



The evolution of vertebral formulae in Hominoidea



Nathan E. Thompson^{a,*}, Sergio Almécija^{b,c}

^a Department of Anatomy, NYIT College of Osteopathic Medicine, Old Westbury, NY 11568, USA

^b Center for the Advanced Study of Human Paleobiology, Department of Anthropology, The George Washington University, Washington, DC 20052, USA

^c Institut Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona, Edifici ICTA-ICP, Carrer de Les Columnes Sense Número, Campus de La UAB, 08193, Cerdanyola Del Vallès, Barcelona, Spain

ARTICLE INFO

Article history:

Received 25 January 2016

Accepted 27 May 2017

Available online 3 July 2017

Keywords:

Bipedalism

Lumbar

Sacrum

Hominin evolution

Ape evolution

ABSTRACT

Primate vertebral formulae have long been investigated because of their link to locomotor behavior and overall body plan. Knowledge of the ancestral vertebral formulae in the hominoid tree of life is necessary to interpret the pattern of evolution among apes, and to critically evaluate the morphological adaptations involved in the transition to hominin bipedalism. Though many evolutionary hypotheses have been proposed based on living and fossil species, the application of quantitative phylogenetic methods for thoroughly reconstructing ancestral vertebral formulae and formally testing patterns of vertebral evolution is lacking. To estimate the most probable scenarios of hominoid vertebral evolution, we utilized an iterative ancestral state reconstruction approach to determine likely ancestral vertebral counts in apes, humans, and other anthropoid out-groups. All available ape and hominin fossil taxa with an inferred regional vertebral count were included in the analysis. Sensitivity iterations were performed both by changing the phylogenetic position of fossil taxa with a contentious placement, and by changing the inferred number of vertebrae in taxa with uncertain morphology. Our ancestral state reconstruction results generally support a short-backed hypothesis of human evolution, with a *Pan-Homo* last common ancestor possessing a vertebral formulae of 7:13:4:6 (cervical:thoracic:lumbar:sacral). Our results indicate that an initial reduction in lumbar vertebral count and increase in sacral count is a synapomorphy of crown hominoids (supporting an intermediate-backed hypothesis for the origins of the great ape-human clade). Further reduction in lumbar count occurs independently in orangutans and African apes. Our results highlight the complexity and homoplastic nature of vertebral count evolution, and give little support to the long-backed hypothesis of human evolution.

© 2017 Elsevier Ltd. All rights reserved.

1. Introduction

The evolution of bipedalism in humans has fundamentally changed the orientation of the vertebral column during terrestrial locomotion compared to any other hominid (i.e., the great ape and human clade). Thus, there has been a long-standing interest in recognizing vertebral adaptations that are indicative of this change (Keith, 1902, 1923; Schultz and Straus, 1945; Schultz, 1953; Robinson, 1972; Rose, 1975; Cook et al., 1983; Schmid, 1991; Latimer and Ward, 1993; Shapiro, 1993; Sanders, 1998; Haeusler et al., 2002, 2011, 2012; Pilbeam, 2004; Ward and Latimer, 2005; Lovejoy, 2005; Whitcome et al., 2007; Lovejoy and McCollum, 2010; Williams, 2011a, 2012a,b; Been et al., 2012, 2014; Whitcome, 2012; Williams et al., 2013; Williams and Russo,

2015). Identifying such adaptations is crucial to understand the functional and biomechanical demands of bipedal gait in general, as well as to understand the nature and efficiency of bipedal locomotion in our early hominin ancestors. In addition to the numerous adaptations in vertebral shape that have been identified in hominins (e.g., Schultz, 1953; Rose, 1975; Latimer and Ward, 1993; Shapiro, 1993; Sanders, 1998; Whitcome et al., 2007), the numerical count of vertebrae within non-cervical spinal regions (thoracic, lumbar, and sacral) has often been investigated as a potential target of selection in response to bipedal posture and locomotion (Keith, 1902; Schultz and Straus, 1945; Filler, 1994; Haeusler et al., 2002; Pilbeam, 2004; McCollum et al., 2010; Williams, 2011a; Williams and Russo, 2015, 2016; Machnicki et al., 2016; Williams et al., 2016).

In comparison to humans, pronograde mammals, including arboreal and terrestrial primates, possess more (Schultz and Straus, 1945; Williams, 2011a), and craniocaudally longer (Jungers, 1984;

* Corresponding author.

E-mail address: nthomp03@nyit.edu (N.E. Thompson).

Susanna et al., 2014) lumbar vertebrae (Fig. 1). Longer lumbar vertebral columns are thought to facilitate greater flexion and extension of the spine, which increases stride length during quadrupedal locomotion, particularly during high-speed gaits (Hildebrand, 1959; English, 1980; Fischer, 1994; Fischer and Lehmann, 1998; Fischer et al., 2002; Schilling and Hackert, 2006). In addition, flexion and extension of the lumbar spine may ultimately play a role in storage and recovery of elastic energy in epaxial musculature (Taylor, 1978; English, 1980; Alexander et al., 1985). Leaping arboreal primates may further gain from longer lumbar columns by increasing the potential for positive work during acceleration for takeoff (Hall-Craggs, 1965; Preuschoft et al., 1979; Johnson and Shapiro, 1998). On the other hand, extant hominoids, and particularly extant great apes, exhibit a reduced number of thoracolumbar (but especially lumbar) vertebrae, and correspondingly an increased number of sacral vertebrae (Fig. 1; Schultz, 1961; Williams, 2011a). This thoracolumbar shortening of the column has been interpreted functionally as a way to increase the stiffness of the trunk (Schultz, 1930; Cartmill and Milton, 1977; Jungers, 1984; Ward, 1993; Hildebrand and Goslow, 2001; Lovejoy, 2005; Lovejoy and McCollum, 2010; but see Thompson et al., 2015 in relation to axial rotations). A stiffer trunk would presumably reduce the stress experienced by intervertebral discs by reducing overall angular excursion (e.g., Jungers, 1984; Ward, 1993). This is thought to be beneficial for primates relying on forelimb-dominated locomotor behaviors in general (Ward, 1993), or more specifically bridging (Cartmill and Milton, 1977) and/or arm swinging (Hildebrand and Goslow, 2001) behaviors. Some or all of these behaviors characterize a portion of the locomotor repertoire of living apes. These activities are thought to incur large intervertebral joint reaction forces, particularly for animals with large body mass (Jungers, 1984). Others believe that the length reduction of the thoracolumbar column was not the primary target of selection, but rather a secondary effect of the dorsal shift of the scapula on the thorax (Lovejoy et al., 2009b; Lovejoy and McCollum, 2010; McCollum et al., 2010; though see Middleton et al., 2017). Under this hypothesis, a dorsally placed scapula required invagination of the vertebral column within the thorax, and a dorsal shift of the vertebral transverse processes. This may have reduced the available space for epaxial muscles which, in turn, may have necessitated an increase in osteological rigidity to maintain upper body stability

during locomotion (Lovejoy et al., 2009b; Lovejoy and McCollum, 2010). Regardless, the outcome is thought to be an osteological rigidification of the vertebral column.

Compared to both extant great apes and quadrupedal monkeys, humans exhibit an intermediate vertebral count (Fig. 1). With a modal vertebral formula of 7:12:5:5 (cervical:thoracic:lumbar:sacral) humans have a thoracic count that is on the low end of primates (but similar to many Old World monkeys), a lumbar count that is higher than most apes but lower than most non-hominoid primates, and a sacral count that is lower than some apes but higher than non-hominoids (Schultz, 1961; Williams, 2011a; Williams et al., 2016). Currently, three major evolutionary scenarios have been put forward explaining how humans have reached their morphology, each of which entails different anatomical, functional, and behavioral assumptions of the *Pan-Homo* last common ancestor (LCA), as well as different assumptions of vertebral column selection and adaption in response to bipedalism in hominins.

The first scenario has been generally referred to as the ‘short-backed’ hypothesis (McCollum et al., 2010; Russo, 2010; Williams, 2011a,b; Williams and Russo, 2015) in reference to Benton’s (1967) division between ‘short-backed’ hominoids and atelids versus the ‘long-backed’ Old World monkeys, (non-atelid) New World monkeys, and lemurs. Therein, humans are hypothesized to have evolved from a *Pan-Homo* LCA that possessed a modal vertebral column similar to living African apes (either 7:13:4:5 or 7:13:4:6; Keith, 1902, 1923; Pilbeam, 1996, 2004; Lovejoy, 2005; Williams, 2011a). Under this hypothesis, this vertebral formula would also likely have characterized the *Gorilla-Pan-Homo* LCA, as well as the hominid LCA (Pilbeam, 2004; Williams, 2011a). Thus, the short-backed morphology of extant great apes, as well as their forelimb dominated forms of arboreal locomotion, would be ancestral for all hominids. From this morphology, humans would have gained an additional lumbar vertebra (through a hypothetical homeotic shift of thoracic to lumbar), and potentially lost a sacral vertebra or incorporated it into the coccyx (Pilbeam, 2004; Williams, 2011a; Williams and Pilbeam, 2017).

The second evolutionary scenario, the long-backed hypothesis, posits that the ancestral vertebral formula at the *Pan-Homo* LCA, as well as the *Gorilla-Pan-Homo*, hominid, and hominoid LCAs was more similar to that of quadrupedal monkeys than to that of any of

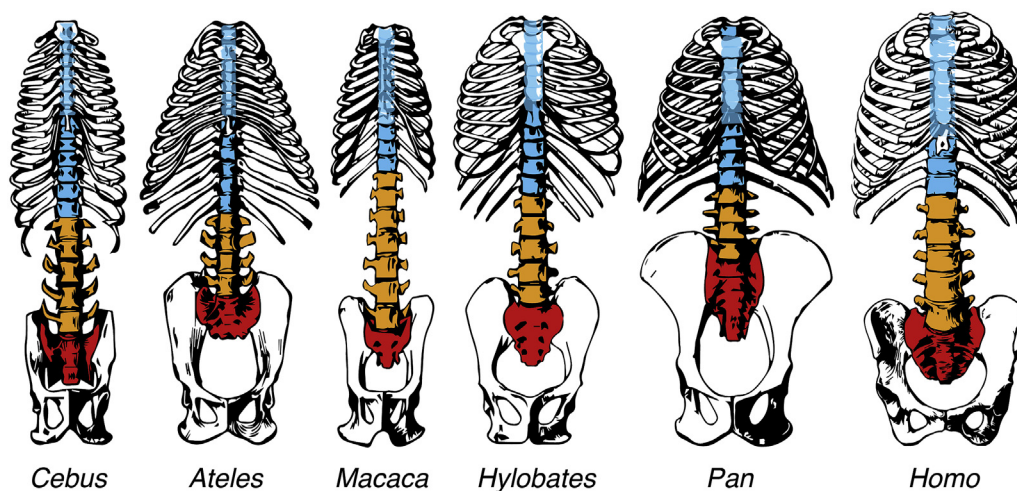


Figure 1. Torso shape and relative vertebral column length in selected anthropoids. Torsos are scaled to the same distance between first thoracic vertebra and caudal end of pelvis to highlight shape differences. Red, sacral vertebrae; orange, lumbar vertebrae; blue, thoracic vertebrae (transparent vertebrae overlay the ribcage). Adapted from Schultz (1950) and Erikson (1963).

Download English Version:

<https://daneshyari.com/en/article/5766866>

Download Persian Version:

<https://daneshyari.com/article/5766866>

[Daneshyari.com](https://daneshyari.com)