPL divided by the geometric mean, GM; right) by species and age group. The middle 95% of each distribution is equivalent to a 95% confidence interval.

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FIGURE 8 Sixth cervical vertebra in lateral view from individuals of *Homo*, *Pan*, *Gorilla*, and *Pongo* from each age group. Note the differences among the genera in the length and angle of the spinous process. Scale bars = 1 cm.

Longer spinous processes can also indicate an increase in the moment arm of associated muscles, improving their mechanical advantage (Cripton, 2000; Shapiro, 1993b; Shapiro & Simons, 2002; Slijper, 1946). In the case of cervical vertebrae, the functional scenario most often invoked in primates is that long spinous processes improve the ability of the nuchal musculature to counter ventral moments of the head and neck related to horizontal neck postures and/or a more prognathic splanchnocranium (Meyer, 2015; Meyer & Williams, 2019a; Meyer & Williams, 2019b; Nalley & Grider-Potter, 2015). Nalley and Grider-Potter (2015), for example, found that primates with more horizontal head and neck postures have relatively long spinous processes. These functional hypotheses have yet to be fully examined via comparative myology and electromyographic studies (McGechie, 2021).

Additional explanations for variation in SPL implicate locomotion and range of motion. Relatively long spinous processes in great apes have been linked functionally with suspensory locomotion and other forelimb dominated behaviors, rather than neck posture per se (Meyer, 2015; Nalley, 2013). For example, in *Gorilla* and *Pan*, the occipital and cervical origins of trapezius are more extensive than in

humans, and the muscle bellies are shortened and thickened (Dean, 1982; Larson et al., 1991; Swindler & Wood, 1982). Larson et al. (1991) suggested that the relatively large size of the cranial portion of trapezius in apes is associated with the muscular requirements of rotating the head and stabilizing the head on the trunk during suspensory locomotion. The proposed link between SPL and suspensory behaviors has received support when only extant hominids are considered (Meyer, 2015; Nalley, 2013), but the correlation breaks down when other suspensory primates—gibbons and spider monkeys—are added to the comparative framework (Arlegi et al., 2017; Nalley, 2013; Schultz, 1961). With regard to differences in neck flexibility and range of motion, longer spinous processes are thought to inhibit extension (Arlegi et al., 2017; Schultz, 1961). Grider-Potter et al. (2020) investigated this hypothesis using range-of-motion data for twelve primate taxa, including chimpanzees and humans, and found that longer spinous processes appear to limit extension at only a single joint—the cervicothoracic junction (C7–T1).

Turning to spinous process angle (SPA), our results support previous observations that humans have more caudally angled cervical spinous processes in comparison to great apes (Arlegi et al., 2017;
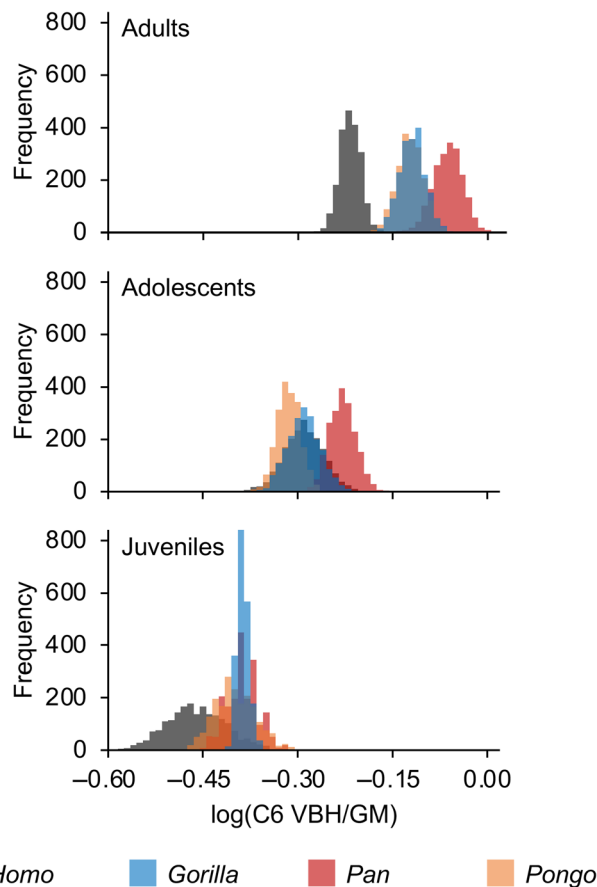
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FIGURE 9 Bootstrap distributions for C6 relative vertebral body craniocaudal height (VBH, divided by the geometric mean, GM) by species and age group. The middle 95% of each distribution is equivalent to a 95% confidence interval.

TABLE 7 Summary of traits that distinguish extant humans from great apes.

Trait	Stages at which humans are differentiated from great apes
C2 odontoid process angle	Juvenile, adolescent†
C2 superior facet angle	Juvenile, adolescent, adult†
C2 spinous process length	Juvenile, adolescent, adult†
C4 spinous process angle	Adolescent†, adult
C4 spinous process length	Adolescent, adult†
C6 spinous process angle	Juvenile†, adolescent, adult
C6 spinous process length	Adolescent†, adult
C6 vertebral body height	Adult†

Note: Crosses indicate the developmental stage at which adultlike morphology emerges in humans. Note that human and chimpanzee adults are not significantly different for odontoid process angle.

Nalley & Grider-Potter, 2015; Schultz, 1961). At the C6 level, humans are distinct from the apes at all developmental stages; at the C4 level, humans are different from all apes at the adult and adolescent stages, but the youngest humans and chimpanzees cannot be statistically distinguished. More caudally oriented spinous processes may be a derived trait of recent human cervical vertebrae, as other fossil hominin taxa—*Australopithecus afarensis*, *Homo erectus*, and *Homo neanderthalensis*—exhibit more horizontal, apelike spinous processes (Arsuaga et al., 2015; Carretero et al., 1999; Gómez-Olivencia et al., 2013; Gómez-Olivencia & Been, 2019; Meyer et al., 2017; Meyer & Williams, 2019b; Nalley, 2013; Williams & Meyer, 2019).

One functional interpretation of more caudally oriented spinous processes is that they permit a greater range of extension when compared to the longer, more horizontal processes observed in apes (Arlegi et al., 2017; Schultz, 1961). As noted above in the discussion of SPL, Grider-Potter et al. (2020) found only limited support for this scenario. Their results showed that humans have a greater range of neck extension at C7–T1 when compared to chimpanzees, but not at C6–C7, one of the levels examined here.

Caudally oriented spinous processes in humans have also been linked with the presence of a nuchal ligament. In humans, the nuchal

ligament extends caudally from the external occipital protuberance and median nuchal line to the spinous processes of the cervical vertebrae and terminates inferiorly at the C7 spinous process (Mercer & Bogduk, 2003). In great apes, the nuchal ligament is either absent or only fascial in nature (Aiello & Dean, 1990; Swindler & Wood, 1982; Vallois, 1926), but cursorial mammals (e.g., ungulates and canids) often display well-developed, tendonlike structures (Bianchi, 1989; Dimery et al., 1985; Gellman & Bertram, 2002). The nuchal ligament is of interest to paleoanthropologists because of its hypothesized role in the evolution of bipedal locomotion, specifically as an adaptation for endurance running in humans (Aiello & Dean, 1990; Bramble & Lieberman, 2004; Yegian et al., 2021). Well-developed nuchal ligaments in humans are thought to improve running by helping to stabilize motions of the head and reduce ventral moments around the atlanto-occipital joint during deceleration (Lieberman, 2011). The functional role of the nuchal ligament is likely to be complex and is worth further comparative investigation because it has also been identified in *Papio* and *Macaca* (Bianchi, 1989; Fielding et al., 1976; Swindler & Wood, 1982), neither of which possess caudally oriented spinous processes or are particularly cursorial. Interestingly, Arlegi et al. (2017) and Schultz (1961) reported that gibbons exhibit humanlike spinous process angles at C6 and C7, and some researchers have noted the presence of a weakly developed nuchal ligament in some gibbon species (Diogo et al., 2012; Donisch, 1973; Plattner, 1923; Sonntag, 1924).

Numerous questions regarding the functional implications of variation in the length and orientation of the cervical spinous processes remain, highlighting the need for experimental biomechanical approaches and soft-tissue data to validate assumptions made in studies of the bony morphology. By establishing differences between humans and great apes at subadult stages, our results provide a foundation for an additional line of inquiry that may prove insightful: testing for developmental covariation between the cervical spinous processes and the cranium, nuchal musculature, neck posture and range of motion, and locomotor behavior.

4.4 | Vertebral body height and cervical lordosis

Results here support previous work showing that humans have craniocaudally short centra when compared to other extant hominids (Arlegi et al., 2017; Meyer, 2005, 2015; Nalley, 2013; Nalley & Grider-Potter, 2015; Schultz, 1961). In contrast to the other traits that separate adult humans from apes, whose differences appear relatively early in development, vertebral body height (VBH) does not distinguish humans until adulthood. The timing of cervical centra growth cessation has only been documented in humans and is observed to correlate with the end of the adolescent growth spurt, occurring between 14 and 17 years of age (Cunningham et al., 2016; Johnson et al., 2016). This benchmark also coincides with the development of the adult configuration of the cervical lordotic curve in humans (Been, Gómez-Olivencia, et al., 2017; Hellsing et al., 1987; Lee et al., 2012;).

The curvature of the cervical vertebral column in most terrestrial mammals is generally described as sigmoidal and is argued to reflect the maintenance of a more vertical, self-stabilizing resting posture of the head and neck (Arnold, 2021; Graf, De Waele, & Vidal, 1995; Graf, De Waele, Vidal, Wang, et al., 1995; Vidal et al., 1986). This resting posture has been observed across many mammalian taxa and variation is likely to be related to differences in torso orientation (Graf, De Waele, & Vidal, 1995; Graf, De Waele, Vidal, Wang, et al., 1995; Vidal et al., 1986). For example, in those taxa with body postures that are relatively more vertical, such as humans and other primates, the neck protrudes from the top of the trunk and the curvatures are much less pronounced (Kapandji, 2008; Kurtz & Edidin, 2006; White & Panjabi, 1990) in comparison to species with body postures that are relatively more horizontal (e.g., rabbits, guinea pigs, and cats) (Graf, De Waele, & Vidal, 1995; Graf, De Waele, Vidal, Wang, et al., 1995; Macpherson & Ye, 1998; Vidal et al., 1988). Regardless of trunk orientation, a more vertical orientation of the cervical vertebrae during rest is thought to play multiple functional roles, such as reducing the distance between the weight of the head and the supporting C7–T1 joint to reduce the energetic requirements of the nuchal musculature (Arnold, 2021; Demes, 1985; Graf, De Waele, & Vidal, 1995; Graf, De Waele, Vidal, Wang, et al., 1995; Macpherson & Ye, 1998; Nalley & Grider-Potter, 2015;).

Across primates, cervical VBH increases as the posture of the head and neck becomes more horizontal, and this relationship may reflect the maintenance of the sigmoidal cervical curve in taxa with more horizontal body postures (Nalley & Grider-Potter, 2015). At a given angular excursion per vertebral pair, longer vertebrae increase the total amount of flexion at that spinal segment and of the column as a whole (Ward, 1993), and thus craniocaudally tall cervical vertebrae may facilitate curve formation in the neck during resting behaviors in taxa with more horizontal body postures (Nalley & Grider-Potter, 2015). Meyer (2005) also suggested this relationship between craniocaudally tall cervical bodies and more horizontal body postures when comparing humans to chimpanzees and gorillas. The lack of comparative documentation of *in situ* cervical lordosis anatomy is a major impediment to understanding extant hominid head and neck postures. Comparing the ontogeny of extant hominid cervical lordosis,

and specifically cervical intervertebral disc morphology, would allow researchers to develop and test more detailed models of fossil hominin head and neck postures and their covariation with the evolution of bipedalism.

5 | CONCLUSION

This study examined the ontogeny of functionally relevant features of the cervical vertebrae of extant hominids to determine how and when the morphologies that are characteristic of adult humans are achieved during development. Of the eighteen variables we examined, only seven distinguish extant humans from great apes at the adult stage: relative lengths of the C2, C4, and C6 spinous processes; angles of the C4 and C6 spinous processes; angle of the C2 superior articular facet; and craniocaudal height of the C6 vertebral body. These differences emerge at different times during development. Some are established by the juvenile stage, especially those that influence the function of the atlantoaxial joint complex. Others emerge in adolescence, and these tend to be related to the nuchal musculature and movement of the subaxial elements. The biomechanical consequences of the features that distinguish humans from great apes are not well understood. Whether the differences in vertebral growth patterns documented here are related to cranial development and/or postural changes requires additional investigation. The results of this study provide a framework for integrating development into tests of biomechanical hypotheses and interpreting the morphology of subadult fossil hominins in functional and phylogenetic contexts.

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DATA AVAILABILITY STATEMENT

The data used in the manuscript are available in the supplementary information.

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