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ABSTRACT

The vertebral column plays a key role in maintaining posture, locomotion, and transmitting loads between body components. Cervical vertebrae act as a bridge between the torso and head and play a crucial role in the maintenance of head position and the visual field. Despite its importance in positional behaviors, the functional morphology of the cervical region remains poorly understood, particularly in comparison to the thoracic and lumbar sections of the spinal column. This study tests whether morphological variation in the primate cervical vertebrae correlates with differences in postural behavior. Phylogenetic generalized least-squares analyses were performed on a taxonomically broad sample of 26 extant primate taxa to test the link between vertebral morphology and posture. Kinematic data on primate head and neck postures were used instead of behavioral categories, in an effort to provide a more direct analysis of our functional hypothesis. Results provide evidence for a function-form link between cervical vertebral shape and postural behaviors. Specifically, taxa with more pronograde heads and necks and less kyphotic orbits exhibit cervical vertebrae with longer spinous processes, indicating increased mechanical advantage for deep nuchal musculature, and craniocaudally longer vertebral bodies and more coronally oriented zygapophyseal articular facets, suggesting an emphasis on curve formation and maintenance within the cervical lordosis, coupled with a greater resistance to translation and ventral displacement. These results not only document support for functional relationships in cervical vertebrae features across a wide range of primate taxa, but highlight the utility of quantitative behavioral data in functional investigations.

Despite the critical role of the vertebral column in postural and locomotor behaviors, our understanding of primate cervical vertebral form and function is markedly limited compared to knowledge of thoracolumbar functional morphology (Schultz, 1942, 1961; Toerien, 1961; Mercer, 1999; Manfreda et al., 2006; Ankel-Simons, 2007; Mitteroecker et al., 2007). Many early descriptions of primate cervical morphology as a whole concluded that skeletal variation was limited and that the region was thus relatively uninformative regarding functional or phylogenetic questions (e.g., Toerien, 1961; Ankel 1967, 1970, 1972). Notable exceptions include Slijper (1946) and Schultz (1961). Slijper's 1946 work investigated the presacral vertebral column across animals and developed several body-axis models stilled used today (e.g., Clauser, 1980; Shapiro, 1991; Dunbar et al., 2008; Stevens, 2013). Furthermore, the author recognized the positive relationship between body size and spinous process size and argued that the differences in cervical spinous process length between humans, great apes, and monkeys was related to head posture and position maintenance (see Toerien (1961) as well). Schultz (1961) focused mostly on measurements of the thoracic and lumbar regions, but described certain generalities of the primate cervical spine and reported relative region length and weight. The relatively long spinous processes of apes were again noted and contrasted with the short processes of monkeys and modern humans. The cervical transverse processes were described as highly variable across primates, specifically referring to process length and projecting angle (Schultz, 1961), but few attempts have been made to support or refute this statement quantitatively in subsequent work (Mercer, 1999; Meyer, 2005; Nalley, 2013).

More recent cervical vertebrae studies have focused on C1 and C2 morphologies and results suggest that primates tend to separate taxonomically, with some variation attributable to

differences in positional behavior (Ankel, 1972; Manfreda et al., 2006; Mitteroecker et al., 2007). Despite these studies, the comparative morphology of lower cervical vertebrae and attaching musculature remain poorly understood in primates, and only very general descriptions prevail in the literature; for example, the terms "monkeylike" and "humanlike" are often used, but few quantitative attempts have established what these terms actually mean or if they are even appropriate descriptors (Nalley, 2013).

Biomechanical and medical research focused on the human cervical vertebral column has demonstrated the functional significance of many features and provides experimental evidence linking function with form (Compere et al., 1958; Penning, 1968; Kapandji, 1974; White and Panjabi, 1990; Milne, 1991; Bogduk and Mercer, 2000; Mercer and Bogduk, 2001; Yoganandan et al., 2001; Kurtz and Edidin, 2006). This previous research has primarily examined the structural role that certain vertebral features play in maintaining proper head and neck posture, specifically regarding injury and surgical implants (e.g., Holness et al., 1984; Yoshida et al., 1992; Panjabi et al., 1993; Whyne et al., 1998:). Researchers have also established normal ranges of motion for the human head and neck, including the proprioceptive role that the nuchal musculature plays during maintenance of the visual field and natural head positions (e.g., Lind et al., 1989; Berthoz et al., 1992; Dvorak et al., 1992; Haymann and Donaldson, 1997; Feipel et al., 1999; Panjabi et al., 2001; Mercer and Bogduk, 2001; Takeuchi and Shono, 2007; Nagamoto et al., 2011). Investigations of nonhuman primates have reported functional patterns in a number of cervical features as well (Slijper, 1946; Schultz, 1961; Toerien, 1961; Ankel, 1972; Gommery, 2000; Manfreda et al., 2006), and as previously mentioned, many of these studies did not document the full range of phylogenetic variation in primate cervical vertebral shape and/or lacked a biomechanical framework (Aiello and Dean, 1990; Dickman et al. 1994; Graf et al.,

1995a,b; Tominaga et al., 1995; Meyer, 2005; Elias et al., 2006). Furthermore, the few functional studies present in the literature have relied on categorical classification of postural and locomotor behaviors and results were therefore limited in scope and application (Mercer, 1999; Nalley, 2013).

A common critique of many function-form studies is the use of discrete postural or locomotor categories. This approach is necessary in some cases, but it can potentially discard real variation that does not fit within defined behavioral categories and thereby oversimplifies species-typical behavioral repertoires and their biomechanical requirements. Moreover, functional signals in skeletal variation can be obscured by "noise" in the data created by the often unclear boundaries between behavioral categories. One solution to this problem is to quantify relevant aspects of behavior instead of assigning postural or locomotor categories, which would provide a more direct and detailed analysis of functional hypotheses. Relatedly, commonly used primate behavioral classifications, such as orthograde and pronograde, are imprecise relative to the head and neck because body posture (the orientation of the trunk) does not always directly reflect head and neck posture. For example, animals with more pronograde body postures can nonetheless display orthograde neck posture and vice versa (e.g., guinea pigs, cats, indriids) (Graf et al., 1995a,b; Keshner, 1994; Selbie et al., 1993; Strait and Ross, 1999; Vidal et al., 1988). By using an integrative approach and utilizing kinematic data on primate head and neck postures, the relationship between posture and craniocervical morphology can be more directly explored.

The cervical vertebral column performs a diverse range of functions as the interface between the head and trunk, including directing head movement and withstanding the forces of gravity and soft-tissue loading associated with the pectoral girdle and forelimb (Schultz, 1942;

Badoux, 1968, 1974; Kapandji, 1974; Mercer and Bogduk, 2001). Several researchers have

suggested that the neck functions as a distinct section of the vertebral column relative to the

thoracic and lumbar regions, and instead of reflecting broad locomotor patterns, cervical

morphology is more strongly influenced by the biomechanical requirements of head movement

and maintenance of the visual field (Vidal et al., 1988; Graf et al., 1995a; Macpherson and Ye,

1998). The head and neck have been commonly modeled as a cantilevered rod (Slijper, 1946;

Badoux, 1968, 1974; Demes, 1985). This scenario suggests that cervical morphology in taxa

with more pronograde head and neck postures (i.e., positioning the head and neck out in front of

the torso and more perpendicular to the gravity vector) would exhibit antigravity mechanisms

and compensation for the reduced mechanical advantage of the nuchal musculature. This might

be accomplished by several means, such as increasing muscle force output of nuchal muscles by

increasing their physiological cross-sectional area or rotating the orientation of their attachments

to increase muscle moment arms. Thus it is reasonable to predict differences in the basic

morphology (e.g., length, orientation, cross-sectional area) for many of these attachments,

specifically the transverse and spinous processes, between taxa that habitually hold their heads

and necks in different postures. Another mechanism to consider is the curvature(s) in the cervical

column. The presence of such curvature is an important reminder that the pronograde primate

neck is not necessarily a simple beam held in a near-horizontal orientation out from the torso.

Radiographic studies of the head and neck in alert mammals (e.g., cats, guinea pigs, rats, and

some monkey species) have demonstrated instead that the cervical region can display complex

curvatures and is often maintained, at least in resting positions, in a more vertical alignment

(Vidal et al., 1986). This morphology is argued to indicate a more energetically efficient

biomechanical system analogous to that of a suspension bridge or inverted bow-and-string

system, which shifts the effort to stabilize the head against gravity from the nuchal musculature to the vertebral bodies in the form of compressive forces (Badoux, 1977; Macpherson and Ye, 1998). This biomechanical model would predict variation in aspects of vertebral body morphology—craniocaudal length, ventrodorsal height, mediolateral width—to reflect the differences in bending stresses related to differences in head and neck postures (Badoux, 1977). Furthermore, the intervertebral joints that govern how cervical vertebral bodies move in relation to one another (i.e., uncovertebral and zygapophyseal joints) could be also expected to exhibit variation related to differences in positional behavior. Support for this function-form relationship has been documented in other regions of the mammalian and primate vertebral spinal columns (e.g., Filler, 1986; Russo, 2010). In either case, these scenarios suggest a functional relationship between head and neck postures and cervical vertebral form. Therefore, the goal of this study is to test whether cervical vertebral features correlate with quantified postural measures specific to the head and neck.

MATERIAL AND METHODS

Sample

The comparative sample comprises individual vertebrae from 221 adult, nonpathological individuals representing 26 primate species, sampling from most major groups (Atelidae, Cebidae, Cercopithecidae, Hominidae, Hylobatidae, and Lemuridae). Though chosen taxa are intentionally limited to those where head and neck postural data is available (i.e., Ross, 1993; Strait and Ross, 1999), they still represent a broad cross-section of primate genera to facilitate comparisons between species that differ in postural and locomotor behaviors. The primate sample is derived from several osteological collections held at the American Museum of Natural History (New York, NY), National Museum of Natural History (Washington, DC), Field

Museum (Chicago, IL), School of Human Evolution and Social Change Arizona State University (Tempe, AZ), and the Muséum national de'Histoire naturelle (Paris, France) (Table 1). Because both the atlas and axis possess unique morphologies (i.e., lack of vertebral body and addition of odontoid process) and are often consider a distinct biomechanical unit from the lower cervical vertebrae (Kapandji, 1974; White and Panjabi, 1990), only levels C3–C7 were included in the skeletal sample.

Vertebral measurements

Seventeen measures designed to capture functionally relevant aspects of vertebral shape (see Nalley, 2013) were collected in two ways: (1) from three-dimensional (3D) landmark data acquired with a MicroScribe G2X digitizer (Immersion Corp.) and (2) using digital calipers (Mituotyo Corp.). Table 2 describes the vertebral variables used for comparison and their method of acquisition and Table 3 describes the vertebral 3D landmarks used to calculate angles of interest. The measures and landmarks are illustrated in Figure 1. Angles were calculated from landmarks relative to the vertebral body using Rhinoceros 4.0 (Robert McNeel & Associates, Seattle).

Posture measurements

Three measurements of head and neck posture were taken directly from the literature, specifically Ravosa (1988), Ross (1993), Ross and Ravosa (1993), and Strait and Ross (1999). First, the *inclination of the neck* is a kinematic measure of neck posture and the authors captured this measurement from video images of primates filmed during locomotion. *Inclination of the neck* was calculated as the angle of its dorsal surface relative to the gravity vector (Strait and Ross, 1999). Head posture was represented by two variables, *head-neck angle* (HNA) and *orbital kyphosis angle* (AOA). *Head-neck angle* is a kinematic measurement that reflects the relative

orientation of the head, specifically the orbits, to the neck. *Head-neck angle* measurements were taken from the same videos used to capture *neck inclination* by Strait and Ross (1999). The authors calculated the angle by subtracting the mean value for orbit inclination (measured as the angle between the line joining the superior and inferior margins of the orbital aperture and the line of gravity) from the mean value for *neck inclination* for each species (Strait and Ross, 1999). Thus, the *head-neck angle* provides information on position of the head in relationship to the neck, such that a large *head-neck angle* indicates a more pronograde posture for the head (or more perpendicular to the line of gravity), while a smaller angle indicates a more orthograde head posture (or more parallel to the line of gravity). The second head posture variable, *orbital kyphosis angle*, is an osteometric measurement taken from Ravosa (1988) and Ross (1993). The authors measured the angle on lateral radiographs and is defined as the angle between the occipital clivus and the axis passing from the optic canal through the center of the orbits (Fig. 2) (Ravosa, 1988; Ross, 1993). Kyphotic orbits, following Dabelow's (1929) definition, are when the orbits are rotated ventrally on the skull, and this case, which is relative to the position of the foramen magnum. More kyphotic orbits have a smaller angle between the clivus and the axis of the optic canal and less kyphotic orbits have larger angles. *Orbital kyphosis angle* is significantly correlated with *head-neck angle* (Strait and Ross, 1999) and was included here to test whether cervical measurements could be directly linked with cranial osteological measurements correlated with head posture. Further detailed descriptions of the three measurements incorporated here are found in Ravosa (1988), Ross and Ravosa (1993), and Strait and Ross (1999).

Statistical analyses

To test whether bony cervical morphology correlated with measurements of head and neck posture, multiple regression analyses were conducted with phylogenetic generalized least-squares (PGLS) on the entire comparative sample. Male and female measurements were combined because no pattern of significant difference in vertebral features was detected in preliminary analyses (student's t-tests, $p < 0.05$). Phylogenetic generalized least-squares estimates the relationship between variables while accounting for the degree of autocorrelation due to phylogenetic relatedness in the dataset (Grafen, 1989; Freckleton, et al., 2002). A phylogenetic comparative approach is necessary here because species may be similar to each other based on the fact that they share a common ancestor and thus do not represent independent observations, an important assumption of regression analyses (Felsenstein, 1985; Harvey and Pagel, 1991). Furthermore, several vertebral features indicated a strong phylogenetic signal (Pagel's $\lambda > 0.5$). A primate consensus phylogeny for the taxa studied here was obtained from the *10kTrees* website (version 3, Arnold et al., 2010) calculated from GenBank data and sampled using Bayesian inference. The PGLS analyses were performed in R v. 3.1.1 (R Development Core Team, 2014) using the CAPER package (Orme et al., 2013). Analyses were performed using species means on each vertebral level separately.

Each vertebral variable was concurrently regressed on two independent variables, body mass and one measure of posture, which estimates the relationship between vertebral variable and posture while controlling for overall differences in organismal size. Body mass data were taken from Smith and Jungers (1997) and Smith and Cheverud (2002); and was used here instead of another size proxy (i.e., cranial or vertebral geometric mean) because body mass has more direct influence on the positional behavior of an animal than the size of the skull or vertebrae,

and is arguably a more relevant feature to adjust for when investigating functional influences of

postural behavior (McMahon, 1975; Pedley, 1977; Heglund, 1984; Jungers and Susman, 1984).

Variables that differed in dimensionality were adjusted accordingly (i.e., square root of areal

measurements [mm^2], cube root of body mass). Linear and areal vertebral variables and body

mass were logged (base e) prior to analysis. Raw angular measurements were transformed to

radians.

Given the number of statistical tests performed in this study, the possibility that some of

the significant results ($p < 0.05$) are type I errors (i.e., false rejections of the null hypothesis) is a

possible concern. A common way of addressing this issue is to lower the level at which a test

achieves statistical significance using Bonferroni adjustments so that the overall error rate is

maintained at $\alpha = 0.05$ (e.g., Holm, 1979; Rice, 1989; Sokal and Rohlf, 1995). This approach is

not adopted here because, given the large number of statistical tests performed, it would reduce

the power to detect significant differences to an unreasonably low level (Perneger, 1998; Moran,

2003; Nakagawa, 2004). As an alternative, following the arguments made by Perneger (1998)

and Moran (2003), the overall pattern of significant differences is used to evaluate significant

results.

RESULTS

The goal of the PGLS analysis was to test whether vertebral morphology was

significantly correlated with measures of posture relative to body mass using a comparative

framework. The majority of results were not significant and do not support a correlation between

the cervical features investigated here and head and neck posture. Nonetheless, certain analyses

do support a link with head and neck posture: craniocaudal vertebral length, spinous process

length, articular facet angle and lamina cross-sectional area. Spinous process length was

significantly correlated with both neck inclination angle and orbital kyphosis angle at all five vertebral levels (C3–C7) and at four of five vertebral levels with head-neck angle (C3-C6). Vertebral body craniocaudal length was also positively correlated with measures of head and neck posture, though with slightly fewer significant results. Vertebral body length was positively correlated with neck inclination angle and head-neck angle at four of five vertebral levels (C3–C6), and three of five vertebral levels with orbital kyphosis angle (C4–C6). The positive nature of the correlations indicates that as the head and neck become more perpendicular to the line of gravity (and the eyes less kyphotic) the length of the cervical spinous processes and the craniocaudal length of the vertebral bodies both increase (Figures 3 and 4).

Results also demonstrated significant correlations found only at particular vertebral levels. For example, at both the midpoint and terminal levels of the cervical column—C4 and C7, respectively—results indicate a major shift in the relationship between the vertebral body and the dorsal vertebral components as the head and neck become more pronograde. Specifically, the angles of the zygapophyseal articular facet exhibit a negative correlation with posture (Figure 5). This result suggests that the articular facets rotate to become more perpendicular to the cranial surface of the vertebral body as the head and neck become more pronograde. Lamina cross-sectional area also exhibits significant positive correlations with all three measures of posture midway along the cervical vertebral column (C4, C5), such that, as the head and neck become more pronograde, cross-sectional area increases.

Though there are other examples of significant correlation between morphology and posture, no other vertebral features demonstrated consistent patterns of correlation. The possible biomechanical significance of those correlations highlighted is further discussed below.

DISCUSSION

This study was primarily concerned with determining whether vertebral bony morphology varies with head and neck posture among primates. And where most other investigations have used behavioral categories with little to varied success (Ankel, 1972; Mercer, 1999; Meyer, 2005; Manfreda et al., 2006; Mitteroecker et al., 2007; Nalley, 2013), we used three morphometric measurements of head and neck posture to test their correlation with bony cervical vertebral traits. Primate-wide PGLS analyses were conducted to achieve these goals. Although most results did not support a link between cervical vertebrae form and posture, some features do strongly suggest functional relevance. Our results indicate that primates with more pronograde heads and necks (and less kyphotic orbits) exhibit cervical vertebrae with longer vertebral bodies and spinous processes. Furthermore, localized patterns observed at the C4 and C7 levels may also indicate a functional response specific to zygapophyseal articular facet orientation, lamina cross-sectional area, and the nature of cervical lordosis. These broad morphological patterns suggest that primates with less kyphotic orbits and more pronograde heads and necks exhibit an increased mechanical advantage for deep nuchal musculature and a number of mechanisms—craniocaudally long vertebral bodies and coronally oriented facets—to facilitate lordosis curve formation with a greater resistance to ventral displacement of the cervical vertebrae.

Vertebral body length

The curvature of the cervical vertebral column in most mammals is often described as S-shaped, or sigmoidal, in nature, though researchers have noted appreciable variation and that the transitions from ventro- to dorsiflexion in some quadrupedal animals (e.g., cats) are often more extreme relative to others, such as macaques and rabbits. Humans exhibit relatively little

curvature of note (Vidal et al., 1988). Variation in the degree of cervical curvature is probably related to an effort to maintain a more vertical (or orthograde) resting head and neck posture. This resting posture in the cervical column has been observed across many mammalian taxa regardless of torso posture or foramen magnum orientation (Vidal et al., 1988; Graf et al., 1995a, b). For example, in those taxa with overall more orthograde body postures, such as humans, the neck protrudes from the top of the trunk and the curvatures are much less pronounced (Kapandji, 1974; White and Panjabi, 1990; Kurtz and Edidin, 2006). The opposite seems to be true in many species with more pronograde body postures, especially smaller-bodied mammals (Vidal et al., 1988; Graf et al., 1995a; Macpherson and Ye, 1998). The role allometry plays in cervical morphology and posture, and whether this relationship is maintained for larger-bodied animals, deserves further examination.

A more vertical orientation of the cervical vertebrae during rest is argued to play multiple possible functional roles, including the incorporation of the vertebral bodies into the mechanical support of the neck against gravity and thereby reducing the role (and energetic requirements) of the nuchal musculature (Demes, 1985; Graf et al., 1995a; Macpherson and Ye, 1998). Researchers have indeed observed that many smaller-bodied mammals in resting position use minimal muscle force, activating only biventer cervicis and occitpito-scapularis to maintain head-neck posture (Richmond et al., 1992). Vertical orientation also allows the rotational axes of the head and sensory organs to become more or less in line with the gravity vector (Vidal et al., 1988; Graf et al., 1995a; Macpherson and Ye, 1998). This head posture adjusts the horizontal semicircular canals to align with earth-horizontal (Graf et al., 1995a). Additionally, as suggested by the sigmoidal shape of the human vertebral column as a whole, which has been argued to act with a damping capability to reduce forces on the spine (Kapandji, 1974; White and Panjabi,

1990; Kurtz and Edidin, 2006), the partial S-shape of the cervical column in nonhuman primates may also act as a shock-absorber during movement (Richmond et al., 1985; Vidal et al., 1988). The positive relationship between vertebral body length and pronograde head and neck postures (at least during locomotion) may reflect the maintenance of this sigmoidal cervical shape, particularly if the role of mechanical efficiency is supported; longer vertebrae would allow for curve formation during resting behaviors, because for 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). This proposed relationship between cranio-caudally long cervical bodies and more pronograde postures has also been noted in more targeted investigations of the hominoid cervical vertebral column, comparing humans to chimpanzees and gorillas (Meyer, 2005).

Results illustrated by Figure 4 also reemphasize that torso/body posture does not necessarily reflect the posture of the head and neck and the importance of quantified behaviors in functional morphology studies. Note that *Alouatta seniculus*, an arboreal quadrupedal taxon that can maintain more orthograde body postures during bouts of locomotion (i.e., climbing, walking, and bridging) (Fleagle and Mittermeier, 1980; Youlatos, 1993, 1998), exhibits a very large angle value and often groups with *Lemur catta* and *Varecia variegata*, both dedicated terrestrial/arboreal quadrupeds (Rowe, 1996; Fleagle, 1999). Such a value indicates pronograde head and neck postures (Strait and Ross, 1999), probably related to this species' enlarged hyo-laryngeal complex (Biegert 1963; Jeffery, 2003).

Articular facet angle

There are two major points of transition in sigmoidal curvature of the cervical column: the cervicothoracic junction (C7-T1) and the midcervical shift at or around C4. The

cervicothoracic junction marks the transition from the ventroflexed thoracic column to the more dorsiflexed lower cervical region. The vertebral relationship shifts again from dorsiflexion to ventroflexion at or near the C4 level. This midcervical shift is more distinct in quadrupedal taxa, where the more caudal cervical vertebrae are primarily held near the limit of dorsiflexion to then become more ventroflexed (Graf et al., 1995a; Macpherson and Yee, 1998). Notably, these two points of transition are at the same vertebral levels where significant correlation between articular facet angle (AFA) and posture are observed. Meyer (2005) also observed a similar significant difference between humans and African apes, but at the C3 level (C4 and C7 levels were not examined), with more pronograde apes exhibiting more coronally oriented articular facets.

Each typical cervical vertebra (C3–C7) articulates with the vertebra above and below it via zygapophyseal processes, and vertebral patterns of movement is heavily dependent on the shape and position of these processes (Kapandji, 1974; White and Panjabi, 1990). Coronal orientation of the facets allows for lateral bending, but restricts translation and motion in the sagittal plane by providing greater resistance to the forward displacement of the cervical vertebrae (Panjabi et al., 1993; Bogduk and Twomey, 2005; Meyer, 2005; Russo, 2010). This relationship has been thoroughly studied in the lumbar region of modern humans, where more coronally oriented facets are argued to reduce the risk of ventral displacement of the lower lumbar vertebrae, particularly at the lumbosacral junction (Keith, 1923; Lewin et al., 1962; Kashimoto et al., 1982; Bogduk and Twomey, 2005). Thus, the more coronal orientation of the zygapophyseal facets at shift points in the cervical column curvature (C4 and C7), may represent a greater resistance to translation and ventral displacement in taxa with more pronograde head and neck postures.

Spinous process length and lamina cross-sectional area

The spinous process is a site of muscle attachment and differences in length can influence the mechanical advantage of cervical musculature. Increased spinous length, or projection, will increase the moment arm of the muscles, and hence their mechanical advantage if all other factors remain equal (Slijper, 1946; Shapiro, 1993; Cripton, 1999). In extant primates, the multifidus muscle attaches along the length of the cervical spinous processes and then spreads onto the laminae and articular pillars (Swindler and Wood, 1982; Anderson et al., 2005). This configuration is important for stability because greater dorsal projection of the spinous processes, as observed at the C3–C7 vertebral levels here, increases the leverage of the multifidus muscles and the cervicis muscles of the erector spinae group. Experimental work has demonstrated that these muscles are key to spinal stability and maintenance of posture in humans (White and Panjabi, 1990; Anderson et al., 2005). Results from the lamina cross-sectional area analyses support this scenario. The laminae are positioned between the spinous process and articular pillars and any forces generated at these sites will be transmitted through them. The laminae are functionally relevant because, with the exception of the prevertebral muscles (longus colli and longus capitis), all muscles acting on lower cervical vertebrae (C3–C7) attach to the dorsal vertebral components (Kapandji, 1974; Dean, 1982; Swindler and Wood, 1982; White and Panjabi, 1990) and it can be assumed that any bending forces generated at these sites will be transmitted through the laminae. Therefore it is not surprising that laminae with relatively greater cross-sectional areas are also found in taxa with other functional signals (longer spinous processes) for increased mechanical advantage of the attaching deep nuchal musculature, perhaps to better resist increased resultant bending loads. Why lamina cross-sectional area is significantly correlated only at the C4 and C5 levels is not immediately evident, however, this may be related

to the midcervical shift and the transition from dorsoflexion to ventroflexion discussed above. Overall, our results supports previous work linking cervical spinous process length with posture (e.g., Slijper, 1946; Schultz, 1961; Meyer, 2005) and suggests that those primates with less kyphotic orbits and more pronograde heads and necks have an increased mechanical advantage for the deep nuchal musculature and perhaps a greater resistance to bending loads at the midcervical shift.

Future work

Considering the support produced here for the functional roles of several cervical vertebral traits, future work is warranted for the development of biomechanical models of the cervical vertebral column among different primate postural groups. There are a few avenues of research that would aid in the development of more accurate cervical models; one in particular, is the incorporation of soft-tissue mechanics. For example, the nuchal ligament, has been considered an important, yet enigmatic, feature of the primate cervical vertebral region; and though it has received little attention outside of medical research, its presence/absence has been incorporated into functional hypotheses regarding bipedal locomotion in fossil hominins (Aiello and Dean, 1990; Bramble and Lieberman, 2004). The nuchal ligament is absent in the great apes (Swindler and Wood, 1982), which has been used to argue that this structure is functionally related to bipedality (Bramble and Lieberman, 2004). However, the nuchal ligament has been documented in *Papio* and *Macaca*, as well as in many other mammals (Fielding, 1976; Swindler and Wood, 1982; Bianchi, 1989), which complicates interpretation of the distribution of this structure and its polarity in hominoids. How the presence or absence of the nuchal ligament affects the functional relationships supported by our results is currently unknown and highlights

the fact that further research is required to understand the functional role of not only the nuchal ligament in head and neck postures, but other soft tissue features as well.

CONCLUSION

While many studies have focused on the thoracic and lumbar regions of the primate vertebral column to investigate primate posture and locomotion, the cervical region has been largely ignored in functional analyses. This study successfully identified a consistent association between direct measures of head and neck posture and cervical vertebral morphology for the first time. Specifically, heads and necks that are more pronograde or more perpendicular to the line of gravity exhibit cervical vertebral morphologies that indicate increased mechanical advantage for deep nuchal musculature (longer spinous processes and greater lamina cross-sectional areas) and an emphasis on lordosis curve formation and maintenance with a greater resistance to translation and ventral displacement (longer vertebral bodies and more coronally oriented articular facets). These results also highlight the advantage of integrating multiple types of morphological data and the use of quantified measures of behavioral data. Finally, results from this work provide a more comprehensive comparative foundation and a clear focus for future research on the primate neck.

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Species	Male (n)	Female (n)	Combined (n)
Alouatta seniculus	2		2
Ateles fusiceps	9	6	15
Ateles geoffroyi	1	4	5
Cebus apella	8	8	16
Cercopithecus diana		1	1
Cercopithecus petaurista		1	1
Chlorocebus aethiops	10	8	18
Colobus angolensis	2		2
Colobus guereza	10	7	17
Erythrocebus patas	4	3	7
Eulemur fulvus		1	1
Gorilla gorilla	6	5	11
Homo sapiens	10	10	20
Hylobates lar	1	1	2
Lagothrix lagotricha	2		2
Lemur catta	7	4	11
Macaca fascicularis	3	2	5
Macaca fuscata	3	2	5
Macaca mulatta	1	12	13
Pan troglodytes	10	9	19
Papio hamadryas	1	1	2
Papio ursinus	1	2	3
Pongo pygmaeus	11	10	21
Saimiri sciureus	4	4	8
Symphalangus syndactylus	1	5	6
Varecia varigata	2	6	8
Total sample size	109	112	221

TABLE 1. Comparative sample

TABLE 2. Cervical vertebrae variables, method of capture, and definition

Variable	Method	Definition
Vertebral body length (VBL)	Caliper	Average of max craniocaudal length along the ventral (VBVL) and dorsal (VBDL) surfaces
Vertebral body height (VBH)	Caliper	Max ventrodorsal height in the midline
Vertebral body width (VBW)	Caliper	Max mediolateral width in the midline
Uncinate process height (UNC)	Caliper	Max length of the uncinate process – VBL
Uncinate angle (UNA)	Landmark	Angle created by the planes of the uncinate process (5-8) and the vertebral body (pts 1-4)
Pedicle cross-sectional area (PCSA)	Caliper	Craniocaudal length X transverse width in the midline
Anterior transverse process length (ATPL)	Caliper	Max length across anterior tubercles
Posterior transverse process length (PTPL)*	Caliper	Max length across posterior tubercles
Transverse process angle - anterior tubercle (TransA)	Landmark	Angle created by the planes of the anterior transverse process margins (9-12) and the vertebral body (1-4)
Transverse process angle - posterior tubercle (TransP)*	Landmark	Angle created by the planes of the posterior transverse process margins (13-16) and the vertebral body (landmarks 1-4)
Articular facet angle (AFA)	Landmark	Angle created by the planes of the superior articular facet (17-20) and the vertebral body (1-4)
Lamina cross-sectional area (LCSA)	Caliper	Craniocaudal length X transverse width in the midline
Lamina angle (LA)	Landmark	Angle created by the planes of the lamina (21-24) and vertebral body (pts 1-4)
Vertebral neural arch angle (NAA)	Landmark	Angle created by the planes of the vertebral neural arch (25-28) and vertebral body (pts 1-4)
Spinous process length (SPL)	Caliper	Max length along the cranial surface
Spinous process cross-sectional area (SCSA)	Caliper	Craniocaudal length X transverse width in the midline
Spinous process angle (SPA)	Landmark	Angle created by the plane of the vertebral body (1-4) and the spinous process line created from landmarks 26 and 29

* In primates, vertebral levels C3 and C7 most commonly exhibit only a single tubercle (Nalley, 2013). This morphology represents the absence or underdevelopment of the anterior component of the transverse process (Scheuer and Black, 2000). Thus transverse

process features at these levels are referred to 'posterior'.

TABLE 3. Three-dimensional vertebral landmarks

No.	Landmark	Definition
1	Vertebral body ventral	Most ventral point on cranial surface of vertebral body in midline
2	Vertebral body dorsal	Most dorsal point on cranial surface of vertebral body in midline
3	Vertebral body right	Most lateral point on right side of cranial surface in midline
4	Vertebral body left	Most lateral point on left side of cranial surface in midline
5	Uncinate cranial ventral	Most cranioventral point on the margin of the medial surface
6	Uncinate cranial dorsal	Most craniodorsal point on the margin of the medial surface
7	Uncinate caudal ventral	Most caudoventral point on the margin of the medial surface
8	Uncinate caudal dorsal	Most caudodorsal point on the margin of the medial surface
9	Transverse process anterior tubercle cranial lateral	Most craniolateral point on the anterior tubercle of the transverse process
10	Transverse process anterior tubercle cranial medial	Most craniomedial point on the anterior tubercle of the transverse process
11	Transverse process anterior tubercle caudal lateral	Most caudolateral point on the anterior tubercle of the transverse process
12	Transverse process anterior tubercle caudal medial	Most caudomedial point on the anterior tubercle of the transverse process
13	Transverse process posterior tubercle cranial lateral	Most craniolateral point on the posterior tubercle of the transverse process
14	Transverse process posterior tubercle cranial medial	Most craniomedial point on the posterior tubercle of the transverse process
15	Transverse process posterior tubercle caudal lateral	Most caudolateral point on the posterior tubercle of the transverse process
16	Transverse process posterior tubercle caudal medial	Most caudomedial point on the posterior tubercle of the transverse process
17	Ventral extent of the superior articular facet	Most ventral point of the superior articular facet
18	Dorsal extent of the superior articular facet	Most dorsal point of the superior articular facet
19	Medial extent of the superior articular facet	Most medial point of the superior articular facet

20	Lateral extent of the superior articular facet	Most lateral point of the superior articular facet
21	Lamina cranial medial	Most craniomedial point on dorsal surface
22	Lamina cranial lateral	Most craniolateral point on dorsal surface
23	Lamina caudal medial	Most caudomedial point on dorsal surface
24	Lamina caudal lateral	Most caudolateral point on dorsal surface
25	Vertebral neural arch ventral	Most ventral point on cranial surface of vertebral neural arch in midline
26	Vertebral neural arch dorsal	Most dorsal point on cranial surface of vertebral neural arch in midline
27	Vertebral neural arch right	Most lateral point on right side of cranial surface
28	Vertebral neural arch left	Most lateral point on left side of cranial surface
29	Spinous process distal	Most distal point in cranial view

TABLE 4. PGLS results of vertebral variable on ln body mass and postural m

Variable	Partial r with neck inclination angle	Partial r with HNA	Partial r with AOA
C3			
LN VBL	0.51.	0.60*	ns
LN VBH	ns	ns	ns
LN VBW	ns	ns	ns
LN UNC	ns	0.46.	0.47.
UNA	ns	ns	ns
LN PCSA	ns	ns	0.46.
LN PTPL	ns	ns	ns
TransP	ns	ns	ns
AFA	ns	ns	ns
LN LCSA	ns	ns	ns
LA	ns	ns	ns
NAA	0.39.	ns	ns
LN SPL	0.71***	0.60**	0.70***
LN SCSA	0.53*	ns	ns
SPA	ns	ns	ns
C4			
LN VBL	0.63.	0.66**	0.46.
LN VBH	ns	ns	0.58*
LN VBW	ns	ns	ns
LN UNC	ns	ns	ns
UNA	ns	ns	ns
LN PCSA	ns	ns	0.49.
LN ATPL	ns	ns	ns
LN PTPL	ns	ns	ns
TransA	0.44.	ns	ns
TransP	ns	ns	ns
AFA	0.68**	0.67**	0.55*
LN LCSA	0.67**	0.73**	0.83***
LA	ns	ns	ns
NAA	ns	ns	ns
LN SPL	0.66***	0.52**	0.72***
LN SCSA	ns	ns	ns

SPA	ns	ns	ns
C5			
LN VBL	0.52*	0.68**	0.49.
LN VBH	ns	ns	ns
LN VBW	ns	ns	ns
LN UNC	ns	ns	ns
UNA	ns	ns	ns
LN PCSA	ns	ns	ns
LN ATPL	ns	ns	ns
LN PTPL	ns	ns	ns
TransA	0.50*	0.62**	0.68*
TransP	ns	ns	ns
AFA	ns	ns	ns
LN LCSA	0.67**	0.68**	0.79***
LA	ns	ns	ns
NAA	ns	ns	ns
LN SPL	0.58**	0.60**	0.76***
LN SCSA	ns	ns	ns
SPA	ns	ns	ns
C6			
LN VBL	0.49.	0.61*	0.52*
LN VBH	0.47.	0.50.	0.49.
LN VBW	ns	ns	ns
LN UNC	ns	ns	ns
UNA	ns	ns	ns
LN PCSA	ns	ns	ns
LN ATPL	ns	ns	ns
LN PTPL	ns	ns	ns
TransA	ns	ns	ns
TransP	ns	ns	ns
AFA	ns	ns	ns
LN LCSA	ns	ns	0.49.
LA	ns	ns	ns
NAA	ns	ns	ns
LN SPL	0.41*	0.38.	0.61**
LN SCSA	ns	ns	ns
SPA	0.44.	ns	ns

C7			
LN VBL	ns	ns	ns
LN VBH	ns	ns	ns
LN VBW	ns	ns	ns
LN UNC	ns	ns	0.65**
UNA	ns	ns	ns
LN PCSA	ns	ns	ns
LN PTPL	ns	ns	ns
TransP	ns	ns	ns
AFA	0.67**	0.68**	0.71**
LN LCSA	ns	ns	ns
LA	ns	0.50*	ns
NAA	0.62**	0.59**	0.78**
LN SPL	0.34.	ns	0.61**
LN SCSA	ns	ns	ns
SPA	ns	ns	ns

Abbreviations are as follows: HNA = head-neck angle, AOA = orbital kyphosis angle, VBL = vertebral body length, VBH = vertebral body height, VBW = vertebral body width, UNC = uncinate process height, UNA = uncinate process angle, PCSA = pedicle cross-sectional area, ATPL = transverse process length (anterior tubercle), TransA = transverse process angle (anterior tubercle), PTPL = transverse process length (posterior tubercle), TransP = transverse process angle (posterior tubercle), AFA = articular facet angle, LCSA = lamina cross-sectional area, LA = lamina angle, NAA = neural arch angle, SPL = spinous process length, SCSA = spinous process cross-sectional area, and SPA = spinous process length angle.

Level of significance indicated as follows: . $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Figure Legends

Figure 1. Vertebral measures and 3-D landmarks captured on cervical vertebrae. (A) and (B) superior view. (C) Lateral view. See Tables 2 and 3 for descriptions.
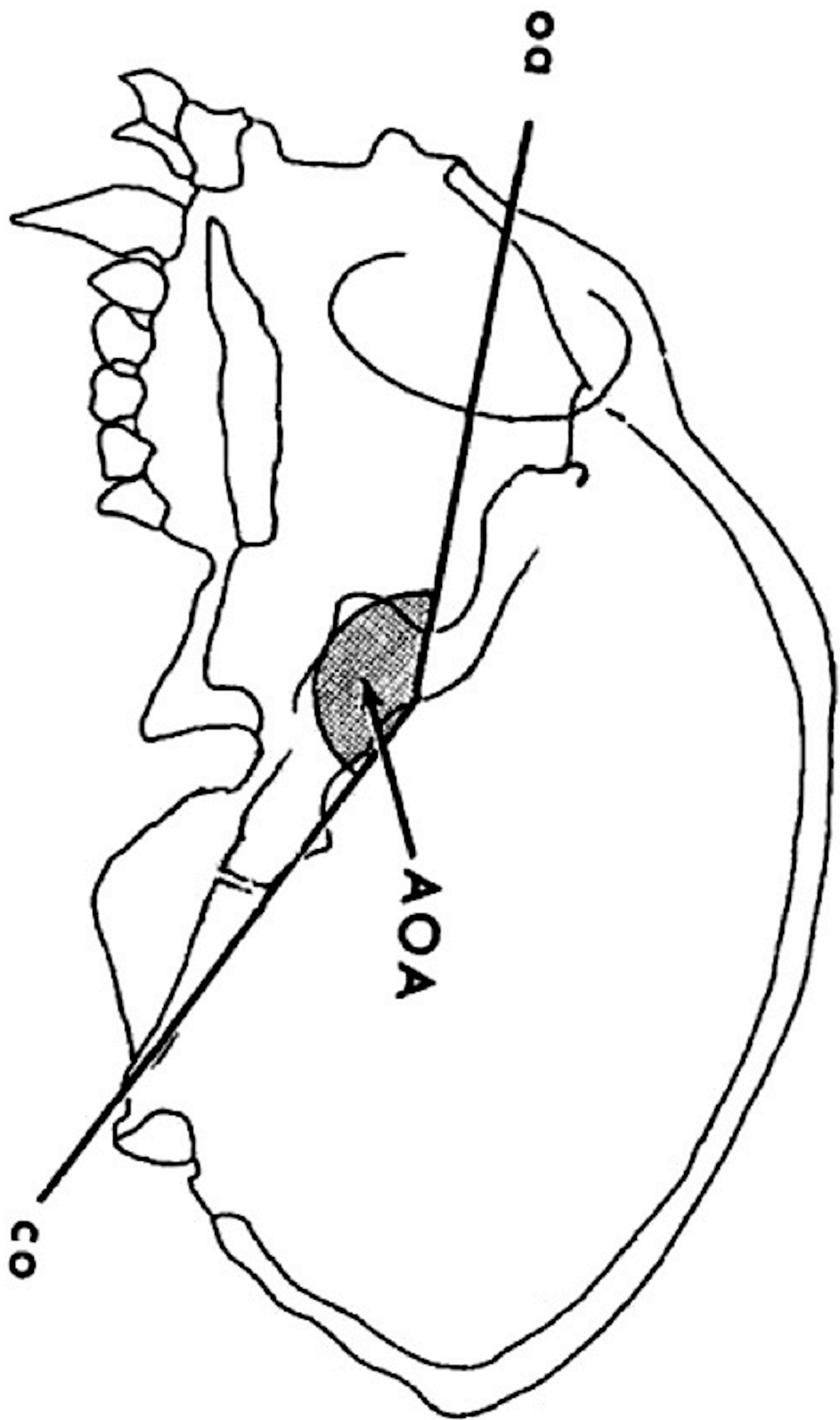
Figure 2. Adapted from Ross and Ravosa (1993). Illustrates axes used to define orbital kyphosis angle (AOA), including the plane of clivus ossis occipitalis (co) and the plane of the orbital axis (oa). More kyphotic orbits will exhibit smaller angles and less kyphotic orbits will demonstrate larger angles.
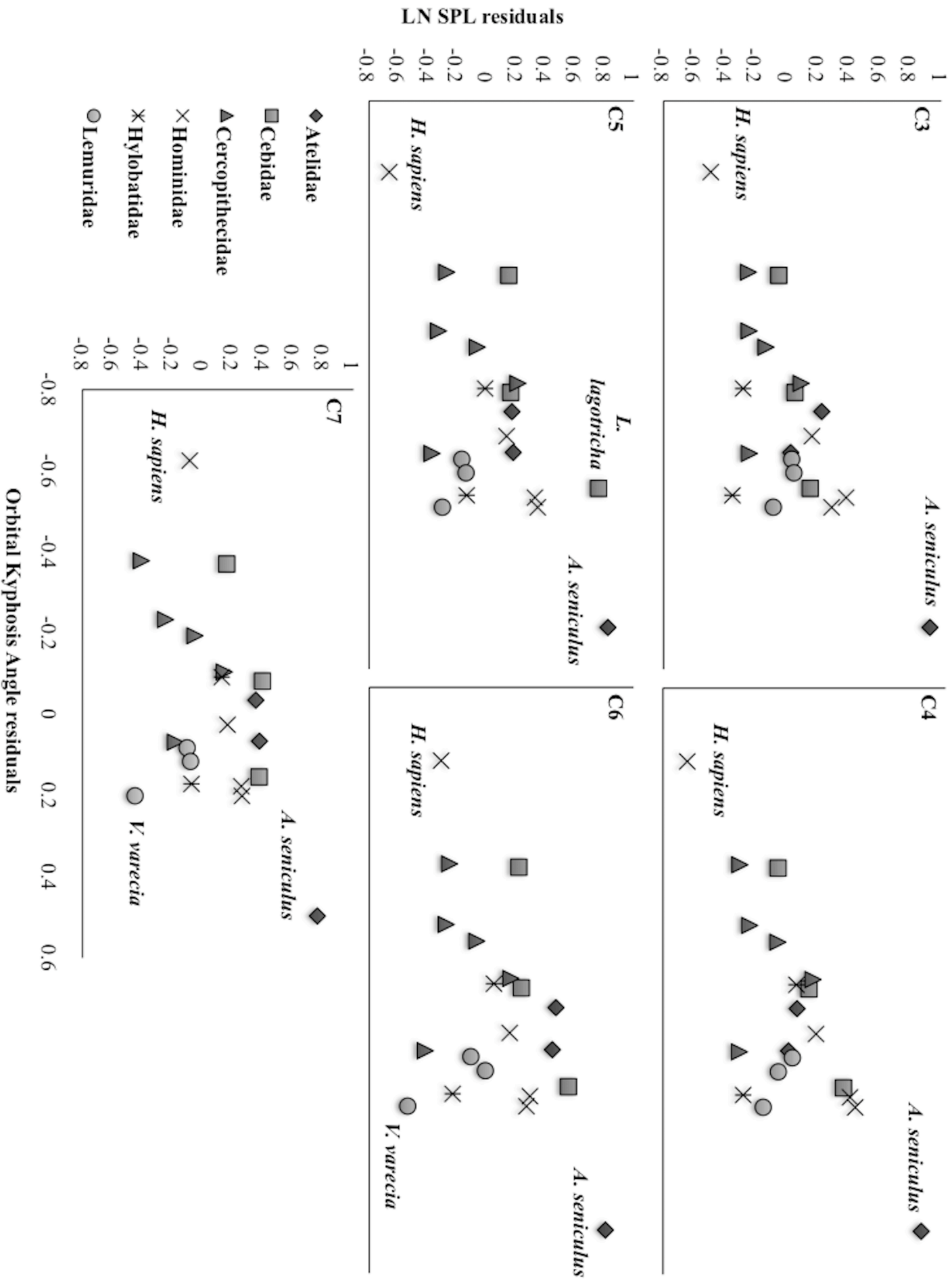
Figure 3. Spinous process length (LN SPL) residuals (relative to body mass) plotted against orbital kyphosis angle residuals (relative to body mass) for C3 through C7 levels ($p<0.05$). Atelidae (diamonds), Cebidae (squares), Cercopithecidae (triangles), Hominidae (X), Hylobatidae (asterisks), and Lemuridae (circles). Similar positive correlations are also observed for head-neck angle and neck inclination angle (not shown). Named taxa highlight more extreme values in dataset.
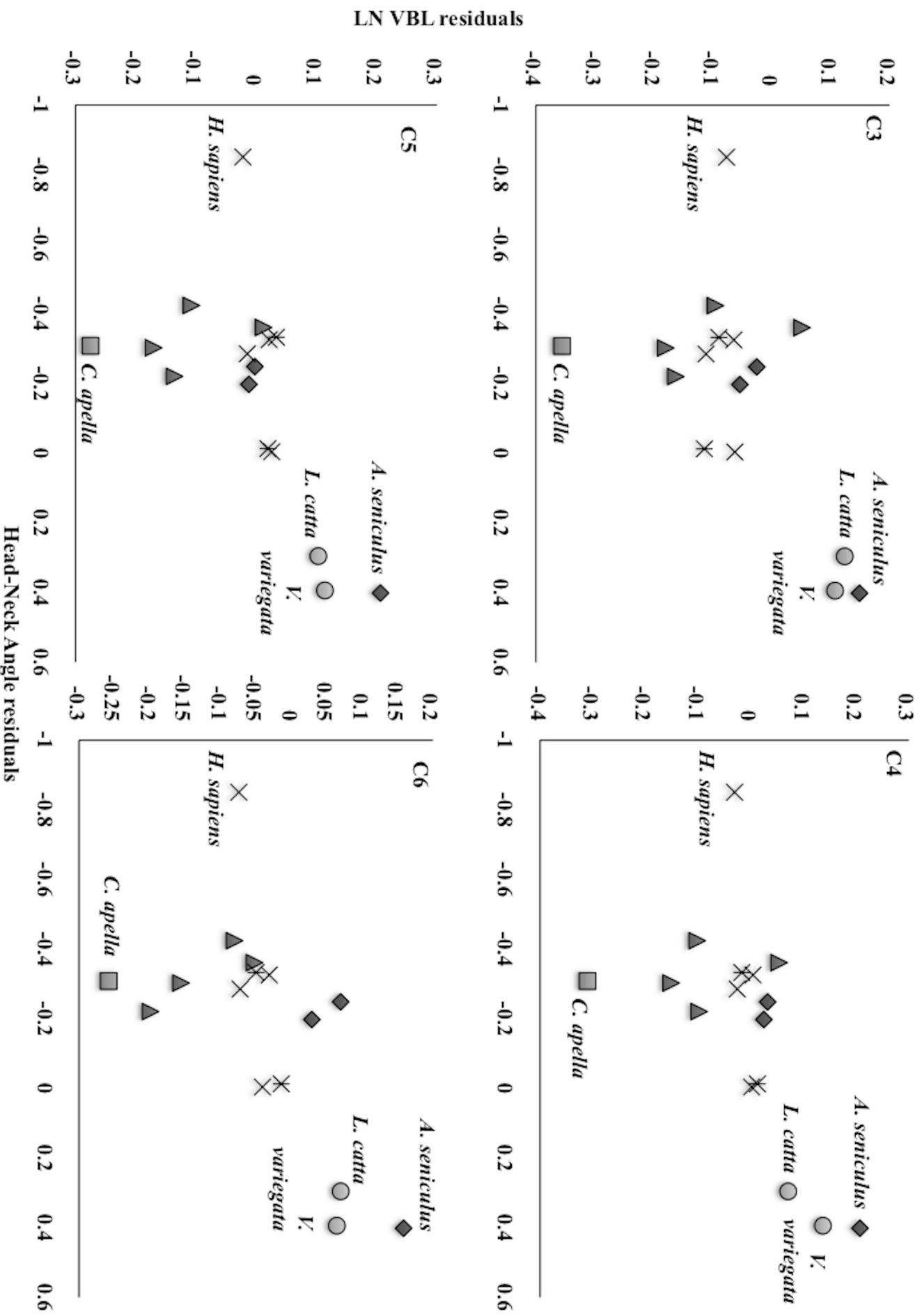
Figure 4. Vertebral body length (LN VBL) residuals (relative to body mass) plotted against head-neck angle residuals (relative to body mass) for C3 through C6 levels ($p<0.05$). Atelidae (diamonds), Cebidae (squares), Cercopithecidae (triangles), Hominidae (X), Hylobatidae (asterisks), and Lemuridae (circles). Similar positive correlations are also observed for neck inclination angle and orbital kyphosis angle (not shown). Named taxa highlight more extreme values in dataset.

Figure 5. Articular facet angle (AFA) residuals (relative to body mass) plotted against the residuals (relative to body mass) of all three measures of posture: neck inclination angle, head-neck angle, and orbital kyphosis angle. A negative relationship is observed at both C4 and C7 levels ($p<0.05$). Atelidae (diamonds), Cebidae (squares), Cercopithecidae (triangles), Hominidae (X), Hylobatidae (asterisks), and Lemuridae (circles). Named taxa highlight more extreme values in dataset.
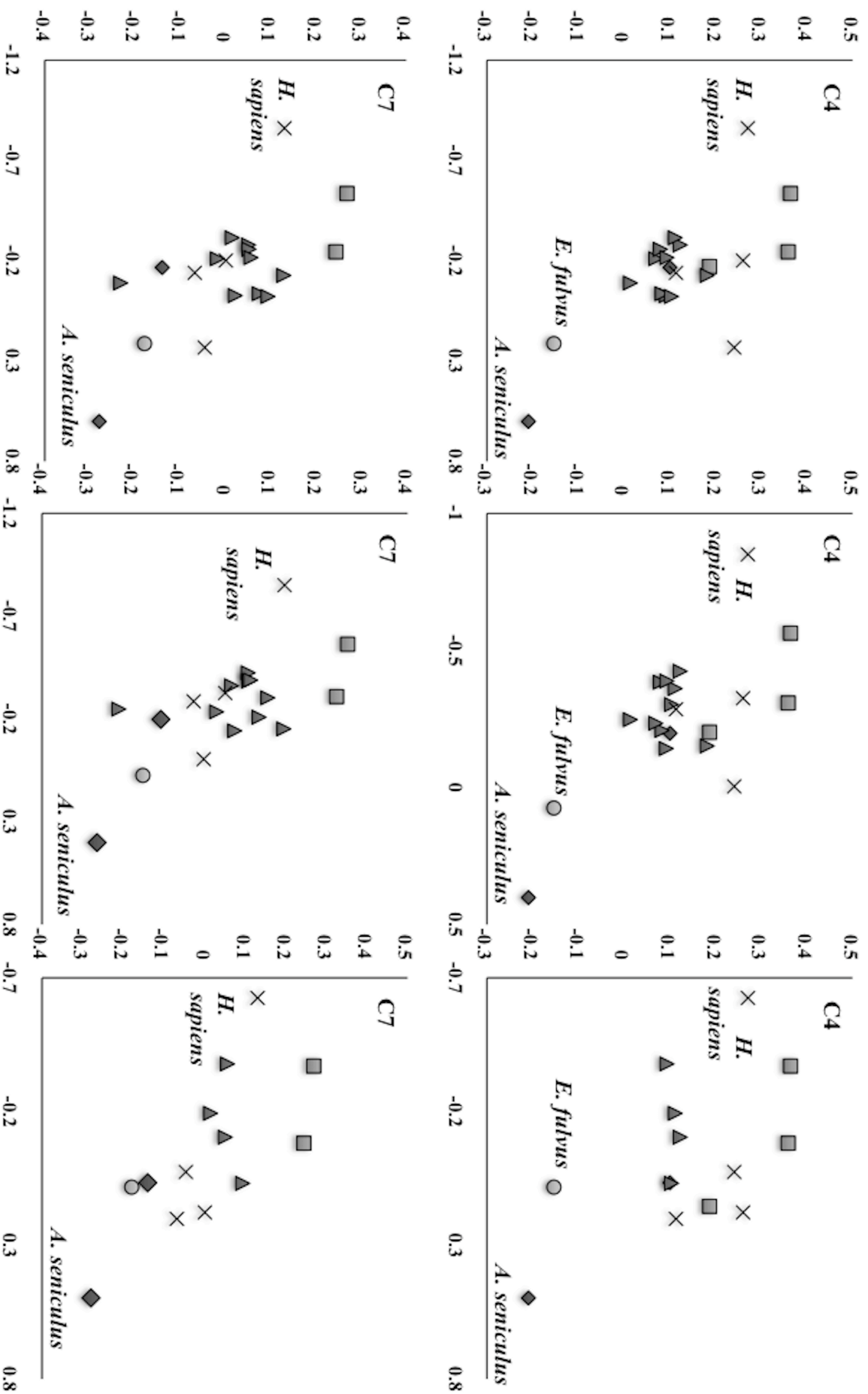
AFA residuals

C4

H. sapiens ×

E. fulvus ○

A. seniculus

C7

H. sapiens ×

A. seniculus

Neck Inclination Angle residuals

C4

H. sapiens ×

E. fulvus ○

A. seniculus

C7

H. sapiens ×

A. seniculus

Head-Neck Angle residuals

C4

H. sapiens ×

E. fulvus ○

A. seniculus

C7

H. sapiens ×

A. seniculus

Orbital Kyphosis Angle residuals

◆ Atelidae ■ Cebidae ▲ Cercopithecidae ✕ Hominidae ✱ Hylobatidae ○ Lemuridae