Giant pandas (*Carnivora: Ailuropoda melanoleuca*) and living hominoids converge on lumbar vertebral adaptations to orthograde trunk posture

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Keywords: Orthograde; Lumbar vertebrae; Convergent evolution; Hominoid evolution; *Ailuropoda melanoleuca*

Abstract

Living hominoids share a common body plan characterized by a gradient of derived postcranial features that distinguish them from their closest living relatives, cercopithecoid monkeys. However, the evolutionary scenario(s) that led to the derived postcranial features of hominoids are uncertain. Explanations are complicated by the fact that living hominoids vary considerably in positional behaviors, and some Miocene hominoids are morphologically, and therefore probably behaviorally, distinct from modern hominoids. Comparative studies that aim to identify morphologies associated with specific components of positional behavioral repertoires are an important avenue of research that can improve our understanding of the evolution and adaptive significance of the hominoid postcranium. Here, we employ a comparative approach to offer additional insight into the evolution of the hominoid lumbar vertebral column. Specifically, we tested whether giant pandas (Carnivora: *Ailuropoda melanoleuca*) converge with living hominoids on lumbar vertebral adaptations for the single component of their respective positional behavioral repertoire that they share—orthograde (i.e., upright) trunk posture. We compare lumbar vertebral morphologies of *Ailuropoda* to those of other living ursids and caniform outgroups (northern raccoons and gray wolves). Mirroring known differences between living hominoids and cercopithecoids, *Ailuropoda* generally exhibits fewer, craniocaudally shorter lumbar vertebral bodies with more dorsally positioned transverse processes that are more dorsally oriented and laterally directed, and taller, more caudally directed spinous processes than other caniforms in the sample. Our comparative evidence lends support to a potential evolutionary scenario in which the acquisition of hominoid-like lumbar vertebral morphologies may have evolved for generalized orthograde behaviors and could have been exapted for

suspensory behavior in crown hominoids and for other locomotor specializations (e.g., brachiation) in extant lineages.

Introduction

Differences in lumbar vertebral morphology between living hominoids and their closest living relatives, cercopithecoid monkeys, are well documented and presumably reflect an evolutionary divergence in the positional behaviors emphasized by these two clades (Keith, 1923; Schultz, 1938, 1961; Benton, 1967; Clauser, 1980; Ward, 1991, 1993; Shapiro, 1993; Sanders and Bodenbender, 1994; Russo, 2010; Williams, 2011). Cercopithecoids and most other primates have long trunks with six or seven craniocaudally tall non-rib-bearing lumbar vertebrae and nine or ten post-transitional vertebrae (Table 1; Keith, 1902; Erikson, 1963; Clauser, 1980; Pilbeam, 2004; Williams, 2012b; Williams and Russo, 2015). Their long lower backs have been argued to satisfy the demands of pronograde quadrupedalism by lengthening the distance over which sagittal plane flexion-extension can occur, thereby increasing stride length during galloping and power during leaping (Table 1; Slijper, 1946; Schultz, 1961; Erikson, 1963; Benton, 1967; Hildebrand and Goslow, 1982; Hurov, 1987). Lumbar column flexibility is further promoted by pronounced ventral keeling that provides a strong attachment surface for the anterior longitudinal ligament to resist stresses along the vertebral bodies' ventral faces, ventrally oriented (transverse plane) and cranially directed (coronal plane) transverse processes arising from the vertebral body that increase the compartment size for the erector spinae muscles and permit lateral flexibility, and narrow, cranially directed spinous processes that permit intervertebral sagittal plane flexibility and improve the mechanical advantage of longissimus for

dorsiflexion (Table 1; Mivart, 1865; Slijper, 1946; Gambaryan, 1974; Shapiro, 1993; Sanders and Bodenbender, 1994). The transversely narrow vertebral bodies and pronounced ventral keels of cercopithecoid lumbar vertebrae give their body articular surfaces a “heart-shaped” (a.k.a. cordiform) appearance (Ward, 1993; Sanders and Bodenbender, 1994; Nakatsukasa et al., 2007; Williams and Russo, 2015). Because these features characterize the lumbar vertebrae of most primate and mammalian quadrupeds, they probably represent the primitive primate and therian condition (Table 1).

By contrast, hominoids have short trunks typically comprised of five or fewer craniocaudally short lumbar vertebrae (Table 1; Keith, 1902; Schultz, 1938; Erikson, 1963; Clauser, 1980; Pilbeam, 2004; Williams, 2012b; Williams and Russo, 2015) that help stiffen the lower back by resisting columnar bending stresses, shearing, and buckling (Slijper, 1946; Clauser, 1980; Jungers, 1984; Shapiro, 1993; Ward, 1993; Sanders and Bodenbender, 1994; Lovejoy, 2005). Lumbar column rigidity is further promoted by laterally (*Hylobates*) to dorsally (*Pongo*, *Gorilla*, *Pan*, and *Homo*) oriented (transverse plane) and laterally directed (coronal plane) transverse processes arising from the pedicle-body junction (*Hylobates*) or pedicle (*Pongo*, *Gorilla*, *Pan*, and *Homo*) that maintain the line of action, and improve the leverage, of longissimus and iliocostalis when bilaterally contracted for achieving extended upright trunk postures and resisting ventral flexion (Table 1; Shapiro, 1993, 1995; Ward, 1993). Additionally, craniocaudally taller and squared-off spinous processes oriented more perpendicular to the vertebral body restrict intervertebral sagittal plane flexibility and improve the mechanical advantage of multifidus for back extension and stabilization* (Table 1; Erikson, 1963; Macintosh

* Surface area for attachment of multifidus is increased by an expanded dorsal sacral surface due to sacralization of lumbar vertebrae (Keith, 1940).

and Bogduk, 1986; Shapiro, 1993). Hominoids also lack a pronounced ventral keel that, in combination with a transversely wide articular surface, gives their vertebral bodies a “kidney-shaped” (a.k.a. reniform) appearance (Ward, 1993; Sanders and Bodenbender, 1994; Nakatsukasa et al., 2007; Williams and Russo, 2015).

Although all living hominoids share a common body plan characterized by a gradient of derived vertebral features discussed above, positional behavior type and frequency varies considerably across extant hominoid genera and even across populations within species (Thorpe and Crompton, 2006). The vertebral features characteristic of living hominoids have thus been linked by researchers to a number of behaviors, including brachiation (Erikson, 1963; Gebo, 1996), quadrumanous climbing and bridging (Cartmill and Milton, 1977; Jungers, 1984; Sarmiento, 1998), vertical climbing (Jungers, 1984; Susanna et al., 2010), arm-hanging suspension (Hunt, 1991), orthograde clambering and arboreal bipedalism (Crompton et al., 2008), generalized orthograde trunk posture (Keith, 1923; Andrews, 1976), or some combination of these positional behaviors (Tuttle, 1975; Tuttle and Basmajian, 1977; Ward, 1993). Moreover, while the ancestral crown hominoid is hypothesized by some workers to have possessed derived vertebral features as well (Keith, 1923; Harrison, 1987; Sarmiento, 1987; Benefit, 1995; MacLatchy et al., 2000, but see Lovejoy et al., 2009; Reno, 2014; Ward, 2014)[†], most known Miocene hominoids exhibit “mosaic” sets of primitive catarrhine-like and derived hominoid-like morphologies (Sanders and Bodenbender, 1994; Kelley, 1997; MacLatchy et al., 2000; Nakatsukasa, 2007, 2008, 2009; Susanna et al., 2014; Ward, 2014), obfuscating our view of

[†] Hominins retain much of this suite of traits, but have enhanced the sagittal mobility of the lower back, particularly by increasing the numerical length of the lumbar spine, probably as an adaptation to achieve effective lordosis and maintain the center of mass over a shifting pelvic platform during bipedal locomotion (Sanders, 1995, 1998).

exactly when and how the positional behaviors characteristic of living apes evolved. The sole use of living apes as models for making fine-grade functional distinctions about the postcranial morphology of extinct apes has thus proven problematic.

Comparative approaches are a demonstrably powerful means of determining the adaptive nature of specific primate morphologies (Coddington, 1994; Orr, 2005; Russo and Kirk, 2013). Previous work demonstrates that lumbar vertebral features (especially lumbar column reduction) known to promote lumbar spine stability are characteristic of some nonhominoid primates (Mivart, 1865; Schultz, 1961; Erikson, 1963; Ankel, 1967; Benton, 1967; Cartmill and Milton, 1977; Shapiro, 1991, 1995, 2007; Johnson and Shapiro, 1998; Shapiro and Simons, 2002; Shapiro et al., 2005). Much attention has been paid to the atelines, particularly *Ateles* and *Brachyteles*, which have the fewest lumbar vertebrae among nonhominoid primates and exhibit vertebral morphologies (e.g., craniocaudal vertebral body length, transverse process position, and dorsoventral orientation) broadly convergent with hylobatids (Mivart, 1865; Schultz, 1961; Erikson, 1963; Ankel, 1972; Benton, 1967; Shapiro, 1993; Johnson and Shapiro, 1998). Work by Shapiro (1995; see also Shapiro and Simons, 2002) further revealed that although orthograde vertical clinging and leaping indriids do not differ from pronograde quadrupedal *Varecia* in post-transitional vertebral numbers, indriids have craniocaudally shorter (but not mediolaterally wider) lumbar vertebral bodies that, at mid-lumbar levels, have more dorsally oriented and laterally directed transverse processes. Shapiro further demonstrated (2007; see also Shapiro and Simons, 2002) that lorises exhibit lumbar vertebrae characterized by spinous process that are shorter and more perpendicularly to caudally oriented relative to the vertebral body, as well as features that promote lateral bending. Shared reduction in lumbar column flexibility (via short lumbar regions and more perpendicularly to caudally directed spinous processes) among

hominoids, atelines, indriids, and lorises has therefore been interpreted to confer an advantage during suspension and/or, more generally, “antipronograde” postures (Shapiro, 1995; see also Shapiro and Simons, 2002; Shapiro, 2007). Some extinct subfossil lemurs (e.g., *Palaeopropithecus*) also appear to possess stability-promoting vertebral morphologies for suspensory behaviors (Shapiro et al., 2005; Granatosky et al., 2014), and inferences about both lorises and these extinct subfossil lemurs are supported by earlier work on extant sloths (Straus and Wislocki, 1932). At the same time, scaling effects are also reflected in lumbar region length, as larger-bodied cercopithecoids, subfossil lemurs, and lorises tend to have shorter lumbar vertebral bodies and/or region lengths than expected (i.e., negative allometry; Rose, 1975; Jungers, 1984; Sanders and Bodenbender, 1994; Shapiro and Simons, 2002; Shapiro et al., 2005; Shapiro, 2007), suggesting that additional bending stresses are imposed by larger body size. Other mammals that appear to converge with hominoids on some aspects of dorsostability of the lower back include perissodactyls and some artiodactyls, probably as adaptations for stiff-spined running by limiting sagittal plane bending and axial rotation movements (Slijper, 1946; Gambaryan, 1974; Townsend and Leach, 1984; Halpert et al., 1987; Boszczyk et al., 2001; Williams, 2012a).

Here, we employ a comparative approach to offer additional insight into the evolution of the hominoid lumbar vertebral column. In our view, extant ursids are an ideal group with which to independently test hypotheses about the functional significance of lumbar vertebral morphologies in hominoids. Ursids are a group of large-bodied quadrupedal caniforms that demonstrate a gradient of arboreal to terrestrial positional behaviors (see below) and evolved over a similar time scale as hominoids during the Miocene (McLellan and Reiner, 1994; Kutschera et al., 2014). Of particular interest is the giant panda (*Ailuropoda melanoleuca*:

Carnivora), which serves as an excellent model species for evaluating vertebral features associated with one central component of all ape positional behaviors—orthograde (i.e., upright) trunk posture. Although the external characteristics and positional behaviors of *Ailuropoda* (Ursidae: Ailuropodinae) broadly resemble those of its closest living relatives—ursine bears (Ursidae: Ursinae; Fig. 1)—the manner and duration of orthograde sitting postures during feeding in *Ailuropoda* is distinctive (Davis, 1964; Schaller et al., 1989). *Ailuropoda* sits in a more reclined position than ursine bears, resting the body weight on the lower back and dorsal aspect of the pelvis so that the forelimbs are completely free to manipulate and transfer bamboo directly to the mouth (Davis, 1964; Chorn and Hoffmann, 1978). Bamboo comprises over 99% of the giant panda’s diet and accordingly, feeding on bamboo to satisfy nutritional requirements demands half to three-quarters of its daily activity budget (Davis, 1964; Chorn and Hoffmann, 1978; Kleiman, 1983; Johnson et al., 1988; Schaller et al., 1989). Behavioral observations thus indicate that *Ailuropoda* spends a substantial amount of its time using orthograde trunk posture. This emphasis on prolonged orthograde posture and deliberate manual manipulation and transfer of food objects appears to distinguish the feeding behaviors of *Ailuropoda* from those of ursine bears, which do not use such stereotyped positional behaviors to feed or subdue prey (Sacco and Van Valkenburgh, 2004).

Indeed, Davis (1964) noted over half a century ago that vertebral “proportions of the giant panda are similar to those of the anthropoid apes and man...” (75), observing that the “short vertebral column give[s] a somewhat non-ursid aspect to [its] skeleton” (42). He demonstrated that the lumbar spine of *Ailuropoda* is numerically reduced, and he even described the spinous processes of *Ailuropoda* lumbar vertebrae as having greater “posterior inclination” than *Ursus sp.* (Davis 1964:77; see also Slijper, 1946). However, Davis did not quantify these

differences nor did he perceive differences in other vertebral morphologies between these taxa. Moreover, Davis (1964:85) interpreted evolutionary modifications in *Ailuropoda* lumbar vertebral number and morphology as “pseudo-adaptations” rather than direct products of natural selection for a mechanical function or positional behavior. Instead, Davis (1964) hypothesized that the likely derived trunk morphology of *Ailuropoda* resulted from a pleiotropic effect of “intense differentiation” (84) of the skull—“an accident of ontogenetic timing” (85) caused by cranial displacement of vertebral regional borders. In doing so, Davis (1964:85) quells possible adaptive significances in *Ailuropoda* for what he calls “lumbosacral peculiarities” and “unintelligible modification of the pelvis.” Yet, that *Ailuropoda* may share with hominoids not only the possession of similar numbers of lumbar vertebrae (Davis, 1964; Williams, 2011) but perhaps other vertebral morphologies (e.g., caudally directed spinous processes), suggests that the lumbar vertebral morphologies that distinguish *Ailuropoda* from ursines could reflect its use of frequent orthograde trunk postures during feeding (contra Davis, 1964). Evidence for convergence on lumbar vertebral adaptations to orthograde trunk postures would be indicated by the presence of lumbar vertebral features shared by *Ailuropoda* and living hominoids to the exclusion of closest living relatives of each, ursine bears and cercopithecoid monkeys, respectively. Therefore, we quantitatively evaluate if, in addition to having fewer lumbar vertebrae, *Ailuropoda* also exhibits craniocaudally shorter, mediolaterally wider lumbar vertebral bodies with more dorsally positioned, dorsally oriented (transverse plane), and laterally directed (coronal plane) transverse processes and caudally directed (sagittal plane) spinous processes that have craniocaudally taller apices, compared to a sample of caniforms including other ursids (American black bear, *Ursus americanus*; brown bear, *U. arctos*; Asiatic black bear, *U. thibetanus*), as well as outgroups of northern raccoons (*Procyon lotor*) and gray wolves (*Canis*

lupus).

Materials and methods

Sample composition

We collected vertebral data for the first (L1), middle (ML), and last (LL) non-rib-bearing lumbar vertebrae of 91 extant caniform individuals from *Ailuropoda*, *U. americanus*, *U. arctos*, *U. thibetanus*, *P. lotor*, and *C. lupus* (Table 2). The first lumbar vertebra was recognized by its lack of rib articulation facets. The middle lumbar vertebra was defined numerically as the midpoint in the vertebral sequence. When an even number of lumbar vertebrae was present, the more caudal vertebra was measured to ensure adequate representation of the lower back (see above). The last lumbar vertebra was the last element in the sequence.

Taxa were chosen based on their evolutionary relatedness to *Ailuropoda*, their positional behaviors, and their availability in museum collections. *Ailuropoda* is recognized as the sister group (Ailuropodinae) to the other living bears (Ursinae; Fig. 1; Fulton and Strobeck, 2006; Nyakatura and Bininda-Emonds, 2012; Kutschera et al., 2014). Within Ursinae, the closest relationships may be between *U. arctos* and polar bears (*U. maritimus*), and either between *U. americanus* and *U. thibetanus* (Nyakatura and Bininda-Emonds, 2012) or between *U. americanus* and the *U. arctos*—*U. maritimus* clade. In this latter scenario, *U. thibetanus* is the outgroup to a sun (*Helarctos malayanus*) and sloth (*Melursus ursinus*) bear clade (Kutschera et al., 2014). *Ursus americanus* (females: 90–140 kg; males: 115–270 kg), and to a lesser extent *U. thibetanus* (females: 65–90 kg; males: 110–150 kg), are particularly useful taxa for comparison

because they are close in body size to *Ailuropoda* (75–160 kg; Davis, 1964; Nowak, 1999). Both *U. americanus* and *U. thibetanus* are scansorial (Van Valkenburgh, 1987), whereas climbing behaviors are infrequent among adult *Ailuropoda* (Kleiman, 1983). *Ursus arctos* is the largest-bodied (95 kg [females]–780 kg [Alaskan males]; Nowak, 1999) and the most terrestrial (Van Valkenburgh, 1987) ursid in the sample. As such, our ursid sample includes taxa representative of a broad range of body sizes and substrate preferences. Polar bears were excluded from the sample because of their marine lifestyle (DeMaster and Stirling, 1981), and sun, sloth, and spectacled (*Tremarctos ornatus*) bears were excluded because of inadequate sample sizes (but see Discussion and Fig. 9 for *Tremarctos*).

Procyon lotor and *C. lupus* were chosen as outgroup taxa for comparison with *Ailuropoda* and ursines. *Procyon lotor* (Procyonidae) belongs to the superfamily Musteloidea, which along with Ursidae (and Pinnipedia) form the Arctoidea infraorder (Fig. 1; Fulton and Strobeck, 2006; Finarelli, 2008). *Procyon lotor* is the smallest-bodied taxon in the sample, but is the largest-bodied procyonid (2–12 kg; Lotze and Anderson, 1979; Nowak, 1999) and is an excellent representative of a generalized scansorial/arboreal quadrupedal carnivoran (Van Valkenburgh, 1987; McClearn, 1992). Like *Ailuropoda*, *P. lotor* is one of the few caniforms that primarily use an ambulatory walking gait (Taylor, 1989). *Canis lupus* is a terrestrial quadruped (Van Valkenburgh, 1987; Nowak, 1999) and belongs to the family Canidae, which is an outgroup to the Arctoidea and together form Caniformia (Fulton and Strobeck, 2006; Finarelli, 2008). *Canis lupus* is the most cursorial taxon in our sample. Unlike *P. lotor* and ursids, *C. lupus* frequently uses trotting and galloping gaits to cover long distances, relying on both speed (up to 55–70 km/hr; covering up to 5 meters per galloping stride) and stamina (maintains rapid pursuit for >20 minutes) to overhaul prey (Taylor, 1989; Nowak, 1999). Therefore, we predict that *C.*

lupus will exhibit the greatest number of craniocaudally taller, mediolaterally narrower, lumbar vertebral bodies bearing more cranially directed (coronal plane) and ventrally oriented (transverse plane) transverse processes arising from the vertebral body, and narrower, more cranially directed spinous processes compared to all other taxa. Members of *Ursus*, and *P. lotor*, are expected to exhibit morphology intermediate between *Ailuropoda* and *C. lupus*.

It is worth noting that the taxa chosen here as outgroup representatives of arboreal and terrestrial caniforms differ from those chosen by Davis (1964), who sampled *Potos flavus* (kinkajous) and *Gulo gulo* (wolverines). We did not use kinkajous for our arboreal representative because the lower lumbar vertebral morphology of kinkajous may be influenced by its considerable vertebral flexibility and the possession of a prehensile tail having well-developed musculature originating from the lumbar region that facilitates feeding in terminal branches (McClern, 1992). Though the lesser or red panda (*Ailurus fogens*, Ailuridae) would also have been an appropriate taxon for comparison, particularly given its historical taxonomic affiliation with *Ailuropoda* (Chorn and Hoffmann, 1978; Mayr, 1985), the vertebrae of the few specimens available in museum collections are mostly articulated and therefore cannot be individually measured. We did not use wolverines for our terrestrial representative because wolverines (like some badgers and skunks) are specialized diggers (Nowak, 1999), and like *A. fogens*, the vertebral columns of the few specimens available in museum collections are mostly articulated. Both gray wolves and northern raccoons are well represented in museum collections and the preservation of their vertebral remains is more amenable to data collection (i.e., disarticulated, non-ligamentous), allowing for comparable sample sizes for outgroups.

Although we endeavored to sample only wild-captured individuals, some individuals from “unknown” or “zoo” localities were included in the sample because of the limited

availability of caniform museum specimens (Table 2). A two-sample *t*-test of mean PC1 scores between the wild-caught and captive individuals was carried out for *C. lupus*, *U. americanus*, and *U. arctos* (the three species with samples most evenly split between wild-caught and captive individuals) to test for possible differences in overall vertebral morphology. For both *C. lupus* and *U. americanus*, the two mean PC1 score subsamples were statistically similar at all vertebral levels (*C. lupus*: L1 $p = 0.501$, ML $p = 0.855$, LL $p = 0.247$; *U. americanus*: L1 $p = 0.640$, ML $p = 0.950$, LL $p = 0.219$). For *U. arctos*, the two subsamples were statistically similar at the L1 ($p = 0.888$) and LL ($p = 0.5645$) levels, but the captive population had significantly higher PC1 mean scores at the level of the ML vertebra ($p = 0.010$). Because these differences were significant only at the ML vertebral level, and because between-group differences in PC1 species mean scores are greater than within-group differences at this vertebral level (see Results), we opted to keep these captive individuals in the sample rather than remove them from all analyses at all three vertebral levels, which would have drastically reduced the sample size. Therefore, captive and wild-caught individuals were pooled for analyses.

Vertebral numbers

We collected data on presacral vertebral numbers for all caniforms in the sample. These data were combined with additional caniform individuals collected during a previous study (Williams, 2011). Additionally, we compared full sets of vertebral formulae of caniforms with published sets of hominoid vertebral formulae (Williams, 2011, 2012b; Russo and Williams, 2015) using interspecific similarity indices that calculate the ratio of frequencies of shared vertebral formulae between two species to total variation within the two species (Pilbeam, 2004;

Williams, 2012b). Following Pilbeam (2004) and Williams (2012b), interspecific similarity in vertebral formulae was quantified by calculating similarity indices between taxa following:

$$\sum \square_{ij} \square_{ij} / (\sum \square_{ij}^2 \sum \square_{ij}^2)^{1/2} ,$$

that measures the frequency of observing shared formulae relative to the total variation in vertebral formulae between the two species and varies from 0 to 1, with 0 indicating no similarity in vertebral formulae and 1 indicating total similarity in vertebral formulae.

Vertebral morphometrics

Measurements are illustrated in Figure 2 and were collected using both digital calipers (recorded to the nearest 0.01 mm) and photographs of vertebrae in dorsal, cranial, and lateral views taken using a Panasonic Lumix DMC-G2 digital camera secured to a professional copy stand. Vertebrae were photographed according to following orientation guidelines to ensure consistency: in dorsal and lateral views, the cranial articular surface of each specimen was positioned perpendicular to the camera lens; in cranial views, the cranial articular surface of each specimen was positioned upright and thus parallel with the camera lens. These guidelines have been employed for orienting mammal vertebrae in previous studies (Russo, 2015). The vertebral variables (shape indices and angles) calculated for the study are described below.

Vertebral body shape (VBS) This is a shape ratio of craniocaudal length (averaged from ventral [measurement 1] and dorsal [measurement 2] dimensions) to mediolateral width (measurement 3) of the vertebral body (Fig. 2; see also Sanders and Bodenbender [1994] for a similar calculation). A value greater than one indicates that the vertebral body is craniocaudally taller

than it is mediolaterally wide; a value equal to one indicates that the vertebral body is as craniocaudally tall as it is mediolaterally wide and a value less than one indicates that the vertebral body is craniocaudally shorter than it is mediolaterally wide. Measurements 1, 2, and 3 for calculating VBS were directly obtained from specimens using calipers.

Transverse process position (TPP) This is the distance from the ventral most point of the cranial articular surface to a chord connecting the roots of the transverse processes (measurement 4), divided by the dorsoventral breadth of the cranial articular surface in the transverse plane (measurement 5; Fig. 2). A value less than one indicates that the transverse processes arise ventral to the dorsal edge of the body's cranial articular surface (i.e., arise from the vertebral body), a value equal to one indicates that the transverse processes are located roughly in the same plane as the dorsal most edge of the vertebral body (i.e., body-pedicle junction), and a value greater than one indicates that the transverse processes arise dorsal to the dorsal most edge of the vertebral body (i.e., pedicle). Measurement 4 was taken from photographs of vertebrae in cranial view and measurement 5 was directly obtained from specimens using calipers.

Transverse process dorsoventral orientation (TPDV) This is the angle between a line that connects the lateral most point on the transverse process apex and the midpoint (dorsoventrally) of the transverse process root, and a line through the midsagittal plane in cranial view (measurement 6; Fig. 2). An angle less than 90° indicates that the transverse process is ventrally oriented, a 90° angle indicates that the transverse process is perpendicular to the midsagittal plane, and an angle greater than 90° indicates that the transverse process is dorsally oriented. TPDV was measured from photographs of vertebrae in cranial view.

Transverse process craniocaudal angle (TPCC) This is the angle between the cranial edge of the transverse process and a line drawn through the midsagittal plane in coronal view (measurement 7; Fig. 2). An angle less than 90° indicates that the transverse process is cranially directed, a 90° angle indicates that the transverse process is directed perpendicular to the midsagittal plane (i.e., laterally directed), and an angle greater than 90° indicates that the transverse process is caudally directed. For some *P. lotor* individuals, this measurement was collected from lumbar vertebrae photographed in ventral view because the prezygapophyses obscured the transverse processes in dorsal view. TPCC was obtained from photographs of vertebrae in dorsal view.

Spinous process craniocaudal angle (SPCC) This is the angle between the cranial edge of the spinous process and a line that connects the dorsal most points on the cranial and caudal articular surfaces of the vertebral body in lateral view (measurement 8; Fig. 2). An angle less than 90° indicates that the spinous process is cranially directed relative to the dorsal surface of the vertebral body, a 90° angle indicates that the spinous process is perpendicular to the dorsal surface of the vertebral body, and an angle greater than 90° indicates that the spinous process is caudally directed relative to the dorsal surface of the vertebral body. SPCC was obtained from photographs of vertebrae in lateral view.

Spinous process craniocaudal height (SPH) We evaluated spinous process craniocaudal height in an attempt to quantitatively distinguish between “broad interlocking” (Erikson, 1963:153) spinous processes and narrower spinous processes. This is the craniocaudal height of the spinous process (measured on the cranial edge at mid-length [i.e., from dorsal edge of the vertebral canal

to the spinous process apex] perpendicular to the long axis of the body; measurement 9) relative to the dorsal height of the vertebral body (measurement 2; Fig. 2). A value greater than one indicates that the spinous process is craniocaudally taller than the dorsal height of the vertebral body, a value of one indicates that the craniocaudal height of the spinous process and that of the dorsal surface of the vertebral body are equal, and a value less than one indicates that the craniocaudal height of the spinous process is less than that of the dorsal surface of the vertebral body. Measurements 2 and 9 for calculating SPH were obtained directly on the specimen using calipers.

Statistical analyses

Differences among species mean ranks for individual vertebral variables were quantified using Kruskal-Wallis tests, followed by Mann-Whitney U-tests pairwise comparisons where H-statistics were significant. Pairwise comparisons were one-tailed because we had directional predictions of how more orthograde giant pandas should differ from the more pronograde caniform species for all variables. Univariate analyses were performed using JMP 11.2.0 (SAS Institute). Variables with significant H-statistics were included in a principal components analysis to determine if composite scores characterizing the total suite of vertebral morphological features could distinguish among taxa. We then examined species mean PC1 score differences by conducting a one-way analysis of variance (ANOVA). Significant F-statistics were followed by Games-Howell (1976) pairwise comparisons.

We did not employ phylogenetically informed statistical methods. Comparative samples comprised of less than 30 species lack the power to detect a phylogenetic signal (Freckleton et

al., 2002), suggesting the use of phylogenetic methods would be inappropriate for our sample of just six caniform species. Further, the phylogenetic relationships of some ursid taxa in our sample are unresolved. For example, although previous workers have assumed a *U. americanus*-*U. thibetanus* “black bear” clade (Nyakatura and Bininda-Emonds, 2012), recent studies support other relationships among ursids, including an *U. americanus*-*U. arctos*-*U. maritimus* clade to the exclusion of *U. thibetanus*, which is instead grouped with *H. malayanus* and *M. ursinus* (Kutschera et al., 2014), and the positioning of *U. thibetanus* as the basal ursine, with *H. malayanus* and *U. americanus* as sister taxa (Gutiérrez and Pine, 2015).

Results

Vertebral numbers

Ailuropoda exhibits the fewest (4.58) and *C. lupus* the greatest (7.03) number of lumbar vertebrae in the sample, with *P. lotor* (5.85) and *Ursus* species (inter-species average 5.84) exhibiting intermediate numbers of lumbar vertebrae (Table 3). *Ailuropoda* exhibits at least two fewer post-transitional vertebrae (i.e., vertebrae caudal to the vertebra with coronally oriented prezygapophyses and sagittally oriented postzygapophyses) than all *Ursus* species and *P. lotor*, and at least three fewer post-transitional vertebrae than *C. lupus* (Table 3). More broadly, *Ailuropoda* has shortened the entire thoracolumbar column by at least two elements, typically exhibiting 18 thoracolumbar vertebrae, compared to all other carnivorans, which possess 20 modally (Narita and Kuratani, 2005; Williams, 2011).

Ailuropoda vertebral formulae share no similarity with other caniforms (i.e., produces similarity indices of zero), but exhibit some degree of similarity with hominoids (similarity indices range from 0.006 to 0.604; Table 4). In fact, *Ailuropoda* and *Hylobates syndactylus* (siamang) produce a higher similarity index than do many intra-hominoid comparisons (only *Pan-Gorilla* is higher), including that of the two hylobatid species analyzed here (*H. lar* and *H. syndactylus*; Table 4).

Vertebral morphometrics

Vertebral body shape (VBS) Species comparisons of VBS are presented in Figure 3 and Table 5. As predicted, *Ailuropoda* has significantly lower VBS values than *C. lupus* or *P. lotor* at all three vertebral levels. *Ailuropoda* also has significantly lower VBS values than *U. americanus* and *U. thibetanus* at all three vertebral levels. However, contrary to predictions, *Ailuropoda* and *U. arctos* are statistically similar across all vertebral levels. Differences between *Ailuropoda*, and *U. americanus* and *U. thibetanus*, in vertebral body shape are driven primarily by changes in the craniocaudal length of the vertebral body, rather than an expansion of the articular surface mediolateral diameter (or total area; Fig. 3; see also Supplementary Online Material [SOM] 1). Figure 3 (right column) shows a natural logarithmic bivariate plot of (from top to bottom) mediolateral width of the cranial articular surface, vertebral body craniocaudal height, and cranial articular surface area, against the geometric mean of postcranial body joint surface area (i.e., body size) at the level of the ML, which is the vertebral level with the greatest inter-group differences. All *Ailuropoda* and some *U. arctos* individuals exhibit craniocaudally shorter vertebrae than the sample predicted for their body size. All *C. lupus* and most *U. americanus* and

U. thibetanus specimens exhibit craniocaudally more elongate vertebrae than the sample predicted for their body size.

Transverse Process Position (TPP) Species comparisons of TPP are presented in Figure 4a and Table 6. As predicted, *Ailuropoda* has significantly higher TPP values, and thus more dorsally positioned transverse processes, than all taxa at the L1 and ML vertebral levels. At the level of the LL, *U. thibetanus*, *C. lupus*, and *P. lotor* have significantly higher TPP values, and thus more dorsally positioned transverse processes, than *U. americanus* and *U. arctos*. *Ursus thibetanus* and *Ailuropoda* are statistically similar at the LL vertebral level.

Transverse Process Dorsoventral Angle (TPDV) Species comparisons of transverse process position are presented in Figure 4b and Table 7. As predicted, *Ailuropoda* has significantly larger TPDV angles, and thus the most dorsally oriented transverse processes, than all other taxa at all three vertebral levels. Also as predicted, *C. lupus* has significantly smaller TPDV angles, and thus the most ventrally oriented transverse processes, than all other taxa at all three vertebral levels. Values for the *Ursus* species are intermediate to *Ailuropoda* and *C. lupus*. *Procyon lotor* has significantly smaller TPDV angles than all ursids, with the exception of *U. americanus* at the ML and LL vertebral levels.

Transverse Process Craniocaudal Angle (TPCC) Species comparisons of TPCC are presented in Figure 4c and Table 8. As predicted, *Ailuropoda* has significantly larger TPCC angles, and thus more laterally directed (caudally directed at the L1 level) transverse processes, than all other taxa at the L1 and LL vertebral levels. However, at the ML vertebral level, *Ailuropoda* and *U. arctos* are not statistically different. Also consistent with predictions, *C. lupus* has significantly smaller

TPCC angles, and thus has more cranially directed transverse processes, than all other taxa at all three vertebral levels. The three *Ursus* species are not statistically different from one another at the L1 and LL vertebral levels, but *U. arctos* differs significantly from *U. thibetanus* and *U. americanus* at the ML level.

Spinous Process Craniocaudal Angle (SPCC) Species comparisons of SPCC are presented in Figure 5a and Table 9. As predicted, *Ailuropoda* has significantly larger SPCC angles, and thus has more caudally directed spinous processes, than all other taxa at all three vertebral levels. As predicted, *C. lupus* has significantly smaller SPCC angles, and thus has more cranially directed spinous processes, than all ursids at all three vertebral levels, with the exception of *U. thibetanus* at the LL. *Procyon lotor* has significantly smaller SPCC angles than all ursids at all vertebral levels and *C. lupus* at the L1 vertebral level. At the LL vertebral level, values for SPCC angle are not statistically different between *C. lupus* and *P. lotor*.

Spinous Process Height (SPH) Species comparisons of SPH are presented in Figure 5b and Table 10. *Ailuropoda* has significantly higher values, and thus craniocaudally taller, spinous processes than *U. americanus*, *C. lupus*, and *P. lotor* at all three vertebral levels, but does not differ significantly from *U. arctos* at the L1 and ML levels or from *U. thibetanus* at any vertebral level. *Procyon lotor* has significantly lower values, and thus craniocaudally narrower spinous processes, than all ursids at all vertebral levels. *Canis lupus* also has significantly lower values than the ursids at all three vertebral levels, with the exception of *U. americanus* at the level of the LL.

Principal Components Analysis Table 11 and Figure 6 present the results of the principal components analysis. Table 12 and Figure 7 present the results of the comparisons among species mean PC1 scores. At all vertebral levels, the greatest differences in lumbar vertebral morphology is between *Ailuropoda*, and *P. lotor* and *C. lupus*, the taxa occupying the most positive and the most negative PC1 scores, respectively, along the major axis of variation (accounting for approximately 66% [L1], 67% [ML], and 58% [LL] of the variance; Fig. 6, Table 11). All three *Ursus* species generally occupy an intermediate position between *Ailuropoda*, and *C. lupus* and *P. lotor*, in the shape space. The positive end of the shape space is associated with vertebrae having more dorsally positioned and oriented (in the transverse plane) transverse processes that are more laterally directed (in the coronal plane), and taller spinous processes that are more caudally directed, in contrast to the negative end of the shape space which is associated with vertebrae having more ventrally positioned and oriented (in the transverse plane) and cranially directed (in the coronal plane) transverse processes, and narrower spinous processes (L1 and LL levels) that are directed more cranially (Table 11 and Fig. 7). PC1 likely represents vertebral shape more so than it does body size as regressions of species mean PC1 scores on the geometric mean of postcranial articular surface joints indicate that only 2.3% (L1), 6.2% (ML), and 2.1% (LL) of the sample variance was accounted for by allometric effects. Figures 6 and 7, which show that the largest-bodied ursid in the sample, *U. arctos*, has PC1 scores that are intermediate between two smaller-bodied ursids, *U. americanus* and *Ailuropoda*, further illustrate this point.

Ailuropoda has significantly higher mean PC1 scores than all other taxa at all three vertebral levels ($p < 0.050$), with the exception of *U. thibetanus* at the LL vertebral level ($p = 0.128$; Table 12, Fig. 7); however, it is likely that the lack of statistical significance for this pair-

wise comparison is due to the small sample size of *U. thibetanus* for the PCA analysis ($N = 4$) and one individual that overlaps with *Ailuropoda* (Fig. 6). The small sample size for *U. thibetanus* in the PCA reflects the variable preservation of vertebral specimens in museum collections. Because PC scores were derived from all lumbar vertebral measurements, an entire vertebra was necessarily excluded from analysis if any measurement could not be collected (e.g., vertebrae were articulated or damaged). Only in the case of *U. thibetanus* (where total number of available skeletons was the primary limiting factor) was this reality of vertebral data collection an issue for analysis. *Canis lupus* exhibits significantly lower mean PC1 scores than all other taxa at all three vertebral levels, with the exception of *P. lotor* at the LL vertebral level ($p = 0.442$). *Ursus arctos* and *U. thibetanus* are not statistically different at any vertebral level (L1, $p = 0.916$; ML, $p = 0.599$; LL, $p = 0.872$). *Ursus americanus* is not statistically different from *U. thibetanus* at the L1 ($p = 0.119$) or ML ($p = 0.990$) vertebral levels, but is statistically different from *U. arctos* at all vertebral levels ($p < 0.050$).

Discussion and conclusion

This study evaluated if giant pandas (*Ailuropoda melanoleuca*) converge with hominoid primates on adaptations to orthograde (i.e., upright) trunk posture by determining if the suite of features characteristic of living hominoid lumbar vertebrae is also characteristic of *Ailuropoda* lumbar vertebrae to the exclusion of their closest living relatives—ursine bears. Mirroring the differences between living hominoids and cercopithecoids (Table 1; Figs. 7 and 8), *Ailuropoda* generally exhibits fewer, shorter (except compared to *U. arctos*) lumbar vertebral bodies with more dorsally positioned transverse processes that are more laterally directed (coronal plane) and

dorsally oriented (transverse plane), and taller, more caudally directed spinous processes than other caniforms in our sample, including *Ursus*. *Ailuropoda* also shares with hominoids more reniform vertebral body shapes and a lack of pronounced sagittal keeling compared to *Ursus* and cercopithecoids, which both exhibit more cordiform vertebral body shapes and exhibit sagittal keeling (Fig. 8). Unlike between living hominoids and cercopithecoids, *Ailuropoda* does not appear to be distinguished from other ursids by vertebral body mediolateral width at similar vertebral levels. Rather, vertebral body shape differences in the sample appear to be driven primarily by changes in vertebral body craniocaudal length (Fig. 3, SOM1; see also Johnson and Shapiro, 1998). Mediolateral width (as well as surface area) of the lumbar vertebral body cranial articular surface also does not distinguish between orthograde vertical clinging and leaping indriids and pronograde quadrupedal *Varecia* (Shapiro, 1995) or orthograde suspensory atelines and pronograde quadrupedal ceboids (Johnson and Shapiro, 1998). Because expanded transverse body dimensions serve to resist coronal plane bending, it is possible that the mediolaterally wider (compared to cercopithecoids) vertebral bodies characteristic of nonhuman hominoids[‡] specifically relate to increased resistance of horizontal (i.e., transverse) plane bending moments during forelimb suspension.

In primates, scaling effects are reflected in overall lumbar length, as larger-bodied cercopithecoids, subfossil lemurs, and lorises tend to have shorter lumbar vertebral bodies and/or region lengths (i.e., negative allometry), suggesting that additional bending stresses are imposed by larger size (Jungers, 1984; Sanders and Bodenbender, 1994; Shapiro and Simons, 2002; Shapiro et al., 2005; Shapiro, 2007). In our caniform sample, only *Ailuropoda* is characterized by

[‡] In humans, mediolateral body width (Rose, 1975) and surface area (Shapiro, 1991; Saunders, 1998) is immense compared to other hominoids and relates to the increased axial compressive loads sustained during habitual bipedalism.

a dramatic reduction in lumbar and post-transitional vertebral numbers (Tables 1 and 3). In fact, *U. arctos*, the largest-bodied ursid in the sample (95 kg [females]–780 kg [Alaskan males]), exhibits similar lumbar vertebral numbers as the smaller-bodied ursids (*Ursus americanus* females: 90–140 kg and males: 115–270 kg; *U. thibetanus* females: 65–90 kg and males: 110–150 kg) and *Procyon lotor* (92–12 kg). However, lumbar reduction is a product of both decreased numbers of lumbar vertebrae and decreased craniocaudal vertebral body height. As *U. arctos* does not differ from *Ailuropoda* in craniocaudal vertebral body length (Table 5, Fig. 3), and the other ursids generally have shorter vertebral bodies than *P. lotor* or *C. lupus*, the craniocaudal short vertebral bodies could be inferred to relate to the larger body sizes of the ursids compared to the other caniforms sampled. Nonetheless, an estimate of the total “length” of the lumbar region that takes into account both vertebral numbers and craniocaudal vertebral body length (calculated following Johnson and Shapiro [1998] and Shapiro and Simons [2002][§]) reveals that *Ailuropoda* possesses the shortest overall lumbar spine in the ursid sample (Table 3). This point reinforces that although ursids generally have shorter lumbar regions and larger body sizes than the other caniforms in the sample (Table 3), spinal reduction in *Ailuropoda* does not appear to be driven by body size.

The hypothesis that the dorsal position and orientation (in the transverse plane) of the transverse processes might reflect an increased abdominal girth associated with a lengthened gut, as has been suggested for large-bodied bovids (Halpert et al., 1987), sloths, and the extinct subfossil lemur *Palaeopropithecus* (Shapiro et al., 2005), should be considered for *Ailuropoda*, given its almost entirely herbaceous diet of bamboo. However, *Ailuropoda* does not have a

[§] Calculated by multiplying mean relative (to our body size proxy) lumbar vertebral body length by the mean number of lumbar vertebrae for each species

lengthened gastrointestinal tract relative to other carnivores; it exhibits a simple (i.e., not sacculated) stomach and colon, does not possess a caecum, does not rely on hindgut fermentation, and has not evolved a specialized (relative to other ursids) gut microbiota compatible with its herbaceous diet (Davis, 1964; Chorn and Hoffmann, 1978; Dierenfeld et al., 1982; Mainka et al., 1989; Xue et al., 2015). Lacking such modification of the digestive system, *Ailuropoda* exhibits anatomical adaptations to its highly specialized feeding ecology primarily in the hand (e.g., elongated radial sesamoid bone) and skull (e.g., enlarged jaw musculature and molar occlusal surface area). These anatomies are related to plant manipulation and effective mastication and are not characteristic of ursines (Lankester, 1901; Davis, 1964; Dierenfeld et al., 1982; Schaller et al., 1989; Endo et al., 1999). Taken together, in our view, the data presented in this study demonstrate that the features characteristic of the lumbar vertebral column of *Ailuropoda* are probably best identified as adaptations to its prolonged orthograde posture during the deliberate manual manipulation of bamboo (contra Davis, 1964).

Even so, given its basal phylogenetic position relative to living ursids, that *Ailuropoda* might represent the primitive condition for vertebral numbers and morphology in ursids must also be considered. Yet, a scenario in which ursines underwent evolutionary reversals by increasing numbers of lumbar vertebrae to obtain the primitive caniform condition is less parsimonious than one in which *Ailuropoda* is derived in reduced thoracolumbar numbers. Additionally, the most basal extant ursine, *Tremarctos ornatus* (spectacled bear), probably presents the most primitive vertebral morphology in ursids, possessing a long lumbar column (13 thoracic and 7 lumbar vertebrae) similar to many carnivorans, in addition to a more primitive appearance of the lumbar vertebrae (Figure 9; Kurtén, 1966). Unfortunately, the rarity of *Tremarctos* skeletons amenable to measurement (i.e., disarticulated, non-pathological) in

museum collections precluded our ability to include it in this study. However, Figure 9 shows a lateral view of *Ailuropoda* and *Tremarctos* lumbar spines and skeletons to permit a visual comparison of their morphologies (see also plate 13 in Kurtén [1966] for an articulated *Tremarctos*). Compared to *Ailuropoda*, *Tremarctos* exhibits more ventrally (transverse plane) and more cranially (coronal plane) directed transverse processes positioned ventrally on craniocaudally longer vertebral bodies, and cranially directed spinous processes. Giant pandas are thus derived relative to ursines in these vertebral morphologies, reduced numbers of lumbar vertebrae, and total thoracolumbar vertebrae (Table 1, Fig. 9), lending further support to the hypothesis that *Ailuropoda* skeletal morphology is evolutionarily derived and adapted for orthograde posture.

What we identify as orthograde adaptations may be evident elsewhere in the *Ailuropoda* skeleton. The articulated pelvis of *Ailuropoda* reveals more coronally flared iliac blades compared to ursines (Fig. 10), and Davis (1964) observed that the manubria of *Ailuropoda* are considerably wider than those of *Ursus* and other carnivores. In hominoids, the iliac blades are more coronally flared than in cercopithecoids, mirroring the shape of the hominoid rib cage, which is mediolaterally broader and dorsoventrally narrower than the rib cages of most cercopithecoids and achieved by increased rib curvature and transversely broadened manubria. The aligned dorsal surfaces of the ribcage and pelvis serve to position the large, superficial back muscles (e.g., trapezius and latissimus dorsi) in a coronal plane to facilitate forelimb dominated arboreal positional behaviors (Keith, 1923; Ward, 1993). The coronally flared iliac blades of hominoids also anchor muscles that bilaterally contract to maintain an erect trunk in upright posture (e.g., erector spinae, quadratus lumborum) and support the pelvis and lower limbs during suspensory behavior (e.g., gluteus medius, iliacus; Waterman, 1929; Ward, 1993). Though

outside the scope of the current study, the presence of similar features in *Ailuropoda* may reflect reorganization to facilitate upright posture during feeding. Moreover, the anchoring of extensor back muscles (e.g., erector spinae) is achieved in *Ailuropoda* by dorsally positioned and oriented transverse processes combined with strong styloid processes (Fig. 8), giving rise to a distinct morphology not seen in hominoids. Ribs with necks that are nearly twice the diameter as those of *Ursus* (Davis, 1964) may also contribute to a stable lumbar spine needed to maintain upright posture during feeding. In sum, we propose that the “ape-like” features of the *Ailuropoda* trunk evolved to support the unique orthograde sitting posture of giant pandas.

Implication for hominoid evolution

Keith (1923) identified generalized orthograde as the most significant behavioral distinction between hominoids and cercopithecoids, whereas Morton (1926) and Gregory (1928) specifically favored brachiation locomotor behaviors. This so called ‘orthodox brachiationist’ model (e.g., Gregory, 1949; Avis, 1962) found further support from the study of atelines, which converge on some aspects of the ape-like body plan and use overhead suspensory locomotion including brachiation (albeit with the assistance of long prehensile tails; Erikson, 1963). Cartmill and Milton (1977) observed that lorises possess ape-like features of the wrist that are absent in atelines and proposed that an evolutionary history of cautious quadrupedal climbing and bridging behavior, in addition to brachiation, explains the hominoid body plan. Following on advances in field studies of primate positional behavior and experimental techniques that improved our biomechanical understanding of locomotion, Fleagle et al. (1981:361) proposed that vertical climbing could explain “as well or better” many aspects of forelimb anatomy traditionally linked

to brachiation (Cartmill and Milton, 1977; Jungers, 1984; Sarmiento, 1998). Jungers (1984) proposed that hylobatids and hominids evolved similar body plans for different locomotor reasons, the former for bridging behaviors and the latter for vertical climbing. Andrews (1976) invoked generalized orthograde trunk posture, whereas others have preferred arm-hanging suspension (Hunt, 1991) or possibly a combination of orthograde clambering and arboreal bipedality (Crompton et al., 2008). Recently, studies of the Miocene hominid *Pierolapithecus catalaunicus* (Moyà-Solà et al., 2004) led Moyà-Solà and colleagues (Almécija et al., 2009; Susanna et al., 2010) to formalize a hypothesis that orthograde and suspensory behaviors were decoupled in hominoid evolution. In this scenario, orthograde initially evolved in the ancestor of hominoids (or at least the great apes), as an adaptation to enhanced vertical climbing capabilities. The orthograde body plan was later independently co-opted for suspensory behaviors in extant hominoids (and presumably bipedalism in hominins), which can be viewed as repeated (i.e., homoplastic) exaptations.

Our study documents an extensive case of convergence between *Ailuropoda melanoleuca*, the giant panda, and extant hominoids in the morphology and numerical composition of the lumbar vertebral column (and potentially other aspects of the skeleton; Fig. 10). In our view, the results of this study may shed light on the evolution of the derived lumbar vertebral features characteristic of hominoids. *Ailuropoda* does not exhibit the arboreal locomotor behaviors characteristic of living hominoids (or atelids, indriids, or lorises). Most notably, *Ailuropoda* (and all other taxa sampled here) does not employ arm hanging, bridging, or brachiation. Although juvenile *Ailuropoda* engage in some vertical climbing, adults use this behavior infrequently unless threatened (Kleiman, 1983). Moreover, many ursid species (e.g., *Ursus americanus*) are skilled vertical climbers (Van Valkenburgh, 1987), with the exception of

large-bodied polar bears (*U. maritimus*) and brown bears (*U. arctos*). During terrestrial locomotion, *Ailuropoda* travels quadrupedally, holding the body axis in pronograde posture in much the same way as do other ursids (Davis, 1964; Chorn and Hoffmann, 1978). All ursids use facultative bipedal standing, and *Ailuropoda* does not stand bipedally more frequently than other ursids (Davis, 1964). Yet, our results demonstrate that the lumbar vertebral morphology of *Ailuropoda* differs significantly from the other ursids at all three vertebral levels (Fig. 7; with the exception of *U. thibetanus* at the LL level, but see above). The striking similarities in lumbar vertebral morphology and lumbar column reduction between *Ailuropoda* and hominoids (Table 1, Figs. 8 and 10) provide evidence for morphological convergence on lumbar vertebral adaptations for the single component of their respective positional behavioral repertoire that they share—orthograde trunk posture. Our finding is particularly interesting given that all primates, and especially cercopithecoids, demonstrate some degree of upright trunk postures compared to most mammals (Straus, 1962). Gelada baboons in particular demonstrate upright feeding postures (Jolly, 1970), but do not appear to converge with hominoids or differ substantially from other large-bodied papionins in vertebral morphologies (S.A.W., pers. obs.). Nevertheless, our comparative evidence lends support to a potential evolutionary scenario in which the acquisition of hominoid-like lumbar vertebral morphologies may have evolved for generalized orthograde behaviors and could have been exapted for suspensory behavior in all crown hominoids and for other locomotor specializations (e.g., brachiation) in extant lineages.

Acknowledgements

The authors thank L. Yao for kindly taking photographs of specimens at the Field Museum for Figure 9; E. Westwig, E. Hoeger, and A. Marcato at the American Museum of Natural History; D. Lunde, J. Ososky, and C. Potter at the Smithsonian Institution; and B. Stanley at the Field Museum of Natural History for assistance with the osteological collections in their care. We also thank J.M. Plavcan, J. DeSilva, and three anonymous reviewers for comments that improved the paper; D. Pilbeam for encouraging this project and examining a giant panda skeleton at the Museum of Comparative Zoology; L. Petrullo for assistance in data collection; and M. Shattuck and L. Shapiro for comments and feedback.

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Figure legends

Figure 1. Simplified phylogeny of the caniform sample (presented in Table 2). Dotted lines indicate alternative phylogenetic relationships. See text for details.

Figure 2. Vertebral measurements obtained on first, middle, and last lumbar vertebrae for all caniforms in the sample: 1) ventral vertebral body craniocaudal height, 2) dorsal vertebral body craniocaudal height, 3) mediolateral breadth of cranial articular surface, 4) transverse process position, 5) dorsoventral height of the cranial articular surface, 6) transverse process dorsoventral orientation, 7) transverse process craniocaudal angle, 8) spinous process craniocaudal angle, 9) spinous process craniocaudal height. Note that measure 2 as shown in the figure overlaps the line depicting the dorsal most points on the cranial and caudal articular surfaces used for calculating measurement 8. See text for details about how measurements were collected and used to calculate vertebral variables. Scale bars approximately 1 cm, same scale for top and bottom picture in cranial view. Vertebra belongs to *Ailuropoda melanoleuca* (AMNH 110453).

Figure 3. The left-hand column shows box plots of variation in vertebral body shape (VBS), defined as the ratio of craniocaudal body height to mediolateral cranial articular surface width. Larger value indicates a relatively taller vertebra; smaller value indicates a relatively shorter vertebra. Arrows indicate the directionality of our one-tailed post hoc test predictions—VBS values should be smallest in *Ailuropoda*. The right-hand column shows log values of craniocaudal vertebral body height and mediolateral width of the vertebral body (used to calculate vertebral body shape VBS), and centrum surface area on the geometric mean of postcranial articular surface areas (our approximation of body mass). The results of the Kruskal-Wallis tests and post hoc Mann-Whitney U-tests pairwise comparisons are presented in Table 5. See also SOM1.

Figure 4. Box plots of variation in A) transverse process position, B) dorsoventral angle, and C) craniocaudal angle. Larger value indicates that the transverse process is more dorsally positioned on the vertebra (A), more dorsally oriented in the transverse plane (B), and more laterally directed in the coronal plane (C); smaller value indicates that the transverse process is more ventrally positioned on the vertebra (A), more ventrally oriented in the transverse plane (B), and more cranially directed in the coronal plane (C). Arrows indicate the directionality of our one-tailed post hoc test prediction—all values should be largest in *Ailuropoda*. Results of the Kruskal-Wallis tests and post hoc Mann-Whitney U-tests pairwise comparisons are presented in Tables 6–8.

Figure 5. Box plots of variation in A) spinous process craniocaudal angle and B) craniocaudal height. Larger value indicates that the spinous process is more caudally directed in the sagittal plane (A) and craniocaudally taller (B); smaller value indicates that the spinous process is more cranially oriented in the sagittal plane (A) and craniocaudally shorter (B). Arrows indicate the directionality of our one-tailed post hoc test predictions—all values should be largest in *Ailuropoda*. Results of the Kruskal-Wallis tests and post hoc Mann-Whitney U-tests pairwise comparisons are presented in Tables 9 and 10.

Figure 6. Scatterplots of PC1 (x-axis) and PC2 (y-axis) for the first, middle, and last lumbar vertebrae (read top to bottom). The positive end of the shape space is associated with vertebrae having more dorsally positioned, dorsally oriented, and laterally directed transverse processes and craniocaudally taller, caudally directed spinous processes; the negative end of the shape space is associated with vertebrae having more ventrally positioned, ventrally oriented, and cranially directed transverse processes and craniocaudally narrower, cranially directed spinous processes (L1 and LL levels). See Table 11 for PCA results, Figure 7 for a comparison of species mean PC scores, and Table 12 for corresponding ANOVA results with Games-Howell pairwise comparisons.

Figure 7. On the left, PC1 species mean scores (with 95% confidence intervals) for the caniforms in the sample for the first, middle, and last lumbar vertebrae (from top to bottom). On right, typical vertebrae from taxa having the highest (*Ailuropoda melanoleuca*), intermediate (*Ursus americanus*), and lowest (*Procyon lotor*) mean scores to illustrate differences. See Table 12 for ANOVA results with Games-Howell pairwise comparisons.

Figure 8. Comparative image of ursid (top set) and catarrhine (bottom set) lumbar vertebrae. The ursine (*Ursus americanus*) and cercopithecoid (*Macaca mulatta*) share traits that represent the probable primitive condition for caniforms, catarrhines, and therians. In contrast, both *Ailuropoda melanoleuca* and *Pan troglodytes* share a number of derived lumbar vertebral traits.

Figure 9. Lateral view of *Ailuropoda melanoleuca* and *Tremarctos ornatus* (spectacled bear) lumbar columns to show distinguishing morphologies. Note that the *Ailuropoda* lumbar column has a thoracic vertebra articulated cranially (i.e., L1 is the second vertebra in the series) and the *Tremarctos* lumbar column is missing L1 (i.e., the first vertebra in the series is L2). Visual comparison underscores differences between *Tremarctos* (the most basal ursine) and derived *Ailuropoda*: the shorter craniocaudal lengths of the vertebral bodies, the more dorsally positioned and laterally oriented transverse processes at the body-pedicle border, and the caudally directed spinous processes in *Ailuropoda* compared to *Tremarctos*, which has craniocaudally taller vertebral bodies, ventrally (in the transverse plane) and cranially (in the coronal plane) directed transverse processes positioned ventrally, and cranially directed spinous processes. See text for more detail.

Figure 10. Cranial view comparison of ursid and catarrhine pelves. The iliac blades of *Ailuropoda melanoleuca* and *Pan troglodytes* are both more para-coronally oriented (more laterally directed arrows) compared to those of their respective outgroups, ursine bears (*Ursus americanus* shown here) and cercopithecoids (*Macaca mulatta* shown here), in which the blades are para-sagittally oriented (more forwardly-directed arrows). The lumbo-sacral joint is roughly parallel with the transverse plane in each image.

Table 1. Summary table of lumbar vertebral features and their biomechanical significance in living hominoids and the presumed primitive catarrhine condition, and the caniform study sample as compared to the presumed primitive caniform condition.^a

Lumbar vertebral feature	Biomechanical significance	Presence in...										
		Presumed primitive catarrhine condition	Hy ¹	GA	<i>Homo sapiens</i>	Presumed primitive caniform condition	<i>C.I.</i>	<i>Pr.I.</i>	<i>U.t.</i>	<i>U.am.</i>	<i>U.ar.</i>	<i>A.m.</i>
Mean numbers of lumbar (L), post-transitional (P), and thoracolumbar (T) vertebrae	<i>Fewer lumbar numbers:</i> Reduces columnar bending; lumbar stability	L: 6 P: 9 T: 19	L: 5 (4–6)	L: 4 (3–5)	L: 5 (4–6)	L: 6–7 P: 9–10 T: 20	L: 7 (6–8)	L: 6 (5–7)	L: 6 (5–6)	L: 6 (5–6)	L: 6 (5–6)	L: 5 (3–5)
	<i>Greater lumbar numbers:</i> Increases columnar bending; lumbar flexibility		P: 5 (4–7)	P: 4 (0–5)	P: 5 (4–6)		P: 10 (10–11)	P: 9 (8–10)	P: 9 (8–9)	P: 9 (8–9)	P: 9 (8–10)	7 (6–8)
			T: 18 (17–19)	T: 17 (15–18)	T: 17 (16–18)		T: 20 (19–21)	T: 20 (19–21)	T: 20 (19–21)	T: 20 (19–20)	T: 20 (19–20)	T: 18 (17–19)
Craniocaudal height of vertebral body	<i>Shorter:</i> Reduces columnar bending; lumbar stability <i>Taller:</i> Increases columnar bending; lumbar flexibility	Relatively taller than apes	Relatively shorter than cercopithecoids	Relatively shorter than cercopithecoids	Relatively shorter than cercopithecoids	Relatively taller than ursids	Relatively taller than ursids	Relatively taller than ursids	Relatively shorter than other caniforms	Relatively shorter than other caniforms	Relatively shorter than other caniforms	Relatively shorter than <i>U.americanus</i> , <i>U.thibetanus</i> , and other caniforms
Mediolateral width of vertebral body	<i>Narrower:</i> Decreases resistance to coronal plane bending; lateral flexibility <i>Wider:</i> Increases resistance to coronal plane bending; lateral stability	Relatively narrower than apes	Relatively wider than cercopithecoids	Relatively wider than cercopithecoids	Relatively wider than cercopithecoids and apes	Relatively narrower than <i>Procyon</i> and ursids	Relatively narrower than <i>Procyon</i> and ursids	Relatively broader than other caniforms	Relatively broader than other caniforms	Relatively broader than other caniforms	Relatively broader than other caniforms	Relatively broader than other caniforms
Transverse process origin ²	<i>More ventral:</i> Improves leverage for ventral flexor muscles; larger compartment for erector spinae muscles	Vertebral body	Pedicle-body junction	Pedicle	Pedicle	Vertebral body	Vertebral body	Pedicle-body junction	Pedicle-body junction	Pedicle-body junction	Pedicle-body junction	Pedicle
Transverse process dorsoventral angle ^c	<i>More lateral to dorsal:</i> Improves leverage for back extensor muscles; resistance to ventroflexion; smaller compartment for erector spinae muscles	Relatively more ventrally oriented than apes	Relatively more laterally oriented than cercopithecoids	Relatively more dorsally oriented than cercopithecoids and hylobatids	Relatively more dorsally oriented than cercopithecoids and hylobatids	Relatively more ventrally-oriented than ursids	Relatively more ventrally oriented than ursids	Relatively more ventrally oriented than ursids	Relatively more laterally oriented than other caniforms	Relatively more laterally oriented than other caniforms	Relatively more laterally oriented than other caniforms	Relatively more laterally to dorsally oriented than ursines and other caniforms

^a Conditions for caniforms are summarized from the results of the first and middle lumbar vertebrae (ML) in this study. See also Figures 3–5, Tables 3 and 4, and the SOM.

^b Average for *Hylobates lar* is 5.6 (range 4–7); average for *Symphalangus syndactylus* is 4.9 (range 4–6).

^c Biomechanical significance of transverse process origin and dorsoventral angle are related and thus listed in conjunction.

^d Great apes generally vary from 3–5 post-transitional vertebrae, but in some mountain gorillas (*Gorilla beringei*) the transitional vertebra occurs lower in the lumbar column, even at the last lumbar level, amounting to zero post-transitional vertebrae.

Transverse process craniocaudal angle	<i>More cranial:</i> Increases lateral flexibility <i>More lateral:</i> Reduces lateral flexibility	Relatively more cranially-oriented than apes	Relatively more laterally oriented	Relatively more laterally oriented	Relatively more laterally oriented		Relatively more cranially oriented	Relatively more cranially oriented	Relatively more cranially oriented	Relatively more laterally oriented	Relatively more laterally oriented	Relatively more laterally oriented	Relatively more laterally oriented ³
Spinous process craniocaudal angle	<i>More cranial:</i> Improves leverage for sagittal plane extension; sagittal mobility <i>More caudal:</i> Decreases leverage for sagittal plane extension; sagittal stability <i>Narrower:</i> Increases interspinous distance for increased sagittal plane flexibility <i>Broader:</i> Reduces interspinous distance for reduced sagittal plane flexibility	Relatively more cranially oriented	Relatively more perpendicular or caudally oriented than cercopithecoids	Relatively more perpendicular or caudally oriented than cercopithecoids	Relatively more perpendicular or caudally oriented than cercopithecoids		Relatively more cranially oriented than ursids	Relatively more cranially oriented than ursids	Relatively more cranially oriented than ursids	Relatively more dorsally oriented than other caniforms	Relatively more dorsally oriented than other caniforms	Relatively more dorsally oriented than other caniforms	Relatively more dorsally oriented than ursines and other caniforms
Spinous process height		Relatively narrower than apes	Relatively broader than cercopithecoids	Relatively broader than cercopithecoids	Relatively broader than cercopithecoids		Relatively narrower than ursids	Relatively narrower than ursids	Relatively narrower than ursids	Relatively broader than other caniforms	Relatively broader than other caniforms	Relatively broader than other caniforms	Relatively broader than other caniforms

Hy = hylobatids, GA = great apes, *C.l.* = *Canis lupus*, *Pr.l.* = *Procyon lotor*, *U. t.* = *Ursus thibetanus*, *U. am.* = *U. americanus*, *U.ar.* = *U. arctos*, *A.l.* = *Ailuropoda melanoleuca*
References: Slijper, 1946; Schultz, 1961; Benton, 1967; Ankel, 1972; Gambaryan, 1974; Rose 1975; Shapiro, 1991, 1993,1995, 2007; Ward, 1991, 1993; Sanders and Bodenbender, 1994; Sanders, 1995, 1998

^e At the level of the first lumbar vertebra, the transverse processes achieve craniocaudal angles of greater than 90° in *A. melanoleuca*, indicating that the transverse processes achieve caudal orientation.

Table 2. Caniform sample composition.

Taxon	N (wild-caught, captive)	Museum^a
<i>Ailuropoda melanoleuca</i>	15 (13, 2)	AMNH, NMNH
<i>Ursus americanus</i>	17 (9, 8)	AMNH, NMNH
<i>Ursus arctos</i>	18 (8, 10)	AMNH, NMNH
<i>Ursus thibetanus</i>	9 (2, 7)	AMNH, NMNH
<i>Procyon lotor</i>	17 (17, 0)	AMNH
<i>Canis lupus</i> ^b	15 (9, 6)	AMNH
Total	91	

^a AMNH = American Museum of Natural History, New York, NY; NMNH = National Museum of Natural History, Smithsonian Institution, Washington, D.C.

^b Includes only North American subspecies

Table 3. Mean vertebral numbers (range, standard deviation) in *Ailuropoda melanoleuca* and the other caniforms in the sample.^a

Taxon (N)	Lumbar vertebrae	Post-transitional vertebrae	Thoracolumbar vertebrae	Sacral vertebrae	Mode (frequency), second highest	Lumbar region “length”
<i>A. melanoleuca</i> (20)	4.58 (3–5, 0.57)	6.70 (6–8, 0.59)	18.00 (17–19, 0.46)	5.08 (4–6, 0.47)	7:13:5:5 (30%), 7:14:4:5 (15%)	3.92
<i>U. americanus</i> (26)	5.94 (5–6, 0.22)	8.92 (8–9, 0.27)	19.81 (19–20, 0.40)	4.48 (3–5, 0.81)	7:14:6:5 (61.5%)	5.94
<i>U. arctos</i> (15)	5.77 (5–6, 0.37)	8.97 (8–10, 0.40)	19.83 (19–20, 0.36)	5.50 (5–6, 0.50)	7:14:6:5 (40%), 7:14:6:6 (25%)	4.96
<i>U. thibetanus</i> (15)	5.80 (5–6, 0.37)	8.77 (8–9, 0.42)	20.03 (19.5–21, 0.30)	5.17 (4–6, 0.65)	7:14:6:5 (26.7%), 7:14:6:6 (26.7%)	5.63
<i>P. lotor</i> (49)	5.85 (5–7, 0.40)	8.83 (8–9.5, 0.39)	19.90 (19–21, 0.37)	3.18 (2.5–4, 0.39)	7:14:6:3 (61.2%)	6.44
<i>C. lupus</i> (16)	7.03 (6–8, 0.39)	10.16 (10–11, 0.35)	20.10 (20–21, 0.27)	3.09 (3–4, 0.27)	7:13:7:3 (81.3%)	8.16

^aData were combined from a previous study (Williams, 2011) and the study presented here, accounting for sample size differences between vertebral number and morphometric data. Modal vertebral formulae (read as number of cervical:thoracic:lumbar:sacral vertebrae) >10% frequency are listed for each taxon. Lumbar region “length” calculated following Johnson and Shapiro (1998) and Shapiro and Simons (2002) as the mean relative lumbar vertebral body length (across L1, ML, LL) multiplied by the mean number of lumbar vertebrae for each species.

Table 4. Interspecific similarity indices of vertebral formulae among caniforms included in this study and hominoids (using previously published data Williams [2012]).^a

	<i>A.mel.</i>	<i>U.amer.</i>	<i>U.arc.</i>	<i>U.thib.</i>	<i>Pr.lotor</i>	<i>C.lupus</i>	<i>Hy. lar</i>	<i>Hy.syn.</i>	<i>Po.pyg.</i>	<i>G.gor.</i>	<i>Pa.tro.</i>	<i>Ho.sap.</i>
<i>A. melanoleuca</i>	1	-	-	-	-	-	-	-	-	-	-	-
<i>U. americanus</i>	0	1	-	-	-	-	-	-	-	-	-	-
<i>U. arctos</i>	0	0.849	1	-	-	-	-	-	-	-	-	-
<i>U. thibetanus</i>	0	0.834	0.906	1	-	-	-	-	-	-	-	-
<i>Pr. lotor</i>	0	0.019	0	0.022	1	-	-	-	-	-	-	-
<i>C. lupus</i>	0	0.008	0	0.016	0.012	1	-	-	-	-	-	-
<i>Hy. lar</i>	0.279	0.012	0	0	0.017	0	1	-	-	-	-	-
<i>Hy. syndactylus</i>	0.604	0	0	0	0.002	0	0.508	1	-	-	-	-
<i>Po. pygmaeus</i>	0.006	0	0	0	0	0	0.003	0.092	1	-	-	-
<i>G. gorilla</i>	0.062	0	0	0	0	0	0.001	0.415	0.138	1	-	-
<i>Pa. troglodytes</i>	0.134	0	0	0	0	0	0.002	0.275	0.125	0.811	1	-
<i>Ho. sapiens</i>	0.013	0	0	0	0	0	0.021	0.014	0.058	0.011	0.010	1

^a Similarity indices are shown in the off-diagonal (lower triangle). See text for index calculation.

Pr. = *Procyon*, *Hy.* = *Hylobates*, *Po.* = *Pongo*, *G.* = *Gorilla*, *Pa.* = *Pan*, *Ho.* = *Homo*

Table 5. Kruskal-Wallis and pairwise Mann-Whitney U results for vertebral body shape (VBS).^a

First lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 58.225	<i>A. melanoleuca</i>	<0.001	0.071	0.035	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	<0.001	0.190	0.008	<0.001
	<i>U. arctos</i>	--	--	0.007	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	<0.001	<0.001
	<i>P. lotor</i>	--	--	--	--	<0.001
Middle lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 68.595	<i>A. melanoleuca</i>	<0.001	0.312	0.028	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	<0.001	0.128	<0.001	<0.001
	<i>U. arctos</i>	--	--	0.027	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	<0.001	<0.001
	<i>P. lotor</i>	--	--	--	--	<0.001
Last lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 61.747	<i>A. melanoleuca</i>	<0.001	0.414	<0.001	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	<0.001	0.416	<0.001	<0.001
	<i>U. arctos</i>	--	--	0.013	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	<0.001	<0.001
	<i>P. lotor</i>	--	--	--	--	<0.001

^a Boldface indicates statistical significance at $\alpha = 0.05$. See also Figure 3.

Table 6. Kruskal-Wallis and pairwise Mann-Whitney U results for transverse process position (TPP).^a

First lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 55.425	<i>A. melanoleuca</i>	<0.001	<0.001	0.004	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.001	0.001	0.035	<0.001
	<i>U. arctos</i>	--	--	0.090	0.017	<0.001
	<i>U. thibetanus</i>	--	--	--	0.005	0.005
	<i>P. lotor</i>	--	--	--	--	<0.001
Middle lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 42.238	<i>A. melanoleuca</i>	<0.001	0.010	0.035	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.002	0.005	<0.001	0.027
	<i>U. arctos</i>	--	--	0.382	0.113	<0.001
	<i>U. thibetanus</i>	--	--	--	0.139	0.001
	<i>P. lotor</i>	--	--	--	--	<0.001
Last lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 38.296	<i>A. melanoleuca</i>	0.014	0.214	0.102	<0.001	0.023
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.063	<0.001	<0.001	<0.001
	<i>U. arctos</i>	--	--	0.014	<0.001	0.001
	<i>U. thibetanus</i>	--	--	--	0.007	0.314
	<i>P. lotor</i>	--	--	--	--	<0.001

^a Boldface indicates statistical significance at $\alpha = 0.05$. See also Figure 4a.

Table 7. Kruskal-Wallis and pairwise Mann-Whitney U results for transverse process dorsoventral angle (TPDV).^a

First lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 57.270	<i>A. melanoleuca</i>	<0.001	<0.001	0.008	<0.001	<0.001
<i>p</i> -value < 0.001	<i>U. americanus</i>	--	0.114	0.086	0.029	<0.001
	<i>U. arctos</i>	--	--	0.368	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	0.002	<0.001
	<i>P. lotor</i>	--	--	--	--	0.006
Middle lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 56.533	<i>A. melanoleuca</i>	<0.001	<0.001	<0.001	<0.001	<0.001
<i>p</i> -value < 0.001	<i>U. americanus</i>	--	<0.001	0.003	0.097	<0.001
	<i>U. arctos</i>	--	--	0.334	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	0.002	<0.001
	<i>P. lotor</i>	--	--	--	--	0.020
Last lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 55.597	<i>A. melanoleuca</i>	<0.001	0.005	0.002	<0.001	<0.001
<i>p</i> -value < 0.001	<i>U. americanus</i>	--	<0.001	0.005	0.381	<0.001
	<i>U. arctos</i>	--	--	0.061	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	0.014	<0.001
	<i>P. lotor</i>	--	--	--	--	<0.001

^a Boldface indicates statistical significance at $\alpha = 0.05$. See also Figure 4b.

Table 8. Kruskal-Wallis and pairwise Mann-Whitney U results for transverse process craniocaudal angle (TPCC).^a

First lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 38.780	<i>A. melanoleuca</i>	<0.001	<0.001	0.007	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.064	0.095	0.241	0.002
	<i>U. arctos</i>	--	--	0.476	0.476	<0.001
	<i>U. thibetanus</i>	--	--	--	0.021	0.003
	<i>P. lotor</i>	--	--	--	--	0.021
Middle lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 62.897	<i>A. melanoleuca</i>	0.026	0.459	0.020	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.012	0.331	<0.001	<0.001
	<i>U. arctos</i>	--	--	0.013	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	<0.001	<0.001
	<i>P. lotor</i>	--	--	--	--	0.003
Last lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 62.300	<i>A. melanoleuca</i>	0.005	<0.001	0.002	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.405	0.194	<0.001	<0.001
	<i>U. arctos</i>	--	--	0.194	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	0.004	<0.001
	<i>P. lotor</i>	--	--	--	--	<0.001

^a Boldface indicates statistical significance at $\alpha = 0.05$. See also Figure 4c.

Table 9. Kruskal-Wallis and pairwise Mann-Whitney U results for spinous process craniocaudal angle (SPCC).^a

First lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 68.842	<i>A. melanoleuca</i>	<0.001	<0.001	<0.001	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.004	0.002	<0.001	<0.001
	<i>U. arctos</i>	--	--	0.112	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	<0.001	<0.001
	<i>P. lotor</i>	--	--	--	--	<0.001
Middle lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 64.693	<i>A. melanoleuca</i>	<0.001	<0.001	0.002	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.007	<0.001	0.007	<0.001
	<i>U. arctos</i>	--	--	0.006	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	<0.001	<0.001
	<i>P. lotor</i>	--	--	--	--	0.031
Last lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 39.936	<i>A. melanoleuca</i>	<0.001	<0.001	0.002	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.077	0.431	0.004	0.092
	<i>U. arctos</i>	--	--	0.143	<0.001	0.011
	<i>U. thibetanus</i>	--	--	--	<0.001	0.217
	<i>P. lotor</i>	--	--	--	--	0.160

^a Boldface indicates statistical significance at $\alpha = 0.05$. See also Figure 5a.

Table 10. Kruskal-Wallis and pairwise Mann-Whitney *U* results for spinous process craniocaudal height (SPH).^a

First lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 49.134	<i>A. melanoleuca</i>	<0.001	0.058	0.187	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	<0.001	0.022	0.034	0.005
	<i>U. arctos</i>	--	--	0.013	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	0.010	0.001
	<i>P. lotor</i>	--	--	--	--	0.275
Middle lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 50.528	<i>A. melanoleuca</i>	<0.001	0.225	0.187	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.001	0.134	0.003	<0.001
	<i>U. arctos</i>	--	--	0.054	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	0.001	<0.001
	<i>P. lotor</i>	--	--	--	--	0.014
Last lumbar vertebra		<i>U. americanus</i>	<i>U. arctos</i>	<i>U. thibetanus</i>	<i>P. lotor</i>	<i>C. lupus</i>
H-statistic = 41.812	<i>A. melanoleuca</i>	<0.001	<0.001	0.060	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.049	0.055	<0.001	0.106
	<i>U. arctos</i>	--	--	0.233	<0.001	0.002
	<i>U. thibetanus</i>	--	--	--	0.008	0.022
	<i>P. lotor</i>	--	--	--	--	0.061

^a Boldface indicates statistical significance at $\alpha = 0.05$. See also Figure 5b.

Table 11. Results of principal components analyses summarizing overall lumbar vertebral morphology in the caniform sample.^a

	PC	Eigenvalue	Percent	Cumulative percent	Positive component loadings: Variable (load)	Negative component loadings: Variable (load)
First lumbar vertebra	PC1	3.967	66.117	66.117	TPDV (0.864), TPP (0.822), TPCC (0.821), SPH (0.765), SPCC (0.821)	VBS (-0.858)
	PC2	0.699	11.142	77.260	SPCC (0.496), TPCC (0.330), VBS (0.298), TPP (0.088)	SPH (-0.466), TPDV (-0.131)
Middle lumbar vertebra	PC1	4.005	66.753	66.753	TPDV (0.882), TPCC (0.871), SPCC (0.802), TPP (0.562)	VBS (-0.940)
	PC2	0.773	12.878	79.632	TPP (0.797), VBS (0.119), SPCC (0.060), TPDV (0.007)	SPH (-0.297), TPCC (-0.178)
Last lumbar vertebra	PC1	3.494	58.239	58.239	TPCC (0.880), SPCC (0.796), TPDV (0.784), SPH (0.647)	VBS (-0.900), TPP (-0.493)
	PC2	0.920	15.330	73.569	TPP (0.820), SPH (0.416), TPDV(0.151), SPCC (0.151)	TPCC (-0.163), VBS (-0.044)

^a See also Figure 6.

Table 12. One-way ANOVA followed by Games-Howell pairwise comparisons of species mean PC scores.^a

U. americanus *U. arctos* *U. thibetanus* *P. lotor* *C. lupus*

First lumbar vertebra

F-statistic = 95.171	<i>A. melanoleuca</i>	<0.001	0.001	0.005	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.001	0.119	0.003	<0.001
	<i>U. arctos</i>	--	--	0.916	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	0.006	0.001
	<i>P. lotor</i>	--	--	--	--	0.001

Middle lumbar vertebra

F-statistic = 211.669	<i>A. melanoleuca</i>	<0.001	<0.001	0.001	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	<0.001	0.004	<0.001	<0.001
	<i>U. arctos</i>	--	--	0.599	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	<0.001	<0.001
	<i>P. lotor</i>	--	--	--	--	<0.001

Last lumbar vertebra

F-statistic = 78.899	<i>A. melanoleuca</i>	<0.001	<0.001	0.128	<0.001	<0.001
<i>p</i> -value <0.001	<i>U. americanus</i>	--	0.010	0.990	<0.001	<0.001
	<i>U. arctos</i>	--	--	0.872	<0.001	<0.001
	<i>U. thibetanus</i>	--	--	--	0.081	0.038
	<i>P. lotor</i>	--	--	--	--	0.442

^a Boldface indicates statistical significance at $\alpha = 0.05$. See also Figure 7.

A. mel. *U. amer.* *U. arc.* *U. thib.* *P. lotor* *C. lupus*

A. mel. *U. amer.* *U. arc.* *U. thib.* *P. lotor* *C. lupus*

CERCOPITHECIDAE

Macaca mulatta

HOMINIDAE

Pan troglodytes

URSIDAE

Ursus americanus

Ailuropoda melanoleuca

A. melanoleuca

T. ornatus