EVOLUTION OF THE HOMINOID VERTEBRAL COLUMN

BY

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DISSERTATION

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ABSTRACT

This is a study of the numerical composition of the vertebral column, the central structure of the vertebrate body plan and one that plays an instrumental role in locomotion and posture. Recent models of hominoid vertebral evolution invoke very different roles for homology and homoplasy in the evolution of vertebral formulae in living and extinct hominoids. These processes are fundamental to the emergence of morphological structures and reflect similarity by common descent (homology) or similarity by independent evolution (homoplasy). Although the "short backs," reflecting reduced lumbar regions, of living hominoids have traditionally been interpreted as homologies and shared derived characters (synapomorphies) of the ape and human clade, recent studies of variation in extant hominoid vertebral formulae have challenged this hypothesis. Instead, a "long-back" model, in which primitive, long lumbar regions are retained throughout hominoid evolution and are reduced independently in six lineages of modern hominoids, is proposed. The recently described skeleton of *Ardipithecus ramidus* is interpreted to support the long-back model. Here, larger samples are collected and placed in a larger phylogenetic context than previous studies. Analyses of over 8,000 mammal specimens, representing all major groups and focusing on anthropoid primates, allow for the reconstruction of ancestral vertebral formulae throughout mammalian evolution and a determination of the uniqueness of hominoid vertebral formulae. This survey, in combination with analyses of intraspecific diversity and interspecific similarity, suggests that reduced lumbar regions are homologous in extant hominoids. Furthermore, hominoid vertebral formulae are unique among primates and relatively unique among mammals in general. Hominins likely evolved five lumbar

vertebrae from a short-backed ancestor with an "African ape-like" vertebral profile. By the appearance of *Australopithecus*, hominins evolved a cranial placement of the diaphragmatic (one that bears a change in articular facet orientation) vertebra, which generates a functionally longer lower spine while maintaining five lumbar vertebrae. In light of these findings, it is proposed that bipedalism evolved in a party arboreal, partly terrestrial African ape-like locomotor context.

For Milena and Oliver,

who provided much-needed distraction and kept me on track,

and for Evan,

my doppelganger, nephew, and fellow naturalist.

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Dan was an excellent teacher and adviser and continues to be a close friend and mentor. The depth and well-roundedness of his knowledge of all aspects of biological anthropology are astounding and turned out to be a wonderful resource for an ambitious and unfocused student. Dan's guidance and courses, especially primate anatomy and evolution, helped me focus in on a master's thesis topic and are largely responsible for my interests in the evolution of orthogrady. It was also in Dan's class that I was first introduced to the lumbar transverse process and its intriguing differences among hominids, hylobatids, and non-hominoid primates, and between the mystery apes of the early Miocene, *Proconsul* and *Morotopithecus*. I consider myself lucky that my short time at NIU coincided with that of Art Durband, who taught human osteology and paleontology. Art is an extremely talented teacher and I learned a lot from him. Fellow (and senior) graduate students Kat Blake, Kierstin Catlett, and Amanda Zika were excellent role models and are still close friends. Amanda, in particular, was an endless source of entertainment.

At the University of Illinois, I have had the good fortune of taking courses and working with a diverse group of faculty, including my co-advisers, John Polk and Charles Roseman, committee members Laura Shackelford, Lyle Konigsberg, and Steve Leigh, and Paul Garber,

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CHAPTER 1

INTRODUCTION

Impetus for this study

This project was originally undertaken as a general morphological study of the hominoid vertebral column to test hypotheses on the role of homology (similarity due to common descent) and homoplasy (similarity due to independent evolution) in the evolution of the hominoid postcranium. Intriguing arguments for predominant roles of both homology (Benefit and McCrossin, 1995; Pilbeam, 1996, 1997; Harrison and Rook, 1997; MacLatchy et al., 2000; Young, 2002, 2003; MacLatchy, 2004; Pilbeam and Young, 2004) and homoplasy (Begun, 1993, 2007; Moyà-Solà and Köhler, 1996; Ward, 1997*a*, 2007; Larson, 1998; Moyà-Solà et al., 2004, 2005; Begun and Ward, 2005; Almécija et al., 2007) had been proposed. Evidence for the latter was largely based on the interpretation of metacarpal and phalangeal morphology in some fossil hominids[1] (*Rudapithecus*, *Hispanopithecus*, and *Pierolapithecus*)[2] (Begun, 1993; Moyà-Solà and

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[1] Here, 'hominid' refers to great apes, including humans, while the term 'hominin' refers specifically to humans and their immediate fossil ancestors. 'Hominine' and 'pongine' refer to members of the African (gorillas, chimpanzees, humans, and their ancestors) and Asian (orangutans and their direct ancestors) great ape clade, respectively.

[2] The taxonomy of European hominids has been revised recently, although there are disagreements in generic-level associations among taxa previously assigned to the single genus *Dryopithecus*. Essentially, the older specimens from Spain, France, and Austria are allocated to *Dryopithecus fontani* by Begun (2009, 2010), while Moyà-Solà and colleagues (Moyà-Solà et al., 2009*a*; Casanovas-Vilar et al., 2011) recognize generic distinctions between the Spanish material from Abocador de Can Mata (*Pierolapithecus catalaunicus*) and the French material from Saint Gaudens (*Dryopithecus fontani*), both from the Middle Miocene (12-13 Ma).[3] The Late Miocene (9.5-11 Ma) taxa are referred to as *Hispanopithecus laietanus* (from Can Llobateres, Spain) and *H. hungaricus* (from Rudabánya, Hungary) by Moyà-Solà and colleagues and *Hispanopithecus laietanus* and *Rudapithecus hungaricus* by Begun. Here, simply for the purpose of clarity and with no intended taxonomic implications, I refer to these taxa as their proposed generic distinctions – *Pierolapithecus*, *Dryopithecus*, *Hispanopithecus*, and *Rudapithecus*.

[3] Recently, Moyà-Solà and colleagues described two additional sets of cranial material from Can Mata, and attribute them to separate genera, *Dryopithecus fontani* (Moyà-Solà et al., 2009*a*) and *Anoiapithecus brevirostris* (Moyà-Solà et al., 2009*b*) (see also Alba et al., 2010). Begun (2009, 2010) considers all three taxa at Can Mata (*Pierolapithecus*, *Dryopithecus*, *Anoiapithecus*) to be synonymous with *Dryopithecus fontani*.

Köhler, 1996; Moyà-Solà et al., 2004; Almécija et al., 2007, 2009), humerus morphology in

Sivapithecus (Larson, 1998; see Pilbeam et al., 1990; Andrews and Pilbeam, 1996; Richmond

and Whalen, 2001), and variation in extant hominoid postcranial morphologies (Ward, 1997*a*;

Larson, 1998; but see Young, 2003). In the former two lines of evidence, humerus and hand

morphologies are argued to be primitive, and given the proposed phylogenetic positions of the

fossil hominoids that possess them (see below), they imply that these primitive features were

retained throughout hominoid evolution (see Ward, 2007 for a review). This necessarily requires

the independent evolution of modern ape-like upper limb morphologies at least three times

among extant taxa, namely in hylobatids, orangutans, and hominines (African apes, including

hominins), a view that the third line of evidence – a high degree of variation in postcranial

features among living hominoids – is interpreted to support (Ward, 1997*a*; Larson, 1998).

Around the same time that data collection for this project was underway, two sets of

studies were published that proposed a ubiquitous role of homoplasy in the hominoid

postcranium and specifically implicated a central role of the vertebral column in this

evolutionary process (Lovejoy et al., 2009*a*; White et al., 2009; Lovejoy and McCollum, 2010;

McCollum et al., 2010). McCollum et al. (2010; originally published online in 2009 prior to the

publication of *Ardipithecus*; see McCollum et al., 2010, p. 133) argue that a primitive, long

lumbar column persisted throughout hominoid evolution and was reduced independently in each

extant clade – hylobatids, orangutans, gorillas, humans, and even separately in chimpanzees and

bonobos (see also Lovejoy and McCollum, 2010). This view is also adopted in the interpretation

of *Ardipithecus* (Lovejoy et al., 2009*a*), in which it is additionally proposed that much of the

postcranium evolved independently in different locomotor contexts in all extant hominoids

(Lovejoy et al., 2009*a*; White et al., 2009; Lovejoy and McCollum, 2010).

In light of these studies, the focus of this dissertation shifted and refocused on the numerical composition of the vertebral column and related topics in order to test the hypotheses proposed by Lovejoy and colleagues (Lovejoy et al., 2009*a*; Lovejoy and McCollum, 2010; McCollum et al., 2010), in addition to previously proposed hypotheses of vertebral column evolution in hominoids (e.g., Filler, 1993; Latimer and Ward, 1993; Haeusler et al., 2002; Pilbeam, 2004; Rosenman, 2008). Because the postcranial axial skeleton (i.e., vertebral column) plays a central role in posture and locomotion, its evolution is fundamental to understanding the evolution of the appendicular skeleton. What follows is a discussion of relevant fossil specimens and their implications for the evolution of upright posture, or orthogrady, including the role of homology and homoplasy in its evolution in hominoid primates.

BACKGROUND

Evidence for homoplasy in hominoid evolution

In a highly anticipated series of papers, White and colleagues (Lovejoy et al., 2009*a*,*b*,*c*,*d*; White et al., 2009) describe and interpret the remarkable 4.4 Ma skeleton of *Ardipithecus ramidus*, from the Middle Awash Valley, Ethiopia. In their arguments, the authors consistently state that *Ardipithecus* lacked specializations for suspension, vertical climbing, and knuckle-walking, and by inference, that the last common ancestors (LCAs) of chimpanzees and hominins, African apes and hominins, and great apes lacked these specializations as well. Instead, Lovejoy et al. (2009*a*,*b*,*c*) interpret the hand and foot anatomy of *Ardipithecus* as indicating arboreal palmigrade quadrupedality, and thus surmise that the aforementioned LCAs were also adapted to arboreal palmigrady and not suspension or vertical climbing. Under this

scenario, orthogrady, or adaptation to upright trunk posture, would have evolved independently in *Pongo*, *Gorilla*, *Pan*, hominins, (Lovejoy et al., 2009*a*) and presumably also in hylobatids (see Lovejoy and McCollum, 2010).

Recent interpretations of metacarpals and phalanges attributed to *Pierolapithecus* (Moyà-Solà et al., 2004, 2005; Almécija et al., 2009) and *Hispanopithecus* (Moyà-Solà et al., 1996; Almécija et al., 2007) suggest that adaptations to arboreal palmigrady may have persisted through much of hominoid evolution and that at least some suspensory features evolved independently in modern lineages (Moyà-Solà et al., 2004, 2005; Almécija et al., 2007, 2009; Alba et al., 2010; but see Begun and Ward, 2005; Deane and Begun, 2008, 2010; Begun, 2009). Likewise, other Miocene taxa are interpreted to provide evidence for extensive homoplasy in hominoid postcranial evolution (Begun, 1993, 2007; Ward, 1997*a*, 2007; Larson, 1998; Harrison, 2002, 2010). However, it remains to be tested whether the extensive homoplasy required to produce orthogrady in at least five different lineages, as suggested by Lovejoy et al. (2009*a*), is reasonable given our current understanding of the evolution of morphological structures and the likelihood of homoplasy.

The living apes share a number of derived morphologies of the trunk and forelimbs, features that distinguish them from many other primates and mammals in general. As opposed to most non-hominoid primates, which have "generalized," albeit arboreally adapted (Gebo, 2010), skeletons (Davis, 1954), hominoids possess a derived set of postcranial features, including a broad, shallow thorax, spinal invagination, long clavicles, dorsally placed scapulae with laterally-oriented glenoid fossae, highly mobile shoulder joints, ulnar deviation and the presence of an intra-articular meniscus between the ulna and the carpals, a short lumbar column and dorsally-placed lumbar transverse processes, visceral fixation, and loss of an external tail (see

Andrews and Groves, 1976; Gebo, 1996, 2010; Ward, 2007). The possession of extensive

postcranial similarities despite a diverse range of locomotor behaviors employed by extant taxa

suggests that these morphologies were inherited from a common ancestor and are homologous

(Corruccini, 1978; Harrison, 1987; Gebo, 1996; Pilbeam, 1996; Young, 2003).

However, Ward (1997*a*), and more explicitly and thoroughly, Larson (1998), have argued

that the existence of significant morphological diversity within the apes and overlap with non-

hominoid taxa suggests that some of these morphologies may have evolved independently in

extant apes. The high degree of variability within hominoids and overlap with non-hominoids

taxa (namely *Ateles*) was later identified by Young (2003) as resulting from the inclusion of

Hylobates in the comparison, without which the total variability and overlap is greatly reduced.

The great apes demonstrate remarkable similarity in postcranial features despite a diverse range

of locomotor behaviors, ranging from quadrumanous clambering in *Pongo*, knuckle-walking in

Gorilla and *Pan*, and bipedalism in *Homo*.

The seemingly homologous situation inferred from living taxa conflicts with the mosaic

pattern of postcranial evolution presented by the fossil record. The fossil hominoids

Rudapithecus (Begun, 1993), *Hispanopithecus* (Moyà-Solà and Köhler, 1996; Almejica et al.,

2007), *Pierolapithecus* (Moyà-Solà et al., 2004, 2005; Almécija et al., 2009), *Nacholapithecus*

(Nakatsukasa et al., 2003; Ishida et al., 2004; Nakatsukasa and Kunimatsu, 2009), *Sivapithecus*

(Pilbeam et al., 1990; Andrews and Pilbeam, 1996; Larson, 1998), and *Morotopithecus*

(Harrison, 2002, 2010*a*; Nakatsukasa, 2008) have been interpreted as providing evidence that at

least some postcranial similarities must have evolved independently in hylobatids and great apes.

The earliest recognized hominoids preserving postcrania are *Proconsul* and *Morotopithecus* of

the early Miocene. The postcranium of *Proconsul* is well-known and has been reconstructed as

belonging to a pronograde arboreal quadruped capable of slow climbing (Napier and Davis, 1959; Preuschoft, 1973; Schon and Ziemer, 1973; Morbeck, 1975; Corruccini et al., 1976; O'Connor, 1976; Rose, 1983, 1993, 1994, 1997; McHenry and Corruccini, 1983; Walker and Pickford, 1983; Beard et al., 1986; Gebo et al., 1988, 2009; Ward, 1993, 1998; Ward et al., 1993; Begun et al., 1994; Walker, 1997).

While the postcranium of *Morotopithecus* is less well known, many of its preserved morphologies suggest it was characterized by orthograde posture and suspensory locomotion (Walker and Rose, 1968; Ward, 1993; Sanders and Bodenbender, 1994; Pilbeam, 1996; Gebo et al., 1997; MacLatchy and Pilbeam, 1999; MacLatchy et al., 2000; MacLatchy, 2004; Young and MacLatchy, 2004). The stark contrast between the postcranial morphology and inferred positional behavior of contemporaneous *Proconsul* and *Morotopithecus* suggests that either 1) *Morotopithecus* is ancestral to extant apes to the exclusion of *Proconsul* and other pronograde Miocene hominoids (Pilbeam, 1996; Gebo et al., 1997; MacLatchy and Pilbeam, 1999; MacLatchy et al., 2000; MacLatchy, 2004; Young and MacLatchy, 2004), or 2) *Morotopithecus* is a large-bodied proconsulid that evolved orthogrady independently of crown hominoids (Harrison, 2002, 2010*a*; Andrews and Harrison, 2005; Nakatsukasa, 2008). Nakatsukasa and colleagues (Nakatsukasa et al., 2003; Ishida et al., 2004; Nakatsukasa and Kunimatsu, 2009) also support the latter scenario in their interpretation of *Nacholapithecus* as an orthograde climber that represents a good model from which extant hominoids evolved suspensory morphologies.

The "*Sivapithecus* dilemma" (Pilbeam and Young, 2001) now exists because the preexisting phylogenetic position of *Sivapithecus* as sister taxon to *Pongo* (Pilbeam, 1982; Andrews and Cronin, 1982; Ward and Pilbeam, 1983; Ward and Kimbel, 1983; Ward and Brown, 1986) is challenged because postcrania attributed to *Sivapithecus* possess traits

characteristic of pronograde quadrupeds (Rose, 1983, 1984, 1994; Pilbeam et al., 1990; Richmond and Whalen, 2001; Madar et al., 2002; but see Rose, 1997). The current debate concerns whether *Sivapithecus* and *Pongo* are sister taxa (Pilbeam et al., 1990; Andrews and Pilbeam, 1996; Ward, 1997*b*; Larson, 1998; Köhler et al., 2001; Pilbeam and Young, 2001). If they are, this implies that 1) orangutans and African apes evolved some suspensory morphologies in parallel (Andrews, 1992; Begun et al., 1997; Larson, 1998) or 2) the *Sivapithecus* lineage evolved from suspensory ancestors but experienced reversals in its postcranial morphology (Ward, 1997*b*; Richmond and Whalen, 2001; Andrews and Harrison, 2005). Alternatively, if *Sivapithecus* and *Pongo* are not sister taxa (Rose, 1997), either 1) extensive facial homoplasy must have occurred in these lineages (Pilbeam, 1996, 1997; Pilbeam and Young, 2001, 2004; Young, 2003) or 2) the facial similarities shared by *Sivapithecus* and *Pongo* are primitive characteristics present in the common ancestor of living great apes and *Sivapithecus* (Shea, 1985, 1988; Benefit and McCrossin, 1995, 1997).

     Pierolapithecus is interpreted by its discoverers as a primitive hominid that possessed a modern ape-like, orthograde thorax, lumbar region, and wrist, but retained short phalanges, suggesting that vertical climbing and suspensory behaviors were decoupled in hominoid evolution, the former gradually producing orthogrady and the latter evolving independently in various living hominoid lineages (Moyà-Solà et al., 2004, 2005; Almécija et al., 2009; Alba et al., 2010; but see Deane and Begun, 2008, 2010; Begun, 2009). The skeleton of *Hispanopithecus* combined long phalanges and short metacarpals and is interpreted as a functional compromise between suspensory behavior and the retention of arboreal palmigrady (Almécija et al., 2007; Lovejoy, 2007; Alba et al., 2010). Both *Pierolapithecus* and *Hispanopithecus* are interpreted to retain adaptations of the metacarpals and phalanges to arboreal palmigrady, but in association

with orthograde body plans, the latter taxon incorporating a significant degree of suspensory behavior in its locomotor repertoire (Moyà-Solà and Köhler, 1996; Moyà-Solà et al., 2004, 2005; Almécija et al., 2007, 2009; Alba et al., 2010).

Ardipithecus is similarly argued to retain features of the hand related to arboreal palmigrady, including a flexible midcarpal joint, short metacarpals, constricted metacarpal heads, and proximal phalanges with basal tubercles (Lovejoy et al., 2009*a,c*). Lovejoy et al. (2009*a*) interpret *Ardipithecus* as orthograde, indeed bipedal when terrestrial, but argue that "advanced" orthogrady in hominins evolved from above-branch palmigrade quadrupedalism, as it did in all living hominoids and extinct *Oreopithecus*. This implies that each genus of living hominoid and fossil "hominoids of modern aspect" (Pilbeam, 1996), including *Morotopithecus*, *Oreopithecus*, and *Pierolapithecus*/*Dryopithecus* and *Hispanopithecus*/*Rudapithecus* independently acquired a set of features related to orthogrady from more or less pronograde ancestors. Whether the shift from pronogrady to orthogrady occurred once in the common ancestor of hominoids or whether it evolved independently in multiple lineages has been debated since the conception of the terms (Keith, 1903; see Appendix A).

Given the propensity of homoplasy in different regions of the body in primates (e.g., Beynon et al., 1991; Disotell, 1994; Begun and Kordos, 1997; Hartwig, 2005), it is difficult to determine *a priori* whether or not extensive homoplasy has occurred in the hominoid postcranium. Levels of homoplasy in different body regions (dentition, cranium, postcranium) of hominoids (Finarelli and Clyde, 2004; Young, 2005), primates (Williams, 2007), and mammals in general (Sánchez-Villagra and Williams, 1998) are very similar. In fact, the postcranium may be less prone to homoplasy than dentition or the cranium (Finarelli and Clyde, 2004; Williams, 2007; but see Young, 2005). Nevertheless, as stated in Wake et al. (2011:1032), "one does not

seek homoplasy—it 'finds' the researcher and compels one to ask appropriate questions." In other words, homoplasy need not be invoked if a simpler explanation (i.e., homology) exists and is not rejected by the phylogeny in question (see also Bolker and Raff, 1996; Begun, 2007).

In some cases, phylogenetic relationships reject homology and instead reveal homoplasy; for example, in the case of brachiation and suspensory adaptations in *Ateles* and *Brachyteles* (Hartwig, 2005) or large body size and facial elongation in *Papio/Theropithecus* and *Mandrillus* (Disotell, 1994). However, when the postcranium of extant hominoids is placed in a modern phylogenetic context, homoplasy is evident only in the knuckle-walking features of chimpanzees and gorillas, which either represent the product of independent evolution (Dainton and Macho, 1999; Kivell and Schmitt, 2009) or reversal in hominins (Begun, 2004; Williams, 2010). It is the interpretation of the morphology and phylogenetic positions of fossil taxa that invoke a large degree of homoplasy in the evolution of the hominoid locomotor skeleton (e.g., Larson, 1998; Almécija et al., 2007, 2009; Lovejoy et al., 2009*a,c,d*; White et al., 2009). This situation is complicated by phylogenetic uncertainty associated with the very fossil taxa around which hypotheses of homoplasy are constructed (e.g., Pilbeam et al., 1990; Pilbeam and Young, 2001; Begun and Ward, 2005; Begun, 2010; Harrison, 2010*b*; Sarmiento, 2010; Wood and Harrison, 2011).

The role of the vertebral column

Vertebral traits that distinguish extant hominoids from cercopithecoids and other primates are thought to be fundamental to the evolution of orthogrady (Mivart, 1865; Keith, 1903; Schultz, 1930, 1961; Erickson, 1963; Ankel, 1967, 1972; Benton, 1967, 1974; Walker and Rose, 1968; Rose, 1975; Kelley, 1986; Shapiro, 1991, 1993*a,b*; Ward, 1991, 1993; Sanders and

Bodenbender, 1994; Sanders, 1995, 1998; MacLatchy et al., 2000; Nakatsukasa et al., 2003, 2007; MacLatchy, 2004; Moyà-Solà et al., 2004; Lovejoy, 2005; Filler, 2007; Nakatsukasa, 2008). Examples include the position of the lumbar transverse processes, lumbar vertebral body width and height, the position of the diaphragmatic vertebra, and the numerical composition of the vertebral column.

Benton (1967) differentiated extant primates among "short-" and "long-backed" groups based on the modal number of lumbar vertebrae and identified other vertebral features, and torso shape in general (see also Ward, 1993), associated with this dichotomy. To generalize, the short-backed primates, including hominoids and atelids, possess five or fewer lumbar vertebrae with short, wide lumbar centra and dorsally-placed lumbar transverse processes (Benton, 1967, 1974). The long-backed group includes sterpsirrhines and non-hominoid, non-atelid primates, which possess six or more lumbar vertebrae with tall centra and ventrally-placed lumbar transverse processes (Benton, 1967, 1974).

Following Benton (1967), various researchers have proposed and supported short-back (Pilbeam, 1996, 1997, 2004; Lovejoy, 2005), long-back (Lovejoy et al., 2009a; Lovejoy and McCollum, 2010; McCollum et al., 2010), and intermediate (Filler, 1993; Latimer and Ward, 1993; Sanders, 1995; Haeusler et al., 2002; Rosenman, 2008) scenarios of hominin ancestry. That is, hominins are argued to have evolved from an ancestor with three to four, six to seven, or five lumbar vertebrae, respectively (notice that Benton's categories are adjusted slightly here, with five lumbar vertebrae representing an "intermediate" category).

These models have important implications for the evolution of bipedalism; indeed, in order to understand the emergence of bipedalism in hominins, it is necessary to reconstruct the locomotor skeleton and positional behavior of the LCA of chimpanzees and humans. The short-

back model implies a "great ape-like" ancestor, or, in some iterations, more specifically, a "chimp-like" one (Pilbeam, 1996, 1997, 2004). Intermediate models tend to be less specific, but propose vertebral formulae for the LCA that can be described as "gibbon-like" (Filler, 1993; Latimer and Ward, 1993) or "human-like" (Haeusler et al., 2002). Finally, the architects of the long-back model propose what is probably best described as a "stem hominoid-like" LCA (Lovejoy et al., 2009*a*; Lovejoy and McCollum, 2010; McCollum et al., 2010).

Each of the three models of vertebral formula evolution invokes a different role for homoplasy; together, they account for nearly all of the possibilities, from extreme amounts of homoplasy to very little at all. The short-back model posits the homology of reduced lumbar regions in hominoids, while the intermediate and long-back models require progressively greater amounts of homoplasy: independent reductions of the lumbar column by one element in orangutans, gorillas, and panins (chimpanzees and bonobos) in the intermediate scenario and by one to three elements in hylobatids, orangutans, gorillas, humans, and even separately in chimpanzees and bonobos in the long-back model. Additional independent reductions would be required for fossil hominoids with reduced lumbar regions (e.g., *Oreopithecus*) in the latter scenario. In this dissertation, I test these hypotheses using the distribution of and variation in vertebral formulae in a broad phylogenetic context of hominoids and other primates and mammals.

CHAPTER OVERVIEWS

This dissertation is structured as a series of semi-autonomous article-chapters flanked by this Introduction chapter (**Chapter 1**) and a Conclusion chapter (**Chapter 5**). Because this

dissertation includes separate article-chapters, each with its own Background and/or

Introduction, detailed accounts of background information specific to the subsequent chapters are

not included in this introduction. Likewise, this dissertation does not include a separate chapter

dedicated to materials and methods since each article-chapter contains its own Materials and

Method section. A short summary of each chapter follows.

Chapter 2. The evolutionary history of hominoid vertebral formulae

In this chapter, I present and analyze a large dataset of mammalian vertebral formulae in

order to test hypotheses of hominin vertebral evolution. To accomplish this, I generate vertebral

profiles, which consist of the most frequent vertebral formulae observed in a taxon. I then

reconstruct ancestral vertebral profiles throughout mammalian evolution and examine the

uniqueness of the hominoids in a broad phylogenetic framework. Results are placed in the

context of recently proposed models of hominin vertebral evolution, with implications for

homology and homoplasy and their roles in the evolution of hominoid vertebral profiles,

including that of humans. An earlier version of this manuscript was accepted for publication in

the Journal of Human Evolution.

Chapter 3: Variation in anthropoid vertebral formulae

This chapter is dedicated to quantifying and comparing intraspecific variation and

interspecific similarity in vertebral formulae among hominoids and other anthropoids included in

this study. To accomplish this, two indices are calculated: 1) the diversity index, which measures

the amount of variation observed in a population compared to the maximum amount of variation

possible, and 2) the similarity index, which measures the extent to which two populations share a set of patterns and compares them in a way analogous to genetic identity calculated from allele frequencies. These indices allow for testing models of hominoid vertebral evolution that call for disparate amounts of homoplasy, and by inference, different patterns of past selection pressures.

Chapter 4: The diaphragmatic vertebra and dorsostability in hominoids

In this chapter, I examine the association between last rib-bearing and diaphragmatic vertebrae in hominoids and other mammals. In most mammals, the diaphragmatic vertebra marks the transition from "thoracic-type" to "lumbar-type" articulations between adjacent vertebrae. Post-diaphragmatic vertebrae resist flexion and extension of the spine; as such, they play a large role in the dorsomobility of the vertebral column. Unlike most mammals, which are dorsomobile, hominoids are dorsostable and accomplish this in part through a caudal placement of the diaphragmatic vertebra, which acts to decrease the length of the post-diaphragmatic spine. The position of the diaphragmatic vertebra is compared within hominoids and among hominoids, cercopithecoids, and other mammals. Fossil Miocene hominoids and Plio-Pleistocene hominins are reexamined in this context.

Chapter 5: Conclusion

In this chapter, I summarize and synthesize my findings and discuss their bearings on homology and homoplasy in the hominoid postcranium and implictations for the evolution of orthogrady and bipedalism. Avenues of future research are outlined.

CHAPTER 1 REFERENCES

Alba, D.M., Almécija, S., Moyà-Solà, S., 2010. Locomotor inferences in *Pierolapithecus* and *Hispanopithecus*: reply to Deane and Begun (2008). J. Hum. Evol. 59, 143-149.

Alba, D.M., Fortuny, J., Moyà-Solà, S., 2010. Enamel thickness in the Middle Miocene great apes *Anoiapithecus*, *Pierolapithecus*, and *Dryopithecus*. Proc. R. Soc. B 277, 2237-2245.

Almécija, S., Alba, D.M., Moyà-Solà, S., 2009. *Pierolapithecus* and the functional morpohlogy of Miocene ape hand phalanges: paleobiolocal and evolutionary implications. J. Hum. Evol. 57, 284-297.

Almécija, S., Alba, D.M., Moyà-Solà, S., Köhler, M., 2007. Orang-like manual adaptations in the fossil hominoid *Hispanopithecus laietanus*: first steps towards great ape suspensory behaviours. Proc. R. Soc. B 274, 2375-2384.

Andrews, P. Evolution and environment in the Hominoidea. Nature 360, 641-646.

Andrews, P., Cronin, J.E., 1982. The relationships of *Sivapithecus* and *Ramapithecus* and the evolution of the orang-utan. Nature 297, 541-546.

Andrews, P., Groves, C.P., 1976. Gibbons and brachiation. In: D.M. Rumbaugh (Ed.), Gibbon and Siamang, Vol. 4. Karger, Basel, pp. 167-218.

Andrews, P., Harrison, T., 2005. The last common ancestor of apes and humans. In: D.E. Lieberman, R.J. Smith, J. Kelley (Eds.), Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam. Brill Academic Publishers, Boston, pp. 103-121.

Ankel, F., 1967. Morphologie von Wirbelsäule und Brustkorb. Primatologia 4, 1-120.

Ankel, F., 1972. Vertebral morphology of fossil and extant primates. In: R. Tuttle (Ed.), Functional and Evolutionary Biology of Primates. Aldine Press, Chicago, pp. 223-240.

Beard, K.C., Teaford, M.F., Walker, A., 1986. New wrist bones of *Proconsul africanus* and *Proconsul nyanzae* from Rusinga Island, Kenya. Folia Primatol. 47, 97-118.

Begun, D.R., 1993. New catarrhine phalanges from Rudabánya (Northeastern Hungary) and the problem of parallelism and convergence in hominoid postcranial morphology. J. Hum. Evol. 24, 373-402.

Begun, D.R., 2004. Knuckle-walking and the origin of human bipedalism. In: D.J. Meldrum, C.E. Hilton (Eds.), From Biped to Strider: The Emergence of Modern Human Walking. Kluwer, New York, pp. 9-33.

Begun, D.R., 2007. How to identify (as opposed to define) a homoplasy: examples from fossils and living great apes. J. Hum. Evol. 52, 559-572.

Begun, D.R., 2009. Dryopithecins, Darwin, de Bonis, and the European origin of the African apes and human clade. Geodiversitas 31, 789-816.

Begun, D.R., 2010. Miocene hominids and the origins of the African apes and humans. Annu. Rev. Anthropol. 39, 67-84.

Begun, D.R., Kordos, L., 1997. Phyletic affinities and functional convergence in Dryopithecus and other Miocene and living hominoids. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 291-316.

Begun, D.R., Teaford, M.F., Walker, A., 1994. Comparative and functional anatomy of *Proconsul* phalanges from the Kaswanga primate site, Rusinga Island, Kenya. J. Hum. Evol. 26, 89-165.

Begun, D.R., Ward, C.V., 2005. Comment on "*Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. Science 308, 203c.

Begun, D.R., Ward, C.V., Rose, M.D., 1997. Events in Hominoid Evolution. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 389-415.

Benefit, B.R., McCrossin, M.L., 1995. Miocene hominoids and hominid origins. Annu. Rev. Anthropol. 24, 237-256.

Benefit, B.R., McCrossin, M.L., 1997. Earliest known Old World monkey skull. Nature 388, 368-371.

Benton, R.S., 1967. Morphological evidence for adaptations within the epaxial region of the primates. In: van der Hoeven, F. (Ed.), The Baboon in Medical Research, Vol. II. University of Texas Press, Austin, pp. 201-216.

Benton, R.S., 1974. Structural patterns in the Pongidae and Cercopithecidae. Y. Phys. Anthropol. 18, 65-88.

Beynon, A.D., Dean, M.C., Reid, D.J., 1991. On thick and thin enamel in hominoids. Am. J. Phys. Anthropol. 86, 295-309.

Bolker, J.A., Raff, R.A., 1996. Developmental genetics and traditional homology. BioEssays 18, 489-494.

Casanovas-Vilar, I., Alba, D.M., Garcés, M., Robles, J.M., Moyà-Solà, S., 2011. Updated chronology for the Miocene hominoid radiation in Western Eurasia. Proc. Natl. Acad. Sci. USA 108, 5554-5559.

Clauser, D., 1980. Functional and comparative anatomy of the primate spinal column: some locomotor and postural adaptations. Ph.D. dissertation, University of Wisconsin-Milwaukee.

Corruccini, R.S., 1978. Primate skeletal allometry and hominoid evolution. Evolution 32, 752-758.

Corruccini, R.S., Ciochon, R.L., McHenry, H.M., 1976. The postcranium of Miocene hominoids: were dryopithecines merely "dental apes"? Primates 17, 205-223.

Dainton, M., Macho, G.A., 1999. Did knuckle-walking evolve twice? J. Hum. Evol. 36, 171-194.

Davis, D.D., 1954. Primate evolution from the viewpoint of comparative anatomy. Hum. Biol. 26, 211-219.

Deane, A.S., Begun, D.R., 2008. Broken fingers: retesting locomotor hypotheses for fossil hominoids using fragmentary proximal phalanges and high-resolution polynomial curve fitting (HR-PCF). J. Hum. Evol. 55, 691-701.

Deane, A.S., Begun, D.R., 2010. *Pierolapithecus* locomotor adaptations: a reply to Alba et al.'s comment on Deane and Begun (2008). J. Hum. Evol. 59, 150-154.

Disotell, T.R., 1994. Generic level relationships of the Papionini (Cercopithecoidea). Am. J. Phys. Anthropol. 94, 47-57.

Erikson, G., 1963. Brachiation in New World monkeys and in anthropoid apes. Symp. Zool. Soc. Lond. 10, 135-163.

Filler, A.G., 1993. Evolution of the sacrum in hominoids. In: Doty, J.R., Rengachary, S.S. (Eds.). Surgical Disorders of the Sacrum. Thieme Medical Publishers, New York, pp. 13-20.

Filler, A.G., 2007. Homeotic evolution in the Mammalia: diversification of therian axial seiation and the morphogenetic basis of human origins. PLoS One. 10, e1019.

Finarelli, J.A., Clyde, W.C., 2004. Reassessing hominoid phylogeny: evaluating congruence in the morphological and temporal data. Paleobiol. 30, 614-651.

Gebo, D.L., 1996. Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. Am. J. Phys. Anthropol. 101, 55-92.

Gebo, D.L., 2010. Locomotor function across primates (including humans). In: C.S. Larson (Ed.), A Companion to Biological Anthropolgoy. Wiley-Blackwell, pp. 530-544.

Gebo, D.L., Beard, K.C., Teaford, M.F., Walker, A., Larson, S.G., Jungers, W.L., Fleagle, J.G., 1988. A hominoid proximal humerus from the Early Miocene of Rusinga Island, Kenya. J. Hum. Evol. 17, 393-401.

Gebo, D.L., Malit, N.R., Nengo, I.O., 2009. New proconsuloid postcranials from the early Miocene of Kenya. Primates 50, 311-319.

Gebo, D.L., MacLatchy, L., Kityo, R., Deino, A., Kingston, J., Pilbeam, D., 1997. A hominoid genus from the early Miocene of Uganda. Science 276, 401-404.

Haeusler M, Martelli SA, Boeni T. 2002. Vertebrae numbers of the early hominid lumbar spine. J. Hum. Evol. 43:621-643.

Harrison, T., 1987. The phylogenetic relationships of the early catarrhine primates: a review of the current evidence. J. Hum. Evol. 16, 41-80.

Harrison, T., 2002. Late Oligocene to middle Miocene catarrhines from Afro-Arabia. In: W.C. Hartwig (Ed.), The Primate Fossil Record. Cambridge University Press, Cambridge, pp. 311-338.

Harrison, T., 2010*a*. Dendropithecoidea, Proconsuloidea, and Hominoidea. In: L. Werdelin, W.J. Sanders (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 429-469.

Harrison, T., 2010*b*. Apes among the tangled branches of human origins. Science 327, 532-534.

Harrison, T., Rook, L., 1997. Enigmatic anthropoid or misunderstood ape: the phylogenetic status of *Oreopithecus bambolii* reconsidered. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 327-362.

Hartwig, W., 2005. Implications of molecular and morphological data for understanding ateline phylogeny. Int. J. Primatol. 26, 999-1015.

Ishida, H., Kunimatsu, Y., Takano, T., Nakano, Y., Nakatsukasa, M., 2004. *Nacholapithecus* skeleton from the Middle Miocene of Kenya. J. Hum. Evol. 69-103.

Keith, A., 1903. The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates. J. Anat. Physiol. 37, 18-40.

Kelley, J.J., 1986. Paleobiology of Miocene hominoids. Ph.D. dissertation, Yale University.

Kivell, T.L., Schmitt, D., 2009. Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. Proc. Natl. Acad. Sci. USA 106, 14241-14246.

Larson, S.G., 1998. Parallel evolution in the hominoid trunk and forelimb. Evol. Anthropol. 6, 87-99.

Latimer, B., Ward, C.V., 1993. The thoracic and lumbar vertebrae. In: Walker, A., Leakey, R. (Eds.). The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 266-293.

Lovejoy, C.O., 2005. The natural history of human gait and posture Part 1. Spine and pelvis. Gait Posture 21, 95-112.

Lovejoy, C.O., 2007. An early ape shows its hand. Proc. R. Soc. B 274, 2373-2374.

Lovejoy, C.O., McCollum, M.A., 2010. Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip–bent-knee gait. Phil. Trans. R. Soc. B 365, 3289-3299.

Lovejoy, C.O., Suwa, G., Simpson, S.W., Matternes, J.H., White, T.D., 2009*a*. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. Science 326, 73, 100-106.

Lovejoy, C.O., Latimer, B., Suwa, G., Asfaw, B., White, T.D., 2009*b*. Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. Science 326, 72.

Lovejoy, C.O., Simpson, S.W., White, TD., Asfaw, B., Suwa, G., 2009*c*. Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. Science 326, 70.

Lovejoy, C.O., Suwa, G., Spurlock, L., Asfaw, B, White, T.D., 2009*d*. The pelvis and femur of *Ardipithecus ramidus*: the emergence of upright walking. Science 326: 71.

MacLatchy, L., 2004. The oldest ape. Evol. Anthropol. 13, 90-103.

MacLatchy, L., Gebo, D., Kityo, R., Pilbeam, D., 2000. Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. J. Hum. Evol. 39, 159-183.

MacLatchy, L.M., Pilbeam, D.P., 1999. Renewed research in the Ugandan early Miocene. In: P. Andrews, P. Banham (Eds.), Late Cenozoic Environments and Hominid Evolution: a tribute to Bill Bishop. The Royal Geological Society, London, pp. 15-25.

Madar, S.I., Rose, M.D., Kelley, J., MacLatchy, L., 2002. New *Sivapithecus* postcranial specimens from the Siwaliks of Pakistan. J. Hum. Evol. 42, 705-752.

McCollum, M.A., Rosenman, B.A., Suwa, G., Meindl, R.S., Lovejoy, C.O., 2010. The vertebral formula of the last common ancestor of African apes and humans. J. Exp. Biol. 314B, 123-134.

McHenry, H.M., Corruccini, R.S., 1983. The wrist of *Proconsul africanus* and the origin of hominoid postcranial adaptations. In: R.L. Ciochon, R.S. Corruccini (Eds.), New Interpretations of Ape and Human Ancestry. Plenum Press, New York, pp. 353-367.

Mivart, G., 1865. Contributions toward a more complete knowledge of the axial skeleton of primates. Proc. Zool. Soc. Lond. 1865, 545-592.

Morbeck, M.E., 1975. *Dryopithecus africanus* forelimb. J. Hum. Evol. 4, 39-46.

Moyà-Solà, S., Alba, D.M., Almécija, S., Casanovas-Vilar, I., Köhler, M., De Esteban-Trivigno, S., Robles, J.M., Galindo, J., Fortuny, J., 2009*b*. A unique Middle Miocene European hominoid and the origins of the great ape and human clade. Proc. Natl. Acad. Sci. USA 106, 9601-9606.

Moyà-Solà, S., Köhler, M., 1996. A *Dryopithecus* skeleton and the origins of great-ape locomotion. Nature 379, 156-159.

Moyà-Solà, S., Köhler, M., Alba, D.M., 2005. Response to comment on "*Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain". Science 308, 203d.

Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., 2004. *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. Science 306, 1339-1344.

Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Cabrera, L., Garcés, M., Almécija, S., Beamud, E., 2009*a*. First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Albocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. Am. J. Phys. Anthropol. 139, 126-145.

Nakatsukasa, M., 2008. Comparative study of Moroto vertebral specimens. J. Hum. Evol. 55, 581-588.

Nakatsukasa, M., Kunimatsu, Y., 2009. *Nacholapithecus* and its importance for understanding hominoid evolution. Evol. Anthropol. 18, 103-119.

Nakatsukasa, M., Kunimatsu, Y., Nakano, Y., Ishida, H., 2007. Vertebral morphology of *Nacholapithecus kerioi* based on KNM-BG 35250. J. Hum. Evol. 52, 347-369.

Nakatsukasa, M., Kunimatsu, Y., Nakano, Y., Takano, T., Ishida, H., 2003. Comparative and functional anatomy of phalanges in *Nacholapithecus kerioi*, a Middle Miocene hominoid from northern Kenya. Primates 44, 371-412.

Napier, J.R., Davis, P.R., 1959. The forelimb skeleton and associated remain of *Proconsul africanus*. Fossil Mammals of Africa. Brit. Mus. (Nat. Hist.) 16, 1-70.

O'Connor, B.L., 1976. *Dryopithecus* (*Proconsul*) *africanus*: quadruped or non-quadruped?

Pilbeam, D.R., 1982. New hominoid skull material from the Miocene of Pakistan. Nature 295, 232-234.

Pilbeam, D., 1996. Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. Mol. Phylogen. Evol. 5, 155-168.

Pilbeam, D., 1997. Research on Miocene hominoids and hominid origins: the last three decades. In: Begun, D.R., Ward, C.V., Rose, M.D. (Eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum Press, New York, pp. 13-28.

Pilbeam, D., 2004. The anthropoid postcranial axial skeleton: comments on development, variation, and evolution. J. Exp. Zool. 302B, 241-267.

Pilbeam, D.R., Rose, M.D., Barry, J.C., Ibrahim Shah, S.M., 1990. New *Sivapithecus* humeri from Pakistan and the relationship of *Sivapithecus* to *Pongo*. Nature 348, 237-239.

Pilbeam, D.R., Young, N.M., 2001. Sivapithecus and hominoid evolution: some brief comments. In: L. de Bonis, G. Koufos (Eds.), Hominoid Evolution and Climate Change in Europe, Vol. 2, Phylogeny of the Neogene Hominoid Primates of Eurasia. Cambridge University Press, Cambridge 349-364.

Pilbeam, D., Young, N., 2004. Hominoid evolution: synthesizing disparate data. C. R. Palevol 3, 305-321.

Preuschoft, H., 1973. Body posture and locomotion in some East African Miocene Dryopithecinae. Symp. Soc. Study Hum. Biol. 11, 13-46.

Richmond, B.G., Whalen, M., 2001. Forelimb function, bone curvature and phylogeny of *Sivapithecus*. In: L. de Bonis, G. Koufos (Eds.), Hominoid Evolution and Climate Change in Europe, Vol. 2, Phylogeny of the Neogene Hominoid Primates of Eurasia. Cambridge University Press, Cambridge, pp. 326-348.

Rose, M.D., 1975. Functional proportions of primate lumbar vertebral bodies. J. Hum. Evol. 4, 21-38.

Rose, M.D., 1983. Miocene hominoid postcranial morphologoy: monkey-like, ape-like, neither, or both? In: R.L. Ciochon, R.S. Corruccini (Eds.), New Interpretations of Ape and Human Ancestry. Plenum Press, New York, pp. 405-417.

Rose, M.D., 1984. Hominoid postcranial specimens from the Middle Miocene Chinji Formation, Pakistan. J. Hum. Evol. 13, 503-516.

Rose, M.D., 1993. Locomotor anatomy of Miocene hominoids. In: D.L. Gebo (Ed.), Postcranial Adaptation in Nonhuman Primates. Northern Illinois University Press, DeKalb, IL, pp. 71-95.

Rose, M.D., 1994. Quadrupedalism in some Miocene catarrhines. J. Hum. Evol. 26, 387-411.

Rose, M.D., 1997. Functional and phylogenetic features of the forelimb in Miocene hominoids. D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 79-100.

Rosenman, B.A., 2008. Triangulating the evolution of the vertebral column in the last common ancestor: thoracolumbar transverse process homology in the hominoidea. Ph.D. dissertation, Kent State University.

Sánchez-Villagra, M., Williams, B.A., 1998. Levels of homoplasy in the evolution of the mammalian skeleton. J. Mammal. Evol. 5, 113-126.

Sanders, W.J., 1995. Function, allometry, and the evolution of the australopithecine lower precaudal spine. Ph.D. dissertation, New York University.

Sanders, W.J., 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J. Hum. Evol. 34, 249-302.

Sanders, W.J., Bodenbender, B.E., 1994. Morphometric analysis of lumbar vertebra UMP 67-28: implications for spinal function and phylogeny of the Miocene Moroto hominoid. J. Hum. Evol. 26, 203-237.

Sarmiento, E.E., 2010. Comment on the paleobiology and classification of *Ardipithecus ramidus*. Science 328, 1105-b.

Schön, M.A., Ziemer, L.K., 1973. Wrist mechanism and locomotor behavior of *Dryopithecus* (*Proconsul*) *africanus*. Folia Primatol. 20, 1-11.

Schultz, A., 1930. The skeleton of the trunk and limbs of higher primates. Hum. Biol. 2, 303-438.

Schultz, A.H., 1961. Vertebral column and thorax. Primatologia 4, 1-66.

Shapiro, L.J., 1991. Functional morphology of the primate spine with special reference to orthograde posture and bipedal locomotion. Ph.D. dissertation, SUNY Stony Brook.

Shapiro, L., 1993*a*. Functional morphology of the vertebral column in primates. In: Gebo, D.L. (Ed.), Postcranial Adaptation in Nonhuman Primates. Northern Illinois University Press, Dekalb, IL.

Shapiro, L., 1993*b*. Evaluation of "unique" aspects of human vertebral bodies and pedicles with a consideration of *Australopithecus africanus*. J. Hum. Evol. 25, 433-470.

Shea, B.T., 1985. On aspects of skull form in African apes and orangutans, with implications for hominoid evolution. Am. J. Phys. Anthropol. 68, 329-342.

Shea, B.T., 1988. Phylogeny and skull form in the hominoid primates. In: J. Schwartz (Ed.), Orang-Utan Biology. Oxford University Press, New York, pp. 233-245.

Wake, D.B., Wake, M.H., Specht, C.D., 2011. Homoplasy: from detecting pattern to determining process and mechanism of evolution. Science 331, 1032-1035.

Walker, A., 1997. *Proconsul*: function and phylogeny. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 209-224.

Walker, A.C., Pickford, M., 1983. New postcranial fossils of *Proconsul africanus* and *Proconsul nyanzae*. In: R.L. Ciochon, R.S. Corruccini (Eds.), New Interpretations of Ape and Human Ancestry. Plenum Press, New York, pp. 325-351.

Walker, A., Rose, M.D., 1968. Fossil hominoid vertebra from the Miocene of Uganda. Nature 217, 980-981.

Ward, C.V., 1991. The functional anatomy of the lower back and pelvis of the Miocene hominoid *Proconsul nyanzae* from the Miocene of Mfangano Island, Kenya. Ph.D. dissertation, The Johns Hopkins University.

Ward, C.V., 1993. Torso morphology and locomotion in *Proconsul nyanzae*. Am. J. Phys. Anthropol. 92, 291-328.

Ward, C.V., 1997a. Functional anatomy and phyletic implications of the hominoid trunk and hindlimb. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 101-130.

Ward, C.V., 1998. *Afropithecus*, *Proconsul*, and the primitive hominoid skeleton. In: E. Strasser, J. Fleagle, A. Rosenberger, McHenry, H. (Eds.), Primate Locomotion: Recent Advances. Plenum Press, New York, pp. 337-352.

Ward, C.V., 2007. Postcranial and locomotor adaptations of hominoids. In: W. Henke, I. Tattersal (Eds.), Handbook of Paleoanthropology. Vol. 2: Primate Evolution and Human Origins. Springer, Berlin, pp. 1011-1030.

Ward, C.V., Walker, A., Teaford, M.F., Odhiambo, I., 1993. Partial skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. Am. J. Phys. Anthropol. 90, 77-111.

Ward, S., 1997*b*. The taxonomy and phyletic relationships of *Sivapithecus* revisited. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 269-290.

Ward, S.C., Brown, B., 1986. The facial skeleton of *Sivapithecus indicus*. In: D.R. Swindler, J. Erwin (Eds.), Comparative Primate Biology, Vol. 1: Systematics, Evolution, and Anatomy. Alan R. Liss, New York, pp. 413-452.

Ward, S.C., Kimbel, W.H., 1983. Subnasal alveolar morphology and the systemic position of *Sivapithecus*. Am. J. Phys. Anthropol. 61, 157-171.

Ward, S.C., Pilbeam, D.R., 1983. Maxillofacial morphology of Miocene hominoids from Africa and Indo-Pakistan. In: R.L. Corruccini, R.S. Ciochon (Eds.), New Interpretation of Ape and Human Ancestry. Plenum, New York, pp. 211-238.

White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G., WoldeGabriel, G., 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. Science 326, 64, 75-86.

Williams, B.A., 2007. Comparing levels of homoplasy in the primate skeleton. J. Hum. Evol. 52, 480-489.

Williams, S.A., 2010. Morphological integration and the evolution of knuckle-walking. J. Hum. Evol. 58, 432-440.

Wood, B., Harrison, T., 2011. The evolutionary context of the first hominins. Nature 470, 347-352.

Young, N.M., 2002. Homology and homoplasy in the evolution of the hominoid postcranium. Ph.D. dissertation, Harvard University.

Young, N.M., 2003. A reassessment of living hominoid postcranial variability: implications for ape evolution. J. Hum. Evol. 45, 441-464.

Young, N.M., 2005. Estimating hominoid phylogeny from morphological data: character choice, phylogenetic signal and postcranial data. In: D.E. Lieberman, R.J. Smith, J. Kelley (Eds.), Interpreting the Past. Brill Academic, Boston, pp.1-13.

Young, N.M., MacLatchy, L., 2004. The phylogenetic position of *Morotopithecus*. J. Hum. Evol. 46, 163-184.

CHAPTER 2

THE EVOLUTIONARY HISTORY OF HOMINOID VERTEBRAL FORMULAE

INTRODUCTION

The numerical composition of the vertebral column has been of interest to biologists for over a quarter of a millennium (e.g., Buffon, 1769; Owen, 1866; Flower, 1884; Welcker, 1881; Keith, 1903). This anatomical region has generated newfound interest in recent years, due in part to the role of *Hox* genes in its evolution (Burke et al., 1995; Belting et al., 1998; Richardson et al., 1998; Wellik and Capecchi, 2003; Ohya et al., 2005; Wellik, 2007, 2009; Alexander et al., 2009; Iimura et al., 2009; Mallo et al., 2010; Mansfield and Abzhanov, 2010) and particularly in light of our modern understanding of phylogenetic relationships among mammals (Pilbeam, 2004; Narita and Kuratani, 2005; Sánchez-Villagra et al., 2007; Asher et al., 2009, 2011; Muller et al., 2010). The role of numerical variation in the vertebral column in the evolution of hominoid primates has likewise experienced a resurgence, in large part due to the implications for hominin origins and the evolution of bipedalism (Haeusler et al., 2002; Pilbeam, 2004; Rosenman, 2008; Lovejoy et al., 2009; Lovejoy and McCollum, 2010; McCollum et al., 2010).

Recently, Haeusler et al. (2002), Pilbeam (2004), and McCollum and colleagues (Lovejoy and McCollum, 2010; McCollum et al., 2010) proposed different evolutionary scenarios to explain the numerical variation of the human vertebral column. According to Haeusler and colleagues, the modal human vertebral formula of 7:12:5:5 (combination of cervical: C, thoracic: T, lumbar: L, and sacral: S vertebrae, abbreviated as C:T:L:S) evolved in

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an ancestral great ape (hominid) and has been retained in humans. This contrasts with the "chimp-like" ancestor with three to four lumbar vertebrae (7:13:3-4:5-6) that Pilbeam proposed. McCollum and colleagues, on the other hand, suggest that hominins evolved from a primitive, "*Proconsul*-like" ancestor with at least six lumbar vertebrae (7:13:6-7:4). These three proposals are drastically different and require different evolutionary scenarios of hominoid evolution, including the evolution of orthogrady and bipedalism.

This study attempts to address two main questions: 1) which, if any, of the existing proposals best explains variation in vertebral formulae among hominoids and other anthropoids, and 2) how unique is the hominoid vertebral column against the diversity represented in all of Mammalia. To address these questions, I compile a large, comparative dataset of mammalian vertebral formulae and analyze it in a modern phylogenetic framework. It is argued here that hominoids are unique among anthropoids and other primates in the possession of a reduced thoracolumbar (thoracic+lumbar = TL) region and concomitantly increased sacrum (sacralization of lumbar vertebrae, or lumbar sacralization; Keith, 1923; Schultz, 1930; Jungers, 1984; Abitbol, 1987). Furthermore, the evolutionary scenario that best accords with the distribution of vertebral formulae among hominoids is the short-back model initially proposed by Keith (1903) and supported in Pilbeam (2004; see also Pilbeam, 1997). Hominins evolved from a short-backed, short-trunked ancestor with an "African ape-like" vertebral profile (7:13:4:5, 7:13:4:6, 7:13:3:6).

BACKGROUND

Two distinct developmental processes control the formation and identification of vertebrae – segmentation, the determination of total vertebral count, and specification, the

regionalization of vertebrae into one of several types (Gomez and Pourquié, 2009; Iimura et al., 2009; Mallo et al., 2010; see excellent reviews as they pertain to hominoid evolution in Pilbeam, 2004 and McCollum et al., 2010). Segmentation occurs through somitogenesis, the production of somites from presomitic mesoderm, the speed of which is determined by a "segmentation clock" (Dequeant and Pourquié, 2008). The speed of the segmentation clock determines the number and size of the somites that are produced; the faster the clock, the smaller and more numerous are the resulting somites (Gomez et al., 2008). Somites are produced at the rate of the segmentation clock until the presomitic mesoderm is exhausted.

Vertebrae are then derived from the somites through a process called resegmentation (Dequeant and Pourquié, 2008; Ilmura et al., 2009). While changes in segmentation involve meristic changes, or changes in the total number of somites that are produced, changes in specification are homeotic in nature (Bateson, 1894) and involve change in the identity of a somite (e.g., a shift from thoracic to lumbar identity). Homeotic changes are associated with alterations in the expression of Hox genes (Gaunt, 1994; Burke et al., 1995; Belting et al., 1998; Ohya et al., 2005; Mallo et al., 2010; Mansfield and Abzhanov, 2010). Mutations of this nature can cause homeotic transformations, as have occurred numerous times in vertebrate evolution to produce regionalization of the mammalian spine.

The mammalian vertebral column has been regionalized into five variably distinct types of vertebrae – cervical, thoracic, lumbar, sacral, and caudal (coccygeal in tail-less mammals). Rib-bearing, thoracic-like vertebrae likely represent the developmental and evolutionary "ground state" for vertebral patterning, suggested by both the fossil record and *Hox* mutant mouse experiments (Hildebrand, 1998; Wellik and Capecchi, 2003; Wellik, 2007). The largest disjunction has formed between caudal and precaudal regions, where precaudal vertebral count is

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relatively conserved and caudal count is highly variable; as such, numerical variation in caudal

and precaudal counts is not significantly correlated (Buchholtz, 2007). This is likely because the

production of caudal somites is controlled by a different process than precaudal segmentation,

the latter produced by the primitive knot and the former by the tail bud (Tam and Tan, 1992),

further demonstrating a developmental dissimilarity between caudal and precaudal regions, as

suggested by Polly et al. (2001) in the case of snakes.

Within the precaudal region, the number of cervical vertebrae is thought to be regulated

by developmental constraints in the form of strong stabilizing selection (Galis, 1999; Galis et al.,

2006). Although other vertebrates are inter- and intra-specifically variable in number of cervical

vertebrae, cervical count became fixed at seven in an ancestral synapsid (Muller et al., 2010) and

persists in nearly all mammals, with three exceptions. Manatees (genus *Trichechus*) deviate from

the modal pattern by one vertebra, possessing six cervical vertebrae (Buchholtz et al., 2007).

Tree sloths, which have independently evolved from separate, ground-dwelling ancestors with

seven cervical vertebrae, evolved divergent numbers of cervical vertebrae independently

(modally six in *Choloepus* and nine in *Bradypus*, with substantial amounts of intraspecific

variation in both taxa) (Buchholtz and Stepien, 2009). Otherwise, regardless of size or neck

length (e.g., giraffes – Van Sittert et al., 2010), all mammals possess a modal number of seven

cervical vertebrae, with little intraspecific variation. Humans are no exception, and it has been

shown that the high frequency of seven cervical vertebrae in humans is not due to a lack of

production of variation for this number but rather to strong stabilizing selection against

modification of the cervico-thoracic border in the developing embryo (Galis et al., 2006).

Offspring with more or fewer cervical vertebrae are usually not viable.

Thoracic and lumbar vertebrae regionalized most recently, deriving from the dorsal region of primitive synapsids prior to the divergence of modern mammals (Jenkins, 1971; Buchholtz, 2007). The thoracolumbar (TL = thoracic + lumbar vertebrae), or trunk, region of mammals coincides with the upper limb and cervical plexus at its cranial border and the lower limb and lumbo-sacral plexus at its caudal border. Like the cervical region, the number of TL vertebrae is conserved across many groups of mammals, although greater amounts of inter- and intra-specific variation in TL number exists compared to the cervical region (Welcker, 1881; Flower, 1885; Todd, 1922; Schultz and Straus, 1945; Narita and Kuratani, 2005; Sánchez-Villagra et al., 2007; Asher et al., 2009, 2011). Most mammals possess a mode of 19 TL vertebrae, although both increases and decreases in this number are observed in various groups of mammals, increases being less common than decreases (Welcker, 1881; Schultz and Straus, 1945; Sánchez-Villagra et al., 2007).

Within Primates, both increases and decreases in the modal number of TL vertebrae occur, the latter occurring via a reduction in the number of lumbar vertebrae (Schultz and Straus, 1945; Erickson, 1963; Benton, 1967). Benton (1967) differentiated primates among "short-" and "long-backed" groups based on the length and number of vertebrae in the lumbar column. Hominoids and atelids (*Alouatta* + atelines: *Ateles*, *Brachyteles*, *Lagothrix*), which generally possess five or fewer lumbar vertebrae, were lumped in the short-backed group, whereas all other primates, including strepsirhines and non-hominoid or non-atelid haplorhines, were relegated to the long-backed group. Members of the latter group generally possess more than five lumbar vertebrae.

Haeusler et al. (2002), Pilbeam (2004), and Lovejoy and colleagues (Lovejoy et al., 2009; Lovejoy and McCollum, 2010; McCollum et al., 2010) invoke very different evolutionary

scenarios of hominoid evolution to explain the numerical composition and variation exhibited by extant hominoids. Pilbeam, like Keith (1903) long before him, argued that a reduced lumbar region is homologous in living hominoids, being synapomorphic for the group and having evolved in their last common ancestor (LCA). In contrast, under Lovejoy and colleagues' scenario, a long, primitive lumbar region persisted throughout hominoid evolution, with the implication that reduced lumbar regions necessarily evolved independently in each extant hominoid (*Hylobates*, *Pongo*, *Gorilla*, *Homo*, and independently in both *Pan paniscus* and *Pan troglodytes*) and probably also in several fossil taxa. The scenario proposed by Haeusler and colleagues is somewhat intermediate, requiring that orangutans, gorillas, and chimpanzees reduced lumbar regions independently, while hylobatids and humans retain the primitive number of 5 lumbar vertebrae.

In this paper, I will test these competing hypotheses by analyzing a combined dataset consisting of data from Pilbeam (2004), McCollum et al. (2010) and other sources (see below), supplemented with my own data. Non-catarrhine primates and non-primate mammals are included for a broad phylogenetic comparison to reconstruct vertebral formula evolution throughout mammalian evolution and to determine the uniqueness of hominoid vertebral formulae. Together, these approaches will allow for discrimination among the short-back, long-back, and intermediate models and the determination of the likelihood of homoplasy in hominoid vertebral formula evolution. If hominoid-like vertebral formulae are relatively common among mammals, then the likelihood of homoplasy within hominoids is increased; conversely, uniqueness of hominoid formulae would increase the likelihood of homology.

MATERIALS AND METHODS

Schultz (1961; Schultz and Straus, 1945) published descriptive statistics and frequencies of vertebral counts but did not include complete vertebral formulae for individual specimens, data that are important for understanding variation and homeotic change within and between taxa. Fortunately, Schultz did keep detailed individual specimen sheets containing hand-written records of quantitative measurements, qualitative observations, and vertebral count information for a subset of specimens. Pilbeam (2004) compiled the Schultz dataset of individual vertebral formulae and supplemented those data with other published sources and his own records.

Overall, the dataset presented in and analyzed by Pilbeam included 181 humans (*Homo sapiens*), 179 chimpanzees (*Pan troglodytes*), 17 bonobos (*Pan paniscus*), 86 western gorillas (*Gorilla gorilla*), 14 eastern gorillas (*Gorilla beringei*)[4], 153 orangutans (*Pongo pygmaeus*), 105 white-handed gibbons (*Hylobates lar*), and 62 siamangs (*Symphalangus syndactylus*). Pilbeam also included other hylobatids (*Hylobates moloch*, *Bunopithecus hoolock*, *Nomascus concolor,* and *Nomascus gabriellae*), cercopithecoids, ceboids, and several rodent species for comparison with the hominoid sample. McCollum et al. (2010) expanded the bonobo sample in Pilbeam's dataset by including specimens from the Royal Museum for Central Africa (RMCA; Tervuren, Belgium). In the end, their efforts contributed 14 additional specimens to the bonobo sample, increasing the sample size to 31.

Here, the Pilbeam/McCollum dataset is supplemented with 1275 primate specimens examined by the author, including 726 hominoids, 360 cercopithecoids, 131 platyrrhines, and 135 strepsirhines (see Appendix B for species and specimen information). This combined dataset

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[4] Here, and throughout, I follow Groves (2001, 2003) and Jensen-Seaman et al. (2003) in allocating gorillas into two species, *Gorilla gorilla* ("western gorillas," including subspecies *G. g. gorilla* and *G. g. diehli*) and *Gorilla beringei* ("eastern gorillas," including subspecies *G. b. graueri*, *G. b. beringei*, and possibly also *G. b. rex-pygmaeorum*).

yields 22 well-sampled (N>30) anthropoid taxa for analysis: 273 humans, 271 chimpanzees, 40

bonobos, 172 western gorillas, 51 eastern gorillas, 182 orangutans, 190 white-handed gibbons,

84 siamangs, 125 lutungs (*Trachypithecus sp.*), 42 snub-nosed monkeys (*Nasalis larvatus*), 128

guenons (*Cercopithecus sp.*), 71 vervets (*Chlorocebus aethiops*), 81 long-tailed macaques

(*Macaca fascicularis*), 883 Japanese macaques (*Macaca fuscata*), 31 *Cercocebus* mangabeys

(*Cercecebus sp.*), 91 *Lophocebus* mangabeys (*Lophocebus sp.*), 120 baboons (*Papio sp.*), 30

geladas (*Theropithecus gelada*), 40 squirrel monkeys (*Saimiri sciureus*), 63 capuchins (*Cebus

sp.*), 39 howler monkeys (*Alouatta sp.*), and 39 spider monkeys (*Ateles sp.*) (Table 2.1).

Additionally, the primate dataset is combined with a large sample of non-primate

mammals compiled from various sources (mainly from Gerrard, 1862; Flower, 1884; Hasebe,

1913; Hatt, 1932; Clauser, 1980; Filler, 1986; Pilbeam, 2004; Sánchez-Villagra et al., 2007;

Asher et al., 2009, 2011; personal communications with E. Buchholtz, C. Lovejoy, D. Pilbeam,

E. Sargis, and A. Zihlman) (see Appendix B for a full list of taxa and sources). This comparative

mammalian dataset includes over 8,000 specimens and represents all major clades and orders of

mammals. It serves as a broad survey in which to reconstruct ancestral vertebral formulae and

interpret the uniqueness of the hominoid vertebral formula. Specimens compiled by researchers

employing non-Schultz-like criteria (see below) (e.g., Gerrard, 1862; Flower, 1884) were used

only for broad comparative purposes and were not included in the more detailed analyses

described below.

Seriation

Both articulated (either naturally by soft tissue or by curatorial rearticulation for display

purposes) and non-articulated museum specimens were examined by the author. Disarticulated

specimens were seriated to check for extra or missing vertebrae. Missing vertebra were identified when it was obvious during seriation that one or more vertebra was not present, indicated by lack of comfortable articulation at adjoining bodies and/or zygapophyses. Specimens found to be missing vertebrae were excluded from further examination and only specimens with complete precaudal vertebral series (full set of cervical, thoracic, lumbar, and sacral elements) were included.

Duplication and repeatability

A potential issue in compiling vertebral formulae from various sources is duplication, where an individual is represented multiple times in a dataset. To avoid this problem, specimen numbers reported in Schultz (1930, 1933) and recorded in the Schultz and Pilbeam datasheets (kindly provided by D. Pilbeam) were combined with the author's own records. Repeated individuals were analyzed only once; in 197 cases (27 chimpanzees, 17 bonobos, 23 western gorillas, 2 eastern gorillas, 21 orangutans, 28 white-handed gibbons, 22 siamangs, 53 lutungs, and 4 spider monkeys), the author recorded the same specimen as did Schultz or Pilbeam. This allowed for an assessment of repeatability, which is 100% in this sample, suggesting that the Schultz method of vertebra classification is highly repeatable.

In the case of bonobos, the Schultz/Pilbeam dataset included 17 individuals. McCollum et al. (2010) supplemented the sample with 14 additional specimens from the Royal Museum for Central Africa (RMCA). Here, 25 bonobos (18 from the RMCA, four from the Royal Belgian Institute of Natural Sciences, two from the Museum of Comparative Zoology, and one from the Field Museum of Natural History) were examined for this study. D. Pilbeam, C. O. Lovejoy, and

W. Wendelin provided accession numbers and assistance in sorting out the bonobo sample, which resulted in the addition of seven specimens to the dataset, now totaling to 38 individuals.

Cervico-thoracic (C-T) transition

Schultz (1930, 1961; Schultz and Straus, 1945) formalized the costal definition of vertebrae and used specific and strict criteria to define vertebrae of different regions. Cervical vertebrae are defined as vertebrae between the skull and thorax, following Turner (1847; see also Buchholtz and Stepien, 2009). Vertebrae with cervical ribs, costal processes that are free distally and do not articulate with the sternum directly or indirectly via an adjacent rib, are considered cervical. It should be noted here that transverse foramina, although common in humans throughout the cervical column, may be present in the first thoracic vertebra or lacking in the ultimate or last several cervical vertebrae in humans and other primates (personal observation; see also Duckworth, 1911).

Thoraco-lumbar (T-L) transition

Schultz defined thoracic vertebrae as those that bear ribs and lumbar vertebrae as those that do not. According to Schultz criteria, thoracic vertebra are those that bear ribs, even in cases where "the last and very short rib of one side was completely fused with the vertebra, giving it the appearance of a transitional vertebra, as which, however, it was not counted" (Schultz, 1930:310). Ankylosed (fused) ribs, therefore, which sometimes appear similar to lumbar transverse processes (LTPs), are counted as ribs under the Schultz definition. Ankylosed ribs are

often accompanied by fovea or foramina at the rib-body/pedicle border, indicating incomplete fusion of the rib (personal observation).

Lumbo-sacral (L-S) transition

Lumbar vertebrae are those situated between the thorax and pelvis. They do not bear ribs, but instead possess LTPs, which are partially homologous to ribs and thoracic transverse processes, or may be novel elements, depending on the taxon (Filler, 1986, 2007; but see Rosenman, 2008). The last lumbar vertebra is one that does not contribute to the sacrum. Schultz considered a vertebra at the L-S border to be sacral if its transverse processes articulate extensively with the ilium and form complete sacral foramina. Vertebrae that are partially fused to the sacrum at the body, zygapophyses, or transverse processes, or articulate with the ilium but do not form complete sacral foramina, are considered lumbar vertebrae.

Sacro-caudal (S-C) transition

Sacral vertebrae are those that form sacral foramina and are differentiated from caudal or coccygeal (hereto after referred to simply as caudal) vertebrae by this criterion. The number of sacral elements is tallied as (total number of sacral foramina)/2 + 1. Here, anterior and posterior foramina are counted together as one foramen.

Transitional vertebrae

At all borders, transitional (half-and-half) vertebrae have been recorded in the literature and observed directly by the author. Transitional vertebrae at the C-T border possess a full first

rib on one side and lack a rib or bear a cervical rib on the other side. At the T-L border, transitional vertebrae possess a costal facet or an ankylosed rib on one side and lack such a structure on the other, instead possessing an LTP. Transitional vertebrae at the L-S and S-C borders form one complete sacral foramen but not two complete foramina. At the L-S border, the non-sacral transverse process will either not articulate with the ilium or will articulate with it but not form a sacral foramen. At the S-C border, a non-sacral side will possess a free transverse process, one that does not articulate with the sacrum, or lacks a transverse process altogether, either way not forming a sacral foramen. Incomplete bony foramina that are nearly complete and were likely connected via cartilage are considered sacral elements (Schultz, 1961). In all cases, transitional vertebrae were counted as half (0.5) in one region and half in the other. A transitional vertebra at the T-L border would be allocated to both regions – 0.5 thoracic and 0.5 lumbar. For example, a column with 7 cervicals, 12 normal thoracics, a T-L transitional vertebra, 4 normal lumbars, and 5 sacrals would be recorded as: 7-12½-4½-5.

Descriptive statistics

Anthropoid taxa represented by at least 30 specimens are included in the comparative statistical analyses. Full precaudal formulae are compiled for each taxon and pattern frequencies are recorded. The modal formula is determined as the most commonly represented (highest frequency) pattern in each taxon. This method of analysis is preferred to a region-specific approach, in which vertebral formulae are not maintained and data for individual specimens are pooled by region. The latter approach is useful in that it allows for calculation of basic descriptive statistics (mean, mode, standard deviation, standard error) for each region and is also employed here. In both treatments, regions are combined into several super-hierarchies:

precaudal (CTLS), presacral (CTL), thoraco-lumbo-sacral (TLS), and thoracolumbar (TL). A vertebral profile, which consists of the mode and other formulae represented at greater than 10% frequency in a population, is determined for each taxon.

RESULTS

Vertebral count data were compiled for over 8,000 mammal specimens belonging to 474 genera and 724 species, including 60 genera and 137 species of primates (Appendix B). Of these, 22 anthropoids are represented at adequate sample sizes (N>30) to permit statistical analyses (Table 2.1). Full lists of vertebral formulae (from the combined dataset) for each of 22 well-sampled taxa are included in Appendix C. A vertebral profile, accounting for the modal formula and other formulae represented at greater than 10% frequency, is listed for each taxon in Table 2.2. Chimpanzees, bonobos, western gorillas, siamangs, guenons, and squirrel monkeys exhibit three vertebral formulae in their profiles, while humans, orangutans, white-handed gibbons, long-tailed macaques, *Cercocebus* mangabeys, baboons, and capuchins exhibit two, and eastern gorillas, lutungs, snub-nosed monkeys, Japanese macaques, *Lophocebus* mangabeys, geladas, and spider monkeys demonstrate just the modal pattern at greater than 10% frequency. The howler monkey vertebral profile includes five formulae, the modal formula (7:14:5:3) at 41% frequency and four subsequent formulae at 10.3% frequency each (7:14:6:3, 7: 7:15:5:3, 7:14:5:4, 7:15:5:4).

For convenience, the four categories of modal super-regional configurations can be reduced to two. Precaudal and CTL count consist of TLS and TL count plus the modal number of cervical vertebrae in each taxon (7), respectively. Therefore, only two of these, precaudal and TL

vertebral number, will be discussed in detail in the text, although all of these combinations, in addition to data for individual vertebral regions, are included in Appendix C.

Survey of Mammals

Here, and in the Discussion, trunk and sacral counts are treated separately for the broad survey of mammals provided. Although this is not ideal, it is necessary because sample sizes and the number of taxa included differ between the two categories. Sacral counts are sometimes not included in published accounts and/or are not recorded by researchers (e.g., Filler 1986; Sánchez-Villagra et al. 2007; Asher et al. 2009, 2011), limiting the number of taxa and specimens that include data for both regions.

TL number

Monotremes possess both 7 cervical and 19 TL vertebrae (17T:2L for *Ornithorhynchus* and 16T:3L for *Tachyglossus*; however the single *Zaglossus* specimen included here demonstrates a 16T:4L pattern). All marsupials demonstrate this pattern (7C:19TL), many possessing 13T:6L vertebrae (35 of 40 genera). Exceptions include feathertail gliders (*Acrobates pygmaeus*, 14T:5L), numbats (*Myrmecobius fasciatus*, 12T:7L), marsupial moles (*Notoryctes typhlops*, 15T:4L), koalas (*Phascolarctos cinereus*, 11T:8L), and common wombats (*Vombatus ursinus*, 15T:4L).

Among afrotherians, 19T:3L is the most common pattern (3 of 22 genera), although this pattern is restricted to three genera of golden moles (*Amblysomus*, *Calcochloris*, *Chrysochloris*). In addition, a variety of combinations exist, with modes ranging from 19 to 31 TL vertebrae.

Tenrecs, elephant shrews, aardvarks, golden moles, and elephants possess between 20 and 24 TL vertebrae modally, while hyraxes possess 29. Although sirenians possess modified vertebral columns that lack sacra, *Trichechus* is characterized by a modal number of 19 TL vertebrae (17T:2L), while *Dungong* has a 19T:4L pattern (23 TL).

Xenarthra is even more variable in TL combination, with modes ranging from 14 to 26 elements, and although 11T:3L is most common (4 of 13 genera), it is restricted to four genera of armadillos (*Chaetophractus*, *Chlamyphorus*, *Tolypeutes*, *Zaedyus*). While armadillos possess modes of 14 to 16 TL vertebrae, anteaters (*Cyclopes*, *Myrmecophaga*, *Tamandua*) are somewhat more conservative and possess between 18 and 20 TL vertebrae. Finally, the two genera of sloths, *Bradypus* and *Choloepus*, are characterized by 19 and 26 TL vertebrae, respectively.

Insectivores most commonly possess a 13T:6L modal pattern (9 of 20 genera; 14T:5L and 15T:5L are the next most common patterns, occurring in three genera each), but are quite interspecifically variable, with one genus exhibiting a highly modified lumbar region (14T:11L in *Scutisorex*, the hero shrew; see also Cullinane et al., 1998). Bats (Chiroptera) possess between 16 and 19 TL vertebrae of various combinations, with 11T:5L as the most common mode (7 of 26 genera; 13T:5L and 13T:6L are the next most common patterns, occurring in four genera each).

Pangolins are quite variable both inter- and intra-specifically, with TL count varying from 18 to 23 vertebrae. The single genus is bimodal at 15T:6L, but if species within *Manis* are treated separately, each of the six demonstrates a different TL number and pattern. Carnivorans (Order Carnivora) have experienced an increase in TL count by one element, resulting in 20 TL vertebrae in most taxa (81 of 88 genera). Among these, 13T:7L is the most common pattern (34 genera), followed by 15T:5L and 14T:6L (22 and 20 genera, respectively). Notable exceptions to

the 20 TL pattern among carnivorans are giant pandas (*Ailuropoda melanoleuca*) and with 18

and skunks (*Mephitis*, *Spilogale*, and *Conepatus*) with 21 to 22 TL vertebrae.

Perissodactyls are characterized by an increased TL count – 22 in rhinoceroses (19T:3L),

23 in tapirs (18T:5L), and 23 to 24 in horses (18T:5L or 18T:6L). Non-cetacean cetartiodactyls

largely possess a 13T:6L pattern (40 of 58 genera; the second most common variant, 14T:5L, is

represented in 11 genera). Cetaceans possess highly modified vertebral columns with highly

variable TL counts, both within and between species, ranging from 15 to 48 elements across the

order. No TL pattern is represented by more than two of 37 genera (9T:10L, 10T:9L, 11T:8L,

10T:12L, 12T:15L, 13T:14T, and 12T:16T are shared by two genera each).

Among lagomorphs, rabbits and hares possess 12T:7L (all four genera included in this

study – *Lepus*, *Oryctolagus*, *Sylvilagus, Pentalagus*), while pikas (genus *Ochotona*) possess 22

TL vertebrae (18T:4L or 17T:5L). In Rodentia, most taxa possess 19 TL vertebrae (74 of 90

genera), and while 12T:7L is the most common pattern (37 genera), 13T:6L is also highly

represented (31 genera). Scaly-tailed squirrels (*Anomalurus*, which are anomalures, not sciurids)

possess a highly modified TL pattern of 15T:10L. Tree shrews are largely modal at 13T:6L

(*Anathana*, *Dendrogale*, *Tupaia*, and *Urogale*; *Ptilocerus* is modal at 14T:5L). Colugos (genus

Cynocephalus) possess a fair amount of variation in TL number, ranging from 18 to 21, but the

modal pattern is 13T:6L.

Within Primates, 12T:7L and 13T:6L are the most common patterns (19 and 18 of 56

genera, respectively). Strepsirhines most commonly possess 13T:6L (7 of 18 genera –

Daubentonia, *Cheirogaleus*, *Euoticus*, *Lemur*, *Varecia*, *Galago*, *Otolemur*), while the 12T:7L

pattern is found in two genera (*Eulemur*, *Hapalemur*). Increases in TL count are observed in

lorisids (*Loris*: 15T:8L; *Nycticebus*: 16T:7L; *Perodicticus*/*Arctocebus*: 15T:7L), indriids

(*Avahi*/*Propithecus*: 12T:8L; *Indri*: 12T:9L), *Phaner* (12T:7L), and *Lepilemur* (12T:9L). Tarsiers are modal at 13T:6L.

Of the 15 platyrrhine genera included in this survey, all but two demonstrate 19 TL vertebrae. A 12T:7L pattern is most common (*Callimico*, *Saguinus*, *Leontopithecus*, *Callicebus*, *Pithecia*), followed by 13T:6L (*Callithrix*, *Cacajao*, *Chiropotes*), 14T:4L (*Ateles*, *Lagothrix*), 14T:5L (*Alouatta*), and 13T:5L *(Brachyteles)*. Greater than 19 TL vertebrae are found modally in *Saimiri* (13T:7L), *Cebus* (14T:6L), and *Aotus* (14T:7L).

Most cercopithecoids are characterized modally by a 12T:7L combination (10 of 17 genera), while four genera (*Lophocebus*, *Papio*, *Theropithecus*, *Miopithecus*) are modal at 13T:6L. Finally, *Colobus* is characterized by a 12T:6L pattern, and *Procolobus* either 11T:8L or 12T:7L (although sample sizes for these taxa are very small at N=3 and N=2, respectively). Hominoids are obviously derived in their reduced TL counts relative to other anthropoids. Hylobatids (*Hylobates*, *Bunopithecus*, *Symphalangus*, *Nomascus*) possess 18 TL (13T:5L), while hominids possess 17 or 16 TL vertebrae (*Homo*: 12T:5L; *Pan*, *Gorilla*: 13T:4L; *Pongo*: 12T:4L).

Sacral number

Monotremes generally possess 3 sacral vertebrae (*Ornithorhynchus*, *Tachyglossus*, *Zaglossus*) and marsupials range from 2 to 4 modally, but most commonly possess 2 (22 of 33 genera; five genera are bimodal at 2/3, four possess 3, and the two wombat genera possess 4). Among afrotherians, sirenians (*Trichechus*, *Dungong*) do not possess sacra. Non-sirenian afrotherians most commonly possess 3 sacral vertebrae (3 of 10 genera: *Rhynchocyon*, *Tenrec*, *Hemicentetes*), although genus modes range from 2 to 7 (*Microgale*: 2; *Setifer*, *Elephas*: 4; *Chrysochloris*: 5; *Orycteropus*, *Dendrohyrax*: 6; *Procavia*: 7). Xenarthrans are even more

variable in sacral count, ranging from 4 to 13 elements. Anteaters possess 4 to 5 (*Cyclopes*: 4; *Myrmercophaga*, *Tamandua*: 5), sloths 6 (*Bradypus*) to 7 (*Choloepus*), and armadillos between 8 and 13 (*Chaetophractus*, *Zaedyus*: 8; *Euphractus*: 8/9; *Dasypus*: 9; *Cabossous*, *Chlamyphorus*: 10; *Priodontes*: 12/13; *Tolypeutes*: 13).

The insectivores (Eulipotyphla) included here most commonly possess 5 sacral elements (7 of 14 genera). Eranceids (hedgehogs and gymnures) possess 3 to 4 (*Echinosorex*, *Hemiechinus*: 3; *Erinaceus*: 4), shrews 4 to 5 (*Sorex*, *Suncus*: 4; *Crocidura*, *Scutisorex*: 5), and talpids 5 to 6 (*Desmana*, *Galemys*, *Talpa*, *Urotrichus*: 5; *Mogera*, *Parascaptor*: 6) sacral vertebrae. The sacro-caudal regions of bats are coalesced and/or otherwise indistinguishable from each other in some taxa. Among the genera included here that possess distinguishable sacral counts, modal numbers range from 3 (six of 14 genera) to 6 (three genera with 4 and 5 each and two genera with 6).

Pangolins most commonly possess 4 sacral vertebrae (four of seven species; of the remaining species, two possess 3 and one 5). Carnivoran modes range from 2 to 5 sacral vertebrae with a mode of 3 (73 of 89 genera). Skunks (*Mephitis*, *Spilogale*, *Conepatus*) are modal at 2, honey (*Mellivora*) and hog (*Arctonyx*) badgers, hyaenas (*Crocuta*, *Hyaena*), sea otters (*Enhydra*), and some pinnipeds (*Phoca*, *Halichoerus*, *Neophoca*, *Otaria*, *Odobenus*) 4, and bears (*Ailuropoda*, *Melursus*, *Ursus*) 5.

Perissodactyl genera possess modes that vary from 3 to 6 sacral elements (3 in *Ceratotherium*, 4 in *Dicerorhinus*, 5 in *Rhinoceros* and *Equus*, and 6 in *Tapirus*). Non-cetacean cetartiodactyls most commonly possess 4 sacral vertebrae (40 of 57 genera; 11 possess 5, three possess 3). Hippopotamuses, the closest living relatives of cetaceans (together, Whippomorpha), possess a mode of 6 sacral vertebrae. Like sirenians (Afrotheria), cetaceans lack sacra altogether.

The only lagomorph taxa with sacral counts included in this survey (*Oryctolagus*, *Pentalagus*, and *Lepus*) are modal at 4 sacral elements. Rodents also commonly possess a 4-element sacrum (37 of 84 genera), although 3 elements are also common (29 genera) and modes range from 2 to 5. In Scandentia, all five tree shrew genera are modal at 3 sacral elements; in Dermoptera, colugos are modal at 5.

Among primates, the majority of non-hominoids are modal at 3 elements in the sacrum (49 of 62 genera); *Cacajao* is characterized by 4-element sacrum, and lorisids (*Nycticebus*, *Arctocebus*, *Perodicticus*) possess 6 sacral elements (*Loris* is modal at 3 elements, but ranges from 2 to 5). Among hominoids, hylobatid genera *Hylobates* and *Bunopithecus* are characterized by modal numbers of 4 sacral elements, while the other hylobatids (*Nomascus* and *Symphalangus*) are modal at 5, along with *Pongo* and *Homo*. *Pan* and *Gorilla* are modal at 6.

Well-sampled taxa

The majority of well-sampled anthropoids included in this study possess modal vertebral formulae that include 29 precaudal elements (15 of 22 taxa: humans, western gorillas, eastern gorillas, white-handed gibbons, howler monkeys, and all 10 cercopithecoids). Of the remaining taxa, five possess 30 (chimpanzees, bonobos, siamangs, capuchins, and squirrel monkeys) and two possess 28 (orangutans and spider monkeys). Cercopithecoid and howler monkey modal formulae contain 19 TL vertebrae, white-handed gibbons, siamangs, and spider monkeys 18, humans, chimpanzees, bonobos, and western gorillas 17, eastern gorillas and orangutans 16, and capuchins and squirrel monkeys 20 TL vertebrae.

Vertebral profiles are constructed for each taxon and include formulae represented at 10% or greater frequency (full lists of vertebral formulae observed in each taxon can be found in

Appendix C). The modal formula is listed first, followed by subsequent formulae. For example, the human modal formula (7:12:5:5) is represented at 63% frequency, followed by a second formula (7:12:5:6) at 12.5% frequency; therefore, the human vertebral profile is (7:12:5:5, 7:12:5:6). Profiles for all 22 well-sampled taxa are listed in Table 2.2.

DISCUSSION

Reconstruction of ancestral vertebral formulae

The broad survey of mammals provided here, along with pertinent fossil specimens (see below), allows for the reconstruction of likely ancestral vertebral formulae throughout mammalian evolution. With the evolution of crown mammals, the cervical count became largely fixed at 7, represented modally by all living mammals except sloths and manatees (Galis, 1999; Buchholtz et al., 2007; Buchholtz and Stepien, 2009). Interestingly, TL count also seems to have stabilized at 19 TL vertebrae during mammalian evolution (Narita and Kuratani, 2005; Sánchez-Villagra et al., 2007). Monotremes, the most basal living mammals, retain both 7 cervical and 19 TL vertebrae, as do most marsupials, many possessing 13T:6L vertebrae. The earliest know placental mammal, *Eomania*, also possessed a 13T:6L pattern (Ji et al., 2002), suggesting that this pattern was retained in the evolution of eutherian mammals.

Among primitive eutherians, Afrotheria and Xenarthra possess highly modified and variable vertebral formulae (Sánchez-Villagra et al., 2007; Buchholtz and Stepien, 2009; Asher et al., 2009, 2011; Hautier et al., 2010; Varela-Lasheras et al., 2011). Because monotremes, marsupials, and boreoeutherian (non-atlantogenatan eutherian) mammals are relatively conservative in this regard, this increase in vertebral variation has been interpreted as support for

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the monophyly of Afrotheria and Xenarthra in the superclade Atlantogenata (Asher et al., 2009). The relaxation of a "constraint" in the form of extreme stabilizing selection allowed for deviation from 7 cervical vertebrae in members of both Afrotheria (*Trichechus*) and Xenarthra (*Bradypus* and *Choloepus*) (Galis, 1999; Galis et al., 2006; Buchholtz and Stepien, 2009), in addition to increased variability in TL count in the clade as a whole (Asher et al., 2009; Galliari et al., 2010; Varela-Lasheras et al., 2011).

Boreoeutheria, sister group to Atlantogenata, is divided into two major clades, Laurasiatheria and Euarchontoglires. Within Laurasiatheria, ordinal relationships are not yet fully resolved (Nishihara et al., 2006; Hou et al., 2009). While "insectivores" (*sensu stricto* Eulipotyphla: Erinaceomorpha + Soricomorpha) are generally agreed to be basal to the rest of the clade and pangolins (Order Pholidota) form the sister-group to Carnivora (together, Ferae), the positions of the Ferae, Perissodactyla, Cetartiodactyla (Artiodactyla + Cetacea), and Chiroptera are disputed (Nishihara et al., 2006; Hou et al., 2009).

Although insectivores are interspecifically quite variable in TL count, 19 TL vertebrae and a 13T:6L pattern is the most commonly represented state. Bats also demonstrate a fair amount of interspecific variation in TL number, with modes ranging from 16 to 19 and 11T:5L as the most common pattern. However, the earliest bats from the fossil record, *Onychonycteris* and *Icaronycteris*, both possess 19 TL vertebrae (12T:7L) (Jepsen, 1966; Simmons et al., 2008), suggesting that the primitive number of TL vertebrae was retained in early bat evolution.

Pangolins possess a large degree of variation in TL number and are clearly derived in this respect. Their sister-taxon relationship with carnivorans, therefore, may not be particularly informative for the primitive condition of Carnivora or Ferae. The majority of carnivorans possess 20 TL vertebrae, with 13T:7L as the most common pattern. The patterns 14T:6L and

15T:5L are also relatively common and are achievable by homeotic exchange at the T-L border within a 20 TL element framework. Fossil carnivorans demonstrate similar patterns of 20 TL vertebrae (Scott and Jepsen 1936), suggesting that the group as a whole is synapomorphic for an increased TL count by one element.

Perissodactyls are also characterized by an increase in TL vertebrae but to a greater degree than in carnivorans, possessing modes of 22 to 23 elements. Fossil perissodactyls are also reconstructed with a similar number of TL vertebrae (e.g., *Moropus*: 15T:6L; *Diceratherium*: 18T:5L; *Hyracotherium*: 17T:7L; *Hipparion*: 17T:6L) (Sánchez-Villagra et al., 2007; Wood et al., 2010), suggesting that increased TL count evolved early in their evolution or may be primitive for the group. In the latter scenario, increased TL count may be a potential morphological synapomorphy supporting the proposed molecular phylogenetic sister-taxon relationship between Perissodactyla and Ferae (Nishihara et al., 2006).

Most non-cetacean cetartiodactyls possess 19 TL vertebrae, commonly with the primitive 13T:6L pattern. Early fossil cetartiodactyls also demonstrate 13T:6L (Rose, 1985), suggesting that this pattern and 19 TL vertebrae are primitive for the group. Hippopotamuses, the closest living relatives of cetaceans, retain 19 TL vertebrae, but possess a mode with the greatest number of thoracic vertebrae and lowest number of lumbar vertebrae observed among extant non-cetacean cetartiodactyls (15T:4L). This suggests that differences among non-cetacean cetartiodactyls are largely homeotic in nature, involving shifts at the T-L border. Finally, although modern cetaceans are highly derived in vertebral number, some early archaeocetes (fossil whales) possessed 19 TL vertebrae (*Remingtonocetus*: 14T:5L; *Rodhocetus*: 13T:6L) (Buchholtz, 1998), although the oldest known archaeocete that preserves a relatively complete

vertebral column, *Ambulocetus*, is reconstructed with 24 TL vertebrae (16T:8L) (Madar et al., 2002).

Euarchontoglires, sister taxon to Laurasiatheria, contains two major groupings. The superorder Glires is sister taxon to Euarchonta, the clade that contains primates and their close relatives (colugos and tree shrews). Glires is divided into two main groups, Lagomorpha and Rodentia. Among lagomorphs, rabbits and hares retain the primitive number of 19 TL vertebrae, while pikas are derived and possess 22 elements. In Rodentia, the majority of taxa possess 19 TL vertebrae, with 12T:7L and 13T:6L as the first and second most common patterns, respectively. It is therefore likely that the ancestral condition for Glires is 12T:7L, although large amounts of variation for 13T:6L is retained in rodents.

Euarchonta consists of tree shrews (Scandentia), colugos (Dermoptera), and Primates. Tree shrews, outgroup to the Primate-Dermoptera clade (Janecka et al., 2007), most commonly possess a 13T:6L pattern. Colugos, the closest living relatives of primates, possess a fair amount of variation in TL number, but the modal pattern for the genus is 13T:6L. Therefore, it is likely that the LCA of primates, and probably euarchontans, was characterized by a 19-element, 13T:6L pattern TL column. Within Primates, variations of 19 TL persist, with 13T:6L and 12T:7L occurring frequently. Although increases in TL count occur in strepsirhines (e.g., lorisids and indriids), the most commonly represented pattern in this group is 13T:6L. Tarsiers are also modal at 13T:6L, suggesting that this pattern was retained in the ancestor of haplorhines.

Most platyrrhines possess 19 TL vertebrae, while increases occur in *Cebus*, *Saimiri*, and *Aotus*, and a decrease by one element occurs in atelines. Although 12T:7L is represented most commonly among platyrrhine genera, it is unknown whether this pattern or the primitive 13T:6L characterized the LCA of platyrrhines (Figure 2.1). Cercopithecoids are interspecifically less

variable than other anthropoids, with all taxa modal at 19 TL vertebrae and all but several clades characterized by a 12T:7L pattern. The possession of a 13T:6L pattern represents a synapomorphy of the *Lophocebus-Papio-Theropithecus* clade (see below and Chapter 3), a pattern that might also characterize *Semnopithecus*, although greater sample sizes are required to confirm these preliminary finding.

The persistence of 12T:7L in colobines and most cercopithecines suggests that it is primitive for cercopithecoids in general; however, as with platyrrhines, it is unknown whether 12T:7L or 13T:6L characterized the LCA of catarrhines. The Middle Miocene stem catarrhine *Pliopithecus* includes a partial vertebral column and was reconstructed by Zapfe (1958) with 12-13T:6-7L. Because most non-hominoid anthropoids and other mammals possess 19 TL vertebrae, it is likely that *Pliopithecus* possessed either 12T:7L or 13T:6L. The Plio-Pleistocene fossil colobine, *Paracolobus*, preserves a significant portion of the vertebral column, which matches extant colobines at 12T:7L (Birchette, 1982) and is therefore largely uninformative for reconstruction of the LCA of catarrhines.

Extant hominoids are clearly derived in TL number, possessing fewer than 19 TL vertebrae. Looking to the hominoid fossil record, *Proconsul*, *Nacholapithecus*, and *Oreopithecus* preserve relatively complete lumbar regions that permit reconstruction of lumbar count. Both *Proconsul* and *Nacholapithecus* are reconstructed with 6 to 7 lumbar vertebrae (although 6 is argued to be the most likely number in both taxa) (Ward, 1993, 2007; Ishida et al., 2004), while *Oreopithecus* is reconstructed with 5 lumbar vertebrae (Straus, 1963; Harrison, 1986). *Proconsul* and *Nacholapithecus*, therefore, are primitive and unlike *Oreopithecus* and extant hominoids in the possession of more than five lumbar vertebrae. Here again, as with cercopithecoids, extant

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and fossil hominoids do not clarify the ancestral condition for catarrhines, although it is likely that 13T:6L, 12T:7L, or high frequencies of both patterns characterized the catarrhine LCA.

Reconstruction of ancestral sacral counts

From the data that are included in the survey compiled here, it is obvious that sacral number is quite variable across Mammalia. Monotremes possess 3, while marsupials are modal at 2. As with TL count, Afrotheria and Xenarthra are quite variable in sacral count, although the most common number among afrotherians is 3 sacral vertebrae. Xenarthrans are highly variable and possess between 4 and 13 sacral vertebrae.

Laurasiatherians are also variable in sacral number. Modal sacral numbers in both insectivores and bats range from 3 to 6, with 5 and 3 elements most commonly represented in each group, respectively, although some bats possess indistinctive sacra that coalesce with the caudal region. The majority of carnivorans possess 3-element sacra, while pangolins possess 4-element sacra. Among perissodactyls, rhinoceroses possess between 3 and 5, horses 5, and tapirs 6 sacral vertebrae. Early fossil perissodactyls possess increased sacral counts like their modern counterparts (e.g., Wood et al., 2010).

Non-cetacean cetartiodactyls most commonly possess 4 sacral vertebrae. Although cetaceans do not possess sacra, early archaeocetes (*Ambulocetus*, *Remingtonocetus*, *Rodhocetus*, *Georgiacetus*) did, and, like most non-cetacean cetartiodactyls, possess 4 elements (Buchholtz, 1998; Madar et al., 2002). The earliest fossil cetartiodactyls (*Diacodexis*, *Cainotherium*), however, are reconstructed with 3 sacral elements (Rose, 1985), suggesting that the group as a whole evolved from an ancestor with a primitive, 3-element sacrum.

Among lagomorphs, only rabbits (*Oryctolagus*, *Pentalagus*) and hares (*Lepus*) are represented by specimens with sacral counts; these taxa possess 4 sacral elements. Rodents also modally possess 4 sacral vertebrae, although 3-element sacra are also common. Therefore, it is likely that the primitive modal number of sacral elements in Lagomorpha, Rodentia, and consequently, Glires, was 4. In Scandentia, all five tree shrew genera are modal at 3 sacral elements; in Dermoptera, colugos are modal at 5.

The vast majority of non-hominoid primates possess 3-element sacra; however, lorisids possess 3 to 6 sacral vertebrae (3 in *Loris* and 6 in *Nycticebus*, *Perodicticus*, and *Arctocebus*) and *Cacajao* is characterized by 4-element sacrum. At the species level, *Macaca arctoides* is also modal at 4 sacral vertebrae, although all other macaque and cercopithecoid species possess 3 sacral vertebrae. Hylobatids are derived in the possession of a 4 to 5 element sacrum, as are hominids with modes of 5 to 6 elements.

Concerning fossil catarrhines, *Pliopithecus* and *Paracolobus* retain primitive, 3-element sacra (Zapfe, 1958; Birchette, 1982). Unfortunately, sacra are not complete enough to infer sacral count in *Proconsul* or *Nacholapithecus*, although both were probably tailless (Ward et al., 1991; Nakatsukasa et al., 2003, 2004). *Oreopithecus* is the only fossil catarrhine with a sacrum consisting of more than 3 elements, and in fact is commonly reconstructed with 6 sacral vertebrae (Schultz, 1960; Straus, 1963; Harrison, 1986), although Haeusler et al. (2002:636) consider that the last element "most likely is an incorporated first caudal vertebra in this individual." Regardless of whether its sacrum consists of 5 or 6 elements, it is clear that, unlike *Proconsul* and *Nacholapithecus*, *Oreopithecus* is a member of the modern hominoid clade (Harrison, 1986, 1991; Sarmiento, 1987; Harrison and Rook, 1997; Moyà-Solà and Köhler, 1997; Alba et al., 2001).

Reconstruction of total precaudal counts

From the broad, albeit shallow survey of mammals conducted here, it seems likely that the possession of 29 precaudal vertebrae (7C:19TL:3S) is primitive for mammals and many mammalian superclades. This formula, likely including 13T:6L, persisted to the LCA of euarchontans and is retained in tree shrews and represented by members of every major primate clade except Hominoidea (Strepsirhini, Tarsiiformes, Platyrrhini, Cercopithecoidea). Indeed, in a review of the numbers of vertebrae in primates, Schultz and Straus (1945) argued that a 7:13:6:3 formula represents the primitive condition for primates.

Since primates are reasonably well represented in this survey, modal formulae are discussed in this section rather than separate TL and sacrum modes, as had been done in the preceding sections. The majority of primates retain 29 precaudal vertebrae (37 of 56 genera), while both increases and decreases in modal patterns are observed (15 and 4 genera, respectively). Increases in total count are both more frequent and greater in range – whereas a decrease to 28 elements occurs in atelines (*Ateles*, *Lagothrix*, *Brachyteles*) and orangutans (*Pongo*), increases range from 30 (*Phaner*, *Avahi*, *Propithecus*, *Cebus*, *Saimiri*, *Cacajao*, *Symphalangus*, *Pan*) to 36 (*Lepilemur*, *Indri*, *Aotus*: 31; *Loris*: 33; *Arctocebus*, *Perodicticus*: 35; *Nycticebus*: 36). Half of the strepsirrhine genera (9 of 18) included in this study retain 29 precaudal vertebrae; departures are limited to increases and occur in lorisids (4 genera), indriids (3 genera), *Phaner*, and *Lepilemur*. Tarsiers retain 29 precaudal vertebrae.

Among platyrrhines, seven of 14 taxa demonstrate 29 precaudal vertebrae, while decreases and increases occur in three and four genera each – 28 in atelines, 30 in *Cebus*, *Saimiri*, *Cacajao*, and 31 in *Aotus*. Among catarrhines, cercopithecoids are unanimous in the possession of 29 precaudal vertebrae, while hominoid genera demonstrate between 28 and 30

elements. If hominoids are grouped at the genus level, six of eight genera possess modal formulae with 29 elements (*Hylobates*, *Bunopithecus*, *Syndactylus*, *Nomascus*, *Gorilla*, *Homo*); *Pongo* has 28 and *Pan* have modes with 30 precaudal vertebrae. If hylobatid species are treated separately, their modal precaudal numbers range from 28 to 31 – *Hylobates pileatus* demonstrates a decreased precaudal number (7:12:5:4), while *Nomascus gabriellae* shows an increase to 31 precaudal elements (7:14:5:5); however, sample sizes are small for these species in particular (N=4 and N=11, respectively). Two hylobatid species, *Hylobates lar* and *Symphalangus syndactylus*, are represented at adequate sample sizes and will be treated in detail in the next section, along with six hominid, ten cercopithecoid, and four platyrrhine taxa.

Vertebral profiles

A vertebral profile is a subset of the full extent of vertebral formulae observed in a population. It includes the modal formula and other formulae represented at greater than 10% frequency in that population. Results produced here (Table 2.2) largely conform to those provided in Pilbeam (2004) and updated for *Pan paniscus* in McCollum et al. (2010), with some differences in the composition and order of certain profiles (compare Table 2.2 to Tables 1-15 in Pilbeam 2004 and Table 2 in McCollum et al. 2010). These differences are to be expected given that sample sizes for anthropoid taxa were more than doubled on average for the purposes of this study.

The representative platyrrhine vertebral profiles are probably derived relative to the primitive platyrrhine condition, which likely included high frequencies of 7:13:6:3 and 7:12:7:3. Only squirrel monkeys (7:13:7:3, 7:13:6:3, 7:14:6:3) exhibit one of these formulae in its profile.

Capuchins (7:14:6:3, 7:14:5:3), howler monkeys (7:14:5:3, 7:14:6:3, 7:15:5:3, 7:14:5:4, 7:15:5:4), and spider monkeys (7:14:4:3) likely evolved even more derived vertebral profiles.

Cercopithecoids demonstrate a narrower range of formulae in their vertebral profiles than platyrrhines (four formulae across ten taxa versus six formulae across four taxa). Colobine profiles include only the modal formula (7:12:7:3 in both lutungs and snub-nosed monkeys), as do vervets and Japanese macaques. Long-tailed macaques (7:12:7:3, 7:12:7:2), guenons (7:12:7:3, 7:13:6:3, 7:12½:6½:3), and *Cercocebus* mangabeys (7:12:7:3, 7:13:6:3) demonstrate more variation in their profiles, but possess the common cercopithecoid modal formulae of 7:12:7:3, which likely represents the primitive condition for cercopithecoids.

Finally, the profiles of baboons (7:13:6:3, 7:12:7:3), geladas (7:13:6:3), and *Lophocebus* mangabeys (7:13:6:3) are distinct and derived from other cercopithecoids. Their shared modal formula represents a previously unidentified morphological synapomorphy of the *Lophocebus-Papio-Theropithecus* clade, a grouping that has received little morphological support (e.g., compared to the *Cercocebus-Mandrillus* clade – Disotell, 1994; Fleagle and McGraw, 1999, 2002; but see Groves, 1978). This observation strengthens arguments that vertebral formulae can be phylogenetically informative (Sánchez-Villagra et al., 2007; Asher et al., 2009).

Among hominoids, white-handed gibbons (7:13:5:4, 7:13:5:5) and siamangs (7:13:5:5, 7:13:5:4, 7:13:4:5) are nearly bimodal and trimodal, respectively, and demonstrate similar vertebral profiles, albeit with different modal formulae. Orangutans (7:12:4:5, 7:12:4:6) are derived in two respects: 1) reduction in the number of thoracic and TL vertebrae, and 2) reduction in total number of precaudal vertebrae in the modal formula.

Chimpanzee (7:13:4:6, 7:13:4:5, 7:13:3:6) and western gorilla (7:13:4:5, 7:13:3:6, 7:13:4:6) vertebral profiles consist of the same formulae in different orders of frequency, while

only the modal formula of the bonobo (7:13:4:6, 7:13:4:7, 7:14:3:7) and eastern gorilla

(7:13:3:6) vertebral profile overlap with those of their respective sister-taxa. If the

chimpanzee/western gorilla profile is viewed as primitive for the hominine clade, then the

bonobo and eastern gorilla profiles are viewed as derived relative to this condition. From a

chimpanzee/gorilla vertebral profile, the human profile (7:12:5:5, 7:12:5:6) requires only one

homeotic shift at the T-L border: 7:12:5:5 from 7:13:4:5, the modal western gorilla formula, and

7:12:5:6 from 7:13:4:6, the modal chimpanzee formula.

Competing hypotheses

Haeusler et al. (2002) reconstruct the primitive catarrhine modal vertebral formula as

7:13:6:3 and the primitive crown hominoid formula as 7:13:5:4, achieved through lumbar

sacralization. They posit a modal pattern of 7:12:5:5 for the common ancestor of hominids, one

that is maintained in the LCA of gorillas, chimpanzees, and humans, rendering the human

vertebral formula plesiomorphic. Haeusler and colleagues, however, developed their

evolutionary scenario in the context of an incorrect and outdated phylogeny in which gorillas and

chimpanzees are sister taxa to the exclusion of humans (see Figure 9 in Haeusler et al., 2002).

The presence of a chimpanzee-human clade to the exclusion of gorillas (Pilbeam, 1996, 2004)

necessarily implies that the reduction of the lumbar and associated increase in the thoracic

column occurred independently in chimpanzees and gorillas under Haeusler et al.'s (2002)

scenario (Figure 2.2).

Using different lines of evidence but employing similarly incorrect phylogenies by

modern standards, other authors previously proposed human-like (7:12:5:5) or hylobatid-like

(7:13:5:4) vertebral formula persisted throughout hominoid evolution, with hominins evolving

directly from an ancestor with a 7:12:5:5 (Filler, 1993) or 7:13:5:4 (Latimer and Ward, 1993) vertebral formula. Rosenman (2008) has recently subscribed to a similar scenario in which gorillas, chimpanzees, and hominins evolved from an ancestor with at least five lumbar vertebrae. Unlike the previously mentioned authors, however, Rosenman constructs a scenario in a modern phylogenetic framework in which gorillas and chimpanzees evolved reduced lumbar regions independently, while early hominins maintain a five-element lumbar region.

In a landmark paper, Pilbeam (2004) supplemented and analyzed the classic datasets presented in Schultz (1930, 1961; Schultz and Straus, 1945) in a modern phylogenetic framework. Pilbeam argued that the primitive catarrhine vertebral formula was 7:13:6-7:3, and that hominoids retained 13 thoracic vertebrae and experienced lumbar sacralization, which resulted in 7:13:4-5:4-5, as evidenced from extant gibbons and siamangs. The common ancestor of extant hominids experienced another lumbar sacralization, resulting in 7:13:3-4:5-6, a formula retained in the common ancestor of panins and hominins. Therefore, hominins evolved from a "short-backed" ancestor with a "chimp-like" vertebral profile (7:13:4:6, 7:13:4:5, 7:13:3:6).

Pilbeam (2004) outlined hominin vertebral evolution as a three step process: 1) early hominins evolved a vertebral profile with five lumbar vertebrae (7:13:5:5, 7:12:5:5), 2) Mid-Pliocene hominins (australopithecines) evolved an extra lumbar vertebra in their vertebral profile (7:12:6:4, 7:12:5:5), and 3) Pleistocene hominins sacralized the sixth lumbar vertebra, resulting in a modal 7:12:5:5 formula once again. The first two steps occurred to allow early hominins to achieve lordosis in the transition to bipedalism; the third step was brought about by changes in iliac shape and orientation and a related need to stabilize the L-S joint in efficient, habitual terrestrial bipedalism (see also Sanders, 1995). Pilbeam's evolutionary scenario supports the homology of reduced lumbar regions in hominoids and accords fairly well with the evolutionary

scenario presented here, with some discrepancies, particularly concerning hominin evolution (Figure 2.3 and see section below entitled "Fossil hominin vertebral columns").

McCollum et al. (2010) add a sample of bonobos to Pilbeam's (2004) dataset and argue that two lines of evidence suggest that at least six lumbar vertebrae (i.e., a long back) persisted throughout hominoid evolution (Figure 2.4): 1) bonobos possess an extra precaudal segment, and 2) fossil hominins possess 6 lumbar vertebrae. To McCollum and colleagues (Lovejoy and McCollum, 2010; McCollum et al., 2010), the presence of 31 precaudal segments is primitive and retained only in bonobos among living hominoids, whereas a segment has been lost, and the lumbar column independently shortened, in all other extant hominoid taxa. Their proposed vertebral profile for the LCA of hominines and that of hominins and panins is the bonobo vertebral profile adjusted to contain six lumbar vertebrae (7:12:6:5, 7:13:6:4, 7:13:6:5). This is not consistent with the scenario proposed here, in which a reduced TL number to 18 elements is considered a synapomorphy of the hominoid clade and a further reduction to 17 TL vertebrae characterized the LCA of hominids, hominines, and the hominin-panin clade. Indeed, McCollum et al.'s scenario posits 18 to 19 TL vertebrae in the LCA of hominines.

McCollum et al. (2010) suggest that a 6- to 7-element lumbar column persisted throughout hominoid evolution and characterized the last common ancestor of panins and hominins (see also Lovejoy et al., 2009; Lovejoy and McCollum, 2010). This necessarily implies that each extant hominoid (hylobatids, orangutans, gorillas, chimpanzees, bonobos, and humans) evolved decreased lumbar regions independently, a scenario that McCollum et al. (2010:123) directly propose: "reduction in the lumbar column occurred independently in humans and in each ape clade, and continued after separation of the two species of *Pan* as well." Among extinct taxa, this would also be the case for at least one Miocene hominoid (*Oreopithecus*). According to

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Lovejoy and McCollum (2010), lumbar reduction occurred independently and in different ways in chimpanzees and bonobos, the former of which reduced the lumbar region by sacralization of lumbar elements and reduction in the number of somites, while the latter retained a long precaudal column and reduced the lumbar column by both thoracization and sacralization of lumbar vertebrae.

McCollum et al.'s scenario of hominin evolution goes as follows. From the vertebral profile of the hominin-panin LCA (7:12:6:5, 7:13:6:4, 7:13:6:5), australopithecines evolved a similar profile with reduced numbers of thoracic and sacral vertebrae (7:12:6:4, 7:12:6:5, 7:13:6:4). Finally, the modern human vertebral profile (7:12:5:5, 7:12:5:6) was achieved through sacralization of the sixth lumbar vertebra.

To sum, Pilbeam (2004) proposes a short-backed, chimp-like vertebral profile for the hominin-panin LCA (7:13:4:6, 7:13:4:5, 7:13:3:6), McCollum et al. (2010) a chimeric vertebral profile with a bonobo-like precaudal number and a *Proconsul*-like long back (7:12:6:5, 7:13:6:4, 7:13:6:5), and several authors an intermediate, human- or hylobatid-like vertebral profile with five lumbar elements (Filler, 1993; Latimer and Ward, 1993; Haeusler et al., 2002; Rosenman, 2008). These competing hypotheses invoke distinct evolutionary histories and allow for different amounts of homoplasy in hominoid postcranial evolution. Pilbeam's short-back model posits the homology of reduced lumbar regions in hominoids, whereas the long-back model of McCollum et al. allow for the greatest amount of homoplasy; the intermediate models fall in between.

Synopsis

Now that the numerical composition of the hominoid vertebral column has been placed in a broad phylogenetic context, its evolution and uniqueness can be addressed. The survey of

mammals provided here, in concert with more detailed analyses on better-sampled taxa, allows for the reconstruction of ancestral vertebral formulae throughout mammalian evolution (Figure 2.5). Following Haeusler et al. (2002) and Pilbeam (2004), it is argued here that the primitive condition for catarrhine primates is a modal vertebral formula of 7:13:6:3. Furthermore, I suggest that this formula is primitive for each node all the way back to the LCA of therian (marsupial + placental) mammals (Catarrhini, Anthropoidea, Haplorhini, Primates, Primatomorpha, Euarchonta, Euarchontoglires, Boreoeutheria, Eutheria, Theria). (It should be noted that Schultz and Straus 1945 also reconstructed the LCA o f primates with a 7:13:6:3 formula.) The LCA of all extant mammals (therians + monotremes) was similarly characterized by a 7C:19TL:3S formula, but probably a different combination of thoracic and lumbar vertebrae.

Although the LCA of cercopithecoids was most certainly modal at 7:12:7:3, this formula need not represent the primitive catarrhine condition from which cercopithecoids and hominoids each evolved (Pilbeam, 2004). Instead, it is likely that cercopithecoids and hominoids are both derived relative to the primitive catarrhine formula of 7:13:6:3. While cercopithecoids evolved a 7:12:7:3 formula by a caudal shift at the T-L border, early hominoids likely retained the primitive formula, 7:13:6:3, evidenced in part by the likely number of six lumbar vertebrae in *Proconsul* and *Nacholapithecus* (Ward, 1993; Ishida et al., 2003). These stem hominoids also demonstrate a primitive, non-ape-like association between the diaphragmatic and last rib-bearing vertebrae (see Chapter 3), supporting this prediction. As in Haeusler and colleagues' (2002) and Pilbeam's (2004) models, it is proposed here that the LCA of crown hominoids evolved a 7:13:5:4 formula via lumbar sacralization.

McCollum et al. (2010), however, provide a different evolutionary scenario. They suggest that tail loss in hominoids was accompanied by caudal sacralization, resulting in the

addition of a fourth sacral element. Furthermore, although the number of sacral vertebrae in *Proconsul* and *Nacholapithecus* is unknown, McCollum and colleagues predict that these taxa possessed 4-element sacra. While this is possible, evidence for an association between tail reduction and increased sacral composition is yet to be demonstrated.

From the data included here, one short-tailed catarrhine (*Macaca arctoides*) and some other short-tailed primates (lorisids and *Cacajao*) demonstrate increased sacral counts; however, the other short-tailed macaques included in this study (*M. fuscata*, *M. maura, M. sylvanus*) possess the same number of sacral elements (3) as the medium- and long-tailed species (here, *M. mulatta*, *M. nemestrina*, *M. fascicularis*, *M. sinica*). In fact, *M. sylvanus* possesses a shorter tail than *M. arctoides* (Fooden, 1980), yet does not demonstrate an increased sacral count. Sacral data made available to the author on additional macaque species confirms this finding – other short-tailed species (*M. nigra*, *M. ochreata*, *M. tonkeana*, *M. thibetana*) do not possess increased sacral counts compared to long-tailed species (*M. cyclopis*); rather, all are modal at 3 sacral elements (J. Polk, unpublished data; tail categories from Russo and Shapiro, 2011).

The relationship between tail reduction and sacral composition remains unexplored among mammals in general and merits a detailed phylogenetic study of its own. Until such an association is firmly established or more complete fossil discoveries demonstrate that the earliest hominoids possessed 4-element sacra, the scenario originally proposed by Keith (1903) and supported in Haeusler et al. (2002) and Pilbeam (2004), in which hominoids initially gained a sacral element by lumbar sacralization, is supported here. The following scenario is proposed to account for the evolutionary history of the hominoid vertebral formula (Figure 2.6).

From a primitive formula of 7:13:6:3, lumbar sacralization resulted in a 7:13:5:4 modal pattern in the LCA of crown hominoids. This formula is represented modally in white-handed

gibbons and in the vertebral profile of siamangs. It is also represented as the modal formula in other hylobatids (*Hylobates moloch*, *Bunopithecus hoolock*, *Nomascus concolor*), although some species are clearly derived relative to the primitive formula (e.g., *Hylobates pileatus* – 7:12:5:4; *Nomascus gabriellae* – 7:14:5:5).

As was evidenced previously in Clauser (1980) and Pilbeam (2004), it is clear that hylobatid vertebral evolution is complicated, with individual gibbon species demonstrating a range of vertebral formulae as diverse as or even more diverse than in hominids. As with hominids, the presence of an extra precaudal element (i.e., 30), generally regionalized to the sacrum, is common in hylobatids and likely characterized the crown hominoid LCA. It is possible that this 30th precaudal element is a result of caudal sacralization, but meristic change is also possible; unfortunately, caudal counts reported in Pilbeam (2004) do not clarify this issue. Regardless, a vertebral profile of (7:13:5:4, 7:13:5:5, 7:13:4:5) is suggested for the hylobatid-hominid LCA. Notice also that this profile contains variation for the formula 7:13:4:5, one that is commonly observed in siamangs and would require the sacralization of a second lumbar element.

From the vertebral profile of the LCA of crown hominoids (7:13:5:4, 7:13:5:5), the LCA of extant hominids evolved a modal vertebral formula of 7:13:4:5. Again, some variation for 30 precaudal vertebrae likely existed in this vertebral profile (7:13:4:5, 7:13:4:6). *Oreopithecus*, a likely crown hominoid (Harrison, 1986; Sarmiento, 1987; Harrison and Rook, 1997; Moyà-Solà and Köhler, 1997; Alba et al., 2001), is reconstructed with 5 lumbar (Schultz, 1960; Straus, 1963; Harrison, 1986) and 6 sacral vertebrae (Harrison, 1986). The thoracic column and ribs are only partially complete, so thoracic number is unknown (Harrison, 1986). Haeusler et al. (2002) infer a 7:12:5:5 formula based on a 29-element precaudal framework and an incorrect assessment of sacral count – they argue that although there are five sacral foramina on the more complete

left side of the sacrum, the last element is actually an incorporated caudal vertebra and not a 'true' sacral vertebra. However, assuming that the right side is symmetrical, there are 6 sacral elements by Schultz criteria, regardless of whether or not the sixth element is a sacralized caudal vertebra. Therefore, if *Oreopithecus* did in fact possess 12 thoracic vertebrae, its formula would be 7:12:5:6.

McCollum et al. (2010) infer a 7:13:5:6 vertebral formula for *Oreopithecus*, rendering its total precaudal count to 31, a number observed only in the vertebral profile of bonobos (7:13:4:6, 7:13:4:7, 7:14:3:7) among extant hominoids. The vertebral formulae inferred for *Oreopithecus* are achievable from the vertebral profile of the crown hominid LCA proposed here (7:13:4:5, 7:13:4:6) by a shift in mode to the secondary formula (7:13:4:6) and either a homeotic shift at the T-L border (7:12:5:6) or the meristic addition of vertebra that is regionalized to the lumbar column (7:13:5:6). However, because the number of thoracic vertebrae is unknown for *Oreopithecus*, the likelihood of either scenario cannot be determined.

From the LCA of crown hominids (7:13:4:5, 7:13:4:6), orangutans evolved a vertebral profile (7:12:4:5, 7:12:4:6) with 28 to 29 precaudal elements. This likely occurred via a homeotic shift across two (7:13:4:5 → 7:12:4:6) to three (7:13:4:5 → 7:12:4:6 → 7:12:4:5) borders and/or the meristic loss of a vertebra (see related discussions in Haeusler et al., 2002; Pilbeam, 2004; Rosenman, 2008). Unfortunately, the relationship between meristic and homeotic change in the vertebral column is not fully understood (Pilbeam, 2004; McCollum et al., 2010), so the exact mechanisms of these changes are unknown. Orangutans do not possess a greater number of caudal vertebrae than other hominids (data from Pilbeam, 2004), so meristic change at some level is unavoidable and may not be entirely separable from homeotic change given the nature of segmentation and specification; in fact, Pilbeam (2004) suggests that the concept of homeotic

versus meristic change is inappropriate and outdated in light of our modern understanding of the production and identification of vertebrae.

The LCA of hominines and that of hominins and panins likely retained the primitive hominid vertebral profile (7:13:4:5, 7:13:4:6) or evolved an expanded profile with variation for three lumbar vertebrae (7:13:4:5, 7:13:4:6, 7:13:3:6). From this ancestral pattern, the LCA of gorillas evolved a higher frequency of three lumbar vertebrae (7:13:4:5, 7:13:3:6, 7:13:4:6). While western gorillas maintain this vertebral profile, eastern gorillas evolved a greater frequency of three lumbar vertebrae, resulting in a specialized vertebral profile (7:13:3:6).

From the vertebral profile of the hominin-panin LCA (7:13:4:5, 7:13:4:6, 7:13:3:6), the LCA of chimpanzees and bonobos evolved a formula containing 30 precaudal elements (7:13:4:6, 7:13:4:5, 7:13:3:6). While both chimpanzees and bonobos retain this modal formula, bonobos have evolved a vertebral profile that includes variation for an increased number of precaudal elements (7:13:4:6, 7:13:4:7, 7:14:3:7). Compared to chimpanzees, which possess 29 elements in the second and third highest frequency vertebral formulae, bonobos possess 31 elements in both of these formulae. These additions to the presacral column are not at the expense of the caudal region (data from Pilbeam, 2004), suggesting that they are meristic in nature. The bonobo vertebral profile does not maintain a primitive number of precaudal elements (contra McCollum et al., 2010; Lovejoy and McCollum, 2010); rather, it is clearly derived relative to that of chimpanzees and other hominids (see also Pilbeam, 2004).

Finally, from the vertebral profile of the panin-hominin LCA, the hominin LCA experienced a cranial homeotic shift at the T-L border, resulting in a 7:12:5:5 modal formula and a likely vertebral profile of (7:12:5:5, 7:13:4:5, 7:13:4:6). Mid-Pliocene hominins, including *Australopithecus* and *Homo ergaster*, may have exhibited some variation for a 7:12:6:4 formula

(7:12:5:5, 7:12:6:4) (but see Chapter 3 and below). The vertebral profile characteristic of modern humans (7:12:5:5, 7:12:5:6) evolved by the appearance of modern humans and Neandertals (Arensburg, 1991; Ogilvie et al., 1998; Bonmati et al., 2010; Walker et al., 2011). Therefore, from a "African ape-like" vertebral profile (7:13:4:5, 7:13:4:6, 7:13:3:6), the human profile (7:12:5:5, 7:12:5:6) requires only a single homeotic shift at the T-L border from the proposed highest frequency formulae in the LCA: 7:12:5:5 from 7:13:4:5 (the modal western gorilla formula), and 7:12:5:6 from 7:13:4:6 (the modal chimpanzee formula) (see also Pilbeam, 1996, 1997, 2004).

Fossil hominin vertebral columns

McCollum and colleagues (Lovejoy and McCollum, 2010; McCollum et al., 2010) argue that Plio-Pleistocene hominins (*Australopithecus* and early members of the genus *Homo*) possessed a long-backed vertebral profile (7:12:6:4, 7:12:6:5, 7:13:6:4) as evidence for their long-back scenario of hominin origins (see also Rosenman, 2008). *A. africanus* and *H. ergaster* are commonly reconstructed with six lumbar vertebrae (Robinson, 1972; Latimer and Ward, 1993; Sanders, 1998; Rosenman, 2008), although other researchers have argued that these specimens possess just five lumbar vertebrae (Haeusler et al., 2002; Toussaint et al., 2003). By Schultz criteria – that operationalized in this study – the Sts 14 *A. africanus* specimen has 5.5 or perhaps only five lumbar vertebrae (Sts 14f bears a costal facet on one side and an LTP or ankylosed rib on the other side; see Haeusler et al., 2002) and not six as originally described (Robinson, 1972). The numerical composition of the lumbar region of a second *A. africanus* specimen, Stw 431, although initially assumed to be six (Sanders, 1998), is now thought to be five (Haeusler et al., 2002; Toussaint et al., 2003).

The vertebral column of KNM-WT 15000 is reasonably complete, but debate over whether or not a vertebra (T12) at the T-L transition is missing (Brown et al., 1985; Walker and Leakey, 1993; Haeusler et al., 2002) complicates assessment of the number of lumbar vertebrae in this specimen. Furthermore, the caudal-next vertebra (KMN-WT 15000 AR/BA) lacks the relevant portion of the posterior body and pedicles to determine whether it possessed a costal facet (Walker and Leakey, 1993; Haeusler et al., 2002), rendering it impossible to determine whether it is a thoracic or lumbar vertebra. It is noteworthy that T11 is the diaphragmatic vertebra (one bearing flat, thoracic-like prezygapophyses and laterally-oriented, lumbar-like postzygapophyses). Therefore, regardless of whether T12 is missing (Walker and Leakey, 1993) or present (KMN-WT 15000 AR/AB; Haeusler et al., 2002), the diaphragmatic vertebra (T11) and last rib-bearing vertebrae are separate elements. A similar cranial displacement of the diaphragmatic vertebra is apparent in Sts 14 (Sts 14g), Stw 431 (Stw 431l) (Haeusler et al., 2002), and in the recently discovered *Australopithecus sediba* skeletons (see Chapter 3).

Two fossil hominin sacra have been interpreted to support a 6L:4S configuration in fossil hominins – AL 288-1 (*A. afarensis*) and KNM-WT 15000 (*H. ergaster*). Although the sacrum of AL 288-1 was initially described as possessing five vertebrae (Johanson et al., 1982; Cook et al., 1983; see also Sanders, 1995), it has been recently suggested that it possesses fewer than five elements – either four or 4.5 (Pilbeam, 2004; Lovejoy and McCollum, 2010; McCollum et al., 2010). However, the AL 288-1 sacrum is broken on both sides at S5/C1, making it impossible to determine if the last element was connected to the rest of the sacrum via sacral foramina.

The Nariokotome sacrum (KNM-WT 15000) is reconstructed with five elements (Walker and Leakey, 1993; Walker and Ruff, 1993); however, McCollum et al. (2010) point out that its fifth segment (KNM-WT 15000AF) is probably the first caudal vertebra rather than the last

sacral. This was the interpretation provided in the initial description of the specimen (Brown et al., 1985), although Brown and colleagues posited that the second element was missing, rendering a total of five sacral elements. The KNM-WT 15000 sacrum is heavily reconstructed (see Fig. 10.3 in Walker and Ruff, 1993), making it difficult to accurately assess sacral count in this specimen.

The recently discovered *A. sediba* sacrum (MH2 88-125) preserves a nearly complete midline with distinct segments from S1 to S5 (personal observation). It also preserves the right side, complete with four complete sacral foramina. Therefore, *A. sediba* possessed five sacral vertebrae and, along with the positioning of the diaphragmatic vertebra, provides evidence that early fossil hominins need not be reconstructed with six lumbar and four sacral vertebrae. Instead, it is likely that fossil hominins retained a high frequency of the primitive hominin vertebral formula (7:12:5:5). Discrepancies arise from the fragmentary nature of many fossil hominin vertebral columns, conflicting reconstructions, and a conflation of two different definitions of thoracic and lumbar vertebrae (i.e., costal versus zygapophyseal definitions; see Chapter 3). However, the debate surrounding the number of lumbar vertebrae in the early hominin vertebral column is not settled and only the recovery of more and better-preserved fossil specimens will resolve this issue.

Consensus and the uniqueness of hominoids

Given the results of the present study, it is argued here that a short-back, "short-trunk" (i.e., 17 TL vertebrae) scenario similar to that supported in Pilbeam (2004) best explains the distribution of vertebral formulae observed among hominoids and other mammals. However, the model proposed here is different from that of Pilbeam (2004) in some ways, particularly

regarding the composition of ancestral vertebral profiles and with regard to hominin vertebral

evolution (see Figure 2.6). An "African ape-like" vertebral profile (7:13:4:5, 7:13:4:6, 7:13:3:6),

one that includes the same formulae as the profiles of chimpanzees (7:13:4:6, 7:13:4:5, 7:13:3:6)

and western gorillas (7:13:4:5, 7:13:3:6, 7:13:4:6) but in a different order of frequency, likely

characterized the LCA of hominines and that of hominins and panins.

Despite far smaller sample sizes and without our modern understanding of the production

and development of vertebrae, Keith (1903:26) devised nearly exactly the same scenario as

presented here, along with a working theory to explain it, over 100 years ago:

> With the evolution of the orthograde from pronograde primates, the lumbar region
> becomes relatively shorter, the process of abbreviation being brought about by the
> transformation of the 26th (lumbar) segment to the 1st sacral; in the evolution of
> the giant primates (the ancestral stock of man, the gorilla, chimpanzee, orang), the
> lumbar region was further shortened, the 25th segment becoming gradually sacral
> in character. In the origin of the human stock, by the assumption of plantigrade
> progression, the lumbar region again became elongated…

An African ape-like vertebral profile is congruent with the hominoid pattern of 18 or fewer TL

vertebrae, a relatively unique and defining characteristic among mammals (Welcker, 1881; Todd,

1922; Schultz and Straus, 1945; Sánchez-Villigra et al., 2007; Asher et al. 2009).

Hominoids are further distinguished by sacralization of lumbar vertebrae. In most other

mammals that demonstrate an increase in sacral count, the TL column remains unreduced and

extra sacral elements therefore must occur via meristic change or caudal shifting of the sacro-

caudal border (caudal sacralization). Unfortunately, these mechanisms cannot be differentiated in

this study because caudal counts are not available for many taxa. For example, many rodents and

non-cetacean cetartiodactyls possess increased sacral counts (e.g., 4 to 6), but do not demonstrate

a reduced presacral column; that is, they retain 19 TL vertebrae and gain sacral elements by

means other than lumbar sacralization (i.e., meristic change or caudal sacralizaiton).

Because the cranial and caudal borders of the TL region are associated with the upper limb and cervical plexus and lower limb and lumbo-sacral plexus, respectively, reduction in TL vertebrae function to shorten the trunk and bring the upper and lower limbs closer together. This is especially exaggerated in hominoids, which demonstrate shortening of the lengths of individual centra in the lumbar column (and therefore a short lumbar column in relation to the rest of the vertebral column) in addition to its reduced numerical composition (Schultz, 1938; Erikson, 1963; Benton, 1967; Rose, 1975; Clauser, 1980). Functionally, a decrease in the number and length of lumbar vertebrae limits flexibility and mobility to resist buckling (Jungers, 1984) and reduces bending moments at the intervertebral discs (Ward, 1993).

Selection for a stiff lower back to resist buckling and prevent injury of the discs during suspensory behavior (Hildebrand, 1974), vertical climbing (Jungers, 1984), bridging (Cartmill and Milton, 1977), or orthogrady in general (Keith, 1923) resulted in the sacralization of lumbar vertebrae. Increased proximity of the upper and lower limbs likely also facilitated all of these behaviors except bridging, which would seem to require the opposite effect. In fact, lorisids possess greatly increased TL regions, supporting this hypothesis and decreasing its significance for hominoid vertebral evolution. Among non-hominoid primates, only atelines (*Ateles*, *Lagothrix*, *Brachyteles*) are characterized by a reduced TL region (18 TL), although these taxa are not characterized by extra sacral elements in their shared modal formula (7:14:4:3, 7:13:5:3).

The only other mammals that demonstrate reduced TL regions are armadillos (all extant genera except *Calyptophractus* are represented in this study: *Chlamyphorus*, *Chaetophractus*, *Euphractus*, *Zaedyus*, *Dasypus*, *Tolypeutes*, *Cabassous*, *Priodontes*), the silky anteater (*Cyclopes*) the giant anteater (*Myrmecophaga*), some bats (*Hipposideros*, *Macrotus*, *Megaderma*, and *Cynopterus* among bats included here), water deer (*Hydropotes*), the giant

panda (*Ailuropida*), and the Cape mole rat (*Georychus*). When the primitive numbers of TL vertebrae are examined for each of these taxa, only armadillos (14 to 16 TL), the giant anteater (18 TL), the silky anteater (18 TL), and the giant panda (18 TL) converge with hominids (16 to 17 TL) in a reduction of TL vertebrae by two or more elements.

Armadillo vertebral formulae are highly derived, with short TL regions and extremely long sacra. The short trunk and long sacrum of armadillos is likely related to rigidity of the carapace (Galliari et al., 2010); indeed, fossil glyptodonts and other armored amniotes (e.g., turtles, anklylosaurian dinosaurs) also possess reduced numbers of trunk vertebrae (Galliari et al., 2010; Muller et al., 2010), supporting this hypothesis. Unfortunately, this case of convergence is probably uninformative in its relevance for hominoid evolution.

The anteaters and the giant panda provide more compelling cases of convergence with hominoids and may shed light on the evolution of the hominoid vertebral column. Although the silky anteater and the giant anteater demonstrate a 130-fold difference in body size (0.23 kg versus 30 kg; Wetzel, 1985) and are characterized by drastically different positional behaviors (Montgomery, 1985; Shaw et al., 1985), both possess modes of 16T:2L (7:16:2:4 in *Cyclopes* and 7:16:2:5 in *Myrmecophaga*). The silky anteater is entirely arboreal, possesses a prehensile tail, and demonstrates greatly expanded ribs and other features related to specialized truncal stability associated with defensive postures and bridging behaviors during locomotion (Jenkins, 1970). In the latter case, it converges with lorisids, which also locomote using slow climbing and bridging behavior (Cartmill and Milton, 1977) and demonstrate adaptations to truncal stability (especially *Arctocebus*, which demonstrates exaggerated costal expansion; Jenkins, 1970).

The giant anteater is a terrestrial knuckle-walker; as such, it exhibits convergent traits with gorillas and chimpanzees related to weight-bearing and stabilization of the wrist and hand

(Orr, 2005). It is also known to adopt a bipedal posture when utilizing its powerful fore claws to excavate and feed from termite mounds, and in defensive posturing (Reynolds, 1931). In such bipedal stances, and during normal quadrupedal locomotion, the giant anteater is plantigrade; that is, its entire heel (i.e., calcaneus) is in contact with the substrate (Reynolds, 1931; Gambaryan et al., 2009). Most other mammals, with several notable exceptions, use heel elevated (the heel does not contact the substrate) or semi-plantigrade (only the distal portion of the heel contacts the substrate) foot positioning (Gebo, 1993). Among the exceptions are African apes (in fact, all hominines, including humans) and ursids (bears), both of which use true plantigrady (Gebo, 1992, 1993).

Paradoxically, the giant panda is the only ursid that is not fully plantigrade (Davis, 1964). Unlike other bears, the giant panda demonstrates a reduced TL region (although the genus *Tremarctos* is not represented in this dataset). The possession of 18 TL vertebrae in giant pandas is especially striking considering nearly all carnivorans are characterized by 20 TL vertebrae. In fact, of the 19 giant pandas included in this dataset, five possess 17 TL vertebrae, a reduction from the primitive carnivoran condition by three elements. Giant pandas are the only non-hominoid mammals that demonstrate a hominoid-like vertebral profile (7:13:5:5, 7:14:4:5, 7:13½:4½:5, 7:13:4:6, 7:13½:3½:6). Like most hominoids (e.g., siamangs, diversity index = 0.889; chimpanzees, $DI = 0.826$; western gorillas, $DI = 0.851$; see Chapter 3), they demonstrate a high amount of intraspecific variation in vertebral formulae (*Ailuropoda*, $DI = 0.860$). Additionally, as can be inferred from the vertebral profile, giant pandas are characterized by a high frequency of transitional vertebrae (32%) that exceeds those observed among primates (bonobos are the highest at 24%). Among all mammals, only two-toed sloths (*Choloepus*) have a higher frequency of transitional vertebrae (48%).

Davis (1964) identified similarities between giant pandas and hominoids and argued that shortened trunks and cranial shifts in vertebral borders "are not themselves adaptive, but are *consequential results of a process of cephalization*" (emphasis in Davis, 1964:84). He argued that disruption of the axial gradient caused by developmental emphasis on the head lead to a pleiotropic effect due to "an accident of ontogenetic timing" – a cranial shift at the L-S boundary – which resulted in a shortened trunk. However, because giant pandas are convergent with hominoids not only in a short trunk but also in other vertebral morphologies (e.g., shorter, broader lumbar centra and more posteriorly-placed LTPs compared to other ursids; Figure 2.7), it is proposed here that these convergences may in fact be adaptive.

Although ursids are capable of standing and even walking bipedally over short distances, giant pandas do not show a greater proclivity at these activities than other bears (Davis, 1964). However, giant pandas are manual manipulators *par excellence*, and use their dexterous forelimbs to handle food and other objects with extreme precision (Davis, 1964; Endo et al., 2001). While feeding on bamboo stalks, giant pandas sit in an upright, reclined position in which weight rests on the lower back and dorsal aspect of the pelvis; this posture frees the forelimbs for food manipulation and feeding (Davis, 1964). Freeing of the hands during upright feeding posture, therefore, is a positional behavior that giant pandas, giant anteaters, and hominoids share in common. Whether or not this behavior played a selective role in their shared and independently evolved short trunks is a hypothesis that will require further testing.

CONCLUSION

Although many different possible scenarios have been proposed to explain the numerical composition of vertebral formulae exhibited by extant and fossil hominoids, and particularly hominins (Keith, 1903; Sanders, 1995; Ward and Latimer, 1993; Filler, 1993; Haeusler et al., 2002; Pilbeam, 2004; Lovejoy and McCollum, 2010; McCollum et al., 2010), a short-back, short-trunk scenario accords best with the distribution of vertebral formulae observed among hominoids and other mammals placed in a modern phylogenetic context, particularly in light of the important and predominant role of homeotic change in vertebral evolution (Muller et al., 2010). Supporting this conclusion, the modern human vertebral profile (7:12:5:5, 7:12:5:6) is just one border shift from the modal formulae represented in western gorillas (7:13:4:5) and chimpanzees (7:13:4:6); this transition does not require the addition, loss, or re-evolution of vertebrae, nor does it represent a reversal. Therefore, an "African ape-like" vertebral profile (7:13:4:5, 7:13:4:6, 7:13:3:6) is proposed to have characterized the LCA of hominins and panins.

TABLE 2.1. Taxa and sample sizes.

Taxon	Species included (if sp.)	Common name	N
Homo sapiens		human	273
Pan troglogytes		chimpanzee	271
Pan paniscus		bonobo	40
Gorilla gorilla		western gorilla	172
Gorilla beringei		eastern gorilla	51
Pongo pygmaeus		orangutan	180
Hylobates lar		white-handed gibbon	190
Hylobates syndactylus		siamang	74
Trachypithecus sp.	*cristatus, phayrei*	lutung (leaf monkey)	125
Nasalis larvatus		snub-nosed monkey	42
Cercopithecus sp.	*ascanius, lhoesti, mitis, mona, neglectus, petaurista*	guenon	128
Chlorocebus aethiops		vervet	71
Macaca fascicularis		long-tailed macaque	81
Macaca fuscata		Japanese macaque	883
Cercocebus sp.	*atys, galeritus, torquatus*	Cercocebus mangabey	31
Lophocebus sp.	*albegina, aterrimus*	crested mangabey	91
Papio sp.	*anubis, cynocephalus, hamadryas, papio, ursinus*	baboon	120
Theropithecus gelada		gelada	30
Saimiri sciureus		squirrel monkey	39
Cebus sp.	*albifrons, apella, capucinus, flavus, frontalis*	capuchin	63
Alouatta sp.	*palliata, pigra, seniculus*	howler monkey	39
Ateles sp.	*ater, fusciceps, geoffroyi, paniscus*	spider monkey	39

TABLE 2.2. Vertebral profiles (formulae represented at >10% frequency).

Taxon	Cervical	Thoracic	Lumbar	Sacral	TL	CTLS	Frequency	Sum freq.
Homo sapiens	7	12	5	5	17	29	62.6	
	7	12	5	6	17	30	12.5	75.1
Pan troglodytes	7	13	4	6	17	30	31.7	
	7	13	4	5	17	29	21.4	
	7	13	3	6	16	29	14.0	67.2
Pan paniscus	7	13	4	6	17	30	15.0	
	7	13	4	7	17	31	10.0	
	7	14	3	7	17	31	10.0	35.0
Gorilla gorilla	7	13	4	5	17	29	26.2	
	7	13	3	6	16	29	20.9	
	7	13	4	6	17	30	16.3	63.4
Gorilla beringei	7	13	3	6	16	29	70.6	70.6
Pongo pygmaeus	7	12	4	5	16	28	39.4	
	7	12	4	6	16	29	15.6	55.0
Hylobates lar	7	13	5	4	18	29	33.2	
	7	13	5	5	18	30	27.9	61.1
Hylobates syndactylus	7	13	5	5	18	30	20.3	
	7	13	5	4	18	29	18.9	
	7	13	4	5	17	29	17.6	56.8

TABLE 2.2 (cont.)

Taxon	Cervical	Thoracic	Lumbar	Sacral	TL	CTLS	Frequency	Sum freq.
Trachypithecus sp.	7	12	7	3	19	29	82.4	82.4
Nasalis larvatus	7	12	7	3	19	29	88.9	88.9
Cercopithecus sp.	7	12	7	3	19	29	43.0	
	7	13	6	3	19	29	23.4	
	7	12.5	6.5	3	19	29	10.9	77.3
Chlorocebus aethiops	7	12	7	3	19	29	66.2	66.2
Macaca fascicularis	7	12	7	3	19	29	70.4	
	7	12	7	2	19	28	18.5	88.9
Macaca fuscata	7	12	7	3	19	29	70.6	70.6
Cercocebus sp.	7	12	7	3	19	29	48.4	
	7	13	6	3	19	29	16.1	64.5
Lophocebus sp.	7	13	6	3	19	29	82.4	82.4
Papio sp.	7	13	6	3	19	29	43.3	
	7	12	7	3	19	29	29.2	72.5
Theropithecus gelada	7	13	6	3	19	29	93.3	93.3
Saimiri sciureus	7	13	7	3	20	30	48.7	
	7	13	6	3	19	29	12.8	
	7	14	6	3	20	30	10.3	71.8
Cebus sp.	7	14	6	3	20	30	36.5	
	7	14	5	3	19	29	28.6	65.1
Alouatta sp.	7	14	5	3	19	29	41.0	
	7	14	6	3	20	30	10.3	
	7	15	5	3	20	30	10.3	
	7	14	5	4	19	30	10.3	
	7	15	5	4	20	31	10.3	82.1
Ateles sp.	7	14	4	3	18	28	74.4	74.4

FIGURE 2.1. Platyrrhine phylogeny (from Perelman et al., 2011) showing taxa included in this study. Vertebral profiles are shown to the right, in this case representing the modal formula and, if present, a second formula represented at >10% frequency (except for Alouatta, which demonstrates four formulae represented at 10.3% frequency each; therefore, only the modal formula is shown). Hypothesized ancestral modal TL patterns are shown at relevant nodes. Notice that the platyrrhine LCA is reconstructed with either 12T:7L or 13T:6L, but which of the two patterns is more likely cannot be determined.
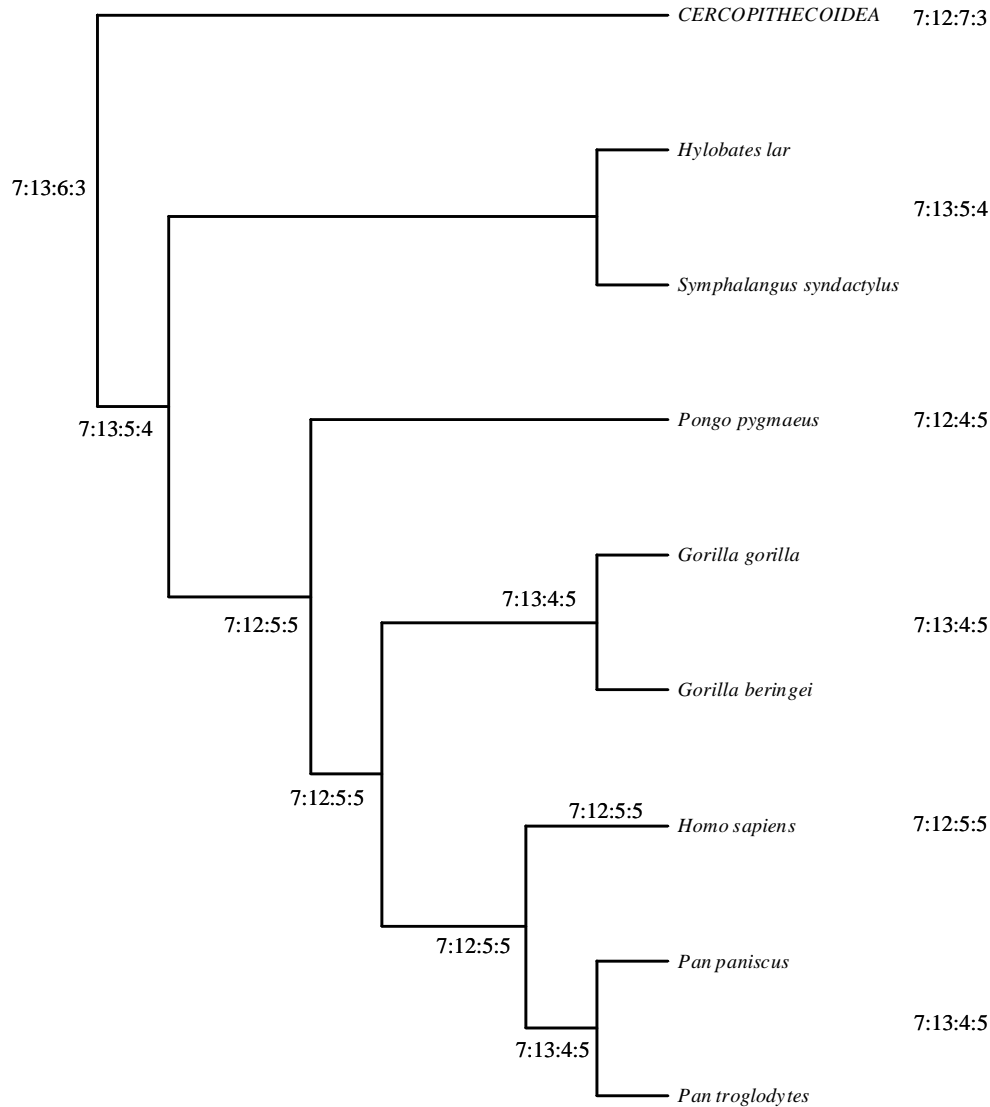
FIGURE 2.2. Catarrhine phylogeny showing Haeusler and colleagues' model. The phylogeny presented in Haeusler et al., which included a *Pan-Gorilla* clade to the exclusion of *Homo*, has been adjusted to a *Pan-Homo* clade to the exclusion of *Gorilla*. Following Haeusler et al., only modal formulae are shown for extant taxa (to the right of taxon names) and hypothesized ancestral conditions (at nodes). Some formulae are shown between extant taxa in cases where Haeusler et al. identified taxa at the genus level; some ancestral formulae are not shown in cases where formulae were not reconstructed. Notice that the human modal formula is proposed to be primitive for hominids. As such, lumbar regions are reduced from five to four elements independently in orangutans, gorillas, and panins. Fossil hominins (shown above the human branch) experience no change in this primitive formula, which modern humans simply retain.
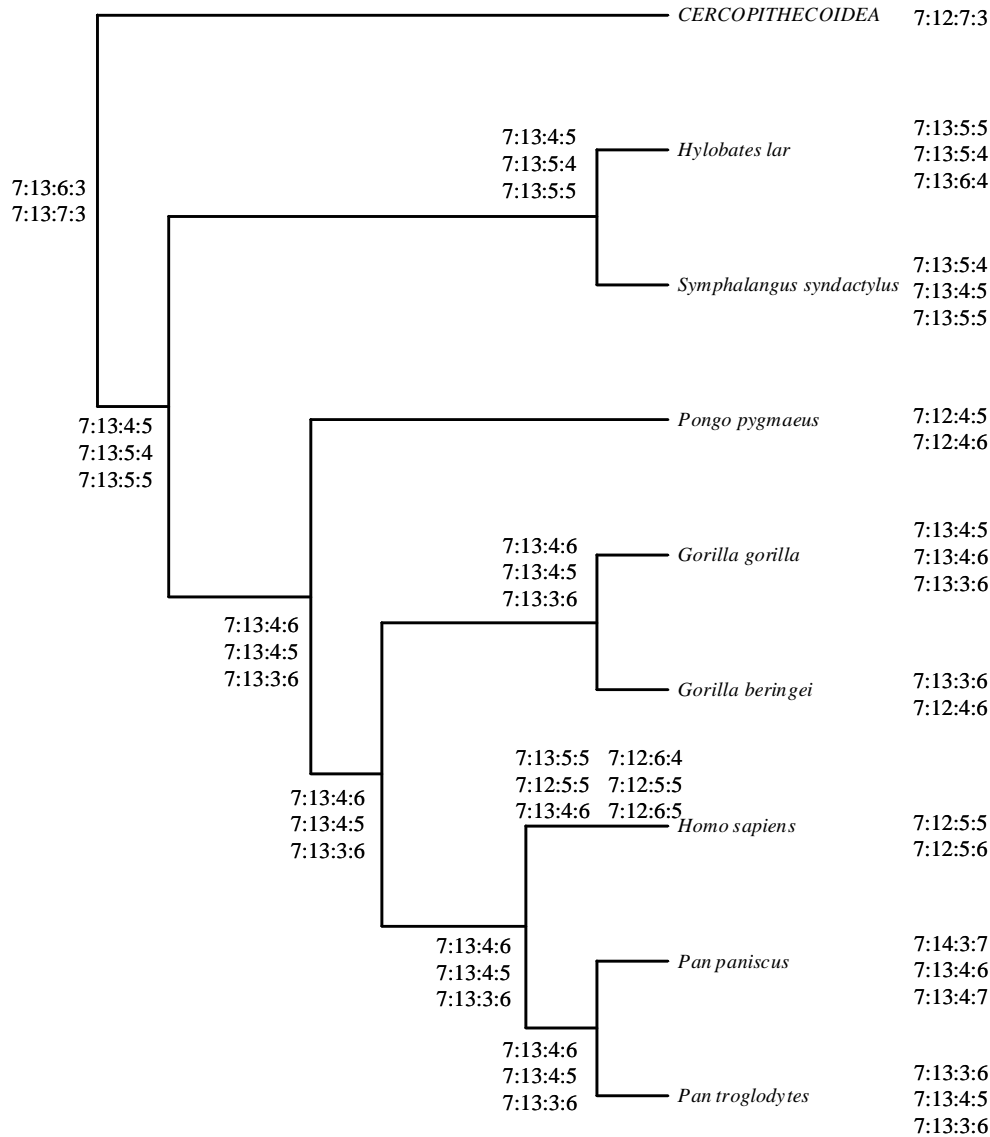
Figure 2.3. Catarrhine phylogeny showing Pilbeam's short-back model. Vertebral profiles for extant taxa are shown on the right and come from data presented in Pilbeam (2004). Hypothesized ancestral vertebral profiles are listed at nodes, with the proposed modal formula listed first (at the top of each set), and were determined from discussions in Pilbeam (2004). Notice that a chimp-like vertebral profile is proposed to be primitive for all hominids, with the implication that reduced lumbar regions are homologous in orangutans, gorillas, and panins. Early fossil hominins evolved a 5L:5S pattern (above the human branch, left), which was modified to 6L:4S in *Australopithecus* (above the human branch, right). Therefore, hominins initially evolved from a short-backed ancestor; the lumbar column was elongated in australopithecines and later reduced in modern humans.
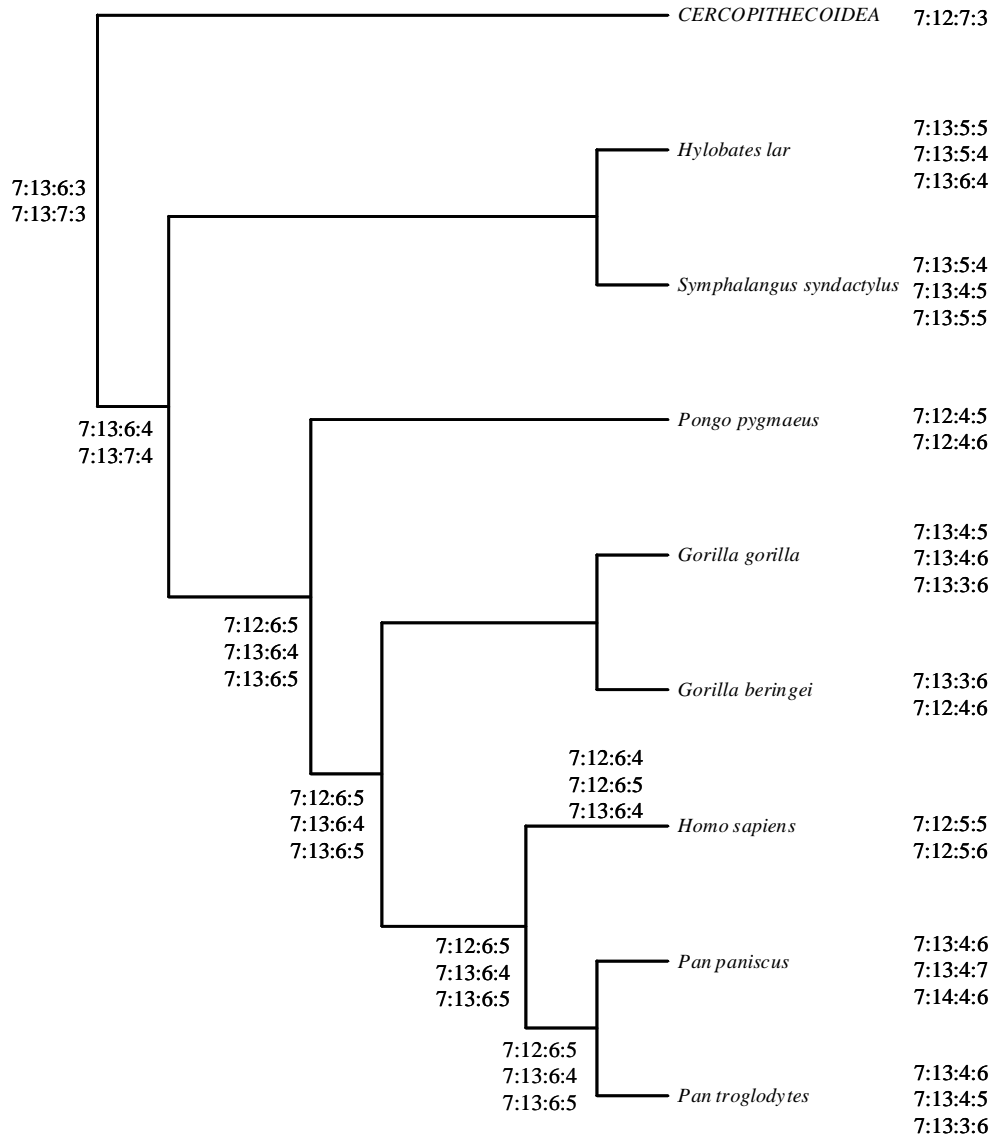
FIGURE 2.4. Catarrhine phylogeny showing McCollum and colleagues' long-back model. Vertebral profiles for extant taxa are shown on the right, and, with the exception of an updated bonobo sample, come from data presented in Pilbeam (2004). Hypothesized ancestral vertebral profiles are listed at nodes, with the proposed modal formula listed first (at the top of each set). Reconstructed hominine profiles come from Figure 4 in McCollum et al. (2010), whereas those of the catarrhine, hominoid, and hominid LCAs are from their Table 3. Notice that a long, primitive lumbar column is retained in the LCAs of hominoids, hominids, hominines, and that of the hominin-panin clade. This necessarily implies that lumbar regions reduced by one to three elements independently in hylobatids, orangutans, gorillas, humans, chimpanzees, and bonobos. Fossil hominins (above the human branch) retain a long lumbar region, which is reduced by one element in modern humans. Therefore, humans evolved from a long-backed ancestor.

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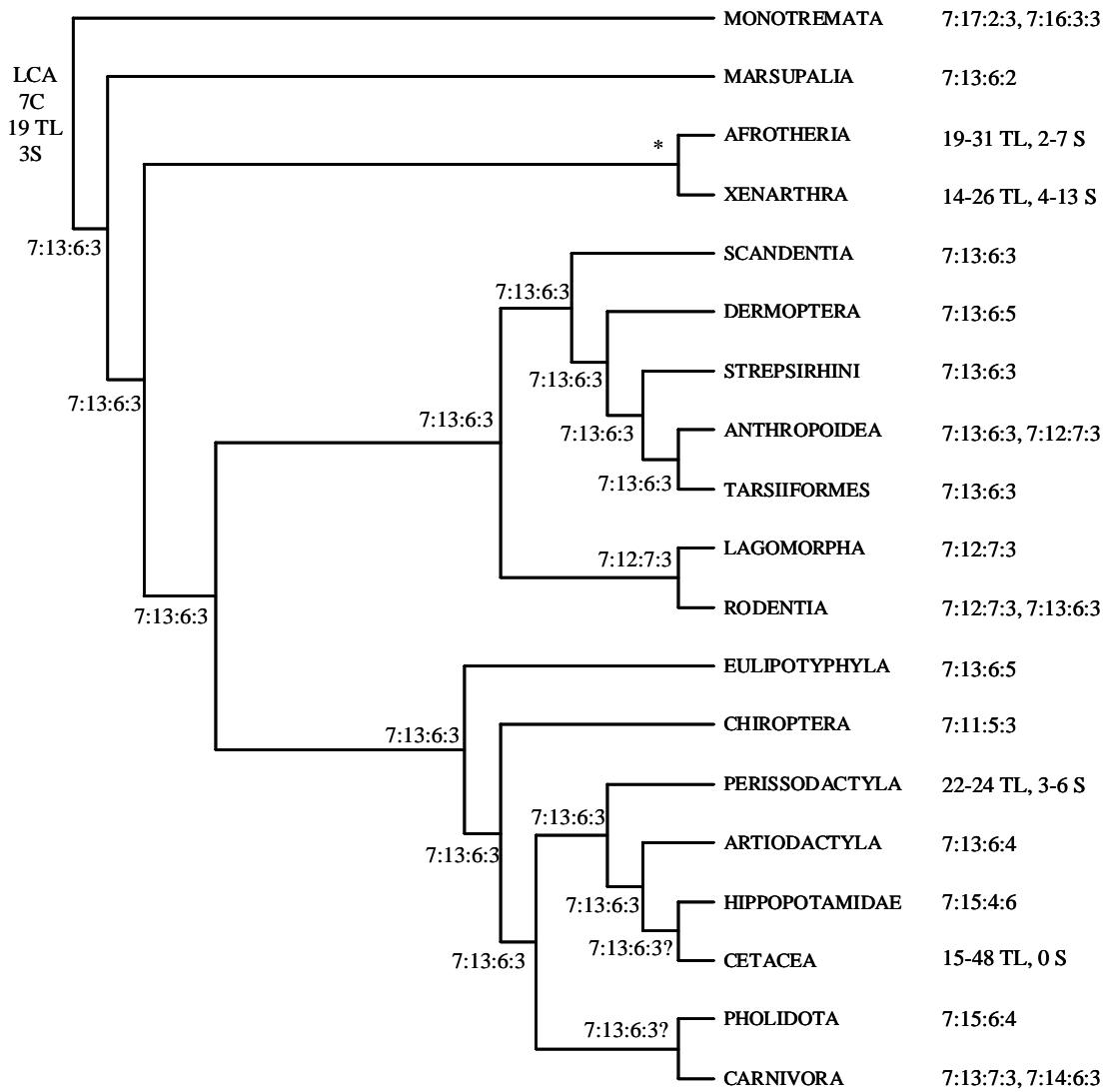
FIGURE 2.5. Phylogeny of mammals showing major clades. Common vertebral formulae represented in each group are shown on the right. Reconstructed vertebral formulae are based on vertebral formulae of both living and fossil mammals (see Discussion) and are shown at relevant nodes. Question marks (?) follow reconstructed ancestral formulae when all descendant taxa are specialized and it is unknown whether the primitive formula or a specialized one characterized the LCA at that node. Notice that the LCA of all mammals likely possessed 19 TL vertebrae, but the specific number of thoracic and lumbar vertebrae at this node is unknown. Phylogenetic structure and nomenclature follow Asher and Helgen (2010), with the use of some alternative relationships (e.g., Scandentia and Dermoptera) and taxonomic synonyms (e.g., Eulipotyphla versus Lipotyphla) (see Tables 1 and 2 in Asher and Helgen, 2010). *Atlantogenata (Afrotheria + Xenarthra) is characterized by a large amount of variation in presacral number and contains the only mammals that demonstrate deviations from modes of seven cervical vertebrae; as such, it is likely that the LCA was also derived in this regard, but its vertebral formula is unknown.
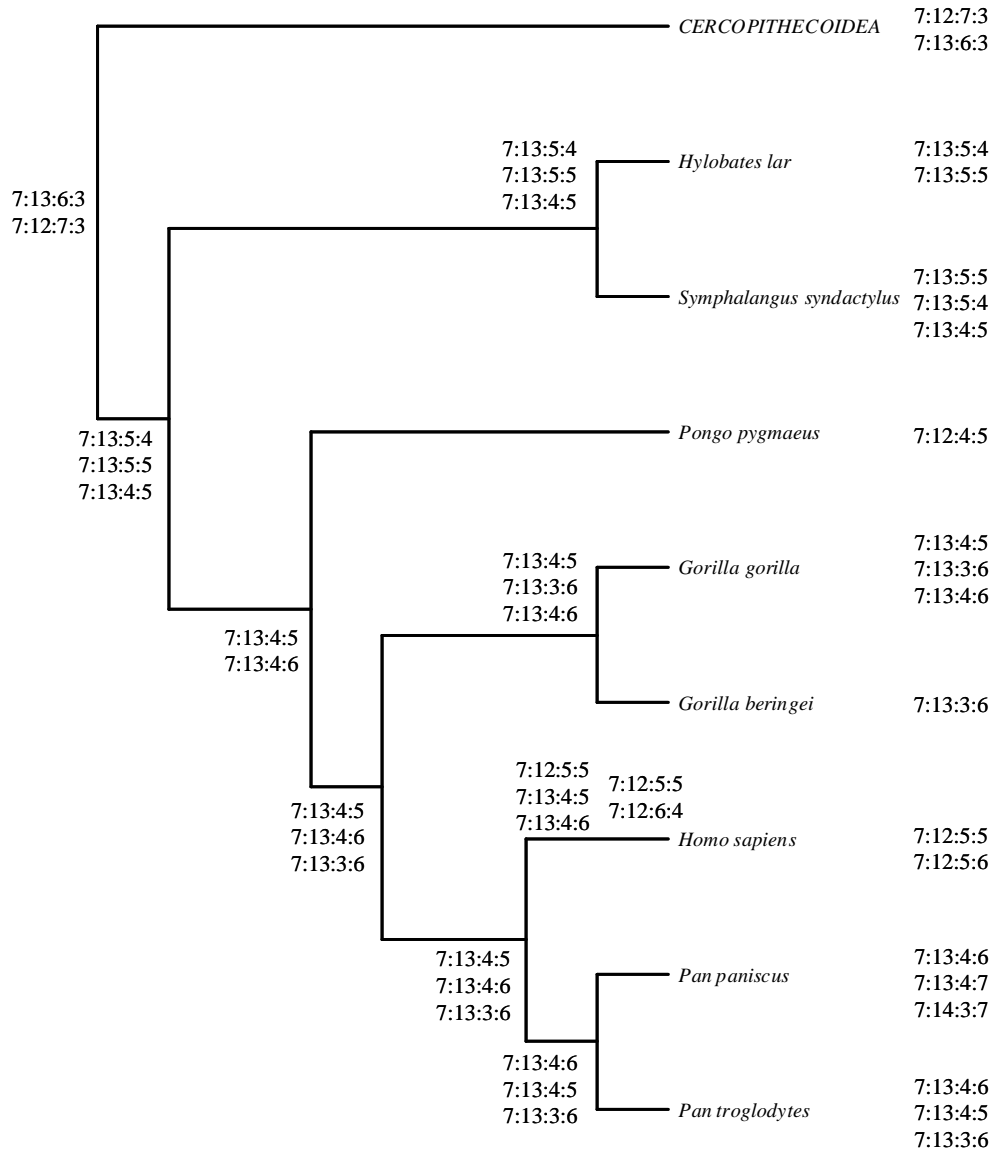
FIGURE 2.6. Catarrhine phylogeny showing the model proposed here. Vertebral profiles for extant taxa are shown on the right and come from the updated dataset presented in this study. Hypothesized ancestral vertebral profiles (from Table 2.1) are listed at nodes, with the proposed modal formula listed first (at the top of each set). Notice that "African ape-like" vertebral profiles are proposed to be primitive for hominids, hominines, gorillas, panins, and the hominin-panin LCA. This implies that reduced lumbar regions are homologous in orangutans, gorillas, and panins. Early fossil hominins evolved the modal human formula (above the human branch, left), which was retained in *Australopithecus* (above the human branch, right). Therefore, hominins evolved five lumbar vertebrae from a short-backed ancestor; modern humans simply retain this modal number.
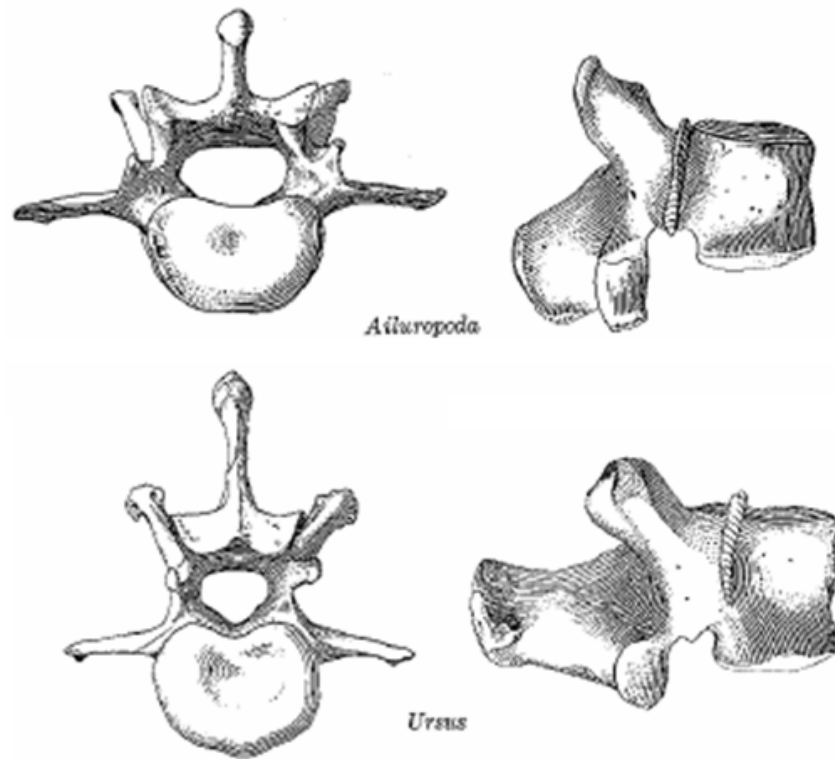
FIGURE 2.7. Giant panda (*Ailuropoda*; top) lumbar vertebra compared to that of another species of bear (*Ursus*; bottom). Caudal view (left) and sagittal views from the right side (right). Notice the shorter, wider centrum, more widely-spaced zygapophyses, larger vertebral canal, and more dorsally-placed lumbar transverse processes of *Ailuropoda* compare to *Ursus*. In these ways, giant pandas differ from other ursids in similar ways that hominoids differ from cercopithecoids. Modified from Davis (1964:81-82).

CHAPTER 2 REFERENCES

Abitbol, M. M., 1987. Evolution of the sacrum in hominoids. Am. J. Phys. Anthropol. 74, 65-81.

Agresti, A., Agresti, B.F., 1978. Statistical analysis of qualitative variation. Sociol. Methodol. 9, 204-237.

Alba, D.M., Moyà-Solà, S., Köhler, M., Rook, L., 2001. Heterochrony and the cranial anatomy of *Oreopithecus*: some cladistic fallacies and the significance of developmental constraints in phylogenetic analysis. In: L. de Bonis, G. Koufos (Eds.), Hominoid Evolution and Climate Change in Europe, Vol. 2, Phylogeny of the Neogene Hominoid Primates of Eurasia. Cambridge University Press, Cambridge, pp. 284-315.

Alexander, T., Nolte, C., Krumlauf, R., 2009. *Hox* genes and segmentation of the hindbrain and axial skeleton. Annu. Rev. Cell Dev. Biol. 25, 431-456.

Allen, J.A., 1917. The skeletal characters of *Scutisorex* Thomas. Bull. Am. Mus. Nat. Hist. 37, 769-784.

Asher, R.J., Bennett, N., Lehmann, T., 2009. The new framework for understanding placental mammal evolution. BioEssays 31, 853-864.

Asher, R.J., Helgen, K.M., 2010. Nomenclature and placental mammal phylogeny. BMC Evol. Biol. 10, 102.

Asher, R.J., Lin, K.H., Kardjilov, N., Hautier, L., 2011. Variability and constraint in the mammalian vertebral column. J. Evol. Biol. 24, 1080-1090.

Bateson, W., 1894. Materials for the Study of Variation: Treated with Especial Regard to Discontinuity in the Origin of Species. MacMillan and Co., London.

Belting, H.G., Shashikant, C.S., Ruddle, F.H., 1998. Modification of expression and cis-regulation of Hoxc8 in the evolution of diverged axial morphology. Proc. Natl. Acad. Sci. USA 95, 2355-2360.

Benton, R.S., 1967. Morphological evidence for adaptations within the epaxial region of the primates. In: van der Hoeven, F. (Ed.), The Baboon in Medical Research, Vol. II. University of Texas Press, Austin, pp. 201-216.

Birchette, M.G., 1982. The postcranial skeleton of *Paracolobus chemeroni*. Ph.D. dissertation, Harvard University.

Bonmati, A., Gómez-Olivencia, A., Arsuaga, J.-L., Carretero, J.M., Gracia, A., Martínez, I., Lorenzo, C., Bérmudez de Castro, J.M., Carbonell, E., 2010. Middle Pleistocene lower back and pelvis from an aged human individual from the Sima de los Huesos site, Spain. Proc. Natl. Acad. Sci. USA 107, 18386-18391.

Brown, F., Harris, J., Leakey, R., Walker, A. 1985., Early *Homo erectus* skeleton from west Lake Turkana, Kenya. Nature. 316, 788-792.

Buchholtz, E.A., 1998. Implications of vertebral morphology for locomotor evolution in early Cetacea. In: Thewissen, J.G.M. (Ed.), The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea. Plenum Press, New York, pp. 325-351.

Buchholtz, E.A., 2007. Modular development of the cetacean vertebral column. Evol. Dev. 9, 278-289.

Buchholtz, E.A., Booth, A.C., Webbink, K.E., 2007. Vertebral anatomy in the Florida manatee, *Trichechus manatus latirostris*: a developmental and evolutionary analysis. Anat. Rec. 290, 624-637.

Buchholtz, E.A., Stepien, C.C., 2009. Anatomical transformation in mammals: developmental origin of aberrant cervical anatomy in tree sloths. Evol. Dev. 11, 69-79.

Buffon, G.L., 1769. Histoire Naturelle, Generale et Particuliere. Pankoucke, Paris.

Burke, A.C., Nelson, C.E., Morgan, B.A., Tabin, C., 1995. Hox genes and the evolution of vertebrate axial morphology. Development. 121, 333-346.

Clauser, D., 1980. Functional and comparative anatomy of the primate spinal column: some locomotor and postural adaptations. Ph.D. dissertation, University of Wisconsin-Milwaukee.

Cullinane, D.M., Aleper, D., Bertram, J.E.A., 1998. The functional and biomechanical modifications of the spine of *Scutisorex somereni*, the hero shrew: skeletal scaling relationships. J. Zool. Lond. 244, 447-452.

Davis, D.D., 1964. The giant panda: a morphological study of evolutionary mechanisms. Fieldiana: Zool. Mem. 8, 1-334.

Dequeant, M.L., Pourquié, O., 2008. Segmental patterning of the vertebrate embryonic axis. Nat. Rev. Genet. 9, 370-382.

Disotell, T.R., 1994. Generic level relationships of the Papionini (Cercopithecoidea). Am. J. Phys. Anthropol. 94, 47-57.

Duckworth, W.L.H., 1911. Report on an abnormal first thoracic vertebra. J. Anat. Physiol. 45, 65-68.

Endo, H., Sasaki, M., Hayashi, Y., Koie, H., Yamaya, Y., Kimura, J., 2001. Carpal bone movements in gripping action of the giant panda (*Ailuropoda melanoleuca*). J. Anat. 198, 243-246.

Erikson, G., 1963. Brachiation in New World monkeys and in anthropoid apes. Symp. Zool. Soc. Lond. 10, 135-163.

Filler, A.G., 1986. Axial character seriation in mammals: an historical and morphological exploration of the origin, development, use, and current collapse of the homology paradigm. Ph.D. dissertation, Harvard University.

Filler, A.G., 1993. Evolution of the sacrum in hominoids. In: Doty, J.R., Rengachary, S.S. (Eds.). Surgical Disorders of the Sacrum. Thieme Medical Publishers, New York, pp. 13-20.

Filler, A.G., 2007. Homeotic evolution in the Mammalia: diversification of therian axial seiation and the morphogenetic basis of human origins. PLoS One 10, e1019.

Fleagle, J.G., McGraw, W.S., 1999. Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. Proc. Natl. Acad. Sci. USA 96, 1157-1161.

Fleagle, J.G., McGraw, W.S., 2002. Skeletal and dental morphology of African papionins: unmasking a cryptic clade. J. Hum. Evol. 42, 267-292.

Flower, W.H., 1884. Catalogue of the Specimens Illustrating the Osteology and Dentition of the Vertebrated Animals, Recent and Extinct, Contained in the Museum of the Royal College of Surgeons of England, Part II. Class Mammalia, other than Man. J. and A. Churchill, London.

Flower, W.H., 1885. An Introduction to the Osteology of the Mammalia. MacMillan and Co., London.

Galis, F., 1999. Why do almost all mammals have seven cervical vertebrae? Developmental constraints, Hox genes, and cancer. J. Exp. Zool. 285, 19-26.

Galis, F., Van Dooren, T.J.M., Feuth, J.D., Metz, J.A.J., Witkam, A., Ruinard, S., Steigenga, M.J., Wijnaendts, L.C.D., 2006. Extreme selection in humans against homeotic transformations of cervical vertebrae. Evolution 60, 2643-2654.

Galliari, F.C., Carlini, A.A., Sánchez-Villagra, M.R., 2010. Evolution of the axial skeleton in armadillos (Mammalia, Dasypodidae). Mammal. Biol. 75, 326-333.

Gambaryan, P.P., Zherebtsova, O.V., Perepelova, A.A., Platonov, V.V., 2009. Pes muscles and their action in giant anteater *Myrmecophaga tridactyla* (Myrmecophagidae, Pilosa) compared with other plantigrade mammals. Russian J. Theriol. 8, 1-15.

Gaunt, S.J., 1994. Conservation in the Hox code during morphological evolution. Int. J. Dev. Biol. 38, 549-552.

Gebo, D.L., 1992. Plantigrady and foot adaptation in African apes. Implications for hominid origins. Am. J. Phys. Anthropol. 89, 29-58.

Gebo, D.L., 1993. Reply to Dr. Meldrum. Am. J. Phys. Anthropol. 91, 382-385.

Gomez, C., Ozbudak, E.M., Wunderlich, J., Baumann, D., Lewis, J., Pourquié, O., 2008. Control of segment number in vertebrate embryos. Nature 454, 335-339.

Gomez, C., Pourquié, O., 2009. Developmental control of segment numbers in vertebrates. J. Exp. Zool. 312B, 533-544.

Groves, C.P., 1978. Phylogenetic and population systematics of the mangabeys (Primates: Cercopithecoidea). Primates 19, 1-34.

Haeusler, M., Martelli, S.A., Boeni, T., 2002. Vertebrae numbers of the early hominid lumbar spine. J. Hum. Evol. 43, 621-643.

Harrison, T., 1986. A reassessment of the phylogenetic relationships of *Oreopithecus bambolii* Gervais. J. Hum. Evol. 15, 541-583.

Harrison, T., 1991. The implications of *Oreopithecus bambolii* for the origins of bipedalism. Cour. Forsch.-Inst. Senckenberg 243, 235-244.

Harrison, T., Rook, L., 1997. Enigmatic anthropoid or misunderstood ape: the phylogenetic status of *Oreopithecus bambolii* reconsidered. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 327-362.

Hasebe, K., 1913. Die wirbelsaule der Japaner. Zeit. Morph. Anth. 15, 259-380.

Hatt, R.T., 1932. The vertebral columns of ricochetal rodents. Bull. Am. Mus. Nat. Hist. 63, 599-738.

Hildebrand, M., 1974. Analysis of Vertebrate Structure. Wiley, New York.

Hou, Z.C., Romero, R., Wildman, D.E., 2009. Phylogeny of the Ferungulata (Mammalia: Laurasiatheria) as determined from phylogenomic data. Mol. Phylogen. Evol. 52, 660-664.

Iimura, T., Denans, N., Pourquié, O., 2009. Establishment of Hox vertebral identities in the embryonic spine precursors. Curr. Topics Develop. Biol. 88, 201-234.

Ishida, H., Kunimatsu, Y., Takano, T., Nakano, Y., Nakatsukasa, M., 2004. *Nacholapithecus* skeleton from the Middle Miocene of Kenya. J. Hum. Evol. 46, 69-103.

Janecka, J.E., Miller, W., Pringle, T.H., Wiens, F., Zitzmann, A., Helgen, K.M., Springer, M.S., Murphy, W.J., 2007. Molecular and genomic data identify the closest living relative of primates. Science 318, 792-794.

Jenkins, F.A., 1970. Anatomy and function of expanded ribs in certain edentates and primates. J. Mammal. 51, 288-301.

Jenkins, F., 1971. The postcranial skeleton of African cynodonts. Bull. Peabody. Mus. Nat. Hist. 36, 1-216.

Jepsen, G.L., 1966. Early Eocene bat from Wyoming. Science 154, 1333-1339.

Jungers, W.L., 1984. Scaling of the hominoid locomotor skeleton with special reference to lesser apes. In: Preuschoft, H., Chivers, D.J., Brockelman, W.Y., Creel, N. (Eds.), The Lesser Apes: Evolutionary and Behavioral Biology. Edinburgh University Press, Edinburgh, pp. 146-169.

Keith, A., 1903. The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates. J. Anat. Physiol. 37, 18-40.

Keith, A., 1923. Man's posture: its evolution and disorders. Brit. Med. J. 1, 451-454, 499-502, 545-548, 587-590, 624-626, 669-672.

Latimer, B., Ward, C.V., 1993. The thoracic and lumbar vertebrae. In: Walker, A., Leakey, R. (Eds.). The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 266-293.

Lovejoy, C.O., McCollum, M.A., 2010. Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip–bent-knee gait. Phil. Trans. R. Soc. B 365, 3289-3299.

Lovejoy, C.O., Suwa, G., Simpson, S.W., Matternes, J.H., White, T.D., 2009. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. Science 326, 100-106.

Madar, S.I., Thewissen, J.G.M., Hussain, S.T., 2002. Additional holotype remains of *Ambulocetus natans* (Cetacea, Ambulocetidae), and their implications for locomotion in early whales. J. Vert. Paleontol. 22, 405-422.

Mallo, M., Wellik, D.M., Deschamps, J., 2010. *Hox* genes and regional patterning of the vertebrate body plan. Develop. Biol. 344, 7-15.

Mansfield, J.H., Abzhanov, A., 2010. Hox expression in the American alligator and evolution of archosaurian axial patterning. J. Exp. Zool. 314B, 629-644.

Matsudaira, K., Ishida, T., 2010. Phylogenetic relationships and divergence dates of the whole mitochondrial genome sequences among three gibbon genera. Mol. Phylogen. Evol. 55, 454-459.

McCollum, M.A., Rosenman, B.A., Suwa, G., Meindl, R.S., Lovejoy, C.O., 2010. The vertebral formula of the last common ancestor of African apes and humans. J. Exp. Biol. 314B, 123-134.

Montgomery, G.G., 1985. Movements, foraging, and food habits of the four extant species of neotropical vermilinguas (Mammalia: Myrmecophagidae). In: Montgomery, G.G. (Ed.). The Evolution and Ecology of Armadillos, Sloths and Vermilinguas. Smithsonian Institution Press, Washington, D.C., pp. 365-377.

Moyà-Solà, S., Köhler, M., 1997. The phylogenetic relationships of *Oreopithecus bambolii* Gervais, 1872. Comp. Rend. Acad. Sci. Paris 324, 141-148.

Muller, J., Scheyer, T.M., Head, J.J., Barrett, P.M., Werneburg, I., Ericson, P.G.P., Pol, D., Sánchez-Villagra, M.R., 2010. Homeotic effects, somitogenesis and the evolution of vertebral numbers in recent and fossil amniotes. Proc. Natl. Acad. Sci. USA 107, 2118-2123.

Nakatsukasa, M., Kunimatsu, Y., 2009. *Nacholapithecus* and its importance for understanding hominoid evolution. Evol. Anthropol. 18, 103-119.

Nakatsukasa, M., Tsujikawa, H., Shimizu, D., Takano, T., Kunimatsu, Y., Nakano, Y., Ishida, H., 2003. Definitive evidence for tail loss in *Nacholapithecus*, an East African Miocene hominoid. J. Hum. Evol. 45, 179-186.

Narita, Y., Kuratani, S., 2005. Evolution of the vertebral formulae in mammals: a perspective on developmental constraints. J. Exp. Zool. 304B, 91-106.

Nishihara, H., Hasegawa, M., Okada, N., 2006. Pegasoferae, an unexpected mammalian clade revealed by tracking anceint retroposon insertions. Proc. Natl. Acad. Sci. USA 103, 9929-9934.

Ohya, Y.K., Kuraku, S., Kuratani, S., 2005. Hox code in embryos of Chinese soft-shelled turtle *Pelodiscus sinensis* correlates with the evolutionary innovation in the turtle. J. Exp. Zool. 304B, 107-118.

Owen, R., 1868. On the Anatomy of Vertebrates, Vol. III. Mammals. Longmans, Green, and Co, London.

Perelman, P., Johnson, W.E., Roos, C., Seuánez, H.N., Horvath, J.E., Moreira, M.A.M., Kessing, B., Pontius, J., Roelke, M., Rumpler, Y., Schneider, M.P.C., Silva, A., O'Brien, S.J., Pecon-Slattery, J., 2011. A molecular phylogeny of living primates. PLoS Genetics 7, e1001342.

Pilbeam, D., 1996. Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. Mol. Phylogen. Evol. 5, 155-168.

Pilbeam, D., 1997. Research on Miocene hominoids and hominid origins: the last three decades. In: Begun, D.R., Ward, C.V., Rose, M.D. (Eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum Press, New York, pp. 13-28.

Pilbeam, D., 2004. The anthropoid postcranial axial skeleton: comments on development, variation, and evolution. J. Exp. Zool. 302B, 241-267.

Polly, P.D., Head, J.J., Cohn, M.J., 2001. Testing modularity and dissociation: the evolution of regional proportions in snakes. In: Zelditch, M.L. (Ed.), Beyond Heterochrony: The Evolution of Development. Wiley-Liss, New York, pp. 305-335.

Reynolds, E., 1931. The evolution of the human pelvis in relation to the mechanics of the erect posture. Papers Peabody Mus. Amer. Archaeol. Ethnol., Harvard 11, 255-334.

Richardson, M.K., Allen, S.P., Wright, G.M., Raynaud, A., Hanken, J., 1998. Somite number and vertebrate evolution. Development 125, 151-160.

Robinson, J., 1972. Early hominid posture and locomotion. University of Chicago Press, Chicago.

Rose, K.D., 1985. Comparative osteology of North American dichobunid artiodactyls. J. Paleontol. 59, 1203-1226.

Rose, M.D., 1975. Functional proportions of primate lumbar vertebral bodies. J. Hum. Evol. 4, 21-38.

Rosenman, B.A., 2008. Triangulating the evolution of the vertebral column in the last common ancestor: thoracolumbar transverse process homology in the hominoidea. Ph.D. dissertation, Kent State University.

Russo, G.A., Shapiro, L.J., 2011. Morphological correlates of tail length in the catarrhine sacrum. J. Hum. Evol. doi:10.1016/j.jhevol.2011.03.006.

Sánchez-Villagra, M.R., Narita, Y., Kuratani, S., 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. Syst. Biodiv. 5, 1-7.

Sanders, W.J., 1995. Function, allometry, and the evolution of the australopithecine lower precaudal spine. Ph.D. dissertation, New York University.

Sanders, W.J., 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J. Hum. Evol. 34, 249-302.

Sargis, E.J., 2001. A preliminary qualitative analysis of the axial skeleton of tupaiids (Mammalia, Scandentia): functional morphology and phylogenetic implications. J. Zool. Lond. 253, 473-483.

Sarmiento, E.E., 1987. The phylogenetic position of *Oreopithecus* and its significance in the origin of the Hominoidea. Am. Mus. Novitates 2881, 1-44.

Schultz, A., 1930. The skeleton of the trunk and limbs of higher primates. Hum. Biol. 2, 303-438.

Schultz, A., 1933. Observations on the growth, classification and evolutionary specialization of gibbons and siamangs (concluded). Hum. Biol. 5, 385-428.

Schultz, A.H., 1938. The relative length of the regions of the spinal column in Old World primates. Am. J. Phys. Anthropol. 24, 1-22.

Schultz, A.H., 1960. Einige beobachtungen und masse am skelett von Oreopithecus. Z. Morph. Anthrop. 50, 136-149.

Schultz, A.H., 1961. Vertebral column and thorax. Primatologia 4, 1-66.

Schultz, A.H., Straus, W.L., 1945. The numbers of vertebrae in primates. Proc. Am. Phil. Soc. 89, 601-626.

Scott, W.B., Jepsen, G.L., 1936. The mammalian fauna of the White River Oligocene. Part I. Insectivora and Carnivora. Trans. Am. Phil. Soc. 28, 1-153.

Shapiro, L., 1993. Functional morphology of the vertebral column in primates. In: Gebo, D.L. (Ed.), Postcranial Adaptation in Nonhuman Primates. Northern Illinois University Press, Dekalb, IL.

Shaw, J.H., Carter, T.S., Machjado-Neto, J.C., 1985. Ecology of the giant anteater Myrmecophaga tridactyla in Serra da Canastra, Minas Gerais, Brazil: a pilot study. In: Montgomery, G.G. (Ed.). The Evolution and Ecology of Armadillos, Sloths and Vermilinguas. Smithsonian Institution Press, Washington, D.C., pp. 379-384.

Simmons, N.B., Seymour, K.L., Habersetzer, J., Gunnell, G.F., 2008. Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451, 818-822.

Slijper, E., 1946. Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. Verh. Kon. Ned. Akad. Wet. (Tweede Sectie). 42, 1-128.

Straus, W.L., 1963. The classification of *Oreopithecus*. In: Washburn SL (Ed.), Classification and Human Evolution. Aldine, Chicago, pp. 146-177.

Tague, R.G., 2009. High assimilation of the sacrum in a sample of American skeletons: prevalence, pelvic size, and obstetrical and evolutionary implications. Am. J. Phys. Anthropol. 138, 429-438.

Tam, P.P.L., Tan, S.S., 1992. The somitogenetic potential of cells in the primitive streak and the tail bud of the organogenesis-stage mouse embryo. Development 115, 703-715.

Todd, T.W., 1922. Numerical significance in the thoracicolumbar vertebrae of the Mammalia. Anat. Rec. 24, 261-286.

Toussaint, M., Macho, G.A., Tobias, P.V., Partridge, T.C., Hughes, A.R., 2003. The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa. S. Af. J. Sci. 99, 215-223.

Turner, H.N., 1847. Observations on the distinction between the cervical and dorsal vertebrae in the Class Mammalia. Proc. Zool. Soc. Lond. 15, 110-114.

Van Sittert, S.J., Skinner, J.D., Mitchell, G., 2010. From fetus to adult – an allometric analysis of the giraffe vertebral column. J. Exp. Zool. 314B, 469-479.

Walker, A., Leakey, R., 1993. The postcranial bones. In: Walker, A., Leakey, R. (Eds.), The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 95-160.

Walker, A., Ruff, C.B., 1993. The reconstruction of the pelvis. In: Walker, A., Leakey, R. (Eds.), The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 221-233.

Walker, M.J., Ortega, J., Parmová, K., López, M.V., Trinkaus, E., 2011. Morphology, body proportions, and postcranial hypertrophy of a female Neandertal from the Sima de las Palomas, southeastern Spain. Proc. Natl. Acad. Sci. USA 108, 10087-10091.

Ward, C.V., 1993. Torso morphology and locomotion in *Proconsul nyanzae*. Am. J. Phys. Anthropol. 92, 291-328.

Ward, C.V., Walker, A., Teaford, M.F., 1991. *Proconsul* did not have a tail. J. Hum. Evol. 21, 215-220.

Welcker, H., 1881. Die nuee anatomische Anstalt zu Halle durch einen Vortrag uber Wirbelsaule und Becken. Arch. Anat. Physiol., Anat. Abth. 161-192.

Wellik, D.M., 2007. *Hox* patterning of the vertebrate axial skeleton. Dev. Dyn. 236, 2454-2463.

Wellik, D.M., 2009. *Hox* genes and vertebrate axial pattern. Curr. Topics Develop. Biol. 88, 257-278.

Wellik, D.M., Capecchi, M.R., 2003. *Hox10* and *Hox11* genes are required to globally pattern the mammalian skeleton. Science 301, 363-367.

Wilcox, A.R., 1971. Indices of qualitative variation and political measurement. West. Pol. Quart. 26, 325-343.

Wood, A.R., Bebej, R.M., Manz, C.L., Begun, D.L., Gingerich, P.D., 2010. Postcranial functional morphology of *Hyracotherium* (Equidae, Perissodactyls) and locomotion in the earliest horses. J. Mammal. Evol. 18, 1-32.

Zapfe, H., 1958. The skeleton of *Pliopithecus* (*Epipliopithecus*) *vindobonesis* Zapfe and Hurzeler. Am. J. Phys. Anthropol. 16, 441-458.

CHAPTER 3

VARIATION IN ANTHROPOID VERTEBRAL FORMULAE

INTRODUCTION

An understanding of the evolution of the numerical composition of the vertebral column in hominoid primates is complicated by high levels of intraspecific variation in vertebral formulae within hominoids. Additionally, the lack of a consistent, sturdy phylogenetic tree throughout much of the history of our discipline has problematized our attempts to reconstruct the evolutionary history of the hominoid vertebral column. Moreover, attempts to place hominin vertebral evolution in the larger hominoid context were likewise obscured, which led to now unsupported scenarios of hominin vertebral evolution (e.g., Filler, 1993; Haeusler et al., 2002; see Pilbeam, 2004). Recently, two evolutionary scenarios (Pilbeam, 2004; McCollum et al., 2010) were proposed to explain the distribution and variation in vertebral formulae observed among extant hominoids, both interpreted in a modern phylogenetic context (e.g., Perelman et al., 2011). Panins (chimpanzees and bonobos) are the closest living relatives of humans, with gorillas as the sister-taxon to the panin-hominin clade, orangutans as the sister-taxon to the African great ape (hominine) clade, and gibbons (hylobatids) as the sister-taxon to the great ape (hominid) clade, together forming the Hominoidea (Wood, 2010).

Pilbeam (2004) interpreted the similarity of western gorilla (*Gorilla gorilla*) and chimpanzee (*Pan troglodytes*) modal vertebral formulae and inter- and intra-specific variation in formulae to indicate that hominins initially evolved from a chimpanzee-like, "short-backed"

ancestor with three to four lumbar vertebrae (hereafter, the "short-back" model). Pilbeam (2004:261) proposed a likely pre-hominin vertebral profile (defined here as a set of vertebral formulae represented at >10% frequency in a population, with each formula shown as Cervical: Thoracic: Lumbar: Sacral) of 7:13:4:6, 7:13:4:5, and 7:13:3:6, a combination shared by both chimpanzees and western gorillas. In this scenario, reduced lumbar regions (five or fewer elements, compared to the primitive catarrhine condition of six or seven lumbar vertebrae) are homologous in extant hominoids and represent a defining characteristic (synapomorphy) of the hominoid clade.

McCollum et al. (2010) do not share this view and instead argue that homoplasy has played a ubiquitous role in hominoid vertebral evolution: "Reduction in the lumbar column occurred independently in humans and in each ape clade, and continued after separation of the two species of *Pan* as well" (McCollum et al., 2010:123). This evolutionary scenario requires the independent reduction of the lumbar region at least six times among extant taxa alone (hylobatids, orangutans, gorillas, humans, chimpanzees and bonobos). McCollum et al. (2010) conclude that hominins and other extant hominoids each evolved from primitive, "long-backed" ancestors with at least six lumbar vertebrae (hereafter, the "long-back" model) and a likely vertebral profile of 7:12:6:5, 7:13:6:4, and 7:13:6:5 (see Figure 4 in McCollum et al., 2010). Their argument is based largely on the presence of an extra pre-caudal element in bonobos (*Pan paniscus*) and their interpretation of fossil hominin vertebral columns.

Modally, each extant hominid species except chimpanzees and bonobos is characterized by a different vertebral formula (from Chapter 2): 7:12:4:5 in orangutans (*Pongo pygmaeus*, here including both Borneo and Sumatran orangutans), 7:13:4:5 in western gorillas (*G. gorilla*), 7:13:3:6 in eastern gorillas (*G. beringei*), 7:12:5:5 in humans (*Homo sapiens*), and 7:13:4:6 in

chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). White-handed gibbons (*Hylobates lar*) and siamangs (*Symphalangus syndactylus*) also demonstrate different modal formulae, at 7:13:5:4 and 7:13:5:5, respectively (Chapter 2). If these modal formulae are placed in a phylogenetic context, the simplest, or most parsimonious, scenario (one that involves the least number of changes) is an "African ape-like," short-backed vertebral profile of 7:13:4:5, 7:13:4:6, and possibly 7:13:3:6 (see Chapter 2).

However, hominoids demonstrate high amounts of intraspecific variation in vertebral formulae (see Pilbeam, 2004; McCollum et al., 2010), which make interpretations of ancestral vertebral formulae difficult. Pilbeam (2004:254) suggested that detectable patterns could be elicited from the diversity he found within species:

> These indices reflect patterning of variation, and suggest that in some cases strong stabilizing selection concentrates most of the variation in a few formulae, generating a low index. This further suggests that cursorial quadrupedalism and bipedalism (cercopithecoids and hominins) are relatively more specialized locomotor adaptations which select for a narrower range of phenotypes.

Here, I calculate new indices of diversity and similarity (see Methods) based on a large sample of anthropoids and interpret the results in the context of patterning of variation and the patterns of selection required to produce it. Strong directional or stabilizing selection should be expected to produce low within-species diversity, the former of which should also be associated with low similarity between species that have experienced divergent selection pressures; alternatively, weak selection should be associated with high diversity and relatively high similarity in closely related taxa.

The diametrically opposed evolutionary scenarios presented by Pilbeam (2004) and McCollum et al. (2010) have drastically different implications not only for the evolution of bipedalism, but also for the way in which evolution works and how we interpret shared derived

traits (synapomorphies) among living taxa. If Pilbeam's short-back model is correct, shared traits are considered homologous and living taxa can be used as models to help us reconstruct hominoid evolution and better understand hominin origins. If, on the other hand, McCollum and colleagues' long-back model is correct, then many postcranial traits shared among extant hominoids are uninformative, non-synapomorphic parallelisms that evolved repeatedly, with the implication that "We can no longer rely on homologies with African apes for accounts of our origins" (Lovejoy, 2009:74e1; see also Lovejoy et al., 2009; Lovejoy and McCollum, 2010). In this study, I will test these competing hypotheses by examining patterns of variation in vertebral formulae demonstrated among extant hominoids to determine if homoplasy or homology played a predominant role in hominoid vertebral evolution.

MATERIALS AND METHODS

Vertebral columns were examined on skeletal specimens at museums and collections in the U.S. and Europe (see Acknowledgments for museum information). Details associated with seriation and measures to avoid specimen duplication, where the same specimen is represented more than once in the dataset, can be found in Chapter 2. Procedures to determine vertebral identity, including the treatment of transitional vertebrae, follow the Schultz criteria, also outlined in Chapter 2. This study focuses on the precaudal vertebral column since caudal or coccygeal vertebrae are often missing or incomplete in museum collections, particularly among non-hominoid specimens. Because analyses of inter- and intraspecific variation are sample size sensitive, even when sample size corrections are employed, only taxa represented by at least 30 specimens are analyzed; however, sample sizes often greatly exceed this minimum threshold

(Table 3.1). Full precaudal formulae are compiled for each taxon and pattern frequencies are recorded. Compared to the datasets analyzed in Pilbeam (2004) and McCollum et al. (2010), sample sizes for anthropoid taxa were more than doubled on average in this study.

Pilbeam (2004) introduced two methods to summarize and compare variation in vertebral formulae, the "morphological heterogeneity" index (p. 252) and the "normalized morphological similarity index" (p. 254). Because vertebral formulae consist of series of meristic data, traditional statistical analyses of quantitative variation cannot be employed. Instead, measures of qualitative (Wilcox, 1973; Agresti and Agresti, 1978) and genetic (Nei, 1972, 1987) variation are used to calculate intraspecific and interspecific variation in vertebral formulae, respectively.

The diversity index measures the amount of variation observed in a population compared to the maximum amount of variation possible (Agresti and Agresti, 1978) and is identical to Pilbeam's (2004) morphological heterogeneity index and Nei's (1987:177) heterozygosity (a.k.a. gene diversity). It is shown here in a sample size standardized form, also known as the index of qualitative variation (Wilcox, 1973; Agresti and Agresti, 1978):

$$DI = 1 - \sum_{i=1}^{n} f_i^2 \ [n/(n\text{-}1)] \ ,$$

where f is the frequency of a single vertebral formula in a population and n is sample size. The diversity index ranges from 0 (no variation) to 1 (maximum variation) and represents the probability of sampling two individuals with different formulae at random from a population.

Pilbeam's (2004) normalized morphological similarity index is analogous to Nei's (1972, 1987:220) genetic identity (a.k.a. normalized identity of genes). It treats variants in vertebral formulae as variants in genes (i.e., alleles) by creating a ratio of shared vertebral patterns to the total variation represented in both species:

$$SI = \sum x_i\, y_i \,/ (\sum x_i^2 \sum y_i^2)^{1/2} \ ,$$

where $x_i\, y_i$ is the probability of sampling pattern i from population x and from population y, and

x_i^2 and y_i^2 are the probabilities of sampling pattern i and then pattern i again from within

population x and from within population y. The product of $x_i^2\, y_i^2$ is the probability of sampling

pattern i twice within x and y. Because it is expressed as a ratio, the *SI* ranges from 0 (no

similarity) to 1 (maximum similarity).

RESULTS

Descriptive statistics for individual regions are included in the Appendix D but are not

discussed in detail here. Instead, full sets of precaudal vertebral formulae are presented and

included in comparative analyses. This latter method is preferred since homeotic (trans-border)

shifts, in which a vertebral element differs between two individuals in a population or between

two populations and is attributable to a change in identity in the same numerical framework (e.g.,

13T:4L in a 17 element framework versus 12T:5L in the same numerical framework), are

common in mammals in both intraspecific and interspecific comparisons (Chapter 2; see also

Muller et al., 2010).

Vertebral profiles are listed in Table 3.2 (see Chapter 2; full sets of vertebral formulae are

listed in Appendix C). Some taxa (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Symphalangus*

syndactylus, *Cercopithecus sp.*, and *Saimiri sciureus*) exhibit three vertebral formulae in their

profiles (those with frequencies >10%), others two (*Homo sapiens*, *Pongo pygmaeus*, *Hylobates*

lar, *Macaca fascicularis*, *Cercocebus sp.*, *Papio sp.*, and *Cebus sp.*) or just the modal formula

(*Gorilla beringei*, *Trachypithecus sp.*, *Nasalis larvatus*, *Macaca fuscata*, *Lophocebus sp.*,

Theropithecus gelada, and *Ateles sp.*). *Alouatta* demonstrates five formulae at greater than 10%

frequency, although the modal formula is represented at a much higher frequency (41%) than the

subsequent formulae, which are tied at 10.3%.

Likewise, the total frequency for which the vertebral profile accounts in each taxon also

varies significantly, ranging from just 35.0% over three formulae in *Pan paniscus* to 93.3% in

Theropithecus gelada at the modal formula alone. Even in closely related species within the

same genus, large differences are observed – for example, *Gorilla gorilla* exhibits three formulae

in its vertebral profile, totaling to 63.4% of the variation observed, while *Gorilla beringei*

demonstrates a greater frequency in its modal formulae alone (70.6%).

Intraspecific variation

A diversity index (*DI*) is calculated to quantify variation in the distribution of observed

vertebral formulae in each taxon (Figure 3.1; Table 3.3). Hominoids demonstrate a wide range of

diversity indices, ranging from 0.496 in eastern gorillas (*Gorilla beringei*) to 0.946 in bonobos

(*Pan paniscus*), with humans (*Homo sapiens*, *DI* = 0.591), orangutans (*Pongo pygmaeus*, *DI* =

0.810), white-handed gibbons (*Hylobates lar*, *DI* = 0.804), chimpanzees (*Pan troglodytes*, *DI* =

0.826), western gorillas (*Gorilla gorilla*, *DI* = 0.851), and siamangs (*Symphalangus syndactylus*,

DI = 0.889) falling in between.

Cercopithecoids also range widely in the diversity index, with geladas (*Theropithecus*

gelada, *DI* = 0.131), snub-nosed monkeys (*Nasalis larvatus*, *DI* = 0.138), *Lophocebus*

mangabeys (*Lophocebus sp.*, *DI* = 0.313), and lutungs (*Trachypithecus sp.*, *DI* = 0.316) on the

low end and baboons (*Papio sp.*, *DI* = 0.721), *Cercocebus* mangabeys (*Cercocebus sp.*, *DI* =

0.742), and guenons (*Cercopithecus sp.*, *DI* = 0.743) on the high end; long-tailed macaques

(*Macaca fascicularis*, *DI* = 0.473), Japanese macaques (*Macaca fuscata*, *DI* = 0.485), and vervets (*Chlorocebus aethiops*, *DI* = 0.550) fall in between. Among the platyrrhines included in this study, spider monkeys (*Ateles sp.*, *DI* = 0.447) generate the lowest diversity index, followed by squirrel monkeys (*Saimiri sciureus*, *DI* = 0.746), capuchins (*Cebus sp.*, *DI* = 0.784), and howler monkeys (*Alouatta sp.*, *DI* = 0.803).

Interspecific variation

Similarity indices (*SI*) for interspecies comparisons are listed in Table 3.3. These range from 0 (no similarity) to 0.995 (nearly identical). Several observations are notable: 1) similarity indices among cercopithecoids are much higher than the other groups are amongst themselves – the average similarity index among cercopithecoids is 0.679, compared to 0.188 in hominoids and 0.180 in platyrrhines. 2) Among cercopithecoids, baboons, and in particular, geladas and *Lophocebus* mangabeys, share less similarity with the other cercopithecoids, including colobines (*Nasalis larvatus* and *Trachypithecus cristata*), than they do with each other (Figure 3.2). Aside from the colobines, which produce a very high similarity index with one another (*SI* = 0.994), this may represent the only strong phylogenetic signal in the dataset, although interrelationships in similarity indices among *Lophocebus sp.* and *Theropithecus gelada* (*SI* = 0.995) and both taxa and *Papio sp.* (*SI* = 0.872 and 0.834, respectively) are complicated by unknown phylogenetic relationships in this group (Harris, 2000; see also Perelman et al., 2011).

3) Hominoids generally produce low intra-group similarity indices, although several comparisons are relatively high. The highest index in the hominoid matrix is that between western gorillas and chimpanzees (*SI* = 0.880). The white-handed gibbon-siamang index is also relatively high (*SI* = 0.795), while the chimpanzee-bonobo (*SI* = 0.614) and western gorilla-

eastern gorilla (*SI* = 0.569) indices are moderate. *Pongo pygmaeus* and *Homo sapiens*, the two hominoid species that commonly possess 12 thoracic vertebrae, produce the lowest average intra-group similarity indices (*SI* = 0.055 and 0.049, respectively) in the hominoid comparison (Table 3.3), although bonobos and eastern gorillas each generate an individual similarity index of 0 (both with *Hylobates lar*). All indices for humans and orangutans, including their own similarly index (*SI* = 0.062) are below or near 0.1 (orangutan-western gorilla *SI* = 0. 105).

4) Among platyrrhines, sister-taxa *Saimiri sciureus* and *Cebus sp.* produce a moderately low index (*SI* = 0.215), while that of *Alouatta sp.* and *Ateles sp.* is extremely low (*SI* = 0.004). The highest index is generated between *Cebus sp.* and *Alouatta sp.* (*SI* = 0.756), while *Saimiri sciureus* and *Ateles sp.* share no common vertebral formulae (*SI* = 0); the *Cebus sp.-Ateles sp.* index is also low (*SI* = 0.037).

5) Hominoid, cercopithecoid, and platyrrhine vertebral formulae share little in common with one another (on average, *SI* = 0.005 for hominoids and cercopithecoids, 0.002 for hominoids and platyrrhines, and 0.078 for cercopithecoids and platyrrhines). In addition, spider monkeys and hominoids demonstrate very little similarity – on average *SI* = 0.001 (ranging from *SI* = 0 to 0.005). Among hominoids, hylobatids (white-handed gibbons and siamangs) share the most similarity with non-hominoids, with average similarity indices of 0.020 (hylobatid-cercopithecoid), 0.009 (hylobatid-platyrrhine), while other hominoids share no common patterns with cercopithecoids or platyrrhines (humans, chimpanzees, and eastern gorillas) or demonstrate similarity indices less than 0.002 (western gorillas and orangutans) (see Table 3.3).

DISCUSSION

Current models of hominin vertebral formula evolution require drastically different amounts of homoplasy. Differentiating between homology and homoplasy is a persistent problem in evolutionary biology and paleoanthropology that persists even in light of our modern understanding of phylogenetic relationships (Young, 2002; Begun, 2007; Williams, 2010; Wake et al., 2011; Wood and Harrison, 2011). Pilbeam's (2004) short-back model postulates the homology of reduced lumbar regions in hominoids, requires very little homoplasy, and is therefore more parsimonious than the homoplasy-driven long-back model introduced by McCollum et al. (2010) and used to support the interpretation of *Ardipithecus ramidus* (Lovejoy et al., 2009; Lovejoy and McCollum, 2010). However, homoplasy is pervasive and must always be considered when reconstructing evolutionary histories and ancestral morphotypes (Wake et al., 2011; Wood and Harrison, 2011), so either scenario is possible, as well as other possibilities.

Pilbeam (2004) found support for the short-back model in the similar vertebral profiles and high similarity index he observed between chimpanzees and western gorillas. McCollum and colleagues, however, present two objections to Pilbeam's argument: 1) mixed phylogenetic signals generated by the similarity index (e.g., closely related hominoids often produce significantly lower similarity indices than the chimpanzee-western gorilla comparison), and 2) non-numerical aspects of lumbar reduction (e.g., bi-iliac lumbar entrapment) differ significantly between chimpanzees and western gorillas and therefore suggest that they evolved independently.

Instead, McCollum et al. (2010) identify two lines of evidence that support a long-back scenario: 1) Bonobos possess more precaudal vertrebra than chimpanzees and other hominines.

McCollum and colleagues interpret this as evidence for the retention of a long vertebral column throughout hominoid evolution – bonobos, like chimpanzees, humans, gorillas, and orangutans, reduced the lumbar column by sacralization (cranially-directed homeotic shift at the lumbo-sacral border) of lumbar vertebrae. Bonobos have further experienced thoracization (caudally-directed homeotic shift at the thoraco-lumbar border) of lumbar vertebrae while retaining the primitive number of elements, while the other hominids reduced their overall precaudal formulae by meristic change (loss of elements). Hylobatids and fossil hominoids with reduced lumbar columns (e.g., *Oreopithecus*) necessarily experienced independent reductions in lumbar vertebrae as well (Lovejoy and McCollum, 2011). 2) Early fossil hominins possessed six lumbar vertebrae and 4-element sacra (see below) – i.e., they preserve a primitive, long back from which humans evolved lumbar reduction via sacralization of the last lumbar vertebra.

Implications of intraspecific variation

The diversity index measures the dispersion of a trait in a population over a number of categories. Here, vertebral formulae are treated as separate categories and their frequencies in a given taxon are used to calculate diversity indices. Low values of this index (approaching 0) indicate a small amount of dispersion and/or a high frequency of one formula, while high values (approaching 1) indicate a large amount of dispersion and/or several medium-frequency formulae. Diversity indices are strongly negatively correlated with the frequency of the modal formula in each taxon ($r = -0.979$, $p < 0.0001$). Therefore, species with high frequencies of the modal formula tend to produce low diversity indices, while those with low frequencies produce high diversity indices.

Most hominoids demonstrate a relatively low frequency of the modal formula and therefore a high diversity index (average hominoid $DI = 0.776$). Humans ($DI = 0.591$) and eastern gorillas ($DI = 0.496$) produce relatively low indices when compared to other hominoids (chimpanzee $DI = 0.826$; bonobo $DI = 0.946$; western gorilla $DI = 0.851$; orangutan $DI = 0.810$; white-handed gibbon $DI = 0.804$; siamang $DI = 0.889$). These differences are most strikingly demonstrated with frequency plots, where the modal frequency and several subsequent frequencies are shown (Figure 3.3). Because it measures the frequency and dispersion of vertebral formulae, the diversity index might be expected to provide a reasonable approximation of the degree of stabilizing selection on vertebral formulae in a given taxon. While vertebral formulae in most hominoids appear to lack strong stabilizing selection on them, humans and eastern gorillas are characterized by a low degree of variation in vertebral formulae, likely due to strong stabilizing selection on the modal formula in both taxa.

In humans, stabilizing selection for the modal formula is likely related to the adoption of habitual terrestrial bipedalism (Pilbeam, 2004) and/or obstetric function. Compared to the modal 7:12:5:5 formula, humans with 30 precaudal vertebrae are more likely to be characterized by "high assimilation sacrum," a condition associated with obstetric disadvantage (Tague, 2009). In the case of eastern gorillas, strong selection for a 7:13:3:6 formula may be related to a highly terrestrial lifestyle, which has been linked to other postcranial differences with the more arboreal western gorillas (Schultz, 1934; Sarmiento, 1994; Inouye, 2003; Tocheri et al., 2011). Strong stabilizing selection on the eastern gorilla modal formula is also evidenced by a complete lack of transitional (half-and-half; see Chapter 2) elements in any of the observed vertebral columns – in other hominines, transitional elements occur at around 10% or greater frequency (10% in western gorillas and chimpanzees, 11% in humans, and 23% in bonobos) (see Appendix C).

In an analogous situation, spider monkeys (*Ateles sp. DI* = 0.447) produce a much lower diversity index than the other platyrrhines included in this study (average non-*Ateles* platyrrhine *DI* = 0.778) and likewise demonstrate a higher frequency of the modal vertebral formula (Figure 3.4). This is consistent with stabilizing selection on the spider monkey modal formula compared to its sister-taxon, *Alouatta*, and other platyrrhines, which are more variable and likely experience relaxed selection on vertebral formulae. While most platyrrhines are considered generalized in terms of locomotor behavior and associated morphologies, spider monkeys and other atelines possess derived features of the trunk and forelimbs associated with tail-assisted brachiation (Erikson, 1963; Johnson and Shapiro, 1998; Jones, 2008).

Jones (2008) outlined scenarios of ateline evolution and concluded that it is likely that the ancestor of atelids [*Alouatta*, (*Ateles*, (*Lagothrix*, *Brachyteles*))] was somewhat generalized and either *Alouatta*-like or *Lagothrix*-like, while specialized brachiation evolved in short, punctuated bursts in *Ateles* and *Brachyteles*. Woolly monkeys (*Lagothrix sp.*) are represented in the dataset provided here by only 26 specimens and so were not initially included in the analyses of variation in this study; however, when the diversity index is calculated for *Lagothrix sp.* (*DI* = 0.831), it is comparable to that of *Alouatta sp.* (*DI* = 0.803) and unlike *Ateles sp.* (DI = 0.447). Unfortunately, too few specimens of *Brachyteles sp.* (N=6) are included in this dataset to address intraspecific variation in this taxon. Nevertheless, the similar and high diversity indices in *Alouatta sp.* and *Lagothrix sp.* are consistent with relaxed selection pressures and more generalized locomotor behaviors, whereas the lower diversity index in *Ateles sp.* is consistent with stabilizing selection on the modal vertebral formula, likely related to relatively recent adaptation to enhanced brachiation.

Another example comes from the *Lophocebus-Papio-Theropithecus* clade. Using molecular genetic studies, Disotell (1994) demonstrated that the *Lophocebus* mangabey (*Lophocebus sp.*) forms a clade with baboons (*Papio* and *Theropithecus*) to the exclusion of *Cercocebus* mangabeys (*Cercocebus sp.*) and mandrills (*Mandrillus sp.*), which are themselves sister-taxa. He also provided morphological support for these groupings, as have others since (Chapter 2; Fleagle and McGraw 2002; Gilbert, 2007). Unlike *Papio sp.* and *Cercocebus sp.*, which are primarily terrestrial but also partly arboreal (semi-terrestrial/semi-arboreal), *Lophocebus* mangabeys are highly arboreal and rarely come to the ground (Waser, 1984). Geladas (*Theropithecus gelada*), on the other hand, are entirely terrestrial and rarely climb trees (Elton, 2002). The more generalized forms, *Papio sp.* and *Cercocebus sp.*, generate relatively high diversity indices (*DI* = 0.721 and 0.742, respectively), while the specialized arborealist (*Lophocebus sp., DI* = 0.313) and terrestrialist (*Theropithecus gelada*, *DI* = 0.131) demonstrate some of the lowest indices in the dataset. Here again, this may provide evidence for stabilizing selection on the modal vertebral formula in *Lophocebus* and *Theropithecus,* and relaxed selection on vertebral formulae in *Papio* and *Cercocebus*.

This hypothesis requires further testing, however, and the inclusion of other groups with members that have recently become specialized might help confirm or reject these predictions. For example, patas monkeys (*Erythrocebus patas*) and vervets (*Chlorocebus aethiops*) are cursorial relatives of guenons that have adapted to terrestriality to different degrees. While both species exhibit morphological adaptations to terrestrial life and cursoriality, patas monkeys are more specialized than the semi-terrestrial/semi-arboreal vervets (Hurov, 1987; Gebo and Sargis, 1994; Isbell et al., 1998). Although patas monkeys were not included in the initial analysis due to an insufficient sample size (N=20), when calculated, their diversity index is quite low (*DI* =

0.279). Accordingly, the vervet diversity index is higher (0.550), but not as high as that of the more generalized and closely related guenons (*Cercopithecus sp.*, *DI* = 0.743). Once again, this may provide evidence for strong stabilizing selection on highly specialized patas monkeys and relaxed selection pressures on more generalized guenons, with somewhat specialized vervets in between, but larger sample sizes and species comparisons are required to test this hypothesis in general.

If hominoids are re-examined in light of this tentative hypothesis, the generally high diversity indices observed among hominoids are interpreted as evidence for relaxed selection pressures on hominoid vertebral formulae. Hylobatids (*Hylobates lar*, *DI* = 0.804; *Symphalangus syndactylus*, *DI* = 0.889), orangutans (*DI* = 0.810), western gorillas (*DI* = 851), chimpanzees (*DI* = 0.826), and bonobos (*DI* = 0.946) demonstrate high variability and dispersion across vertebral formulae and therefore exhibit little evidence for stabilizing selection. Humans (*DI* = 0.591) and eastern gorillas (*DI* = 0.496), on the other hand, are less variable and more stable at their respective modal formulae (63% and 71%, respectively; Figure 3.3). Therefore, although hominoids are clearly a specialized group of primates, they do not currently exhibit strong patterns of selection pressures on vertebral formulae, with two exceptions. Humans and eastern gorillas likely experienced strong stabilizing selection on their modal vertebral formulae associated with adaptation to terrestriality, albeit in different ways and for different reasons.

Alternatively, the relatively low diversity indices observed in humans and eastern gorillas might be explained by demographic history. Both groups likely experienced population bottlenecks in the recent past (Harpending et al., 1998; Fay and Wu, 1999; Jensen-Seaman and Kidd, 2001; Anthony et al., 2007; Fagundes et al., 2007), which might be expected to produce similar results (i.e., high frequencies of the modal formula) through reduced genetic variation.

Following a bottleneck and subsequent increase in population size, previously rare alleles are largely eliminated and replaced by higher frequencies of common alleles and new mutations that arise during population expansion (Nei et al., 1975). While human and eastern gorilla vertebral profiles are concordant with this pattern of genetic drift, that of bonobos is not, and is in fact quite the opposite of what would be expected given a recent bottleneck. Although, like eastern gorillas (Jensen-Seaman and Kidd, 2001; Anthony et al., 2007), bonobo population genetic structure has been influenced by Pleistocene forest refugia and rivers (Eriksson et al., 2004), bonobos may (Jensen-Seaman et al., 2001; Yu et al., 2003) or may not (Eriksson et al., 2004) have experienced recent bottlenecks. Clearly, more research on hominine population genetics and its implications for morphological variation are required to differentiate between natural selection and genetic drift in vertebral formulae evolution.

Nevertheless, the maintenance of a high degree of variation in vertebral formulae throughout hominoid evolution does not support the hypothesis of independently reduced lumbar regions in extant hominoids, as proposed by McCollum et al. (2010). Under the long-back scenario, we might expect to find low diversity indices in all or at least some extant hominoids if directional selection has acted to reduce lumbar regions independently and repeatedly, particularly in closely related taxa that diverged relatively recently (e.g., *Pan troglodytes* and *Pan paniscus*). Rather, high diversity indices suggest that most hominoid lineages have not experienced strong directional or stabilizing selection on vertebral formulae, and instead elicit patterns consistent with relaxed selection associated with gradual change and stasis. Again, humans and eastern gorillas are exceptions, and suggest that changes in the diversity index are associated with changes in apparent selection pressures related to locomotor and habitat specializations. Pilbeam's (2004) short-back model, which supports the homology of reduced

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lumbar regions in hominoids, is congruent with the patterns of intraspecific variation observed

and described here.

Implications of interspecific variation

The similarity index measures the extent to which two populations share a set of patterns.

It accounts for both the presence and frequency of vertebral formulae and compares the two

populations in a way analogous to genetic identity calculated from allele frequencies (Pilbeam,

2004). Unlike genetic identity, however, the similarity index should not be expected to reflect

phylogenetic relatedness, as was stated and demonstrated in Pilbeam (2004), although the

Lophocebus-Papio-Theropithecus clade does generate a phylogenetic signal amongst the

cercopithecoids (Figure 3.2), likely because the three taxa demonstrate a different modal formula

(7:13:6:3) than the other cercopithecoids (7:12:7:3). Otherwise, mixed phylogenetic/functional

signals are generally produced; for example, in the case of the atelids *Alouatta sp.* and *Ateles sp.*

(SI = 0.004). Although they are closely related, spider monkeys experienced modifications to

their vertebral formulae that howler monkeys have not, resulting in a low similarity index.

Similarly, humans obviously experienced different selection pressures than their closest

relatives, chimpanzees and bonobos, since their common ancestry, and should not be expected to

generate high similarity indices with them despite their close relatedness. As expected, humans

generate low indices with both chimpanzees (SI = 0.043) and bonobos (SI = 0.044).

Chimpanzees and bonobos themselves, on the other hand, generate a higher similarity index (SI

= 0.581). This is also true for closely related taxa like western gorillas and eastern gorillas (SI =

0.569) and white-handed gibbons and siamangs (SI = 0.779).

The highest similarity index among hominoids is observed between chimpanzees and western gorillas ($SI = 0.880$). Pilbeam (2004) found a similar relationship (Pilbeam $SI = 0.86$) and suggested that eastern gorillas and bonobos, although represented at inadequate sample sizes in his dataset (N=14 and N=17, respectively), were somewhat derived from each other's closest relatives and in opposite directions. These observations are confirmed here (and in McCollum et al. in the case of bonobos) at larger sample sizes (N=51 and N=40, respectively), and indeed, bonobos and eastern gorillas generate a low similarity index ($SI = 0.032$). This suggests one of two evolutionary scenarios to explain the high similarity index generated by chimpanzees and western gorillas: 1) their shared vertebral profile characterized the last common ancestor of hominines (African apes, including humans), from which bonobos, eastern gorillas, and humans evolved their unique vertebral profiles, or 2) they evolved similar vertebral profiles independently. The former scenario is congruent with Pilbeam's short-back model, while the latter supports the long-back model proposed by McCollum and colleagues.

McCollum et al. (2010) argue that the lack of high similarity indices among hominoids in general, and particularly those between chimpanzees and bonobos (Pilbeam $SI = 0.39$) and white-handed gibbons and siamangs (Pilbeam $SI = 0.50$), weaken Pilbeam's hypothesis that the high chimpanzee-western gorilla similarity index provides evidence for the short-back model. However, McCollum et al. did not recalculate similarity indices in light of their increased bonobo sample and instead reproduce Pilbeam's original results, which were based on an inadequate sample size for bonobos. Here, new indices are calculated in light of significantly increased sample sizes, which reveal higher similarity indices for chimpanzees and bonobos ($SI = 0.614$) and white-handed gibbons and siamangs ($SI = 0.779$), in addition to all other

comparisons with the exception of *Gorilla gorilla-Pongo pygmaeus*, which is slightly lower in this study (0.105 versus 0.118; compare Table 3.3 with Table 24 in Pilbeam, 2004).

Long- and short-back models in light of intra- and inter-specific variation

Results of this study demonstrate that the intraspecific variation observed among hominoids and other anthropoids does not support the independent evolution of reduced lumbar regions in hominoids (i.e., the long-back model). Hominoid diversity indices suggest relaxed selection on extant lineages and not strong directional or stabilizing selection, as might be expected if vertebral formula evolution occurred recently and independently in each lineage. The two exceptions (humans and eastern gorillas), which do demonstrate patterns congruent with strong stabilizing selection, likely evolved high frequencies of their modal vertebral formulae associated with efficient terrestrial locomotion and/or obstetric demands in the case of humans. Analyses of interspecific variation also fail to support the long-back model; rather, given the high similarity index generated between chimpanzees and western gorillas in a modern phylogenetic context, it is likely that their shared vertebral profile characterized their last common ancestor and necessarily also the last common ancestor of panins and hominins.

Bonobos share most similarity in vertebral formulae with their closest relatives, chimpanzees, but are clearly divergent in some ways, including the possession of an extra precaudal vertebra. McCollum et al. (2010) interpret these differences as evidence for the retention of a primitive number of precaudal vertebrae in bonobos, and that orangutans, gorillas, chimpanzees, and humans independently reduced both total precaudal number via meristic change and lumbar number via homeotic change, the latter of which would have also occurred independently in bonobos. However, in a far more parsimonious scenario where reduced lumbar

regions are homologous in hominoids, bonobos simply evolved a different vertebral profile (7:13:4:6; 7:13:4:7, 7:14:3:7) than chimpanzees (7:13:4:6, 7:13:4:5, 7:13:3:6) while still maintaining the same modal formula (7:13:4:6). Likewise, eastern gorillas and humans evolved different modal formulae (7:13:3:6 and 7:12:5:5) from similar "African ape-like" profiles.

The claim by McCollum and colleagues (Lovejoy and McCollum, 2010; McCollum et al., 2011) that an increased number of vertebral elements in bonobos runs counter to the hominoid trend of reduction in precaudal vertebral number is false. If modal vertebral formulae are examined, only orangutans demonstrate reduced numbers of precaudal vertebrae. Humans (7:12:5:5), western gorillas (7:13:4:5), eastern gorillas (7:13:3:6) and white-handed gibbons (7:13:5:4) demonstrate the primitive number of 29 precaudal elements (also retained in cercopithecoids and many other groups of mammals; see Table 2 and Chapter 2). Siamangs (7:13:5:5) and chimpanzees (7:13:4:6) possess modes containing 30 precaudal vertebrae each, but the other formulae in their vertebral profiles contain 29 elements (7:13:4:5, 7:13:5:4 and 7:13:4:5, 7:13:3:6, respectively). Bonobos possess 30 elements in their modal formula (7:13:4:6) and 31 elements in the other formulae of their vertebral profile (7:13:4:7, 7:14:3:7).

Compared to a primitive formula containing 29 elements, the panin (chimpanzee-bonobo) clade experienced an increase in total precaudal number (see Chapter 2). Bonobos have simply continued this trend to a greater degree than chimpanzees, all the while maintaining a short lumbar region (both bonobos and chimpanzees possess modes of four lumbar vertebrae, with averages of 3.6 and 3.7, respectively; see Appendix D), the purported target of selection and namesake of the short- and long-back models. Furthermore, all hominids except eastern gorillas (humans, chimpanzees, bonobos, western gorillas, and orangutans) possess modes of four lumbar vertebrae (eastern gorillas possess three), and all but eastern gorillas and orangutans possess 17

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thoracolumbar (TL) vertebrae. The human thoracic-lumbar pattern (12T:5L) is attainable from the mode shared by chimpanzees, bonobos, and western gorillas (13T:4L) by a simple homeotic shift at the thoraco-lumbar border, a common occurrence among mammals (see Chapter 2).

McCollum et al. (2010) also criticize the short-back model and find support for the independent reduction in lumbar regions based on differences in "lumbar entrapment," or the number of elements contained and immobilized within the iliac blades, among hominids and particularly between western gorillas and chimpanzees. They ask, "If *Pan* and *Gorilla* evolved from a common ancestor with a short back, why has stabilizing selection not maintained similar morphology?" (McCollum et al., 2010:128). The answer becomes clear upon a wider survey of mammals – despite large differences in body size, locomotor behavior, and vertebral morphology, the mammalian vertebral formula is relatively conserved (Chapter 2; see also Narita and Kuratani, 2005; Sánchez-Villagra et al., 2007; Asher et al., 2009, 2011; Hautier et al., 2010).

Nearly all mammals possess seven cervical vertebrae despite drastic differences in neck lengths (e.g., whales versus giraffes), and most mammals possess 19 TL vertebrae (Chapter 2; see also Narita and Kuratani, 2005). Furthermore, when departures from these primitive numbers are observed (e.g., 20 thoracolumbar vertebrae in carnivorans), they tend to be phylogenetically structured (Chapter 2; see also Narita and Kuratani, 2005; Sánchez-Villagra et al., 2007; Asher et al., 2009, 2011). Hominoids are no exception – while cercopithecoids possess the primitive number of 19 TL vertebrae, hominoids have sacralized lumbar vertebrae, resulting in 18 TL vertebrae in hylobatids and 17 TL vertebrae in hominids (with the exceptions of eastern gorillas and orangutans, which possess 16). Given the strong conservation and phylogenetic structuring of vertebral formulae among mammals in general, morphological modifications in a similar numerical framework such as that described in McCollum et al. should not be unexpected.

Indeed, mammals as morphologically and behaviorally distinct as opossums (*Didelphis sp.*) and kangaroos (*Macropus sp.*) possess the same vertebral formula (7:13:6:2), as do springhares (*Pedetes sp.*) and flying squirrels (*Petaurista sp.*) (7:12:7:3), which in both cases were likely inherited from their respective marsupial and rodent common ancestors (see Chapter 2).

Finally, McCollum et al. (McCollum et al., 2010:128) argue that the short-back model is "problematic" because hominins would have "re-evolved" a long lumbar spine. This is based on observations that fossil hominins possessed six lumbar vertebrae (Robinson, 1972; Latimer and Ward, 1993; Sanders, 1998; Rosenman, 2008) and the sacra of *Australopithecus afarensis* (A.L. 288-1) and *Homo ergaster* (KNM-WT 15000) may have fewer than five elements (Pilbeam, 2004; McCollum et al., 2010). As outlined in Chapters 2 and 4, respectively, conflicting reconstructions and conflated definitions of thoracic and lumbar vertebrae have led to general confusion surrounding the vertebral formulae of fossil hominins.

The pertinent fossil specimens have either been reexamined and reconstructed with just five lumbar vertebrae (Haeusler et al., 2002; Toussaint et al., 2003) or remain unsettled due to heavy reconstruction and/or potential missing elements (KNM-WT 15000: Brown et al., 1985; Walker and Leakey, 1993; Haeusler et al., 2002). The latter is also true for the sacra of A.L. 288-1 (Johanson et al., 1982; Sanders, 1995; Pilbeam, 2004; McCollum et al., 2010) and KNM-WT 15000 (Brown et al., 1985; Walker and Ruff, 1993; McCollum et al., 2010). The recently discovered sacrum of *Australopithecus sediba* (MH2 UW88) preserves the entire sacral midline from the first sacral body to the articulation for the coccyx and four strong, complete sacral foramena on the right side, revealing five distinct sacral vertebrae (personal observation).

MH2 also includes the ultimate and penultimate thoracic vertebrae, which demonstrate a dissociation between the diaphragmatic and last rib-bearing (thoracic) vertebrae (personal

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observation); that is, the change in zygapophysis orientation that generally occurs at the level of the last thoracic vertebra in extant hominoids occurs at the level of the penultimate thoracic vertebra in MH2 and other early fossil hominins (Chapter 4; see also Haeusler et al., 2002). This dissociation has been a source of confusion and has led to erroneous interpretations of the numerical composition of fossil hominin thoraco-lumbar columns (see Chapter 4). Instead of 6 lumbar (non-rib-bearing) vertebrae, early fossil hominins evolved a more mobile spine by shifting the diaphragmatic vertebra one element cranially, resulting in six postdiaphragmatic vertebra but only five lumbar vertebrae (Chapter 4). This process likely allowed early fossil hominins to effectively achieve lordosis during the transition to efficient terrestrial bipedalism while maintaining a 7:12:5:5 vertebral formula. By the Middle Pleistocene, common placement was re-established, as demonstrated by Neandertal (Arensburg, 1991; Ogilvie et al., 1998) and modern human vertebral columns.

Therefore, there is no need for early fossil hominins to "re-evolve" a long lumbar spine; the human and likely early fossil hominin modal TL pattern (12T:5L) is only one border shift away from that expressed modally in chimpanzees, bonobos, and western gorillas (13T:4L), a change that would not require the gain or loss of elements. The analyses of inter- and intra-specific variation presented here support this interpretation of the short-back model and are not congruent with the expectations of the long-back model. An African ape-like ancestry should not be unexpected given our phylogenetic position within the African ape clade. Indeed, although our closest relatives are certainly not living fossils, there is still much they can tell us about our evolutionary past (Begun, 2010; Sarmiento 2010; Whitten et al. 2010; Williams 2010; Young et al. 2010).

TABLE 3.1. Taxa and sample sizes.

Taxon	Species included (if sp.)	Common name	N
Homo sapiens		human	273
Pan troglogytes		chimpanzee	271
Pan paniscus		bonobo	40
Gorilla gorilla		western gorilla	172
Gorilla beringei		eastern gorilla	51
Pongo pygmaeus		orangutan	180
Hylobates lar		white-handed gibbon	190
Hylobates syndactylus		siamang	74
Trachypithecus sp.	*cristatus, phayrei*	lutung (leaf monkey)	125
Nasalis larvatus		snub-nosed monkey	42
Cercopithecus sp.	*ascanius, lhoesti, mitis, mona, neglectus, petaurista*	guenon	128
Chlorocebus aethiops		vervet	71
Macaca fascicularis		long-tailed macaque	81
Macaca fuscata		Japanese macaque	883
Cercocebus sp.	*atys, galeritus, torquatus*	Cercocebus mangabey	31
Lophocebus sp.	*albegina, aterrimus*	crested mangabey	91
Papio sp.	*anubis, cynocephalus, hamadryas, papio, ursinus*	baboon	120
Theropithecus gelada		gelada	30
Saimiri sciureus		squirrel monkey	39
Cebus sp.	*albifrons, apella, capucinus, flavus, frontalis*	capuchin	63
Alouatta sp.	*palliata, pigra, seniculus*	howler monkey	39
Ateles sp.	*ater, fusciceps, geoffroyi, paniscus*	spider monkey	39

TABLE 3.2. Vertebral profiles (formulae represented at >10% frequency).

Taxon	Cervical	Thoracic	Lumbar	Sacral	TL	CTLS	Frequency	Sum freq.
Homo sapiens	7	12	5	5	17	29	62.6	
	7	12	5	6	17	30	12.5	75.1
Pan troglodytes	7	13	4	6	17	30	31.7	
	7	13	4	5	17	29	21.4	
	7	13	3	6	16	29	14.0	67.2
Pan paniscus	7	13	4	6	17	30	15.0	
	7	13	4	7	17	31	10.0	
	7	14	3	7	17	31	10.0	35.0
Gorilla gorilla	7	13	4	5	17	29	26.2	
	7	13	3	6	16	29	20.9	
	7	13	4	6	17	30	16.3	63.4
Gorilla beringei	7	13	3	6	16	29	70.6	70.6
Pongo pygmaeus	7	12	4	5	16	28	39.4	
	7	12	4	6	16	29	15.6	55.0
Hylobates lar	7	13	5	4	18	29	33.2	
	7	13	5	5	18	30	27.9	61.1
Hylobates syndactylus	7	13	5	5	18	30	20.3	
	7	13	5	4	18	29	18.9	
	7	13	4	5	17	29	17.6	56.8

TABLE 3.2 (cont.)

Taxon	Cervical	Thoracic	Lumbar	Sacral	TL	CTLS	Frequency	Sum freq.
Trachypithecus sp.	7	12	7	3	19	29	82.4	82.4
Nasalis larvatus	7	12	7	3	19	29	88.9	88.9
Cercopithecus sp.	7	12	7	3	19	29	43.0	
	7	13	6	3	19	29	23.4	
	7	12.5	6.5	3	19	29	10.9	77.3
Chlorocebus aethiops	7	12	7	3	19	29	66.2	66.2
Macaca fascicularis	7	12	7	3	19	29	70.4	
	7	12	7	2	19	28	18.5	88.9
Macaca fuscata	7	12	7	3	19	29	70.6	70.6
Cercocebus sp.	7	12	7	3	19	29	48.4	
	7	13	6	3	19	29	16.1	64.5
Lophocebus sp.	7	13	6	3	19	29	82.4	82.4
Papio sp.	7	13	6	3	19	29	43.3	
	7	12	7	3	19	29	29.2	72.5
Theropithecus gelada	7	13	6	3	19	29	93.3	93.3
Saimiri sciureus	7	13	7	3	20	30	48.7	
	7	13	6	3	19	29	12.8	
	7	14	6	3	20	30	10.3	71.8
Cebus sp.	7	14	6	3	20	30	36.5	
	7	14	5	3	19	29	28.6	65.1
Alouatta sp.	7	14	5	3	19	29	41.0	
	7	14	6	3	20	30	10.3	
	7	15	5	3	20	30	10.3	
	7	14	5	4	19	30	10.3	
	7	15	5	4	20	31	10.3	82.1
Ateles sp.	7	14	4	3	18	28	74.4	74.4

TABLE 3.3. Martix of similarity (lower triangle) and distance (1-*SI* ; upper triangle) indices; diversity indices along diagonal.

TAXON	H.sap	P.tro	P.pan	G.gor	G.ber	P.pyg	H.lar	S.syn	N.larv	Trach	C.aet	Cercop	M.fas	M.fus	Cercoc	T.gel	Papio	Lopho	S.sci	Cebus	Aloua	Ateles
H. sapiens	**0.591**	0.9567	0.9564	0.9585	0.9972	0.9379	0.9400	0.9136	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P. troglodytes	0.0433	**0.826**	0.9567	0.1199	0.6359	0.9420	0.9941	0.6757	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P. paniscus	0.0436	0.6135	**0.946**	0.5581	0.9680	0.9479	1	0.8236	1	1	1	1	1	1	1	1	1	1	1	1	1	1
G. gorilla	0.0415	0.8801	0.4419	**0.851**	0.4309	0.8952	0.9990	0.6203	1	1	1	1	1	1	1	1	1	1	1	1	1	0.9985
G. beringei	0.0028	0.3641	0.0320	0.5691	**0.496**	0.9334	1	0.9968	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P. pygmaeus	0.0621	0.0580	0.0521	0.1048	0.0666	**0.810**	0.9978	0.9291	1	1	1	1	1	0.9998	1	1	1	1	1	1	1	0.9991
H. lar	0.0600	0.0059	0	0.0010	0	0.0022	**0.804**	0.2213	0.9952	0.9991	0.9863	0.9542	0.9968	0.9791	0.9714	0.9059	0.9148	0.8963	0.9769	0.9851	0.9799	0.9992
S. syndactylus	0.0864	0.3243	0.1764	0.3797	0.0032	0.0709	0.7787	**0.889**	1	1	1	1	1	0.9996	1	1	1	0.9924	1	1	0.9915	0.9947
N. larvatus	0	0	0	0	0	0	0.0048	0	**0.138**	0.9938	0.9866	0.8614	0.9658	0.9884	0.9284	0.0867	0.5903	0.1696	0.9359	0.9600	0.9944	1
Trachypithecus sp.	0	0	0	0	0	0	0.0009	0	0.0062	**0.316**	0.9811	0.8552	0.9852	0.9802	0.8411	0.0451	0.5599	0.1287	0.9142	0.9647	0.9989	1
C. aethiops	0	0	0	0	0	0	0.0137	0	0.0134	0.0189	**0.550**	0.9170	0.9657	0.9845	0.9709	0.1804	0.6789	0.2615	0.8846	0.9475	0.9840	1
Cercopithecus sp.	0	0	0	0	0	0	0.0458	0	0.1386	0.1448	0.0830	**0.743**	0.8670	0.8989	0.9632	0.5133	0.1279	0.4426	0.6703	0.9074	0.9497	1
M. fascicularis	0	0	0	0	0	0	0.0032	0	0.0342	0.0148	0.0343	0.1330	**0.473**	0.9544	0.9132	0.0868	0.4079	0.8510	0.9095	0.9629	0.9963	1
M. fuscata	0	0	0	0	0	0.0002	0.0209	0.0004	0.0116	0.0198	0.0155	0.1011	0.0456	**0.485**	0.9445	0.0555	0.3433	0.7459	0.8274	0.9462	0.9851	1
Cercocebus sp.	0	0	0	0	0	0	0.0286	0	0.0716	0.1589	0.0291	0.0368	0.0868	0.0555	**0.742**	0.6642	0.2134	0.5886	0.8092	0.9274	0.9666	1
T. gelada	0	0	0	0	0	0	0.0941	0	0.9133	0.9549	0.8196	0.4867	0.9132	0.9445	0.3358	**0.131**	0.8342	0.1658	0.7531	0.8662	0.8902	1
Papio sp.	0	0	0	0	0	0	0.0852	0	0.4097	0.4401	0.3211	0.8721	0.5921	0.6567	0.7866	0.1658	**0.721**	0.1278	0.6967	0.8720	0.9108	1
Lophocebus sp.	0	0	0	0	0	0	0.1037	0.0076	0.8304	0.8713	0.7385	0.5574	0.1490	0.2541	0.4114	0.8342	0.8722	**0.313**	0.7260	0.8243	0.8880	1
S. sciureus	0	0	0	0	0	0	0.0231	0	0.0641	0.0858	0.1154	0.3297	0.0905	0.1726	0.1908	0.2469	0.3033	0.2740	**0.746**	0.7848	0.9298	1
Cebus sp.	0	0	0	0	0	0	0.0149	0	0.0400	0.0353	0.0525	0.0926	0.0371	0.0538	0.0726	0.1338	0.1280	0.1757	0.2152	**0.784**	0.2444	0.9626
Alouatta sp.	0	0	0	0	0	0	0.0201	0.0085	0.0056	0.0011	0.0160	0.0503	0.0037	0.0149	0.0334	0.1098	0.0892	0.1120	0.0702	0.2444	**0.803**	0.9962
Ateles sp.	0	0	0	0.0015	0	0.0009	0.0008	0.0053	0	0	0	0	0	0	0	0	0	0	0	0.0374	0.0038	**0.447**

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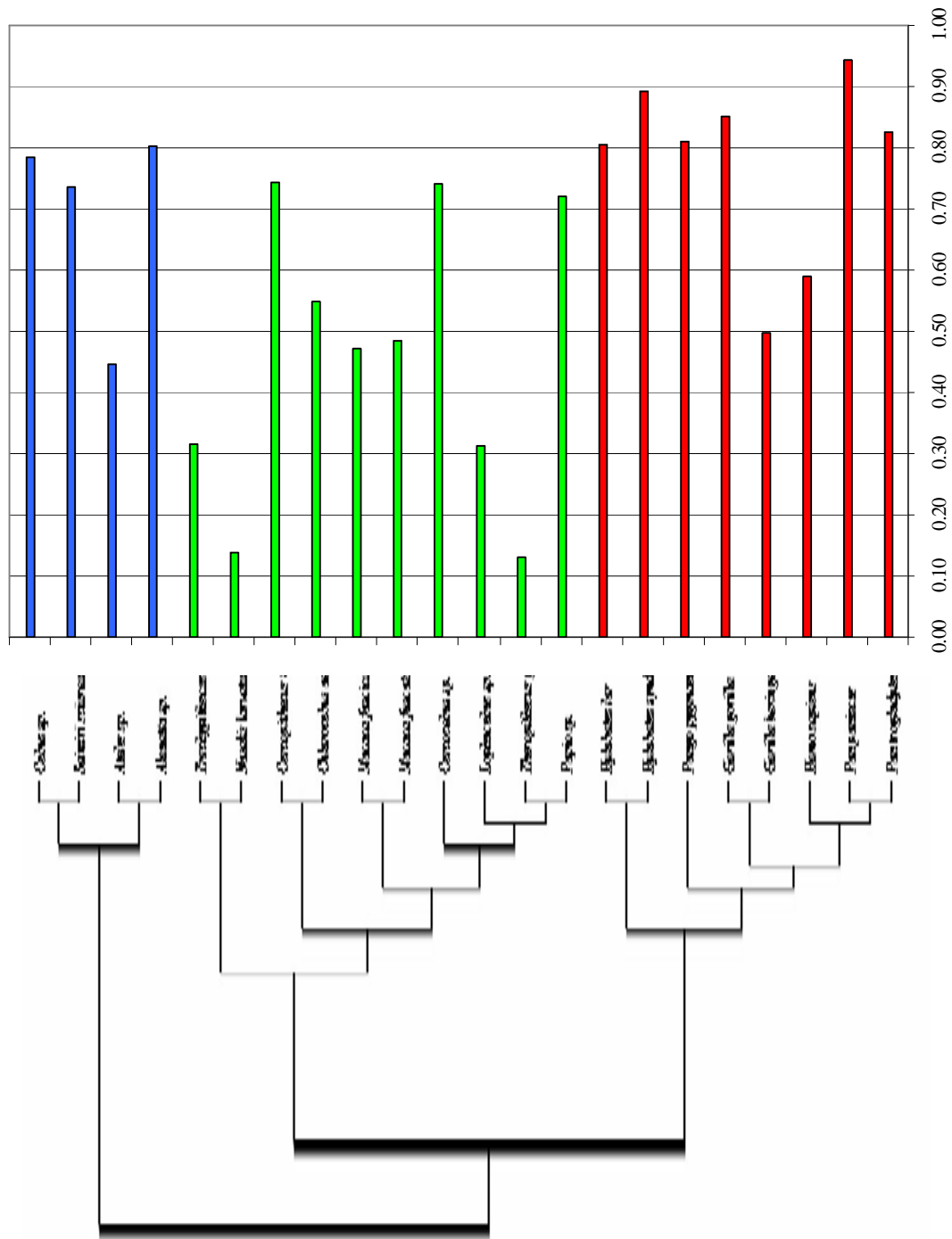
FIGURE 3.1. Diversity indices in a phylogenetic context. Red bars = hominoids; green = cercopithecoids; blue = platyrrhines.
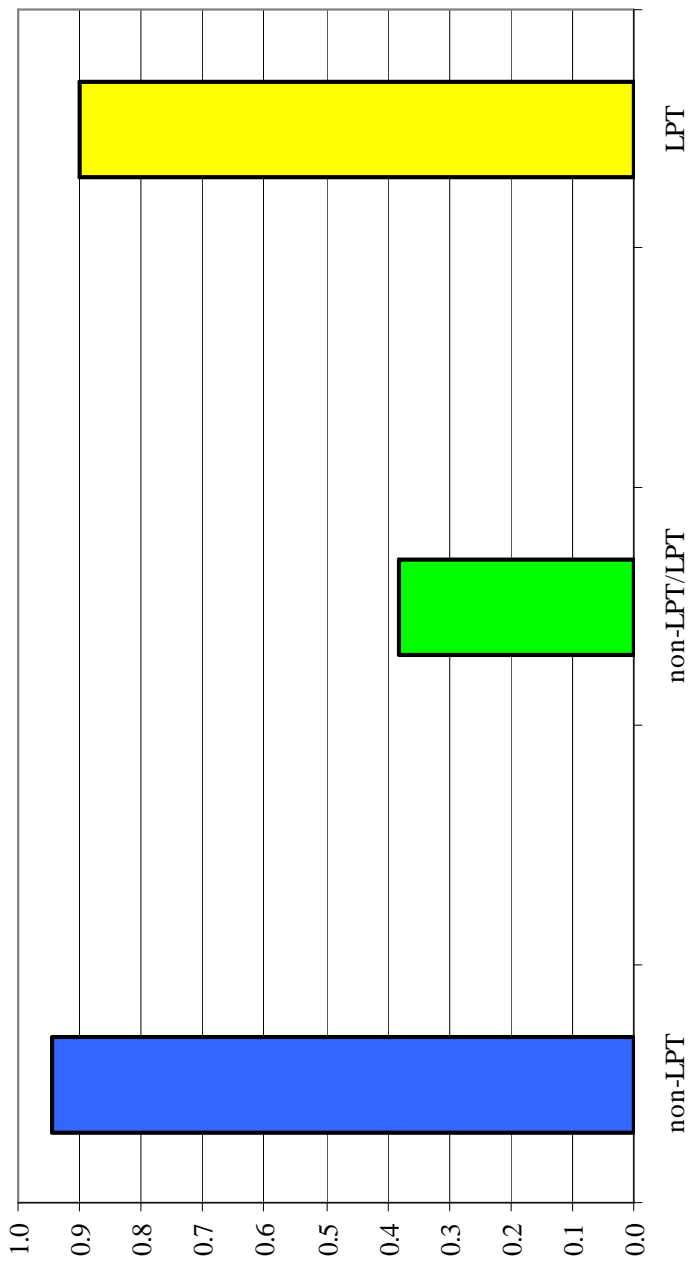
FIGURE 3.2. Average similarity indices for the *Lophocebus-Papio-Theropithecus* clade compared to other cercopithecoids. LPT = *Lophocebus-Papio-Theropithecus* group; non-LPT = non-LPT cercopithecoids. Left: average non-LPT similarity index. Right: average LPT similarity index. Middle: average similarity index between LPT and non-LPT taxa.
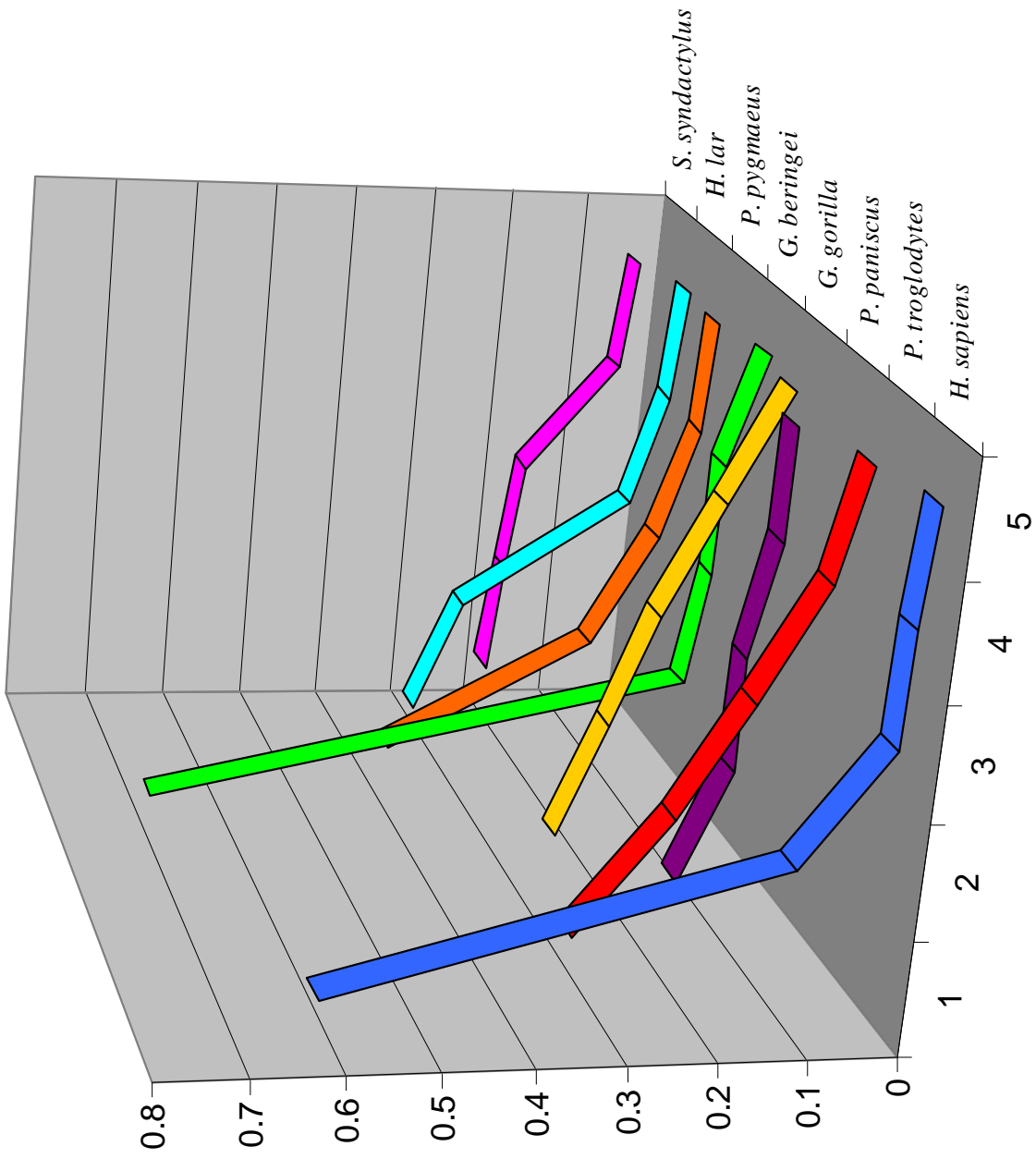
FIGURE 3.3. Frequencies of modal (1) and subsequent formulae (2-5) in hominoid taxa.

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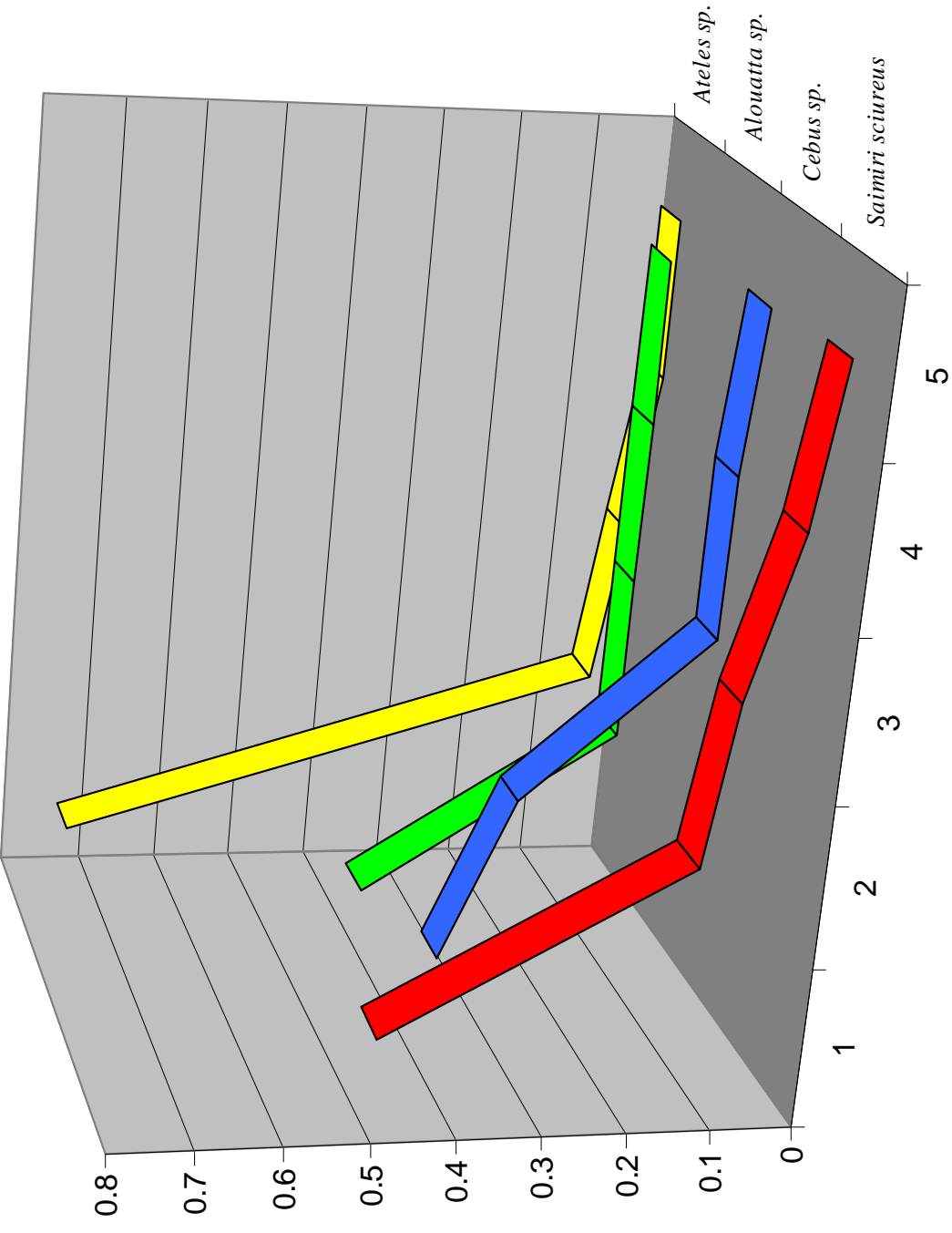
FIGURE 3.4. Frequencies of modal (1) and subsequent formulae (2-5) in platyrrhine taxa.

CHAPTER 3 REFERENCES

Agresti, A., Agresti, B.F., 1978. Statistical analysis of qualitative variation. Sociol. Methodol. 9, 204-237.

Arensburg, B., 1991. The vertebral column, thoracic cage and hyoid bone. In: O. Bar Yosef, B. Vandermeersch (Eds.), Le Squelette Mousterian de Kebara 2. Editions du C.N.R.S., Paris, pp. 113-146.

Asher, R.J., Bennett, N., Lehmann, T., 2009. The new framework for understanding placental mammal evolution. BioEssays 31, 853-864.

Asher, R.J., Lin, K.H., Kardjilov, N., Hautier, L., 2011. Variability and constraint in the mammalian vertebral column. J. Evol. Biol. 24, 1080-1090.

Begun, D.R., 2007. How to identify (as opposed to define) a homoplasy: examples from fossils and living great apes. J. Hum. Evol. 52, 559-572.

Begun, D.R., 2010. Miocene hominids and the origins of the African apes and humans. Annu. Rev. Anthropol. 39, 67-84.

Brown, F., Harris, J., Leakey, R., Walker, A. 1985., Early *Homo erectus* skeleton from west Lake Turkana, Kenya. Nature. 316, 788-792.

Disotell, T.R., 1994. Generic level relationships of the Papionini (Cercopithecoidea). Am. J. Phys. Anthropol. 94, 47-57.

Elton, S., 2002. A reappraisal of the locomotion and habitat preference of *Theropithecus oswaldi*. Folia Primatol. 73, 252-280.

Erikson, G., 1963. Brachiation in New World monkeys and in anthropoid apes. Symp. Zool. Soc. Lond. 10, 135-163.

Eriksson, J., Hohmann, G., Boesch, C., Vigilant, L., 2004. Rivers influence the population genetic structure of bonobos (*Pan paniscus*). Mol. Ecol. 13, 3425-3435.

Fagundes, N.J.R., Ray, N., Beaumont, M., Neuenschwander, S., Salzano, F.M., Bonatto, S.L., Excoffier, L., 2007. Statistical evaluation of alternative models of human evolution. Proc. Natl. Acad. Sci. USA 104, 17614-17619.

Fay, J.C., Wu, C.-I., 1999. A human population bottleneck can account for the discordance between patterns of mitochondrial versus nuclear DNA variation. Mol. Biol. Evol. 16, 1003-1005.

Filler, A.G., 1993. Evolution of the sacrum in hominoids. In: Doty, J.R., Rengachary, S.S. (Eds.). Surgical Disorders of the Sacrum. Thieme Medical Publishers, New York, pp. 13-20.

Fleagle, J.G., McGraw, W.S., 2002. Skeletal and dental morphology of African papionins: unmasking a cryptic clade. J. Hum. Evol. 42, 267-292.

Gebo, D.L., Sargis, E.J., 1994. Terrestrial adaptations in the postcranial skeletons of guenons. Am. J. Phys. Anthropol. 93, 341-371.

Gilbert, C.C., 2007. Craniomandibular morphology supporting the diphyletic origin of mangabeys and a new genus of the *Cercocebus*/*Mandrillus* clade, *Procercocebus*. J. Hum. Evol. 53, 69-102.

Groves, C., 2001. Primate Taxonomy. Smithsonian Institution Press, Washington, D.C.

Groves, C.P., 2003. A history of gorillas taxonomy. In: A.B. Taylor, M.L. Goldsmith (Eds.), Gorilla Biology: A Multidisciplinary Perspective. Cambridge University Press, Cambridge, pp. 15-34.

Haeusler, M., Martelli, S.A., Boeni, T., 2002. Vertebrae numbers of the early hominid lumbar spine. J. Hum. Evol. 43, 621-643.

Harpending, H.C., Batzer, M.A., Gurven, M., Jorde, L.B., Rogers, A.R., Sherry, S.T., 1998. Genetic traces of ancient demography. Proc. Natl. Acad. Sci. USA 95, 1961-1967.

Harris, E.E., 2000. Molecular systematics of the Old World monkey tribe Papionini: analysis of the total available genetic sequences. J. Hum. Evol. 38, 235-256.

Hautier, L., Weisbecker, V., Sánchez-Villagra, M.R., Goswami, A., Asher, R.J., 2010. Skeletal development in sloths and the evolution of mammalian vertebral patterning. Proc. Natl. Acad. Sci. USA 107, 18903-18908.

Hurov, J.R., 1987. Terrestrial locomotion and back anatomy in vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*). Am. J. Primatol. 13, 297-311.

Inouye, S.E., 2003. Intraspecific and ontogenetic variation in the forelimb morphology of *Gorilla*. In: A.B. Taylor, M.L. Goldsmith (Eds.), Gorilla Biology: A Multidisciplinary Perspective. Cambridge University Press, Cambridge, pp. 194-235.

Isbell, L.A., Pruetz, J.D., Lewis, M., Young, T.P., 1998. Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): implications for the evolution of long hindlimb length in *Homo*. Am. J. Phys. Anthropol. 105, 199-207.

Jensen-Seaman, M.I., Kidd, K.K., 2001. Mitochondrial DNA variation and biogeography of eastern gorillas. Mol. Ecol. 10, 2241-2247.

Jensen-Seaman, M.I., Deinard, A.S., Kidd, K.K., 2001. Modern African ape populations as genetic and demographic models of the last common ancestor of humans, chimpanzees, and gorillas. J. Heredity 92, 475-480.

Jensen-Seaman, M.I., Deinard, A.S., Kidd, K.K., 2003. Mitochondrial and nuclear DNA estimates of divergence between western and eastern gorillas. In: A.B. Taylor, M.L. Goldsmith (Eds.), Gorilla Biology: A Multidisciplinary Perspective. Cambridge University Press, Cambridge, pp. 247-268.

Johanson, D.C., Lovejoy, C.O., Kimbel, W.H., White, T.D., Ward, S.C., Bush, M.E., Latimer, B.M., Coppens, Y., 1982. Morphology of the Pliocene partial hominid skeleton (A.L. 288-1) from the Hadar Formation, Ethiopia. Am. J. Phys. Anthropol. 57, 403-452.

Johnson, S.E., Shapiro, L.J., 1998. Positional behavior and vertebral morphology in atelines and cebines. Am. J. Phys. Anthropol. 105, 333-354.

Jones, A.L., 2008. The evolution of brachiation in ateline primates, ancestral character states and history. Am, J, Phys, Anthropol. 137, 123-144.

Latimer, B., Ward, C.V., 1993. The thoracic and lumbar vertebrae. In: Walker, A., Leakey, R. (Eds.). The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 266-293.

Lovejoy, C.O., 2009. Reexamining human origins in light of *Ardipithecus ramidus*. Science 326, 74.

Lovejoy, C.O., McCollum, M.A., 2010. Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip–bent-knee gait. Phil. Trans. R. Soc. B 365, 3289-3299.

Lovejoy, C.O., Suwa, G., Simpson, S.W., Matternes, J.H., White, T.D., 2009. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. Science 326, 100-106.

McCollum, M.A., Rosenman, B.A., Suwa, G., Meindl, R.S., Lovejoy, C.O., 2010. The vertebral formula of the last common ancestor of African apes and humans. J. Exp. Biol. 314B, 123-134.

Muller, J., Scheyer, T.M., Head, J.J., Barrett, P.M., Werneburg, I., Ericson, P.G.P., Pol, D., Sanchez-Villagra, M.R., 2010. Homeotic effects, somitogenesis and the evolution of vertebral numbers in recent and fossil amniotes. Proc. Natl. Acad. Sci. USA 107, 2118-2123.

Narita, Y., Kuratani, S., 2005. Evolution of the vertebral formulae in mammals: a perspective on developmental constraints. J. Exp. Zool. 304B, 91-106.

Nei, M., 1972. Genetic distance between populations. Am. Nat. 106, 283-292.

Nei, M., 1987. Molecular Evolutionary Genetics. Columbia University Press: New York.

Nei, M., Maruyama, T., Chakraborty, R., 1975. The bottleneck effect and genetic variability in populations. Evolution 29, 1-10.

Ogilvie, M.D., Hilton, C.E., Ogilvie, C.D., 1998. Lumbar anomalies in the Shanidar 3 Neandertal. J. Hum. Evol. 35, 597-610.

Perelman, P., Johnson, W.E., Roos, C., Seuánez, H.N., Horvath, J.E., Moreira, M.A.M., Kessing, B., Pontius, J., Roelke, M., Rumpler, Y., Schneider, M.P.C., Silva, A., O'Brien, S.J., Pecon-Slattery, J., 2011. A molecular phylogeny of living primates. PLoS Genetics 7, e1001342.

Pilbeam, D., 2004. The anthropoid postcranial axial skeleton: comments on development, variation, and evolution. J. Exp. Zool. 302B, 241-267.

Robinson, J., 1972. Early hominid posture and locomotion. University of Chicago Press, Chicago.

Rosenman, B.A., 2008. Triangulating the evolution of the vertebral column in the last common ancestor: thoracolumbar transverse process homology in the hominoidea. Ph.D. dissertation, Kent State University.

Sánchez-Villagra, M.R., Narita, Y., Kuratani, S., 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. Syst. Biodiv. 5, 1-7.

Sanders, W.J., 1995. Function, allometry, and the evolution of the australopithecine lower precaudal spine. Ph.D. dissertation, New York University.

Sanders, W.J., 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J. Hum. Evol. 34, 249-302.

Sarmiento, E.E., 1994. Terrestrial traits in the hands and feet of gorillas. Am. Mus. Novit. 3091, 1-56.

Sarmiento, E.E., 2010. Comment on the paleobiology and classification of *Ardipithecus ramidus*. Science 328, 1105-b.

Schultz, A.H., 1934. Some distinguishing characters of the mountain gorilla. J. Mammal. 15, 51-61.

Tague, R.G., 2009. High assimilation of the sacrum in a sample of American skeletons: prevalence, pelvic size, and obstetrical and evolutionary implications. Am. J. Phys. Anthropol. 138, 429-438.

Tocheri, M.W., Solhan, C.R., Orr, C.M., Femiani, J., Frohlich, B., Groves, C.P., Harcourt-Smith, W.E., Richmond, B.G., Shoelson, B., Jungers, W.L., 2011. Ecological divergence and medial cuneiform morphology in gorillas. J. Hum. Evol. 60,171-184.

Toussaint, M., Macho, G.A., Tobias, P.V., Partridge, T.C., Hughes, A.R., 2003. The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa. S. Af. J. Sci. 99, 215-223.

Wake, D.B., Wake, M.H., Specht, C.D., 2011. Homoplasy: from detecting pattern to determining process and mechanism of evolution. Science 331, 1032-1035.

Waser, P., 1984. Ecological differences and behavioral contrasts between two mangabey species. In: P.S. Rodman, J.G.H. Cant (Eds.), Adaptations for Foraging in Non-human Primates. Columbia University Press, pp. 195-216.

Whitten, A., McGrew, W.C., Aiello, L.C., Boesch, C., Boyd, R., Byrne, R.W., Dunbar, R.I.M., Matsuzawa, T., Silk, J.B., Tomasello, M., van Schaik, C.P., Wrangham, R., 2010. Studying extant species to model our past. Science 327, 410.

Wilcox, A.R., 1971. Indices of qualitative variation and political measurement. West. Pol. Quart. 26, 325-343.

Williams, S.A., 2010. Morphological integration and the evolution of knuckle-walking. J. Hum. Evol. 58, 432-440.

Wood, B., 2010. Reconstructing human evolution: achievements, challenges, and opportunities. Proc. Natl. Acad. Sci. USA 107, 8902-8908.

Wood, B., Harrison, T., 2011. The evolutionary context of the first hominins. Nature 470, 347-352.

Young, N.M., 2002. Homology and homoplasy in the evolution of the hominoid postcranium. Ph.D. dissertation, Harvard University.

Young, N.M., Wagner, G.P., Hallgrimsson, B., 2010. Development and the evolvability of human limbs. Proc. Natl. Acad. Sci. USA 107, 3400-3405.

Yu, N., Jensen-Seaman, M.I., Chemnick, L., Kidd, J.R., Deinard, A.S., Ryder, O., Kidd, K.K., Li, W.-H., 2003. Low nucleotide diversity in chimpanzees and bonobos. Genetics 164, 1511-1518.

CHAPTER 4

THE DIAPHRAGMATIC VERTEBRA AND DORSOSTABILITY IN HOMINOIDS

"The study of the direction of the articular processes in the several regions, usually regarded as a rather dry part of human anatomy, becomes interesting on taking a wider survey."
– Struthers (1892: 134)

INTRODUCTION

Interspecific variation in vertebral formulae is both functionally and phylogenetically informative (Narita and Kuratani, 2005; Sánchez-Villagra et al., 2007; Asher et al., 2009, 2011). Mammals are characterized by regionalization of the vertebral column into five variably distinct types – cervical, thoracic, lumbar, sacral, and caudal (coccygeal in tailless mammals such as humans and other hominoids) regions. Rib-bearing, thoracic-like vertebrae likely represent the developmental and evolutionary "ground state" for vertebral patterning, suggested by both the fossil record and *Hox* mutant mouse experiments (Hildebrand, 1995; Wellik and Capecchi, 2003; Wellik, 2007).

Thoracic and lumbar vertebrae regionalized most recently, deriving from the dorsal region of primitive synapsids prior to the divergence of modern mammals (Jenkins, 1971; Buchholtz, 2007). The thoracolumbar (TL = thoracic + lumbar vertebrae) region of mammals coincides with the upper limb and cervical plexus at its cranial border and the lower limb and lumbo-sacral plexus at its caudal border. When examined separately, the thoracic and lumbar regions demonstrate a fair degree of inter- and intraspecific variation, but as a whole the TL

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region is relatively conserved across mammals (Welcker, 1881; Flower, 1885; Todd, 1922; Schultz and Straus, 1945; Narita and Kuratani, 2005; Sánchez-Villagra et al., 2007; Asher et al., 2009, 2011).

This suggests that inter- and intraspecific differences in thoracic and lumbar number can often be attributed to homeotic change (border shifts) within a 19 or 20 element framework. Humans and other hominoids depart from this primitive number and instead commonly possess 18 or fewer TL vertebrae (18 in hylobatids, 17 in western gorillas, chimpanzees, bonobos, and humans, and 16 in orangutans and eastern gorillas; Chapter 1), with departures from the primitive 19 TL pattern attributable to homeotic shifts at the lumbo-sacral border, or lumbar sacralization (Chapter 1; see also Abitbol, 1987).

In this sense, cercopithecoids, the closest living relatives of hominoids, are similar to most other mammals – they possess 19 TL vertebrae with little intraspecific variation and no interspecific variation (see Chapters 1 and 2). The reduced TL regions of hominoids are due to a reduction in the number of lumbar vertebrae by one to several elements. A reduced lumbar region resists buckling and reduces bending moments at the intervertebral discs during antipronograde (climbing and hindlimb and/or forelimb suspensory postures and locomotion) and orthograde (upright) positional behaviors (Jungers, 1984; Ward, 1993; Sanders, 1995); thus, it contributes to the dorsostability (stability in the sagittal plane) of the vertebral column. Another important mechanism of dorsostability involving the level at which the zygapophyses, the processes that bear the articular facets, change orientation and thus resist certain intervertebral movements that were allowed by preceding vertebrae, has received little attention despite its important role in hominoid evolution.

This study has three aims: 1) to critically evaluate the use of multiple definitions of TL vertebrae, 2) to explore variation in the thoraco-lumbar and zygapophyseal transitions in hominoids, and 3) to place the hominoid condition in a wide phylogenetic framework in order to address its uniqueness. To accomplish these aims, I collect data on a large sample of catarrhine primates and interpret the results in the context of a wide survey of mammals.

Aim 1: Definitions of trunk vertebrae

The thoraco-lumbar transition marks the intersection between the thoracic and lumbar regions of the vertebral column and is defined using several methods: 1) costal (rib-bearing/non rib-bearing) criteria, 2) zygapophyseal (orientation of the articular facets and location of the diaphragmatic vertebra, or one that bears transitional facets) criteria, and 3) combined costal-zygapophyseal criteria.

Traditionally, the thoraco-lumbar transition is identified as the juncture of the last rib-bearing vertebra and the first non rib-bearing trunk vertebra (costal definition); therefore, the presence or absence of ribs is used to differentiate thoracic and lumbar vertebrae (Flower, 1885; Schultz, 1930, 1961; Schultz and Straus, 1945; Bornstein and Peterson, 1966; Haeusler et al., 2002). Ribs function to protect the heart, lungs, and other organs, serve as areas of muscle attachment, and assist the lungs and diaphragm in respiration. Due to constraints associated with respiration, true ribs articulate with the sternum and limit flexion, extension, and lateral bending of the anterior thorax (Filler, 1986). Lower ribs may also limit lateral bending of the torso when the lower rib cage approximates the iliac blades, a situation that has been termed lumbar or iliac entrapment (Lovejoy, 2005; Kimbel and Delezene, 2009; Lovejoy et al., 2009; Lovejoy and McCollum, 2010; McCollum et al., 2010).

Somewhat more recently, and largely within anthropology, the thoraco-lumbar transition has been identified by the orientation of the zygapophyses, the processes bearing the articular facets that act as the synovial joints of the vertebral column (Washburn and Buettner-Janusch, 1952; Erickson, 1963; Washburn, 1963; Clauser, 1980; Shapiro, 1993). Under the so-called zygapophyseal definition, thoracic vertebrae are defined as those that bear flat, dorsally and ventrally facing zygapophyses, while lumbar vertebrae possess curved, sagittally-orientated zygapophyses. The vertebra that bears flat, dorsal upper zygapophyses and curved, laterally-facing lower ones is identified as the ultimate thoracic vertebra and termed the diaphragmatic vertebra (Slijper, 1946). In the past, this vertebra has been termed "transitional" (Danforth, 1930; Haeusler et al., 2002), "junctional" (Allbrook, 1955), and intermediate (Lucae, 1876; Stromer, 1902; both cited in Slijper, 1946), or was otherwise described as the vertebra with thoracic-type articulations cranially and lumbar-type ones caudally (Struthers, 1874; Stewart, 1932; Lanier, 1939).

The zygapophyseal criterion has been termed the "functional" definition (Washburn, 1963; Shapiro, 1995; Nakatsukasa et al., 2007) because zygapophyses assist the vertebral centra in load bearing and permit or resist intervertebral movement. Curved, sagitally-oriented zygapophyses ("lumbar-type," or postdiaphragmatic) allow movement in the sagittal plane (i.e., flexion and extension) and constrain rotation, while flat, coronally-oriented zygapophyses ("thoracic-like," or prediaphragmatic) allow lateral bending and resist flexion and extension (Rockwell et al., 1938; Clauser, 1980; Shapiro, 1995; Russo, 2010). Therefore, zygapophyseal orientation, including the position of the diaphragmatic vertebra, is generally structured to either allow or restrict the dorsomobility of the spine during locomotion.

A recent attempt to combine the costal and zygapophyseal definitions has recently been proposed (Stevens, 2004; Rosenman, 2008). According to Rosenman (2008:168), Stevens (2004) devised a scoring system for the identification of thoracic and lumbar vertebrae. In this system, flat zygapophyses and rib facets were scored as "thoracic" and curved zygapophyses and absence of rib facets were scored as "lumbar." Since each zygapophysis (4 criteria – left and right pre- and post-zygapophyses) is scored, zygapophysis orientation is weighed more heavily than the presence or absence of rib facets (2 criteria – left and right). In cases where the costal and zygapophyseal definition produce different results, the Stevens-Rosenman system agrees with the zygapophyseal definition in two of three possible scenarios and thus does not treat the two definitions equally. Moreover, a combination of the two methods may be unwarranted because ribs and zygapophyses are separate morphologies that may evolve independently of one other (see below).

In some studies, the costal and zygapophyseal definitions are presented together, which allows for a comparison of the two methods in a variety of taxa (Erickson, 1963; Washburn, 1963; Clauser, 1980; Shapiro, 1993, 1995; Aimi, 1994; Nakatsukasa and Hirose, 2003). When just one method is used, this approach can be burdensome and confusing because authors must explain that there are two definitions and then identify which one they are using for their particular study (e.g., Shapiro, 1991; Ward, 1993; Haeusler et al., 2002; Pilbeam, 2004; Shapiro et al., 2005; Nakatsukasa et al., 2007). In some studies, it is not entirely clear which definition is being used (e.g., McCollum et al., 2010; Lovejoy and McCollum, 2010). This can lead to a conflation of the two definitions, as has occurred with the Sts 14 *Australopithecus africanus* vertebral column (see below).

An earlier and simpler approach, in which the *relationship* between the diaphragmatic vertebra and the last rib-bearing vertebra is presented (Hasebe, 1913; Stewart, 1932; Lanier, 1939; Slijper, 1946; Allbrook, 1955; Filler, 1986), is preferred here and still allows for a comparison of costal (thoracic and lumbar) and zygapophyseal (pre-diaphragmatic and post-diaphragmatic) criteria of trunk vertebrae, without the burden and confusion involved in using multiple definitions of thoracic and lumbar vertebrae.

Aim 2: Intraspecific variation in hominoids

In humans, as in other hominids ("great apes"), the diaphragmatic and last rib-bearing vertebrae commonly occur at the same level (Shapiro, 1993; Sanders, 1995), but in hylobatids, they are sometimes distinct, with the diaphragmatic vertebra placed cranially relative to the last rib-bearing vertebra by one element (Erickson, 1963; Washburn, 1963; Shapiro, 1993). In non-hominoid catarrhines, platyrrhines, and most other mammals, these morphologies are separated by one or more vertebral elements (Slijper, 1946; Erickson, 1963; Washburn, 1963; Shapiro, 1993, 1995; Argot, 2003). The observation that the diaphragmatic vertebra and last rib-bearing vertebra do not occur together at the same vertebral level in non-hominoid primates and most other mammals suggests that they are distinct morphologies that can be acted upon independently by the forces of evolution.

An examination of the integration between these morphologies in hominoids and other catarrhines will highlight their intra- and interspecific variation, and as within-species variation provides the raw material for the forces of evolution to act upon and generates between-species differences, this study will allow for a better understanding of their evolution. I show that while all hominoids are characterized by a common placement of diaphragmatic and last rib-bearing

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vertebrae on average, individual species and groups demonstrate different intraspecific patterns of variation in these traits. Humans and chimpanzees are nearly identical in this regard, which reflects their close phylogenetic affinities and has important implications for the interpretation of fossil taxa.

Aim 3: Survey of mammals

Hominoids are known to differ from other anthropoids in the placement of the diaphragmatic and last rib-bearing vertebrae (Erikson, 1963; Washburn, 1963; Shapiro, 1993). Here, this trait is examined in a broad survey of mammals to address the uniqueness of the hominoid condition. I demonstrate that hominoids are relatively unique among primates and other mammals in a common placement of these morphologies and argue that this feature is related to dorsostability of the vertebral column. Dorsostability has evolved several times in mammals in two very different locomotor contexts – stiff-spined running (Slijper, 1946; Gambaryan, 1974; Shapiro et al., 2005) and suspensory, antipronograde climbing (Slijper, 1946; Sanders and Bodenbender, 1994; Sanders, 1995; Shapiro et al., 2005). I argue that "common placement" or "caudal displacement" (see Methods) of the diaphragmatic vertebra relative to the last rib-bearing vertebra accompanied the evolution of dorsostability in these groups.

MATERIALS

A total of 700 catarrhine specimens from nine species were examined and form the main focus of this study. These include *Homo sapiens* (humans; N=117), *Pan troglodytes* (chimpanzees; N=104), *Pan paniscus* (bonobos; N=22), *Gorilla gorilla* (western gorillas;

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N=106), *Pongo pygmaeus* (orangutans; N=82), *Hylobates lar* (white-handed gibbons; N=74),

Symphalangus syndactylus (siamangs; N=34), *Papio hamadryas* (baboons; N=73), and

Trachypithecus cristatus (silvery leaf monkeys; N=88). The former seven species encompass all

major clades of Hominoidea except the hylobatid genera/subgenera *Nomascus* and *Bunopithecus*.

The two cercopithecoids were chosen because they represent arboreal (*T. cristatus*) and large-

bodied, terrestrial (*P. hamadryas*) forms from the two major divisions of Cercopithecoidea,

Colobinae and Cercopithecinae, respectively.

For comparative purposes, 272 non-catarrhine euarchontan mammals (platyrrhines,

tarsiers, sterpsirhines, colugos, and tree shrews) were also examined (Table 4.1). Additionally,

published records of the relationship between diaphragmatic and last rib-bearing vertebrae

(Slijper, 1946; Erikson, 1963; Washburn, 1963; Filler, 1986; Shapiro, 1993; Breit and Kunzel,

2002; Argot, 2003) and the author's personal observations on non-euarchontan mammals were

utilized to provide a larger mammalian framework in which to interpret the hominoid condition.

Due to small sample sizes for some taxa (in some cases, N=1) for species other than those nine

that form the focus of this study, this latter analysis should be viewed merely as a superficial

survey for purposes of comparison and in need of more detailed study in the future. Despite

small sample sizes, every major clade of mammals is represented in this survey[5]. Together,

previously published and new data included in this study combine to result in a survey consisting

of 1416 specimens representing 245 mammalian species and to 195 genera (Appendix E).

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[5] Monotremata, Marsupalia, Afrotheria, Xenarthra, Lagomorpha, Rodentia, Scandentia, Dermoptera, Primates, Eulipotyphla, Chiroptera, Pholidota, Carnivora, Perissodactyla, Cetartiodactyla. Although early cetaceans are similar to most non-hominoid mammals in vertebral morphology and diaphragmatic placement (Gingerich et al., 2009), extant cetaceans are not included in the analysis because their zygapophyses are reduced or vestigial in terms of functionality and morphology, or are absent altogether in the posterior thoracic and lumbar regions (Slijper, 1946; Buchholtz and Schur, 2004; Buchholtz et al., 2005). Therefore, with a few exceptions, the cetacean vertebral column does not possess a diaphragmatic vertebra (Slijper, 1946).

METHODS

Thoracic and lumbar vertebrae were distinguished using both costal and zygapophyseal definitions, the criteria for which are discussed below, along with relevant sub-definitions.

Costal definition

The costal definition identifies thoracic vertebrae as those that bear ribs and lumbar vertebrae as those that do not. Schultz (1930, 1961; Schultz and Straus, 1945) formalized an iteration of this definition by providing specific criteria for differentiating thoracic and lumbar vertebra and dealing with transitional vertebrae. Transitional vertebrae, those that bear a rib or costal facet on one side and a lumbar transverse process on the other, are recorded as half-counts (e.g., a transitional vertebra at the thoraco-lumbar border is recorded as 0.5 thoracic and 0.5 lumbar). According to Schultz criteria, thoracic vertebrae are those that bear ribs, even in cases where "the last and very short rib of one side was completely fused with the vertebra, giving it the appearance of a transitional vertebra, as which, however, it was not counted" (Schultz, 1930:310).

A second costal definition, one proposed by Bornstein and Peterson (1966), counts vertebrae that do not bear a costal facet (and therefore a free, moveable rib) as lumbar. This definition is similar to that of Schultz but does not allow for transitional vertebrae (half counts) and ignores the possibility of ankylosed (fused) ribs. It was preferred by Haeusler et al. (2002) as a matter of convenience to avoid the allocation of a single vertebra to more than one category. In this study, both of these methods are employed and their results presented.

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Zygapophyseal definition

The zygapophyseal definition classifies vertebrae that bear flat, coronally-oriented zygapophyses as thoracic and curved, sagitally-oreinted zygapophyses as lumbar (Washburn and Buettner-Janusch, 1952; Erickson, 1963; Washburn, 1963; Clauser, 1980; Shapiro, 1993). The diaphragmatic vertebra is identified here as one that possesses posteriorly facing prezygapophyses and laterally facing postzygapophyses, and is considered the ultimate thoracic vertebra.

Although the angulations of articular facets are sometimes asymmetrical and involve a larger degree of sagittalization (curvature) on one side than the other (Odgers, 1933; Clauser, 1980), a completely transitional set of zygapophyses, in which one side is flat and the other is curved, is rare (personal observation). Some authors (e.g., Pridmore, 1992:144; Slijper, 1946) identify a "diaphragmatic region" rather than a distinct diaphragmatic vertebra because a vertebra with intermediate, only partially sagittalized postzygapophyses is observed, followed by a vertebra with distinct sagittalization of its postzygapophyses. However, different patterns of sagittalization are observed among taxa (Filler, 1986; Russo, 2010), some occurring gradually (Filler's lateral curving) and others more abruptly (Filler's sagittalization). Here, with several notable exceptions (see below), the first vertebra to demonstrate any moderate degree of sagittalization on the postzygapophyses is considered the diaphragmatic vertebra, regardless of the degree of sagittalization that is achieved further down the column.

Thoracic and lumbar vs. prediaphragmatic and postdiaphragmatic

As opposed to lumbar vertebrae, which are defined here by the absence of ribs, vertebrae caudal to the diaphragmatic vertebra are referred to here as postdiaphragmatic, allowing a comparison of lumbar and postdiaphragmatic vertebrae. The total number of diaphragmatic/prediaphragmatic TL vertebrae (hereafter, prediaphragmatic vertebrae) is then comparable to the number of thoracic vertebrae. This system eliminates confusion and burden associated with two definitions of thoracic and lumbar vertebrae and better acknowledges the evolutionary autonomy of ribs and zygapophyses and recognizes their unique functional implications for vertebral mobility and locomotion. Lumbar and postdiaphragmatic regions are compared statistically (using t- and F-tests with an alpha level of 0.10) in the nine focus species included in this study.

Terminology associated with the placement of diaphragmatic and last rib-bearing vertebrae

The position of the diaphragmatic vertebra relative to the last rib-bearing vertebra (Figure 4.1) underlies the difference (or lack thereof) between the thoracic and prediaphragmatic regions and the lumbar and postdiaphragmatic regions in an individual or species. When the diaphragmatic vertebra is cranially-positioned relative to the last rib-bearing vertebra ("cranial displacement"), there are more postdiaphragmatic than lumbar vertebrae; conversely, when the diaphragmatic vertebra is caudally-positioned ("caudal displacement"), there are more lumbar than postdiaphragmatic vertebrae. Only in instances when both morphologies exist at the same vertebral level ("common placement") are the number of lumbar and postdiaphragmatic vertebrae equal.

Cranial or caudal displacement may occur by one or more vertebral levels. On an individual level, positive/negative numerical system is used here to symbolize displacement, positive values representing cranial displacement, negative values caudal displacement, with common placement receiving a zero value ("0"). One-element cranial and caudal displacements are therefore shown as "+1" and "-1," respectively, two-element displacements as "+2" and "-2," and so on (Figure 2), for individual specimens. In intraspecific comparisons, the average level of displacement is calculated and shown as a positive, negative, or neutral (0) value.

RESULTS

Intraspecific variation

Within hominoid species, the modal number of thoracic and prediaphragmatic vertebrae and lumbar and postdiaphragmatic trunk vertebrae do not differ, but their means and variances do (Table 4.2). Because the two methods of costal classification produce very similar results, the traditional half-count method outlined and formalized by Schultz is presented here. All catarrhine taxa included in this analysis except *Gorilla* and *Pongo* possess a significantly greater number of postdiaphragmatic than lumbar vertebrae. Modern humans (p<0.001), chimpanzees (p=0.005), bonobos (p=0.095; borderline significance is likely an artifact of low sample size), gibbons (p<0.001), siamangs (p<0.05), baboons (p<0.001), and silvery leaf monkeys (p<0.001) possess a greater average number of post-diaphragmatic than lumbar vertebrae. These regions are not significantly different in western gorillas (p=0.840). In orangutans, the number of postdiaphragmatic vertebrae is significantly lower than the number of lumbar vertebrae (p=0.068).

Perhaps more importantly, the position of the diaphragmatic vertebra relative to the last rib-bearing vertebra presents unique population-level patterns and differs among taxa (Table 4.3; Figure 4.2). In 82% of western gorillas, these elements exist at a common vertebral level. The diaphragmatic vertebra is positioned one element cranial to the last rib-bearing vertebra (+1) in 9% and one element caudal (-1) in the other 9% of the remaining sample. Therefore, western gorillas are not characterized by a tendency toward displacement in either direction (0).

Humans and chimpanzees, on the other hand, are nearly identical in this relationship and demonstrate slightly positive values (+0.21 and +0.19, respectively). In humans, 72% are characterized by common placement (0), whereas 25% are characterized by a one-element cranial shift (+1) and 3% are characterized by a one-element caudal shift (-1) of the diaphragmatic vertebra. Similarly, common placement characterizes 74% of chimpanzees, while 23% possess a cranially-placed (+1), and 3% a caudally-placed (-1), diaphragmatic vertebra. Bonobos, although represented by a cautiously low sample size (N=22), largely conform to the situation in humans and chimpanzees – 23% of bonobos are characterized by cranial displacement (+1), while no cases of caudal displacement are observed. This is hardly surprising considering the low frequency of this relationship in humans and chimpanzees in concert with the small sample of bonobos.

Orangutans are unique among catarrhines and possibly among primates overall in the possession of an average caudal displacement (-0.20). While 74% of orangutans are characterized by a common placement, 21% of specimens possess a caudally displaced diaphragmatic vertebra (-1) and 5% are characterized by a cranial displacement (+1).

In hylobatids, 62% of white-handed gibbons and 65% of siamangs possess common placement. Neither is characterized by a full caudal shifting of the diaphragmatic vertebra (-1; a

single gibbon specimen exhibited -0.5), while 37% of white-handed gibbons and 35% of siamangs are characterized by cranial displacement (+1). Both species of cercopithecoid included in this study are characterized by cranial displacement by at least two elements. Cranial displacement in silvery leaf monkeys ranges from +2 to +3 elements, with an average of +2, while in baboons it ranges from +2 to +4 elements with an average of +2.5.

Survey of Mammals

In a survey of Mammalia (235 species; 193 genera; see Appendix E), specimens were found to range from a cranial displacement of 6 vertebra (+6, represented by *Ochotona rufescens*) to a 2-element caudal displacement (-2, represented by *Equus quagga*). The amount of cranial and caudal displacement observed among mammals is even greater when two observations are taken into account: 1) Tapirs (*Tapirus bairdii* and *T. terrestris*) and rhinoceroses (*Diceros bicornis* and *Rhinoceros sondaicus*) are characterized by an extreme degree of caudal displacement that results in no post-diaphragmatic vertebrae (-3 in rhinoceroses, -5 in tapirs).

2) Some taxa, including elephants and sirenians, demonstrate a diaphragmatic region encompassing between three and eight elements and generally spanning the T-L transition. On the one hand, if the vertebra with intermediately-oriented zygapophyses is treated as the diaphragmatic vertebra, manatees (*Trichechus inungius*) demonstrate the highest degree of cranial displacement among non-cetacean mammals at +8; however, if, on the other hand, the first vertebra with strong sagittalization is counted as the diaphragmatic vertebra, dugongs (*Dugong dugon*) are characterized by an extreme caudal displacement (-3) and posses no post-diaphragmatic vertebrae, as in tapirs and rhinoceroses. These discrepancies highlight the ambiguities sometimes associated with the zygapophyseal definition of trunk vertebrae.

Because, as previously stated, this survey of non-catarrhine mammals is superficial and certainly not all encompassing, it should be noted that both intraspecific variation and interspecific dispersion are not well estimated here based on low sample size and representation of taxonomic diversity, respectively. Most mammals are characterized by cranial displacement: +3 to +5 elements in Monotremata (+5 in *Ornithorhynchus*, +3 in *Tachyglossus*), +2 to +4 in Marsupalia, +1 to +8 in Afrotheria, +1 to +4 in Xenarthra (except *Bradypus* and *Choloepus*, which sometimes demonstrate common placement), +1 to +5 in Eulipotyphla (except *Scuitsorex*, which demonstrates common placement), +1 to +5 in non-cetacean artiodactyls (except *Bos*, which demonstrates common placement), +1 to +4 in Carnivora, +2 to +6 in Lagomorpha (+2 in *Lepus* and *Sylvilagus*; +6 in *Ochotona*), +1 to 4 in Rodentia (except *Cuniculus*, *Dolichotis*, and *Hydrochoerus*, which demonstrate common placement), +2 to +4 in Scandentia, +1 in Dermoptera, and +1 to +4 in non-hominoid primates. Members of Chiroptera included here range from -1 to +3, and those in Perissodactyla from -5 to +3.

DISCUSSION

Definition of thoracic and lumbar vertebrae

Here, it is proposed that the traditional rib-bearing criterion be retained as the sole definition of thoracic and lumbar vertebrae, and that the zygapophysis definition be discarded as a working definition of thoracic and lumbar vertebrae. This is not to suggest that either method is more reliable or functionally relevant than the other; rather, it is proposed for practical reasons. While all mammals possess caudal, rib-less TL vertebrae that can be differentiated as lumbar, not all mammals possess diaphragmatic or post-diaphragmatic vertebrae (e.g., rhinoceroses, tapirs,

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hyraxes, and some cetaceans), and therefore would lack altogether lumbar vertebra when defined by zygapophysis orientation. Furthermore, the transition from flat to curved zygapophyses is not clearly marked in some taxa (e.g., elephants, sirenians, monotremes), rendering it difficult and even somewhat arbitrary to identify its position (Slijper, 1946; Pridmore, 1992). Additionally, Aimi (1994) showed that if the zygapophyseal definition is adhered to in a strict sense, the first thoracic vertebra (T1) of Japanese macaques (*Macaca fuscata*) generally bears cervical-like zygapophyses and not thoracic-like ones, thus reducing the number of vertebrae identified as "thoracic" in such a comparison. This is unlikely to be restricted to Japanese macaques and likely occurs in other taxa as well. Similar issues also likely exist at the lumbo-sacral border, where the postzygapophyses of the last lumbar vertebra and the prezygapophses of the sacrum often bear flat, "thoracic-like" facets rather than curved "lumbar-like" ones (personal observation).

Another definition of thoracic and lumbar vertebrae was introduced in the past but has since been abandoned on similar grounds. The terminal thoracic vertebra was identified as one with a vertical spinous process; this vertebra marks a change in direction of the spinous processes, those located cranial to it having spines that are directed caudally and those located caudal to it having spines directed cranially. According to Slijper (1946) and Haeusler et al. (2002), Giebel (1853) originally termed this vertebra "diaphragmatic," but it was later renamed "anticlinal" (Giebel, 1900). In fact, Lucae (1876) suggested that a different morphology should be used to identify thoracic versus lumbar vertebrae because the anticlinal vertebra is not present in many mammals (see Table 3 in Slijper, 1946); in addition, it is not clearly marked and identifiable in some other mammals, including humans and other hominoids (Danforth, 1930).

Here, instead of attributing the pre- and postdiaphragmatic vertebrae to the thoracic or lumbar regions, as has been done in the past, particularly in anthropology (e.g., Washburn and

Buettner-Janusch, 1952; Erickson, 1963; Washburn, 1963; Clauser, 1980; Shapiro, 1993, 1995; Nakatsukasa and Hirose, 2003), the presence of the diaphragmatic vertebra is recorded in relation to the last rib-bearing vertebra, as was done by Slijper (1946), Filler (1986), and others (Struthers, 1874; Hasebe, 1913; Danforth, 1930; Stewart, 1932; Lanier, 1939; Allbrook, 1955; Breit and Kunzel, 2002; Argot, 2003; Nakatsukasa et al., 2007; Gingerich et al., 2009). This treatment avoids the confusion associated with the maintenance of multiple definitions of thoracic and lumbar vertebrae and allows for comparisons of prediaphragmatic and thoracic vertebrae and postdiaphragmatic and lumbar vertebrae. Because the zygapophyses and ribs are separate morphologies that can be manipulated independently by the forces of evolution, as evidenced in the survey of mammals presented here, combined or conflated costal-zygapophyseal definitions (Robinson, 1972; Stevens, 2004; Rosenman, 2008) are problematic and applicable largely only to hominoids, and therefore are unwarranted.

Dorsostability and reduced postdiaphragmatic regions in hominoids and other mammals

Given the diversity of the thoraco-lumbar transition in a modern phylogenetic context, it is likely that the primitive condition for Primates, Anthropoidea, and Catarrhini is a 2-3 element cranial displacement of the diaphragmatic vertebra. Hominoids likely evolved common placement and dorsostability from a primitive, dorsomobile condition with cranial displacement that characterizes most primates and mammals in general. In hominoids, this likely evolved along with the lumbar sacralization (Keith, 1903; Abitbol, 1987; Pilbeam, 2004) and reduction in erector spinnae mass (Benton, 1967; Ward, 1993) that accompanied the evolution of crown hominoid primates.

Relevant portions of the TL vertebral column exist for two Miocene hominoids (KNM-MW 13142 *Proconsul nyanzae* and KNM-BG 35250 *Nacholapithecus kerioi*). The diaphragmatic vertebra is cranially displaced by at least one element in *Proconsul* (Ward, 1993; Sanders and Bodenbender, 1994) and two to three elements in *Nacholapithecus* (Ishida et al., 2004; Nakatsukasa et al., 2007; Nakatsukasa and Kunimatsu, 2009). The *Proconsul* KNM-MW 13142 fossil specimen preserves five thoracolumbar elements: one thoracic (H) and four lumbar (I, J, K, L) vertebrae, both of which represent incomplete regions. This includes the thoraco-lumbar transition since H is the last thoracic and I is the first lumbar. Unfortunately, the penultimate thoracic vertebra is not preserved (Ward, 1991). In this specimen, the last thoracic (H) is interpreted as T13. It bears rib facets and is post-diaphragmatic (i.e., is a post-diaphragmatic thoracic vertebra), but since more cranial lower thoracic vertebrae are not present, it is unknown whether the diaphragmatic vertebra was T10, T11, or T12.

The *Nacholapithecus* skeleton (KNM-BG 35250) preserves nine to ten thoracic vertebrae (BH, BI, BJ, BW, BL, BM, BK, BO, BP, and BN, if in fact the last specimen represents a separate element and is not associated with another specimen) and a complete or nearly complete lumbar column, consisting of six elements (P, R, BQ, BR, BS, and BT) (Ishida et al., 2004; Nakatsukasa et al., 2007). The thoraco-lumbar transition is represented by a prediaphragmatic thoracic vertebra (BK), the diaphragmatic vertebra (BO), a post-diaphragmatic thoracic vertebra (BP), and the lumbar series. Because it is unknown whether BO and BP are adjacent or whether BP is the last rib-bearing vertebra, the position of the diaphragmatic vertebra relative to the last rib-bearing vertebra is unknown, although it is certainly cranially displaced by at least two, and possibly three elements (Nakatsukasa et al., 2007; Nakatsukasa and Kunimatsu, 2009).

Since it is likely that *Nacholapithecus* is derived relative to the more primitive *Proconsul*, it seems reasonable to speculate that *Proconsul* too was characterized by cranial displacement by at least two elements. In this light, *Proconsul* and *Nacholapithecus* are unlike crown hominoids and similar to cercopithecoids, other non-hominoid primates, and most mammals in general (Figure 4.2). This is consistent with their number of lumbar and TL vertebrae, which in *Proconsul* and *Nacholapithecus* is also primitive and unlike the reduced region of modern hominoids (Ward, 1993; Ishida et al., 2004; Nakatsukasa et al., 2007).

Although extant hominoids modally demonstrate common placement, unique population-level patterns of variation in cranial and caudal displacement exist (Figure 4.1). Hylobatids show a relatively high degree of cranial displacement (~35 to 37%) and no caudal displacement. Hylobatids likely represent the primitive crown hominoid condition in this regard. Orangutans are quite the opposite and are unique among hominoids in displaying a high degree of caudal displacement (21%) and little variation for cranial displacement (5%). Caudal displacement functions to decrease the number of elements composing the postdiaphragmatic region, which further enhances the sagittal stability of the vertebral column.

Gorillas demonstrate an even distribution of cranial and caudal displacement (~9% each). Humans and chimpanzees are very similar to each other in a moderate degree of cranial displacement (25% and 23%, respectively) and a low frequency of caudal displacement (~3% each). Bonobos, although represented at a much lower sample size, demonstrate a very similar pattern, with 23% of individuals characterized by cranial displacement. Given the close phylogenetic relatedness of this clade, their similarity in this trait may reflect a population-level synapomorphy, although two lines of evidence need to be addressed to confirm this hypothesis:

1) diversity of this trait among modern human populations, and 2) the thoraco-lumbar transition in fossil hominins.

Modern human population diversity

Allbrook (1955) provided a summary of human population-level variation in the position of the diaphragmatic vertebra relative to the last rib-bearing vertebra from his own records and those previously published in Hasebe (1913), Stewart (1932), and Lanier (1939) on East Africans, Japanese, Inuit, and Americans of African and European descent, respectively, and concluded that human population-level differences do exist. In these samples, Japanese and Inuit demonstrate a high degree of common placement (75 to 77%), whereas East Africans and African and European Americans show a lower degree of common placement (58 to 51%). In addition, all groups except Inuit are characterized by a high frequency of cranial displacement compared to caudal displacement (76 to 89%) among individuals without common placement. In the Inuit sample, the converse was found, where only 20% of non-common placement was cranial.

The sample of modern humans included in this analysis comes mainly from the Cleveland Museum of Natural History and consists of African Americans (labeled "B" for black; N=34) and European Americans (labeled "W" for white; N=59). It also includes a number of individuals from India (N=17) from the teaching collection at Northern Illinois University and several individuals of unknown identity (N=7) from the University of Illinois teaching collection. Therefore, although human populations included in this study do not appear to differ significantly in frequencies of common placement or cranial and caudal displacement, sample sizes are not sufficient to permit a proper statistical analysis in this study. It should be noted that

a related line of research documents "shifting" of the thoraco-lumbar border in various aspects of morphology and provides a different approach and perspective on this issue (see Barnes, 1994; Ogilvie et al., 1998), but is not comparable to this study.

Implications for and interpretation of fossil hominins

The thoraco-lumbar transition is fully or partially preserved in five Pliocene and Plio-Pleistocene hominins (A.L. 288-1 *Australopithecus afarensis*, Sts 14 *A. africanus*, Stw 431 *A. africanus*, MH1/MH2 *A. sediba*, and KNW-WT 15000 *Homo ergaster*), although fragmentation and discrepancies in reconstructions make it difficult to determine the association between the diaphragmatic and last rib-bearing vertebrae. What follows is a description of the relevant specimens and the implications of different reconstructions.

The fossil hominins *A. africanus* (Sts 14 and Stw 431) and *H. ergaster* (KNM-WT 15000) may be characterized by a cranial displacement of the diaphragmatic vertebra by one element (Haeusler et al., 2002). The Sts 14 partial skeleton, which includes a consecutive, 15-element TL vertebral column, was described and interpreted by Robinson (1972). Using a definition of lumbar vertebrae based on overall morphology (including the presence or absence or ribs, the medio-lateral orientation of zygapophyses, and the cranio-caudal orientation of the spinous process), he described six lumbars, the first of which (Sts 14f) includes a "costal process" on the right side and a "transverse process" on the left. Robinson (1972) interpreted the costal process as non-functional; however, Haeusler et al. (2002) identified a matching right rib that articulates with the costal facet, making it functional. In addition, the transverse process is not like normal lumbar transverse processes in that it is not fully fused and bears a complete transverse foramen (Haeusler et al., 2002). In this light, the process is best interpreted as an

ankylosed last rib rather than a lumbar transverse process, although it must be recognized that these structures are at least partially homologous (Rosenman, 2008; personal observations). Partial fusions of this sort were encountered in varying degrees by the author in several hominoid specimens, nearly always accompanied by a similar process on the opposing side or by a costal facet for a last rib, and were accordingly classified as thoracic vertebrae.

Another *A. africanus* fossil, Stw 431, includes nine (Toussaint et al., 2003) or ten (Haeusler et al., 2002) consecutive vertebrae in the TL column, identified as T8 or T9 to L5. This specimen was argued to have possessed six lumbar vertebrae by various authors in the past (Sanders, 1995). Haeusler et al.'s (2002) reconstruction is slightly different than that of Toussaint et al., although they too argued that this specimen likely possessed just five lumbar vertebrae. This discrepancy results in a cranially displaced diaphragmatic vertebra (Sts 431l) in Haeusler et al.'s reconstruction and a common placement according to that of Toussaint et al. Similar issues, including missing or fragmentary vertebrae, plague the interpretation of other fossil hominins with relatively complete thoraco-lumbar transitions – A.L. 288-1 ("Lucy") and KNW-WT 15000 ("Nariokotome Boy").

The A.L. 288-1 vertebral column consists of three (Cook et al., 1983) or four (Johanson et al., 1982) consecutive thoracic vertebrae (AG, AD, AC, and AI, or just AD, AC, and AI). The discrepancy lies in whether or not a vertebra is missing between AG and AD. While Johanson et al. (1982:434) found that AG articulates "reasonably well" with AD, Cook et al. (1983) argue that it does not, and instead infer that a vertebra is missing between them. Cook et al. (1983) identify a second consecutive series, AH, AF, and AG. If Johanson et al. (1982) are correct in their association of AG and AD, it is possible that six consecutive vertebrae are present in this series (AH, AF, AG, AD, AC, AI). In Johanson et al.'s description, vertebra AG is T9; in Cook

et al.'s reconstruction, it is T8. The three terminal thoracic elements (AD, AC, and AI) are identified in both studies as T10-T12 based on zygapophysis orientation; that is, AI is the diaphragmatic vertebra and so it is inferred to be the terminal thoracic vertebra. The presence of a costal facet confirms its status as a thoracic vertebra, but the next caudal vertebra, which is inferred to be L1 but could in fact be the terminal thoracic, is missing or unidentifiable. The next vertebra is either L2 (Cook et al., 1983) or L3 (Johanson et al., 1982). Therefore, it is possible that the diaphragmatic vertebra is cranially placed relative to the last rib-bearing vertebra, but because a continuous TL series is not present, this relationship remains unknown.

The Nariokotome Boy, KNM-WT 15000, preserves 16 precaudal vertebrae, with two (Haeusler et al. 2002) or three (Latimer and Ward, 1993; Walker and Leakey, 1993) missing elements throughout. The two elements that are agreed to be missing are from the upper thoracic region (probably T4 and T6). The remaining 11 vertebrae may form a consecutive series (w, v, bi, x, y, ar/ba, av/aa, z/bw, ab, bm, and ac) (Haeusler et al., 2002) or may be divided between y and ar/ba by a missing vertebra (Walker and Leakey, 1993). In the original description of KNM-WT 15000, AC was classified as L5, which is in agreement with Haeusler et al.'s interpretation. It was in the formal description of the skeleton (Latimer and Ward, 1993; Walker and Leakey, 1993) that a vertebra was determined to be missing and AC relegated as L6. Two observations are relevant: 1) Y is the diaphragmatic vertebra and 2) the relevant portions of AR/BA are not preserved to determine if costal facets are present. According to Walker and Leakey (1993), Y is T11 (diaphragmatic), T12 is missing, and AR/BA is the first lumbar. Haeusler et al. (2002) agree that Y is T11, but question the absence of a vertebra and instead suggest that AR/BA is T12. In either situation, the diaphragmatic vertebra would be cranially displaced by one element.

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Finally, two recently discovered *Australopithecus sediba* skeletons (MH1 and MH2) preserve a number of thoracic and lumbar vertebrae each (Berger et al., 2010). Importantly, MH2 preserves the ultimate and penultimate thoracic vertebrae (personal observation). The penultimate (MH2 88-43), likely T11, is complete and undistorted. It bears a full, rounded costal facet for a floating rib at the body-pedicle border on each side. The transverse processes do not bear costal articulations and as such are not knob-like, but short, narrow, and somewhat caudally-directed. The transverse process on the left side is somewhat obscured by matrix and the presence of a disarticulated rib. The right transverse process bears a noticeable split into cranio-medial and caudo-lateral portions, recognizable as precursors of the mammillary process and accessory process/lumbar transverse process, respectively. The penultimate thoracic vertebra bears flat prezygapophyses and curved, laterally-oriented postzygapophyses (as with the left transverse process, the left postzygapophysis is partially obscured, but the upper portion of the corresponding prezygapophysis on the ultimate thoracic vertebra is visible and is clearly curved and medially-oriented); therefore, it is the diaphragmatic vertebra.

The ultimate thoracic vertebra (MH2 88-44), which is likely T12, is complete and undistorted, but is mostly obscured on the left side by matrix and the aforementioned disarticulated rib. On its right side, it bears an ovoid-shaped costal facet at the body-pedicle border for the last rib. The transverse process is nearly non-existent, consisting of a small, bifurcated process, the cranial aspect of which is likely homologous to a lumbar transverse process, and the latter an accessory process, of a lumbar vertebra. The mammillary process is completely incorporated into the prezygapophysis, which is curved and medially-oriented. Likewise, the postzygapophysis is curved and laterally-oriented. This vertebra is the last thoracic

and first postdiaphragmatic vertebra; therefore, MH2 is characterized by cranial displacement (+1).

In light of these findings, several possible scenarios of hominin vertebral evolution are proposed: 1) As with chimpanzees and modern humans, early hominins maintained a modal frequency of common placement of diaphragmatic and last rib-bearing vertebrae. The *H. ergaster* Nariokotome skeleton, MH2 *A. sediba*, Sts 14 *A. africanus*, and possibly other potential examples of cranial displacement in fossil hominins (i.e., Stw 431 and A.L. 288-1) represent a less frequent pattern (at <50% frequency) than the modal pattern of common placement. 2) Early (Mio-Pliocene) hominins evolved cranial displacement in order to gain a functionally longer lower back (i.e., postdiaphgramatic) region during the evolution of bipedalism, likely to achieve effective lordosis. 3) Common placement was retained in early hominins; Mid-Pliocene to Plio-Pleistocene hominins (e.g., australopithecines, early *Homo*, *H. ergaster*) evolved cranial displacement to gain a more flexible trunk in the adoption of efficient terrestrial bipedalism. In evolutionary scenarios 2 and 3, common placement is re-established by the appearance of Neandertals (Arensburg, 1991; Ogilvie et al., 1998) and modern humans, possibly in response to obstetric demands (e.g., Tague, 2009). These scenarios are more likely than scenario 1, which seems unlikely given the apparent prevalence of cranial displacement in fossil hominins.

Dorsostability in hominoids and other mammals

Common placement or caudal displacement is relatively uncommon in mammals and restricted to several species and larger taxonomic groups – *Scutisorex*, Cavioidea (Agoutidae, Dasyproctidae, Caviidae), Perissodactyla, *Bos* (and possibly a larger group of bovines), Folivora (sloths), *Nycticebus*, and Hominoidea among specimens included in this survey. *Scutisorex*, the

hero shrew, possesses an extremely specialized vertebral column in both its morphology and numerical composition (Allen, 1917; Cullinane et al., 1998). The reason for its highly modified nature is unknown, although it may be a safety mechanism to withstand large dorso-ventral loading (Allen, 1917; Cullinane and Aleper, 1998; Cullinane and Bertram, 2000).

In mammals that use flexible spinal columns to increase stride length or as a spring mechanism for leaping or hopping, the diaphragmatic vertebra is cranially-placed relative to the last rib-bearing vertebra, which itself precedes a long lumbar column (Slijper, 1946; Erickson 1963). This allows for a spring-like mechanism in which a long, dorsoventrally flexible postdiaphragmatic region permits bending and stretching (flexion and extension) of the spine, with the extremely mobile diaphragmatic region at its center, which allows increase propulsion and stride length during running, leaping, and hopping (Slijper, 1946, 1947; Hildebrand, 1959; Hurov, 1987). These "dorsomobile" mammals (Gambaryan, 1974; Sanders and Bodenbender, 1994; Sanders, 1995) are probably best exemplified by cercopithecoids and carnivorans (Order Carnivora), but also include many non-hominoid primates, glirians (rodents and lagomorphs), "insectivores" (Lipotyphla), and marsupials, including both arboreal and terrestrial forms and even bipedal jumpers like kangaroos, springhares, and jerboas (Slijper, 1946).

In contrast with the dorsomobile "leaping-gallop," "bipedal jumping," and "walking-climbing" forms (Slijper, 1946, 1947), "dorsostable" mammals (Gambaryan, 1974; Sanders and Bodenbender, 1994; Sanders, 1995) possess little flexibility in the diaphragmatic region and the trunk in general and include hominoid primates, elephants, perissodactyls, and large-bodied artiodactyls[6] (Slijper, 1946; Halpert et al., 1987). Perissodactyls represent an extreme version of dorsostability for both speed and endurance and are characterized by a caudally-placed

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[6] Here, I refer to non-cetacean cetartiodactyls, including hippopotamuses, as "artiodactyls" as a matter of convenience; however, I recognize phylogenetic position of whales within Cetartiodactyla, and by implication, the resultant paraphyly of the term.

diaphragmatic vertebra or lack of one altogether, which, along with other stabilizing vertebral morphologies, creates a stiff spine that moves very little during galloping except at the lumbo-sacral joint (Slijper, 1946, 1947; Smith and Savage, 1955; Hildebrand, 1959; Gambaryan, 1974). Artiodactyls are best viewed on a spectrum, from large-bodied, dorsostable forms such as bovines, to primitive, dorsomobile suiforms (pigs and peccaries) and tragulids (chevrotains), with small- and medium-bodied deer and antelope occupying an intermediate type (Slijper, 1946; Smith and Savage, 1955; Gambaryan, 1974; Halpert et al., 1987).

Gambaryan (1974) identified three groups of mammals that independently evolved dorsostable modes of running – Ungulata, Proboscidea, and Dasyproctidae. There is some doubt as to whether Ungulata, or Euungulata, as the clade to which cetartiodactyls and perissodatctyls belong is currently known (Asher and Helgen, 2010), is a true taxonomic group (e.g., Nishihara et al., 2006); either way, extreme dorsostability likely evolved independently in perissodactyls and large-bodied artiodactyls, exemplified by horses and cattle (Bovinae), respectively. Although Gambaryan (1974) discussed a variety of mechanisms that contribute to the stability and mobility of the vertebral column, he did not include a treatment of zygapophyseal orientation and its relevance for these strategies of locomotion. Both perissodactyls and large-bodied artiodactyls (exemplified here by *Bos*) exhibit caudally-placed diaphragmatic vertebrae (common placement in cattle and horses and caudal displacement in rhinos and tapirs). Given the paucity of common placement and caudal displacement among other artiodactyls (see Appendix E), it is likely that these morphologies are the result of convergence on similar strategies to enhance dorsostability in large-bodied running forms.

A third independent strategy of dorsostability is found in Proboscoidea. Elephants demonstrate a reduced number of lumbar vertebrae and achieve what amounts to iliac

entrapment, where the lower ribs approximate and directly attach via soft tissue connections to the iliac blades (Gambaryan, 1974). In addition, elephants possess a 4 to 5 element diaphragmatic region that culminates in an abrupt change in zygapophyseal orientation at the first lumbar vertebra. The intermediate zygapophyses of the diaphragmatic region limit sagittal movement and further enhance stabilization.

Gambaryan (1974) characterized running in the agouti (Family Dasyproctidae) as a stiff-backed, ungulate-like gallop, and he therefore included Dasyproctidae in the dorsostable group of runners. As in galloping euungulates, the agouti vertebral column remains rigid during running and thus does not actively facilitate locomotion (Gambaryan, 1974). The phylogenetic position of agoutis, acouchis, and pacas among cavioid hystricomorph rodents has been reexamined and revised with the emergence and increasing utility of molecular phylogenetic approaches (Rowe and Honeycutt, 2002). Of the four cavioid rodents included in this survey, the paca (*Cuniculus paca*), mara (*Dolichotis patagonum*), and capybara (*Hydrochoerus hydrochaeris*) are characterized by common placement. The fourth member of this group, the guinea pig (*Cavia porcellus*), is characterized by a one-element cranial displacement; however, one of the two paca specimens included in this survey also demonstrates a one-element cranial displacement. Therefore, it is possible that the entire clade is characterized by a tendency towards common placement, although a larger study is required to confirm such a synapomorphy.

Hominoids, Slijper's (1946) "hanging-climbing" mammals, represent the other group of dorsostable mammals, and possess both reduced lumbar regions and caudally-placed diaphragmatic vertebrae. Rigidity of the lower back of hominoids, and orangutans, gorillas, and chimpanzees in particular, is achieved not only by reduction of the lumbar region and caudal

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placement of the diaphragmatic vertebra, which results in a shortened postdiaphragmatic region, but also by close approximation of the rib cage and iliac blades. All together, these morphologies limit both sagittal flexion and extension (dorsomobility) and lateral bending, creating a rigid trunk that allows rotation but resists other movements for truncal stability during orthograde posture, suspensory locomotion, ape-like vertical climbing, and bridging and transferring behaviors (Keith, 1923; Cartmill and Milton, 1977; Jungers, 1984; Sanders and Bodenbender, 1994; Sanders, 1995; Hildebrand and Goslow, 2001).

Extant tree sloths exist in separate families, three-toed sloths (genus *Bradypus*) in Bradypodidae and two-toed sloths (genus *Choloepus*) along with extinct ground sloths in Megalonychidae (Hoos et al., 1996). Both two-toed and three-toed tree sloths demonstrate common placement, although there appears to be a large amount of variation in this trait in these taxa. Only two of seven *Bradypus* specimens demonstrate common placement, while the other five specimens range from -1 to +1. In *Choloepus*, three of eight specimens demonstrate common placement, while the other five range from -1 to +3.

Convergences among tree sloths, hominoids, and lorisids on certain postcranial morphologies are notable (Straus and Wislocki, 1932; Carleton, 1936; Cartmill and Milton, 1977; Mendel, 1979; Gebo, 1989; White, 1993; Shapiro et al., 2005). However, lorisids, which are reasonably well-sampled in this study (Table 4.1), are not characterized by common placement (although one specimen each of *Arctocebus* and *Nycticebus* demonstrate common placement; both species are +1 modally, as is *Perodicticus*; *Loris* is modal at +2). Similarities observed between hominoids and sloths, particularly in the vertebral column, are likely related to convergence on similar locomotor demands that require dorsostability of the vertebral column. Dorsostability acts to resist buckling and reduce bending moments at the intervertebral discs

during orthograde and antipronograde behaviors (Jungers, 1984; Ward, 1993; Sanders, 1995). Along with other hard and soft tissue traits (e.g., Ward, 1991, 1993; Nakatsukasa et al., 2007), this was achieved via reduction of the lumbar column and caudal migration of the diaphragmatic vertebra.

CONCLUSION

I question the utility of multiple definitions of TL vertebrae and suggest that the costal definition be retained as the sole criterion for identifying thoracic and lumbar vertebrae. The orientation of the zygapophyses should be treated as a separate morphology under a different named system; prediaphragmatic and postdiaphragmatic regions are suggested here and are comparable to thoracic and lumbar regions as defined by the presence or absence of ribs. This reduces confusion and conflation associated with multiple definitions of thoracic and lumbar vertebrae and eliminates the need to repeatedly explain, identify, and justify the use of one definition over the other. Both aspects of the vertebral column are functionally important and should be recognized separately as such.

Although extant hominoids are relatively unique among mammals in the common placement of diaphragmatic and last rib-bearing vertebrae, unique population-level patterns of variation in cranial and caudal displacement exist. In particular humans and chimpanzees are very similar to each other in a high degree of common placement (72% and 74%, respectively), a moderate degree of cranial displacement (25% and 23%, respectively), and a low frequency of caudal displacement (~3% each). This may represent a population-level synapomorphy of the

chimp-human clade, although a better understanding of these morphologies across human populations and in fossil hominins is necessary.

Unlike most mammals, including proconsuloids, cercopithecoids, and most other non-hominoid primates, which possess dorsomobile vertebral columns, hominoids are characterized by various mechanisms that prohibit sagittal spine movements and therefore promote dorsostability. Other mammals that are characterized by common placement or caudal displacement either converge with hominoids on antipronograde, suspensory behaviors (sloths) or possess dorsostable spines for specialized running (perissodactyls, large-bodied artiodactyls, and cavioids). Therefore, although dorsostability and common placement are uncommon and almost certainly derived, they have been achieved multiple times in one of two very different locomotor contexts.

TABLE 4.1. Non-catarrhine euarchontan mammals included in the comparative sample.

Platyrrhini			Tarsiiformes			Strepsirhini			Dermoptera			Scandentia		
Genus	No. species	N	Genus	No. species	N	Genus	No. species	N	Genus	No. species	N	Genus	No. species	N
Alouatta	1	21	Tarsius	2	3	Arctocebus	1	23	Cynocephalus	1	1	Ptilocercus	1	2
Aotus	1	9		2	3	Avahi	1	3		1	1	Tupaia	2	5
Ateles	3	32				Cheirogaleus	1	2					3	7
Brachyteles	1	3				Daubentonia	1	1						
Cacajao	2	10				Eulemur	3	8						
Callicebus	1	5				Galago	1	1						
Callithrix	1	10				Hapalemur	1	4						
Cebus	1	7				Indri	1	12						
Chiropotes	1	2				Lemur	1	8						
Lagothrix	1	26				Lepilemur	2	5						
Leontopithecus	1	2				Loris	1	4						
Saguinus	1	6				Nycticebus	1	7						
Saimiri	1	16				Otolemur	2	4						
						Perodicticus	1	13						
						Propithecus	2	13						
						Varecia	1	4						
13	16	149	1	2	3	16	21	112						

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TABLE 4.2. Descriptive statistics of number of lumbar and postdiaphragmatic vertebrae.

Species	N	Mean L	Mean P	t-stat.	p-value	Var. L	Var. P	F-stat.	p-value
H. sapiens	117	4.93	5.14	-3.654	<0.001	0.138	0.231	1.681	0.006
P. trog.	106	3.77	3.96	-2.698	0.005	0.205	0.302	1.477	0.050
P. paniscus	22	3.59	3.77	-1.366	0.095	0.229	0.160	1.432	0.417
G. gorilla	104	3.58	3.57	0.134	0.839	0.225	0.308	1.370	0.110
P. pygmaeus	81	3.94	3.79	1.749	0.068	0.238	0.393	1.654	0.026
H. lar	74	5.28	5.61	-3.449	<0.001	0.241	0.470	1.951	0.005
S. syndact.	33	4.48	4.77	-2.283	0.027	0.226	0.298	1.318	0.439
T. cristatus	88	6.98	8.98	-61.364	<0.001	0.034	0.060	1.768	0.008
P. hamad.	73	6.44	8.92	-30.178	<0.001	0.277	0.215	1.288	0.285

Means and variances of the number of lumbar (L) and postdiaphragmatic (P) vertebrae are shown, along with the results of t- and F-tests for differences in means and variances, respectively. Postdiaphragmatic regions are significantly longer than lumbar regions in all taxa except *G. gorilla* (p<0.10). Variances are also higher in taxa with postdiaphragmatic regions that are significantly different from lumbar regions.

TABLE 4.3. Position of the diaphragmatic vertebra relative to the last rib-bearing vertebra.

Species	%cr. shift	Avg. cr. shift	%ca. shift	Avg. ca. shift	Avg. shift	Total %shift	%common	Range
H. sapiens	24.79	0.24	3.42	-0.03	0.21	28.21	71.79	0-1 cr., 0-1 ca.
P. trog.	23.08	0.22	2.88	-0.03	0.19	25.96	74.04	0-1 cr., 0-1 ca.
P. paniscus	22.73	0.20	0.00	0.00	0.20	22.73	77.27	0-1 cr.
G. gorilla	8.49	0.08	9.43	-0.08	0.00	17.92	82.08	0-1.5 cr., 0-1 ca.
P. pygmaeus	4.88	0.05	20.73	-0.20	-0.15	25.61	74.39	0-1 cr., 0-1 ca.
H. lar	36.49	0.34	1.35	-0.01	0.34	37.84	62.16	0-1 cr., 0-0.5 ca.
S. syndact.	35.29	0.30	0.00	0.00	0.30	35.29	64.71	0-1 cr.
I. cristatus	100.0	2.01	0.00	0.00	2.01	100.0	0.00	1.5-3 cr.
P. hamadr	100.0	2.48	0.00	0.00	2.48	100.0	0.00	2-4 cr.

The position is shown as a cranial (cr.) or caudal (ca.) shift, in both average number of elements (Avg. shift) and frequency (% shift) in each species. The average shift (regardless of direction) is also shown, along with the total frequency of shifting (Total % shift) and frequency of common placement of diaphragmatic and last rib-bearing vertebrae (% common, representing no shift) in each species.

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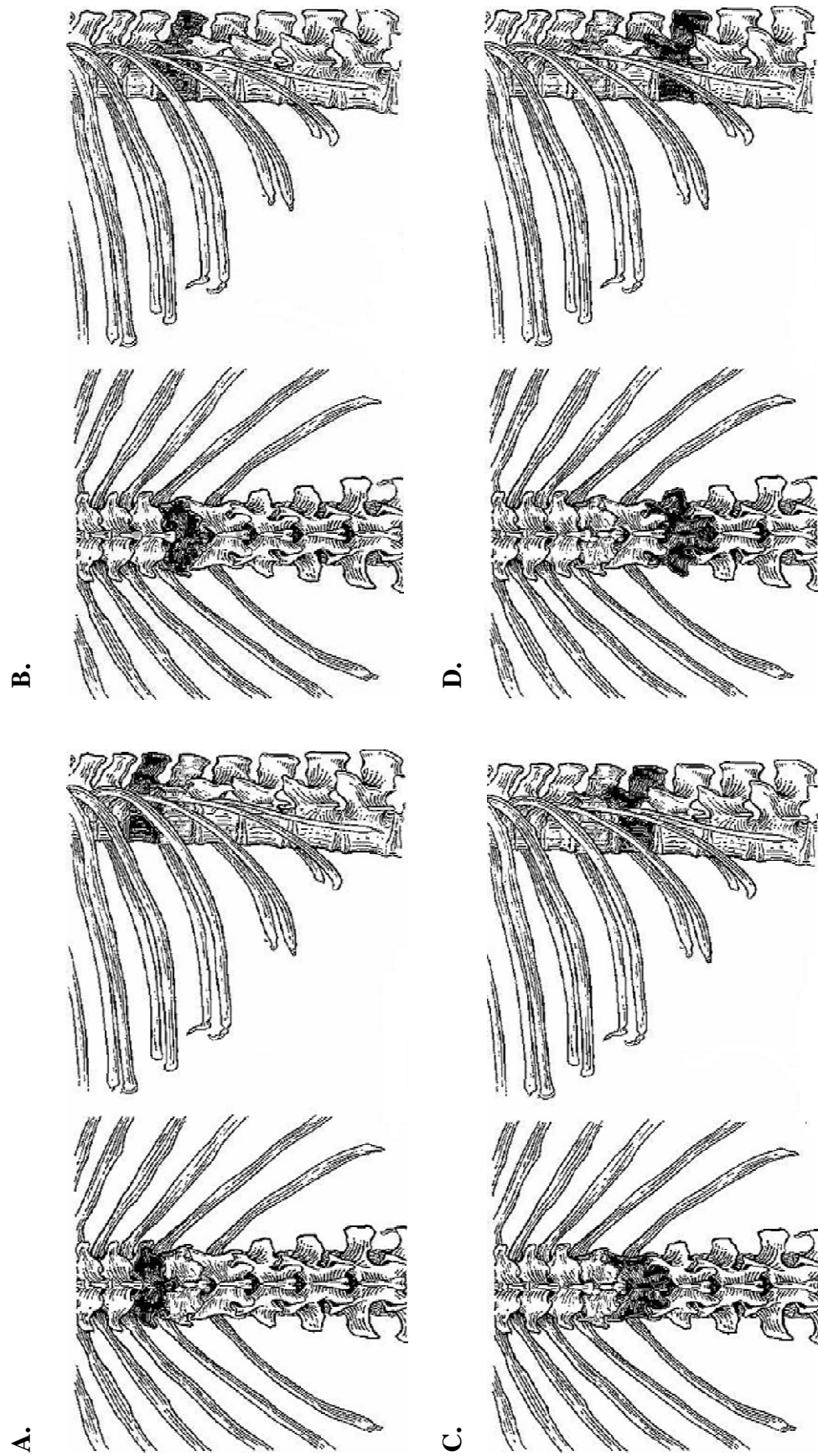
FIGURE 4.1. Illustration of common placement and cranial and caudal displacement. The diaphragmatic vertebra is shaded in black to demonstrate its position relative to the last rib-bearing vertebra. A.) Cranial displacement by two elements (+2), B.) Cranial displacement by one element (+1), C.) Common placement (0), D.) Caudal displacement by one element (-2). Modified from Erikson (1963).

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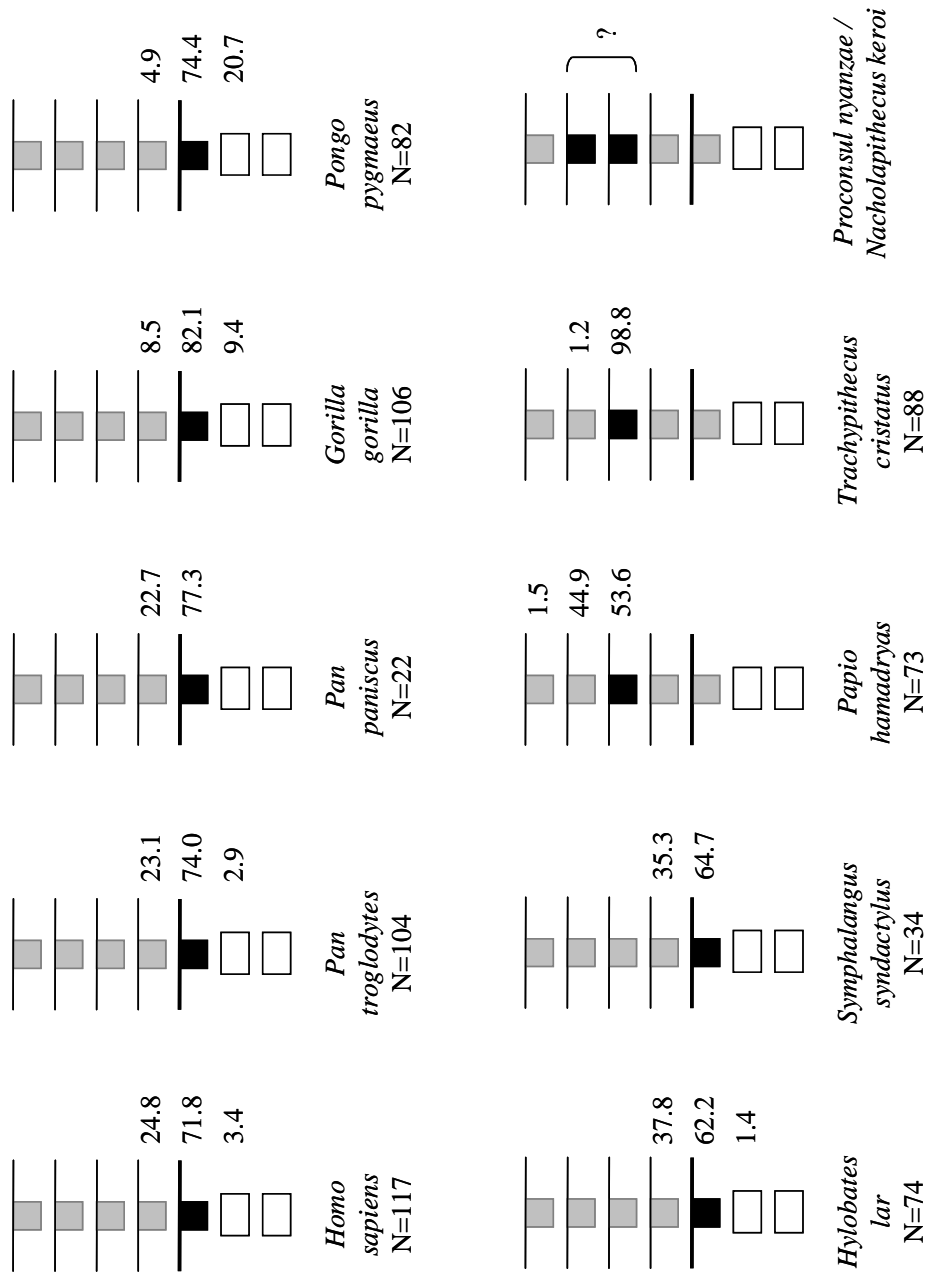
FIGURE 4.2. Intraspecific variation in placement of the diaphragmatic vertebra relative to the last rib-bearing vertebrae. Schematics symbolize the last five thoracic vertebrae (boxes with 'ribs') and the first two lumbar vertebrae ('unribbed' rectangles). The last set of ribs is bolded to symbolize the ultimate thoracic vertebra. For each species, the modal position of the diaphragmtic vertebra is shaded in black. Numbers to the right of each vertebral column represent frequencies (%) of types of placement observed in each species. *Proconsul* and *Nacholapithecus* are shown for comparison (see text).

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CHAPTER 4 REFERENCES

Abitbol, M. M., 1987. Evolution of the sacrum in hominoids. Am. J. Phys. Anthropol. 74, 65-81.

Aimi, M., 1994. Numerical variation of vertebrae in Japanese macaques, *Macaca fuscata*. Anthropol. Sci. 102, 1-10.

Allbrook, D.B., 1955. The East African vertebral column: a study in racial variability. Am. J. Phys. Anthropol. 13, 489-514.

Allen, J.A., 1917. The skeletal characters of *Scutisorex* Thomas. Bull. Am. Mus. Nat. Hist. 37, 769-784.

Arensburg, B., 1991. The vertebral column, thoracic cage and hyoid bone. In: O. Bar Yosef, B. Vandermeersch (Eds.), Le Squelette Mousterian de Kebara 2. Editions du C.N.R.S., Paris, pp. 113-146.

Argot, C., 2003. Functional-adaptive anatomy of the axial skeleton of some extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J. Morph. 255, 279-300.

Asher, R.J., Bennett, N., Lehmann, T., 2009. The new framework for understanding placental mammal evolution. BioEssays 31, 853-864.

Asher, R.J., Helgen, K.M., 2010. Nomenclature and placental mammal phylogeny. BMC Evol. Biol. 10, 102.

Asher, R.J., Lin, K.H., Kardjilov, N., Hautier, L., 2011. Variability and constraint in the mammalian vertebral column. J. Evol. Biol. 24, 1080-1090.

Barnes, E., 1994., Developmental Defects of the Axial Skeleton in Paleopathology. University of Colorado Press, Boulder, CO.

Benton, R.S., 1967. Morphological evidence for adaptations within the epaxial region of the primates. In: F. van der Hoeven (Ed.), The Baboon in Medical Research, Vol. II. University of Texas Press, Austin, pp. 201-216.

Berger, L.R., de Ruiter, D.J., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P.H.G.M., Kibii, J.M., 2010. *Australopithecus sediba*: a new species of *Homo*-like australopiths from South Africa. Science 328, 195-204.

Bornstein, P.E., Peterson, R.R., 1966. Numerical variation of the presacral vertebral column in three population groups in North America. Am. J. Phys. Anthropol. 25, 139-146.

Breit, S., Künzel, W., 2002. The diameter of the vertebral canal in dogs in cases of lumbosacral transitional vertebrae or numerical vertebral variations. Anat. Embryol. 205, 125-133.

Buchholtz, E.A., 2007. Modular development of the cetacean vertebral column. Evol. Dev. 9, 278-289.

Buchholtz, E.A., Schur, S.A., 2004. Vertebral osteology in Delphinidae (Cetacea). Zool. J. Linn. Soc. 140, 383-401.

Buchholtz, E.A., Wolkovich, E.M., Cleary, R.J., 2005. Vertebral osteology and complexity in *Lagenorhynchus acutus* (Delphinidae) with comparison to other delphinoid genera. Mar. Mamm. Sci. 21, 411-428.

Carleton, A.C., 1936. The limb-bones and vertebrae of the extinct lemurs of Madagascar. J. Zool. 106, 281-307.

Cartmill, M., Milton, K., 1977. The lorisiform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. Am. J. Phys. Anthropol. 47, 249-272.

Clauser, D., 1980. Functional and comparative anatomy of the primate spinal column: some locomotor and postural adaptations. Ph.D. dissertation, University of Wisconsin-Milwaukee.

Cook, D.C., Buikstra, J.E., DeRousseau, C.J., Johanson, D.C., 1983. Vertebral pathology in the Afar australopithecines. Am. J. Phys. Anthropol. 60, 83-101.

Cullinane, D.M., Aleper, D., 1998. The functional and biomechanical modifications of the spine of *Scutisorex somereni*, the hero shrew: spinal musculature. J. Zool. Lond. 244, 453-458.

Cullinane, D.M., Aleper, D., Bertram, J.E.A., 1998. The functional and biomechanical modifications of the spine of *Scutisorex somereni*, the hero shrew: skeletal scaling relationships. J. Zool. Lond. 244, 447-452.

Cullinane, D.M., Bertram, J.E.A., 2000. The mechanical behavior of a novel mammalian intervertebral joint. J. Anat. 197, 627-634.

Danforth, C.H., 1930. Numerical variation and homologies in vertebrae. Am. J. Phys. Anthropol. 14, 463-481.

Erikson, G., 1963. Brachiation in New World monkeys and in anthropoid apes. Symp. Zool. Soc. Lond. 10, 135-163.

Filler, A.G., 1986. Axial character seriation in mammals: an historical and morphological exploration of the origin, development, use, and current collapse of the homology paradigm. Ph.D. dissertation, Harvard University.

Flower, W.H., 1885. An Introduction to the Osteology of the Mammalia. MacMillan and Co: London.

Gambaryan, P.P., 1974. How Mammals Run. John Wiley and Sons, New York.

Gebo, D.L., 1989. Postcranial adaptation and evolution in Lorisidae. Primates 30, 347-367.

Giebel, C.G., 1853. Uber die Granze zwischen Brust- und Lendengegend in der Wirbelsaule der Saugetiere. Zeitschr ges Naturw. 1853 I, 261.

Giebel, C.G., 1900. Mammalia. In: H.G. Bronn (Ed.), Klassen und Ordnungen des Tierreichs, Bd. 6, Abt. 5., Leipzig.

Gingerich, P.D., ul-Haq, M., von Koenigswald, W., Sanders, W.J., Smith, B.H., Zalmout, I.S., 2009. New protocetid whale from the Middle Eocene of Pakistan: birth on land, precocial development, and sexual dimorphism. PLoS One 4, 4366.

Haeusler, M., Martelli, S.A., Boeni, T., 2002. Vertebrae numbers of the early hominid lumbar spine. J. Hum. Evol. 43, 621-643.

Halpert, A.P., Jenkins, F.A., Franks, H., 1987. Structure and scaling of the lumbar vertebrae in African bovids (Mammalia: Artiodactyla). J. Zool. Lond. 211, 239-258.

Hasebe, K., 1913. Die wirbelsaule der Japaner. Zeit. Morph. Anth. 15, 259-380.

Hildebrand, M., 1959. Motions of the running cheetah and horse. J. Mammal. 40, 481-495.

Hildebrand, M., 1995. Analysis of Vertebrate Structure, 4th Ed. Wiley, New York.

Hildebrand, M., Goslow, G., 2001. Analysis of Vertebrate Structure, 5th Ed. Wiley, New York.

Hoos, M., Dilling, A., Currant, A., Paabo, S., 1996. Molecular phylogeny of the extinct ground sloth *Mylodon darwinii*. Proc. Natl. Acad. Sci. USA 93, 181-185.

Hurov, J.R., 1987. Terrestrial locomotion and back anatomy in vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*). Am. J. Primatol. 13, 297-311.

Ishida, H., Kunimatsu, Y., Takano, T., Nakano, Y., Nakatsukasa, M., 2004. *Nacholapithecus* skeleton from the Middle Miocene of Kenya. J. Hum. Evol. 46, 69-103.

Jenkins, F., 1971. The postcranial skeleton of African cynodonts. Bull. Peabody Mus. Nat. Hist. 36, 1-216.

Johanson, D.C., Lovejoy, C.O., Kimbel, W.H., White, T.D., Ward, S.C., Bush, M.E., Latimer, B.M., Coppens, Y., 1982. Morphology of the Pliocene partial hominid skeleton (A.L. 288-1) from the Hadar Formation, Ethiopia. Am. J. Phys. Anthropol. 57, 403-452.

Jungers, W.L., 1984. Scaling of the hominoid locomotor skeleton with special reference to lesser apes. In: H. Preuschoft, D.J. Chivers, W.Y. Brockelman, N. Creel (Eds.), The Lesser Apes: Evolutionary and Behavioral Biology. Edinburgh University Press, Edinburgh, pp. 146-169.

Keith, A., 1903. The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates. J. Anat. Physiol. 37, 18-40.

Keith, A., 1923. Man's posture: its evolution and disorders. Brit. Med. J. 1, 451-454, 499-502, 545-548, 587-590, 624-626, 669-672.

Kimbel, W.H., Delezene, L.K., 2009. "Lucy" redux: a review of research on *Australopithecus afarensis*. Y. Phys. Anthropol. 52, 2-48.

Lanier, R.R., 1939. The presacral vertebrae of American white and negro males. Am. J. Phys. Anthropol. 25, 341-420.

Latimer, B., Ward, C.V., 1993. The thoracic and lumbar vertebrae. In: A. Walker, R. Leakey (Eds.), The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 266-293.

Lovejoy, C.O., 2005. The natural history of human gait and posture Part 1. Spine and pelvis. Gait Posture 21, 95-112.

Lovejoy, C.O., McCollum, M.A., 2010. Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip–bent-knee gait. Phil. Trans. R. Soc. B 365, 3289-3299.

Lovejoy, C.O., Suwa, G., Simpson, S.W., Matternes, J.H., White, T.D., 2009. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. Science 326, 100-106.

Lucae, J.C.G., 1867. Die Robbe und die Otter. Frankfurt am Main.

McCollum, M.A., Rosenman, B.A., Suwa, G., Meindl, R.S., Lovejoy, C.O., 2010. The vertebral formula of the last common ancestor of African apes and humans. J. Exp. Biol. 314B, 123-134.

Mendel, F.C., 1979. The wrist joint of two-toed sloths and its relevance to brachiating adaptations in the Hominoidea. J. Morphol. 162, 413-424.

Nakatsukasa, M., Hirose, Y., 2003. Scaling of lumbar vertebrae in anthropoids and implications for evolution of the hominoid axial skeleton. Primates 44, 127-135.

Nakatsukasa, M., Kunimatsu, Y., 2009. *Nacholapithecus* and its importance for understanding hominoid evolution. Evol. Anthropol. 18, 103-119.

Nakatsukasa, M., Kunimatsu, Y., Nakano, Y., Ishida, H., 2007. Vertebral morphology of *Nacholapithecus kerioi* based on KNM-BG 35250. J. Hum. Evol. 52, 347-369.

Narita, Y., Kuratani, S., 2005. Evolution of the vertebral formulae in mammals: a perspective on developmental constraints. J. Exp. Zool. 304B, 91-106.

Odgers, P.N.B., The lumbar and lumbo-sacral diarthrodial joints. J. Anat. 67, 301-317.

Ogilvie, M.D., Hilton, C.E., Ogilvie, C.D., 1998. Lumbar anomalies in the Shanidar 3 Neandertal. J. Hum. Evol. 35, 597-610.

Pilbeam, D., 2004. The anthropoid postcranial axial skeleton: comments on development, variation, and evolution. J. Exp. Biol. 302B, 241-267.

Pridmore, P.A., 1992. Trunk movements during locomotion in the marsupial *Monodelphis domestica* (Didelphidae). J. Morph. 211, 137-146.

Robinson, J., 1972. Early hominid posture and locomotion. University of Chicago Press, Chicago.

Rockwell, H., Evans, F.G., Pheasant, H.C., 1938. The comparative morphology of the vertebrate spinal column. Its form as related to function. J. Morphol. 63, 87–117.

Rosenman, B.A., 2008. Triangulating the evolution of the vertebral column in the last common ancestor: thoracolumbar transverse process homology in the Hominoidea. Ph,D. dissertation, Kent State University.

Rowe, D.L., Honeycutt, R.L., 2002. Phylogenetic relationships, ecological correlates, and molecular evolution within the Cavioidea (Mammalia, Rodentia). Mol. Biol. Evol. 19, 236-277.

Russo, G.A., 2010. Prezygapophyseal articular facet shape in the catarrhine thoracolumbar vertebral column. Am. J. Phys. Anthropol. 142, 600-612.

Sánchez-Villagra, M.R., Narita, Y., Kuratani, S., 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. Syst. Biodiv. 5, 1-7.

Sanders, W.J., 1995. Function, allometry, and the evolution of the australopithecine lower precaudal spine. Ph.D. dissertation, New York University.

Sanders, W.J., Bodenbender, B.E., 1994. Morphometric analysis of lumbar vertebra UMP 67-28: implications for spinal function and phylogeny of the Miocene Moroto hominoid. J. Hum. Evol. 26, 203-237.

Schultz, A.H., 1930. The skeleton of the trunk and limbs of higher primates. Hum. Biol. 2, 303-438.

Schultz, A.H., 1961. Vertebral column and thorax. Primatologica 5, 1–66.

Schultz, A.H., Straus, W.L., 1945. The numbers of vertebrae in primates. Proc. Am. Phil. Soc. 89, 601-626.

Shapiro, L.J., 1991. Functional morphology of the primate spine with special reference to orthograde posture and bipedal locomotion. Ph.D. dissertation, SUNY Stony Brook.

Shapiro, L., 1993. Functional morphology of the vertebral column in primates. In: D.L. Gebo (Ed.), Postcranial Adaptation in Nonhuman Primates. Northern Illinois University Press, DeKalb, IL.

Shapiro, L., 1995. Functional morphology of indrid lumbar vertebrae. Am. J. Phys. Anthropol. 98, 323-342.

Shapiro, L.J., Seiffert, C.V.M., Godfrey, L.R., Jungers, W.L., Simons, E.L., Randria, G.F.N., 2005. Morphometric analysis of lumbar vertebrae in extinct Malagasy strepsirrhines. Am. J. Phys. Anthropol. 128, 823-839.

Slijper, E.J., 1946. Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. Verh. Kon. Ned. Akad. Wet. (Tweede Sectie) 42, 1-128.

Slijper, E.J., 1947. Observations on the vertebral column of the domestic animals. Vet. Journal 103, 376-387.

Stevens, L.S., 2004. Morphological variation in the hominoid vertebral column. Master's thesis, Kent State University.

Stewart, T.D., 1932. The vertebral column of the Eskimo. Am. J. Phys. Anthropol. 17, 123-136.

Straus, W.L., Wislocki, G.B., 1942. On certain similarities between sloths and sloth lemurs. Bull. Mus. Comp. Zool. (Harvard) 74, 45-56.

Stromer von Reichenbach, E., 1902. Die Wirbel der Land-Raubtiere. Zoologica 15, 1.

Struthers, J., 1874. On variations of the vertebrae and ribs in man. J. Anat. Phys. 9, 17-96.

Struthers, J., 1892. On the articular processes of the vertebrae in the gorilla compared with those in man, and on cost-vertebral variation in the gorilla. J. Anat. Phys. 27, 131-138.

Tague, R.G., 2009. High assimilation of the sacrum in a sample of American skeletons: prevalence, pelvic size, and obstetrical and evolutionary implications. Am. J. Phys. Anthropol. 138, 429-438.

Todd, T.W., 1922. Numerical significance in the thoracolumbar vertebrae of the Mammalia. Anat. Rec. 24, 261-286.

Toussaint, M., Macho, G.A., Tobias, P.V., Partridge, T.C., Hughes, A.R., 2003. The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa. S. Af. J. Sci. 99, 215-223.

Walker, A., Leakey, R., 1993. The postcranial bones. In: A. Walker, R. Leakey (Eds.), The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 95-160.

Ward, C.V., 1993. Torso morphology and locomotion in *Proconsul nyanzae*. Am. J. Phys. Anthropol. 92, 291-328.

Washburn, S.L., 1963. Behavior and human evolution. In: S.L. Washburn (Ed.). Classification and Human Evolution. Aldine, Chicago, pp. 190-203.

Washburn, S.L., Buettner-Janusch, J., 1952. The definition of thoracic and lumbar vertebrae. Am. J. Phys. Anthropol. Suppl. 10, 251-252.

Welcker, H., 1881. Die nuee anatomische Anstalt zu Halle durch einen Vortrag uber Wirbelsaule und Becken. Arch. Anat. Physiol Anat. Abth., 161-192.

Wellik, D.M., 2007. *Hox* patterning of the vertebrate axial skeleton. Dev. Dyn. 236, 2454-2463.

Wellik, D.M., Capecchi, M.R., 2003. *Hox10* and *Hox11* genes are required to globally pattern the mammalian skeleton. Science 301, 363-367.

White, J.L., 1993. Indicators of locomotor habits in xenarthrans: evidence for locomotor heterogeneity among fossil sloths. J. Vert. Paleontol. 13, 230-242.

CHAPTER 5

CONCLUSION

Overview of concepts and hypotheses

Homology has been described as "the central concept for *all* of biology" (Wake, 1994:268; see also Hall, 1994). Julian Huxley (1928) identified it as "morphology's central concept." Indeed, homology and its counterpart, homoplasy, underlie the evolution of any and all phenotypes. Descent with modification implies a continuity of information and underlying commonality of structure (Bolker and Raff, 1996). This is the core of homology and evolution in general. Homoplasies, or similar structures of distinct evolutionary origins, arise through independent evolution (via convergence or parallelism) or reversal (Wake et al., 2011). Because evolution is a process of descent (over time and generations, intraspecific variation is converted into interspecific variation), a phylogenetic framework is required to differentiate between homology and homoplasy (Bolker and Raff, 1996; Begun, 2007; Wake et al., 2011). Fortunately, the field of molecular phylogenetics has made available robust, well-supported phylogenies for many branches of life (e.g., http://timetree.org/; Hedges et al., 2006). Homoplasies, however, are not sought – they are identified on a phylogeny when common descent (i.e., homology) fails to account for them (Wake et al., 2011); nevertheless, homoplasy is commonplace in evolution (Wake et al., 2011; Wood and Harrison, 2011).

Drastically different degrees of homoplasy have recently been proposed to account for the evolution of shared or similar postcranial morphologies in hominoid primates (see Chapter 1). Some invoke a predominate role for homology (Benefit and McCrossin, 1995; Pilbeam, 1996;

Harrison and Rook, 1997; MacLatchy et al., 2000; Young, 2003; MacLatchy, 2004; Pilbeam and

Young, 2004), suggesting that many of these features are synapomorphies (shared, derived traits)

of the crown hominoid clade, while others call for extreme levels of homoplasy (Larson, 1998;

Ward, 2007; Moyà-Solà et al., 2004, 2005; Begun and Ward, 2005; Almécija et al., 2007, 2009;

Lovejoy et al., 2009*a*; Alba et al., 2010). These scenarios have obvious implications for the

evolution of locomotor and other positional behaviors in extant hominoids, including hominins.

At the two extremes of homology (Pilbeam and Young, 2004) and homoplasy (Lovejoy et al.,

2009*a*), bipedalism is set to emerge in very different locomotor contexts from drastically

disparate evolutionary histories. In the former, hominins would evolve bipedalism from a

knuckle-walking (e.g., Pilbeam, 1996) or otherwise African ape-like locomotor ancestry (e.g.,

vertical climbing and suspensory behavior). On the other hand, Lovejoy et al. (2009*a*:104) argue

that hominins evolved from a primitive ancestor that practiced "above-branch quadrupedal

palmigrady" and "advanced bridging" behaviors. These authors specifically rule out the roles of

knuckle-walking, vertical climbing, and suspensory behavior in the evolution of bipedalism (see

Lovejoy et al., 2009*a,b,c*; White et al., 2009).

Summary and synthesis of findings

In this dissertation, I approach this problem by testing scenarios of hominoid vertebral

column evolution (Haeusler et al., 2002; Pilbeam, 2004; McCollum et al., 2010) to determine the

likelihood of homoplasy in this important region. The vertebral column plays a central role in

posture and locomotion; as such, its evolution is fundamental to and instrumental in the

emergence of novel positional behaviors (i.e., orthograde and bipedalism) and their

morphological correlates. In Chapter 1, I review recent hypotheses on the role of homology and

homoplasy in the evolution of hominoid postcrania based on interpretations of fossil and extant hominoids. I then discuss current models of vertebral column evolution in this context.

In Chapter 2, I update the Schultz-Pilbeam-McCollum dataset with many new records of vertebral formulae and place hominoids in a larger mammalian framework. This approach allows for the reconstruction of ancestral vertebral profiles throughout mammalian evolution and the determination of the uniqueness of the hominoid vertebral formulae amongst other primates and mammals in general. I conclude that an "African ape-like" vertebral profile evolved in the ancestor of hominids and persisted to the hominin-panin last common ancestor. This profile was modified, along with other morphological aspects of the vertebral column (Shapiro, 1993; Sanders, 1998; Lovejoy, 2005), during hominin evolution. The hominoid condition of a reduced trunk (combined thoracic and lumbar regions) is unique among primates and relatively unique among mammals in general. Although reduced trunk and lumbar regions are found in some other mammals (namely, armadillos and giant anteaters), only the vertebral profile of giant pandas converge with that of hominoids. The uniqueness of hominoid vertebral formulae further supports the homology of reduced lumbar regions in hominoids, and therefore a short-back, short-trunk model of hominoid vertebral evolution and hominin emergence.

In Chapter 3, I calculate diversity and similarity indices for the full extent of vertebral formulae observed in hominoid and other anthropoid taxa and interpret them in the context of long- (McCollum et al., 2010) and short-back (Pilbeam, 2004) models of vertebral formula evolution. These models imply very different pattern of evolution, patterns that should be detectable in variation observed among and between extant hominoids. Under the long-back scenario, in particular, we should expect to see reduced variation in vertebral formulae associated with adaptively driven homoplasy (independently and repeatedly reduced lumbar regions) and

the relatively strong directional selection presumably associated with it, especially in closely related taxa that diverged relatively recently (e.g., *Pan troglodytes* and *Pan paniscus*). Instead, high amounts of variation are observed among all hominoids except humans and eastern gorillas, taxa that have likely experienced strong stabilizing selection on vertebral formulae associated with locomotor and habitat specializations. Furthermore, analyses of interspecific similarity support an evolutionary scenario in which the vertebral formulae observed in gorillas and chimpanzees represent a reasonable approximation of the ancestral condition for hominines, from which eastern gorillas, humans, and bonobos derived their unique vertebral profiles.

In Chapter 4, I examine the association between last rib-bearing (i.e., last thoracic) and diaphragmatic vertebrae in hominoids and other mammals. The diaphragmatic vertebra marks the transition in vertebral articular facet (zygapophysis) orientation, which either resists (prediaphragmatic) or allows (postdiaphragmatic) trunk movement in the sagittal plane (i.e., flexion and extension). Therefore, its position represents an alternative and complementary strategy of dorsostability or dorsomobility to changes in the number and morphology of lumbar vertebrae. Unlike most mammals, which have dorsomobile spines (long lumbar columns and cranially-placed diaphragmatic vertebrae) for running and leaping, hominoids possess dorsostable spines (short lumbar columns and caudally-placed diaphragmatic vertebrae). Dorsostability via caudal placement of the diaphragmatic vertebra has evolved several times in mammals for two very different reasons – orthogrady and antipronogrady in hominoids and sloths, and specialized, stiff-spined running in perissodactyls, large-bodied artiodactyls, and cavioids. Within hominoids, patterns of variation are strikingly similar in humans and chimpanzees (comparable to gibbons and siamangs), supporting the homology of this feature and that of reduced lumbar regions in hominoids in general.

Together, these findings provide strong support for a short-back model of hominin evolution, a view that has been supported in the past (e.g., Keith, 1903; Pilbeam, 2004) and receives support from other studies of vertebral morphology (e.g., Lovejoy, 2005). It is suggested that hominins evolved bipedalism in the context of an African ape-like positional behavioral repertoire, likely involving suspensory behavior and vertical climbing in the trees, knuckle-walking on the ground, and facultative bipedal posture and locomotion in both the arboreal and terrestrial milieu. It bears mentioning and reinforcing here that a knuckle-walking, African ape-like ancestor does not preclude the role of arboreal positional behaviors (i.e., vertical climbing, suspension, arboreal bipedalism) in the evolution of bipedalism (Richmond et al., 2001; Begun et al., 2007; Williams, 2010). The short-back model of vertebral column evolution also implies a predominant role of homology in the evolution of the hominoid vertebral formulae. Therefore, although homoplasy is clearly implicated in some aspects of hominoid evolution (e.g., Andrews and Pilbeam, 1996; Begun and Kordos, 1997; Nakatsukasa and Kunimatsu, 2009; Wood and Harrison, 2011), it does not play a major role in the evolution of the numerical composition of the hominoid vertebral column.

This scenario is incompatible with that proposed in the recent interpretation of *Ardipithecus ramidus* (Lovejoy et al., 2009*a,b,c*; White et al., 2009; Lovejoy and McCollum, 2010). The phylogenetic affinities of *Ardipithecus* have been questioned (Harrison, 2010; Sarmiento, 2010; Wood and Harrison, 2011), which, if correct, would invalidate the specific claims of extensive homoplasy outlined in the *Ardipithecus* papers, but would also require homoplasy between *Ardipithecus* and hominins in other features (White et al., 2010). In particular, morphologies of the hip (Lovejoy et al., 2009*c*) and dentition (Suwa et al., 2009; White et al., 2010) of *Ardipithecus* would be convergent with those of hominins, features that

were used to erroneously link *Oreopithecus* and "*Ramapithecus*" (i.e., *Sivapithecus*) to the hominin lineage in the past (reviewed in Wood and Harrison, 2011). However, an alternative interpretation is proposed by Begun (2010:1009) – that the morphological pattern observed in *Ardipithecus* is entirely compatible with an ape-like, suspensory ancestry, and the interpretation of extreme homoplasy in extant hominoid postcrania is unnecessary; moreover, "*Ardipithecus* actually fits in well as an intermediate genus between arboreal, suspensory, knuckle-walking chimpanzee-like common ancestors and our fully bipedal more direct ancestors" (see also Young et al., 2010). This is directly opposed to the interpretation provided in Lovejoy et al. (2009*a*:73): "It [*Ardipithecus*] is so rife with anatomical surprises that no one could have imagined it without direct fossil evidence."

Any of these alternatives – that *Ardipithecus* is not a hominin, that *Ardipithecus* is a hominin that fits well with what we should expect for a panin-hominin common ancestor, or that *Ardipithecus* challenges so much of what can and have learned about hominin evolution from studies our closest living relatives that "We can no longer rely on homologies with African apes for accounts of our origins" (Lovejoy, 2009:74e1) – are possible; however, the latter is not compatible with the model of vertebral evolution supported in this study. Since the vertebral formula and numerical composition of the lumbar column of *Ardipithecus* is unknown (indeed, the interpretation of six lumbar vertebrae in *Ardipithecus* is entirely theoretical; see Lovejoy and McCollum, 2010), this does not have any bearing on the *Ardipithecus* skeleton itself, which in fact could have possessed a vertebral formula not unlike that proposed here for early hominins.

This study has more limited implications for the hypothesis that vertical climbing and suspensory behaviors were decoupled in hominoid evolution, the former resulting in orthogrady and the latter evolving independently in extant hominoid lineages (Moyà-Solà et al., 2004, 2005;

Almécija et al., 2007, 2009; Alba et al., 2010). This hypothesis is based on short phalanges in *Pierolapithecus* (Moyà-Solà et al., 2004, 2005; Almécija et al., 2009), short and robust metacarpals in *Hispanopithecus* (Moyà-Solà et al., 1996; Almécija et al., 2007), and purported features related to palmigrady (e.g., dorsally constricted metacarpal heads and dorsal extension of the proximal articular surface of phalanges) in both taxa. Crompton and colleagues (Crompton et al., 2003, 2008, 2010; Crompton and Thorpe, 2007; Thorpe et al., 2007) propose a similar hypothesis based not on the interpretation of fossil taxa, but on orangutan positional behavior. Like Moyà-Solà and colleagues, they argue that orthogrady evolved initially in hominoid evolution and independently of suspensory behavior, thus requiring the independent acquisition of suspensory-related morphologies (seemingly restricted to the hands in both sets of hypotheses) in extant genera.

However, these hypotheses are questionable on several grounds: 1) Deane and Begun (2008, 2010) found the phalanges of *Pierolapithecus* to be consistent in length, curvature, and secondary shaft features with below-branch suspensory behavior (but see Alba et al., 2010). 2) Begun's (2009:805-806) interpretation of the metacarpophalangeal joint in *Hispanopithecus* is that it is unique and unlike that of palmigrade monkeys, instead reflecting a wide range of flexed postures rather than hyperextension associated with palmigrady. 3) To these ends, it bears mentioning that this research group (Almécija, Alba, Moyà-Solà, and colleagues) has consistently downplayed the significance of suspensory traits, and even suggested that the hand of *Oreopithecus* is short and therefore "inconsistent with extensive suspensory adaptations in this taxon" (Alba et al., 2011:11; see also Moyà-Solà et al., 1999; Köhler and Moyà-Solà, 2003; contra Susman, 2004 and references therein). 4) Finally, the underlying hypothesis that orthogrady and suspensory behavior are dissociated is far from established and will require

further analyses of fossil and extant hominoid postcrania. Future discoveries and functional and phylogenetic analyses of contentious Neogene taxa such as *Sivapithecus*, *Morotopithecus*, *Ardipithecus ramidus*, *Ardipithecus kadabba* (Haile-Selassie, 2001; Begun, 2004; Haile-Selassie et al., 2009), *Orrorin tugenensis* (Senut et al., 2001; Pickford et al., 2002; Galik et al., 2004; Eckhardt et al., 2005; Ohman et al., 2005; Richmond and Jungers, 2008) and *Sahelanthropus tchadensis* (Brunet, 2002, Brunet et al., 2002; Wolpoff et al., 2002, 2006; Zollikofer et al., 2005; Senut, 2007) will no doubt contribute to our understanding of hominoid postcranial evolution and hominin origins.

Future directions

As explained in Chapter 1, this study began as a broader project on the evolution of the vertebral column, including not only vertebral formulae and the relationship between the last thoracic and diaphragmatic vertebrae, but also other vertebral morphologies. As such, upwards of 200 (depending on the number of vertebrae possessed by a individual specimen) linear measurements and a number of qualitative observations were collected on the vertebral columns of 700 catarrhine (seven hominoid and two cercopithecoid) specimens. These data were used in a study of morphological integration in the hominoid vertebral column (Williams, 2009) and will be utilized in future studies.

This dissertation focused on the numerical composition of the vertebral column, with implications for its length (i.e., "short" versus "long" backs); however, individual lengths of the vertebra that make up the column also contribute to its overall length and the length of its regions. Since lengths of every vertebra, including the sacrum, were measured for this study, a future one will focus on this quantitative aspect of region lengths and its implications for the

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evolution of the hominoid vertebral column. Hominoids have reduced the length of individual lumbar vertebrae in addition to their number (e.g., Keith, 1903; Erikson, 1963; Benton, 1967; Rose, 1975; Clauser, 1980), but well-sampled interspecific comparisons within hominoids are few and intraspecific studies are lacking altogether. Estimation of the variability and evolvability (Houle, 1992; Hansen and Houle, 2008) of vertebral region lengths and other vertebral morphologies (e.g., lumbar transverse process position) would be major contributions to our understanding of the evolution of the vertebral column.

Finally, the narrowed focus on vertebral formulae in this dissertation actually allowed for a broadened phylogenetic perspective, which became an integral part of the study. Mammals that converge with hominoids on vertebral and other skeletal traits are of particular interest, comparative studies on which may contribute to our understanding of hominoid evolution. Among primates, atelines, lorisids, and subfossil lemurs are convergent on some aspects of hominoid postcranial morphology and positional behavior, as are sloths. The giant panda presents an unexpected convergence with hominoids in its vertebral profile. Like hominoids, giant pandas also possess a reduced trunk and lumbar column. A comparative study of hominoid and ursid positional behaviors and postcranial morphologies with a special focus on the vertebral column may or may not elucidate adaptive explanations for this intriguing case of convergence.

CHAPTER 5 REFERENCES

Alba, D.M., Almécija, S., Moyà-Solà, S., 2010. Locomotor inferences in *Pierolapithecus* and *Hispanopithecus*: reply to Deane and Begun (2008). J. Hum. Evol. 59, 143-149.

Alba, D.M., Moyà-Solà, S., Almécija, S., 2011. A partial hominoid humerus from the Middle Miocene of Castell de Barberá (Vallès-Penedès Basin, Catalonia, Spain). Am. J. Phys. Anthropol. 144, 365-381.

Almécija, S., Alba, D.M., Moyà-Solà, S., 2009. *Pierolapithecus* and the functional morpohlogy of Miocene ape hand phalanges: paleobiolocal and evolutionary implications. J. Hum. Evol. 57, 284-297.

Almécija, S., Alba, D.M., Moyà-Solà, S., Köhler, M., 2007. Orang-like manual adaptations in the fossil hominoid *Hispanopithecus laietanus*: first steps towards great ape suspensory behaviours. Proc. R. Soc. B 274, 2375-2384.

Andrews, P., Pilbeam, D., 1996. The nature of the evidence. Nature 379, 123-124.

Begun, D.R., 2004. The earliest hominins – is less more? Science 303, 1478-1480.

Begun, D.R., 2007. How to identify (as opposed to define) a homoplasy: examples from fossils and living great apes. J. Hum. Evol. 52, 559-572.

Begun, D.R., 2009. Dryopithecins, Darwin, de Bonis, and the European origin of the African apes and human clade. Geodiversitas 31, 789-816.

Begun, D.R., 2010. Miocene hominids and the origins of the African apes and humans. Annu. Rev. Anthropol. 39, 67-84.

Begun, D.R., Kordos, L., 1997. Phyletic affinities and functional convergence in Dryopithecus and other Miocene and living hominoids. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 291-316.

Begun, D.R., Richmond, R.G., Strait, D.S., 2007. Comment on "Origin of human bipedalism as an adaptation for locomotion on flexible branches". Science 318, 1066d.

Begun, D.R., Ward, C.V., 2005. Comment on "*Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. Science 308, 203c.

Benefit, B.R., McCrossin, M.L., 1995. Miocene hominoids and hominid origins. Annu. Rev. Anthropol. 24, 237-256.

Benton, R.S., 1967. Morphological evidence for adaptations within the epaxial region of the primates. In: F. van der Hoeven (Ed.), The Baboon in Medical Research, Vol. II. University of Texas Press, Austin, pp. 201-216.

Bolker, J.A., Raff, R.A., 1996. Developmental genetics and traditional homology. BioEssays 18, 489-494.

Brunet, M., 2002. Reply. Nature 419, 582.

Brunet, M., Guy, F., Pilbeam, D., Mackaye, H.T., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Bolsserie, J.-R., de Bonis, L., Coppens Y., Dejax, J., Denys, C., Duringer, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Campomanes, P.P., Ponce de Leon, M., Rage, J.-C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A., Zollikofer, C., 2002. A new hominid from the Upper Miocene of Chad, Central Africa. Nature 418, 145-151.

Clauser, D., 1980. Functional and comparative anatomy of the primate spinal column: some locomotor and postural adaptations. Ph.D. dissertation, University of Wisconsin-Milwaukee.

Crompton, R.H., Sellers, W.I., Thorpe, S.K.S., 2010. Arboreality, terrestriality and bipedalism. Phil. Trans. R. Soc. B 365, 3301-3314.

Crompton, R.H., Thorpe, S.K.S., 2007. Response to comment on "Origin of human bipedalism as an adaptation for locomotion on flexible branches". Science 318, 1066e.

Crompton, R.H., Thorpe, S., Welite, W., Yu, L., Payne, R., Savage, R., Carey, T., Aerts, P., Elsacker, V., Hofstetter, A., Günther, M., Richardson, J., 2003. The biomechanical evolution of erect bipedality. Cour. Forsch.-Inst. Seneckenberg 243, 135-146.

Crompton, R.H., Vereecke, E.E., Thorpe, S.K.S., 2008. Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. J. Anat. 212, 501-543.

Deane, A.S., Begun, D.R., 2008. Broken fingers: retesting locomotor hypotheses for fossil hominoids using fragmentary proximal phalanges and high-resolution polynomial curve fitting (HR-PCF). J. Hum. Evol. 55, 691-701.

Deane, A.S., Begun, D.R., 2010. *Pierolapithecus* locomotor adaptations: a reply to Alba et al.'s comment on Deane and Begun (2008). J. Hum. Evol. 59, 150-154.

Eckhardt, R.B., Galik, K., Kuperavage, A.J., 2005. Response. Science 307, 845.

Erikson, G., 1963. Brachiation in New World monkeys and in anthropoid apes. Symp. Zool. Soc. Lond. 10, 135-163.

Galik, K., Senut, B., Pickford, M., Gommery, D., Treil, J., Kuperavage, A.J., Eckhardt, R.B., 2004. External and internal morphology of BAR 1002'00 *Orrorin tugenensis* femur. Science 305, 1450-1453.

Haeusler M, Martelli SA, Boeni T. 2002. Vertebrae numbers of the early hominid lumbar spine. J. Hum. Evol. 43:621-643.

Haile-Selassie, Y., 2001. Late Miocene hominids from the Middle Awash, Ethiopia. Nature 412, 178-181.

Haile-Selassie, Y., Suwa, G., White, T., 2009. Hominidae. In: Y. Haile-Selassie, G. WoldeGabriel (Eds.), *Ardipithecus Kadabba*: Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley, pp. 159-236.

Hall, B.K., 1994. Homology: The Hierarchical Basis of Comparative Biology. Academic Press, San Diego, CA.

Hansen, T.F., Houle, D., 2008. Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. 21, 1201-1219.

Harrison, T., 2010. Apes among the tangled branches of human origins. Science 327, 532-534.

Harrison, T., Rook, L., 1997. Enigmatic anthropoid or misunderstood ape: the phylogenetic status of *Oreopithecus bambolii* reconsidered. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 327-362.

Hedges, S.B., Dudley, J., Kumar, S., 2006. TimeTree: a public knowledge-base of divergence times among organisms. Bioinformatics 22, 2971-2972.

Houle, D., 1992. Comparing evolvability and variability of quantitative traits. Genetics 130, 195-204.

Huxley, J., 1928. Introduction. In: G.R. De Beer (Ed.), Vertebrate Zoology. Macmillan Co., New York.

Keith, A., 1903. The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates. J. Anat. Physiol. 37, 18-40.

Köhler, M., Moyà-Solà, S., 2003. Understanding the enigmatic ape *Oreopithecus bambolii*. Cour. Forsch.-Inst. Senckenberg 243, 111-123.

Lovejoy, C.O., 2005. The natural history of human gait and posture Part 1. Spine and pelvis. Gait Posture 21, 95-112.

Lovejoy, C.O., 2009. Reexamining human origins in light of *Ardipithecus ramidus*. Science 326, 74.

Lovejoy, C.O., McCollum, M.A., 2010. Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip–bent-knee gait. Phil. Trans. R. Soc. B 365, 3289-3299.

Lovejoy, C.O., Suwa, G., Simpson, S.W., Matternes, J.H., White, T.D., 2009*a*. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. Science 326, 73, 100-106.

Lovejoy, C.O., Simpson, S.W., White, TD., Asfaw, B., Suwa, G., 2009*b*. Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. Science 326, 70.

Lovejoy, C.O., Suwa, G., Spurlock, L., Asfaw, B, White, T.D., 2009*c*. The pelvis and femur of *Ardipithecus ramidus*: the emergence of upright walking. Science 326: 71.

MacLatchy, L., 2004. The oldest ape. Evol. Anthropol. 13, 90-103.

MacLatchy, L., Gebo, D., Kityo, R., Pilbeam, D., 2000. Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. J. Hum. Evol. 39, 159-183.

McCollum, M.A., Rosenman, B.A., Suwa, G., Meindl, R.S., Lovejoy, C.O., 2010. The vertebral formula of the last common ancestor of African apes and humans. J. Exp. Biol. 314B, 123-134.

Moyà-Solà, S., Köhler, M., Alba, D.M., 2005. Response to comment on "*Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain". Science 308, 203d.

Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., 2004. *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. Science 306, 1339-1344.

Moyà-Solà, S., Köhler, M., Rook, L., 1999. Evidence of hominid-like precision grip capability in the hand of the Miocene ape *Oreopithecus*. Proc. Natl. Acad. Sci. USA 96, 313-317.

Nakatsukasa, M., Kunimatsu, Y., 2009. *Nacholapithecus* and its importance for understanding hominoid evolution. Evol. Anthropol. 18, 103-119.

Ohman, J.C., Lovejoy, C.O., White, T.D., 2005. Questions about *Orrorin* femur. 307, 845.

Pickford, M., Senut, B., Gommery, D., Treil, J., 2002. Bipedalism in *Orrorin tugenensis* revealed by its femora. CR Palevol. 1, 191-203.

Pilbeam, D., 1996. Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. Mol. Phylogen. Evol. 5, 155-168.

Pilbeam, D., 2004. The anthropoid postcranial axial skeleton: comments on development, variation, and evolution. J. Exp. Zool. 302B, 241-267.

Pilbeam, D., Young, N., 2004. Hominoid evolution: synthesizing disparate data. C. R. Palevol 3, 305-321.

Richmond, B.G., Jungers, W.L., 2008. *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. Science 319, 1662-1665.

Rose, M.D., 1975. Functional proportions of primate lumbar vertebral bodies. J. Hum. Evol. 4, 21-38.

Sanders, W.J., 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J. Hum. Evol. 34, 249-302.

Sarmiento, E.E., 2010. Comment on the paleobiology and classification of *Ardipithecus ramidus*. Science 328, 1105-b.

Senut, B., 2007. The earliest putative hominids. In: W. Henke, I. Tattersal (Eds.), Handbook of Paleoanthropology. Vol. 3: Phylogeny of Hominids. Springer, Berlin, 1519-1538.

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., Coppens, Y., 2001. First hominid from the Miocene (Lukeino Formation, Kenya). CR Acad. Sci. Paris 332, 137-144.

Shapiro, L., 1993. Functional morphology of the vertebral column in primates. In: Gebo, D.L. (Ed.), Postcranial Adaptation in Nonhuman Primates. Northern Illinois University Press, Dekalb, IL.

Susman, R.L., 2004. *Oreopithecus bambolii*: an unlikely case of hominidlike grip capability in a Miocene ape. J. Hum. Evol. 46, 105-117.

Suwa, G., Kono, R.T., Simpson, S.W., Asfaw, B., Lovejoy, C.O., White, T.D., 2009. Paleobiological implications of the *Ardipithecus ramidus* dentition. Science 236, 69, 94-99.

Thorpe, S.K.S., Holder, R.L., Crompton, R.H., 2007. Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science 316, 1328-1331.

Wake, D.B., 1994. Comparative terminology. Science 265, 268-269.

Wake, D.B., Wake, M.H., Specht, C.D., 2011. Homoplasy: from detecting pattern to determining process and mechanism of evolution. Science 331, 1032-1035.

White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G., WoldeGabriel, G., 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. Science 326, 64, 75-86.

White, T.D., Suwa, G., Lovejoy, C.O., 2010. Response to comment on the paleobiology and classification of *Ardipithecus ramidus*. Science 328, 1105-c.

Williams, S.A., 2009. Modularity in the hominoid vertebral column: implications for the evolution of orthogrady. Am. J. Phys. Anthropol. Suppl. 47, 366.

Wolpoff, M.H., Hawks, J., Senut, B., Pickford, M., Ahern, J., 2006. An ape or *the* ape: is the Toumaï cranium TM 266 a hominid? Paleoanthropol. 2006, 36-50.

Wolpoff, M.H., Senut, B., Pickford, M., Hawks, J., 2002. *Sahelanthropus* or '*Sahelpithecus*'? Nature 419, 581-582.

Wood, B., Harrison, T., 2011. The evolutionary context of the first hominins. Nature 470, 347-352.

Young, N.M., 2003. A reassessment of living hominoid postcranial variability: implications for ape evolution. J. Hum. Evol. 45, 441-464.

Young, N.M., Wagner, G.P., Hallgrimsson, B., 2010. Development and the evolvability of human limbs. Proc. Natl. Acad. Sci. USA 107, 3400-3405.

Zollikofer, C.P.E., Ponce de León, M.S., Lieberman, D.E., Guy, F., Pilbeam, D., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2005. Virtual cranial reconstruction of *Sahelanthropus tchadensis*. Nature 434, 755-759.

APPENDIX A

ORTHOGRADY: A HISTORY OF THOUGHT CONCERNING ITS EVOLUTION

Keith (1903:18-19) coined the terms "orthograde" and "pronograde" to describe the upright and horizontal positions of the body axis, respectively, in anthropoid primates. The hominoids were designated as orthograde, the derived condition (Keith, 1903, 1923, 1940), while the New and Old World monkeys were described as pronograde, presumably a primitive mammalian condition. Straus (1962), however, had been careful to point out that primates in general are prone to orthogrady and that a tendency towards upright posture is a defining primate characteristic. This was noted early on by Keith (1891:80), who recognized that all primates are characterized by a "semi-upright position," within which anthropoids are further characterized by "upright" and "downright" postures. Although all primates are capable of orthograde postures, only apes (and to a lesser degree, brachiating atelines) are specifically adapted to orthogrady.

In this context, positional behavior studies may describe locomotor or postural behavior as orthograde – the main body axis is held in a vertical position to the substrate (Hunt et al., 1996) – but only primates specifically adapted to orthogrady should be considered orthograde. Likewise, most primates, including orthograde apes, are capable of pronograde locomotion and postures, where the body is held relatively horizontal to the substrate. Indeed, non-hominin hominids (orangutans, gorillas, chimpanzees) utilize an intermediate orientation of the body axis during quadrupedal locomotion and postural bouts. Filler (2007) has coined the term 'diagonograde' to describe this posture. It is clear, however, that living great apes and humans are adapted similarly to orthogrady, which presumably underlies the locomotor modes currently

employed by them. Therefore, the evolution of orthogrady is crucial to understanding the locomotor behaviors of living hominoids – brachiation, quadrumanous clambering, knuckle-walking, and bipedalism. A historical account of the locomotor behaviors of extant apes and their purported roles in hominoid ancestry follow.

Keith (1903, 1923) proposed a four-stage model for the evolution of bipedalism – the pronograde stage, the orthograde ("hylobatian") stage, the giant ("troglodytian") stage, and the plantigrade stage. Therefore, Keith's model required that all living apes passed through a small-bodied orthograde stage. Hominids then experienced a significant increase in body size and passed through a large-bodied orthograde stage. Keith's plantigrade stage is restricted to humans and is synonymous to bipedalism. To Keith, orthograde posture in the trees preadapted hominins for bipedal progression on the ground. Keith (1899), following Owen (1859) described the gibbons as brachiators, but whereas Owen had restricted the term to gibbons, Keith extended it to orangutans and chimpanzees. Keith was an anatomist, not a primatologist, so his observations were largely anatomical. Keith (1899:305-307) described the forelimb of the chimpanzee as "that of the brachiators, anthropoids like the Orang and the Gibbon," that it "approaches the conditions found in the brachiating Apes and shows features adapted to climbing." Keith did not describe humans as brachiators or having descended from a brachiating ancestry and he argued that the gorilla forelimb was not adapted for brachiation.

Interestingly, although Keith is considered the founder and champion of the brachiationist theory, Keith's (1903, 1923) four-stage model for the evolution of orthogrady and bipedalism did not include a locomotor phase called brachiation. Indeed, the word 'brachiation' cannot be found in either of Keith's (1903, 1923) major works on the subject. Straus (1949) and later Tuttle (1974) misconstrued Keith's model as including explicit brachiating stages, which with it has

been incorrectly associated ever since (e.g., Crompton et al., 2008). To Keith, the key was orthogrady and not a specific locomotor behavior that was associated with its evolution, a point only rarely appreciated or even realized by modern authorities (e.g., Jungers, 1984). It was Gregory (1916, 1927, 1928*a,b*, 1930, 1934) and Morton (1922, 1924, 1926) who found in Keith's term brachiation a mechanism to explain the evolution of upright posture (it should be noted that these authors did not follow Keith in the use of the term orthograde). Only following the establishment of the brachiationist theory by Gregory and Morton did Keith (1934:51) invoke a "brachiating method of climbing" to explain the evolution of orthogrady.

Washburn (1950, 1963, 1968, 1971) Avis (1962), and Lewis (1969, 1971, 1972, 1974, 1985*a,b*) supported Gregory and Morton's general premise that brachiation was the locomotor behavior that elicited upright posture in the ancestor of living apes. All of these authors subscribed to generalized forelimb-dominated, suspensory behavior, not necessarily a high-speed, ricochetal form of brachiation. According to Gregory (1930:646), the ancestors of living apes were "partly brachiating ancestors" that "avoided the extreme brachiating specializations of the gibbon and orang" (Gregory, 1934:29).

Indeed, the exact meaning of the term brachiation has differed over time and lack of a solid definition has led to different uses by different authors (see Avis, 1962; Napier, 1963; Trevor, 1963; Stern and Oxnard, 1973; Tuttle, 1975; Andrews and Groves, 1976). Keith (1899:305) originally provided a cursory definition of brachiation as, "use of the arms as one of the main organs of locomotion." Gregory (1916:333) specified the type of arm use as "swinging from branch to branch with the arms." Avis (1962) attempted to sort out the confusion by defining brachiation as a particular set of locomotor movements, characterized by trunk rotation and forearm supination, employed during bimanual progression. She argued that gibbons differ

from apes only in a limited sense: "The gibbon has compensated for its relatively small size by developing elbow flexion and humeral retraction to bring arm-swinging to its maximum speed. The large apes have capitalized on trunk rotation and forearm supination, movements which enable them to lift their heavier bodies relatively great distances even among flimsy supporting structures" (Avis, 1962:135).

This is similar to Gebo's (1996:63) definition of brachiation, "slow to moderate arm swinging where the trunk undergoes rotation under the supporting hand," who argued that specializations of the hominoid forearm and thorax are "primarily due to increased mobility at the shoulder and relate to brachiation and prolonged arm suspensory capabilities" (Gebo, 1996:75). The fast, specialized locomotor behavior of hylobatids was termed ricochetal arm-swinging (Tuttle, 1969), but it was also recognized that hylobatids, especially siamangs, commonly employ brachiation at slower speeds (Fleagle, 1974, 1976), of which all living hominoids are capable. Many types are brachiation are now recognized, including the ricochetal brachiation of hylobatids and the tail-assisted brachiation of some atelines (Hunt et al., 1996; Cant et al., 2003). Recently, several authors have also documented brachiation in some wild colobines (Byron and Covert, 2004; Wright et al., 2008).

Tuttle (1969, 1974, 1975, 1981) traced his "hylobatian" model back to the work of Morton (1926:162), who described "vertical climbing" in association with the evolution of brachiation. Initially, he proposed that the ancestor of living hominoids possessed postcranial features "developed in response to orthograde positional behavior, including some arboreal bipedalism, vertical climbing, and forelimb suspension" (Tuttle, 1975:465). Later, however, he suggested that the ancestral hominoid rarely practiced arm-swinging or fed in suspensory

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postures, instead moving and feeding by hoisting, bridging, reaching, and vertical and versatile climbing (Tuttle, 1981).

Over the years, Tuttle's model increasingly emphasized vertical climbing at the expense of brachiation and suspensory behavior, no doubt influenced by the work of Stern and colleagues (Stern et al., 1977, 1980*a,b*; Jungers and Stern, 1980; Fleagle et al., 1981). In a series of studies, Stern and colleagues (Stern et al., 1977, 1980*a,b*; Jungers and Stern, 1980) demonstrated that shoulder and forelimb muscles of hominoids and atelids experience higher levels of recruitment during vertical climbing than during brachiation. Based on these findings, it was suggested that, "many aspects of forelimb anatomy that have previously been identified as brachiating adaptations can be explained as well or better as adaptations to vertical climbing" (Fleagle et al., 1981:361).

Although Washburn (1950, 1963, 1968, 1971) initially supported a brachiating ancestor, he later de-emphasized the role of brachiation, instead suggesting that "reaching in many directions while climbing and feeding" was responsible for the evolution of the hominoid postcranium and that "the anatomy of climbing-feeding makes brachiation possible" (Washburn, 1973:478). To characterize this generalized form of climbing and suspension, Stern (1976:59) coined the term antipronograde, defined as "behavior in which either the upper or lower limbs, or both, are employed in tension during activities of climbing, feeding, and suspensory locomotion."

Andrews and Groves (1976) argued that hominoid postcranial adaptations are not related to locomotor behaviors, but instead to use of the forelimbs during feeding in upright posture. Hunt (1991) also suggested that a postural mode – arm-hanging during feeding – was largely responsible for shared derived hominoid postcranial morphology. Stern and Larson (2001)

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support Hunt's hang-feeding hypothesis and emphasize one-arm hanging during feeding as the fundamental positional adaptation of hominoids. Sarmiento (2002:94) described the ancestral hominoid as employing all of the aforementioned behaviors – brachiation, vertical climbing, and one-arm hanging – as "the derived subsets of a cautious climbing locomotor repertoire" (Sarmiento, 1987, 1988, 2002). Fleagle (1976:245) observed that siamangs brachiate less and climb more than smaller-bodied gibbons, and noting that all apes climb during feeding, he proposed that "quadrumanous climbing during feeding is the basic hominoid locomotor adaptation." Crompton and colleagues (2003, 2008, 2010; Crompton and Thorpe, 2007; Thorpe et al., 2007) have argued that orthograde clambering and arm-assisted bipedalism, as demonstrated by the living orangutan, characterized the ancestral great ape.

Finally, a set of hypotheses related to varying degrees of pronogrady have been proposed, starting with those of Straus (1940, 1949, 1962, 1968). Founded initially on an incorrect phylogeny – hominins were proposed to have been primitive catarrhines, not members of the hominoid family – Straus (1968:196) argued that hominins evolved from a pronograde quadruped, "essentially a monkey, rather than a true anthropoid ape." Straus also proposed that the human hand is too primitive, and those of living apes too specialized, for the former to have been derived from anything like the latter.

Cartmill and Milton (1977) argued that living hominoids evolved from cautious quadrupedal ancestors, and that while hylobatids evolved postcranial morphologies related to brachiation, the hominid LCA evolved postcranial features in relation to cautious quadrupedalism and bridging at a larger body size. The basis of their argument is one structured in a comparative study of lorisids and hominoids. They observed that lorisids, and particularly the slow loris (*Nycticebus*), share with hominoids derived features of the wrist joint not present

in brachiating atelines, namely ulnar deviation from the carpus. The apparent similarities

between loris and hominoid wrist joints suggested to Cartmill and Milton (1977:251) that "the

hominoid peculiarities of the wrist may originally have had nothing to do with brachiation." In

addition, lorises and two-toed sloths (*Choloepus*) possess features of the shoulder, thorax, and

caudal region that approach the hominoid condition (Straus and Wislocki, 1932; Ashton and

Oxnard, 1964; Oxnard, 1967; Cartmill and Milton, 1977; Mendel, 1979). Although apes, lorises,

and sloths commonly employ suspensory behaviors, Cartmill and Milton (1977) dismiss the

influence of suspension on the shared anatomy of these taxa; instead, they suggest that cautious

quadrupedalism, involving reaching, grasping, and bridging behavior as a non-leaping means to

cross gaps, produced the similarities among these taxa (Cartmill and Milton, 1977, but see

Lewis, 1985*a*).

Cartmill and Milton's (1977) cautious quadrupedalism hypothesis has been very

influential (Mendel, 1979; Fleagle et al., 1981) and persists in various forms (e.g., Sarmiento,

1995, 1998). The evolutionary scenario proposed by Lovejoy et al. (2009*a,b*) in the

interpretation of *Ardipithecus* is structured around the work of Cartmill and Milton (1977) and

Straus (1940, 1949, 1962, 1968). Cartmill and Milton (1977) proposed that the ancestral hominid

was an "only partially orthograde quadruped" that "had not completely abandoned pronograde

quadrupedality" (Cartmill and Milton, 1977:269); thus, "advanced orthogrady" would have

evolved independently from a more or less pronograde form in separate lineages (Lovejoy et al.,

2009*d*:104).

The preceding overview has briefly covered many of the hypotheses to explain the

postcranial anatomy of living apes. In the past, these models have been grouped into discrete

categories (Tuttle, 1974; Richmond et al., 2001), but it is clear that many categories overlap with

one another. For example, although Lewis (1972) and Fleagle (1976) argued that brachiation and quadrumanous climbing best explain living ape morphology, respectively, their descriptions of the locomotor repertoire of the ancestral hominoid are strikingly similar: "the use of efficient, mobile, grasping forelimbs which play a leading role in climbing and in suspensory locomotion and feeding activities" (Lewis, 1972:164) and "quadrumanous climbing, forelimb-dominated locomotion during feeding" (Fleagle, 1976:264). In fact, many of the "brachiationists" emphasized the role of climbing in hominoid evolution (see Morton, 1922, 1924, 1926; Gregory, 1928*b*; Washburn, 1950; Lewis, 1972, 1974).

APPENDIX B

SPECIMENS AND SAMPLE SIZES ANALYZED IN CHAPTER 2

TABLE B.1. List of specimens, species, genera, major clades, and sample sizes used in Ch. 2.

Major clade	Genus (#)	Species (#)	N*	References
Monotremata	3	3	44	
	Ornithorhynchus	*anatinus*	18	1, 2, 3, 4, 5
	Tachyglossus	*aculeatus*	25	1, 2, 4, 5
	Zaglossus	*bruijni*	1	6
Marsupalia	40	59	166	
	Acrobates	*pygmaeus*	1	1
	Aepyprymnus	*rufescens*	1	1
	Antechinus	*adustus, minimus*	3	1, 2
	Bettongia	*gaimardi, lesueur*	4	1, 2
	Caenolestes	*sp.*	1	7
	Caluromys	*philander*	1	8
	Cercaretus	*nanus*	1	1
	Chaeropus	*ecaudatus*	1	2
	Chironectes	*minimus*	1	2
	Dasyuroides	*byrnei*	1	4
	Dasyurus	*maculatus, ursinus, viverrinus*	9	1, 2, 7
	Dendrolagus	*goodfellowi, ursinus*	3	2, 4, 7
	Didelphis	*albiventris, marsupalis, virginiana*	37	1, 2, 4, 5, 8
	Echymipera	*sp.*	1	1

TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Lasiorhinus	*latifrons*	1	2
	Macropus	*antilopinus, eugenii, fuliginosus, giganteus, rufogriseus, rufus*	9	1, 2, 4
	Marmosa	*murina*	1	1
	Metachirus	*nudicaudatus, rufogriseus*	2	8
	Micoureus	*demerarae*	1	8
	Monodelphis	*brevicaudata*	1	8
	Myrmecobius	*fasciatus*	2	2, 4
	Notoryctes	*typhlops*	1	7
	Perameles	*gunnii, nasuta, obesula*	4	2, 4, 7, 9
	Petauroides	*volans*	2	1, 2
	Petaurus	*australis, breviceps, norfolcensis*	5	1, 2, 4
	Petrogale	*penicillata*	2	1, 7
	Phalanger	*orientalis*	1	7
	Phascogale	*tapoatafa*	1	1
	Phascolarctos	*cinereus*	13	2, 5, 7
	Phascolomys	*mitchelli*	1	4
	Philander	*opossum*	4	1, 4, 8
	Potorous	*tridactylus*	1	1
	Pseudocheirus	*peregrinus*	4	1, 2, 7
	Rhyncholestes	*raphanurus*	1	4
	Sarcophilis	*harrisi, laniarius*	2	4, 7

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Thylacinus	*cynocephalus*	6	1, 2
	Thylogale	*billardierii, thetis*	3	1, 7
	Trichosurus	*vulpecula*	25	1, 2, 5
	Vombatus	*ursinus*	7	1, 2, 4
	Wallabia	*bicolor*	1	1
Afrotheria	22	31	408	
	Amblysomus	*hottentotus*	121	5, 10
	Calcochlorix	*obtusirostris*	1	7
	Chrysochloris	*asiatica*	12	2, 4, 7, 10
	Chrysospalax	*trevelyani*	2	7
	Dendrohyrax	*arboreus, dorsalis, validus*	43	2, 4, 7, 5, 10
	Dugong	*dugong*	7	1, 2
	Elephantulus	*intufi, myurus, rufescens*	5	4, 7
	Elephas	*maximus*	4	1, 2, 4
	Eremitalpa	*granti*	40	10
	Hemicentetes	*nigriceps, semispinosus*	4	2, 4, 7
	Limnogale	*mergulus*	2	7
	Macroscelides	*proboscideus*	1	4
	Microgale	*cowani, longicaudata, talazaci*	5	2, 7
	Orycteropus	*afer*	9	1, 2, 4, 6, 7, 11
	Oryzorictes	*tetradactylus*	1	7

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Petrodromus	*tetradactylus*	2	7
	Potamogale	*velox*	2	7
	Procavia	*capensis*	70	1, 2, 4, 5, 10, 12
	Rhynchocyon	*chrysopygus, cirnei*	3	2, 7, 13
	Setifer	*setosus*	14	2, 4, 5, 7, 10
	Tenrec	*ecaudatus*	26	1, 2, 4, 5, 7, 10
	Trichechus	*inunguis, manatus, senegalensis*	34	2, 4, 14
Xenarthra	13	19	197	
	Bradypus	*torquatus, tridactylus, variegatus*	63	1, 2, 4, 5, 15
	Cabassous	*unicinctus*	2	1, 2
	Chaetophractus	*villosus*	2	1, 2
	Chlamyphorus	*truncatus*	2	1, 2
	Choloepus	*didactylus, hoffmanni*	71	2, 15
	Cyclopes	*didactylus*	2	1, 2
	Dasypus	*hybrida, novemcinctus, septemcinctus*	18	1, 2, 4, 5, 10
	Euphractus	*sexcinctus*	2	1, 2
	Myrmecophaga	*tridactyla*	5	1, 2, 4, 7
	Priodontes	*maximus*	3	1, 2, 4
	Tamandua	*mexicana, tetradactyla*	23	1, 2, 4, 14
	Tolypeutes	*conurus*	1	2
	Zaedyus	*pichiy*	3	2, 7

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
Eulipotyphla	20	26	204	
	Atelerix	algirus	1	7
	Blarina	brevicauda	1	4
	Condylura	cristata	1	4
	Crocidura	foxi, nyansae	4	4, 7, 16
	Cryptotis	parva	47	5
	Desmana	moschata	1	2
	Echinosorex	albus, gymnura	4	2, 3, 4, 7
	Erinaceus	europaeus	32	1, 2, 4, 5, 10
	Galemys	pyrenaicus	3	1, 2
	Hemiechinus	auritus	5	1, 7
	Hylomys	suillus	1	7
	Mogera	wogura	2	1, 7
	Paraechinus	aethiopica	1	4
	Parascaptor	leucura	1	1
	Scutisorex	congicus, somereni	7	4, 16
	Solenodon	cubanus, paradoxus	3	2, 4, 7
	Sorex	araneus	39	1, 2, 10
	Suncus	etruscus, madagascarensis, murinus	10	1, 10
	Talpa	europaea	40	1, 2, 4, 5, 10
	Urotrichus	talpoides	1	1

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
Chiroptera	26	33	35	
	Artibeus	*obscurus*	1	2
	Asellia	*tridens*	1	2
	Balantiopteryx	*io*	1	4
	Chaerephon	*plicata*	1	1
	Cheiromeles	*parvidens*	1	1
	Cynopterus	*brachyotis*	2	1, 2
	Desmodus	*rufus*	1	2
	Emballonura	*sp.*	1	1
	Epomops	*franqueti*	1	2
	Eptesicus	*serotinus*	1	2
	Hipposideros	*caffra, commersonii, diadema*	4	1, 2, 4
	Lasionycteris	*noctivagans*	1	4
	Lavia	*frons*	1	2
	Lonchorhina	*aurita*	1	4
	Macroglossus	*minimus*	1	1
	Megaderma	*lyra*	1	1
	Miniopterus	*schreibersi*	1	2
	Molossus	*molossus*	1	1
	Nyctalus	*noctula*	1	2
	Nycticeius	*sp.*	1	1

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Phyloderma	*stenops*	1	4
	Pipistrellus	*nanulus, pipistrellus*	2	2
	Pteropus	*dasymallus, medius, ornatus, rufus, vampyrus*	5	2, 4, 7
	Rhinolophus	*ferrum*	1	4
	Saccolaimus	*saccolaimus*	1	1
	Scotophilus	*leucogaster*	1	1
Ferae	88	132	714	
	Manis	*crassicaudata, culionensis, gigantea, javanica, pentadactyla, temminckii, tetradactyla*	23	2, 4, 7, 17, 18, 19, 20
	Acinonyx	*jubatus*	4	1, 2, 7, 14
	Ailuropoda	*melanoleuca*	19	2, 20, 21, 22, 23
	Ailurus	*fulgens*	4	1, 2, 4, 22
	Alopex	*lagopus*	4	1, 2
	Aonyx	*cinerea*	1	2
	Arctictis	*binturong*	4	1, 2, 7
	Arctonyx	*collaris*	2	1, 2
	Atilax	*paludinosus*	2	1, 14
	Bassaricyon	*alleni*	1	14
	Bassariscus	*astutus*	3	2, 14, 24
	Callorhinus	*ursinus*	5	2, 7, 14
	Canis	*aureus, familiaris, latrans, lupus*	195	2, 7, 14, 22
	Caracal	*caracal*	2	2, 14

TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Cerdocyon	thous	1	1
	Conepatus	chinga	2	1, 25
	Crocuta	crocuta	4	1, 2, 7, 14
	Crossarchus	obscurus	2	1, 2
	Cryptoprocta	ferox	3	2, 7, 26
	Cuon	alpinus	6	1, 2, 14
	Cystophora	cristata	3	2, 4, 14
	Eira	barbara	2	1, 4
	Enhydra	lutris	5	1, 2, 7, 14
	Erignathus	barbatus	1	1
	Eumetopias	jubatus	5	2, 4, 7, 14
	Eupleres	goudotii	1	2
	Felis	domestica	6	1, 2
	Fossa	fossa	1	14
	Galictis	vittata	2	1, 2
	Galidia	elegans	1	2
	Genetta	genetta, tigrina	2	1, 2
	Gulo	gulo	3	1, 2
	Halichoerus	grypus	1	2
	Hemigalus	derbyanus	2	1, 2
	Herpestes	auropunctatus, edwardsii, ichneumon, smithii, vitticollis	9	1, 2, 4, 7, 14

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Hyaena	*brunnea, hyaena*	10	1, 2, 4, 14, 27
	Hydrurga	*leptonyx*	1	1, 2
	Ictonyx	*striatus*	1	1
	Leopardus	*pajeros, pardalis*	2	1, 14
	Leptailurus	*serval*	1	1
	Lobodon	*carcinophagus*	1	2
	Lontra	*felina, longicaudis*	2	1, 14
	Lutra	*lutra*	7	1, 2, 28
	Lycaon	*pictus*	2	2, 4
	Lynx	*canadensis, lynx*	3	1, 2
	Martes	*domestica, martes, pennanti, zibellina*	6	1, 2, 7, 14
	Meles	*meles*	4	2
	Melivora	*capensis*	2	2, 7
	Melogale	*everetti*	1	14
	Melursus	*ursinus*	3	1, 2
	Mephitis	*mephitis*	3	2, 14, 25
	Mirounga	*leonina*	3	1, 2
	Monachus	*monachus, tropicalis*	4	1, 2, 7, 29
	Mungos	*mungo*	1	1
	Mustela	*erminea, frenata, nivalis, putorius, siberica, vison*	172	1, 2, 7, 30, 31, 32
	Mydaus	*javanicus*	1	2

TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Nandinia	binotata	1	2
	Nasua	narica, nasua	5	1, 2, 4, 7
	Neofelis	nebulosa	2	1, 22
	Neophoca	cinerea	3	2
	Nyctereutes	procyonoides	3	1, 2, 14
	Odobenus	rosmarus	4	2, 4, 7, 14
	Ommatophoca	rossii	2	1, 14
	Otaria	flavescens	2	2
	Otocyon	megalotis	5	2, 4, 7
	Paguma	larvata	1	1
	Panthera	concolor, leo, onca, pardus, tigris, uncia	20	1, 2, 4, 7, 14, 22
	Paradoxurus	hermaphroditus	2	1, 2
	Phoca	groenlandica, hispida, vitulina	8	1, 2, 14
	Potos	flavus	6	1, 2, 4
	Prionailurus	bengalensis	1	1
	Procyon	cancrivorus, lotor	8	1, 2, 4, 14
	Profelis	chrysothrix	1	2
	Proteles	cristatus	1	2
	Pseudalopex	culpaeus, fulvipes	2	1
	Pteronura	brasiliensis	1	1
	Puma	yagouaroundi	2	1

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Pusa	caspica	1	1
	Salanoia	concolor	1	14
	Spethos	venaticus	1	2
	Spilogale	gracilis	1	25
	Suricata	suricata	5	1, 2, 7, 14
	Taxidea	taxus	2	1, 2
	Urocyon	cineroargenteus	1	14
	Ursus	americanus, arctos, malayanus, maritimus, spelaeus, thibetanus	23	1, 2, 4, 7, 14, 20, 22, 33
	Viverra	civettina, zibetha	3	1, 2, 7
	Viverricula	indica	2	1, 14
	Vulpes	bengalensis, vulpes	33	1, 2, 10, 14, 34
Perissodactyla	5	14	294	
	Ceratotherium	simum	2	4, 35
	Dicerorhinus	sumatrensis	3	2
	Equus	africanus, ferus, grevyi, hemionus, kiang, quagga, zebra	278	1, 2, 4, 5, 7, 36, 37
	Rhinoceros	sondaicus, unicornis	4	1, 2, 7
	Tapirus	bairdii, indicus, terrestris	7	1, 2, 4, 38
Artiodactyla	57	76	518	
	Addax	nasomaculatus	1	1
	Alcelaphus	buselaphus	2	1, 7
	Alces	alces	3	1, 2

TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Ammotragus	*lervia*	3	1, 2, 7
	Antidorcas	*marsupalis*	1	1
	Antilocapra	*americana*	1	4
	Antilope	*cervicapra*	1	2
	Axis	*axis, porcinus*	2	1
	Babirussa	*alfurus*	1	2
	Bison	*bison, bonasus*	6	1, 2, 7
	Bos	*frontalis, gaurus, javanicus, primigenius*	8	1, 2
	Boselaphus	*tragocamelus*	4	1, 2
	Camelus	*bactrianus, dromedarius*	3	1, 2
	Capra	*hircus, ibex*	162	1, 2, 39
	Capreolus	*capreolus*	3	1, 2
	Cephalophus	*maxwellii, monticola, natalensis*	3	1, 4
	Cervus	*canadensis, elaphus*	7	1, 2
	Connochaetes	*gnu*	2	1, 2
	Dama	*dama*	4	2
	Elaphurus	*davidianus*	1	2
	Gazella	*bennettii, dorcas, soemmerringii*	4	1, 2, 4
	Giraffa	*camelopardalis*	3	1, 2, 40
	Hemitragus	*hylocrius*	1	2
	Hippotragus	*equinus*	1	2

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Hydropotes	*inermis*	1	2
	Hyemoschus	*aquaticus*	2	1, 2
	Kobus	*ellipsiprymnus*	1	1
	Lama	*glama*	1	2
	Litocranius	*walleri*	1	4
	Mazama	*rufina*	1	1
	Moschiola	*meminna*	1	1
	Moschus	*moschiferus*	4	2
	Muntiacus	*muntjac*	2	1, 2
	Odocoileus	*virginianus*	2	1, 2
	Okapia	*johnstoni*	2	4, 7
	Ovibos	*moschatus*	1	1
	Ovis	*ammon, aries,*	36	1, 2, 41, 42
	Ozotoceros	*bezoarticus*	1	1
	Pecari	*tajacu*	4	1, 2
	Pelea	*capreolus*	1	1
	Phacochoerus	*aethiopicus, africanus*	2	1, 2
	Potamochoerus	*porcus*	1	1
	Pseudois	*nayaur*	1	2
	Puda	*puda*	1	2
	Rangifer	*tarandus*	5	1, 2

Major clade	Genus (#)	Species (#)	N*	References
	Rucervus	duvaucelii	1	1
	Rupicapra	rupicapra	1	1
	Saiga	tatarica	2	2
	Sus	scrofa, verrucosus	196	1, 2, 4, 5
	Sylvicapra	grimmia	2	1
	Syncerus	caffer	2	1
	Taurotragus	oryx	1	1
	Tayassu	pecari	1	1, 4
	Tetracerus	quadricornis	1	2
	Tragelaphus	scriptus, strepsiceros, sylvaticus	3	1
	Tragulus	javanicus, kanchil, napu	5	1, 2, 4
	Vicugna	pacos, vicugna	5	1, 2
Whippomorpha 38		52	234	
	Hippopotamus	amphibius	5	2, 4, 7
	Balaena	mysticetus	10	2, 14
	Balaenoptera	acutorostrata, borealis, musculus, physalus, rostrata,	34	1, 2, 14
	Berardius	arnuxii	1	2
	Caperea	marginata	28	14, 43
	Cephalorhynchus	commersonii	3	2, 12
	Delphinapterus	leucas	4	1, 2, 12
	Delphinus	delphis	11	1, 2, 12

TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Eschrichus	*robustus*	6	14
	Eubalaena	*australis, glacialis*	18	2, 14
	Feresa	*attenuata*	1	12
	Globicephala	*macrorhynchus, melas*	9	1, 2, 12
	Grampus	*griseus*	1	12
	Hyperoodon	*rostratus*	1	2
	Inia	*geoffrensis*	1	14
	Kogia	*simus*	1	14
	Lagenodelphis	*hosei*	2	12, 14
	Lagenorhynchus	*acutus, albirostris, obliquidens*	34	1, 2, 12, 44
	Lipotes	*vexillifer*	1	44
	Lissodelphis	*borealis*	2	12
	Megaptera	*novaeangliae*	7	14
	Mesoplodon	*grayi, europaeus*	2	2, 14
	Monodon	*monoceros*	6	1, 2, 12, 14
	Neophocoena	*phocaenoides*	2	14, 44
	Orcaella	*brevirostris*	1	12
	Orcinus	*orca*	5	2, 12
	Peponocephala	*electra*	1	12
	Phocoena	*phocoena, spinipinnis*	3	1, 44
	Phocoenoides	*dalli*	1	44

TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Physeter	*macrocephalus*	13	2, 14
	Platanista	*gangetica*	2	2
	Pontoporia	*blainvillei*	1	14
	Pseudorca	*crassidens*	4	2, 12
	Sotalia	*fluviatilis, sinensis*	2	2, 12
	Stenella	*coeruleoalba, frontalis, longirostris*	3	12
	Steno	*bredanensis*	1	12
	Tursiops	*truncatus*	6	2, 12, 14
	Ziphius	*cavirostris*	1	14
Lagomorpha	5	10	522	
	Lepus	*alleni, americanus, europaeus, timidus, townsendii*	19	1, 2, 4, 5
	Ochotona	*hyperborea, rufescens*	6	4, 10
	Oryctolagus	*cuniculus*	495	1, 2, 7
	Pentalagus	*furnessi*	1	45
	Sylvilagus	*floridanus*	1	4
Rodentia	93	128	468	
	Abrocoma	*bennettii*	1	1
	Aconaemys	*fuscus*	1	1
	Allactaga	*jaculus, sibirica, tetradactyla*	5	1, 2, 46
	Anomalurus	*pelii*	2	1, 4
	Aplodontia	*rufa*	1	4

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Apodemus	*sylvaticus*	1	1
	Arvicola	*agrestis, terrestris*	3	1, 2
	Bathyergus	*suillus*	5	1, 2
	Callistomys	*pictus*	1	1
	Callosciurus	*prevosti*	1	4
	Cannomys	*badius*	1	1
	Capromys	*pilorides*	2	1, 2
	Castor	*canadensis, fiber*	8	1, 2, 4
	Cavia	*aperea, porcellus*	5	1, 2
	Chaetodipus	*fallax, penicillatus*	4	46
	Chaetomys	*subspinosus*	1	1
	Chinchilla	*lanigera*	4	1, 2, 4, 47
	Clethrionomys	*glareolus*	1	1
	Coendou	*prehensilis*	2	1, 4
	Conilurus	*albipes*	1	2
	Cricetomys	*gambianus*	1	1
	Cricetulus	*migratorius*	1	1
	Cricetus	*cricetus*	2	1, 2
	Ctenodactylus	*gundi*	1	1
	Ctenomys	*boliviensis, talarum*	13	1, 5
	Cuniculus	*paca*	5	1, 2, 4

TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Cynomys	*ludovicianus*	3	2, 48
	Dasyprocta	*leporina*	1	1
	Dicrostonyx	*groenlandicus*	1	1
	Dipodomys	*murinus, ordii*	19	1, 2, 46
	Dipus	*sagitta, sowerbyi*	4	2, 46
	Dolichotis	*patagonum*	2	1, 2, 4
	Eliomys	*melanurus*	1	1
	Eliurus	*penicillatus*	1	46
	Ellobius	*talpinus*	1	2
	Erethizon	*dorsatum*	2	1
	Eutamias	*sibiricus*	1	2
	Galea	*spixii*	1	1
	Geocapromys	*brownii, thoracatus*	2	1, 49
	Geomys	*bursarius*	1	2
	Georychus	*capensis*	2	2, 4
	Gerbillus	*sp.*	1	46
	Glaucomys	*sabrinus, volucella*	3	2, 48
	Heteromys	*anomalus, lonicaudus*	2	46
	Hydrochoerus	*hydrochaeris*	5	1, 2, 4
	Hydromys	*chrysogaster*	2	2
	Hystrix	*brachyura, cristata, indica, javanica*	11	1, 2, 4, 50

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Ictidomys	*mexicanus*	1	48
	Jaculus	*jaculus, orientalis*	9	46
	Lagidium	*viscacia*	1	1
	Lagostomus	*trichodactylus*	2	2, 4
	Laonastes	*aenigmamus*	2	51
	Lemmus	*lemmus*	1	2
	Macrotus	*waterhousii*	1	52
	Marmota	*bobak, flaviventris, marmota, monax*	5	1, 2, 48
	Maxomys	*panglima*	1	4
	Microsciureus	*alfari, flaviventer, mimulus*	41	23, 53
	Microtus	*oeconomus*	25	10
	Mus	*musculus*	2	1, 2
	Muscardinus	*avellanarius*	2	1, 2
	Myocastor	*coypus*	3	1, 2
	Myoprocta	*acouchy*	1	2
	Neotamias	*townsendii*	3	48
	Notomys	*sp.*	1	46
	Octodon	*degus*	2	1, 2
	Ondatra	*zibethicus*	2	1, 2
	Onychomys	*leucogaster*	71	23, 53
	Orthogeomys	*hispidus*	1	1

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Paramys	*delicatus*	1	46
	Parotomys	*brantsii*	1	1
	Pedetes	*capensis*	17	2, 5, 46
	Peromyscus	*leucopus, melanophrys*	3	4, 5
	Petaurista	*philippensis*	2	1, 4
	Petromus	*typicus*	1	1
	Psammomys	*obesus*	1	1
	Pygeretmus	*pumilio*	1	2
	Rattus	*fuscipes, norvegicus, rattus*	9	1, 2, 20, 46
	Ratufa	*bicolor, indicus*	3	1, 2
	Rhabdomys	*pumillo*	8	5
	Rhizomys	*pruinosus, sumatrensis*	2	2, 4
	Scirtopoda	*telum*	1	46
	Sciurus	*aberti, aestuans, carolinensis, griseus, niger, vulgaris*	78	1, 2, 5, 20, 23, 48, 53
	Sicista	*subtilis*	1	2
	Sigmodon	*hispidus*	1	4
	Spalacopus	*poeppigi*	1	4
	Spalax	*ehrenbergi, leucodon, microphthalmus*	4	1, 2, 4, 54
	Spermophilus	*dauricus, parryii*	3	1, 2
	Sphiggurus	*insidiosus, mexicanus*	2	1, 2
	Tatera	*afra, robusta*	2	46

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Thryonomys	*gregorianus, swinderianus*	3	1, 2, 4
	Zapus	*hudsonius*	5	2, 4, 46
Scandentia	5	7	16	
	Anathana	*ellioti*	1	55
	Dendrogale	*melanura*	1	55
	Ptilocerus	*lowii*	5	4, 55, 56
	Tupaia	*glis, javanica, minor*	8	2, 4, 20, 56
	Urogale	*everetti*	1	55
Dermoptera	1	1		
	Cynocephalus	*volans*	9	1, 2, 4, 7
Primates	60	132	4470	
	Alouatta	*guariba, palliata, pigra, seniculus*	47	2, 20, 56, 57, 58
	Aotus	*azarae, trivirgatus, vociferans*	17	1, 2, 4, 20, 59
	Arctocebus	*calabarensis*	24	2, 20, 60
	Ateles	*ater, belzebuth, chamek, fusciceps, geoffroyi, marginatus, paniscus*	51	1, 2, 20, 57, 58
	Avahi	*laniger*	8	2, 7, 20, 59
	Brachyteles	*arachnoides*	7	1, 20, 57, 59
	Bunopithecus	*hoolock*	20	20, 23, 53, 58, 61
	Cacajao	*calvus, melanocephalus*	17	1, 20, 59, 60, 62
	Callicebus	*moloch*	9	20, 59, 60, 63
	Callimico	*goeldii*	8	20

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Callithrix	*aurita, jacchus,*	14	1, 2, 20
	Cebus	*albifrons, apella, capucinus, flavus, frontalis*	94	1, 2, 4, 20, 56, 57, 58
	Cercocebus	*atys, galeritus, torquatus*	32	1, 4, 20, 56, 58
	Cercopithecus	*albogularis, ascanius, cephus, diana, lhoesti, mitis, mona, neglectus, petaurista*	136	1, 2, 20, 56, 58
	Cheirogaleus	*major, medius,*	9	2, 4, 20, 59, 60
	Chiropotes	*satanas*	11	20, 64
	Chlorocebus	*aethiops*	75	1, 2, 56, 58
	Colobus	*guereza, vellerosus*	3	1, 2, 20
	Daubentonia	*madagascariensis*	5	2, 7, 20, 65
	Erythrocebus	*patas*	23	1, 2, 4, 56, 59, 60
	Eulemur	*albifrons, fulvus, macaco, mongoz*	26	1, 2, 4, 7, 20
	Euoticus	*elegantulus*	15	20
	Galago	*alleni, senegalensis*	3	2, 4, 7
	Gorilla	*beringei, gorilla*	273	2, 20, 23, 33, 53, 57, 58
	Hapalemur	*griseus*	5	2, 20
	Homo	*sapiens*	837	20, 53, 56, 66
	Hylobates	*agilis, klossi, lar, moloch, muelleri, pileatus*	261	2, 4, 20, 23, 53, 58, 61
	Indri	*indri*	15	2, 7, 20, 60
	Lagothrix	*lagotricha, lugens, poeppigii*	29	1, 2, 7, 20, 56
	Lemur	*catta*	8	1, 2, 20
	Leontopithecus	*sp.*	5	4, 20, 59

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Lepilemur	leucopus, mustelinus	20	5, 10, 20
	Lophocebus	albigena, aterrimus	92	4, 56
	Loris	tardigradus	11	1, 2, 4, 20
	Macaca	arctoides, fascicularis, fuscata, maura, mulatta, nemestrina, nigra, radiata, silenus, sylvanus	1056	1, 2, 4, 20, 23, 53, 56, 58, 67
	Mandrillus	leucophaeus, sphinx	15	1, 2, 20, 58
	Microcebus	myoximus, rufus	2	20
	Miopithecus	talapoin	11	1, 20
	Nasalis	larvatus	46	1, 2, 4, 20, 23, 53
	Nomascus	concolor, gabriellae, leucogenys	31	4, 20, 61
	Nycticebus	coucang	17	2, 4, 7, 20
	Otolemur	crassicaudatus, garnettii	5	2, 20
	Pan	paniscus, troglodytes	340	2, 20, 23, 53, 57, 58, 68, 69, 70
	Papio	anubis, cynocephalus, hamadryas, neumanni, papio, ursinus	128	1, 2, 4, 20, 58
	Perodicticus	potto	21	2, 20
	Phaner	furcifer	1	2
	Pithecia	monachus, pithecia	17	2, 20, 59, 64
	Pongo	pygmaeus	220	2, 4, 20, 23, 53, 57, 58
	Presbytis	melalophos, rubicunda	13	2, 20
	Procolobus	badius	2	2, 20
	Propithecus	diadema, verreauxi	14	2, 4, 20
	Pygathrix	nemaeus	6	20

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TABLE B.1 (cont).

Major clade	Genus (#)	Species (#)	N*	References
	Saguinus	*oedipus*	7	1, 2, 20
	Saimiri	*sciureus*	44	1, 2, 4, 20, 56
	Semnopithecus	*entellus, schistaceus*	9	1, 2, 20
	Symphalangus	*syndactylus*	88	1, 2, 20, 58, 61
	Tarsius	*bancanus, spectrum, syrichta*	6	1, 2, 4, 20
	Theropithecus	*gelada*	32	2, 20, 56, 60
	Trachypithecus	*cristatus, johnii, obscurus, phayrei*	128	1, 2, 20, 23, 53
	Varecia	*variegata*	1	1, 2, 20
TOTAL	**476**	**723**	**8297**	

* N = sample size for each genus, including incomplete vertebral formulae in some cases (e.g., missing sacral count) and specimens not included in the detailed analyses of well-sampled taxa (e.g., pre-Schultz criteria records compiled in Schultz 1930, 1933, and Clauser 1980 – these were not included because they sometimes do not record half-counts and therefore may bias the frequencies of formulae and similarity and diversity indices. Ferae = Pholidota + Carnivora. Whippomorpha = Hippopotamidae + Cetacea. References are as follows: 1 (Gerrard, 1862); 2 (Flower, 1884); 3 (Todd, 1922); 4 (Filler, 1986); 5 (Asher et al., 2011); 6 (Flower, 1885); 7 (Sánchez-Villagra et al., 2007); 8 (Argot, 2003); 9 (Seebeck, 2001); 10 (Asher et al., 2009); 11 (Shoshani et al., 1998); 12 (Buchholtz and Schur, 2004); 13 (Rathbun, 1979); 14 (E. Buchholtz, personal communication); 15 (Buchholtz and Stepien, 2009); 16 (Allen, 1917); 17 (Heath, 1992a); 18 (Heath, 1992b); 19 (Heath, 1995); 20 (S. Williams, new data); 21 (Davis, 1964); 22 (Yang and Fang, 1982); 23 (D. Pilbeam, personal communication); 24 (Poglayen-Neuwall and Toweill, 1988); 25 (Verts et al., 2001); 26 (Köhncke and Leonhardt, 1986); 27 (Tecirlioglu, 1983); 28 (Yilmaz et al., 2000); 29 (Adam, 2004); 30 (Hall, 1951); 31 (Sheffield and King, 1994); 32 (Plant and Lloyd, 2010); 33 (D. Gebo, personal communication); 34 (Gultekin and Ucar, 1980); 35 (Chang and Jang, 2004); 36 (Stecher, 1962); 37 (Stubbs et al., 2006); 38 (Padilla and Dowler, 1994); 39 (Simoens et al., 1983); 40 (Dagg, 1971); 41 (Shackleton, 1985); 42 (Ghazi and Gholami, 1994); 43 (Buchholtz, 2011); 44 (Buchholtz et al., 2005); 45 (Yamada and Cervantes, 2006); 46 (Hatt, 1932); 47 (Spotorno et al., 2004); 48 (Bryant, 1945); 49 (Morgan, 1989); 50 (Yilmaz, 1998); 51 (Jenkins et al., 2005); 52 (Anderson, 1969); 53 (Pilbeam, 2004); 54 (Özkan, 2007); 55 (Sargis, 2001); 56 (Clauser, 1980); 57 (Schultz, 1930); 58 (A. Schultz, data sheets); 59 (Schultz and Straus, 1945); 60 (Schultz, 1961); 61 (Schultz, 1933); 62 (Barnett, 2005); 63 (Jones and Anderson, 1978); 64 (Fleagle and Meldrum, 1988); 65 (Quinn and Wilson, 2004); 66 (Hasebe, 1913); 67 (Aimi, 1994); 68 (McCollum et al., 2010); 69 (C. Lovejoy, personal communication); 70 (A. Zihlman, personal communication).

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APPENDIX C

FULL SETS OF VERTEBRAL FORMULAE FOR WELL-SAMPLED TAXA

TABLE C.1. Full sets of vertebral formulae for well-sampled (N>30) anthropoid taxa.

TAXON	N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Homo sapiens	171	62.6	7	12	5	5	17	29	24	22
	34	12.5	7	12	5	6	17	30	24	23
	8	2.9	7	13	4	5	17	29	24	22
	7	2.6	7	13	5	5	18	30	25	23
	5	1.8	7	12	4.5	5.5	16.5	29	23.5	22
	5	1.8	7	12	5	5.5	17	29.5	24	22.5
	5	1.8	7	12	6	5	18	30	25	23
	4	1.5	7	11	5	5	16	28	23	21
	4	1.5	7	13	4	6	17	30	24	23
	3	1.1	7	12	4	6	16	29	23	22
	3	1.1	7	12.5	4.5	6	17	30	24	23
	3	1.1	6.5	12.5	5	5	17.5	29	24	22.5
	3	1.1	7	12	5.5	5.5	17.5	30	24.5	23
	2	0.7	7	12	4	5	16	28	23	21
	2	0.7	7	12.5	4.5	5	17	29	24	22
	1	0.4	7	11	4	6	15	28	22	21
	1	0.4	7	11.5	4.5	5	16	28	23	21
	1	0.4	7	11	5	6	16	29	23	22
	1	0.4	7	12	5	4.5	17	28.5	24	21.5
	1	0.4	7	11.5	5.5	5	17	29	24	22
	1	0.4	7	11	6	5	17	29	24	22
	1	0.4	7.5	11.5	5.5	5.5	17	30	24.5	22.5
	1	0.4	7	12.5	5	4.5	17.5	29	24.5	22
	1	0.4	7	12	5.5	4.5	17.5	29	24.5	22
	1	0.4	7.5	12.5	5	5	17.5	30	25	22.5
	1	0.4	7	13	4.5	5.5	17.5	30	24.5	23
	1	0.4	6.5	11.5	6	6	17.5	30	24	23.5
	1	0.4	7	12	6	4	18	29	25	22
	1	0.4	7	12.5	5.5	5	18	30	25	23
Total N	273	100.0								

TABLE C.1 (cont).

TAXON		N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Pan troglodytes		86	31.7	7	13	4	6	17	30	24	23
		58	21.4	7	13	4	5	17	29	24	22
		38	14.0	7	13	3	6	16	29	23	22
		19	7.0	7	14	3	6	17	30	24	23
		11	4.1	7	13	3	7	16	30	23	23
		10	3.7	7	14	3	5	17	29	24	22
		8	3.0	7	13	3.5	5.5	16.5	29	23.5	22
		7	2.6	7	13	3	5	16	28	23	21
		4	1.5	7	13.5	3.5	6	17	30	24	23
		4	1.5	7	14	4	5	18	30	25	23
		3	1.1	7	12	4	5	16	28	23	21
		2	0.7	7	13	3.5	6.5	16.5	30	23.5	23
		2	0.7	7	13	4	5.5	17	29.5	24	22.5
		2	0.7	7	13	4	7	17	31	24	24
		2	0.7	7	14	4	6	18	31	25	24
		1	0.4	7	14	2	6	16	29	23	22
		1	0.4	7	12.5	3.5	6	16	29	23	22
		1	0.4	7	12	4	6	16	29	23	22
		1	0.4	7	12.5	4	4.5	16.5	28	23.5	21
		1	0.4	7.5	12.5	4	5	16.5	29	24	21.5
		1	0.4	6.5	13.5	3	6	16.5	29	23	22.5
		1	0.4	7	12	5	4.5	17	28.5	24	21.5
		1	0.4	7	13.5	3.5	5	17	29	24	22
		1	0.4	7	12.5	4.5	6	17	30	24	23
		1	0.4	7	12	5	6	17	30	24	23
		1	0.4	7	14	3	6.5	17	30.5	24	23.5
		1	0.4	6.5	13.5	4	5	17.5	29	24	22.5
		1	0.4	7	13	4.5	5.5	17.5	30	24.5	23
		1	0.4	7	13	5	5	18	30	25	23
		1	0.4	7	13	5	5.5	18	30.5	25	23.5
	Total N	271	100.0								

TABLE C.1 (cont).

TAXON		N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Pan paniscus		6	15.0	7	13	4	6	17	30	24	23
		4	10.0	7	14	3	7	17	31	24	24
		4	10.0	7	13	4	7	17	31	24	24
		3	7.5	7	13	4	5	17	29	24	22
		3	7.5	7	14	3	6	17	30	24	23
		3	7.5	7	14	3	6.5	17	30.5	24	23.5
		3	7.5	7	14	3	8	17	32	24	25
		3	7.5	7	14	4	6	18	31	25	24
		1	2.5	7	12	4	6	16	29	23	22
		1	2.5	7	12.5	3.5	5	16	28	23	21
		1	2.5	7	13	3	7	16	30	23	23
		1	2.5	7	13	3	7.5	16	30.5	23	23.5
		1	2.5	7	14	3	5.5	17	29.5	24	22.5
		1	2.5	7	12	5	6	17	30	24	23
		1	2.5	8	13	4	6	17	31	25	23
		1	2.5	7	13	4	6.5	17	30.5	24	23.5
		1	2.5	6.5	13.5	4	5	17.5	29	24	22.5
		1	2.5	7	14	4	7	18	32	25	25
		1	2.5	7.5	14.5	4	5	18.5	31	26	23.5
	Total N	40	100.0								
Gorilla beringei		36	70.6	7	13	3	6	16	29.0	23.0	22
		4	7.8	7	12	4	6	16	29.0	23.0	22
		3	5.9	7	13	3	5	16	28.0	23.0	21
		3	5.9	7	13	3	7	16	30.0	23.0	23
		1	2.0	7	13	2	5	15	27.0	22.0	20
		1	2.0	7	12	4	5	16	28.0	23.0	21
		1	2.0	6	13	3	6	16	28.0	22.0	22
		1	2.0	6	13	3	7	16	29.0	22.0	23
		1	2.0	7	13	4	6	17	30.0	24.0	23
	Total N	51	100.0								

TABLE C.1 (cont).

TAXON		N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Gorilla gorilla		45	26.2	7	13	4	5	17	29	24	22
		36	20.9	7	13	3	6	16	29	23	22
		28	16.3	7	13	4	6	17	30	24	23
		17	9.9	7	13	3	5	16	28	23	21
		7	4.1	7	13	3.5	5.5	16.5	29	23.5	22
		5	2.9	7	14	3	6	17	30	24	23
		4	2.3	7	12	4	6	16	29	23	22
		4	2.3	7	14	3	5	17	29	24	22
		3	1.7	7	12	4	5	16	28	23	21
		3	1.7	7	13	3	7	16	30	23	23
		3	1.7	7	13	4	4	17	28	24	21
		2	1.2	7	12	3	5	15	27	22	20
		2	1.2	7	13	3	6.5	16	29.5	23	22.5
		2	1.2	7	13	3.5	6.5	16.5	30	23.5	23
		2	1.2	7	14	4	5	18	30	25	23
		1	0.6	7	12	3	6	15	28	22	21
		1	0.6	7	13	3	4	16	27	23	20
		1	0.6	7	12.5	3.5	6	16	29	23	22
		1	0.6	7	13.5	3.5	5	17	29	24	22
		1	0.6	7	13.5	3.5	6	17	30	24	23
		1	0.6	7	14	3	6.5	17	30.5	24	23.5
		1	0.6	7	13	4	7	17	31	24	24
		1	0.6	7	13.5	3.5	8	17	32	24	25
		1	0.6	7	13.5	4.5	5	18	30	25	23
	Total N	172	100.0								

TABLE C.1 (cont).

TAXON	N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Pongo pygmaeus	71	39.4	7	12	4	5	16	28	23	21
	28	15.6	7	12	4	6	16	29	23	22
	15	8.3	7	12	4	4	16	27	23	20
	8	4.4	7	11	4	6	15	28	22	21
	7	3.9	7	12	3	6	15	28	22	21
	5	2.8	7	11	4	5	15	27	22	20
	4	2.2	7	12	3	5	15	27	22	20
	4	2.2	7	12	5	4	17	28	24	21
	3	1.7	7	12	5	5	17	29	24	22
	3	1.7	7	11.5	3.5	6	15	28	22	21
	3	1.7	7	13	3	5	16	28	23	21
	3	1.7	7	11	5	5	16	28	23	21
	3	1.7	7	13	4	5	17	29	24	22
	2	1.1	7	11.5	3.5	5	15	27	22	20
	2	1.1	7	11	5	6	16	29	23	22
	2	1.1	7	13	4	4	17	28	24	21
	2	1.1	7	12	5	6	17	30	24	23
	1	0.6	7	11	3.5	5.5	14.5	27	21.5	20
	1	0.6	7	11	4	4	15	26	22	19
	1	0.6	7	12	3.5	5.5	15.5	28	22.5	21
	1	0.6	7	13	3	4	16	27	23	20
	1	0.6	7	11	5	4	16	27	23	20
	1	0.6	6	12	4	5	16	27	22	21
	1	0.6	7	12.5	3.5	5	16	28	23	21
	1	0.6	7	11.5	4.5	5	16	28	23	21
	1	0.6	7	12	4	5.5	16	28.5	23	21.5
	1	0.6	7	12	4	7	16	30	23	23
	1	0.6	6.5	11.5	5	5	16.5	28	23	21.5
	1	0.6	7	12	4.5	5.5	16.5	29	23.5	22
	1	0.6	6	13	4	5	17	28	23	22
	1	0.6	6	13	4	6	17	29	23	23
	1	0.6	7	13	4	6	17	30	24	23
Total N	180	100.0								

TABLE C.1 (cont).

TAXON		N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Hylobates lar		63	33.2	7	13	5	4	18	29	25	22
		53	27.9	7	13	5	5	18	30	25	23
		15	7.9	7	13	6	4	19	30	26	23
		8	4.2	7	13	6	3	19	29	26	22
		6	3.2	7	13	6	5	19	31	26	24
		4	2.1	7	13.5	5.5	4	19	30	26	23
		4	2.1	7	14	5	5	19	31	26	24
		3	1.6	7	12	5	5	17	29	24	22
		3	1.6	7	12.5	5.5	4	18	29	25	22
		3	1.6	7	12	6	4	18	29	25	22
		3	1.6	7	13	5	6	18	31	25	24
		3	1.6	7	13	6	3.5	19	29.5	26	22.5
		3	1.6	7	14	5	4	19	30	26	23
		2	1.1	7	14	4	4	18	29	25	22
		2	1.1	7	13	5.5	3.5	18.5	29	25.5	22
		2	1.1	7	13	5.5	4.5	18.5	30	25.5	23
		1	0.5	7	13	4	4	17	28	24	21
		1	0.5	7	12.5	4.5	4	17	28	24	21
		1	0.5	7	12	5	4	17	28	24	21
		1	0.5	7	13	5	3	18	28	25	21
		1	0.5	7	13	5	3.5	18	28.5	25	21.5
		1	0.5	7	13.5	4.5	4	18	29	25	22
		1	0.5	7	13	5	4.5	18	29.5	25	22.5
		1	0.5	7	14	4	5	18	30	25	23
		1	0.5	7	13.5	4.5	5	18	30	25	23
		1	0.5	7	12	6	5	18	30	25	23
		1	0.5	7	13.5	5.5	3	19	29	26	22
		1	0.5	6	14	5	4	19	29	25	23
		1	0.5	6	13	6	4	19	29	25	23
	Total N	190	100.0								

TABLE C.1 (cont).

TAXON	N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Symphalangus syndactylus	15	20.3	7	13	5	5	18	30	25	23
	14	18.9	7	13	5	4	18	29	25	22
	13	17.6	7	13	4	5	17	29	24	22
	5	6.8	7	14	4	4	18	29	25	22
	4	5.4	7	13	4	4	17	28	24	21
	3	4.1	7	14	4	5	18	30	25	23
	3	4.1	7	13.5	4.5	5	18	30	25	23
	2	2.7	7	12	5	4	17	28	24	21
	2	2.7	7	13	4	6	17	30	24	23
	2	2.7	7	13	4.5	4.5	17.5	29	24.5	22
	2	2.7	7	14	5	5	19	31	26	24
	1	1.4	7	12	4	4	16	27	23	20
	1	1.4	7	12	4	5	16	28	23	21
	1	1.4	7	12	5	5	17	29	24	22
	1	1.4	7	13	4	5.5	17	29.5	24	22.5
	1	1.4	7	12.5	4.5	6	17	30	24	23
	1	1.4	7	13.5	4.5	4	18	29	25	22
	1	1.4	7	13	5	6	18	31	25	24
	1	1.4	7	13.5	5	4.5	18.5	30	25.5	23
	1	1.4	7	14	5	4	19	30	26	23
Total N	74	100.0								

TABLE C.1 (cont).

TAXON		N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Nasalis larvatus		39	92.9	7	12	7	3	19	29	26	22
		2	4.8	7	13	6	3	19	29	26	22
		1	2.4	7	12	6	3	18	28	25	21
	Total N	42	100.0								
Trachypithecus sp.		103	82.4	7	12	7	3	19	29	26	22
		10	8.0	7	12	7	2	19	28	26	21
		3	2.4	7	12	6	3	18	28	25	21
		3	2.4	7	13	7	3	20	30	27	23
		1	0.8	7	12	6.5	2.5	18.5	28	25.5	21
		1	0.8	7	13	6	3	19	29	26	22
		1	0.8	7	12.5	6.5	3	19	29	26	22
		1	0.8	7	11.5	7.5	3	19	29	26	22
		1	0.8	7	12.5	7.5	2	20	29.0	27.0	22
		1	0.8	7	12	8	2	20	29.0	27.0	22
	Total N	125	100.0								
Chlorocebus aethiops		47	66.2	7	12	7	3	19	29	26	22
		7	9.9	7	13	6	3	19	29	26	22
		5	7.0	7	12	6	3	18	28	25	21
		4	5.6	7	12.5	6.5	3	19	29	26	22
		2	2.8	7	12	7	2	19	28	26	21
		1	1.4	7	11	7	3	18	28	25	21
		1	1.4	7	12	6	3.5	18	28.5	25	21.5
		1	1.4	7	12	6	4	18	29	25	22
		1	1.4	7	13	6	2	19	28	26	21
		1	1.4	7	11.5	7.5	3	19	29	26	22
		1	1.4	7	13	7	3	20	30	27	23
	Total N	71	100.0								

TABLE C.1 (cont).

TAXON	N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Cercopithecus sp.	55	43.0	7	12	7	3	19	29	26	22
	30	23.4	7	13	6	3	19	29	26	22
	14	10.9	7	12.5	6.5	3	19	29	26	22
	10	7.8	7	12	7	2	19	28	26	21
	8	6.3	7	13	7	3	20	30	27	23
	2	1.6	7	12	6	3	18	28	25	21
	2	1.6	7	12	6.5	2.5	18.5	28	25.5	21
	2	1.6	7	13	7	2	20	29	27	22
	1	0.8	7	11	7	3	18	28	25	21
	1	0.8	7	13	5.5	2.5	18.5	28	25.5	21
	1	0.8	7	13	6	2	19	28	26	21
	1	0.8	7	13	6	4	19	30	26	23
	1	0.8	7	13	6.5	2.5	19.5	29	26.5	22
Total N	128	100.0								
Macaca fascicularis	57	70.4	7	12	7	3	19	29	26	22
	15	18.5	7	12	7	2	19	28	26	21
	4	4.9	7	12	6	3	18	28	25	21
	2	2.5	7	13	6	3	19	29	26	22
	1	1.2	7	12	6.5	3.5	18.5	29	25.5	22
	1	1.2	7	13	7	2	20	29	27	22
	1	1.2	7	13	7	3	20	30	27	23
Total N	81	100.0								

TABLE C.1 (cont).

TAXON		N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Macaca fuscata		623	70.6	7	12	7	3	19	29	26	22
		86	9.7	7	13	6	3	19	29	26	22
		60	6.8	7	13	7	3	20	30	27	23
		40	4.5	7	12	7	4	19	30	26	23
		29	3.3	7	13	6	4	19	30	26	23
		13	1.5	7	12	8	3	20	30	27	23
		8	0.9	7	12	6	3	18	28	25	21
		7	0.8	7	13	6.5	3.5	19.5	30	26.5	23
		3	0.3	7	12	5	4	17	28	24	21
		3	0.3	7	12	6.5	3.5	18.5	29	25.5	22
		3	0.3	7	12	7.5	3.5	19.5	30	26.5	23
		2	0.2	7	12	8	2	20	29	27	22
		2	0.2	7	12.5	6.5	3	19	29	26	22
		2	0.2	7	13	7	2	20	29	27	22
		1	0.1	7	13	6.5	2.5	19.5	29	26.5	22
		1	0.1	7	13	7	4	20	31	27	24
	Total N	883	100.0								
Cercocebus sp.		15	48.4	7	12	7	3	19	29	26	22
		5	16.1	7	13	6	3	19	29	26	22
		3	9.7	7	12.5	6.5	3	19	29	26	22
		2	6.5	7	12	6	3	18	28	25	21
		2	6.5	7	12	6	4	18	29	25	22
		1	3.2	7	13	6	2	19	28	26	21
		1	3.2	7	12.5	6.5	2	19	28	26	21
		1	3.2	7	12	7	2	19	28	26	21
		1	3.2	7	13	7	3	20	30	27	23
	Total N	31	100.0								

TABLE C.1 (cont).

TAXON		N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Theropithecus gelada		28	93.3	7	13	6	3	19	29.0	26.0	22
		1	3.3	7	12	7	3	19	29.0	26.0	22
		1	3.3	7	12	7	4	19	30.0	26.0	23
	Total N	30	100.0								
Papio sp.		52	43.3	7	13	6	3	19	29	26	22
		35	29.2	7	12	7	3	19	29	26	22
		9	7.5	7	12	6	3	18	28	25	21
		7	5.8	7	12	7	2	19	28	26	21
		4	3.3	7	12.5	6.5	3	19	29	26	22
		4	3.3	7	13	7	3	20	30	27	23
		3	2.5	7	13	6	4	19	30	26	23
		2	1.7	7	13	6	2	19	28	26	21
		1	0.8	7	12	5	3	17	27	24	20
		1	0.8	7	11.5	5.5	3	17	27	24	20
		1	0.8	7	12	6	4	18	29	25	22
		1	0.8	7	12.5	6.5	4	19	30	26	23
	Total N	120	100.0								
Lophocebus sp.		75	82.4	7	13	6	3	19	29	26	22
		9	9.9	7	12	7	3	19	29	26	22
		2	2.2	7	13	7	3	20	30	27	23
		1	1.1	7	13	5	4	18	29	25	22
		1	1.1	7	13	5.5	3.5	18.5	29	25.5	22
		1	1.1	7	14	5	4	19	30	26	23
		1	1.1	7	13	6	4	19	30	26	23
		1	1.1	7	13	7	2	20	29	27	22
	Total N	91	100.0								

TABLE C.1 (cont).

TAXON		N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Saimiri sciureus		16	48.5	7	13	7	3	20	30	27	23
		4	12.1	7	13	6	3	19	29	26	22
		4	12.1	7	14	6	3	20	30	27	23
		2	6.1	7	12	6	3	18	28	25	21
		1	3.0	7	12	7	2	19	28	26	21
		1	3.0	7	12	7	3	19	29	26	22
		1	3.0	7	12	7.5	2.5	19.5	29	26.5	22
		1	3.0	7	12	8	3	20	30	27	23
		1	3.0	7	13	6.5	3.5	19.5	30	26.5	23
		1	3.0	7	13	8	2	21	30	28	23
		1	3.0	7	14	7	3	21	31	28	24
	Total N	33	100.0								
Cebus sp.		30	32.3	7	14	5	3	19	29	26	22
		29	31.2	7	14	6	3	20	30	27	23
		8	8.6	7	13	6	3	19	29	26	22
		7	7.5	7	15	5	3	20	30	27	23
		3	3.2	7	12	7	3	19	29	26	22
		2	2.2	7	13	5	3	18	28	25	21
		2	2.2	7	14	6	2	20	29	27	22
		2	2.2	7	14	4	3	18	28	25	21
		1	1.1	7	15	5.5	3.5	20.5	31	27.5	24
		1	1.1	7	14	5	2	19	28	26	21
		1	1.1	7	14	5	2.5	19	28.5	26	21.5
		1	1.1	7	13	6	2	19	28	26	21
		1	1.1	7	13	7	3	20	30	27	23
		1	1.1	7	14.5	5.5	3	20	30	27	23
		1	1.1	7	15	5	3.5	20	30.5	27	23.5
		1	1.1	7	15	6	3	21	31	28	24
		1	1.1	7	14	5	4	19	30	26	23
		1	1.1	7	13	5	3	18	28	25	21
	Total N	93	100.0								

TABLE C.1 (cont).

TAXON		N	Freq. (%)	C	T	L	S	TL	CTLS	CTL	TLS
Alouatta sp.		16	41.0	7	14	5	3	19	29	26	22
		4	10.3	7	14	6	3	20	30	27	23
		4	10.3	7	15	5	3	20	30	27	23
		4	10.3	7	14	5	4	19	30	26	23
		4	10.3	7	15	5	4	20	31	27	24
		2	5.1	7	13	5	3	18	28	25	21
		2	5.1	7	13	6	3	19	29	26	22
		1	2.6	7	13.5	5.5	3	19	29	26	22
		1	2.6	7	16	5	3	21	31	28	24
		1	2.6	7	15.5	5.5	3	21	31	28	24
	Total N	39	100.0								
Ateles sp.		29	74.4	7	14	4	3	18	28	25	21
		3	7.7	7	15	4	3	19	29	26	22
		2	5.1	7	13	4	3	17	27	24	20
		1	2.6	7	13.5	3.5	4	17	28	24	21
		1	2.6	7	13	4	4	17	28	24	21
		1	2.6	6	14	4	3	18	27	24	21
		1	2.6	7	13	5	3	18	28	25	21
		1	2.6	7	14	5	2	19	28	26	21
	Total N	39	100.0								

APPENDIX D

DESCRIPTIVE STATISTICS AND FREQUENCIES OF INDIVIDUAL REGIONS

TABLE D.1. *Homo sapiens* (N=273). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.06	4.95	5.19	Mean	29.20	24.01	22.21
St. Dev.	0.074	0.331	0.333	0.396	St. Dev.	0.467	0.348	0.468
St. Err.	0.004	0.020	0.020	0.024	St. Err.	0.028	0.021	0.028
1					18			
2					19			
3					20			
4			8.8	0.9	21			3.1
5			87.0	79.1	22		0.4	73.4
6	0.7		4.2	20.0	23		4.9	23.3
7	98.9				24		87.9	0.2
8	0.4				25		6.8	
9					26			
10					27			
11		3.3			28	3.1		
12		87.4			29	73.6		
13		9.3			30	23.3		
14					31			
15					32			
16					33			

TABLE D.2. *Homo sapiens* (N=273). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	5.19	Mean	17.01
St. Dev.	0.396	St. Dev.	0.348
St. Err.	0.024	St. Err.	0.021
2		14	
3		15	0.4
4	0.9	16	4.9
5	79.1	17	87.5
6	20.0	18	7.1
7		19	
8		20	
9		21	

TABLE D.3. *Pan troglodytes* (N=271). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	13.12	3.66	5.70	Mean	29.48	23.78	22.48
St. Dev.	0.053	0.394	0.503	0.556	St. Dev.	0.607	0.474	0.608
St. Err.	0.003	0.024	0.031	0.034	St. Err.	0.037	0.029	0.037
1					18			
2			0.4		19			
3			35.1		20			
4			62.7	0.4	21			4.4
5			1.8	34.3	22			44.6
6	0.4			60.0	23		25.3	49.1
7	99.4			5.4	24		71.6	1.8
8	0.2				25		3.1	
9					26			
10					27			
11					28	4.2		
12		3.0			29	45.2		
13		82.1			30	48.7		
14		14.9			31	1.8		
15					32			
16					33			

TABLE D.4. *Pan troglodytes* (N=271). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	5.70	Mean	16.78
St. Dev.	0.556	St. Dev.	0.474
St. Err.	0.034	St. Err.	0.029
2		14	
3		15	
4	0.4	16	25.3
5	34.3	17	71.4
6	60.0	18	3.3
7	5.4	19	
8		20	
9		21	

TABLE D.5. *Pan paniscus* (N=40). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.03	13.44	3.61	6.33	Mean	30.40	24.08	23.38
St. Dev.	0.194	0.622	0.537	0.836	St. Dev.	0.921	0.572	0.897
St. Err.	0.031	0.098	0.085	0.132	St. Err.	0.146	0.090	0.142
1					18			
2					19			
3			41.3		20			
4			56.3		21			
5			2.5	16.3	22			7.5
6	1.3			43.8	23		10.0	7.5
7	95.0			31.3	24		75.0	40.0
8	3.8			8.8	25		12.5	35.0
9					26		2.5	10.0
10					27			
11					28	2.5		
12		6.3			29	13.8		
13		45.0			30	35.0		
14		47.5			31	38.8		
15		1.3			32	10.0		
16					33			

TABLE D.6. *Pan paniscus* (N=40). Sacral and thoracolumbar regions

Region	S	Super region	TL
Mean	6.33	Mean	17.05
St. Dev.	0.836	St. Dev.	0.516
St. Err.	0.132	St. Err.	0.082
2		14	
3		15	
4		16	10.0
5	10.3	17	76.3
6	47.1	18	12.5
7	36.8	19	1.3
8	5.9	20	
9		21	

TABLE D.7. *Gorilla beringei* (N=51). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	6.96	12.90	3.10	5.98	Mean	28.94	22.96	21.98
St. Dev.	0.196	0.300	0.361	0.424	St. Dev.	0.506	0.280	0.510
St. Err.	0.027	0.042	0.051	0.059	St. Err.	0.071	0.039	0.071
1					18			
2			2.0		19			
3			86.3		20			2.0
4			11.8		21			7.8
5				9.8	22		5.9	80.4
6	3.9			82.4	23		92.2	9.8
7	96.1			7.8	24		2.0	
8					25			
9					26			
10					27	2.0		
11					28	9.8		
12		9.8			29	80.4		
13		90.2			30	7.8		
14					31			
15					32			
16					33			

TABLE D.8. *Gorilla beringei* (N=51). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	5.98	Mean	16.00
St. Dev.	0.424	St. Dev.	0.200
St. Err.	0.059	St. Err.	0.028
2		14	
3		15	2.0
4		16	96.1
5	9.8	17	2.0
6	82.4	18	
7	7.8	19	
8		20	
9		21	

TABLE D.9. *Gorilla gorilla* (N=172). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	13.02	3.55	5.54	Mean	29.11	23.57	22.11
St. Dev.	0.000	0.368	0.484	0.621	St. Dev.	0.731	0.551	0.731
St. Err.	0.000	0.028	0.037	0.047	St. Err.	0.056	0.042	0.056
1					18			
2					19			
3			45.6		20			1.7
4			54.1	2.3	21			14.0
5			0.3	45.6	22		1.7	57.6
6				47.7	23		41.6	25.3
7	100.0			3.8	24		54.9	0.9
8				0.6	25		1.7	0.6
9					26			
10					27	1.7		
11					28	14.0		
12		6.1			29	57.6		
13		85.8			30	25.3		
14		8.1			31	0.9		
15					32	0.6		
16					33			

TABLE D.10. *Gorilla gorilla* (N=172). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	5.54	Mean	16.57
St. Dev.	0.621	St. Dev.	0.551
St. Err.	0.047	St. Err.	0.042
2		14	
3		15	1.7
4	2.3	16	41.6
5	45.6	17	54.9
6	47.7	18	1.7
7	3.8	19	
8	0.6	20	
9		21	

TABLE D.11. *Pongo pygmaeus* (N=180). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	6.98	11.93	3.99	5.18	Mean	28.08	22.90	21.10
St. Dev.	0.133	0.437	0.432	0.649	St. Dev.	0.697	0.513	0.708
St. Err.	0.010	0.033	0.032	0.048	St. Err.	0.052	0.038	0.053
1					18			
2					19			0.6
3			10.6		20			16.1
4			80.0	13.3	21		0.27778	58.9
5			9.4	56.1	22		17.8	21.7
6	1.9			30.0	23		73.3	2.8
7	98.1			0.6	24		8.6	
8					25			
9					26	0.6		
10					27	16.7		
11		13.6			28	59.2		
12		79.4			29	21.4		
13		6.9			30	2.2		
14					31			
15					32			
16					33			

TABLE D.12. *Pongo pygmaeus* (N=180). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	5.18	Mean	15.92
St. Dev.	0.649	St Dev	0.523
St. Err.	0.048	St Err	0.039
2		14	0.3
3		15	17.2
4	13.3	16	72.5
5	56.1	17	10.0
6	30.0	18	
7	0.6	19	
8		20	
9		21	

TABLE D.13. *Hylobates lar* (N=190). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	6.99	13.02	5.20	4.33	Mean	29.54	25.21	22.56
St. Dev.	0.102	0.338	0.445	0.617	St. Dev.	0.654	0.475	0.653
St. Err.	0.007	0.025	0.032	0.045	St. Err.	0.047	0.034	0.047
1					18			
2					19			
3				6.8	20			
4			2.9	54.5	21			2.4
5			74.5	37.1	22			46.6
6	1.1		22.6	1.6	23			44.2
7	98.9				24		3.2	6.8
8					25		72.6	
9					26		24.2	
10					27			
11					28	2.4		
12		5.3			29	47.6		
13		87.1			30	43.2		
14		7.6			31	6.8		
15					32			
16					33			

TABLE D.14. *Hylobates lar* (N=190). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	4.33	Mean	18.22
St. Dev.	0.617	St Dev	0.481
St. Err.	0.045	St Err	0.035
2		14	
3	6.8	15	
4	54.5	16	
5	37.1	17	3.2
6	1.6	18	71.6
7		19	25.3
8		20	
9		21	

TABLE D.15. *Symphalangus syndactylus* (N=74). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	13.11	4.55	4.66	Mean	29.32	24.66	22.32
St. Dev.	0.000	0.477	0.477	0.580	St. Dev.	0.757	0.608	0.757
St. Err.	0.000	0.055	0.055	0.067	St. Err.	0.088	0.071	0.088
1					18			
2					19			
3					20			1.4
4			45.3	39.9	21			9.5
5			54.7	54.1	22			49.3
6				6.1	23		2.7	35.8
7	100.0				24		33.8	4.1
8					25		58.8	
9					26		4.7	
10					27	1.4		
11					28	9.5		
12		7.4			29	49.3		
13		74.3			30	35.8		
14		18.2			31	4.1		
15					32			
16					33			

TABLE D.16. *Symphalangus syndactylus* (N=74). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	4.66	Mean	17.66
St. Dev.	0.580	St Dev	0.608
St. Err.	0.067	St Err	0.071
2		14	
3		15	
4	39.9	16	2.7
5	54.1	17	33.8
6	6.1	18	58.8
7		19	4.7
8		20	
9		21	

TABLE D.17. *Nasalis larvatus* (N=42). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.05	6.93	3.00	Mean	28.98	25.98	21.98
St. Dev.	0.000	0.216	0.261	0.000	St. Dev.	0.154	0.154	0.154
St. Err.	0.000	0.033	0.040	0.000	St. Err.	0.024	0.024	0.024
1					18			
2					19			
3				100.0	20			
4					21			2.4
5					22			97.6
6			7.1		23			
7	100.0		92.9		24			
8					25		2.4	
9					26		97.6	
10					27			
11					28	2.4		
12		95.2			29	97.6		
13		4.8			30			
14					31			
15					32			
16					33			

TABLE D.18. *Nasalis larvatus* (N=42). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	3.00	Mean	18.98
St. Dev.	0.000	St Dev	0.154
St. Err.	0.000	St Err	0.024
2		14	
3	100.0	15	
4		16	
5		17	
6		18	2.4
7		19	97.6
8		20	
9		21	

TABLE D.19. *Trachypithecus sp.* (N=125). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.04	6.98	2.90	Mean	28.91	26.01	21.91
St. Dev.	0.000	0.192	0.219	0.298	St. Dev.	0.360	0.258	0.360
St. Err.	0.000	0.017	0.020	0.027	St. Err.	0.032	0.023	0.032
1					18			
2				10.0	19			
3				90.0	20			
4					21			11.2
5					22			86.4
6			4.0		23			2.4
7	100.0		94.4		24			
8			1.6		25			2.8
9					26		93.2	
10					27		4.0	
11		0.4			28	11.2		
12		95.6			29	86.4		
13		4.0			30	2.4		
14					31			
15					32			
16					33			

TABLE D.20. *Trachypithecus sp.* (N=125). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	2.90	Mean	19.01
St. Dev.	0.298	St Dev	0.258
St. Err.	0.027	St Err	0.023
2	10.0	14	
3	90.0	15	
4		16	
5		17	
6		18	2.8
7		19	93.2
8		20	4.0
9		21	

TABLE D.21. *Chlorocebus aethiops* (N=71). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.13	6.77	2.98	Mean	28.88	25.90	21.88
St. Dev.	0.000	0.378	0.421	0.245	St. Dev.	0.363	0.345	0.363
St. Err.	0.000	0.045	0.050	0.029	St. Err.	0.043	0.041	0.043
1					18			
2				4.2	19			
3				93.7	20			
4				2.1	21			13.4
5					22			85.2
6			23.9		23			1.4
7	100.0		75.4		24			
8			0.7		25		11.3	
9					26		87.3	
10					27		1.4	
11		2.1			28	13.4		
12		82.4			29	85.2		
13		15.5			30	1.4		
14					31			
15					32			
16					33			

TABLE D.22. *Chlorocebus aethiops* (N=71). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	2.98	Mean	18.90
St. Dev.	0.245	St Dev	0.345
St. Err.	0.029	St Err	0.041
2	4.2	14	
3	93.7	15	
4	2.1	16	
5		17	
6		18	11.3
7		19	87.3
8		20	1.4
9		21	

TABLE D.23. *Cercopithecus sp.* (N=128). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.39	6.66	2.89	Mean	28.94	26.05	21.94
St. Dev.	0.000	0.478	0.447	0.326	St. Dev.	0.448	0.329	0.448
St. Err.	0.000	0.042	0.040	0.029	St. Err.	0.040	0.029	0.040
1					18			
2				11.7	19			
3				87.5	20			
4				0.8	21			13.3
5			0.4		22			79.7
6			33.6		23			7.0
7	100.0		66.0		24			
8					25		3.5	
9					26		88.3	
10					27		8.2	
11		0.8			28	13.3		
12		59.4			29	79.7		
13		39.8			30	7.0		
14					31			
15					32			
16					33			

TABLE D.24. *Cercopithecus sp.* (N=128). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	2.89	Mean	19.05
St. Dev.	0.326	St Dev	0.329
St. Err.	0.029	St Err	0.029
2	11.7	14	
3	87.5	15	
4	0.8	16	
5		17	
6		18	3.5
7		19	88.3
8		20	8.2
9		21	

TABLE D.25. *Macaca fascicularis* (N=81). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.05	6.92	2.81	Mean	28.78	25.97	21.78
St. Dev.	0.000	0.218	0.268	0.407	St. Dev.	0.447	0.278	0.447
St. Err.	0.000	0.024	0.030	0.045	St. Err.	0.050	0.031	0.050
1					18			
2				19.8	19			
3				79.6	20			
4				0.6	21			24.7
5					22			74.1
6			8.0		23			1.2
7	100.0		92.0		24			
8					25		6.8	
9					26		90.7	
10					27		2.5	
11					28	24.7		
12		96.3			29	74.1		
13		3.7			30	1.2		
14					31			
15					32			
16					33			

TABLE D.26. *Macaca fascicularis* (N=81). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	2.81	Mean	18.97
St. Dev.	0.407	St Dev	0.278
St. Err.	0.045	St Err	0.031
2	19.8	14	
3	79.6	15	
4	0.6	16	
5		17	
6		18	6.8
7		19	90.7
8		20	2.5
9		21	

TABLE D.27. *Macaca fuscata* (N=883). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.21	6.87	3.08	Mean	29.16	26.08	22.16
St. Dev.	0.000	0.408	0.395	0.290	St. Dev.	0.404	0.330	0.404
St. Err.	0.000	0.014	0.013	0.010	St. Err.	0.014	0.011	0.014
1					18			
2				0.5	19			
3				90.5	20			
4				9.0	21			1.2
5			0.3		22			81.4
6			14.7		23			17.2
7	100.0		83.1		24		0.3	0.1
8			1.9		25		1.1	
9					26		89.1	
10					27		9.5	
11					28	1.2		
12		78.8			29	81.4		
13		21.2			30	17.2		
14					31	0.1		
15					32			
16					33			

TABLE D.28. *Macaca fuscata* (N=883). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	3.08	Mean	19.08
St. Dev.	0.290	St Dev	0.330
St. Err.	0.010	St Err	0.011
2	0.5	14	
3	90.5	15	
4	9.0	16	
5		17	0.3
6		18	1.1
7		19	89.1
8		20	9.5
9		21	

TABLE D.29. *Cercocebus sp.* (N=31). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.29	6.61	2.97	Mean	28.87	25.90	21.87
St. Dev.	0.000	0.424	0.460	0.407	St. Dev.	0.428	0.396	0.428
St. Err.	0.000	0.076	0.083	0.073	St. Err.	0.077	0.071	0.077
1					18			
2				9.7	19			
3				83.9	20			
4				6.5	21			16.1
5					22			80.6
6			38.7		23			3.2
7	100.0		61.3		24			
8					25		12.9	
9					26		83.9	
10					27		3.2	
11					28	16.1		
12		71.0			29	80.6		
13		29.0			30	3.2		
14					31			
15					32			
16					33			

TABLE D.30. *Cercocebus sp.* (N=31). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	2.97	Mean	18.90
St. Dev.	0.407	St Dev	0.396
St. Err.	0.073	St Err	0.071
2	9.7	14	
3	83.9	15	
4	6.5	16	
5		17	
6		18	12.9
7		19	83.9
8		20	3.2
9		21	

TABLE D.31. *Theropithecus gelada* (N=30). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.93	6.07	3.03	Mean	29.03	26.00	22.03
St. Dev.	0.000	0.254	0.254	0.183	St. Dev.	0.183	0.000	0.183
St. Err.	0.000	0.046	0.046	0.033	St. Err.	0.033	0.000	0.033
1					18			
2					19			
3				96.7	20			
4				3.3	21			
5					22			96.7
6			93.3		23			3.3
7	100.0		6.7		24			
8					25			
9					26		100.0	
10					27		0.0	
11					28			
12		6.7			29	96.7		
13		93.3			30	3.3		
14					31			
15					32			
16					33			

TABLE D.32. *Theropithecus gelada* (N=30). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	3.03	Mean	19.00
St. Dev.	0.183	St Dev	0.000
St. Err.	0.033	St Err	0.000
2		14	
3	96.7	15	
4	3.3	16	
5		17	
6		18	
7		19	100.0
8		20	
9		21	

TABLE D.33. *Papio sp.* (N=120). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.53	6.39	2.97	Mean	28.88	25.92	21.88
St. Dev.	0.000	0.497	0.503	0.341	St. Dev.	0.522	0.422	0.522
St. Err.	0.000	0.045	0.046	0.031	St. Err.	0.048	0.039	0.048
1					18			
2				7.5	19			
3				88.3	20			1.7
4				4.2	21			15.0
5			1.3		22			76.7
6			58.3		23			6.7
7	100.0		40.4		24			1.7
8					25		15.8	
9					26		75.8	
10					27	1.7	6.7	
11		0.4			28	15.0		
12		46.7			29	76.7		
13		52.9			30	6.7		
14					31			
15					32			
16					33			

TABLE D.34. *Papio sp.* (N=120). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	2.97	Mean	18.92
St. Dev.	0.341	St Dev	0.422
St. Err.	0.031	St Err	0.039
2	7.5	14	
3	88.3	15	
4	4.2	16	
5		17	1.7
6		18	8.3
7		19	86.7
8		20	3.3
9		21	

TABLE D.35. *Lophocebus sp.* (N=91). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	12.91	6.10	3.03	Mean	29.04	26.02	22.04
St. Dev.	0.000	0.321	0.384	0.216	St. Dev.	0.206	0.217	0.206
St. Err.	0.000	0.034	0.040	0.023	St. Err.	0.022	0.023	0.022
1					18			
2				1.1	19			
3				95.1	20			
4				3.8	21			
5			2.7		22			95.6
6			84.1		23			4.4
7	100.0		13.2		24			
8					25		1.6	
9					26		95.1	
10					27		3.3	
11					28			
12		9.9			29	95.6		
13		89.0			30	4.4		
14		1.1			31			
15					32			
16					33			

TABLE D.36. *Lophocebus sp.* (N=91). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	3.03	Mean	19.02
St. Dev.	0.216	St Dev	0.217
St. Err.	0.023	St Err	0.023
2	1.1	14	
3	95.1	15	
4	3.8	16	
5		17	
6		18	1.6
7		19	95.1
8		20	3.3
9		21	

TABLE D.37. *Saimiri sciureus* (N=39). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	6.97	13.00	6.77	2.92	Mean	29.67	26.74	22.69
St. Dev.	0.160	0.562	0.548	0.293	St. Dev.	0.662	0.668	0.655
St. Err.	0.026	0.090	0.088	0.047	St. Err.	0.106	0.107	0.105
1					18			
2				9.0	19			
3				89.7	20			
4				1.3	21			7.7
5					22			17.9
6	2.6		29.5		23			71.8
7	97.4		64.1		24			2.6
8			6.4		25		5.1	
9					26		23.1	
10					27		64.1	
11					28	7.7	7.7	
12		15.4			29	20.5		
13		69.2			30	69.2		
14		15.4			31	2.6		
15					32			
16					33			

TABLE D.38. *Saimiri sciureus* (N=39). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	2.92	Mean	19.77
St. Dev.	0.293	St Dev	0.657
St. Err.	0.047	St Err	0.105
2	9.0	14	
3	89.7	15	
4	1.3	16	
5		17	
6		18	5.1
7		19	20.5
8		20	66.7
9		21	7.7

TABLE D.39. *Cebus sp.* (N=63). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	13.94	5.52	2.98	Mean	29.44	26.47	22.44
St. Dev.	0.000	0.540	0.585	0.276	St. Dev.	0.685	0.628	0.685
St. Err.	0.000	0.068	0.074	0.035	St. Err.	0.086	0.079	0.086
1					18			
2				5.6	19			
3				91.3	20			
4			1.6	3.2	21			8.7
5			47.6		22			40.5
6			47.6		23			48.4
7	100.0		3.2		24			2.4
8					25		6.3	
9					26		41.3	
10					27		51.6	
11					28	8.7	0.8	
12		1.6			29	40.5		
13		12.7			30	48.4		
14		75.4			31	2.4		
15		10.3			32			
16					33			

TABLE D.40. *Cebus sp.* (N=63). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	2.98	Mean	19.47
St. Dev.	0.276	St Dev	0.628
St. Err.	0.035	St Err	0.079
2	5.6	14	
3	91.3	15	
4	3.2	16	
5		17	
6		18	6.3
7		19	41.3
8		20	51.6
9		21	0.8

TABLE D.41. *Alouatta sp.* (N=39). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	7.00	14.18	5.18	3.21	Mean	29.56	26.36	22.56
St. Dev.	0.000	0.674	0.371	0.409	St. Dev.	0.821	0.668	0.821
St. Err.	0.000	0.108	0.059	0.066	St. Err.	0.131	0.107	0.131
1					18			
2					19			
3				79.5	20			
4				20.5	21			5.1
5			82.1		22			48.7
6			17.9		23			30.8
7	100.0				24			15.4
8					25		5.1	
9					26		59.0	
10					27		30.8	
11					28	5.1	5.1	
12					29	48.7		
13		11.5			30	30.8		
14		62.8			31	15.4		
15		21.8			32			
16		3.8			33			

TABLE D.42. *Alouatta sp.* (N=39). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	3.21	Mean	19.36
St. Dev.	0.409	St Dev	0.668
St. Err.	0.066	St Err	0.107
2		14	
3	79.5	15	
4	20.5	16	
5		17	
6		18	5.1
7		19	59.0
8		20	30.8
9		21	5.1

TABLE D.43. *Ateles sp.* (N=39). Vertebral regions and super regions.

Region	C	T	L	S	Super region	CTLS	CTL	TLS
Mean	6.97	13.96	4.04	3.03	Mean	28.00	24.97	21.03
St. Dev.	0.160	0.435	0.240	0.280	St. Dev.	0.397	0.486	0.362
St. Err.	0.026	0.070	0.038	0.045	St. Err.	0.064	0.078	0.058
1					18			
2				2.6	19			
3			1.3	92.3	20			5.1
4			93.6	5.1	21			87.2
5			5.1		22			7.7
6	2.6				23			
7	97.4				24		12.8	
8					25		76.9	
9					26		10.3	
10					27	7.7		
11					28	84.6		
12					29	7.7		
13		11.5			30			
14		80.8			31			
15		7.7			32			
16					33			

TABLE D.44. *Ateles sp.* (N=39). Sacral and thoracolumbar regions.

Region	S	Super region	TL
Mean	3.03	Mean	18.00
St. Dev.	0.280	St Dev	0.459
St. Err.	0.045	St Err	0.073
2	2.6	14	
3	92.3	15	
4	5.1	16	
5		17	10.3
6		18	79.5
7		19	10.3
8		20	
9		21	

APPENDIX E

SPECIMENS AND SAMPLE SIZES ANALYZED IN CHAPTER 4

TABLE E.1. List of specimens, species, genera, major clades, and sample sizes used in Ch. 4.

Major clade	Genus (#)	Species (#)	Placement*	N	References
Monotremata	2	2		2	
	Ornithorhynchus	*anatinus*	+5	1	2
	Tachyglossus	*aculeatus*	+3	1	2
Marsupalia	19	22		24	
	Caluromys	*philander*	+4	1	3
	Dasyuroides	*byrnei*	+3	1	2
	Dendrolagus	*goodfellowi*	+2	1	2
	Didelphis	*albiventris*	+4	1	2
	Didelphis	*marsupalis*	+4	1	3
	Dorcopsis	*muelleri*	+2	1	1
	Macropus	*fuliginosus*	+2	1	2
	Macropus	*giganteus*	+3	1	1
	Macropus	*rufogriseus*	+2	1	1
	Metachirus	*nudicaudatus*	+3.5	2	1, 3
	Micoureus	*demerarae*	+3	1	3
	Monodelphis	*brevicaudata*	+3	1	3
	Myrmecobius	*fasciatus*	+3	1	2
	Perameles	*gunnii*	+2	1	2
	Petaurus	*australis*	+4	1	2
	Phalanger	*orientalis*	+4	1	1
	Phascolomys	*mitchelli*	+3	1	2
	Philander	*opossum*	+4	2	1, 2

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
	Rhyncholestes	*raphanurus*	+2	1	2
	Sarcophilis	*harrisi, laniarius*	+3	1	2
	Thylacinus	*cynocephalus*	+4	1	2
	Vombatus	*ursinus*	+3	1	2
Afrotheria	14	15		17	
	Chrysochloris	*asiatica*	+4	1	2
	Dendrohyrax	*arboreus*	ND	1	2
	Dugong	*dugong*	+7 (ND)	1	1
	Elephantulus	*rufescens*	+1	1	2
	Elephas	*maximus*	+4	2	1, 2
	Hemicentetes	*nigriceps*	+4	1	2
	Loxodonta	*africana*	+3	1	1
	Macroscelides	*proboscideus*	+4	1	2
	Macroscelides	*sp.*	+1	1	1
	Orycteropus	*afer*	+3	2	1, 2
	Petrodromus	*tetradactylus*	+2	1	2
	Procavia	*capensis*	ND	1	2
	Setifer	*setosus*	+4	1	2
	Tenrec	*ecaudatus*	+5	1	2
	Trichechus	*inunguis*	+8	1	1
	Trichechus	*sp.*	ND	1	2

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
Xenarthra	6	8		20	
	Bradypus	*tridactylus*	-0.5	2	4
	Bradypus	*variegatus*	+0.5	5	2, 4
	Choloepus	*didactylus*	0	5	1, 2, 4
	Choloepus	*hoffmanni*	+0.5	3	4
	Dasypus	*novemcinctus*	+3.5	2	1, 2
	Myrmecophaga	*tridactyla*	+2	1	2
	Priodontes	*maximus*	+3	1	2
	Tamandua	*mexicana*	+3	1	2
Eulipotyphla	10	10		12	
	Blarina	*brevicauda*	+1	1	2
	Condylura	*cristata*	+1	1	2
	Crocidura	*foxi*	+2	1	2
	Echinosorex	*albus*	+3	1	2
	Erinaceus	*europaeus*	+3	2	1, 2
	Galemys	*pyrenaicus*	+1	1	2
	Paraechinus	*aethiopica*	+5	1	2
	Scutisorex	*somereni*	0	1	2
	Solenodon	*paradoxus*	+3	1	2
	Talpa	*europaea*	+1	2	1, 2

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
Chiroptera	7	7		7	
	Balantiopteryx	*io*	0	1	2
	Hipposideros	*commersonii*	+3	1	2
	Lasionycteris	*noctivagans*	+1	1	2
	Lonchorhina	*aurita*	0	1	2
	Phyloderma	*stenops*	+1	1	2
	Pteropus	*sp.*	+2	1	2
	Rhinolophus	*sp.*	-1	1	2
Ferae	22	26		166	
	Manis	*javanica*	+3	1	2
	Manis	*temminckii*	+1	1	5
	Manis	*sp.*	+3.5	1	1, 5
	Ailuropoda	*melanoleuca*	+2	1	5
	Ailurus	*fulgens*	+3	1	2
	Canis	*familiaris*	+3	139	1, 6
	Cystophora	*cristata*	+4	1	2
	Eira	*barbara*	+3	1	2
	Eumetopias	*jubatus*	+3	1	2
	Herpestes	*ichneumon*	+3	1	2
	Hyaena	*hyaena*	+3	1	2
	Lutra	*lutra*	+2	1	1
	Lycaon	*pictus*	+3	1	2
	Mustela	*putorius*	+4	1	1

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
	Mydaus	*javanicus*	+1	1	2
	Nasua	*narica*	+3	1	2
	Odobenus	*rosmarus*	+1	1	2
	Otocyon	*megalotis*	+3	1	2
	Panthera	*leo*	+2	2	1, 2
	Phoca	*vitulina*	+4	1	1
	Potos	*flavus*	+3	1	2
	Procyon	*lotor*	+3	1	2
	Ursus	*americanus*	+4	1	1
	Ursus	*arctos*	+4	1	2
	Ursus	*malayanus*	+4	1	1
	Ursus	*maritimus*	+3	1	5
	Zalophus	*californianus*	+3	1	1
Perissodactyla	5	7		7	
	Ceratotherium	*simum*	+3	1	2
	Diceros	*bicornis*	-3	1	1
	Equus	*ferus*	-2	1	1
	Equus	*quagga*	+2	1	2
	Rhinoceros	*sondaicus*	-3	1	1
	Tapirus	*bairdii*	-5	1	2
	Tapirus	*terrestris*	-5	1	1

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
Artiodactyla	15	17		18	
	Antilocapra	*americana*	+2	1	2
	Bos	*primigenius*	0	1	1
	Camelus	*bactrianus*	+1	1	1
	Capra	*aegagrus*	+2	1	1
	Capreolus	*capreolus*	+1	1	1
	Cephalophus	*natalensis*	+2	1	2
	Gazella	*soemmerringii*	+2	1	2
	Gazella	*sp.*	+2	1	1
	Lama	*glama*	+1	1	1
	Litocranius	*walleri*	+1	1	2
	Mazama	*americana*	+1	1	1
	Odocoileus	*virginianus*	+2	1	1
	Okapia	*johnstoni*	+2	1	1
	Sus	*scrofa*	+4	2	1, 2
	Tayassu	*pecari*	+3	1	2
	Tragulus	*javanicus*	+2	1	1
	Tragulus	*kanchil*	+2	1	2
Whippomorpha	9	11		13	
	Hippopotamus	*amphibius*	+4	2	1, 2
	Balaenoptera	*acutorostrata*	ND	1	1
	Balaenoptera	*borealis*	ND	1	1
	Balaenoptera	*musculus*	ND	1	1

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
	Delphinapterus	*leucas*	ND	1	1
	Delphinus	*delphis*	+9	1	1
	Grampus	*griseus*	+10	1	1
	Hyperoodon	*ampullatus*	ND	1	1
	Phocoena	*phocoena*	ND	2	1
	Pseudorca	*crassidens*	+6	1	1
	Tursiops	*truncatus*	+8	1	1
Lagomorpha	3	3		3	
	Lepus	*alleni*	+2	1	2
	Ochotona	*rufescens*	+2	1	2
	Sylvilagus	*floridans*	+6	1	2
Rodentia	29	31		32	
	Allactaga	*sibirica*	+1	1	1
	Allactaga	*tetradactyla*	+2	1	2
	Anomalurus	*pelii*	+3	1	2
	Aplodontia	*rufa*	+3	1	2
	Arvicola	*terrestris*	+2	1	1
	Callosciurus	*prevosti*	+3	1	2
	Castor	*canadensis*	+4	1	2
	Cavia	*porcellus*	+1	1	1
	Chinchilla	*lanigera*	+3	1	2
	Coendou	*prehensilis*	+3	1	2
	Cricetus	*cricetus*	+2	1	1

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
	Cuniculus	*paca*	+0.5	2	1, 2
	Dipodomys	*spectabilis*	+1	1	1
	Dolichotis	*patagonum*	0	1	2
	Georychus	*capensis*	+2	1	2
	Hydrochoerus	*hydrochaeris*	0	1	2
	Hystrix	*cristata*	+2	1	2
	Jaculus	*jaculus*	+1	1	1
	Jaculus	*orientalis*	+1	1	1
	Lagostomus	*trichodactylus*	+2	1	2
	Maxomys	*panglima*	+2	1	2
	Peromyscus	*leucopus*	+2	1	2
	Petaurista	*annamensis*	+3	1	2
	Psammomys	*obesus*	+2	1	1
	Rhizomys	*sumatrensis*	+2	1	2
	Sciurus	*vulgaris*	+2	1	1
	Sigmodon	*hispidus*	+2	1	2
	Spalacopus	*poeppigi*	+3	1	2
	Spalax	*ehrenbergi*	+4	1	2
	Thryonomys	*gregorianus*	+2	1	2
	Zapus	*hudsonius*	+1	1	2

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
Scandentia	2	4		7	
	Ptilocerus	*lowii*	+3.5	2	1, 2
	Tupaia	*glis*	+3	2	2, 5
	Tupaia	*javanica*	+3	1	5
	Tupaia	*minor*	+3	1	5
	Tupaia	*sp.*	+2	1	1
Dermoptera	1	1		1	
	Cynocephalus	*volans*	+1	1	2
Primates	51	81		1087	
	Alouatta	*palliata*	+3	7	2, 5
	Alouatta	*villosa*	+3	2	7
	Alouatta	*sp.*	+2	12	8, 5
	Aotus	*trivirgatus*	+1.5	2	2, 5
	Aotus	*sp.*	+1.5	7	5
	Arctocebus	*calabarensis*	+1	23	5
	Ateles	*fusciceps*	+1	1	2
	Ateles	*geoffroyi*	+2	5	5
	Ateles	*paniscus*	+1.5	1	1
	Ateles	*sp.*	+1.5	25	8, 5
	Avahi	*laniger*	+1	3	5
	Brachyteles	*arachnoides*	+1.5	3	8, 5
	Bunopithecus	*hoolock*	0	1	7
	Cacajao	*calvus*	+2	2	5

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
	Cacajao	*melanocephalus*	+2	7	5
	Callicebus	*moloch*	+2	5	5
	Callithrix	*jacchus*	+3	1	5
	Callithrix	*sp.*	+3	9	1, 5
	Cebus	*albifrons*	+3	1	2
	Cebus	*nigrivittatus*	+4	1	7
	Cebus	*sp.*	+3	5	9, 5
	Cercocebus	*atys*	+2.5	2	7
	Cercocebus	*torquatus*	+3	3	5
	Cercopithecus	*ascanius*	+2.5	51	5
	Cercopithecus	*mona*	+2.5	2	5
	Cheirogaleus	*major*	+2	2	2, 5
	Chiropotes	*satanas*	+3	2	5
	Chlorocebus	*aethiops*	+2	1	10
	Daubentonia	*madagascariensis*	+3	1	5
	Erythrocebus	*patas*	+1.5	2	1, 2
	Eulemur	*fulvus*	+2	2	5
	Eulemur	*macaco*	+2	5	2, 5
	Eulemur	*mongoz*	+2	1	5
	Galago	*senegalensis*	+2	1	2
	Gorilla	*beringei*	0	2	5
	Gorilla	*gorilla*	0	106	5
	Hapalemur	*griseus*	+2	3	5

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
	Hapalemur	*sp.*	+3	1	5
	Homo	*sapiens*	0	117	5
	Hylobates	*agilis*	0	7	7, 5
	Hylobates	*klossi*	0	1	5
	Hylobates	*lar*	0	74	5
	Hylobates	*muelleri*	0	1	5
	Hylobates	*pileatus*	0	4	5
	Indri	*indri*	+1	12	9, 5
	Lagothrix	*lagotricha*	+2	6	5
	Lagothrix	*poeppigii*	+2	1	5
	Lagothrix	*sp.*	+2	19	8, 5
	Lemur	*catta*	+2	8	1, 5
	Leontopithecus	*sp.*	+2	2	2, 5
	Lepilemur	*leucopus*	+2	1	5
	Lepilemur	*mustelinus*	+2	1	5
	Lepilemur	*sp.*	+2	3	5
	Lophocebus	*aterrimus*	+3	1	2
	Loris	*tardigradus*	+2	4	2, 5
	Macaca	*arctoides*	+2	6	2, 5
	Macaca	*mulatta*	+3	1	1
	Macaca	*nigra*	+2	1	5
	Macaca	*silenus*	+2	1	5
	Macaca	*sylvanus*	+2	3	5

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
	Macaca	*sp.*	+2	5	5
	Mandrillus	*leucophaeus*	+2	2	5
	Mandrillus	*sp.*	+2	1	5
	Nasalis	*larvatus*	+2	3	2, 5
	Nomascus	*concolor*	0	1	5
	Nycticebus	*coucang*	+1	6	2, 5
	Nycticebus	*sp.*	0	1	1
	Otolemur	*crassicaudatus*	+1	3	5
	Otolemur	*garnettii*	+2	1	5
	Pan	*paniscus*	0	22	5
	Pan	*troglodytes*	0	104	5
	Papio	*anubis*	+3	2	5
	Papio	*cynocephalus*	+2	1	5
	Papio	*hamadryas*	+2	73	5
	Papio	*papio*	+3	1	2
	Papio	*ursinus*	+3	1	5
	Perodicticus	*potto*	+1	13	5
	Pongo	*pygmaeus*	0	82	5
	Presbytis	*melalophos*	+2	7	5
	Presbytis	*rubicunda*	+2	3	5
	Propithecus	*diadema*	+1	2	5
	Propithecus	*verreauxi*	+1	1	2
	Propithecus	*sp.*	+2	10	5

TABLE E.1 (cont).

Major clade	Genus (#)	Species (#)	Placement*	N	References
	Pygathrix	*nemaeus*	+2	1	5
	Saguinus	*sp.*	+2	6	5
	Saimiri	*sciureus*	+2	11	1, 2, 5
	Saimiri	*sp.*	+2	5	5
	Semnopithecus	*entellus*	+3	2	5
	Symphalangus	*syndactylus*	0	34	5
	Tarsius	*bancanus*	+2	1	2
	Tarsius	*sp.*	+3	2	1, 5
	Theropithecus	*gelada*	+2.5	4	5
	Trachypithecus	*cristatus*	+2	88	5
	Varecia	*variegata*	+3	2	5
	Varecia	*sp.*	+3	2	9, 5
TOTAL	**195**	**245**		**1416**	

* Placement = position of the diaphragmatic vertebra relative to the last rib-bearing vertebra (cranial = '+', caudal = '-', common = '0'; see Chapter 4 for more details). References are as follows: 1 (Slijper, 1946), 2 (Filler, 1986), 3 (Argot, 2003), 4 (E. Buchholtz, personal communication), 5 (S. Williams, new data), 6 (Breit and Kunzel, 2002), 7 (Clauser, 1980), 8 (Erikson, 1963), 9 (Shapiro, 1993), 10 (Washburn, 1963).

APPENDICES REFERENCES

Adam, P.J., 2004. *Monachus tropicalis*. Mammalian Species 747, 1-9.

Aimi, M., 1994. Numerical variation of vertebrae in Japanese macaques, *Macaca fuscata*. Anthropol. Sci. 102, 1-10.

Allen, J.A., 1917. The skeletal characters of *Scutisorex* Thomas. Bull. Am. Mus. Nat. Hist. 37, 769-784.

Anderson, S., 1969. *Macrotus waterhousii*. Mammalian Species 1, 1-4.

Andrews, P., Groves, C.P., 1976. Gibbons and brachiation. In: D.M. Rumbaugh (Ed.), Gibbon and Siamang, Vol. 4. Karger, Basel, pp. 167-218.

Argot, C., 2003. Functional-adaptive anatomy of the axial skeleton of some extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J. Morph. 255, 279-300.

Asher, R.J., Bennett, N., Lehmann, T., 2009. The new framework for understanding placental mammal evolution. BioEssays 31, 853-864.

Asher, R.J., Lin, K.H., Kardjilov, N., Hautier, L., 2011. Variability and constraint in the mammalian vertebral column. J. Evol. Biol. 24, 1080-1090.

Ashton, E.H., Oxnard, C.E., 1964. Locomotor patterns in primates. Proc. Zool. Soc. Lond. 142, 1-28.

Avis, V., 1962. Brachiation: the crucial issue for man's ancestry. Southwestern J. Anthropol. 18, 119-148.

Barnett, A.A., 2005. *Cacajao melanocephalus*. Mammalian Species 776, 1-6.

Breit, S., Künzel, W., 2002. The diameter of the vertebral canal in dogs in cases of lumbosacral transitional vertebrae or numerical vertebral variations. Anat. Embryol. 205, 125-133.

Bryant, M.D., 1945. Phylogeny of Nearctic Sciuridae. Am. Mid. Nat. 33, 257-390.

Buchholtz, E.A., 2011. Vertebral and rib anatomy in *Caperea marginata*: implications for evolutionary patterning of the mammalian vertebral column. Marine Mammal Science 27, 382-397.

Buchholtz, E.A., Schur, S.A., 2004. Vertebral osteology in Delphinidae (Cetacea). Zool. J. Linn. Soc. 140, 383-401.

Buchholtz, E.A., Stepien, C.C., 2009. Anatomical transformation in mammals: developmental origin of aberrant cervical anatomy in tree sloths. Evol. Dev. 11, 69-79.

Buchholtz, E.A., Wolkovich, E.M., Cleary, R.J., 2005. Vertebral osteology and complexity in *Lagenorhynchus acutus* (Delphinidae) with comparison to other delphinoid genera. Mar. Mamm. Sci. 21, 411-428.

Cartmill, M., Milton, K., 1977. The lorisiform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. Am. J. Phys. Anthropol. 47, 249-272.

Chang, C.-H., Jang, C.-M., 2004. On the processing and mounting of a skeleton of a white rhinoceros, *Ceratotherium sinum*. Coll. Res. 17, 58-69.

Clauser, D., 1980. Functional and comparative anatomy of the primate spinal column: some locomotor and postural adaptations. Ph.D. dissertation, University of Wisconsin-Milwaukee.

Crompton, R.H., Sellers, W.I., Thorpe, S.K.S., 2010. Arboreality, terrestriality and bipedalism. Phil. Trans. R. Soc. B 365, 3301-3314.

Crompton, R.H., Thorpe, S.K.S., 2007. Response to comment on "Origin of human bipedalism as an adaptation for locomotion on flexible branches". Science 318, 1066e.

Crompton, R.H., Thorpe, S., Welite, W., Yu, L., Payne, R., Savage, R., Carey, T., Aerts, P., Elsacker, V., Hofstetter, A., Günther, M., Richardson, J., 2003. The biomechanical evolution of erect bipedality. Cour. Forsch.-Inst. Seneckenberg 243, 135-146.

Crompton, R.H., Vereecke, E.E., Thorpe, S.K.S., 2008. Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. J. Anat. 212, 501-543.

Dagg, A.I., 1971. *Giraffa camelopardalis*. Mammalian Species 5, 1-8.

Davis, D.D., 1964. The giant panda: a morphological study of evolutionary mechanisms. Fieldiana: Zool. Mem. 8, 1-334.

Erikson, G., 1963. Brachiation in New World monkeys and in anthropoid apes. Symp. Zool. Soc. Lond. 10, 135-163.

Filler, A.G., 1986. Axial character seriation in mammals: an historical and morphological exploration of the origin, development, use, and current collapse of the homology paradigm. Ph.D. dissertation, Harvard University.

Filler, A.G., 2007. The Upright Ape. New Page Books, Franklin Lakes, NJ.

Fleagle, J.G., 1976. Locomotion and posture of the Malayan siamang and implications for hominoid evolution. Folia Primatol. 26, 245-269.

Fleagle, J.G., Meldrum, D.J., 1988. Locomotor behavior and skeletal morphology of two sympatric pitheciine monkeys, *Pithecia pithecia* and *Chiropotes satanas*. Am. J. Primatol. 16, 227-249.

Fleagle, J.G., Stern, J.T., Jungers, W.L., Susman, R.L., Vangor, A.K., Wells, J.P., 1981. Climbing: a biomechanical link with brachiation and with bipedalism. Symp. Zool. Soc. Lond. 48, 359-375.

Flower, W.H., 1884. Catalogue of the Specimens Illustrating the Osteology and Dentition of the Vertebrated Animals, Recent and Extinct, Contained in the Museum of the Royal College of Surgeons of England, Part II. Class Mammalia, other than Man. J. and A. Churchill, London.

Flower, W.H., 1885. An Introduction to the Osteology of the Mammalia. MacMillan and Co., London.

Gebo, D.L., 1996. Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. Am. J. Phys. Anthropol. 101, 55-92.

Gerrard, E., 1862. Bones of Mammalia in the Collection of the British Museum. Taylor and Francis, London.

Ghazi, S.R., Gholami, S., 1994. Allometric growth of the spinal cord in relation to the vertebral column during prenatal and postnatal life in the sheep (*Ovis aries*). J. Anat. 185, 427-431.

Gregory, W.K., 1916. Studies on the evolution of the primates. Part II. Phylogeny of recent and extinct anthropoids with special reference to the origin of man. Bull. Am. Mus. Nat. Hist. 35, 258-355.

Gregory, W.K., 1927. Two views on the origin of man. Science 65, 601-605.

Gregory, W.K., 1928*a*. Were the ancestors of man primitive brachiators? Proc. Am. Phil. Soc. 67, 129-150.

Gregory, W.K., 1928*b*. The upright posture of man: a review of its origin and evolution. Proc. Am. Phil. Soc. 67, 339-374.

Gregory, W.K., 1930. The origin of man from a brachiating anthropoid stock. Science 71, 645-650.

Gregory, W.K., 1934. Man's Place Among the Anthropoids. Clarendon, Oxford.

Gültekin, M., Ucar, Y., 1980. Terli Tilki (*Canis vulpes*) ve Cakal (*Canis aureus*) iskelet kemiklerinin, yerli köperginkilerine (*Canis familiaris*) göre gösterdikleri makro-anatomik ayirimlar üzerinde arastirmalar. Ankara Üniv. Vet. Fak. Derg. 27, 201-214.

Hall, E.R., 1951. American weasels. Univ. Kansas Pub. Mus. Nat. Hist. 4, 1-466.

Hasebe, K., 1913. Die wirbelsaule der Japaner. Zeit. Morph. Anth. 15, 259-380.

Hatt, R.T., 1932. The vertebral columns of ricochetal rodents. Bull. Am. Mus. Nat. Hist. 63, 599-738.

Heath, M.E., 1992*a*. *Manis pentadactyla*. Mammalian Species 414, 1-6.

Heath, M.E., 1992*b*. *Manis temminckii*. Mammalian Species 415, 1-5.

Heath, M.E., 1995. *Manis crassicaudata*. Mammalian Species 513, 1-4.

Hunt, K.D., 1991. Positional behavior in the Hominoidea. Int. J. Primatol. 12, 95-118.

Hunt, K.D., Cant, J.G.H., Gebo, D.L., Rose, M.D., Walker, S.E., Youlatos, D., 1996. Standardized descriptions of primate locomotor and postural modes. Primates 37, 363-387.

Jenkins, P.D., Kilpatrick, C.W., Robinson, M.F., Timmins, R.J., 2005. Morphological and molecular investigations of a new family, genus and species of rodent (Mammalia: Rodentia: Hystricognatha) from Lao PDR. Syst. Biodiv. 2, 419-454.

Jones, C., Anderson, S., 1978. *Callicebus moloch*. Mammalian Species 112, 1-5.

Jungers, W.L., 1984. Scaling of the hominoid locomotor skeleton with special reference to lesser apes. In: Preuschoft, H., Chivers, D.J., Brockelman, W.Y., Creel, N. (Eds.), The Lesser Apes: Evolutionary and Behavioral Biology. Edinburgh University Press, Edinburgh, pp. 146-169.

Jungers, W.L., Stern, J.T., 1980. Telemetered electromyography of forelimb muscle chains in gibbons (*Hylobates lar*). Science 208, 617-617.

Keith, A., 1891. Anatomical notes on Malay apes. J. Straits Branch Roy. Asiatic Soc. 23, 77-94.

Keith, A., 1899. On the chimpanzees and their relationship to the gorilla. Proc. Zool. Soc. Lond. 67, 296-312.

Keith, A., 1903. The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates. J. Anat. Physiol. 37, 18-40.

Keith, A., 1923. Man's posture: its evolution and disorders. Brit. Med. J. 1, 451-454, 499-502, 545-548, 587-590, 624-626, 669-672.

Keith, A., 1934. The Construction of Man's Family Tree. Watts, London.

Keith, A., 1940. Fifty years ago. Am. J. Phys. Anthropol. 26, 251-267.

Köhncke, M., Leonhardt, K., 1986. *Cryptoprocta ferox*. Mammalian Species 254, 1-5.

Lewis, O.J., 1969. The hominoid wrist joint. Am. J. Phys. Anthropol. 30, 251-267.

Lewis, O.J., 1971. Brachiation and the early evolution of the Hominoidea. Nature 230, 577-579.

Lewis, O.J., 1972. Osteological features characterizing the wrists of monkeys and apes, with a reconsideration of this region in *Dryopithecus* (*Proconsul*) *africanus*. Am. J. Phys. Anthropol. 36, 45-58.

Lewis, O.J., 1974. The wrist articulations of the Anthropoidea. In: F.A. Jenkins (Ed.), Primate Locomotion. Academic Press, New York, pp. 143-169.

Lewis, O.J., 1985*a*. Derived morphology of the wrist articulations and theories of hominoid evolution. Part I. The lorisine joints. J. Anat. 140, 447-460.

Lewis, O.J., 1985*b*. Derived morphology of the wrist articulations and theories of hominoid evolution. Part II. The midcarpal joints of higher primates. J. Anat. 142, 151-172.

Lovejoy, C.O., Suwa, G., Simpson, S.W., Matternes, J.H., White, T.D., 2009*b*. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. Science 326, 73, 100-106.

Lovejoy, C.O., Simpson, S.W., White, TD., Asfaw, B., Suwa, G., 2009*a*. Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. Science 326, 70.

McCollum, M.A., Rosenman, B.A., Suwa, G., Meindl, R.S., Lovejoy, C.O., 2010. The vertebral formula of the last common ancestor of African apes and humans. J. Exp. Biol. 314B, 123-134.

Mendel, F.C., 1979. The wrist joint of two-toed sloths and its relevance to brachiating adaptations in the Hominoidea. J. Morphol. 162, 413-424.

Morgan, G.S., 1989. *Geocapromys thoracatus*. Mammalian Species 341, 1-5.

Morton, D.J., 1922. Evolution of the human foot. I. Am. J. Phys. Anthropol. 5, 305-336.

Morton, D.J., 1924. Evolution of the human foot. II. Am. J. Phys. Anthropol. 7, 1-52.

Morton, D.J., 1926. Evolution of man's erect posture. J. Morph. Physiol. 43, 147-179.

Napier, J.R., 1963. Brachiation and brachiators. Symp. Zool. Soc. Lond. 10, 183-195.

Oxnard, C.E., 1967. The functional morphology of the primate shoulder as revealed by comparative anatomical, osteometric and discriminant function techniques. Am. J. Phys. Anthropol. 26, 219-240.

Owen, R., 1859. On the Classification and Geographical Distribution of the Mammalia. Appendix B. On the orang, chimpanzee and gorilla. Parker, London.

Özkan, Z.E., 2007. Macro-anatomical investigations on the skeletons of mole-rat (*Spalax leucodon* Nordmann) III. Skeleton axiale. Veterinarski Arhiv 77, 281-289.

Padilla, M., Dowler, R.C., 1994. *Tapirus terrestris*. Mammalian Species 481, 1-8.

Pilbeam, D., 2004. The anthropoid postcranial axial skeleton: comments on development, variation, and evolution. J. Exp. Zool. 302B, 241-267.

Poglayen-Neuwall, I., Toweill, D.E., 1988. *Bassariscus astutus*. Mammalian Species 327, 1-8.

Quinn, A., Wilson, D.E., 2004. *Daubentonia madagascariensis*. Mammalian Species 740, 1-6.

Rathbun, G.B., 1979. *Rhynchocyon chrysopygus*. Mammalian Species 117, 1-4.

Richmond, B.G., Begun, D.R., Strait, D.S., 2001. Origin of human bipedalism: the knuckle-walking hypothesis revisited. Y. Phys. Anthropol. 44, 70-105.

Sánchez-Villagra, M.R., Narita, Y., Kuratani, S., 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. Syst. Biodiv. 5, 1-7.

Sarmiento, E.E., 1987. The phylogenetic position of *Oreopithecus* and its significance in the origin of the Hominoidea. Am. Mus. Novitates 2881, 1-44.

Sarmiento, E.E., 1988. Anatomy of the hominoid wrist joint: its evolutionary and functional implications. Int. J. Primatol. 9, 281-345.

Sarmiento, E.E., 1995. Cautious climbing and folivory: a model of hominoid differentiation. Hum. Evol. 10, 289-321.

Sanders, W.J., 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J. Hum. Evol. 34, 249-302.

Sargis, E.J., 2001. A preliminary qualitative analysis of the axial skeleton of tupaiids (Mammalia, Scandentia): functional morphology and phylogenetic implications. J. Zool. Lond. 253, 473-483.

Sarmiento, E.E., 2002. Forearm rotation and the "Origin of the hominoid lifestyle": a reply to Stern and Larson (2001). Am. J. Phys. Anthropol. 119, 92-94.

Schultz, A., 1930. The skeleton of the trunk and limbs of higher primates. Hum. Biol. 2, 303-438.

Schultz, A., 1933. Observations on the growth, classification and evolutionary specialization of gibbons and siamangs (concluded). Hum. Biol. 5, 385-428.

Schultz, A.H., 1961. Vertebral column and thorax. Primatologia 4, 1-66.

Schultz, A.H., Straus, W.L., 1945. The numbers of vertebrae in primates. Proc. Am. Phil. Soc. 89, 601-626.

Seebeck, J.H., 2001. *Perameles gunnii*. Mammalian Species 645, 1-8.

Shackleton, D.M., 1985. *Ovis canadensis*. Mammalian Species 230, 1-9.

Shapiro, L., 1993. Functional morphology of the vertebral column in primates. In: Gebo, D.L. (Ed.), Postcranial Adaptation in Nonhuman Primates. Northern Illinois University Press, Dekalb, IL.

Sheffield, S.R., King, C.M., 1994. *Mustela nivalis*. Mammalian Species 454, 1-10.

Shoshani, J., Goldman, C.A., Thewissen, J.G.M., 1988. *Orycteropus afer*. Mammalian Species 300, 1-8.

Simoens, P., de Vos, N.R., Lauwers, H., Nicaise, M., 1983. Numerical vertebral variations and transitional vertebrae in the goat. Zbl. Vet. Med. C. Anat. Histol. Embryol. 12, 97-103.

Slijper, E.J., 1946. Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. Verh. Kon. Ned. Akad. Wet. (Tweede Sectie) 42, 1-128.

Spotorno, A.E., Zuleta, C.A., Valladares, J.P., Deane, A.L., Jiménez, J.E., 2004. *Chinchilla laniger*. Mammalian Species 785, 1-9.

Stern, J.T., 1976. Before bipedality. Y. Phys. Anthropol. 19, 59-68.

Stern, J.T., Larson, S.G., 2001. Telemetered electromyography of the supinators and pronators of the forearm in gibbons and chimpanzees: implications for the fundamental positional adaptation of hominoids. Am. J. Phys. Anthropol. 115, 253-268.

Stern, J.T., Oxnard, C.E., 1973. Primate locomotion: some links with evolution and morphology. Primatologia 4, 1-93.

Stern, J.T., Wells, J.P., Jungers, W.L., Vangor, A.K., 1980*b*. An electromyographic study of serratus anterior in atelines and *Alouatta*: implications for hominoid evolution. Am. J. Phys. Anthropol. 52, 323-334.

Stern, J.T., Wells, J.P., Jungers, W.L., Vangor, A.K., Fleagle, J.G., 1980*a*. An electromyographic study of the pectoralis major in atelines and *Hylobates*, with special reference to the evolution of a pars clavicularis. Am. J. Phys. Anthropol. 52, 18-25.

Stern, J.T., Wells, J.P., Vangor, A.K., Fleagle, J.G., 1977. Electryomyography of some muscles of the upper limb in *Ateles* and *Lagothrix*. Y. Phys. Anthropol. 20, 498-507.

Stecher, R.M., 1962. Anatomical variations of the spine in the horse. J. Mammal. 43, 205-219.

Straus, W.L., 1940. The posture of the great ape hand in locomotion, and its phylogenetic implications. Am. J. Phys. Anthropol. 27, 199-207.

Straus, W.L., 1942. Rudimentary digits in primates. Q. Rev. Biol. 17, 228-243.

Straus, W.L., 1949. The riddle of man's ancestry. Q. Rev. Biol. 24, 200-223.

Straus, W.L., 1962. Fossil evidence of the evolution of the erect, bipedal posture. Clin. Orthop. 25, 9-19.

Straus, W.L., 1968. Huxley's evidence as to man's place in nature – a century later. In: L.G. Stevenson, R.P. Multhauf (Eds.), Medicine Science and Culture: Historical Essays in Honor of Owsei Temkin. The Johns Hopkins Press, Baltimore, pp. 160-167.

Straus, W.L., Wislocki, G.B., 1942. On certain similarities between sloths and sloth lemurs. Bull. Mus. Comp. Zool. (Harvard) 74, 45-56.

Stubbs, N.C., Hodges, P.W., Jeffcott, L.B., Cowin, G., Hodgson, D.R., McGowan, C.M., 2006. Functional anatomy of the caudal thoracolumbar and lumbosacral spine in the horse. Equine Vet. J. Suppl. 36, 393-399.

Tecirlioglu, S., 1983. Sirtlan ve köpegin iskelet kemikleri üzerinde makro-anatomik arastirmalar. Ankara Üniv. Vet. Fak. Derg. 30, 149-166.

Todd, T.W., 1922. Numerical significance in the thoracicolumbar vertebrae of the Mammalia. Anat. Rec. 24, 261-286.

Trevor, J.C., 1963. The history of the word "brachiator" and a problem of authorship in primate nomenclature. Symp. Zool. Soc. Lond. 10, 197-198.

Tuttle, R.H., 1969*a*. Quantitative and functional studies on the hands of the Anthropoidea. I. The Hominoidea. J. Morpohol. 128, 309-364.

Tuttle, R.H., 1969*b*. Knuckle-walking and the problem of human origins. Science 166, 953-961.

Tuttle, R.H., 1974. Darwin's apes, dental apes, and the descent of man: normal science in evolutionary anthropology. Curr. Anthropol. 15, 389-426.

Tuttle, R.H., 1975. Parallelism, brachiation, and hominoid phylogeny. In: W.P. Luckett, F.S. Szalay (Eds.), Phylogeny of the Primates: A Multidisciplinary Approach. Plenus Press, New York, pp. 447-480.

Tuttle, R.H., 1981. Evolution of hominid bipedalism and prehensile capabilities. Phil. Trans. R. Soc. Lond. 292, 89-94.

Verts, B.J., Carraway, L.N., Kinlaw, A., 2001. *Spilogale gracilis*. Mammalian Species 674, 1-10.

Washburn, S.L., 1950. The analysis of primate evolution with particular reference to the origin of man. Cold Spring Harbor Symposia on Quantitative Biology 15, 67-77.

Washburn, S.L., 1963. Behavior and human evolution. In: S.L. Washburn (Ed.), Classification and Human Evolution. Aldine, Chicago, pp. 190-203.

Washburn, S.L., 1968. Speculations on the problem of man's coming to the ground. In: B. Rothblatt (Ed.), Changing Perspectives on Man. University of Chicago Press, Chicago, pp. 191-206.

Washburn, S.L., 1971. The study of human evolution. In: P. Dolhinow, V. Sarich (Eds.), Background for Man: Readings in Physical Anthropology. Little, Brown and Co., Boston, pp. 82-117.

Washburn, S.L., 1973. Human evolution: science or game? Y. Phys. Anthropol. 17, 67-70.

Yamada, F., Cervantes, F.A., 2005. *Pentalagus furnessi*. Mammalian Species 782, 1-5.

Yang, A., Fang, L., 1982. The vertebral column and the thorax of the giant panda, *Ailuropoda melanoleuca*. Acta Theriologica Sinica 2, 1-8.

Yilmaz, S., 1998. Macro-anatomical investigations on the skeletons of porcupine (*Hystrix cristata*). Part III: skeleton axiale. Anat. Histol. Embryol. 27, 293-296.

Yilmaz, S., Dinc, G., Toprak, B., 2000. Macro-anatomical investigations on skeletons of otter (*Lutra lutra*). III. Skeleton axiale. Veterinarski Arhiv 70, 191-198.

BIBLIOGRAPHY

Abitbol, M. M., 1987. Evolution of the sacrum in hominoids. Am. J. Phys. Anthropol. 74, 65-81.

Adam, P.J., 2004. *Monachus tropicalis*. Mammalian Species 747, 1-9.

Agresti, A., Agresti, B.F., 1978. Statistical analysis of qualitative variation. Sociol. Methodol. 9, 204-237.

Aimi, M., 1994. Numerical variation of vertebrae in Japanese macaques, *Macaca fuscata*. Anthropol. Sci. 102, 1-10.

Alba, D.M., Almécija, S., Moyà-Solà, S., 2010. Locomotor inferences in *Pierolapithecus* and *Hispanopithecus*: reply to Deane and Begun (2008). J. Hum. Evol. 59, 143-149.

Alba, D.M., Fortuny, J., Moyà-Solà, S., 2010. Enamel thickness in the Middle Miocene great apes *Anoiapithecus*, *Pierolapithecus*, and *Dryopithecus*. Proc. R. Soc. B 277, 2237-2245.

Alba, D.M., Moyà-Solà, S., Almécija, S., 2011. A partial hominoid humerus from the Middle Miocene of Castell de Barberá (Vallès-Penedès Basin, Catalonia, Spain). Am. J. Phys. Anthropol. 144, 365-381.

Alba, D.M., Moyà-Solà, S., Köhler, M., Rook, L., 2001. Heterochrony and the cranial anatomy of *Oreopithecus*: some cladistic fallacies and the significance of developmental constraints in phylogenetic analysis. In: L. de Bonis, G. Koufos (Eds.), Hominoid Evolution and Climate Change in Europe, Vol. 2, Phylogeny of the Neogene Hominoid Primates of Eurasia. Cambridge University Press, Cambridge, pp. 284-315.

Alexander, T., Nolte, C., Krumlauf, R., 2009. *Hox* genes and segmentation of the hindbrain and axial skeleton. Annu. Rev. Cell Dev. Biol. 25, 431-456.

Allbrook, D.B., 1955. The East African vertebral column: a study in racial variability. Am. J. Phys. Anthropol. 13, 489-514.

Allen, J.A., 1917. The skeletal characters of *Scutisorex* Thomas. Bull. Am. Mus. Nat. Hist. 37, 769-784.

Almécija, S., Alba, D.M., Moyà-Solà, S., 2009. *Pierolapithecus* and the functional morpohlgy of Miocene ape hand phalanges: paleobiolocal and evolutionary implications. J. Hum. Evol. 57, 284-297.

300

Almécija, S., Alba, D.M., Moyà-Solà, S., Köhler, M., 2007. Orang-like manual adaptations in the fossil hominoid *Hispanopithecus laietanus*: first steps towards great ape suspensory behaviours. Proc. R. Soc. B 274, 2375-2384.

Anderson, S., 1969. *Macrotus waterhousii*. Mammalian Species 1, 1-4.

Andrews, P. Evolution and environment in the Hominoidea. Nature 360, 641-646.

Andrews, P., Cronin, J.E., 1982. The relationships of *Sivapithecus* and *Ramapithecus* and the evolution of the orang-utan. Nature 297, 541-546.

Andrews, P., Groves, C.P., 1976. Gibbons and brachiation. In: D.M. Rumbaugh (Ed.), Gibbon and Siamang, Vol. 4. Karger, Basel, pp. 167-218.

Andrews, P., Harrison, T., 2005. The last common ancestor of apes and humans. In: D.E. Lieberman, R.J. Smith, J. Kelley (Eds.), Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam. Brill Academic Publishers, Boston, pp. 103-121.

Andrews, P., Pilbeam, D., 1996. The nature of the evidence. Nature 379, 123-124.

Ankel, F., 1967. Morphologie von Wirbelsäule und Brustkorb. Primatologia 4, 1-120.

Ankel, F., 1972. Vertebral morphology of fossil and extant primates. In: R. Tuttle (Ed.), Functional and Evolutionary Biology of Primates. Aldine Press, Chicago, pp. 223-240.

Arensburg, B., 1991. The vertebral column, thoracic cage and hyoid bone. In: O. Bar Yosef, B. Vandermeersch (Eds.), Le Squelette Mousterian de Kebara 2. Editions du C.N.R.S., Paris, pp. 113-146.

Argot, C., 2003. Functional-adaptive anatomy of the axial skeleton of some extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J. Morph. 255, 279-300.

Asher, R.J., Bennett, N., Lehmann, T., 2009. The new framework for understanding placental mammal evolution. BioEssays 31, 853-864.

Asher, R.J., Helgen, K.M., 2010. Nomenclature and placental mammal phylogeny. BMC Evol. Biol. 10, 102.

Asher, R.J., Lin, K.H., Kardjilov, N., Hautier, L., 2011. Variability and constraint in the mammalian vertebral column. J. Evol. Biol. 24, 1080-1090.

Ashton, E.H., Oxnard, C.E., 1964. Locomotor patterns in primates. Proc. Zool. Soc. Lond. 142, 1-28.

Avis, V., 1962. Brachiation: the crucial issue for man's ancestry. Southwestern J. Anthropol. 18, 119-148.

Barnes, E., 1994., Developmental Defects of the Axial Skeleton in Paleopathology. University of Colorado Press, Boulder, CO.

Barnett, A.A., 2005. *Cacajao melanocephalus*. Mammalian Species 776, 1-6.

Bateson, W., 1894. Materials for the Study of Variation: Treated with Especial Regard to Discontinuity in the Origin of Species. MacMillan and Co., London.

Beard, K.C., Teaford, M.F., Walker, A., 1986. New wrist bones of *Proconsul africanus* and *Proconsul nyanzae* from Rusinga Island, Kenya. Folia Primatol. 47, 97-118.

Begun, D.R., 1993. New catarrhine phalanges from Rudabánya (Northeastern Hungary) and the problem of parallelism and convergence in hominoid postcranial morphology. J. Hum. Evol. 24, 373-402.

Begun, D.R., 2004. Knuckle-walking and the origin of human bipedalism. In: D.J. Meldrum, C.E. Hilton (Eds.), From Biped to Strider: The Emergence of Modern Human Walking. Kluwer, New York, pp. 9-33.

Begun, D.R., 2004. The earliest hominins – is less more? Science 303, 1478-1480.

Begun, D.R., 2007. How to identify (as opposed to define) a homoplasy: examples from fossils and living great apes. J. Hum. Evol. 52, 559-572.

Begun, D.R., 2009. Dryopithecins, Darwin, de Bonis, and the European origin of the African apes and human clade. Geodiversitas 31, 789-816.

Begun, D.R., 2010. Miocene hominids and the origins of the African apes and humans. Annu. Rev. Anthropol. 39, 67-84.

Begun, D.R., Kordos, L., 1997. Phyletic affinities and functional convergence in Dryopithecus and other Miocene and living hominoids. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 291-316.

Begun, D.R., Richmond, R.G., Strait, D.S., 2007. Comment on "Origin of human bipedalism as an adaptation for locomotion on flexible branches". Science 318, 1066d.

Begun, D.R., Teaford, M.F., Walker, A., 1994. Comparative and functional anatomy of *Proconsul* phalanges from the Kaswanga primate site, Rusinga Island, Kenya. J. Hum. Evol. 26, 89-165.

Begun, D.R., Ward, C.V., 2005. Comment on "*Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. Science 308, 203c.

Begun, D.R., Ward, C.V., Rose, M.D., 1997. Events in Hominoid Evolution. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 389-415.

Belting, H.G., Shashikant, C.S., Ruddle, F.H., 1998. Modification of expression and cis-regulation of Hoxc8 in the evolution of diverged axial morphology. Proc. Natl. Acad. Sci. USA 95, 2355-2360.

Benefit, B.R., McCrossin, M.L., 1995. Miocene hominoids and hominid origins. Annu. Rev. Anthropol. 24, 237-256.

Benefit, B.R., McCrossin, M.L., 1997. Earliest known Old World monkey skull. Nature 388, 368-371.

Benton, R.S., 1967. Morphological evidence for adaptations within the epaxial region of the primates. In: van der Hoeven, F. (Ed.), The Baboon in Medical Research, Vol. II. University of Texas Press, Austin, pp. 201-216.

Benton, R.S., 1974. Structural patterns in the Pongidae and Cercopithecidae. Y. Phys. Anthropol. 18, 65-88.

Berger, L.R., de Ruiter, D.J., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P.H.G.M., Kibii, J.M., 2010. *Australopithecus sediba*: a new species of *Homo*-like australopiths from South Africa. Science 328, 195-204.

Beynon, A.D., Dean, M.C., Reid, D.J., 1991. On thick and thin enamel in hominoids. Am. J. Phys. Anthropol. 86, 295-309.

Birchette, M.G., 1982. The postcranial skeleton of *Paracolobus chemeroni*. Ph.D. dissertation, Harvard University.

Bolker, J.A., Raff, R.A., 1996. Developmental genetics and traditional homology. BioEssays 18, 489-494.

Bonmati, A., Gómez-Olivencia, A., Arsuaga, J.-L., Carretero, J.M., Gracia, A., Martínez, I., Lorenzo, C., Bérmudez de Castro, J.M., Carbonell, E., 2010. Middle Pleistocene lower back and pelvis from an aged human individual from the Sima de los Huesos site, Spain. Proc. Natl. Acad. Sci. USA 107, 18386-18391.

Bornstein, P.E., Peterson, R.R., 1966. Numerical variation of the presacral vertebral column in three population groups in North America. Am. J. Phys. Anthropol. 25, 139-146.

Breit, S., Künzel, W., 2002. The diameter of the vertebral canal in dogs in cases of lumbosacral transitional vertebrae or numerical vertebral variations. Anat. Embryol. 205, 125-133.

Brown, F., Harris, J., Leakey, R., Walker, A. 1985., Early *Homo erectus* skeleton from west Lake Turkana, Kenya. Nature. 316, 788-792.

Brunet, M., 2002. Reply. Nature 419, 582.

Brunet, M., Guy, F., Pilbeam, D., Mackaye, H.T., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Bolsserie, J.-R., de Bonis, L., Coppens Y., Dejax, J., Denys, C., Duringer, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Campomanes, P.P., Ponce de Leon, M., Rage, J.-C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A., Zollikofer, C., 2002. A new hominid from the Upper Miocene of Chad, Central Africa. Nature 418, 145-151.

Bryant, M.D., 1945. Phylogeny of Nearctic Sciuridae. Am. Mid. Nat. 33, 257-390.

Buchholtz, E.A., 1998. Implications of vertebral morphology for locomotor evolution in early Cetacea. In: Thewissen, J.G.M. (Ed.), The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea. Plenum Press, New York, pp. 325-351.

Buchholtz, E.A., 2007. Modular development of the cetacean vertebral column. Evol. Dev. 9, 278-289.

Buchholtz, E.A., 2011. Vertebral and rib anatomy in *Caperea marginata*: implications for evolutionary patterning of the mammalian vertebral column. Marine Mammal Science 27, 382-397.

Buchholtz, E.A., Booth, A.C., Webbink, K.E., 2007. Vertebral anatomy in the Florida manatee, *Trichechus manatus latirostris*: a developmental and evolutionary analysis. Anat. Rec. 290, 624-637.

Buchholtz, E.A., Schur, S.A., 2004. Vertebral osteology in Delphinidae (Cetacea). Zool. J. Linn. Soc. 140, 383-401.

Buchholtz, E.A., Stepien, C.C., 2009. Anatomical transformation in mammals: developmental origin of aberrant cervical anatomy in tree sloths. Evol. Dev. 11, 69-79.

Buchholtz, E.A., Wolkovich, E.M., Cleary, R.J., 2005. Vertebral osteology and complexity in *Lagenorhynchus acutus* (Delphinidae) with comparison to other delphinoid genera. Mar. Mamm. Sci. 21, 411-428.

Buffon, G.L., 1769. Histoire Naturelle, Generale et Particuliere. Pankoucke, Paris.

Burke, A.C., Nelson, C.E., Morgan, B.A., Tabin, C., 1995. Hox genes and the evolution of vertebrate axial morphology. Development. 121, 333-346.

Carleton, A.C., 1936. The limb-bones and vertebrae of the extinct lemurs of Madagascar. J. Zool. 106, 281-307.

Casanovas-Vilar, I., Alba, D.M., Garcés, M., Robles, J.M., Moyà-Solà, S., 2011. Updated chronology for the Miocene hominoid radiation in Western Eurasia. Proc. Natl. Acad. Sci. USA 108, 5554-5559.

Cartmill, M., Milton, K., 1977. The lorisiform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. Am. J. Phys. Anthropol. 47, 249-272.

Chang, C.-H., Jang, C.-M., 2004. On the processing and mounting of a skeleton of a white rhinoceros, *Ceratotherium sinum*. Coll. Res. 17, 58-69.

Clauser, D., 1980. Functional and comparative anatomy of the primate spinal column: some locomotor and postural adaptations. Ph.D. dissertation, University of Wisconsin-Milwaukee.

Cook, D.C., Buikstra, J.E., DeRousseau, C.J., Johanson, D.C., 1983. Vertebral pathology in the Afar australopithecines. Am. J. Phys. Anthropol. 60, 83-101.

Corruccini, R.S., 1978. Primate skeletal allometry and hominoid evolution. Evolution 32, 752-758.

Corruccini, R.S., Ciochon, R.L., McHenry, H.M., 1976. The postcranium of Miocene hominoids: were dryopithecines merely "dental apes"? Primates 17, 205-223.

Crompton, R.H., Sellers, W.I., Thorpe, S.K.S., 2010. Arboreality, terrestriality and bipedalism. Phil. Trans. R. Soc. B 365, 3301-3314.

Crompton, R.H., Thorpe, S.K.S., 2007. Response to comment on "Origin of human bipedalism as an adaptation for locomotion on flexible branches". Science 318, 1066e.

Crompton, R.H., Thorpe, S., Welite, W., Yu, L., Payne, R., Savage, R., Carey, T., Aerts, P., Elsacker, V., Hofstetter, A., Günther, M., Richardson, J., 2003. The biomechanical evolution of erect bipedality. Cour. Forsch.-Inst. Seneckenberg 243, 135-146.

Crompton, R.H., Vereecke, E.E., Thorpe, S.K.S., 2008. Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. J. Anat. 212, 501-543.

Cullinane, D.M., Aleper, D., 1998. The functional and biomechanical modifications of the spine of *Scutisorex somereni*, the hero shrew: spinal musculature. J. Zool. Lond. 244, 453-458.

Cullinane, D.M., Aleper, D., Bertram, J.E.A., 1998. The functional and biomechanical modifications of the spine of *Scutisorex somereni*, the hero shrew: skeletal scaling relationships. J. Zool. Lond. 244, 447-452.

Cullinane, D.M., Bertram, J.E.A., 2000. The mechanical behavior of a novel mammalian intervertebral joint. J. Anat. 197, 627-634.

Dagg, A.I., 1971. *Giraffa camelopardalis*. Mammalian Species 5, 1-8.

Dainton, M., Macho, G.A., 1999. Did knuckle-walking evolve twice? J. Hum. Evol. 36, 171-194.

Danforth, C.H., 1930. Numerical variation and homologies in vertebrae. Am. J. Phys. Anthropol. 14, 463-481.

Davis, D.D., 1954. Primate evolution from the viewpoint of comparative anatomy. Hum. Biol. 26, 211-219.

Davis, D.D., 1964. The giant panda: a morphological study of evolutionary mechanisms. Fieldiana: Zool. Mem. 8, 1-334.

Deane, A.S., Begun, D.R., 2008. Broken fingers: retesting locomotor hypotheses for fossil hominoids using fragmentary proximal phalanges and high-resolution polynomial curve fitting (HR-PCF). J. Hum. Evol. 55, 691-701.

Deane, A.S., Begun, D.R., 2010. *Pierolapithecus* locomotor adaptations: a reply to Alba et al.'s comment on Deane and Begun (2008). J. Hum. Evol. 59, 150-154.

Dequeant, M.L., Pourquié, O., 2008. Segmental patterning of the vertebrate embryonic axis. Nat. Rev. Genet. 9, 370-382.

Disotell, T.R., 1994. Generic level relationships of the Papionini (Cercopithecoidea). Am. J. Phys. Anthropol. 94, 47-57.

Duckworth, W.L.H., 1911. Report on an abnormal first thoracic vertebra. J. Anat. Physiol. 45, 65-68.

Eckhardt, R.B., Galik, K., Kuperavage, A.J., 2005. Response. Science 307, 845.

Elton, S., 2002. A reappraisal of the locomotion and habitat preference of *Theropithecus oswaldi*. Folia Primatol. 73, 252-280.

Endo, H., Sasaki, M., Hayashi, Y., Koie, H., Yamaya, Y., Kimura, J., 2001. Carpal bone movements in gripping action of the giant panda (*Ailuropoda melanoleuca*). J. Anat. 198, 243-246.

Erikson, G., 1963. Brachiation in New World monkeys and in anthropoid apes. Symp. Zool. Soc. Lond. 10, 135-163.

Eriksson, J., Hohmann, G., Boesch, C., Vigilant, L., 2004. Rivers influence the population genetic structure of bonobos (*Pan paniscus*). Mol. Ecol. 13, 3425-3435.

Fay, J.C., Wu, C.-I., 1999. A human population bottleneck can account for the discordance between patterns of mitochondrial versus nuclear DNA variation. Mol. Biol. Evol. 16, 1003-1005.

Fagundes, N.J.R., Ray, N., Beaumont, M., Neuenschwander, S., Salzano, F.M., Bonatto, S.L., Excoffier, L., 2007. Statistical evaluation of alternative models of human evolution. Proc. Natl. Acad. Sci. USA 104, 17614-17619.

Filler, A.G., 1986. Axial character seriation in mammals: an historical and morphological exploration of the origin, development, use, and current collapse of the homology paradigm. Ph.D. dissertation, Harvard University.

Filler, A.G., 1993. Evolution of the sacrum in hominoids. In: Doty, J.R., Rengachary, S.S. (Eds.). Surgical Disorders of the Sacrum. Thieme Medical Publishers, New York, pp. 13-20.

Filler, A.G., 2007. The Upright Ape. New Page Books, Franklin Lakes, NJ.

Filler, A.G., 2007. Homeotic evolution in the Mammalia: diversification of therian axial seiation and the morphogenetic basis of human origins. PLoS One 10, e1019.

Fleagle, J.G., 1976. Locomotion and posture of the Malayan siamang and implications for hominoid evolution. Folia Primatol. 26, 245-269.

Fleagle, J.G., McGraw, W.S., 1999. Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. Proc. Natl. Acad. Sci. USA 96, 1157-1161.

Fleagle, J.G., McGraw, W.S., 2002. Skeletal and dental morphology of African papionins: unmasking a cryptic clade. J. Hum. Evol. 42, 267-292.

Fleagle, J.G., Meldrum, D.J., 1988. Locomotor behavior and skeletal morphology of two sympatric pitheciine monkeys, *Pithecia pithecia* and *Chiropotes satanas*. Am. J. Primatol. 16, 227-249.

Fleagle, J.G., Stern, J.T., Jungers, W.L., Susman, R.L., Vangor, A.K., Wells, J.P., 1981. Climbing: a biomechanical link with brachiation and with bipedalism. Symp. Zool. Soc. Lond. 48, 359-375.

Flower, W.H., 1884. Catalogue of the Specimens Illustrating the Osteology and Dentition of the Vertebrated Animals, Recent and Extinct, Contained in the Museum of the Royal College of Surgeons of England, Part II. Class Mammalia, other than Man. J. and A. Churchill, London.

Flower, W.H., 1885. An Introduction to the Osteology of the Mammalia. MacMillan and Co., London.

Galik, K., Senut, B., Pickford, M., Gommery, D., Treil, J., Kuperavage, A.J., Eckhardt, R.B., 2004. External and internal morphology of BAR 1002'00 *Orrorin tugenensis* femur. Science 305, 1450-1453.

Galis, F., 1999. Why do almost all mammals have seven cervical vertebrae? Developmental constraints, Hox genes, and cancer. J. Exp. Zool. 285, 19-26.

Galis, F., Van Dooren, T.J.M., Feuth, J.D., Metz, J.A.J., Witkam, A., Ruinard, S., Steigenga, M.J., Wijnaendts, L.C.D., 2006. Extreme selection in humans against homeotic transformations of cervical vertebrae. Evolution 60, 2643-2654.

Galliari, F.C., Carlini, A.A., Sánchez-Villagra, M.R., 2010. Evolution of the axial skeleton in armadillos (Mammalia, Dasypodidae). Mammal. Biol. 75, 326-333.

Gambaryan, P.P., 1974. How Mammals Run. John Wiley and Sons, New York.

Gambaryan, P.P., Zherebtsova, O.V., Perepelova, A.A., Platonov, V.V., 2009. Pes muscles and their action in giant anteater *Myrmecophaga tridactyla* (Myrmecophagidae, Pilosa) compared with other plantigrade mammals. Russian J. Theriol. 8, 1-15.

Gaunt, S.J., 1994. Conservation in the Hox code during morphological evolution. Int. J. Dev. Biol. 38, 549-552.

Gebo, D.L., 1989. Postcranial adaptation and evolution in Lorisidae. Primates 30, 347-367.

Gebo, D.L., 1992. Plantigrady and foot adaptation in African apes. Implications for hominid origins. Am. J. Phys. Anthropol. 89, 29-58.

Gebo, D.L., 1993. Reply to Dr. Meldrum. Am. J. Phys. Anthropol. 91, 382-385.

Gebo, D.L., 1996. Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. Am. J. Phys. Anthropol. 101, 55-92.

Gebo, D.L., 2010. Locomotor function across primates (including humans). In: C.S. Larson (Ed.), A Companion to Biological Anthropolgoy. Wiley-Blackwell, pp. 530-544.

Gebo, D.L., Beard, K.C., Teaford, M.F., Walker, A., Larson, S.G., Jungers, W.L., Fleagle, J.G., 1988. A hominoid proximal humerus from the Early Miocene of Rusinga Island, Kenya. J. Hum. Evol. 17, 393-401.

Gebo, D.L., Malit, N.R., Nengo, I.O., 2009. New proconsuloid postcranials from the early Miocene of Kenya. Primates 50, 311-319.

Gebo, D.L., MacLatchy, L., Kityo, R., Deino, A., Kingston, J., Pilbeam, D., 1997. A hominoid genus from the early Miocene of Uganda. Science 276, 401-404.

Gebo, D.L., Sargis, E.J., 1994. Terrestrial adaptations in the postcranial skeletons of guenons. Am. J. Phys. Anthropol. 93, 341-371.

Gerrard, E., 1862. Bones of Mammalia in the Collection of the British Museum. Taylor and Francis, London.

Ghazi, S.R., Gholami, S., 1994. Allometric growth of the spinal cord in relation to the vertebral column during prenatal and postnatal life in the sheep (*Ovis aries*). J. Anat. 185, 427-431.

Giebel, C.G., 1853. Uber die Granze zwischen Brust- und Lendengegend in der Wirbelsaule der Saugetiere. Zeitschr ges Naturw. 1853 I, 261.

Giebel, C.G., 1900. Mammalia. In: H.G. Bronn (Ed.), Klassen und Ordnungen des Tierreichs, Bd. 6, Abt. 5., Leipzig.

Gilbert, C.C., 2007. Craniomandibular morphology supporting the diphyletic origin of mangabeys and a new genus of the *Cercocebus*/*Mandrillus* clade, *Procercocebus*. J. Hum. Evol. 53, 69-102.

Gingerich, P.D., ul-Haq, M., von Koenigswald, W., Sanders, W.J., Smith, B.H., Zalmout, I.S., 2009. New protocetid whale from the Middle Eocene of Pakistan: birth on land, precocial development, and sexual dimorphism. PLoS One 4, 4366.

Gomez, C., Ozbudak, E.M., Wunderlich, J., Baumann, D., Lewis, J., Pourquié, O., 2008. Control of segment number in vertebrate embryos. Nature 454, 335-339.

Gomez, C., Pourquié, O., 2009. Developmental control of segment numbers in vertebrates. J. Exp. Zool. 312B, 533-544.

Gregory, W.K., 1916. Studies on the evolution of the primates. Part II. Phylogeny of recent and extinct anthropoids with special reference to the origin of man. Bull. Am. Mus. Nat. Hist. 35, 258-355.

Gregory, W.K., 1927. Two views on the origin of man. Science 65, 601-605.

Gregory, W.K., 1928. Were the ancestors of man primitive brachiators? Proc. Am. Phil. Soc. 67, 129-150.

Gregory, W.K., 1928. The upright posture of man: a review of its origin and evolution. Proc. Am. Phil. Soc. 67, 339-374.

Gregory, W.K., 1930. The origin of man from a brachiating anthropoid stock. Science 71, 645-650.

Gregory, W.K., 1934. Man's Place Among the Anthropoids. Clarendon, Oxford.

Groves, C.P., 1978. Phylogenetic and population systematics of the mangabeys (Primates: Cercopithecoidea). Primates 19, 1-34.

Groves, C., 2001. Primate Taxonomy. Smithsonian Institution Press, Washington, D.C.

Groves, C.P., 2003. A history of gorillas taxonomy. In: A.B. Taylor, M.L. Goldsmith (Eds.), Gorilla Biology: A Multidisciplinary Perspective. Cambridge University Press, Cambridge, pp. 15-34.

Gültekin, M., Ucar, Y., 1980. Terli Tilki (*Canis vulpes*) ve Cakal (*Canis aureus*) iskelet kemiklerinin, yerli köperginkilerine (*Canis familiaris*) göre gösterdikleri makro-anatomik ayirimlar üzerinde arastirmalar. Ankara Üniv. Vet. Fak. Derg. 27, 201-214.

Haeusler M, Martelli SA, Boeni T. 2002. Vertebrae numbers of the early hominid lumbar spine. J. Hum. Evol. 43:621-643.

Haile-Selassie, Y., 2001. Late Miocene hominids from the Middle Awash, Ethiopia. Nature 412, 178-181.

Haile-Selassie, Y., Suwa, G., White, T., 2009. Hominidae. In: Y. Haile-Selassie, G. WoldeGabriel (Eds.), *Ardipithecus Kadabba*: Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley, pp. 159-236.

Hall, B.K., 1994. Homology: The Hierarchical Basis of Comparative Biology. Academic Press, San Diego, CA.

Hall, E.R., 1951. American weasels. Univ. Kansas Pub. Mus. Nat. Hist. 4, 1-466.

Halpert, A.P., Jenkins, F.A., Franks, H., 1987. Structure and scaling of the lumbar vertebrae in African bovids (Mammalia: Artiodactyla). J. Zool. Lond. 211, 239-258.

Hansen, T.F., Houle, D., 2008. Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. 21, 1201-1219.

Harpending, H.C., Batzer, M.A., Gurven, M., Jorde, L.B., Rogers, A.R., Sherry, S.T., 1998. Genetic traces of ancient demography. Proc. Natl. Acad. Sci. USA 95, 1961-1967.

Harris, E.E., 2000. Molecular systematics of the Old World monkey tribe Papionini: analysis of the total available genetic sequences. J. Hum. Evol. 38, 235-256.

Harrison, T., 1986. A reassessment of the phylogenetic relationships of *Oreopithecus bambolii* Gervais. J. Hum. Evol. 15, 541-583.

Harrison, T., 1987. The phylogenetic relationships of the early catarrhine primates: a review of the current evidence. J. Hum. Evol. 16, 41-80.

Harrison, T., 1991. The implications of *Oreopithecus bambolii* for the origins of bipedalism. Cour. Forsch.-Inst. Senckenberg 243, 235-244.

Harrison, T., 2002. Late Oligocene to middle Miocene catarrhines from Afro-Arabia. In: W.C. Hartwig (Ed.), The Primate Fossil Record. Cambridge University Press, Cambridge, pp. 311-338.

Harrison, T., 2010. Dendropithecoidea, Proconsuloidea, and Hominoidea. In: L. Werdelin, W.J. Sanders (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 429-469.

Harrison, T., 2010. Apes among the tangled branches of human origins. Science 327, 532-534.

Harrison, T., Rook, L., 1997. Enigmatic anthropoid or misunderstood ape: the phylogenetic status of *Oreopithecus bambolii* reconsidered. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 327-362.

Hartwig, W., 2005. Implications of molecular and morphological data for understanding ateline phylogeny. Int. J. Primatol. 26, 999-1015.

Hasebe, K., 1913. Die wirbelsaule der Japaner. Zeit. Morph. Anth. 15, 259-380.

Hatt, R.T., 1932. The vertebral columns of ricochetal rodents. Bull. Am. Mus. Nat. Hist. 63, 599-738.

Hautier, L., Weisbecker, V., Sánchez-Villagra, M.R., Goswami, A., Asher, R.J., 2010. Skeletal development in sloths and the evolution of mammalian vertebral patterning. Proc. Natl. Acad. Sci. USA 107, 18903-18908.

Heath, M.E., 1992. *Manis pentadactyla*. Mammalian Species 414, 1-6.

Heath, M.E., 1992. *Manis temminckii*. Mammalian Species 415, 1-5.

Heath, M.E., 1995. *Manis crassicaudata*. Mammalian Species 513, 1-4.

Hedges, S.B., Dudley, J., Kumar, S., 2006. TimeTree: a public knowledge-base of divergence times among organisms. Bioinformatics 22, 2971-2972.

Hildebrand, M., 1959. Motions of the running cheetah and horse. J. Mammal. 40, 481-495.

Hildebrand, M., 1974. Analysis of Vertebrate Structure. Wiley, New York.

Hildebrand, M., 1995. Analysis of Vertebrate Structure, 4th Ed. Wiley, New York.

Hildebrand, M., Goslow, G., 2001. Analysis of Vertebrate Structure, 5th Ed. Wiley, New York.

Hoos, M., Dilling, A., Currant, A., Paabo, S., 1996. Molecular phylogeny of the extinct ground sloth *Mylodon darwinii*. Proc. Natl. Acad. Sci. USA 93, 181-185.

Hou, Z.C., Romero, R., Wildman, D.E., 2009. Phylogeny of the Ferungulata (Mammalia: Laurasiatheria) as determined from phylogenomic data. Mol. Phylogen. Evol. 52, 660-664.

Houle, D., 1992. Comparing evolvability and variability of quantitative traits. Genetics 130, 195-204.

Hunt, K.D., 1991. Positional behavior in the Hominoidea. Int. J. Primatol. 12, 95-118.

Hunt, K.D., Cant, J.G.H., Gebo, D.L., Rose, M.D., Walker, S.E., Youlatos, D., 1996. Standardized descriptions of primate locomotor and postural modes. Primates 37, 363-387.

Hurov, J.R., 1987. Terrestrial locomotion and back anatomy in vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*). Am. J. Primatol. 13, 297-311.

Huxley, J., 1928. Introduction. In: G.R. De Beer (Ed.), Vertebrate Zoology. Macmillan Co., New York.

Iimura, T., Denans, N., Pourquié, O., 2009. Establishment of Hox vertebral identities in the embryonic spine precursors. Curr. Topics Develop. Biol. 88, 201-234.

Inouye, S.E., 2003. Intraspecific and ontogenetic variation in the forelimb morphology of *Gorilla*. In: A.B. Taylor, M.L. Goldsmith (Eds.), Gorilla Biology: A Multidisciplinary Perspective. Cambridge University Press, Cambridge, pp. 194-235.

Isbell, L.A., Pruetz, J.D., Lewis, M., Young, T.P., 1998. Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): implications for the evolution of long hindlimb length in *Homo*. Am. J. Phys. Anthropol. 105, 199-207.

Ishida, H., Kunimatsu, Y., Takano, T., Nakano, Y., Nakatsukasa, M., 2004. *Nacholapithecus* skeleton from the Middle Miocene of Kenya. J. Hum. Evol. 69-103.

Janecka, J.E., Miller, W., Pringle, T.H., Wiens, F., Zitzmann, A., Helgen, K.M., Springer, M.S., Murphy, W.J., 2007. Molecular and genomic data identify the closest living relative of primates. Science 318, 792-794.

Jenkins, F.A., 1970. Anatomy and function of expanded ribs in certain edentates and primates. J. Mammal. 51, 288-301.

Jenkins, F., 1971. The postcranial skeleton of African cynodonts. Bull. Peabody Mus. Nat. Hist. 36, 1-216.

Jenkins, P.D., Kilpatrick, C.W., Robinson, M.F., Timmins, R.J., 2005. Morphological and molecular investigations of a new family, genus and species of rodent (Mammalia: Rodentia: Hystricognatha) from Lao PDR. Syst. Biodiv. 2, 419-454.

Jensen-Seaman, M.I., Kidd, K.K., 2001. Mitochondrial DNA variation and biogeography of eastern gorillas. Mol. Ecol. 10, 2241-2247.

Jensen-Seaman, M.I., Deinard, A.S., Kidd, K.K., 2001. Modern African ape populations as genetic and demographic models of the last common ancestor of humans, chimpanzees, and gorillas. J. Heredity 92, 475-480.

Jensen-Seaman, M.I., Deinard, A.S., Kidd, K.K., 2003. Mitochondrial and nuclear DNA estimates of divergence between western and eastern gorillas. In: A.B. Taylor, M.L. Goldsmith (Eds.), Gorilla Biology: A Multidisciplinary Perspective. Cambridge University Press, Cambridge, pp. 247-268.

Jepsen, G.L., 1966. Early Eocene bat from Wyoming. Science 154, 1333-1339.

Johanson, D.C., Lovejoy, C.O., Kimbel, W.H., White, T.D., Ward, S.C., Bush, M.E., Latimer, B.M., Coppens, Y., 1982. Morphology of the Pliocene partial hominid skeleton (A.L. 288-1) from the Hadar Formation, Ethiopia. Am. J. Phys. Anthropol. 57, 403-452.

Johnson, S.E., Shapiro, L.J., 1998. Positional behavior and vertebral morphology in atelines and cebines. Am. J. Phys. Anthropol. 105, 333-354.

Jones, A.L., 2008. The evolution of brachiation in ateline primates, ancestral character states and history. Am, J, Phys, Anthropol. 137, 123-144.

Jones, C., Anderson, S., 1978. *Callicebus moloch*. Mammalian Species 112, 1-5.

Jungers, W.L., 1984. Scaling of the hominoid locomotor skeleton with special reference to lesser apes. In: Preuschoft, H., Chivers, D.J., Brockelman, W.Y., Creel, N. (Eds.), The Lesser Apes: Evolutionary and Behavioral Biology. Edinburgh University Press, Edinburgh, pp. 146-169.

Jungers, W.L., Stern, J.T., 1980. Telemetered electromyography of forelimb muscle chains in gibbons (*Hylobates lar*). Science 208, 617-617.

Keith, A., 1891. Anatomical notes on Malay apes. J. Straits Branch Roy. Asiatic Soc. 23, 77-94.

Keith, A., 1899. On the chimpanzees and their relationship to the gorilla. Proc. Zool. Soc. Lond. 67, 296-312.

Keith, A., 1903. The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates. J. Anat. Physiol. 37, 18-40.

Keith, A., 1923. Man's posture: its evolution and disorders. Brit. Med. J. 1, 451-454, 499-502, 545-548, 587-590, 624-626, 669-672.

Keith, A., 1934. The Construction of Man's Family Tree. Watts, London.

Keith, A., 1940. Fifty years ago. Am. J. Phys. Anthropol. 26, 251-267.

Kimbel, W.H., Delezene, L.K., 2009. "Lucy" redux: a review of research on *Australopithecus afarensis*. Y. Phys. Anthropol. 52, 2-48.

Köhler, M., Moyà-Solà, S., 2003. Understanding the enigmatic ape *Oreopithecus bambolii*. Cour. Forsch.-Inst. Senckenberg 243, 111-123.

Köhncke, M., Leonhardt, K., 1986. *Cryptoprocta ferox*. Mammalian Species 254, 1-5.

Lanier, R.R., 1939. The presacral vertebrae of American white and negro males. Am. J. Phys. Anthropol. 25, 341-420.

Larson, S.G., 1998. Parallel evolution in the hominoid trunk and forelimb. Evol. Anthropol. 6, 87-99.

Latimer, B., Ward, C.V., 1993. The thoracic and lumbar vertebrae. In: Walker, A., Leakey, R. (Eds.). The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 266-293.

Lewis, O.J., 1969. The hominoid wrist joint. Am. J. Phys. Anthropol. 30, 251-267.

Lewis, O.J., 1971. Brachiation and the early evolution of the Hominoidea. Nature 230, 577-579.

Lewis, O.J., 1972. Osteological features characterizing the wrists of monkeys and apes, with a reconsideration of this region in *Dryopithecus* (*Proconsul*) *africanus*. Am. J. Phys. Anthropol. 36, 45-58.

Lewis, O.J., 1974. The wrist articulations of the Anthropoidea. In: F.A. Jenkins (Ed.), Primate Locomotion. Academic Press, New York, pp. 143-169.

Lewis, O.J., 1985. Derived morphology of the wrist articulations and theories of hominoid evolution. Part I. The lorisine joints. J. Anat. 140, 447-460.

Lewis, O.J., 1985. Derived morphology of the wrist articulations and theories of hominoid evolution. Part II. The midcarpal joints of higher primates. J. Anat. 142, 151-172.

Lovejoy, C.O., 2005. The natural history of human gait and posture Part 1. Spine and pelvis. Gait Posture 21, 95-112.

Lovejoy, C.O., 2007. An early ape shows its hand. Proc. R. Soc. B 274, 2373-2374.

Lovejoy, C.O., 2009. Reexamining human origins in light of *Ardipithecus ramidus*. Science 326, 74.

Lovejoy, C.O., Latimer, B., Suwa, G., Asfaw, B., White, T.D., 2009. Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. Science 326, 72.

Lovejoy, C.O., McCollum, M.A., 2010. Spinopelvic pathways to bipedality: why no hominids ever relied on a bent-hip–bent-knee gait. Phil. Trans. R. Soc. B 365, 3289-3299.

Lovejoy, C.O., Simpson, S.W., White, TD., Asfaw, B., Suwa, G., 2009. Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. Science 326, 70.

Lovejoy, C.O., Suwa, G., Simpson, S.W., Matternes, J.H., White, T.D., 2009. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. Science 326, 100-106.

Lovejoy, C.O., Suwa, G., Spurlock, L., Asfaw, B, White, T.D., 2009. The pelvis and femur of *Ardipithecus ramidus*: the emergence of upright walking. Science 326: 71.

Lucae, J.C.G., 1867. Die Robbe und die Otter. Frankfurt am Main.

MacLatchy, L., 2004. The oldest ape. Evol. Anthropol. 13, 90-103.

MacLatchy, L., Gebo, D., Kityo, R., Pilbeam, D., 2000. Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. J. Hum. Evol. 39, 159-183.

MacLatchy, L.M., Pilbeam, D.P., 1999. Renewed research in the Ugandan early Miocene. In: P. Andrews, P. Banham (Eds.), Late Cenozoic Environments and Hominid Evolution: a tribute to Bill Bishop. The Royal Geological Society, London, pp. 15-25.

Madar, S.I., Rose, M.D., Kelley, J., MacLatchy, L., 2002. New *Sivapithecus* postcranial specimens from the Siwaliks of Pakistan. J. Hum. Evol. 42, 705-752.

Madar, S.I., Thewissen, J.G.M., Hussain, S.T., 2002. Additional holotype remains of *Ambulocetus natans* (Cetacea, Ambulocetidae), and their implications for locomotion in early whales. J. Vert. Paleontol. 22, 405-422.

Mallo, M., Wellik, D.M., Deschamps, J., 2010. *Hox* genes and regional patterning of the vertebrate body plan. Develop. Biol. 344, 7-15.

Mansfield, J.H., Abzhanov, A., 2010. Hox expression in the American alligator and evolution of archosaurian axial patterning. J. Exp. Zool. 314B, 629-644.

Matsudaira, K., Ishida, T., 2010. Phylogenetic relationships and divergence dates of the whole mitochondrial genome sequences among three gibbon genera. Mol. Phylogen. Evol. 55, 454-459.

McCollum, M.A., Rosenman, B.A., Suwa, G., Meindl, R.S., Lovejoy, C.O., 2010. The vertebral formula of the last common ancestor of African apes and humans. J. Exp. Biol. 314B, 123-134.

McHenry, H.M., Corruccini, R.S., 1983. The wrist of *Proconsul africanus* and the origin of hominoid postcranial adaptations. In: R.L. Ciochon, R.S. Corruccini (Eds.), New Interpretations of Ape and Human Ancestry. Plenum Press, New York, pp. 353-367.

Mendel, F.C., 1979. The wrist joint of two-toed sloths and its relevance to brachiating adaptations in the Hominoidea. J. Morphol. 162, 413-424.

Mivart, G., 1865. Contributions toward a more complete knowledge of the axial skeleton of primates. Proc. Zool. Soc. Lond. 1865, 545-592.

Montgomery, G.G., 1985. Movements, foraging, and food habits of the four extant species of neotropical vermilinguas (Mammalia: Myrmecophagidae). In: Montgomery, G.G. (Ed.). The Evolution and Ecology of Armadillos, Sloths and Vermilinguas. Smithsonian Institution Press, Washington, D.C., pp. 365-377.

Morbeck, M.E., 1975. *Dryopithecus africanus* forelimb. J. Hum. Evol. 4, 39-46.

Morgan, G.S., 1989. *Geocapromys thoracatus*. Mammalian Species 341, 1-5.

Morton, D.J., 1922. Evolution of the human foot. I. Am. J. Phys. Anthropol. 5, 305-336.

Morton, D.J., 1924. Evolution of the human foot. II. Am. J. Phys. Anthropol. 7, 1-52.

Morton, D.J., 1926. Evolution of man's erect posture. J. Morph. Physiol. 43, 147-179.

Moyà-Solà, S., Alba, D.M., Almécija, S., Casanovas-Vilar, I., Köhler, M., De Esteban-Trivigno, S., Robles, J.M., Galindo, J., Fortuny, J., 2009*b*. A unique Middle Miocene European hominoid and the origins of the great ape and human clade. Proc. Natl. Acad. Sci. USA 106, 9601-9606.

Moyà-Solà, S., Köhler, M., 1996. A *Dryopithecus* skeleton and the origins of great-ape locomotion. Nature 379, 156-159.

Moyà-Solà, S., Köhler, M., 1997. The phylogenetic relationships of *Oreopithecus bambolii* Gervais, 1872. Comp. Rend. Acad. Sci. Paris 324, 141-148.

Moyà-Solà, S., Köhler, M., Alba, D.M., 2005. Response to comment on "*Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain". Science 308, 203d.

Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., 2004. *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. Science 306, 1339-1344.

Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Cabrera, L., Garcés, M., Almécija, S., Beamud, E., 2009*a*. First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Albocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. Am. J. Phys. Anthropol. 139, 126-145.

Moyà-Solà, S., Köhler, M., Rook, L., 1999. Evidence of hominid-like precision grip capability in the hand of the Miocene ape *Oreopithecus*. Proc. Natl. Acad. Sci. USA 96, 313-317.

Muller, J., Scheyer, T.M., Head, J.J., Barrett, P.M., Werneburg, I., Ericson, P.G.P., Pol, D., Sanchez-Villagra, M.R., 2010. Homeotic effects, somitogenesis and the evolution of vertebral numbers in recent and fossil amniotes. Proc. Natl. Acad. Sci. USA 107, 2118-2123.

Napier, J.R., 1963. Brachiation and brachiators. Symp. Zool. Soc. Lond. 10, 183-195.

Napier, J.R., Davis, P.R., 1959. The forelimb skeleton and associated remain of *Proconsul africanus*. Fossil Mammals of Africa. Brit. Mus. (Nat. Hist.) 16, 1-70.

Nakatsukasa, M., 2008. Comparative study of Moroto vertebral specimens. J. Hum. Evol. 55, 581-588.

Nakatsukasa, M., Hirose, Y., 2003. Scaling of lumbar vertebrae in anthropoids and implications for evolution of the hominoid axial skeleton. Primates 44, 127-135.

Nakatsukasa, M., Kunimatsu, Y., 2009. *Nacholapithecus* and its importance for understanding hominoid evolution. Evol. Anthropol. 18, 103-119.

Nakatsukasa, M., Kunimatsu, Y., Nakano, Y., Ishida, H., 2007. Vertebral morphology of *Nacholapithecus kerioi* based on KNM-BG 35250. J. Hum. Evol. 52, 347-369.

Nakatsukasa, M., Kunimatsu, Y., Nakano, Y., Takano, T., Ishida, H., 2003. Comparative and functional anatomy of phalanges in *Nacholapithecus kerioi*, a Middle Miocene hominoid from northern Kenya. Primates 44, 371-412.

Nakatsukasa, M., Tsujikawa, H., Shimizu, D., Takano, T., Kunimatsu, Y., Nakano, Y., Ishida, H., 2003. Definitive evidence for tail loss in *Nacholapithecus*, an East African Miocene hominoid. J. Hum. Evol. 45, 179-186.

Narita, Y., Kuratani, S., 2005. Evolution of the vertebral formulae in mammals: a perspective on developmental constraints. J. Exp. Zool. 304B, 91-106.

Nei, M., 1972. Genetic distance between populations. Am. Nat. 106, 283-292.

Nei, M., 1987. Molecular Evolutionary Genetics. Columbia University Press: New York.

Nei, M., Maruyama, T., Chakraborty, R., 1975. The bottleneck effect and genetic variability in populations. Evolution 29, 1-10.

Nishihara, H., Hasegawa, M., Okada, N., 2006. Pegasoferae, an unexpected mammalian clade revealed by tracking anceint retroposon insertions. Proc. Natl. Acad. Sci. USA 103, 9929-9934.

O'Connor, B.L., 1976. *Dryopithecus* (*Proconsul*) *africanus*: quadruped or non-quadruped?

Odgers, P.N.B., The lumbar and lumbo-sacral diarthrodial joints. J. Anat. 67, 301-317.

Ogilvie, M.D., Hilton, C.E., Ogilvie, C.D., 1998. Lumbar anomalies in the Shanidar 3 Neandertal. J. Hum. Evol. 35, 597-610.

Ohman, J.C., Lovejoy, C.O., White, T.D., 2005. Questions about *Orrorin* femur. 307, 845.

Ohya, Y.K., Kuraku, S., Kuratani, S., 2005. Hox code in embryos of Chinese soft-shelled turtle *Pelodiscus sinensis* correlates with the evolutionary innovation in the turtle. J. Exp. Zool. 304B, 107-118.

Oxnard, C.E., 1967. The functional morphology of the primate shoulder as revealed by comparative anatomical, osteometric and discriminant function techniques. Am. J. Phys. Anthropol. 26, 219-240.

Owen, R., 1859. On the Classification and Geographical Distribution of the Mammalia. Appendix B. On the orang, chimpanzee and gorilla. Parker, London.

Owen, R., 1868. On the Anatomy of Vertebrates, Vol. III. Mammals. Longmans, Green, and Co, London.

Özkan, Z.E., 2007. Macro-anatomical investigations on the skeletons of mole-rat (*Spalax leucodon* Nordmann) III. Skeleton axiale. Veterinarski Arhiv 77, 281-289.

Padilla, M., Dowler, R.C., 1994. *Tapirus terrestris*. Mammalian Species 481, 1-8.

Perelman, P., Johnson, W.E., Roos, C., Seuánez, H.N., Horvath, J.E., Moreira, M.A.M., Kessing, B., Pontius, J., Roelke, M., Rumpler, Y., Schneider, M.P.C., Silva, A., O'Brien, S.J., Pecon-Slattery, J., 2011. A molecular phylogeny of living primates. PLoS Genetics 7, e1001342.

Pickford, M., Senut, B., Gommery, D., Treil, J., 2002. Bipedalism in *Orrorin tugenensis* revealed by its femora. CR Palevol. 1, 191-203.

Pilbeam, D.R., 1982. New hominoid skull material from the Miocene of Pakistan. Nature 295, 232-234.

Pilbeam, D., 1996. Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. Mol. Phylogen. Evol. 5, 155-168.

Pilbeam, D., 1997. Research on Miocene hominoids and hominid origins: the last three decades. In: Begun, D.R., Ward, C.V., Rose, M.D. (Eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum Press, New York, pp. 13-28.

Pilbeam, D., 2004. The anthropoid postcranial axial skeleton: comments on development, variation, and evolution. J. Exp. Zool. 302B, 241-267.

Pilbeam, D.R., Rose, M.D., Barry, J.C., Ibrahim Shah, S.M., 1990. New *Sivapithecus* humeri from Pakistan and the relationship of *Sivapithecus* to *Pongo*. Nature 348, 237-239.

Pilbeam, D.R., Young, N.M., 2001. Sivapithecus and hominoid evolution: some brief comments. In: L. de Bonis, G. Koufos (Eds.), Hominoid Evolution and Climate Change in Europe, Vol. 2, Phylogeny of the Neogene Hominoid Primates of Eurasia. Cambridge University Press, Cambridge 349-364.

Pilbeam, D., Young, N., 2004. Hominoid evolution: synthesizing disparate data. C. R. Palevol 3, 305-321.

Poglayen-Neuwall, I., Toweill, D.E., 1988. *Bassariscus astutus*. Mammalian Species 327, 1-8.

Polly, P.D., Head, J.J., Cohn, M.J., 2001. Testing modularity and dissociation: the evolution of regional proportions in snakes. In: Zelditch, M.L. (Ed.), Beyond Heterochrony: The Evolution of Development. Wiley-Liss, New York, pp. 305-335.

Preuschoft, H., 1973. Body posture and locomotion in some East African Miocene Dryopithecinae. Symp. Soc. Study Hum. Biol. 11, 13-46.

Pridmore, P.A., 1992. Trunk movements during locomotion in the marsupial *Monodelphis domestica* (Didelphidae). J. Morph. 211, 137-146.

Quinn, A., Wilson, D.E., 2004. *Daubentonia madagascariensis*. Mammalian Species 740, 1-6.

Rathbun, G.B., 1979. *Rhynchocyon chrysopygus*. Mammalian Species 117, 1-4.

Reynolds, E., 1931. The evolution of the human pelvis in relation to the mechanics of the erect posture. Papers Peabody Mus. Amer. Archaeol. Ethnol., Harvard 11, 255-334.

Richardson, M.K., Allen, S.P., Wright, G.M., Raynaud, A., Hanken, J., 1998. Somite number and vertebrate evolution. Development 125, 151-160.

Richmond, B.G., Begun, D.R., Strait, D.S., 2001. Origin of human bipedalism: the knuckle-walking hypothesis revisited. Y. Phys. Anthropol. 44, 70-105.

Richmond, B.G., Jungers, W.L., 2008. *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. Science 319, 1662-1665.

Richmond, B.G., Whalen, M., 2001. Forelimb function, bone curvature and phylogeny of *Sivapithecus*. In: L. de Bonis, G. Koufos (Eds.), Hominoid Evolution and Climate Change in Europe, Vol. 2, Phylogeny of the Neogene Hominoid Primates of Eurasia. Cambridge University Press, Cambridge, pp. 326-348.

Robinson, J., 1972. Early hominid posture and locomotion. University of Chicago Press, Chicago.

Rockwell, H., Evans, F.G., Pheasant, H.C., 1938. The comparative morphology of the vertebrate spinal column. Its form as related to function. J. Morphol. 63, 87–117.

Rose, K.D., 1985. Comparative osteology of North American dichobunid artiodactyls. J. Paleontol. 59, 1203-1226.

Rose, M.D., 1975. Functional proportions of primate lumbar vertebral bodies. J. Hum. Evol. 4, 21-38.

Rose, M.D., 1983. Miocene hominoid postcranial morphologoy: monkey-like, ape-like, neither, or both? In: R.L. Ciochon, R.S. Corruccini (Eds.), New Interpretations of Ape and Human Ancestry. Plenum Press, New York, pp. 405-417.

Rose, M.D., 1984. Hominoid postcranial specimens from the Middle Miocene Chinji Formation, Pakistan. J. Hum. Evol. 13, 503-516.

Rose, M.D., 1993. Locomotor anatomy of Miocene hominoids. In: D.L. Gebo (Ed.), Postcranial Adaptation in Nonhuman Primates. Northern Illinois University Press, DeKalb, IL, pp. 71-95.

Rose, M.D., 1994. Quadrupedalism in some Miocene catarrhines. J. Hum. Evol. 26, 387-411.

Rose, M.D., 1997. Functional and phylogenetic features of the forelimb in Miocene hominoids. D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 79-100.

Rosenman, B.A., 2008. Triangulating the evolution of the vertebral column in the last common ancestor: thoracolumbar transverse process homology in the hominoidea. Ph.D. dissertation, Kent State University.

Rowe, D.L., Honeycutt, R.L., 2002. Phylogenetic relationships, ecological correlates, and molecular evolution within the Cavioidea (Mammalia, Rodentia). Mol. Biol. Evol. 19, 236-277.

Russo, G.A., 2010. Prezygapophyseal articular facet shape in the catarrhine thoracolumbar vertebral column. Am. J. Phys. Anthropol. 142, 600-612.

Russo, G.A., Shapiro, L.J., 2011. Morphological correlates of tail length in the catarrhine sacrum. J. Hum. Evol. doi:10.1016/j.jhevol.2011.03.006.

Sánchez-Villagra, M.R., Narita, Y., Kuratani, S., 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. Syst. Biodiv. 5, 1-7.

Sánchez-Villagra, M., Williams, B.A., 1998. Levels of homoplasy in the evolution of the mammalian skeleton. J. Mammal. Evol. 5, 113-126.

Sanders, W.J., 1995. Function, allometry, and the evolution of the australopithecine lower precaudal spine. Ph.D. dissertation, New York University.

Sanders, W.J., 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. J. Hum. Evol. 34, 249-302.

Sanders, W.J., Bodenbender, B.E., 1994. Morphometric analysis of lumbar vertebra UMP 67-28: implications for spinal function and phylogeny of the Miocene Moroto hominoid. J. Hum. Evol. 26, 203-237.

Sargis, E.J., 2001. A preliminary qualitative analysis of the axial skeleton of tupaiids (Mammalia, Scandentia): functional morphology and phylogenetic implications. J. Zool. Lond. 253, 473-483.

Sarmiento, E.E., 1987. The phylogenetic position of *Oreopithecus* and its significance in the origin of the Hominoidea. Am. Mus. Novitates 2881, 1-44.

Sarmiento, E.E., 1988. Anatomy of the hominoid wrist joint: its evolutionary and functional implications. Int. J. Primatol. 9, 281-345.

Sarmiento, E.E., 1994. Terrestrial traits in the hands and feet of gorillas. Am. Mus. Novit. 3091, 1-56.

Sarmiento, E.E., 1995. Cautious climbing and folivory: a model of hominoid differentiation. Hum. Evol. 10, 289-321.

Sarmiento, E.E., 2002. Forearm rotation and the "Origin of the hominoid lifestyle": a reply to Stern and Larson (2001). Am. J. Phys. Anthropol. 119, 92-94.

Sarmiento, E.E., 2010. Comment on the paleobiology and classification of *Ardipithecus ramidus*. Science 328, 1105-b.

Schön, M.A., Ziemer, L.K., 1973. Wrist mechanism and locomotor behavior of *Dryopithecus* (*Proconsul*) *africanus*. Folia Primatol. 20, 1-11.

Schultz, A., 1930. The skeleton of the trunk and limbs of higher primates. Hum. Biol. 2, 303-438.

Schultz, A., 1933. Observations on the growth, classification and evolutionary specialization of gibbons and siamangs (concluded). Hum. Biol. 5, 385-428.

Schultz, A.H., 1934. Some distinguishing characters of the mountain gorilla. J. Mammal. 15, 51-61.

Schultz, A.H., 1938. The relative length of the regions of the spinal column in Old World primates. Am. J. Phys. Anthropol. 24, 1-22.

Schultz, A.H., 1960. Einige beobachtungen und masse am skelett von Oreopithecus. Z. Morph. Anthrop. 50, 136-149.

Schultz, A.H., 1961. Vertebral column and thorax. Primatologia 4, 1-66.

Schultz, A.H., Straus, W.L., 1945. The numbers of vertebrae in primates. Proc. Am. Phil. Soc. 89, 601-626.

Scott, W.B., Jepsen, G.L., 1936. The mammalian fauna of the White River Oligocene. Part I. Insectivora and Carnivora. Trans. Am. Phil. Soc. 28, 1-153.

Seebeck, J.H., 2001. *Perameles gunnii*. Mammalian Species 645, 1-8.

Senut, B., 2007. The earliest putative hominids. In: W. Henke, I. Tattersal (Eds.), Handbook of Paleoanthropology. Vol. 3: Phylogeny of Hominids. Springer, Berlin, 1519-1538.

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., Coppens, Y., 2001. First hominid from the Miocene (Lukeino Formation, Kenya). CR Acad. Sci. Paris 332, 137-144.

Shackleton, D.M., 1985. *Ovis canadensis*. Mammalian Species 230, 1-9.

Shapiro, L.J., 1991. Functional morphology of the primate spine with special reference to orthograde posture and bipedal locomotion. Ph.D. dissertation, SUNY Stony Brook.

Shapiro, L., 1993. Functional morphology of the vertebral column in primates. In: Gebo, D.L. (Ed.), Postcranial Adaptation in Nonhuman Primates. Northern Illinois University Press, Dekalb, IL.

Shapiro, L., 1993. Evaluation of "unique" aspects of human vertebral bodies and pedicles with a consideration of *Australopithecus africanus*. J. Hum. Evol. 25, 433-470.

Shapiro, L., 1995. Functional morphology of indrid lumbar vertebrae. Am. J. Phys. Anthropol. 98, 323-342.

Shapiro, L.J., Seiffert, C.V.M., Godfrey, L.R., Jungers, W.L., Simons, E.L., Randria, G.F.N., 2005. Morphometric analysis of lumbar vertebrae in extinct Malagasy strepsirrhines. Am. J. Phys. Anthropol. 128, 823-839.

Shaw, J.H., Carter, T.S., Machjado-Neto, J.C., 1985. Ecology of the giant anteater Myrmecophaga tridactyla in Serra da Canastra, Minas Gerais, Brazil: a pilot study. In: Montgomery, G.G. (Ed.). The Evolution and Ecology of Armadillos, Sloths and Vermilinguas. Smithsonian Institution Press, Washington, D.C., pp. 379-384.

Shea, B.T., 1985. On aspects of skull form in African apes and orangutans, with implications for hominoid evolution. Am. J. Phys. Anthropol. 68, 329-342.

Shea, B.T., 1988. Phylogeny and skull form in the hominoid primates. In: J. Schwartz (Ed.), Orang-Utan Biology. Oxford University Press, New York, pp. 233-245.

Sheffield, S.R., King, C.M., 1994. *Mustela nivalis*. Mammalian Species 454, 1-10.

Shoshani, J., Goldman, C.A., Thewissen, J.G.M., 1988. *Orycteropus afer*. Mammalian Species 300, 1-8.

Simmons, N.B., Seymour, K.L., Habersetzer, J., Gunnell, G.F., 2008. Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451, 818-822.

Simoens, P., de Vos, N.R., Lauwers, H., Nicaise, M., 1983. Numerical vertebral variations and transitional vertebrae in the goat. Zbl. Vet. Med. C. Anat. Histol. Embryol. 12, 97-103.

Slijper, E.J., 1946. Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. Verh. Kon. Ned. Akad. Wet. (Tweede Sectie) 42, 1-128.

Slijper, E.J., 1947. Observations on the vertebral column of the domestic animals. Vet. Journal 103, 376-387.

Spotorno, A.E., Zuleta, C.A., Valladares, J.P., Deane, A.L., Jiménez, J.E., 2004. *Chinchilla laniger*. Mammalian Species 785, 1-9.

Stern, J.T., 1976. Before bipedality. Y. Phys. Anthropol. 19, 59-68.

Stern, J.T., Larson, S.G., 2001. Telemetered electromyography of the supinators and pronators of the forearm in gibbons and chimpanzees: implications for the fundamental positional adaptation of hominoids. Am. J. Phys. Anthropol. 115, 253-268.

Stern, J.T., Oxnard, C.E., 1973. Primate locomotion: some links with evolution and morphology. Primatologia 4, 1-93.

Stern, J.T., Wells, J.P., Jungers, W.L., Vangor, A.K., 1980. An electromyographic study of serratus anterior in atelines and *Alouatta*: implications for hominoid evolution. Am. J. Phys. Anthropol. 52, 323-334.

Stern, J.T., Wells, J.P., Jungers, W.L., Vangor, A.K., Fleagle, J.G., 1980. An electromyographic study of the pectoralis major in atelines and *Hylobates*, with special reference to the evolution of a pars clavicularis. Am. J. Phys. Anthropol. 52, 18-25.

Stern, J.T., Wells, J.P., Vangor, A.K., Fleagle, J.G., 1977. Electryomyography of some muscles of the upper limb in *Ateles* and *Lagothrix*. Y. Phys. Anthropol. 20, 498-507.

Stecher, R.M., 1962. Anatomical variations of the spine in the horse. J. Mammal. 43, 205-219.

Stevens, L.S., 2004. Morphological variation in the hominoid vertebral column. Master's thesis, Kent State University.

Stewart, T.D., 1932. The vertebral column of the Eskimo. Am. J. Phys. Anthropol. 17, 123-136.

Straus, W.L., 1940. The posture of the great ape hand in locomotion, and its phylogenetic implications. Am. J. Phys. Anthropol. 27, 199-207.

Straus, W.L., 1942. Rudimentary digits in primates. Q. Rev. Biol. 17, 228-243.

Straus, W.L., 1949. The riddle of man's ancestry. Q. Rev. Biol. 24, 200-223.

Straus, W.L., 1962. Fossil evidence of the evolution of the erect, bipedal posture. Clin. Orthop. 25, 9-19.

Straus, W.L., 1963. The classification of *Oreopithecus*. In: Washburn SL (Ed.), Classification and Human Evolution. Aldine, Chicago, pp. 146-177.

Straus, W.L., 1968. Huxley's evidence as to man's place in nature – a century later. In: L.G. Stevenson, R.P. Multhauf (Eds.), Medicine Science and Culture: Historical Essays in Honor of Owsei Temkin. The Johns Hopkins Press, Baltimore, pp. 160-167.

Straus, W.L., Wislocki, G.B., 1942. On certain similarities between sloths and sloth lemurs. Bull. Mus. Comp. Zool. (Harvard) 74, 45-56.

Stromer von Reichenbach, E., 1902. Die Wirbel der Land-Raubtiere. Zoologica 15, 1.

Stubbs, N.C., Hodges, P.W., Jeffcott, L.B., Cowin, G., Hodgson, D.R., McGowan, C.M., 2006. Functional anatomy of the caudal thoracolumbar and lumbosacral spine in the horse. Equine Vet. J. Suppl. 36, 393-399.

Struthers, J., 1874. On variations of the vertebrae and ribs in man. J. Anat. Phys. 9, 17-96.

Struthers, J., 1892. On the articular processes of the vertebrae in the gorilla compared with those in man, and on cost-vertebral variation in the gorilla. J. Anat. Phys. 27, 131-138.

Susman, R.L., 2004. *Oreopithecus bambolii*: an unlikely case of hominidlike grip capability in a Miocene ape. J. Hum. Evol. 46, 105-117.

Suwa, G., Kono, R.T., Simpson, S.W., Asfaw, B., Lovejoy, C.O., White, T.D., 2009. Paleobiological implications of the *Ardipithecus ramidus* dentition. Science 236, 69, 94-99.

Tague, R.G., 2009. High assimilation of the sacrum in a sample of American skeletons: prevalence, pelvic size, and obstetrical and evolutionary implications. Am. J. Phys. Anthropol. 138, 429-438.

Tam, P.P.L., Tan, S.S., 1992. The somitogenetic potential of cells in the primitive streak and the tail bud of the organogenesis-stage mouse embryo. Development 115, 703-715.

Tecirlioglu, S., 1983. Sirtlan ve köpegin iskelet kemikleri üzerinde makro-anatomik arastirmalar. Ankara Üniv. Vet. Fak. Derg. 30, 149-166.

Thorpe, S.K.S., Holder, R.L., Crompton, R.H., 2007. Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science 316, 1328-1331.

Tocheri, M.W., Solhan, C.R., Orr, C.M., Femiani, J., Frohlich, B., Groves, C.P., Harcourt-Smith, W.E., Richmond, B.G., Shoelson, B., Jungers, W.L., 2011. Ecological divergence and medial cuneiform morphology in gorillas. J. Hum. Evol. 60,171-184.

Todd, T.W., 1922. Numerical significance in the thoracicolumbar vertebrae of the Mammalia. Anat. Rec. 24, 261-286.

Toussaint, M., Macho, G.A., Tobias, P.V., Partridge, T.C., Hughes, A.R., 2003. The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa. S. Af. J. Sci. 99, 215-223.

Trevor, J.C., 1963. The history of the word "brachiator" and a problem of authorship in primate nomenclature. Symp. Zool. Soc. Lond. 10, 197-198.

Turner, H.N., 1847. Observations on the distinction between the cervical and dorsal vertebrae in the Class Mammalia. Proc. Zool. Soc. Lond. 15, 110-114.

Tuttle, R.H., 1969. Quantitative and functional studies on the hands of the Anthropoidea. I. The Hominoidea. J. Morpohol. 128, 309-364.

Tuttle, R.H., 1969. Knuckle-walking and the problem of human origins. Science 166, 953-961.

Tuttle, R.H., 1974. Darwin's apes, dental apes, and the descent of man: normal science in evolutionary anthropology. Curr. Anthropol. 15, 389-426.

Tuttle, R.H., 1975. Parallelism, brachiation, and hominoid phylogeny. In: W.P. Luckett, F.S. Szalay (Eds.), Phylogeny of the Primates: A Multidisciplinary Approach. Plenus Press, New York, pp. 447-480.

Tuttle, R.H., 1981. Evolution of hominid bipedalism and prehensile capabilities. Phil. Trans. R. Soc. Lond. 292, 89-94.

Van Sittert, S.J., Skinner, J.D., Mitchell, G., 2010. From fetus to adult – an allometric analysis of the giraffe vertebral column. J. Exp. Zool. 314B, 469-479.

Verts, B.J., Carraway, L.N., Kinlaw, A., 2001. *Spilogale gracilis*. Mammalian Species 674, 1-10.

Wake, D.B., 1994. Comparative terminology. Science 265, 268-269.

Wake, D.B., Wake, M.H., Specht, C.D., 2011. Homoplasy: from detecting pattern to determining process and mechanism of evolution. Science 331, 1032-1035.

Walker, A., 1997. *Proconsul*: function and phylogeny. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 209-224.

Walker, A., Leakey, R., 1993. The postcranial bones. In: Walker, A., Leakey, R. (Eds.), The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 95-160.

Walker, A.C., Pickford, M., 1983. New postcranial fossils of *Proconsul africanus* and *Proconsul nyanzae*. In: R.L. Ciochon, R.S. Corruccini (Eds.), New Interpretations of Ape and Human Ancestry. Plenum Press, New York, pp. 325-351.

Walker, A., Rose, M.D., 1968. Fossil hominoid vertebra from the Miocene of Uganda. Nature 217, 980-981.

Walker, A., Ruff, C.B., 1993. The reconstruction of the pelvis. In: Walker, A., Leakey, R. (Eds.), The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 221-233.

Walker, M.J., Ortega, J., Parmová, K., López, M.V., Trinkaus, E., 2011. Morphology, body proportions, and postcranial hypertrophy of a female Neandertal from the Sima de las Palomas, southeastern Spain. Proc. Natl. Acad. Sci. USA 108, 10087-10091.

Ward, C.V., 1991. The functional anatomy of the lower back and pelvis of the Miocene hominoid *Proconsul nyanzae* from the Miocene of Mfangano Island, Kenya. Ph.D. dissertation, The Johns Hopkins University.

Ward, C.V., 1993. Torso morphology and locomotion in *Proconsul nyanzae*. Am. J. Phys. Anthropol. 92, 291-328.

Ward, C.V., 1997. Functional anatomy and phyletic implications of the hominoid trunk and hindlimb. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 101-130.

Ward, C.V., 1998. *Afropithecus*, *Proconsul*, and the primitive hominoid skeleton. In: E. Strasser, J. Fleagle, A. Rosenberger, McHenry, H. (Eds.), Primate Locomotion: Recent Advances. Plenum Press, New York, pp. 337-352.

Ward, C.V., 2007. Postcranial and locomotor adaptations of hominoids. In: W. Henke, I. Tattersal (Eds.), Handbook of Paleoanthropology. Vol. 2: Primate Evolution and Human Origins. Springer, Berlin, pp. 1011-1030.

Ward, C.V., Walker, A., Teaford, M.F., 1991. *Proconsul* did not have a tail. J. Hum. Evol. 21, 215-220.

Ward, C.V., Walker, A., Teaford, M.F., Odhiambo, I., 1993. Partial skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. Am. J. Phys. Anthropol. 90, 77-111.

Ward, S., 1997. The taxonomy and phyletic relationships of *Sivapithecus* revisited. In: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum, New York, pp. 269-290.

Ward, S.C., Brown, B., 1986. The facial skeleton of *Sivapithecus indicus*. In: D.R. Swindler, J. Erwin (Eds.), Comparative Primate Biology, Vol. 1: Systematics, Evolution, and Anatomy. Alan R. Liss, New York, pp. 413-452.

Ward, S.C., Kimbel, W.H., 1983. Subnasal alveolar morphology and the systemic position of *Sivapithecus*. Am. J. Phys. Anthropol. 61, 157-171.

Ward, S.C., Pilbeam, D.R., 1983. Maxillofacial morphology of Miocene hominoids from Africa and Indo-Pakistan. In: R.L. Corruccini, R.S. Ciochon (Eds.), New Interpretation of Ape and Human Ancestry. Plenum, New York, pp. 211-238.

Waser, P., 1984. Ecological differences and behavioral contrasts between two mangabey species. In: P.S. Rodman, J.G.H. Cant (Eds.), Adaptations for Foraging in Non-human Primates. Columbia University Press, pp. 195-216.

Washburn, S.L., 1950. The analysis of primate evolution with particular reference to the origin of man. Cold Spring Harbor Symposia on Quantitative Biology 15, 67-77.

Washburn, S.L., 1963. Behavior and human evolution. In: S.L. Washburn (Ed.), Classification and Human Evolution. Aldine, Chicago, pp. 190-203.

Washburn, S.L., 1968. Speculations on the problem of man's coming to the ground. In: B. Rothblatt (Ed.), Changing Perspectives on Man. University of Chicago Press, Chicago, pp. 191-206.

Washburn, S.L., 1971. The study of human evolution. In: P. Dolhinow, V. Sarich (Eds.), Background for Man: Readings in Physical Anthropology. Little, Brown and Co., Boston, pp. 82-117.

Washburn, S.L., 1973. Human evolution: science or game? Y. Phys. Anthropol. 17, 67-70.

Washburn, S.L., Buettner-Janusch, J., 1952. The definition of thoracic and lumbar vertebrae. Am. J. Phys. Anthropol. Suppl. 10, 251-252

Welcker, H., 1881. Die nuee anatomische Anstalt zu Halle durch einen Vortrag uber Wirbelsaule und Becken. Arch. Anat. Physiol., Anat. Abth. 161-192.

Wellik, D.M., 2007. *Hox* patterning of the vertebrate axial skeleton. Dev. Dyn. 236, 2454-2463.

Wellik, D.M., 2009. *Hox* genes and vertebrate axial pattern. Curr. Topics Develop. Biol. 88, 257-278.

Wellik, D.M., Capecchi, M.R., 2003. *Hox10* and *Hox11* genes are required to globally pattern the mammalian skeleton. Science 301, 363-367.

White, J.L., 1993. Indicators of locomotor habits in xenarthrans: evidence for locomotor heterogeneity among fossil sloths. J. Vert. Paleontol. 13, 230-242.

White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G., WoldeGabriel, G., 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. Science 326, 64, 75-86.

White, T.D., Suwa, G., Lovejoy, C.O., 2010. Response to comment on the paleobiology and classification of *Ardipithecus ramidus*. Science 328, 1105-c.

Whitten, A., McGrew, W.C., Aiello, L.C., Boesch, C., Boyd, R., Byrne, R.W., Dunbar, R.I.M., Matsuzawa, T., Silk, J.B., Tomasello, M., van Schaik, C.P., Wrangham, R., 2010. Studying extant species to model our past. Science 327, 410.

Wilcox, A.R., 1971. Indices of qualitative variation and political measurement. West. Pol. Quart. 26, 325-343.

Williams, B.A., 2007. Comparing levels of homoplasy in the primate skeleton. J. Hum. Evol. 52, 480-489.

Williams, S.A., 2009. Modularity in the hominoid vertebral column: implications for the evolution of orthogrady. Am. J. Phys. Anthropol. Suppl. 47, 366.

Williams, S.A., 2010. Morphological integration and the evolution of knuckle-walking. J. Hum. Evol. 58, 432-440.

Wolpoff, M.H., Hawks, J., Senut, B., Pickford, M., Ahern, J., 2006. An ape or *the* ape: is the Toumaï cranium TM 266 a hominid? Paleoanthropol. 2006, 36-50.

Wolpoff, M.H., Senut, B., Pickford, M., Hawks, J., 2002. *Sahelanthropus* or '*Sahelpithecus*'? Nature 419, 581-582.

Wood, A.R., Bebej, R.M., Manz, C.L., Begun, D.L., Gingerich, P.D., 2010. Postcranial functional morphology of *Hyracotherium* (Equidae, Perissodactyls) and locomotion in the earliest horses. J. Mammal. Evol. 18, 1-32.

Wood, B., 2010. Reconstructing human evolution: achievements, challenges, and opportunities. Proc. Natl. Acad. Sci. USA 107, 8902-8908.

Wood, B., Harrison, T., 2011. The evolutionary context of the first hominins. Nature 470, 347-352.

Yamada, F., Cervantes, F.A., 2005. *Pentalagus furnessi*. Mammalian Species 782, 1-5.

Yang, A., Fang, L., 1982. The vertebral column and the thorax of the giant panda, *Ailuropoda melanoleuca*. Acta Theriologica Sinica 2, 1-8.

Yilmaz, S., 1998. Macro-anatomical investigations on the skeletons of porcupine (*Hystrix cristata*). Part III: skeleton axiale. Anat. Histol. Embryol. 27, 293-296.

Yilmaz, S., Dinc, G., Toprak, B., 2000. Macro-anatomical investigations on skeletons of otter (*Lutra lutra*). III. Skeleton axiale. Veterinarski Arhiv 70, 191-198.

Young, N.M., 2002. Homology and homoplasy in the evolution of the hominoid postcranium. Ph.D. dissertation, Harvard University.

Young, N.M., 2003. A reassessment of living hominoid postcranial variability: implications for ape evolution. J. Hum. Evol. 45, 441-464.

Young, N.M., 2005. Estimating hominoid phylogeny from morphological data: character choice, phylogenetic signal and postcranial data. In: D.E. Lieberman, R.J. Smith, J. Kelley (Eds.), Interpreting the Past. Brill Academic, Boston, pp.1-13.

Young, N.M., MacLatchy, L., 2004. The phylogenetic position of *Morotopithecus*. J. Hum. Evol. 46, 163-184.

Young, N.M., Wagner, G.P., Hallgrimsson, B., 2010. Development and the evolvability of human limbs. Proc. Natl. Acad. Sci. USA 107, 3400-3405.

Yu, N., Jensen-Seaman, M.I., Chemnick, L., Kidd, J.R., Deinard, A.S., Ryder, O., Kidd, K.K., Li, W.-H., 2003. Low nucleotide diversity in chimpanzees and bonobos. Genetics 164, 1511-1518.

Zapfe, H., 1958. The skeleton of *Pliopithecus* (*Epipliopithecus*) *vindobonesis* Zapfe and Hurzeler. Am. J. Phys. Anthropol. 16, 441-458.

Zollikofer, C.P.E., Ponce de León, M.S., Lieberman, D.E., Guy, F., Pilbeam, D., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2005. Virtual cranial reconstruction of *Sahelanthropus tchadensis*. Nature 434, 755-759.