

## Caudal vertebral body articular surface morphology correlates with functional tail use in anthropoid primates

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Prehensile tails, capable of suspending the entire body weight of an animal, have evolved in parallel in New World monkeys (Platyrrhini): once in the Atelinae (*Alouatta*, *Ateles*, *Brachyteles*, *Lagothrix*), and once in the Cebinae (*Cebus*, *Sapajus*). Structurally, the prehensile tails of atelines and cebines share morphological features that distinguish them from non-prehensile tails, including longer proximal tail regions, well-developed hemal processes, robust caudal vertebrae resistant to higher torsional and bending stresses, and caudal musculature capable of producing higher contractile forces. The functional significance of shape variation in the articular surfaces of caudal vertebral bodies, however, is relatively less well understood. Given that tail use differs considerably among prehensile and non-prehensile anthropoids, it is reasonable to predict that caudal vertebral body articular surface area and shape will respond to use-specific patterns of mechanical loading. We examine the potential for intervertebral articular surface contour curvature and relative surface area to discriminate between prehensile- and nonprehensile-tailed platyrrhines and cercopithecoids. The proximal and distal intervertebral articular surfaces of the first (Ca1), transitional (TV) and longest (LV) caudal vertebrae were examined for individuals representing 10 anthropoid taxa with differential patterns of tail-use. Study results reveal significant morphological differences consistent with the functional demands of unique patterns of tail use for all vertebral elements sampled. Prehensile-tailed platyrrhines that more frequently use their tails in suspension (atelines) had significantly larger and more convex

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intervertebral articular surfaces than all nonprehensile-tailed anthropoids examined here, although the intervertebral articular surface contour curvatures of large, terrestrial cercopithecoids (i.e. *Papio*) converge on the ateline condition. Prehensile-tailed platyrrhines that more often use their tails in tripodal bracing postures (cebines) are morphologically intermediate between atelines and nonprehensile tailed anthropoids.

**Keywords:** Prehensile, Caudal Vertebrae, Curvature, Atelinae, Cebinae, Intervertebral disc articulation

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## Introduction

Positional behaviors are one of the most basic functional parameters defining a primate species. Behavioral studies establish that primates represent a greater diversity of locomotor adaptations than any other mammalian order (Hunt *et al.*, 1996; Fleagle, 2013). Among primates, only members of the Atelinae (*Alouatta*, *Ateles*, *Brachyteles*, *Lagothrix*) and the Cebinae (*Cebus*, *Sapajus*) possess prehensile tails that may be used as a postural support and/or suspensory grasping appendage capable of supporting an animal's entire body mass during feeding and locomotion (Emmons and Gentry, 1983). Although similar in structure and function (Lemelin, 1995; Organ *et al.*, 2009; Organ, 2010), prehensile tails in atelines and cebines are thought to have evolved in parallel (Napier, 1976; Rosenberger, 1983; Organ and Lemelin, 2011).

The mammalian tail is subdivided into three regions based on caudal vertebral morphology: proximal, transitional, and distal. Proximal caudal vertebrae articulate with one another by way of zygapophyseal and intervertebral disc joints. Depending on their orientation and shape, zygapophyses serve to govern spinal movements by permitting movement in some planes, while restricting it in others (Shapiro, 1993; Bogduk and Twomey, 2005; Russo, 2010). By contrast, distal caudal vertebrae articulate only through intervertebral disc joints (i.e., they lack zygapophyses), and are capable of more degrees

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of freedom in movement compared to proximal caudal vertebrae. The proximal tail region includes all caudal vertebrae from the first caudal vertebra (Ca1) to the transition vertebra (TV). The morphology of the TV is distinct among caudal vertebrae by the presence of zygapophyseal and intervertebral disc articulations proximally, but only an intervertebral disc articulation distally (Schmidt, 1886; Ankel, 1962, 1965, 1972). More recent analyses of anthropoid caudal vertebrae describe a third region of the tail, the transitional region, that includes all vertebrae between the TV and the craniocaudally longest vertebra (LV) in the tail sequence (German, 1982; Lemelin, 1995; Schmitt et al., 2005; Organ et al., 2009; Organ, 2010; Organ and Lemelin, 2011; Russo and Young, 2011).

Previous research has identified functionally significant differences in musculoskeletal morphology between prehensile- and nonprehensile- tailed platyrrhines. Compared to nonprehensile-tailed taxa, prehensile-tailed taxa have more craniocaudally expanded sacroiliac joints, longer proximal regions comprised of a greater number of vertebrae, craniocaudally shorter and transversely wider distal region vertebrae, more expanded transverse and hemal processes (sites of muscle attachment), caudal flexor musculature structured to produce higher contractile forces (i.e. muscle with greater physiological cross sectional areas [PCSA]), and vertebral cross-sectional geometry consistent with greater resistance to bending and torsion (Schmidt, 1886; Ankel, 1962, 1965, 1972; German, 1982; Lemelin, 1995; Schmitt et al., 2005; Organ et al., 2009; Organ, 2010; Organ and Lemelin, 2011; Russo and Young, 2011). The differences

between prehensile- and nonprehensile-tailed platyrrhine muscle attachments, PCSA,

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caudal vertebral robusticity, and resistance to bending and torsion are accentuated in the distal caudal region (Organ et al., 2009; Organ, 2010; Organ and Lemelin, 2011; Russo and Young, 2011). Proximal caudal vertebrae are thought to be less divergent morphologically between prehensile- and nonprehensile-tailed taxa given the presumably similar functional demands in this region of the tail (i.e. both groups abduct, adduct, flex and extend their tails) (German, 1982). Organ (2010), however, has more recently demonstrated that the cross-sectional geometric structure of proximal caudal vertebrae distinguishes prehensile-tailed platyrrhines from nonprehensile-tailed platyrrhines. The one exception in these results was *Pithecia monachus*, who exhibited more robust caudal vertebrae than expected, perhaps due to that taxon's use of 'tail draping' postures where the proximal region is used as a brace during hind limb suspension (Walker, 1993; 1996; Meldrum, 1998; Organ and Lemelin, 2011).

Prehensile-tailed platyrrhines differ in their frequency and mode of tail-use (Bergeson, 1992, 1995, 1996; Gebo 1992, Bezanson, 2012). Cebines use their prehensile tails to brace themselves against a vertical substrate in a tripod posture during feeding and resting, but infrequently use their tails to suspend their entire body weight (Bergeson, 1992, 1995, 1996; Bezanson, 2012). Like cebines, atelines use their tails in postural and feeding behaviors, but also employ their tails in hindlimb-assisted tail suspension and during tail-only suspensory locomotor behaviors (Bergeson, 1996; Schmitt et al., 2005; Bezanson, 2012). Despite these behavioural differences, ateline and cebine tails differ morphologically only by the presence of a hairless ventral friction

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pad (Organ et al., 2011) and more well-developed dorsal caudal musculature in the former (Lemelin, 1999; Organ et al., 2009). In contrast, the cebine prehensile tail is completely covered with hair (Organ et al., 2011) and the dorsal caudal musculature is developed as in nonprehensile-tailed platyrrhines (Lemelin, 1999). Nonetheless, features such as the well-developed ventral caudal musculature, the strong estimated structural mechanical properties of the caudal vertebrae, and the relatively longer proximal tail region in cebines are convergent with those properties of the ateline prehensile tail (Organ et al., 2009; Organ, 2010). Therefore, cebine prehensile tails appear as a morphological intermediate between the tails of atelines and the tails of nonprehensile-tailed platyrrhines.

Although there have been numerous studies examining the anatomy of prehensile and nonprehensile anthropoid tails with respect to function, none of these directly addresses the functional significance of articular surfaces of the caudal vertebrae. This study will specifically address the scaling relationships and surface curvature of intervertebral disc joint articulations among prehensile- and nonprehensile-tailed anthropoids. Bones from closely related taxa with dissimilar positional behaviors should respond in unique ways to locomotor specific loading patterns. One such adaptive response is the relative increase in joint surface area in response to increased mechanical loading (Jungers, 1988, 1991; Ruff, 1988; Godfrey *et al.*, 1991; Ruff and Runstead, 1992; Rafferty and Ruff, 1994; Lieberman *et al.*, 2001). Joint stress is a function of the force applied to a joint relative to articular surface area. Larger joint surfaces effectively

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minimize the concentration of these forces on the articular surfaces and preserve joint function by minimizing the potential for damage to the cartilaginous and osseous joint components (Currey, 1984; Jungers, 1988). Similarly, the contour morphology of articular surfaces can significantly influence joint function and excursion (e.g., Organ and Ward, 2006). We hypothesize that intervertebral articular surface area and contour curvature are correlates of tail-use (e.g., prehensile-tailed versus nonprehensile-tailed). This hypothesis will be validated by confirmation of the following predictions:

1. Prehensile-tailed anthropoids have relatively larger intervertebral articular surfaces compared to their nonprehensile-tailed relatives, presumably as a consequence of the increased mechanical loading of the caudal vertebrae resulting from tail use during locomotion, suspension and/or support during tripodal postures.
2. Prehensile-tailed anthropoids will have more pronounced intervertebral articular surface curvatures (i.e. greater convexity) compared to nonprehensile-tailed anthropoids consistent with increased dorsoventral and mediolateral tail flexibility.

## **Methods and Materials**

### *Data sample*

The first caudal vertebra (Ca1), transition vertebra (TV), and longest vertebra (LV) were identified for a mixed taxonomic sample (n=56 individuals) representing ten

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distinct anthropoid genera (Table 1). Specimens were from the Field Museum of Natural History (FMNH), the Department of Anthropology at the University of Texas at Austin, and the Department of Anatomy and Neurobiology in the College of Medicine at the University of Kentucky. These vertebrae were chosen because they possess unique and consistent morphologies that make them readily identifiable. Vertebral identification follows the descriptions of Ca1, TV and LV vertebral morphology in Organ (2010). All genera were identified as belonging to one of two discrete tail function groupings (i.e. prehensile-tailed vs. nonprehensile-tailed). Specimens identified as nonprehensile-tailed were further segregated into nonprehensile-tailed New World monkey (NWM) and nonprehensile-tailed Old World monkey (OWM) groupings (Table 1). Functional groupings are based on behavioral observations (Gebo, 1992; Garber and Rehg, 1999; Youlatos, 1999; Bezanson, 2004; 2005; 2006a, 2006b; 2009; 2012) and prior functional analyses of caudal musculoskeletal anatomy (Schmidt, 1886; Dor, 1937; Ankel, 1962, 1965, 1972; German, 1982; Lemelin, 1995; Youlatos, 2003; Schmitt et al., 2005; Organ et al., 2009; Organ, 2010).

#### **TABLE 1 HERE**

##### *Data collection*

3D surface models of the proximal and distal articular surfaces of Ca1, TV and LV vertebral bodies were generated using a NextEngine HD portable laser scanner and ScanStudio HD software or from available CT scan data using Mimics 11.0.

Zygapophyseal articular surfaces, which are quite small in most study taxa, were not

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considered in the present study due to the resolution limitations of the laser scanning equipment (but see below). Geomagic 11.0 was used to isolate and measure the absolute surface area ( $\text{mm}^2$ ) of individual 3D models.

Articular contour curvature was quantified for all isolated articular surface models using the quadric-based method described by Tocheri (2007; see also Marzke et al., 2010). This method fits a quadric surface to a 3D surface and then compares the coefficients describing that quadric surface. In 3D, a quadric surface is defined by the equation

$$z = ax^2 + by^2 + 2cxy + 2dx + 2ey + f$$

Using the following rigid body transform

$$\begin{bmatrix} \hat{x} \\ \hat{y} \\ \hat{z} \end{bmatrix} = R \begin{bmatrix} x - x_0 \\ y - y_0 \\ z - z_0 \end{bmatrix}$$

then

$$\hat{z} = A\hat{x}^2 + B\hat{y}^2$$

$A$  and  $B$  represent the magnitude of contour curvature of the quadric surface in perpendicular axes (i.e.,  $A$  represents mediolateral [ML] contour curvature,  $B$  represents dorsoventral [DV] contour curvature) and are analogous to the fitted principle curvatures ( $k_{\max}$  and  $k_{\min}$ ) of the fitted quadric surface (Tocheri, 2007).  $A$  and  $B$  values derived from the fitting of a quadric surface to each vertebral specimen were used for direct comparisons among taxonomic and functional groupings. In total, twelve articular contours were examined (i.e., ML and DV contours for the proximal and distal

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articular surfaces of three individual skeletal elements).

#### *Data analysis*

All average body mass and articular surface areas were naturally log-transformed.

Ordinary least squares (OLS) regression analysis of the log-transformed data was used to evaluate scaling relationships between vertebral body articular surface area and average body mass. Slope,  $R^2$  fit statistics, and standardized residuals were recorded and bivariate plots of log-normalized average body mass and articular surface area values were generated. One-way ANOVA with a post-hoc Bonferroni correction was used to evaluate the statistical significance of differences in mean standardized residual values among the three tail-use groupings (prehensile-tailed, nonprehensile-tailed NWM, nonprehensile-tailed OWM). Although it has been suggested that ratios are better at identify shape similarities among individuals (Jungers et al. 1995), ratios are incapable of removing completely the effects of size related scaling in morphometric data (Albrecht et al. 1993). Regression residuals, however, are independent of size and therefore not influenced by comparisons between sample taxa with dissimilar body masses. The average body mass of the smallest taxon used in this study (*Saimiri*) is only 3% of the average body mass of the largest taxon (*Papio*). Statistically significant differences ( $p < 0.05$ ) in coefficients *A* (ML contour curvature) and *B* (DV contour curvature) were evaluated with one-way ANOVA with a post-hoc Bonferroni correction.

## **Results**

### *Articular Surface Area*

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OLS regression analyses demonstrate that only the TV proximal articular surface area scales with positive allometry (slope = 0.681) and that all other articular surfaces scale with slight negative allometry (i.e., the slope for all regression lines were < 0.667 and range between 0.541 and 0.626). Atelines are consistently positioned above the regression line, and most specimens fall outside the upper boundary of the 95% confidence interval for all articular surface samples. *Sapajus*, *Cebus*, and *Saimiri* cluster around the regression line and most specimens fall within the upper and lower boundaries of the 95% confidence interval. In contrast, *Aotus* and most nonprehensile-tailed OWM's are typically positioned below the regression line and many specimens fall outside the lower boundary of the 95% confidence interval (Figures 1).

**FIGURE 1 HERE**

Results of a one-way ANOVA with a post-hoc Bonferroni correction reveal that the mean standardized regression residual values for prehensile-tailed taxa are significantly larger than those for either nonprehensile-tailed group (OWM and NWM) in the analysis of the Ca1 distal articular sample and the proximal and distal TV and LV articular samples (Figure 2; Table 2). Although mean standardized regression residuals reported for the prehensile group were significantly different from the nonprehensile-tailed OWM group for the proximal Ca1 and distal LV samples, they were not statistically different from the nonprehensile NWM group (Figure 4; Table 2). Likewise, the mean standardized regression residuals reported for atelines are significantly larger than those

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reported for cebines in the proximal and distal Ca1, proximal TV and distal LV samples (Figure 3).

**FIGURE 2 HERE**

**TABLE 2 HERE**

**FIGURE 3 HERE**

#### *Articular Surface Contour Curvature*

The results of the analyses of articular surface contour curvature identify statistically significant differences in the coefficients describing a best-fit quadric surface for eight of the twelve articular contours examined in the present study (Figure 4; Table 3). These include the ML and DV contours of the proximal TV and distal Ca1 and LV articular surfaces, the DV contour of the distal TV articular surface and the ML contour of the distal LV articular surface. One-way ANOVA results reveal statistically significant differences among mean quadric coefficient values for each of the three tail-use groupings and a post-hoc Bonferroni correction reveals that prehensile-tailed taxa are significantly more curved (i.e their coefficient values are negative indicating convexity and further removed from 0.0 which indicates flatness) than are nonprehensile-tailed NWM for all eight articular contours. Likewise, nonprehensile-tailed OWM's are generally less curved than prehensile-tailed platyrrhines, however there are no significant differences between these groups for three of the eight variables (DV contour of the proximal and distal TV articular surfaces, ML contour of the distal LV articular surface). There is little difference in the articular contour curvatures of nonprehensile-

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tailed OWM's and NWM's, however the former has significantly more curved ML contours for the distal Ca1 articular surface and DV contours for the proximal TV articular surface.

**FIGURE 4 HERE**

**TABLE 3 HERE**

Within the prehensile-tailed sample, independent samples T-tests identify statistically significant differences between atelines and cebines. Atelines have greater ML and DV contour curvatures for both the proximal and distal articular surfaces of Ca1, ML contour curvatures for the proximal and distal TV and proximal LV articular surfaces and DV contours for the distal LV articular surface (Figure 5).

**FIGURE 5 HERE**

## **Discussion**

### *Intervertebral articular surface size and scaling*

The results described above demonstrate that prehensile-tailed platyrrhines have relatively larger distal Ca1, and proximal and distal TV and LV intervertebral articular surfaces than nonprehensile-tailed NWM's and OWM's (Figure 1, 2; Table 2). Two of the vertebral elements used in this study to differentiate prehensile and nonprehensile-tailed anthropoids (Ca1 and TV) are located in the proximal caudal region; the region that is most affected by mechanical loading during prehensile tail grasping and suspension. Prior research has identified numerous skeletal characteristics that distinguish prehensile tailed from nonprehensile-tailed anthropoids, however the

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majority of these are accentuated in the distal caudal region (i.e. craniocaudally shorter and transversely wider distal vertebrae, expanded transverse and hemal processes, and higher vertebral torsional/bending strength in the former) (German, 1982; Organ, 2007, 2010). Although it has been suggested that the proximal caudal regions of prehensile- and nonprehensile-tailed anthropoids have a similar function and similar magnitude and pattern of mechanical loading (German, 1982), this is contra-indicated by the results of the present study. Our results are consistent with a pattern of increased mechanical loading in prehensile-tailed platyrrhines relative to all nonprehensile-tailed anthropoids, presumably as a consequence of tail use in suspensory and tripod support postures.

Similarly, atelines included in the study sample (*Ateles*, *Lagothrix*) have larger relative proximal and distal Ca1, proximal TV and distal LV intervertebral articular surface areas than do cebines (*Cebus*, *Sapajus*) (Figure 3). This result is consistent with the interpretation that, although atelines and cebines have convergent prehensile tail skeletal structure, differences in prehensile tail use have resulted in larger articular surface areas in the former. Specifically, prehensile tail use in suspensory postures and locomotion may be mechanically more demanding than prehensile tail use during tripod support postures, and that difference in the magnitude of the mechanical loading is likely concentrated in the proximal tail segment. Larger intervertebral articular surfaces would effectively provide a greater area over which to distribute the increased mechanical loading associated with suspensory tail-assisted postures.

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### *Intervertebral articular surface contour curvature*

The results of the analysis of intervertebral articular surface contour curvature confirm that prehensile-tailed platyrrhines have generally more pronounced (e.g. more convex) articular surface contour curvatures relative to nonprehensile-tailed NWM's and OWM's (Figure 4,5,6; Table 3). Relative to nonprehensile-tailed anthropoids, prehensile-tailed platyrrhines are likely afforded a greater range of ML and DV tail flexion as a consequence of the more pronounced contour curvatures of the distal Ca1 articular surface and the proximal and distal articular surfaces of the TV and LV. This is consistent with the conclusion that increased intervertebral articular surface contour curvatures are correlated with enhanced caudal mobility in the proximal and transitional caudal region and are more beneficial to primates that routinely support their entire body weight during locomotor and postural events. Moreover, the observation that atelines have more pronounced caudal vertebral articular surface curvatures than nocebines supports the conclusion that prehensile tail-use during suspensory postural and locomotor activities requires additional ML and DV tail flexion, particularly between Ca1 and Ca2, relative to prehensile tail-use in tripod support postures.

Despite the broad discrimination between prehensile- and nonprehensile-tailed anthropoids, and between atelines and cebines, prehensile-tailed platyrrhines and nonprehensile-tailed OWM articular contour morphology overlaps for a limited number (n=3) of the eight study variables for which statistically significant variation was reported (Figure 4, Table 3). These similarities likely represent a morphological

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convergence resulting from similar selection pressures associated with unique and distinctive patterns of tail use. Unlike prehensile-tailed platyrrhines, OWM tail structure and function is not directly related to locomotor and postural behaviours (Karrer, 1970, Ohja, 1974; Bernstein et al. 1978; Stevens et al. 2008). Large and terrestrial OWM's (i.e. *Papio*) often have a prominent tail kink that is located near the transition vertebra or subadjacent vertebra (i.e. the proximal caudal segment arches upward from the base of the sacrum and then quickly reverses direction on or near the level of the TV and the distal caudal segment is directed inferiorly) (Figure 7). This tail configuration has the advantage of making the individual appear larger for agonistic display or defense purposes. Likewise, it exposes the individual's hindquarters that may be useful for mating related display behaviour and/or exposure of the ischial callosities for sitting. Alternatively the kinked tail morphology in large terrestrial OWM's may function to stabilize an infant during transportation, also known as "rump riding" (Karrer, 1970, Ohja, 1974; Bernstein et al. 1978). Increased intervertebral articular surface contour curvature of the vertebrae associated with the proximal and transitional caudal regions may be associated with the formation of this unique tail kink morphology and increased articular surface convexity may contribute to the abrupt change in tail orientation in this region. In contrast, similar contour curvatures in prehensile-tailed platyrrhines are likely the result of enhanced joint mobility in the proximal and transitional caudal regions.

## **Conclusion**

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The results of the present study demonstrate that analyses of intervertebral articular size and articular contour morphology possess the necessary resolution to effectively discriminate prehensile-tailed anthropoids from nonprehensile-tailed anthropoids and confirm both study predictions. In general, prehensile-tailed anthropoids have larger and more convex articular surfaces relative to nonprehensile-tailed anthropoids. Similarly, within the prehensile-tailed group, atelines that more frequently use their tails in suspensory locomotor activities have larger and more convex articular surfaces than cebines that more frequently use their tails in tripodal bracing postures and less often during locomotor events. These findings are counter to the suggestion that, despite differential patterns of anthropoid tail use, the proximal caudal regions of prehensile- and nonprehensile-tailed anthropoids have a similar function, and presumably a similar magnitude and pattern of mechanical loading (German, 1982). In light of these findings, it is recommended that analyses of the intervertebral articular size and articular contour morphology of vertebral elements in the proximal tail region be employed in future analyses of fossil platyrrhines to better understand the evolution of use-specific patterns of anthropoid functional tail use. Nevertheless, intervertebral articulations are only one set of articulations found in the proximal tail region and must be considered with respect to zygapophyseal articular function. Although not included in the present study owing to the resolution limitations of portable scanning equipment, future analyses of zygapophyseal articular surface casts using a higher resolution non-portable laser scanner are planned.

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## Figure Captions

**Figure 1.** A). Relationship between proximal Ca1 articular area and body mass. B). Relationship between distal Ca1 articular area and body mass. C). Relationship between proximal TV articular area and body mass. D). Relationship between proximal TV articular area and body mass. E). Relationship between proximal LV articular area and body mass. F). Relationship between proximal LV articular area and body mass. Linear regression lines of best fit are passed through the raw data space with the 95% confidence intervals indicated by the curved lines above and below.

**Figure 2.** Boxplots of standardized residuals for individual locomotor groups from linear regression analyses of A) proximal Ca1 articular surface area, B) distal Ca1 articular surface area, C) proximal TV articular surface area and D) distal TV articular surface area, E) proximal LV articular surface area, and F) distal LV articular surface area against average body size. Darkened bars represent the median value for each group, while the boxes show the 50% confidence interval and the whiskers extend to the highest and lowest values for each taxon, excluding outliers.

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**Figure 3.** Boxplots of standardized residuals for atelines and a group including *Cebus* and *Sapajus* from linear regression analyses of A). proximal Ca1 articular surface area and B). distal Ca1 articular surface area C). proximal TV articular surface area and D). distal LV articular surface area against average body size. Darkened bars represent the median value for each group, while the boxes show the 50% confidence interval and the whiskers extend to the highest and lowest values for each taxon, excluding outliers.

**Figure 4.** Boxplots of articular surface contour curvature coefficients where statistically significant differences were identified among locomotor groupings. Darkened bars represent the median value for each group, while the boxes show the 50% confidence interval and the whiskers extend to the highest and lowest values for each taxon, excluding outliers.

**Figure 5.** Boxplots of articular surface contour curvature coefficients where statistically significant differences were identified between atelines and cebines. Darkened bars represent the median value for each group, while the boxes show the 50% confidence interval and the whiskers extend to the highest and lowest values for each taxon, excluding outliers.

**Figure 6.** 3D articular surface models of the i. proximal Ca1, ii. distal Ca1, iii. proximal TV, iv. distal TV, v. proximal LV and vi. distal LV for A) *Lagothrix lagotricha*, B) *Sapajus apella*, C) *Saimiri sciurius*, D) *Colobus guereza*, and E) *Semnopithecus entellus*.

**Figure 7.** *Papio anubis* female with notable tail kink. Photo by Andrew Deane

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Table 1. Study sample and locomotor group designations

<b>Taxon</b>	<b>Locomotor group</b>	<b>Ca1</b>	<b>LV</b>	<b>TV</b>
<i>Ateles fusciceps</i>	prehensile	n=3	n=3	n=3
<i>Lagothrix lagotricha</i>	prehensile	n=20	n=20	n=20
<i>Cebus capuchinus</i>	prehensile	n=1	n=1	n=1
<i>Sapajus apella</i>	prehensile	n=5	n=5	n=5
<i>Aotus lemurinus</i>	non-prehensile NWM	n=1	n=1	n=1
<i>Saimiri sciurius</i>	non-prehensile NWM	n=6	n=6	n=6
<i>Colobus guereza</i>	non-prehensile OWM	n=3	n=3	n=3
<i>Semnopithecus entellus</i>	non-prehensile OWM	n=1	n=1	n=1
<i>Trachypithecus obscura</i>	non-prehensile OWM	n=2	n=2	n=2
<i>Papio cynocephalus</i>	non-prehensile OWM	n=6	n=8	n=5
<b>Total</b>		n=48	n=50	n=47

Table 2. Bonferroni significance values; articular surface area

Ca1 prox.	Nonprehensile-tailed NWM	Nonprehensile-tailed OWM
Prehensile	$p \leq 0.000$	
Nonprehensile-tailed NWM		$p \leq 0.042$
Ca1 dist.	Nonprehensile-tailed NWM	Nonprehensile-tailed OWM
Prehensile	$p \leq 0.043$	$p \leq 0.000$
Nonprehensile-tailed NWM		$p \leq 0.027$
TV prox.	Nonprehensile-tailed NWM	Nonprehensile-tailed OWM
Prehensile	$p \leq 0.037$	$p \leq 0.000$
Nonprehensile-tailed NWM		
TV dist.	Nonprehensile-tailed NWM	Nonprehensile-tailed OWM
Prehensile	$p \leq 0.024$	$p \leq 0.000$
Nonprehensile-tailed NWM		
LV prox.	Nonprehensile-tailed NWM	Nonprehensile-tailed OWM
Prehensile	$p \leq 0.025$	$p \leq 0.000$
Nonprehensile-tailed NWM		
LV dist.	Nonprehensile-tailed NWM	Nonprehensile-tailed OWM
Prehensile	$p \leq 0.012$	$p \leq 0.000$
Nonprehensile-tailed NWM		

Table 3. Bonferroni significance values; articular surface contour curvature

Ca1 dist. mediolateral axis	non-prehensile NWM	non-prehensile OWM
prehensile	$p \leq 0.000$	$p \leq 0.019$
non-prehensile NWM		$p \leq 0.008$
Ca1 dist. dorsoventral axis	non-prehensile NWM	non-prehensile OWM
prehensile	$p \leq 0.000$	$p \leq 0.007$
non-prehensile NWM		
TV prox. mediolateral axis	non-prehensile NWM	non-prehensile OWM
prehensile	$p \leq 0.002$	$p \leq 0.018$
non-prehensile NWM		
TV prox. dorsoventral axis	non-prehensile NWM	non-prehensile OWM
prehensile	$p \leq 0.007$	
non-prehensile NWM		
TV dist. dorsoventral axis	non-prehensile NWM	non-prehensile OWM
prehensile	$p \leq 0.029$	
non-prehensile NWM		
LV prox. mediolateral axis	non-prehensile NWM	non-prehensile OWM
prehensile	$p \leq 0.026$	$p \leq 0.011$
non-prehensile NWM		
LV dist. mediolateral axis	non-prehensile NWM	non-prehensile OWM
prehensile	$p \leq 0.052$	
non-prehensile NWM		
LV dist. dorsoventral axis	non-prehensile NWM	non-prehensile OWM
prehensile	$p \leq 0.001$	$p \leq 0.039$
non-prehensile NWM		

# Figure 1.

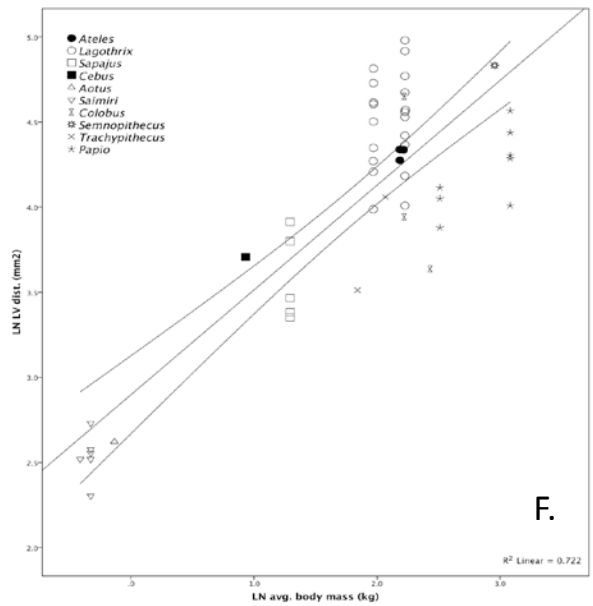
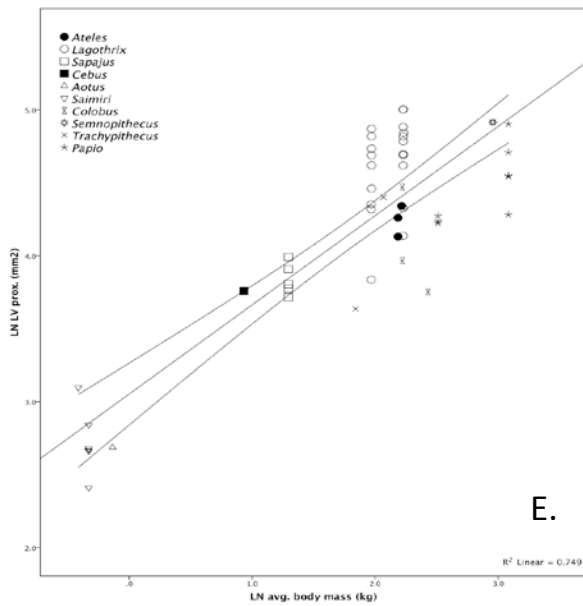
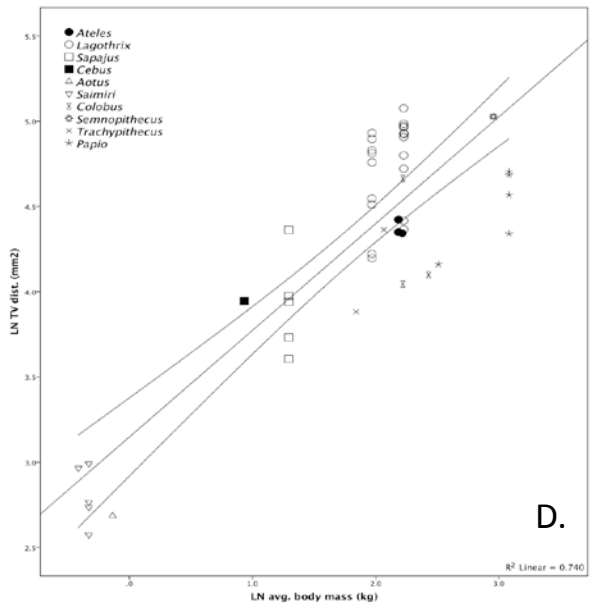
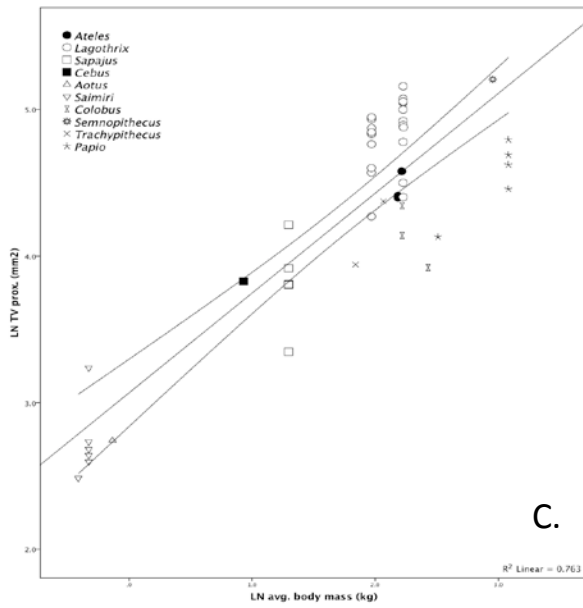
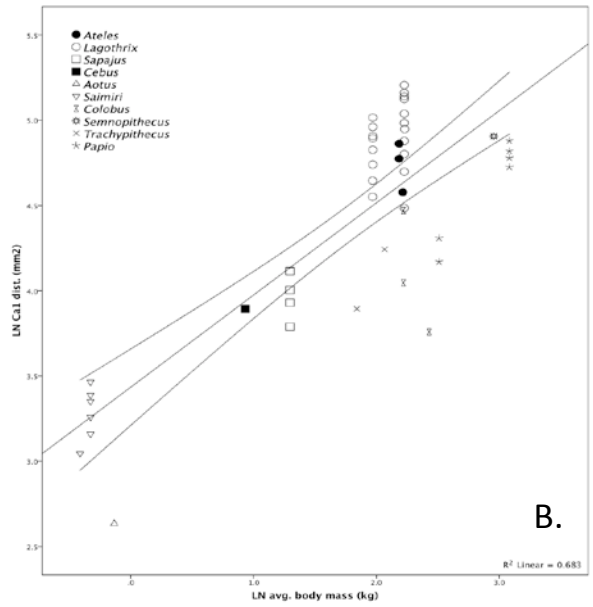
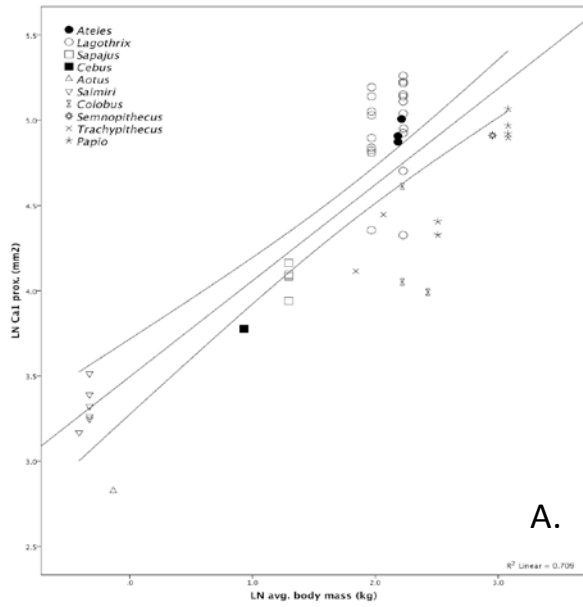


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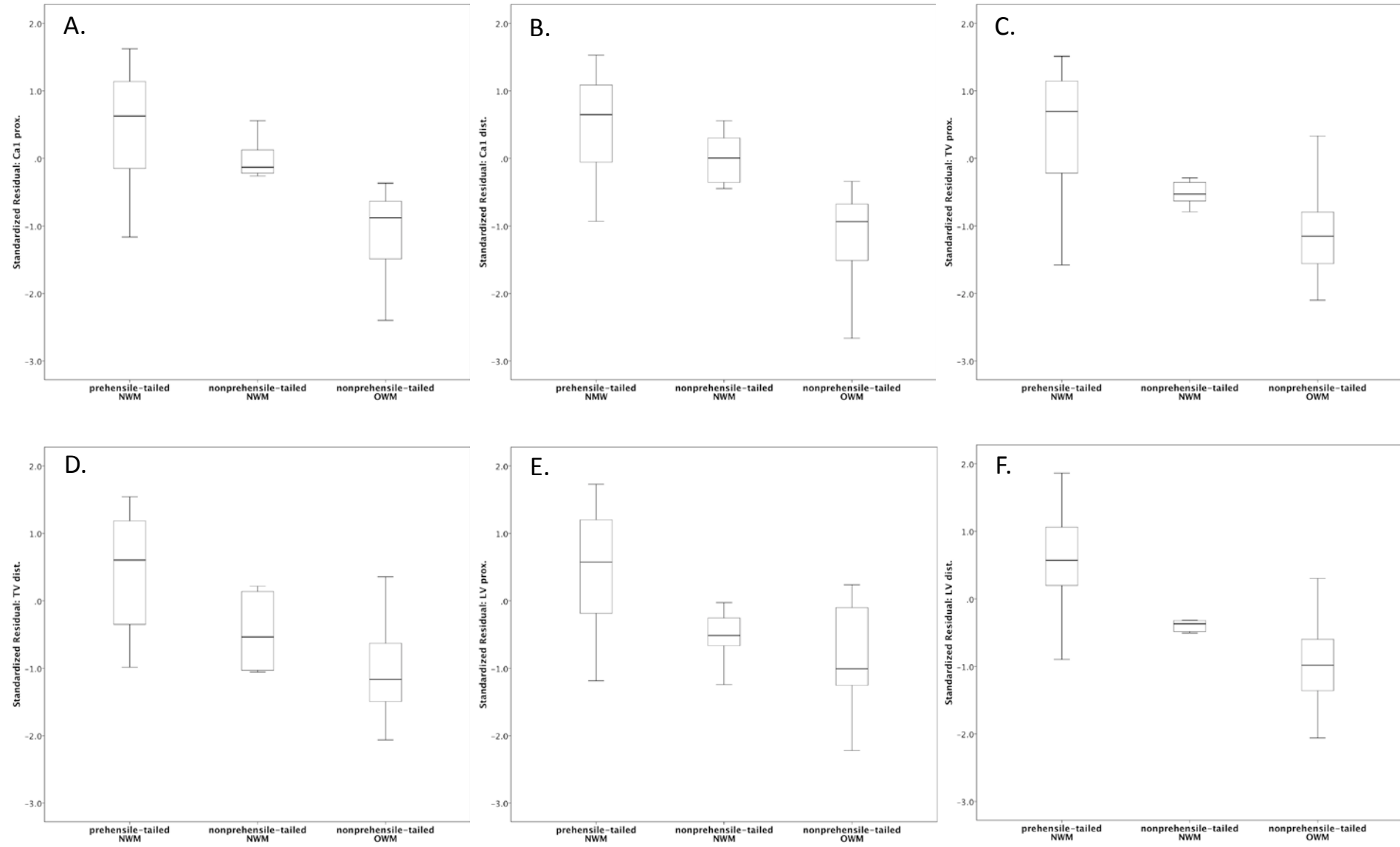


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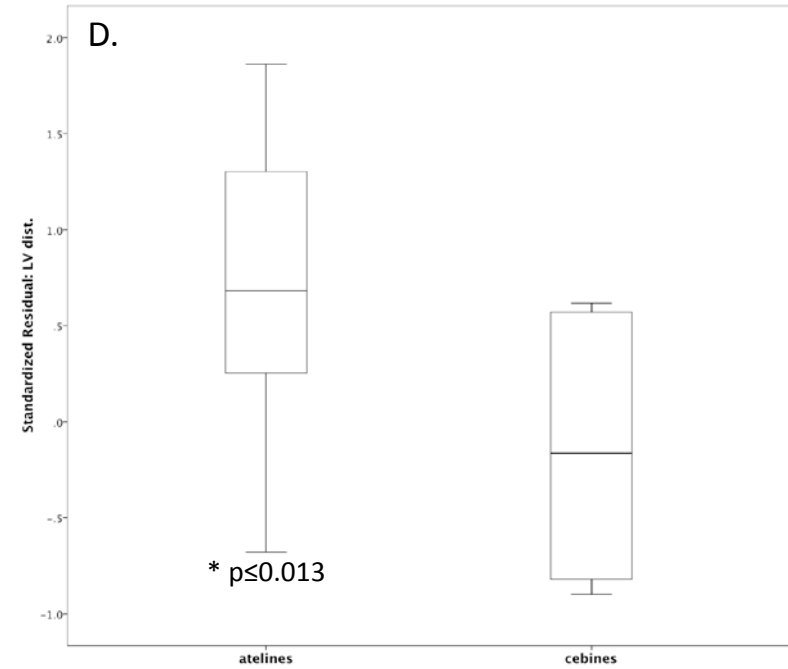
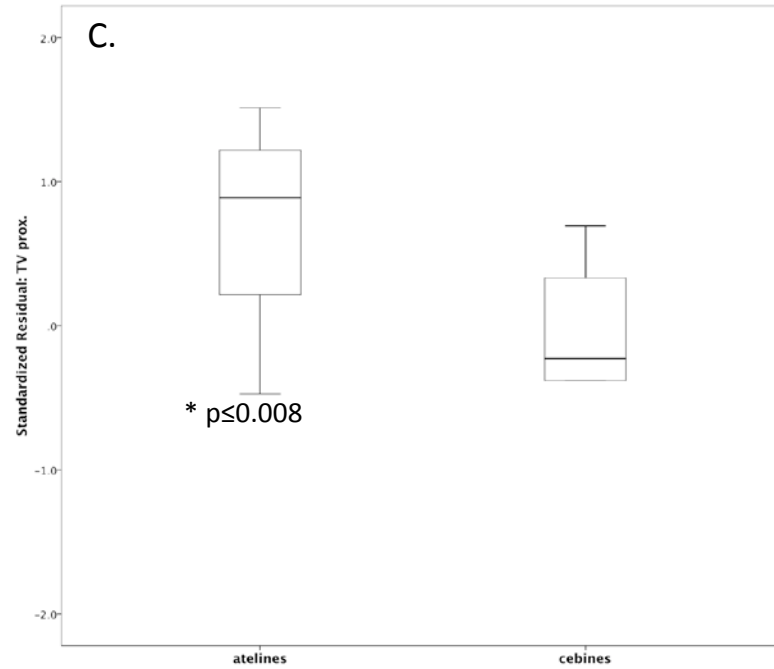
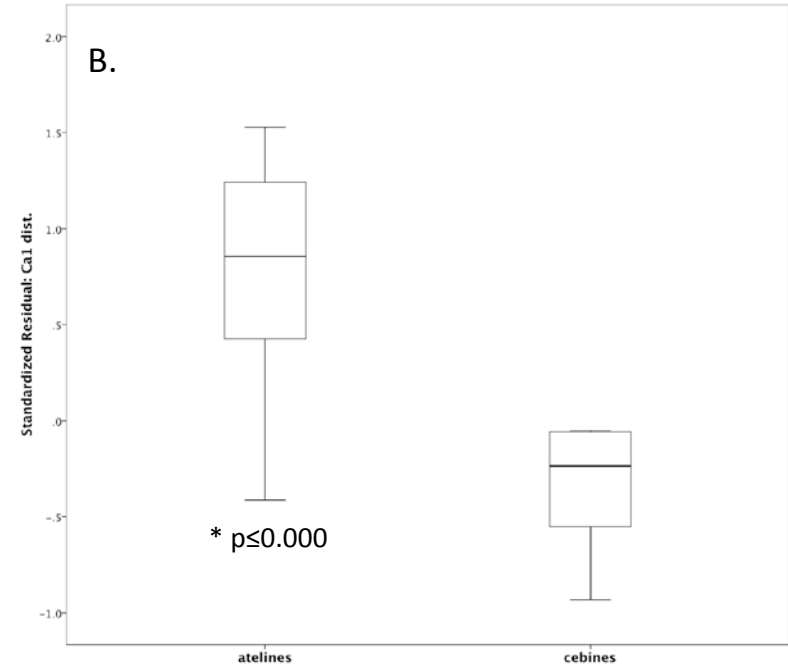
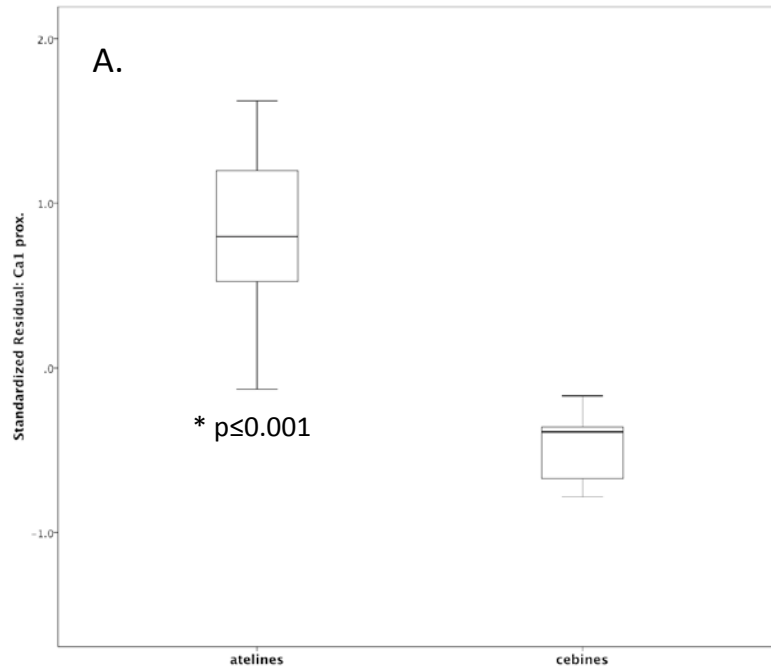


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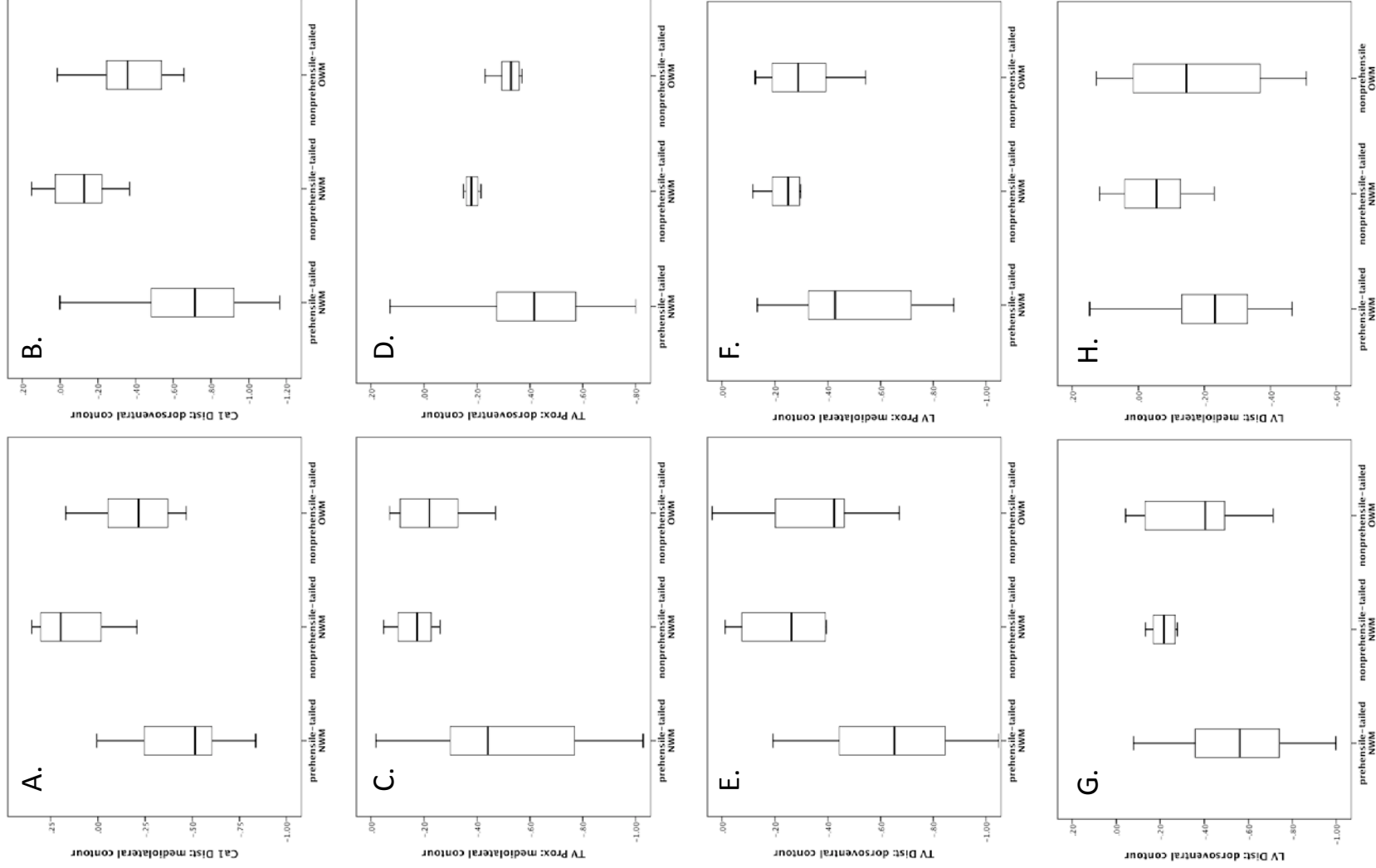




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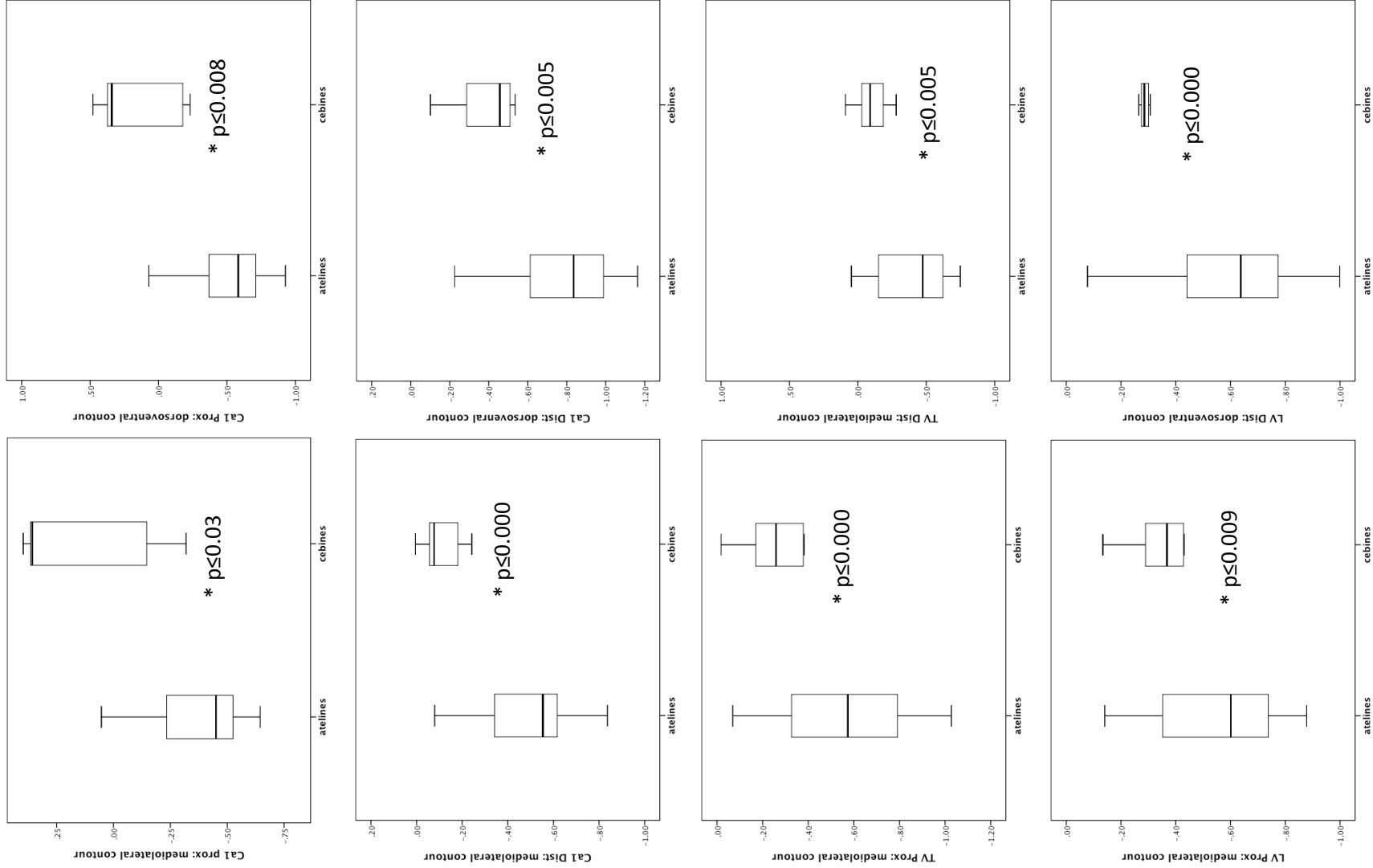


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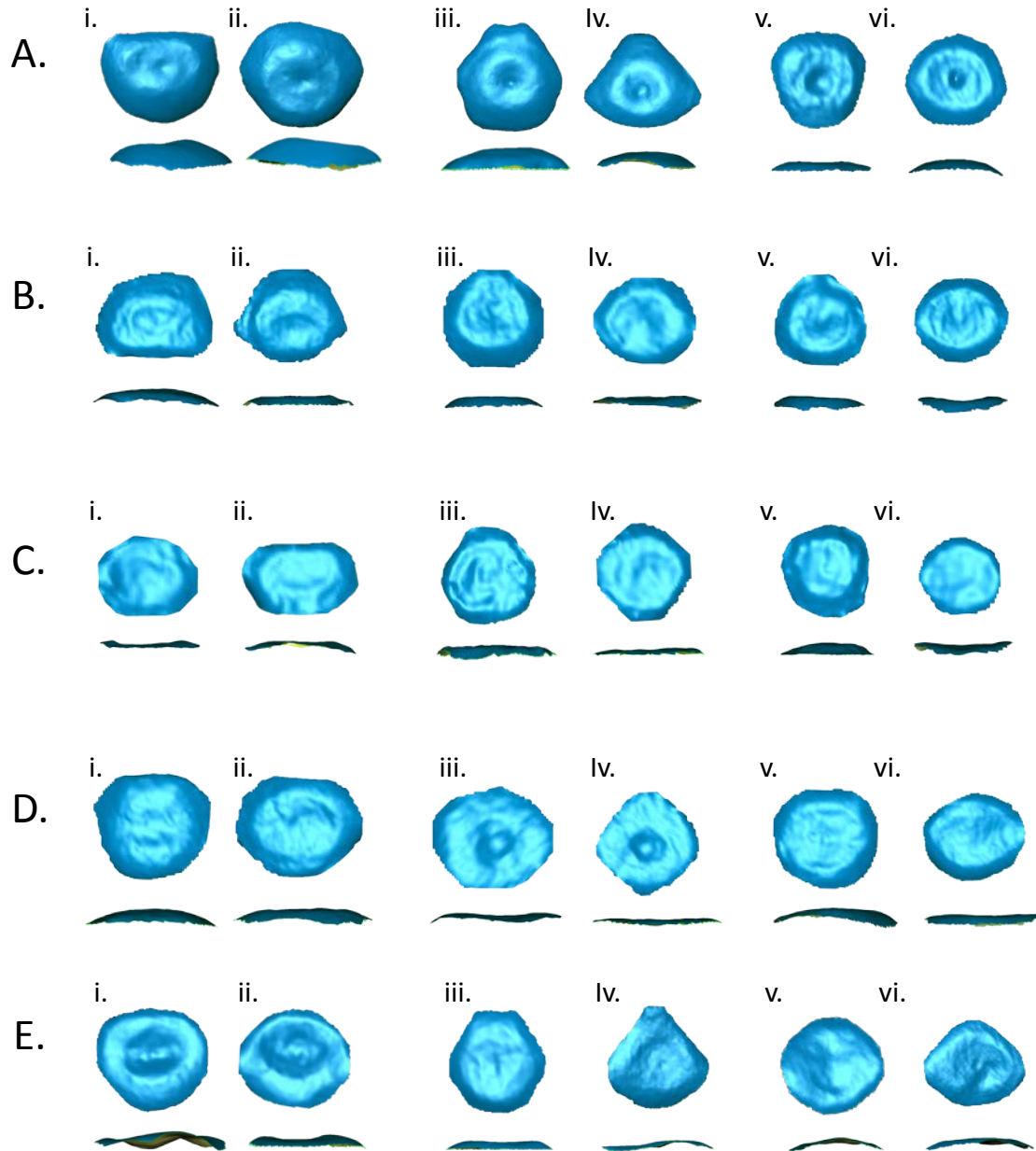


Figure 7.

