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Phylogenetic and functional signal in prezygapophyseal articular facet shape of the first post-transitional vertebra in anthropoids

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Abstract

Objectives: Previous studies of the prezygapophyseal articular facet (PAF) of the thoracolumbar vertebrae in primates have suggested that the morphology of this feature reflects relative mobility of the lower back, and therefore corresponds to locomotor behavior. Specifically, these studies suggest that the PAF morphology found in cercopithecoids reflects greater mobility of the lower back compared to a stiffer lower back adapted for forelimb-dominated suspensory behaviors in hominoids. In this study, we sought to re-examine this question in terms of both locomotor behavior and phylogenetic signal in a broad sample of anthropoid taxa.

Materials and Methods: The study sample consisted of 291 first post-transitional vertebrae of wild-caught individuals representing 27 extant anthropoid species (16 genera). Vertebrae were 3D scanned, and 19 landmarks were digitized. PAF shape was tested for the presence of a phylogenetic signal using the multivariate version of the *K*-statistic (K_{mult}), and a chronometric consensus phylogenetic tree was mapped onto the major axes of shape space using species means to produce a phylomorphospace.

Results: Results showed that phylogenetic signal is statistically significant in PAF shape ($K_{\text{mult}} = 0.3$; $p < 0.0001$), and phylogenetic separation is apparent in the phylomorphospace, with some exceptions. However, certain aspects of PAF shape also appear to be associated with locomotor behavior within major taxonomic groups, such as hominoids and platyrrhines.

Discussion: Our results suggest that both phylogenetic relatedness and function may contribute to PAF shape variation in anthropoids.

KEYWORDS
functional morphology, phylomorphospace, primate locomotion, thoracolumbar vertebral column, zygapophyses

1 | INTRODUCTION

Due to its functional role during primate locomotion and posture, vertebral column morphology has been studied in relation to various primate positional behaviors (Benton, 1967; Erikson, 1963; Johnson & Shapiro, 1998; Latimer & Ward, 1993; Linden et al., 2019; Meyer et al., 2018; Nalley & Grider-Potter, 2015, 2017; Pal & Routal, 1987; Rose, 1975; Russo et al., 2020; Schultz, 1960;

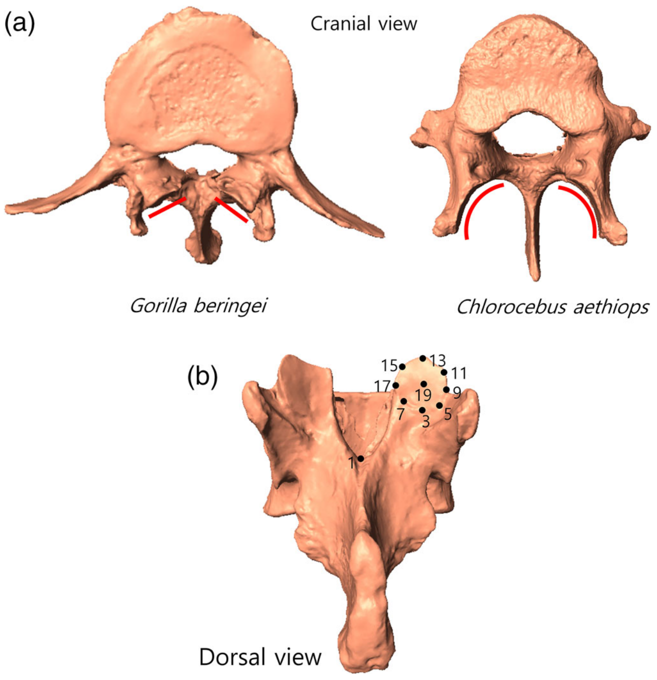

FIGURE 1 Prezygapophyseal articular facet (PAF) shape in the 3D scan and landmarks on it. (a) Comparison of PAF shape in the 3D scan of the first post-transitional vertebra between *Gorilla beringei* and *Chlorocebus aethiops* male specimens. The *G. beringei* specimen shows more obliquely oriented and flatter PAF shape in cranial view than the *Chlorocebus aethiops* specimen. Added lines indicate orientation and curvature of the PAF; (b) Landmarks on the PAF of the first post-transitional vertebra of male gorilla. Bilateral landmarks are presented only on the left side of the PAF

Shapiro, 1993, 1995, 2007; Shapiro et al., 2001; Shapiro & Simons, 2002; Slijper, 1946). One example of this is lumbar vertebral column length, which is cranio-caudally greater in cercopithecoids compared to hominoids, both through increased craniocaudal vertebral body length and an increase in lumbar vertebrae number. This morphology allows for relatively more flexion-extension movement during leaping and/or running behaviors in primates such as the cercopithecoids (Shapiro, 1993). In contrast, hominoids tend to have shorter and stiffer lumbar vertebral columns to reduce lower back mobility and provide stability during fore-limb dominated suspensory behaviors, such as vertical climbing, arm-swinging and bridging (Cartmill, 1985). Similarly, atelines, which also engage in suspensory locomotor behaviors but which are widely separated from hominoids phylogenetically, also possess relatively short lumbar vertebral columns when compared to cebids (Johnson & Shapiro, 1998; Shapiro, 1993).

Another aspect of vertebral morphology that has been used as an indicator of relative lower back mobility in distinguishing between suspensory and non-suspensory primate species is the shape of the prezygapophyseal articular facet (PAF) (e.g., Nalley et al., 2019; Russo, 2010). Zygapophyseal articular facets are the facets on the cranial (or superior) and caudal (or inferior) articular processes, which form synovial joints that dorsally connect two adjacent vertebrae for intervertebral movement (Bogduk & Twomey, 1987; Pal & Routal, 1987; Shapiro, 1993; Russo, 2010; Nalley et al., 2019; Figure 1). The PAFs are the cranial zygapophyseal articular facet on a given vertebra, and its morphology has been argued to be related to its functional role in spinal movements and transmission of body weight (Bogduk & Twomey, 1987; Nalley et al., 2019; Pal & Routal, 1987; Russo, 2010; Shapiro, 1993). For example, Pal and Routal (1987) reported that zygapophyseal articular facet size in humans increases in absolute term and relative to vertebral body area from T12 throughout the lumbar vertebrae as the magnitude of compressive force per unit surface area can be reduced by enlarging total facet surface area.

In terms of spinal movements, it has been suggested that sagittally oriented PAFs permit flexion-extension movement in the sagittal plane, but resists axial rotation, while more obliquely-oriented (relative to the sagittal plane) PAFs allow axial rotation but resist flexion-extension movement in the sagittal plane (Latimer & Ward, 1993; Shapiro, 1993; figure 1a,b in Russo, 2010). For instance, gorillas have more obliquely-oriented PAFs in the lumbar region to reduce sagittal plane bending between their vertebrae, allowing for a stiffer and more stable trunk in suspensory behaviors (Cartmill, 1985; Russo, 2010). As another example, lorisids have relatively coronally oriented zygapophyses in the lumbar region, which may be beneficial for coronal plane spinal mobility during antipronograde suspensory behaviors including bridging, hanging, and reaching, while galagids have more sagittally oriented prezygapophyses to facilitate more leaping and quadrupedal behaviors (Shapiro, 2007). Additionally, flatter joint surfaces in obliquely-oriented PAFs may resist axial rotation but permit lateral flexion in species like gorillas (figure 1c in Russo, 2010). Finally, the interfacet distance between PAFs on the right and left sides of vertebrae may also be related to lower back mobility. For instance, Russo (2010: 610) reported that *Hylobates* had greater interfacet distance than *Pongo* to enhance the control of truncal rotation during ricochetal brachiation. Alternatively, greater interfacet distance may reflect body size differences between *Hylobates* and *Pongo* (Russo, 2010, p. 610). Thus, it has been shown that PAF shape generally has functional significance in relation to spinal movement during locomotion, in particular for distinguishing between adaptations for stability versus mobility in suspensory and non-suspensory species (Latimer & Ward, 1993; Nalley et al., 2019; Russo, 2010).

One factor that complicates functional interpretations of PAF morphology is the confounding effects of phylogeny. Differences between the morphology of cercopithecoids and hominoids could be due to phylogenetic separation in addition to frequency of use of suspensory behaviors. Nalley et al. (2019) demonstrated the possible confounding effects of phylogeny in an investigation of PAF shape in hominids and fossil hominins. They found similar zygapophyseal facet morphology in chimpanzees and hominins, which was distinct from the morphology in gorillas and orangutans. Their finding, that chimpanzees more closely resembled humans than gorillas, suggests phylogeny might be a better determinant of PAF morphology than locomotor behavior. Russo (2010) minimized the effects of phylogenetic history and locomotor variability in PAF morphology by looking within nonhuman hominoids, and using *Papio* as an outgroup.

However, formal statistical tests for phylogenetic effects on PAF morphology were not conducted in either of these previous studies.

One way to statistically assess the impact of phylogeny on the morphology of a given trait is through the calculation of a *K*-statistic, which shows the degrees of similarity between closely related taxonomic groups relative to a null model assuming Brownian motion evolution (Blomberg et al., 2003). As an example of the application of this method to vertebral morphology, Linden et al. (2019) showed that atlas shape can be explained by phylogenetic relatedness and body size but not locomotor behaviors and head size when analyzed in the orders Primates, Rodentia, Lagomorpha, Dermoptera, and Scandentia. Another approach is to expand the diversity of species analyzed to include clades outside of catarrhines with variable locomotor behaviors, which can then be compared to cercopithecoids and hominoids. Platyrrhines make an ideal group for this comparison, since they include species such as the atelines that engage in suspensory behavior, and therefore should converge anatomically with hominoids. In a study of platyrrhine monkeys in central Suriname, Fleagle and Mittermeier (1980) observed a broad range of suspensory and non-suspensory locomotor behaviors. From their observations, *Ateles* used suspensory behaviors for 70% of travel, *Alouatta* used an intermediate frequency of suspensory behavior (16% of travel), and *Cebus*, *Chiropotes*, *Saimiri*, and *Saguinus* mostly used leaping and/or quadrupedal behaviors during travel. Given this locomotor diversity, investigation of platyrrhine species could potentially shed light on the phylogenetic versus functional determinants of vertebral morphology in anthropoids more generally.

In the present study, PAF shape of the first post-transitional vertebra was tested for functional and phylogenetic signal in a diverse sample of anthropoid species, including catarrhines and platyrrhines. This study expands on previous work (e.g., Russo, 2010) by including platyrrhines as well as a broad sample of cercopithecoid species, and by employing phylogenetic comparative methods. The "transitional vertebra" (traditionally the diaphragmatic vertebra in the thoracolumbar region) is defined as the vertebra with cranial articular facets with flat and coronal orientation and caudal articular facets with curved and parasagittal orientation (Williams et al., 2016). It was shown that changes in PAF orientation were more abrupt in the first post-transitional vertebra of *Papio* than hominoids (Russo, 2010), which may reflect locomotor behaviors and/or phylogenetic effects. The PAF shape of anthropoids is especially suited for a phylogenetic comparative approach, as anthropoids display a large amount of variation in both axial skeletal morphology (Latimer & Ward, 1993; Nalley & Grider-Potter, 2015, 2017; Shapiro, 1993) and in locomotor behaviors (Fleagle, 2013).

In this study, we examined whether there is significant phylogenetic signal in PAF shape across anthropoids, and whether platyrrhine species show morphological convergence with catarrhine species depending on their use of suspensory locomotor behaviors. Specifically, we tested the hypothesis that PAF morphology reflects phylogeny. Following this hypothesis, we predicted that anthropoid taxa would cluster together according to major taxonomic groups (cercopithecoids, hominoids, platyrrhines) in phylomorphospace, and the *K*-statistics would be significant. We also tested the alternative hypothesis that PAF shape would be more strongly dictated by functional demands than by phylogeny. According to this hypothesis, non-human hominoids and atelines should have convergent PAF morphology due to shared functional requirements of suspensory locomotion. Among the hominoids, there is differing frequency of use of suspensory locomotion, with the African apes more frequently engaging in terrestrial quadrupedalism. However, all hominoids have orthogrady-adapted body plans reflecting suspensory adaptations (Fleagle, 2013), and thus we feel that they can all be considered "suspensory" for the purpose of testing hypotheses about trunk anatomy in this study. Therefore, we predicted that atelines would cluster with hominoids in phylomorphospace and would separate to some degree from platyrrhines that engage in suspensory behavior less frequently, such as cebids. However, we recognize that all of the platyrrhine species in this study engage in some amount of suspensory behavior (Fleagle & Mittermeier, 1980), and thus distinctions between these species may be relatively subtle.

2 | MATERIALS AND METHODS

2.1 | Skeletal materials and geometric morphometric method

For this study, 291 vertebrae of wild anthropoid primate individuals representing 27 extant species (16 genera) were used (Table 1). Data collection was conducted by 3D scanning the first post-transitional vertebra using HDI and Macro R5X structured-light scanners (LMI technologies Inc., Vancouver, Canada). In the present study, the "transitional vertebra" in the thoracolumbar region is the diaphragmatic vertebra, defined as vertebrae with cranial articular facets with flat and coronal orientation and caudal articular facets with curved and parasagittal orientation (Williams et al., 2016). On the 3D scanned first post-transitional vertebra, 19 landmarks were digitized using the Landmark program (Wiley et al., 2005) with reference to Russo (2010) (Figure 1b; Table 2).

Procrustes superimposition was applied to the digitized landmarks to produce Procrustes coordinate data (Zelditch et al., 2012). This procedure includes scaling the centroid size of coordinate configurations to unit centroid size, translating the centroid locations of coordinate configurations to the origin point in a Cartesian coordinate system, and rotating the coordinate configurations to minimize the distances among landmarks using a least-squares method (Zelditch et al., 2012). Reiteration of this procedure is known as a generalized Procrustes analysis (GPA). GPA was conducted until the sum of distances among homologous landmarks are minimized. Any differences that remain among the landmark configurations are by definition shape differences, as the information of size (i.e., isometric size), location, and rotation was removed by GPA. In this study, the species mean of Procrustes coordinates was used for the subsequent analyses as described below. In order to achieve this, the mean form for each taxon was extracted following Procrustes superimposition conducted

TABLE 1 Sample of anthropoid taxa used in this study

Genus	Species/subspecies	Female	Male	Unknown sex	Total
Homo	*sapiens*	20	17	0	37
Pan	*troglodytes troglodytes*	8	6	0	14
Gorilla	*gorilla gorilla*	5	6	0	11
	beringei	0	3	0	3
Pongo	*pygmaeus*	5	8	0	13
	abelii	1	1	0	2
Hylobates	*lar*	22	19	0	41
Papio	*hamadryas*	1	3	1	5
	anubis	0	2	0	2
	cynocephalus	2	0	0	2
	ursinus	1	1	0	2
Macaca	*fascicularis*	3	7	0	10
Cercopithecus	*ascanius*	8	9	0	17
	mitis	5	7	0	12
Chlorocebus	*pygerythrus*	1	4	0	5
	aethiops	6	11	0	17
Lophocebus	*albigena*	5	5	0	10
Nasalis	*larvatus*	2	3	0	5
Trachypithecus	*cristatus*	5	5	0	10
Colobus	*angolensis*	0	2	0	2
	guereza	4	10	0	14
Cebus	*albifrons*	10	10	2	22
Alouatta	*seniculus*	5	1	1	7
	caraya	3	4	0	7
	palliata	3	7	0	10
Ateles	*paniscus*	3	1	0	4
	fusciceps	3	4	0	7
Total sample		131	156	4	291

separately within each taxon with scaling re-established. Thereafter, another GPA was conducted on the mean forms of taxa as described above.

2.2 | Phylogenetic comparative approach

Phylogenetic relationships were examined using a chronometric consensus tree based on molecular data from "The 10KTrees Project" (Arnold et al., 2010) (Figure 2). This tree was used to test for phylogenetic signal, and to examine the major axes of shape variation in a phylogenetic context using a phylomorphospace (Almécija et al., 2015; Rohlf, 2002; Sidlauskas, 2008). A phylomorphospace illustrates the magnitude and direction of shape change relative to the evolutionary history of morphological diversification (Almécija et al., 2015; Klingenberg & Gidaszewski, 2010; Rohlf, 2002; Sidlauskas, 2008). Hypothesized ancestral states were reconstructed with shape considered as a single and multidimensional character and squared-change parsimony was used to minimize the sum of the squared changes along the branches of the tree (Klingenberg & Gidaszewski, 2010; Maddison, 1991). In other words, the cost function *f*(x,y) is the squared Procrustes distance between shapes x and y instead of squared Euclidian distance (Klingenberg & Gidaszewski, 2010). Then, shapes of ancestral nodes are mapped onto phylomorphospace along with the original shape data, which are connected by the branches of the tree (Almécija et al., 2015; Klingenberg & Gidaszewski, 2010; Rohlf, 2002; Sidlauskas, 2008). An advantage of the squared-change parsimony method is that it can be directly related to a Brownian motion model of evolution, as the squared-change parsimony estimates correspond to a maximum likelihood estimate under a Brownian motion model when branch lengths are weighted for reconstruction of ancestral states (Maddison, 1991; Nunn, 2011). Moreover, the squared-change parsimony method is invariant to the effects of rotation, which is important as the data are rotated in the phylomorphospace (Adams, 2014; Rohlf, 2002). Phylomorphospace was generated using "plotGMPhyloMorphoSpace" function in the *geomorph* package (Adams & Otárola-Castillo, 2013) in R 3.6.3 (R core team, 2020).

TABLE 2 Landmarks used in this study adopted from Russo (2010)

#	Landmark description
Midline	
1	Point on the cranial ridge of the laminae where the spinous process meets the vertebral foramen
Bilateral	
2, 3	Most caudal point on the articulating surface of the prezygapophysis
4, 5	Most caudolateral point on the articulating surface of the prezygapophysis
6, 7	Most caudomedial point on the articulating surface of the prezygapophysis
8, 9	Most lateral point on the articulating surface of the prezygapophysis
10, 11	Most craniolateral point on the articulating surface of the prezygapophysis
12, 13	Most cranial point on the articulating surface of the prezygapophysis
14, 15	Most craniomedial point on the articulating surface of the prezygapophysis
16, 17	Most medial point on the articulating surface of the prezygapophysis
18, 19	Most concave point on the articulating surface of the prezygapophysis

The degree of phylogenetic signal in PAF shape was evaluated under a Brownian motion model of evolution using the multivariate version of the *K*-statistic (K_{mult}) (Adams, 2014; Blomberg et al., 2003; Nunn, 2011). This method evaluates the similarity between closely related taxonomic groups relative to a null model under a Brownian motion model of evolution (Adams, 2014; Blomberg et al., 2003; Nunn, 2011). It is assumed in the Brownian motion model that "evolutionary changes in a trait are randomly distributed around a mean of zero, independent of previous changes and changes on other branches, and the larger changes are more likely to occur on longer branches (Nunn, 2011, p. 81)." In other words, evolution in a Brownian motion model is treated as a random walk along the branches of the phylogenetic tree where the variance accumulates proportional to time (Nunn, 2011, p. 81). A K_{mult} value under or over 1 shows that taxa resemble each other phenotypically less or more than expected, respectively, under a Brownian motion model of evolution (Adams, 2014; Blomberg et al., 2003; Nunn, 2011).

In order to reject the null hypothesis of no phylogenetic signal, close taxonomic groups should be more similar to each other than to distant species. Thus, to obtain significant phylogenetic signal, the observed variance in distribution (i.e., distance-based sums of squares) should be significantly lower than a null distribution with randomly permuted data under the given phylogenetic tree (i.e., morphometric values among tip taxa; Adams, 2014; Blomberg et al., 2003; Nunn, 2011). This permutation was conducted by randomly distributing species mean shape configurations (Procrustes coordinates) to the tips of the phylogenetic tree (Adams, 2014; Adams & Otárola-Castillo, 2013). In this study, if more than 95% of the resulting variances from random permutations were greater than the observed variance, the null hypothesis of no phylogenetic signal in the data was rejected. Statistical significance ($p < 0.05$) was tested by 10,000 rounds of permutation for phylogenetic signal analyses using the "physignal" function in the *geomorph* package (Adams & Otárola-Castillo, 2013) in R 3.6.3 (R core team, 2020).

In addition, ordinary least squares regression (statistically significant when $p < 0.05$) was conducted with log centroid size of PAF and PAF shape (Procrustes coordinates) to evaluate the effect of PAF size on its shape using "procD.lm" function in the *geomorph* package (Adams & Otárola-Castillo, 2013) in R 3.6.3 (R core team, 2020). Centroid size of the PAF was logged to control the probable non-linear relationship between PAF size and shape.

3 | RESULTS

3.1 | Phylogenetic signal in PAF shape variation in anthropoids

The phylogenetic signal analysis found statistically significant phylogenetic effects in PAF shape variation in anthropoids ($K_{\text{mult}} = 0.3$; $p < 0.0001$). Thus, PAF shape variation reflects phylogenetic history in anthropoids, but taxa resembled each other in PAF shape less than expected under a Brownian motion model of evolution, in which case K_{mult} would have been close to 1. Figure 3 presents a phylomorphospace of PAF shape. The first principal component (PC1) axis (explaining 33.2% of the variation) separated catarrhines and platyrrhines. Positive values on PC1 were associated with a more obliquely oriented PAF, a greater interfacet distance, and a shorter distance between the PAF and the lamina (Figure 3). *Ateles* and *Alouatta* species were located at the most positive PC scores, while *Colobus angolensis* was located at the most negative PC scores on PC1 axis. On PC2 (17.6% variation), hominoids and cercopithecoids were separated, while platyrrhines were intermediate. Positive values on PC2 were associated with a more curved and sagittally oriented PAF shape, which distinguished most cercopithecoids from hominoids and platyrrhines. The shape variation associated with PC2 in hominoids, and to a lesser extent platyrrhines, was a flatter PAF than in cercopithecoids. However, hominoids were distinguished from platyrrhines on PC1 by a less obliquely oriented PAF. Flatness of PAF was distinct in *Gorilla beringei*, but not in *G. gorilla*, among anthropoids. On PC3 (12.8% variation), *G. beringei*, *Cebus*, and *Colobus* species showed flatter PAF shape, a more ventrally located point where the spinous process meets the vertebral foramen, and a shorter distance between PAF and laminae than other taxa (Figure S1). However, on PC1 and 2, *G. beringei* and *Colobus* species showed relatively more distance between PAFs and laminae, while *Cebus* and *Colobus* species showed relatively more curved PAF surface (Figure 3).

Within hominoids, *Homo sapiens*, *Pan troglodytes*, and *G. gorilla* were clustered together, while *Pongo*, *Hylobates lar*, and *G. beringei* were separated (Figure 3). Within platyrrhines, *Ateles* showed more

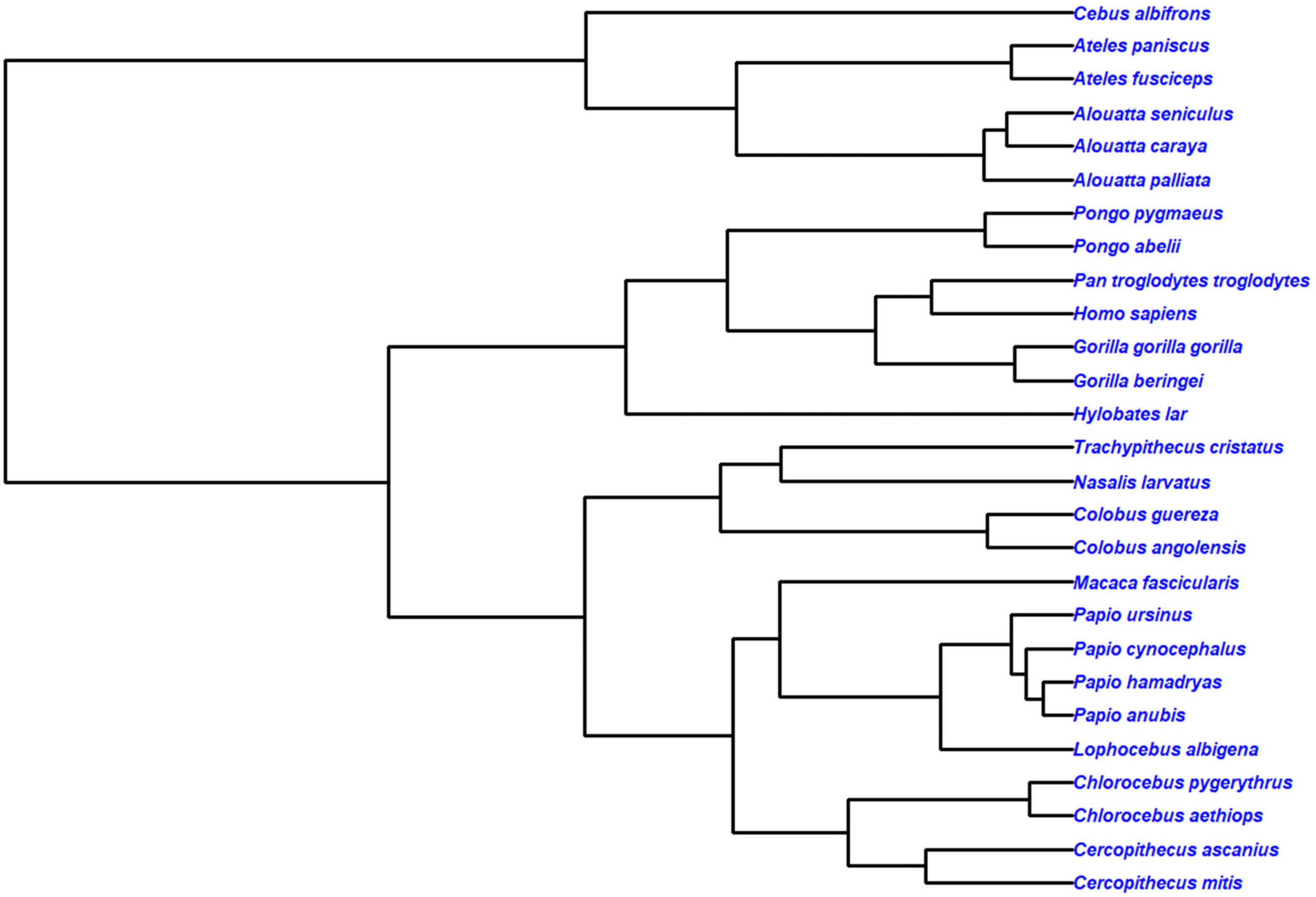

FIGURE 2 Phylogenetic tree of anthropoid taxa used in this study

obliquely-oriented PAF and a greater interfacet distance than *Cebus*. *Trachypithecus cristatus* and *Lophocebus albigena* were close in morphospace to *Pongo* and *Hylobates lar*, respectively (Figure 3).

3.2 | Effect of PAF size on its shape

Results of the regression analysis on logged centroid size of PAF and PAF shape found a non-significant relationship between these variables ($r^2 = 0.071$, $F_{[1,25]} = 1.9266$, $p = 0.0685$). This result indicates that PAF shape is not significantly affected by its size, which is in agreement with Russo (2010).

4 | DISCUSSION

4.1 | Phylogenetic signal in PAF shape variation in anthropoids

The results of this study supported our first hypothesis, indicating that phylogenetic history is likely a major contributing factor to PAF shape variation in anthropoids. This is visually apparent in the phylomorphospace plot (Figure 3), which separates the major anthropoid taxa (e.g., catarrhines vs. platyrrhines). Moreover, the PAF shape of *H. sapiens* was not distinct among anthropoids in spite of their distinct locomotor behavior (i.e., obligate bipedalism) and was located close to *P. troglodytes* and *G. gorilla* in phylomorphospace (Figure 3). Nalley et al. (2019) also reported that adult chimpanzees, humans, and fossil hominins had similar zygapophyseal facet morphology from antepenultimate thoracic (i.e., rib-bearing) vertebra to the first lumbar vertebra, which contrasted with gorillas and orangutans. This similarity might be a synapomorphy of the *Pan-Homo* clade or it could have independently evolved in both chimpanzees and humans, as it is unclear whether the similarity between gorillas and orangutans is plesiomorphic (Nalley et al., 2019). In the present study, the similarity in PAF shape between chimpanzees and humans seems synapomorphic, as *H. sapiens*, *P. troglodytes*, and *G. gorilla* clustered together in phylomorphospace (Figure 3). Moreover, the cluster made up of *H. sapiens*, *P. troglodytes*, and *G. gorilla* was most similar to the LCA of hominoids and catarrhines (Figure 3), which could suggest that these species are most similar to the ancestral condition. Thus, the results of Nalley et al. (2019) and the present study suggest that the PAF shape of humans should be interpreted in terms of phylogenetic history and not solely through a lens of functional significance. The different results obtained by Nalley et al. (2019) for gorillas may be related to differences in the research methods used to analyze the sample.

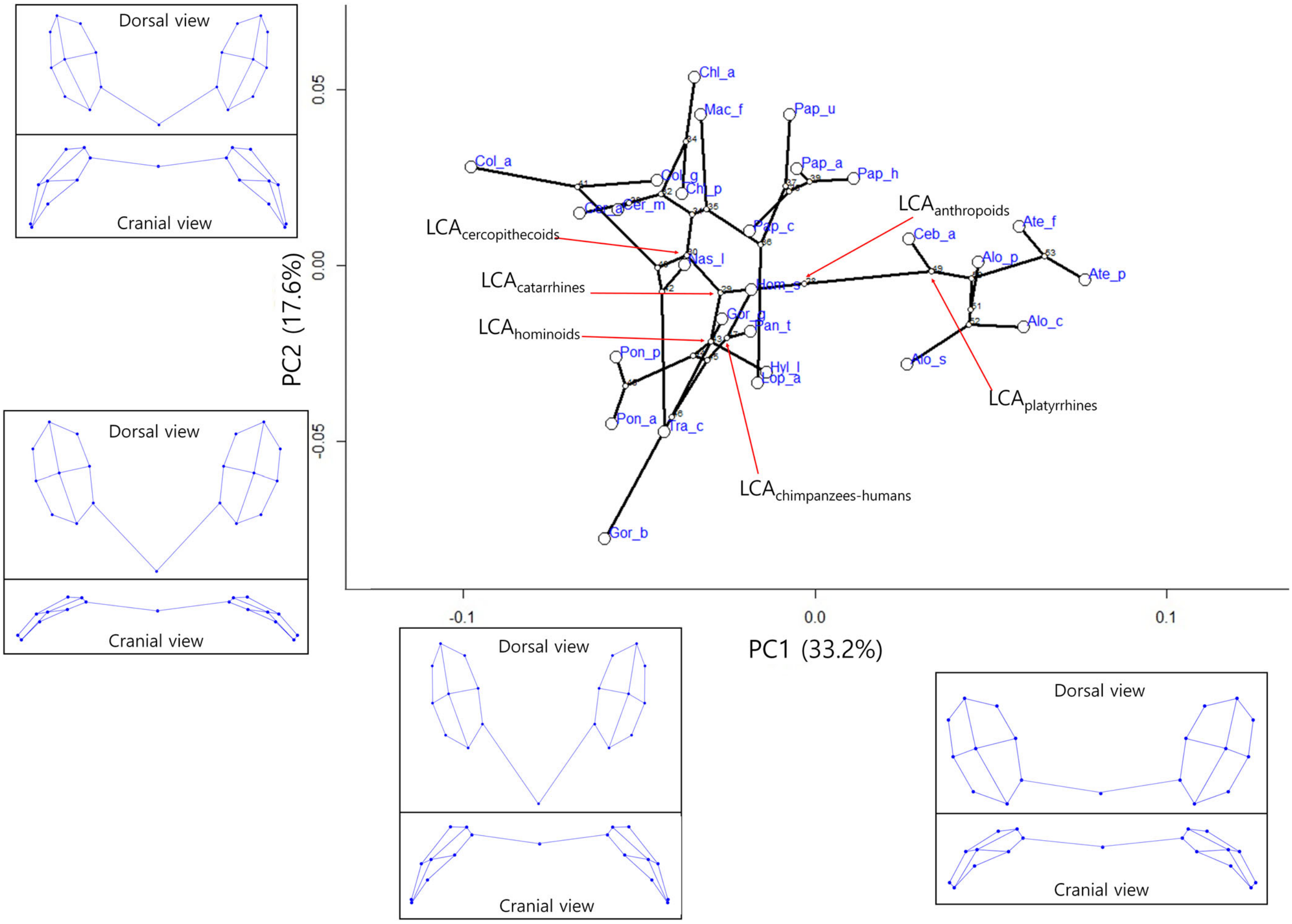

FIGURE 3 Phylomorphospace of prezygapophyseal articular facet (PAF) shape of the first post-transitional vertebra in anthropoids. Principal component (PC) 1 (explaining 33.2% of the variation) presents the variation in orientation of PAF, interfacet distance, and distance between the PAFs and the laminae. PC2 (17.6% variation) presents the variation in curvature of PAF surface. Alo_c/p/s, *Alouatta caraya/palliata/seniculus*; Ate_f/p, *Ateles fusciceps/paniscus*; Ceb_a, *Cebus albifrons*; Cer_a/m, *Cercopithecus ascanius/mitis*; Chl_a/p, *Chlorocebus aethiops/pygerythrus*; Col_a/g, *Colobus angolensis/guereza*; Gor_b/g, *Gorilla beringei/gorilla*; Hom_s, *Homo sapiens*; Hyl_l, *Hylobates lar*; LCA, last common ancestor; Lop_a, *Lophocebus albigena*; Mac_f, *Macaca fascicularis*; Nas_l, *Nasalis larvatus*; Pan_t, *Pan troglodytes*; Pap_a/c/h/u, *Papio anubis/cynocephalus/hamadryas/ursinus*; Pon_a/p, *Pongo abelii/pygmaeus*; Tra_c, *Trachypithecus cristatus*

Nalley et al. (2019) analyzed the vertebra caudal to the last rib-bearing vertebra as L1, whereas in this study we analyzed the first post-transitional vertebra, which could be T13, L1, or L2. Thus, the choice of vertebra for comparison may affect the degree of similarity in PAF morphology between gorillas and the human-chimpanzee clade.

In several cases, taxa with different locomotor repertoires occupied similar locations in phylomorphospace (Figure 3). For instance, *Ateles* was located closer to *Cebus* than to hominoids in phylomorphospace despite similar locomotor behaviors between hominoids and *Ateles* (e.g., bridging, climbing, and/or suspensory behaviors) (Fleagle, 2013). *Ateles* and *Cebus* showed more obliquely-oriented PAFs, a greater interfacet distance, and a shorter distance between PAF and laminae than hominoids. Moreover, *Trachypithecus* and *Lophocebus* were closer to *Pongo* and *Hylobates* in phylomorphospace, respectively, in spite of very different locomotor behaviors. PC3 shows considerable overlap among species with different locomotor behaviors and among phylogenetically distant taxa (Figure S1). However, PC3 mostly reflects variation in the location of the point where the spinous process meets the vertebral foramen, which does not have clear functional significance. Thus, the results showed that locomotor behavior may not reflect PAF morphology as strongly as phylogenetic history.

4.2 | Relationship between suspensory locomotor behavior and PAF shape variation in anthropoids

Our second hypothesis, that PAF morphology of *Ateles* would converge on that of hominoids due to shared reliance on suspensory locomotor behaviors, was not supported. Our results showed that hominoids and *Ateles* were widely separated on the PC1 axis (Figure 3). Nevertheless, there was evidence in support of PAF shape reflecting variation in the relative frequency of suspensory locomotor behaviors within taxonomic groups, as indicated by the results for platyrrhines and hominoids.

Orientation of the PAF was most oblique in *Ateles*, intermediate in *Alouatta*, and most sagittal in *Cebus* (Figure 3). As mentioned above, more obliquely oriented (relative to the sagittal plane) PAFs allow axial rotation but resist flexion-extension movement in the sagittal plane (Russo, 2010). This finding may reflect the fact that *Ateles* has a more forelimb-dominated suspensory locomotor repertoire, while *Cebus* is primarily an arboreal quadruped that only occasionally engages in suspensory locomotion, and *Alouatta* is intermediate between *Ateles* and *Cebus* in terms of suspensory and arboreal quadrupedal locomotor behaviors (Fleagle, 2013; Gebo, 1996). As mentioned above, more sagittally oriented PAFs permit flexion-extension spinal movements in the sagittal plane but resists rotational movement (Bogduk & Twomey, 1987; figure 1a in Russo, 2010). Thus, variation in PAF orientation among platyrrhine taxa in this study may reflect this variability in their locomotor behaviors. However, curvature of the PAF was similar in *Cebus* and *Ateles* (Figure 3), and therefore curvature of the PAF does not appear to be related to different locomotor behaviors in platyrrhines.

The PAF was more sagittally oriented in *Pongo* and *G. beringei* than in *Homo*, *Pan*, *G. gorilla*, and *Hylobates* (Figure 3). Moreover, the PAF was flatter in *Pongo*, *Hylobates*, *G. beringei* than in *Homo*, *Pan*, and *G. gorilla* (Figure 3). Russo (2010) suggested that the flatter surface of the PAF in hominoids may help to resist axial rotational movement while permitting lateral flexion. However, the more suspensory *Pongo* and *Hylobates* (Fleagle, 2013; Gebo, 1996) did not consistently show more curvature in PAF surface in relation to suspensory locomotor behaviors. Nevertheless, *Hylobates* did show more obliquely-oriented PAFs than other hominoids, which allows for axial rotation but resists flexion-extension movement in the sagittal plane (Russo, 2010). In this regard, *Ateles* and *Hylobates* showed that orientation of PAF (but not curvature) may be associated with suspensory locomotion. Surprisingly, *G. beringei* had the flattest PAF shape among hominoid taxa, while *G. gorilla* had a more curved joint surface (Figure 3). Russo (2010) reported that genus *Gorilla* had a flatter PAF shape than other hominoids and *Papio* and interpreted this result as indicating that the flatter PAF shape of gorillas may be related to their large body size. She argued that a flatter PAF shape would distribute the load more evenly over the surface area of the PAF (Russo, 2010). However, intrageneric variation in gorillas was not examined by Russo (2010), as that study combined *G. gorilla* and *G. beringei* into a single taxon. As there is no clear functional explanation for the differences in PAF morphology between these species, one possibility is that these differences may be a product of genetic drift. Having said that, previous studies have reported that *G. gorilla* talar morphology is better suited for a wider range of positions/motions such as climbing and other arboreal behaviors, while *G. beringei* talar morphology reflects the need for stability and load-bearing associated with more terrestrial behaviors (Dunn et al., 2014; Knigge et al., 2015). Thus, the possibility cannot be excluded that function-induced PAF shape differences between *G. gorilla* and *G. beringei* were not adequately captured in this study. Alternatively, the results of the present study could be an artifact of sample size, as there were only three male specimens of *G. beringei* in the present study. A more balanced (i.e., sex) and larger sample is therefore needed to adequately address this issue in future studies.

In addition, the present study also found a greater interfacet distance in *Hylobates* compared to other hominoids and in *Ateles* compared to *Alouatta* and *Cebus* (Figure 3). Russo (2010) found that *Hylobates* has a greater interfacet distance than *Pongo*, and suggested that this is to enhance control of trunk during ricochetal brachiation. In previous studies, it was reported that hylobatids and *Ateles* have similar morphologies in several skeletal elements due to suspensory and/or (semi)brachiating locomotor behaviors (e.g., the clavicle [Squyres & DeLeon, 2015], the scapula [Young, 2008], lumbar vertebrae [Johnson & Shapiro, 1998], and the pelvis [Machnicki et al., 2016]). Focusing on vertebrae, the overall morphology of lumbar vertebrae of *Ateles* has been interpreted as convergent with that of hylobatids in terms of orientation of transverse processes, and ventrodorsally elongated and craniocaudally shorter vertebral bodies, which may be an adaptation to resist bending stress on the spine during suspensory and/or (semi)brachiating behaviors (Johnson & Shapiro, 1998). Thus, it is also tempting to interpret a relatively greater interfacet distance in *Hylobates* and *Ateles* as being driven by these taxa engaging in more brachiation than other hominoids or platyrrhines, respectively (but not *ricochetal* brachiation per se, which is only used by hylobatids). Thus, our results find some support for Russo (2010)'s argument but also show that just because morphology is convergent across lineages does not mean the resultant morphologies will end up looking similar in all regards. Our interpretation is mainly based on PC1 loadings, and it remains to be determined if relative interfacet distance would be found to be greatest in *Hylobates* (as expected due to their use of ricochetal brachiation), if this distance were directly measured and scaled to body size. In this regard, more research that focuses on the relationship between spinal movement and interfacet distance measurements needs to be conducted to interpret our results more precisely.

Although our results seemingly support a relationship between PAF mobility and shape variation within primate groups, these results need to be assessed with caution. Previous experimental studies reported that the relationship between bony structure and (passive) range of motion (ROM) is complex and not straightforward in the hip joint of anthropoids (Hammond et al., 2016), the avian hip joint (Manafzadeh & Padian, 2018), snake vertebrae (Jurestovsky et al., 2020), and cervical vertebrae of primates (Grider-Potter et al., 2020). Moreover, it may be hard to find a definitive relationship between vertebral morphology and intervertebral ROM without considering soft tissue (e.g., muscles, ligaments, intervertebral discs, nerves, blood vessels, and connective tissues) (Grider-Potter et al., 2020). Digitally removing the zygosphene (a median process on the front part of the neural arch) generally increased yaw (lateral bending) and dorsal pitch (dorsoventral bending) ROM in snake vertebrae (Jurestovsky et al., 2020). In contrast, only few morphological variables were significantly correlated to the passive intervertebral

ROM in cervical vertebrae, such as the relationship between range of lateral flexion and transverse process angle in C4-C5 (Grider-Potter et al., 2020). Thus, there has been inconsistent support for the assumption that skeletal morphology can provide enough bony stoppage to constrain spinal movements, and therefore some caution is prudent when inferring PAF joint mobility from bone morphology.

5 | CONCLUSIONS

The results of this study showed that PAF shape largely reflects phylogenetic history, as major anthropoid groups, including hominoids, cercopithecoids, and platyrrhines, were separated in phylomorphospace. Moreover, suspensory nonhuman hominoids and *Ateles* did not show convergent PAF morphology in phylomorphospace. However, some functional significance may be associated with PAF shape variation within taxonomic groups. For instance, *Hylobates* and *Ateles* may show similar adaptations in PAF shape within their phylogenetic groups, such as more obliquely-oriented PAF and greater interfacet distances, when compared with closely related taxa. Thus, while PAF shape seems to mainly reflect phylogeny across anthropoids, it may also reflect locomotor function within taxonomic groups, such as platyrrhines and hominoids (e.g., more forelimb-dominated suspensory behaviors). The functional hypothesis and interpretation in the present study was mainly focused on how PAF shape varies in association with forelimb-dominated suspensory behavior, but additional questions should be investigated. In future studies, hypotheses about the functional significance of specific features (e.g., PAF surface curvature, interfacet distance) should be tested experimentally. Additionally, comparative studies should look at other primate and non-primate mammalian taxa that have different positional behaviors (e.g., bipedal vs. forelimb-dominated suspensory vs. quadrupedal; terrestrial vs. arboreal; orthograde vs. pronograde etc.). This research will deepen our knowledge of the relationship between positional behavior and PAF shape variation.

AUTHOR CONTRIBUTIONS

Hyunwoo Jung: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Evan A. Simons:** Conceptualization (supporting); investigation (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting). **Nicholas B. Holowka:** Conceptualization (supporting); investigation (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting). **Noreen von Cramon-Taubadel:** Conceptualization (supporting); funding acquisition (lead); investigation (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting).

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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