Journal of Human Evolution 144 (2020) 102791

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Great apes and humans evolved from a long-backed ancestor

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ARTICLE INFO

Article history:
Received 26 April 2019
Accepted 23 March 2020
Available online xxx

Keywords:
Lumbar lordosis
Parallel evolution
Human evolution
Bipedalism
Morotopithecus
Pierolapithecus

ABSTRACT

There is current debate whether the *Homo*/*Pan* last common ancestor (LCA) had a short, stiff lumbar column like great apes or a longer, flexible column observed in generalized Miocene hominoids. Beyond having only four segments, three additional features contribute to lumbar stiffening: the position of the transitional vertebra (TV), orientation of the lumbar spinous processes, and entrapment of lumbar vertebrae between the iliac blades. For great apes, these features would be homologous if inherited from a short-backed LCA but likely functionally convergent through dissimilar phenotypes if evolved from a long-backed LCA. We quantitatively and qualitatively analyzed human, ape, and monkey thoracic and lumbar vertebrae using 3D surface scanning and osteological measurements to compare spinous process morphology and sacral depth. We also used a large sample of hominoid vertebral counts to assess variation in the position of the TV and lumbosacral boundary. All extant hominoids modally place the TV at the ultimate thoracic. However, humans and orangutans place the TV at the 19th postcranial vertebral segment, whereas other apes place the TV at the 20th. Furthermore, chimpanzees, gorillas, and orangutans each have distinct patterns of spinous process angulation and morphology associated with lumbar stiffening, while human spinous process morphology is similar to that of longer backed gibbons, monkeys, and Miocene hominoids *Morotopithecus* and *Pierolapithecus*. Finally, chimpanzees are unique compared with other hominoids with a greater sacral depth facilitating lumbar entrapment, and there are differences among African apes with respect to the mechanisms governing variation in the lumbosacral boundary. These differences suggest that lumbar stiffening is convergent among great apes and that human bipedalism evolved from a more generalized long-backed ancestor. Such a model is more consistent with evidence of TV placement in *Australopithecus*.

1. Introduction

The nature of the last common ancestor (LCA) of humans and chimpanzees from which bipedalism evolved is a fundamental question of human evolution (Keith, 1902, 1923; Schultz, 1930; Straus, 1962; Huxley, 2003). Debate revolves around whether the LCA was more similar to the highly derived modern great apes or if it was more generalized like monkeys or many extinct Miocene hominoids (Larson, 1998; Richmond et al., 2001; Crompton et al., 2008; Begun, 2010; Reno, 2014; Ward, 2015; Pilbeam and Lieberman, 2017). All extant hominoids share a broad, shallow thorax with a dorsally placed scapula and to varying degrees an invaginated vertebral column (Larson, 1998; Lovejoy and McCollum, 2010). Living great apes (*Pongo*, *Gorilla*, and *Pan*) also share long forelimbs, short hind limbs, and short, stiff lumbar columns (Schultz, 1930). These features are commonly attributed to the frequent use of orthograde postures and suspensory locomotion in contrast to the arboreal quadrupedal form of locomotion used by most monkeys (Keith, 1923; Schultz, 1930; Benton, 1967). However, given the morphological diversity in living hominoids it can be difficult to determine when these great ape specializations occurred in the course of hominoid evolution. For example, both humans and gibbons (*Hylobates* sp.) have long hind limbs (Schultz, 1973; Jungers et al., 1984) and mobile lumbar spines (Schultz and Straus, 1945). Phylogenetically, humans (*Homo sapiens*) exist squarely within the African ape clade and are more closely related to chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) than to gorillas (Prado-Martinez et al., 2013). If features associated with suspension had a common origin in African apes, then humans

Abbreviations: LCA, last common ancestor; PCS, postcranial segment; PSV, presacral vertebra; TV, transitional vertebra.

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https://doi.org/10.1016/j.jhevol.2020.102791
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must have evolved from a suspensory ancestor with a short back. As yet, no fossil hominoids have been found that display the full suite of derived features found in great apes. Archaic hominoids such as *Ekembo* (*Proconsul*) retained postcranial features found in living monkeys (Pilbeam, 1996; McNulty et al., 2015; Ward, 2015), and other Miocene hominoids such as *Morotopithecus*, *Pierolapithecus*, and *Hispanopithecus* display a mixture of ancestral and derived characters (MacLatchy, 2004; Alba, 2012). Furthermore, the lack of derived suspensory characters in early fossil hominids, such as *Ardipithecus ramidus*, indicates that many African ape suspensory features evolved in parallel (Lovejoy et al., 2009a; White et al., 2015). If so, human bipedalism likely evolved from a more generalized 'multigrade' ancestor with a longer lumbar spine (Lovejoy and McCollum, 2010; Reno, 2014; White et al., 2015).

The vertebral column has undergone adaptations related to both great ape suspension and human bipedalism. The mammalian spine is divided into functionally distinct cervical, thoracic, lumbar, and sacral regions (Müller et al., 2010; Jones et al., 2018). Thoracic and lumbar vertebrae are defined here by their respective presence or absence of ribs (Schultz and Straus, 1945). In hominoids, these vertebrae also tend to differ in the orientation of their articular facets (zygapophyses), with dorsoventrally oriented facets in thoracic vertebrae and mediolaterally oriented facets in lumbar vertebrae (Rockwell et al., 1938; Washburn and Buettner-Janusch, 1952; Kashimoto et al., 1982; Singer et al., 1988; Shapiro, 1993; Russo, 2010; Williams, 2012). This change typically occurs within a single segment known as the transitional vertebra (TV), or the diaphragmatic vertebra, where the cranial articular facets are oriented dorsally (coronally) and the caudal articular facets oriented laterally (parasagittally) (Fig. 1A) (Slijper, 1946; Erikson, 1963; Washburn, 1963; Clauser, 1980; Shapiro, 1993, 1995; Filler, 2007; Williams, 2012). To distinguish from thoracic and lumbar identity based on ribs, we will refer to pre- and post-TV to identify vertebrae with coronal versus parasagittal facet orientations. The presence of the ribs and sternum and the orientation of the articular facets enable different ranges of motion between the thoracic and lumbar regions (Horton et al., 2005). For humans, both regions contribute similarly to the degree of lateral flexion of the spine, but the vast majority of axial rotation is accounted for by the thorax (~35° vs. 5° in lumbar), while dorsoventral flexion in the sagittal plain occurs in the lumbar region (~60° of a total of 105°) (Masharawi et al., 2004). Therefore, changing the number of thoracic and lumbar vertebrae and the location of the TV can impact the degree of dorsoventral flexion and extension in a particular species (Shapiro, 1993).

Old World monkeys have a generalized mammalian vertebral formula consisting of 7 cervical, 12–13 thoracic, 6–7 lumbar, 3 sacral, and numerous caudal vertebrae (producing a vertebral formula of 7:12-13:6-7:3, not counting caudal segments, Table 1) (Keith, 1902; Schultz and Straus, 1945; Schultz, 1961; Shapiro, 1993; Narita and Kuratani, 2005). Like many other mammals, the New and Old World monkey TV tends to occur about 2–3 segments cranial to the last thoracic vertebra [vertebral formula 7:12-13(+3/2):7:3 indicating the cranial placement of the TV] (Table 1) (Filler, 1986; Johnson and Shapiro, 1998; Russo, 2010; Williams, 2012). The approximately 9 mobile post-TV segments produce a spine with substantial dorsoventral flexibility necessary for arboreal quadrupedalism and leaping (Shapiro, 1993). In extant hominoids, the number of lumbar vertebrae is reduced, and the position of the TV has shifted caudally to correspond to the last thoracic vertebra (Fig. 1A). Humans and hylobatids [gibbons and siamangs (*Symphalangus syndactylus*)] have 5 lumbar vertebrae, retaining

Table 1
Vertebral formulae and the number of precaudal segments (cervical + thoracic + lumbar + sacral, CTLS) for a variety of extant catarrhines.

Species	Vertebral formula[a]	CTLS (mean)
Homo sapiens	7:12(+1-0):5:5	29 (29.1)
Pan troglodytes	7:13(+1/0):3-4:5-6	29–30 (29.6)
Pan paniscus	7:13-14(+1/0):3-4:6	30-31 (30.5)
Gorilla gorilla	7:13(+0):3-4:5-6	29-30 (29.2)
Gorilla beringei	7:13(+1/0):3:6	29 (28.9)
Pongo pygmaeus	7:12(+0/-1):4:4-6	27-28 (28.0)
Hylobates lar	7:13(+1/0):5-6:4	29-30 (29.3)
Symphalangus syndactylus[b]	7:13(0)re:4-5:5-4	29-30 (29.4)
Papio sp.[b]	7:12-13(+3/2):6-7:3	29
Colobus sp.[c]	7:12(+3/2):7:3	29

TV = transitional vertebra.
[a] Vertebral formula indicated as cervical:thoracic(+TV):lumbar:sacral, where +TV is the number of segments the transitional vertebra is placed cranial to the ultimate thoracic. Formula and segment count ranges include any frequencies ≥0.20. Data from Williams et al. (2016) unless noted.
[b] Williams (2011b) and Williams et al. (2019).
[c] Schultz (1961) and this study.

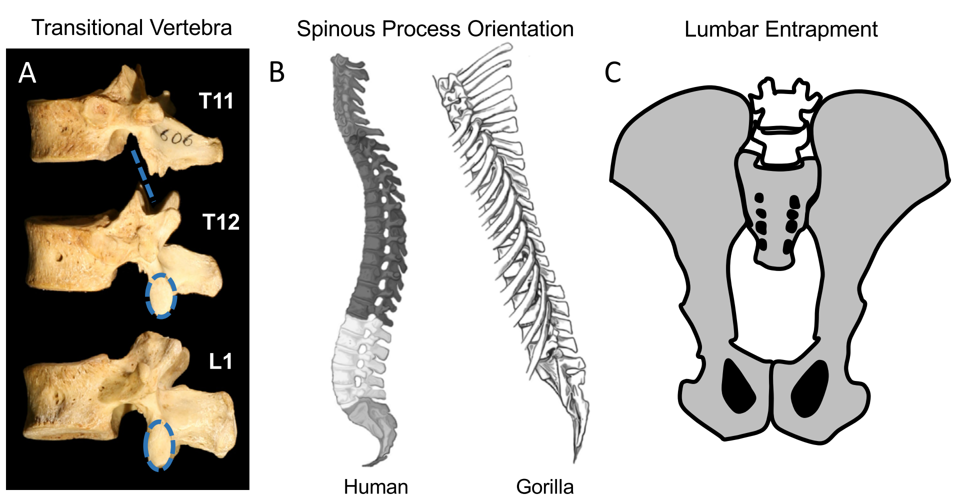

Figure 1. Mechanisms of stiffening the lumbar spine. (A) The T12 in this human specimen is the transitional vertebra that has dorsally facing superior articular facets and laterally facing inferior articular facets. This demarcates the boundary between rotational motions permitted in the thoracic region and dorsoventral mobility in the lumbar region. (B) In humans, the spinous processes change from caudally oriented in thoracic vertebrae (dark gray) to dorsally oriented in lumbar vertebrae (light gray). In contrast, gorillas maintain caudal orientation into the lumbar region (Slijper, 1946). Gorilla figure modified from (Slijper, 1946). (C) Lower lumbar vertebrae (white) can be entrapped in apes owing to the high iliac crests and narrow sacrum (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

substantial dorsoventral flexibility (Table 1). Great apes typically have only 3 to 4 lumbar vertebrae, resulting in dorsoventrally stiff vertebral columns providing support during below-branch suspension and bridging in these large-bodied primates (Schultz, 1961; Erikson, 1963).

The fact that great apes have shortened lumbar columns while both hylobatids and humans have 5 lumbar segments makes it difficult to infer the vertebral formula for the LCA. Like other suspensory characters, a short lumbar column could have either evolved in the ancestor of great apes requiring a reversion in humans or it could have reduced in parallel among great apes. Unfortunately, the Miocene hominoid fossil record is too incomplete to resolve this debate. Archaic hominoids such as *Ekembo* (17–20 Ma) and *Nacholapithecus* (~15 Ma) had a more generalized Old World monkey-like vertebral count and TV placement (Table 2) (Ward, 1993; Ishida et al., 2004; Nakatsukasa and Kunimatsu, 2009). Derived vertebral morphologies, such as a reduced vertebral body length and more dorsally placed transverse process on the base of the pedicle, occurred in *Morotopithecus bishopi* (20.6 Ma), *Pierolapithecus catalaunicus* (11.9 Ma), and *Hispanopithecus laietanus* (9.7 Ma) (Walker and Rose, 1968; Moyà-Solà and Köhler, 1996; MacLatchy, 2004; Moyà-Solà et al., 2004; Susanna et al., 2010, 2014). Although there are no sufficient vertebral specimens to infer lumbar numbers in *Pierolapithecus* and *Hispanopithecus*, possible attribution of additional vertebral fragments to the same *Morotopithecus* individual would indicate that this species may have had a long back with 6–7 lumbar vertebrae (Nakatsukasa, 2008). The more complete *Oreopithecus bambolii* (8.3–6.7 Ma) clearly contains more derived features shared with living hominoids, yet it retains 5 lumbar vertebrae (Jungers, 1987; Harrison, 1991; Rook et al., 2001; Sarmiento, 2001; Russo and Shapiro, 2013; Hammond et al., 2020). As such, there are no fossil hominoids before the *Homo*/*Pan* LCA that display a shortened back similar to extant great apes.

When considering hominins, the earliest vertebral column belongs to the *Australopithecus afarensis* specimen DIK-1-1 which preserves a full thoracic column with 12 ribbed vertebrae and a TV at the 11th thoracic, but no lumbar vertebrae (Table 2) (Ward et al., 2017). A.L. 288-1 ('Lucy') also does not preserve sufficient lumbar vertebrae to determine a total count, but she has a TV at the 11th thoracic (Meyer et al., 2015). Thus, *Au. afarensis* likely had 12 thoracic vertebrae with a cranially positioned TV (Ward et al., 2017). The *Au. africanus* specimen Sts 14 has a better preserved lower vertebral column containing 15 consecutive vertebrae ending at the last lumbar (Robinson, 1972; Sanders, 1998; Haeusler et al., 2002; Rosenman, 2008). Counting from the last lumbar, there are 5 presacral vertebrae (PSVs) lacking ribs. The next cranial vertebra (6th PSV), Sts 14f, has a rib facet on the right side and a transverse process on the left, giving it a partial lumbar identity. The TV is Sts 14g, which is the 7th PSV. If the 6th PSV is considered a partial lumbar, this results in 5.5 lumbars and the TV at +0.5. Stw 431 has 5 serial lumbar vertebrae and several ambiguous elements at the thoracolumbar border (Haeusler et al., 2002; Rosenman, 2008). There is debate whether a feature on the vertebral body of the 6th PSV (Stw 431qa-b) is an abnormal costal facet, indicating it is the ultimate thoracic (Haeusler et al., 2002), or an osteophytic knob of no diagnostic value (Rosenman, 2008). The next most cranial recovered vertebra (Stw 431l) preserves only the neural arch and is very likely the TV (Haeusler et al., 2002; Rosenman, 2008). Rosenman (2008) argues that Stw 431qa-b and Stw 431l are noncontiguous, necessitating a missing 7th PSV; therefore, Stw 431 preserved 5 or 6 lumbar vertebrae with the TV at the penultimate or antepenultimate thoracic segment. A later australopithecine, *Australopithecus sediba* (MH2), has 5 lumbar vertebrae with the TV at the penultimate thoracic vertebra (Williams et al., 2013). Similarly, the *Homo erectus* specimen WT 15000 has the TV at the 11th (penultimate) thoracic vertebra and 5 lumbar vertebrae (Haeusler et al., 2011; Williams, 2011a). Thus, early hominins appear to have 12 thoracics, 5 to 6 lumbar vertebrae, and a cranially placed TV (Table 2).

Given the variation observed among extant hominoids and the fossil record, the nature of the vertebral column of the LCA has been long debated (for a thorough review, see Williams et al., 2016). There are currently two distinct scenarios with respect to lumbar numbers in the *Homo*/*Pan* LCA (Pilbeam and Lieberman, 2017). These can be distinguished by either relying on a common origin of a short lumbar column requiring fewer evolutionary steps or the parallel evolution of lumbar reduction requiring fewer reversals to attain a human-like spine (Reno, 2014; Williams and Russo, 2015). In the first, the LCA was characterized by a great ape–like lumbar column containing 4 or fewer segments (Pilbeam, 1996, 2004; Williams, 2011a). If this were the case, then great apes retain the ancestral condition, and humans have re-evolved a longer 5-lumbar spine. This 'short-back' scenario finds support from Pilbeam (2004) and Williams (2011a) who identified similarly high levels of intraspecific vertebral count variation in chimpanzees and western gorillas (*Gorilla gorilla*) and high homogeneity in humans. They concluded that humans have undergone recent directional selection from an African ape-like short back with the modal chimpanzee formula [7:13(+0):3-4:5-6]. Thus, the similarity in lumbar column length between humans and gibbons reflects a reversion on the part of humans who converge on a mobile spine (Pilbeam, 1996).

In contrast, the 'long-back' scenario proposes that the LCA had 5 or more lumbar vertebrae (Rosenman, 2008; Lovejoy et al., 2009a; Lovejoy and McCollum, 2010; McCollum et al., 2010). In this case, humans need not have reverted to a longer back, and the great apes would have evolved their short lumbar columns in parallel. McCollum et al. (2010) cite the greater total precaudal segment counts in bonobos than in chimpanzees (Table 1) and the fossil evidence indicating that early hominids had 6 or more post-transitional mobile vertebrae (Table 2) to support a long-backed

Table 2
Observed or reasonably inferred vertebral counts and transitional vertebra (TV) position for key hominoid fossil specimens.

Miocene hominoids	Vertebral formula[a]	TV PSV	TV PCS
Ekembo[d]	7:12-13(+2/1):6:?	7–8	17–18
Nacholapithecus[e]	7:12(+3/2):6-7:3-4	8–10	16–17
Hominins			
Australopithecus afarensis			
DIK-1-1[f]	7:12(+1):?:?	?	18
A.L. 288-1 (Lucy)[g]	7:?(+1):?:4.5 (TV at T11)	?	18
Au. africanus			
Sts 14[h]	7:?(+0.5):5.5:?	7	18[c]
Stw 431[h]	7:?(+1 or +2):5 or 6:?	7–8	18[c]
Au. sediba			
MH2[i]	7:?(+1):5:5	7	18[c]
Homo erectus			
KNM-WT 15000[j]	7:12(+1):5:4-5	7	18

PSV = presacral vertebra, PCS = postcranial segment.
[a] If not actually observed, 7 cervical vertebrae are inferred for all specimens.
[c] Based on 12 thoracic vertebrae.
[d] Ward (1993).
[e] Ishida et al. (2004); Nakatsukasa et al. (2007); Nakatsukasa and Kunimatsu (2009).
[f] Ward et al. (2017).
[g] Lovejoy et al. (1982); Meyer et al. (2015); Machnicki et al. (2016a).
[h] Haeusler et al. (2002); Rosenman (2008).
[i] Williams et al. (2013).
[j] Latimer and Ward (1993); Walker and Leakey (1993); Haeusler et al. (2011); Machnicki et al. (2016a).

ancestor capable of lordosis as the more likely *Homo*/*Pan* LCA. A slightly different version of the long-back model by Haeusler et al. (2002) proposes that the LCA had a human-like vertebral formula [7:12(+0):5:5], with the instances of a cranially shifted TV in most Plio-Pleistocene hominids being explained as falling within the natural variation of most hominoids (Haeusler et al., 2002, 2012). While others have also suggested the LCA had 5 lumbar vertebrae (Filler, 1993; Latimer and Ward, 1993), these models also require parallel evolution in the great apes and no reversals from a short-backed ancestor in humans (Haeusler et al., 2002). The predictions with respect to the evolution of lumbar stiffening are essentially the same whether the LCA is posited to have 5 or 6 lumbar vertebrae, so both scenarios will be considered under the long-back model.

Two additional features beyond elimination of lumbar vertebrae and caudal shifts of TV placement can contribute to stiffening the vertebral column. In many mammals, there is a change in shape and orientation of the spinous processes between thoracic and lumbar vertebrae (Benton, 1967; Shapiro, 1993; Shapiro and Simons, 2002; Russo, 2010). Thoracic spinous processes are rod-like and angled caudally, overlapping with the next caudal vertebra (Fig. 1B). Experiments on human cadaver material suggest the caudal orientation of the spinous process serves to limit extension of the vertebral column (Panjabi et al., 1984). Near the thoracolumbar transition, the spinous process abruptly changes shape to become more dorsally oriented with greater craniocaudal breadth (Slijper, 1946). In mammals with greater dorsoventral mobility, the spinous processes of the subsequent vertebrae continue with a dorsal or even somewhat cranial orientation to permit greater flexion and extension (Slijper, 1946; Latimer and Ward, 1993; Nakatsukasa et al., 2007). A fourth means of stiffening the spine is through lumbar entrapment between the iliac blades (Lovejoy and McCollum, 2010). When the transverse processes of the most caudal lumbar vertebrae articulate directly to form a syndesmosis with the iliac blades, they become effectively immobilized (Fig. 1C). In apes, the sacrum is narrowed relative to monkeys, facilitating contact between lumbar vertebrae and the iliac blades (Machnicki et al., 2016b), such that the frequency of entrapping the last lumbar is high ranging from 74% of gibbons to 100% of bonobos (McCollum et al., 2010).

Hypotheses in science are frequently evaluated based on their relative parsimony. For example, phylogenetic analyses use large data sets of ideally developmentally independent characters with limited functional value to identify preferred phylogenies requiring the fewest evolutionary transitions (Skelton and McHenry, 1992; Strait et al., 1997; Strait, 2001). Similar logic has been applied to the ancestral reconstruction of vertebral counts (Thompson and Almécija, 2017). Easily enumerable vertebral counts would seem to be well suited for such an analysis. There are, however, a number of key differences between phylogenetic analyses and the reconstruction of ancestral traits. First, relative to the number of characters used in cladistic analyses, the characters of interest are typically few and have strong functional values that are subject to strong selection. Suspensory and vertical climbing behaviors—-which clearly favor a stiff lumbar spine in great apes—are examples of such relevant characters. Second, there is substantial intraspecific variation in vertebral counts within hominoids (Pilbeam, 2004; McCollum et al., 2010; Williams, 2011a). Such standing variation can allow for rapid genetic and morphological change in the face of selection (Haldane, 1932; Jones et al., 2012). Third, many phenotypes are patterned by highly conserved and organized developmental pathways that produce integrated morphologies (Lovejoy et al., 1999; Wagner, 2007; Rolian, 2014; Reno, 2016). In such cases, the potential for convergence and homoplasy increases (Gompel and Prud'homme, 2009; Wake et al., 2011; Jones et al., 2012). Because the characters associated with lumbar stiffening are limited in number, under selection, and at least somewhat developmentally interdependent, simply counting evolutionary transitions to identify most parsimonious pathways is unlikely to accurately resolve ancestral character states (Reno, 2014).

The structure of the vertebral column is plainly reflected by its embryological origin (Burke et al., 1995; Christ et al., 1998, 2000; Burke, 2000; Nowicki and Burke, 2000; Pilbeam, 2004). It is formed through cranial to caudal segmentation of paraxial mesoderm into somites (Burke et al., 1995; Christ et al., 1998, 2000; Saga and Takeda, 2001; Iimura et al., 2009; Pourquie, 2011). The overlapping expression domains of various patterning genes determine the individual identity of each vertebra and its phenotype appropriate to its segmental position (Burke et al., 1995; Wellik, 2009). Vertebral count and identity are regulated by a complex Hox gene combinatorial code during somite formation (Burke, 2000; Wellik, 2009). Intraspecific and interspecific variation in segment numbers and identity are produced by variation in Hox and other gene function (Pilbeam, 2004; Machnicki et al., 2016a). For example, sacral-to-lumbar transitions are produced by changes in Hoxa11 and Hoxd11 and can also shift the position of the sacrum within the pelvis in mice (Davis and Capecchi, 1994; Favier et al., 1996; Zakany et al., 1996; Gerard et al., 1997; Branford et al., 2000). Alternatively, Gdf11 secreted from the paraxial mesoderm integrates sacral and hind limb positioning such that altered expression can shift the pelvis, creating a longer or shorter lumbar column (Matsubara et al., 2017). As such, changes in vertebral count and identity are potentially highly evolvable and can easily follow non-'parsimonious' pathways (Wagner and Altenberg, 1996; Reno, 2014). Furthermore, vertebral development is modular such that costal and neural arch features can be patterned independently (Verbout, 1985; Saga and Takeda, 2001; Rawls and Fisher, 2010). Hoxb9 and Hoxc9 mouse knockouts can shift the position of the TV relative to the last rib-bearing thoracic vertebra (Suemori et al., 1995; personal observation). Thus, different features associated with lumbar stiffening (TV placement, spinous process morphology, and degree of lumbar entrapment) may be all under at least somewhat separate genetic control and may evolve independently.

Given the multiple means of vertebral stiffening beyond simple lumbar numbers and their potential evolutionary and developmental independence, we test how compatible each is with models of the *Homo*/*Pan* LCA. If the short-back model is correct, then a long and common history (15–20 My) of selection (Langergraber et al., 2012; Besenbacher et al., 2019) on stiffening adaptations with respect to TV placement, spinous process morphology, and lumbar entrapment was all inherited from the great ape, or at least the African ape common ancestor, and humans would have undergone reversion to facilitate lumbar flexibility. In this case, great ape adaptations associated with lumbar stiffening are predicted to be developmentally and phenotypically similar. Alternatively, if the long-back model is correct, then humans, gibbons, and Old World monkeys reflect the ancestral condition with respect to lumbar mobility, and great apes have functionally converged to produce a stiff lumbar spine. Under this hypothesis, functionally similar lumbar stiffening mechanisms in great apes may be phenotypically distinct, reflecting their independent evolutionary origins, while greater similarity would be observed among less derived, longer backed primates. More specifically, we make the following predictions.

1.1. TV placement

The short-back model predicts a more caudal ancestral placement of the TV for humans as in extant hominoids, whereas the long-back scenario allows for a more cranial position of the ancestral TV with parallel caudal shifts in great apes. We will assess TV placement in three ways: (1) using the traditional method relative to the thoracolumbar boundary, (2) by identifying its PSV position to indicate the number of mobile segments, and (3) by its absolute postcranial segment (PCS) number reflecting the process of cranial to caudal patterning of the vertebral column. We determine not only the modal placements of the TV but also the patterns of variation around the modes. If the short-back model is correct, then we predict a shared TV placement and distribution of variation among great apes. In contrast, the long-back model hypothesizes relatively recent caudal shifts in each ape lineage, and we predict there will be notable variation in the placement and patterns of variation of the TV among great apes.

1.2. Spinous process morphology

In most primates, the spinous process becomes craniocaudally broader and is dorsally oriented (block-shaped) near the thoracolumbar boundary (Fig. 1). This morphology is continued in the remaining PSV in monkeys and humans, enabling greater flexion and extension (Slijper, 1946; Latimer and Ward, 1993). Slijper has previously noted that great ape lumbar spinous processes maintain a more dorsal orientation in accordance with their stiff spine (Fig. 1) (Slijper, 1946). This provides a simple hypothesis regarding the evolution of spinous process orientation in hominoids. If a short-backed primate was the LCA, then caudally oriented spinous processes would have been present in the ancestors of great apes and humans. Novel functional changes in spinous processes would have evolved in humans to facilitate greater lumbar mobility. Alternatively, if the LCA was a long-backed primate, then spinous process stiffening mechanisms would have evolved in parallel among the great apes. Either case requires functional convergence from a dissimilar phenotype. In the former, we hypothesize convergence in long-backed primates would result in greater morphological divergence than in conserved great apes, while in the latter case, the converged functional similarity of short-backed great apes would have greater morphological differences than long-backed forms.

1.3. Degree of lumbar entrapment

A lower lumbar column is stiffened by frequent entrapment of the ultimate and penultimate lumbar vertebrae in nonhuman hominoids owing to their narrowed sacrum and high iliac blades. Under the short-back scenario, lumbar entrapment would have evolved in the great ape or African ape common ancestor. In this case, we would predict similar degrees and mechanisms of lumbar entrapment. Alternatively, if lumbar entrapment evolved in parallel among the great apes, we predict that variation can occur in the mechanisms underlying lower lumbar stiffening. To test this hypothesis, we will assess the relative craniocaudal position of the sacrum relative to the iliac crest (sacral depth) among hominoids. The short-back model predicts that sacral depth will be similar across great apes, whereas variation in sacral depth supports the long-back scenario.

2. Materials and methods

2.1. TV placement

We identified TV position from the following extant catarrhine species: *Ho. sapiens* (modern humans), *Pa. troglodytes* (chimpanzees), *G. gorilla* (lowland gorillas), *Pongo pygmaeus* (orangutans), *Hylobates lar* (lar gibbons), *Papio cynocephalus* (baboons), and *Colobus* sp. (colobus monkeys) (Table 3). These specimens were housed at the American Museum of Natural History, Cleveland Museum of Natural History, Field Museum, Museum of Comparative Zoology at Harvard University, Smithsonian Institution National Museum of Natural History, and University of Florida Museum of Natural History. Only complete wild-caught disarticulated specimens without vertebral pathologies (e.g., fusion or osteophytes) and containing species-specific modal numbers of vertebrae based on rib definition were examined. All specimens were adults in dentition; however, some orangutans had vertebral centra epiphyses that were still undergoing fusion.

We also used the data set of cervical, thoracic, lumbar, and sacral counts and TV position provided by Williams et al. (2016) for the following extant hominoids: *Ho. sapiens* (n = 1159), *Pa. troglodytes* (n = 239), *Pa. paniscus* (bonobo, n = 47), *G. gorilla* (n = 199), *Gorilla beringei* (mountain gorilla, n = 65), *Po. pygmaeus* (n = 103), *Hy. lar* (118), and *S. syndactylus* (siamang, n = 36). TV position in this data set was reported as a vertebral identity (i.e., T12, T13, L1, and so on). We converted each to a numerical value as the segment count from the thoracolumbar boundary for each individual accounting for the number of reported thoracic segments. Specimens in which the change in right and left facet orientation was offset at different vertebral levels (i.e., T11/T12) or the transition was gradual across multiple levels were given an average value to the nearest 0.5 (Haeusler et al., 2002; Williams, 2012; Ward et al., 2017). The number of post-transitional PSVs was computed as the number of segments between the TV and first sacral (Fig. 2). The postcranial vertebral segment number of the TV was computed as the number of segments counting from the C1 to the TV.

2.2. Spinous process orientation

Qualitative assessment of spinous process morphology was accomplished from lateral and dorsal photographs of the 5 most caudal thoracic and first 3 lumbar vertebrae for the specimens in our sample (Table 3). We also collected surface scans for 15 individuals from each species in our sample using either a NextEngine or Artec Space Spider for qualitative assessment of spinous process orientation. Spinous process angle was measured from 3D surfaces using Avizo (9.0) relative to a line formed by the dorsal wall of the intersection of the median plane through the centrum in two ways: (1) to the line formed by the cranial margin of the centrum and the cranial-dorsal margin of the spinous process (cranial angle) and (2) the line formed by the caudal margin of the centrum to the dorsal-caudal margin of the spinous process (caudal angle) (Fig. 3).

We also estimated spinous process angle in fossil hominoid specimens. For the *M. bishopi* (UMP-67-28), *P. catalaunicus* (ISP-21350.64), *Au. afarensis* (A.L. 288-1ac and A.L. 288-1aa), *Au. africanus* (Sts 14d, Sts 14e, Sts 14f, Sts 14g, and Sts 14h), and *Au. sediba* (MH1 U.W. 88-92 and MH2 U.W. 88-43 and MH2 U.W. 88-114) vertebrae, caudal angle was approximated by aligning published lateral and cranial/caudal photographs to determine the intersection of the two lines (Johanson et al., 1982; MacLatchy, 2004; Susanna et al., 2010; Meyer et al., 2015; Williams et al., 2016, 2018). Each of the hominin specimens (other than MH1) preserves a measurable TV, so each vertebra was compared with our extant sample based on its inferred relative TV position (except for A.L. 288-1aa which is plotted as the third post-TV, see the following sections). The two Miocene hominoids represent isolated lumbar vertebrae, making their specific segment identities less certain. In these cases, their values are compared across the range of pre- and post-TV angulations in our sample (Fig. 3).

2.3. Sacral depth

We measured sacral depth in the following catarrhine species: *Ho. sapiens* (4 lumbar, n = 10; 5 lumbar, n = 46; 6 lumbar, n = 9), *Pa.*

Table 3
Species included for the spinous process analysis and frequency of transitional vertebra (TV) placement in our sample.

Species	←	Cranial shift (+)	Mode	Caudal shift (−)	→		
Humans	**T11**	**T11/T12**	**T12**	**T12/L1**	**L1**		
(*Homo sapiens*)	7 (35%)	2 (10%)	9 (45%)	1 (5%)	2 (10%)		
Chimpanzees	**T12**	**T12/T13**	**T13**	**T13/L1**	**L1**		
(*Pan troglodytes*)	3 (15%)	4 (20%)	11 (55%)	0	2 (10%)		
Lowland gorillas		**T12**	**T13**	**T13/L1**	**L1**	**L1/L2**	**L2/L3**
(*Gorilla gorilla*)			14 (63.6%)	2 (9.1%)	2 (9.1%)	2 (9.1%)	1 (4.5%)
Orangutans		**T11**	**T12**	**T12/L1**	**L1**		
(*Pongo pygmaeus*)			9 (47.4%)	3 (15.8%)	7 (36.8%)		
Gibbons	**T12**	**T12/T13**	**T13**				
(*Hylobates lar*)	8 (44.4%)	1 (5.6%)	9 (50%)				
Baboons	**T10**	**T10/T11**	**T11**				
(*Papio* sp.)	2 (8%)	1 (4%)	22 (88%)				
Colobus monkeys		**T8**	**T9**	**T9/T10**	**T10**		
(*Colobus* sp.)		1 (5%)	11 (55%)	1 (5%)	7 (35%)		

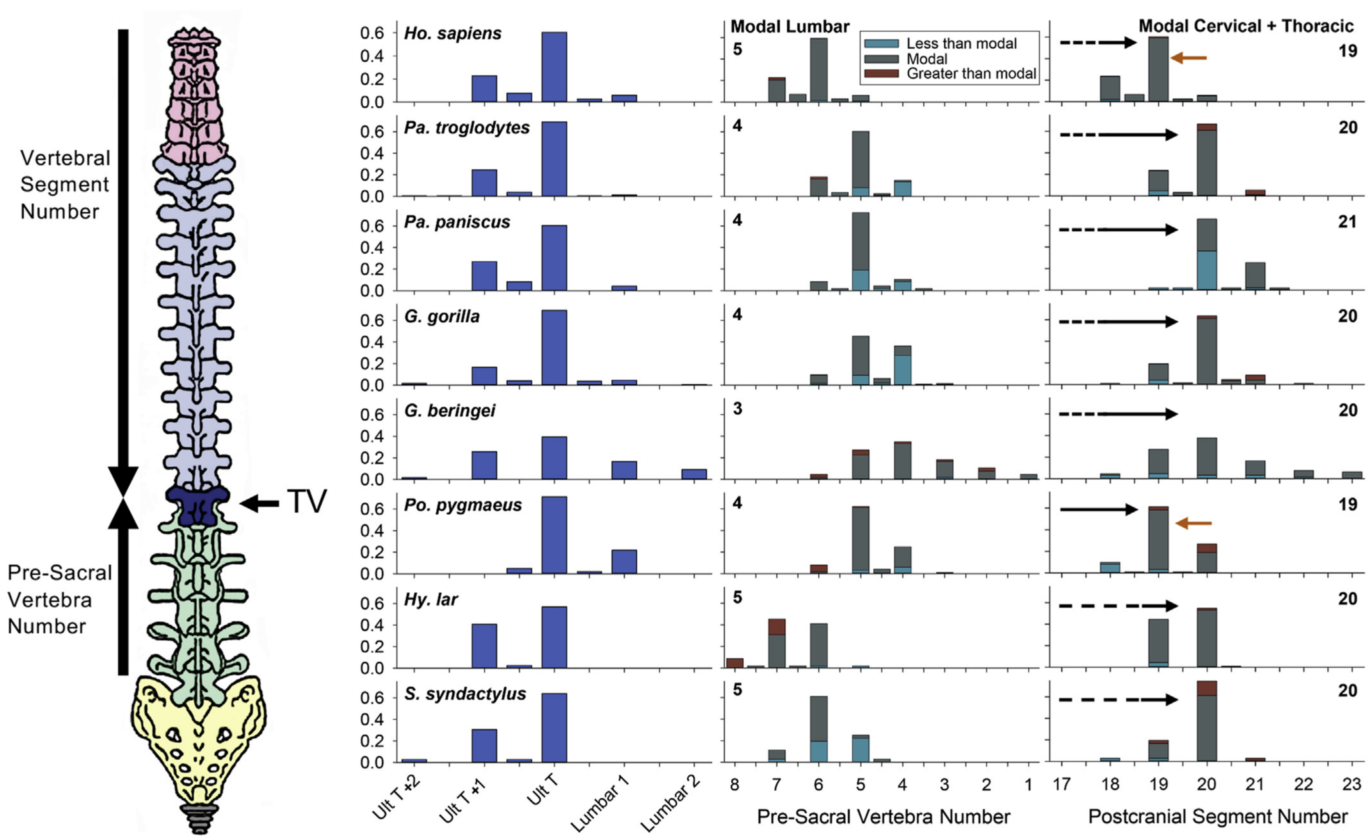

Figure 2. Placement of the transitional vertebra (TV). Modal human vertebral column indicating the cervical (pink), thoracic (blue), lumbar (green), and sacral (yellow) regions. The transitional vertebra (TV; dark blue) is placed at the last thoracic. Histograms of TV placement in hominoids compiled and computed from vertebral counts provided by Williams et al. (2016). All hominoids share a modal placement of the TV at the ultimate thoracic vertebra. Except for orangutans, the most frequent nonmodal position is the next cranial vertebra (Ult T +1, cranial displacement) for all other taxa. Dorsoventral mobility is indicated by the presacral vertebral number of the TV which distinguishes long-backed humans and hylobatids from short-backed great apes. Modal lumbar count is provided for each species, and color indicates frequencies of individuals with at least a full lumbar count higher or less than the species' modal value. The majority of chimpanzees, bonobos, gorillas, and siamangs with less than modal pre-sacral vertebra (PSV) counts results from the loss of a lumbar vertebra (blue) and not a caudally shifted TV (gray). Developmental position of the TV is determined by its postcranial segment (PCS) number counted from the first cervical. Compared with other hominoids, humans and orangutans have a more cranially placed TV on the 19th segment. Note that the next most common placement of the TV for all other hominoids is the 19th segment, with the exception of bonobos which have an additional thoracic vertebra. Arrows indicate the evolutionary trajectories required under the alternative scenarios. In the short-back model (orange), the TV would shift from an ancestral position at the 20th segment in humans and orangutans. The long-back model (black) predicts the parallel caudal shift of the TV. The dashed lines indicate caudal shifts that likely occurred in the respective ancestral African ape/human and hylobatid lineages before final divergence. PSV = presacral vertebra. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

troglodytes (3 or 3.5 lumbar, n = 11; 4 lumbar, n = 33), *G. gorilla* (3 or 3.5 lumbar, n = 18; 4 lumbar, n = 29), *Po. pygmaeus* (n = 29), *Hylobates* sp. (n = 45), and *Papio* sp. (n = 43). The vast majority were wild caught, but a few specimens were derived from zoos. The *Hylobates* sp. sample includes 35 *Hy. lar* and 10 non−lar gibbons (6 *Hylobates muelleri*, 3 *Hylobates moloch*, and 1 *Hylobates hoolock* × *Hylobates agilis* hybrid). There was no significant difference in sacral

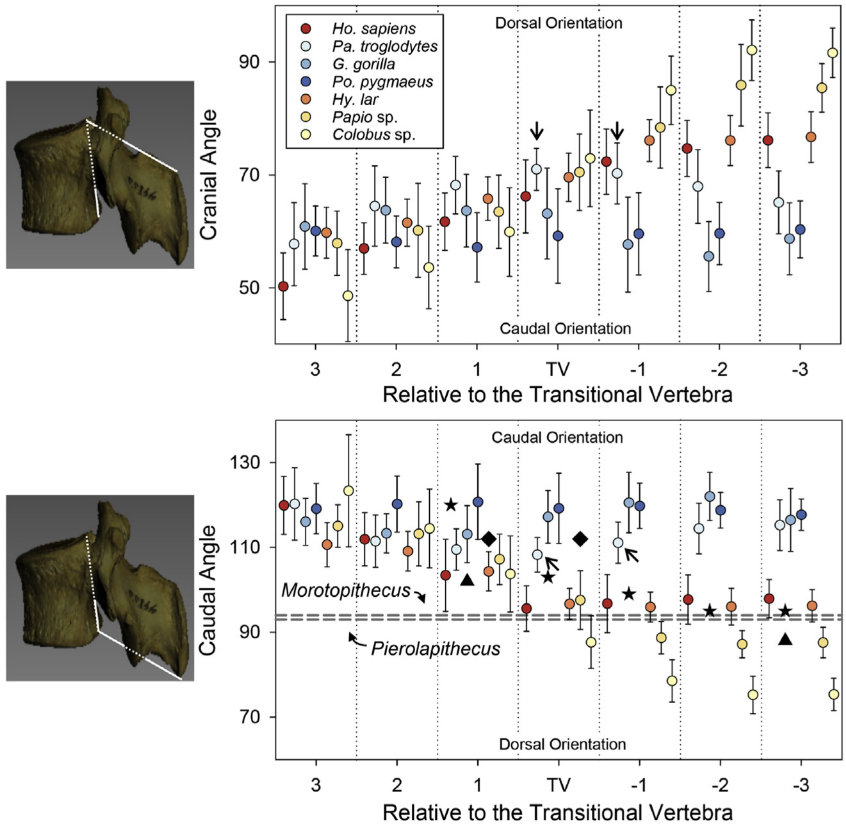

Figure 3. Spinous process angulation across the thoracolumbar transition. Cranial and caudal spinous angle measurements are illustrated on the surface scans (left). Angle values (mean ± standard deviation) are similar among species in pre-TV but diverge between short- and long-backed catarrhines in post-TV. Arrows identify chimpanzees that initially follow a long-back pattern with more dorsally oriented spinous processes before returning to caudal angulation in subsequent lumbar vertebrae. Hominin caudal angle estimates are provided for specific vertebral levels (▲, *Au. afarensis* A.L. 288-1; ★, *Au. africanus* Sts 14; and ◆, *Au. sediba* MH2). The dashed lines indicate the caudal angle measurements for midlumbar vertebrae attributed to Miocene hominoids *Morotopithecus* (UMP 67.28) and *Pierolapithecus* (IPS21350-64). TV = transitional vertebra.

depth between the two samples ($t = 1.434$, $df = 43$, $p = 0.159$), so they were pooled into a *Hylobates* sp. sample for further analysis.

Sacral depth was measured using digital sliding calipers and an osteometric board as the vertical distance from the most cranial margin of the iliac crest to the superior margin of the sacroiliac joint auricular surface. We express sacral depth as a negative number and account for body size by calculating the ratio between sacral depth and acetabulum diameter. The average of the left and right sides was computed for each individual using the following formula:

$$\text{Average Relative Sacral Depth} = -\left(\frac{\text{Rt.Sacral.Depth}}{\text{Rt.Acetabulum}} + \frac{\text{Lt.Sacral.Depth}}{\text{Lt.Acetabulum}}\right) \Big/ 2$$

Differences in sacral depth between multiple groups were compared using analysis of variance (ANOVA) and Bonferroni post hoc tests (SPSS version 22). The independent samples t-test was used to compare means between 3 and 4 lumbar chimpanzees or gorillas. For the comparison of vertebral counts and lumbosacral boundary (see the following section), we used the large sample provided by Williams et al. (2016), except that we eliminated specimens with a partial cervical, thoracic, lumbar, or sacral transition (i.e., any individual with a half segment count). This produced a sample containing 1082 humans, 211 chimpanzees, and 168 lowland gorillas. We tested differences in frequency of lumbosacral boundary modification types using a χ^2 test.

3. Results

3.1. TV placement

We recorded the location of the TV with respect to the thoracolumbar boundary for each individual in our sample and confirm previous observations that hominoids have a modal position at the last thoracic vertebra, while the TV is placed more cranially in Old World monkeys, reflecting the ancestral mammalian condition (Table 3). To better evaluate intraspecific and interspecific variation in hominoids, we analyzed the large sample by Williams et al. (2016) (Fig. 2). In both our and the Williams et al. (2016) samples, the modal placement of the TV for each hominoid species is at the ultimate thoracic vertebra. Humans, chimpanzees, bonobos, lowland gorillas, and siamangs have approximately 20–25% of individuals showing some degree of cranial displacement in TV position (Table 3, sum of bars to the left of the mode in Fig. 2). Cranial displacement was even more common in gibbons, producing a bimodal placement at the penultimate and ultimate thoracic vertebra. In contrast, orangutans showed greater propensity for caudal displacement of TV position, with approximately 20% of individuals placing the TV at the first lumbar. Mountain gorillas are notably variable in TV position, ranging from the penultimate thoracic to the third lumbar, with a greater proportion having a caudally displaced TV. The common placement at the ultimate thoracic fits the short-back prediction. However, for all species other than orangutans, the second most frequent position of the TV is at the penultimate thoracic, which would be expected under the long-back model if more recent selection events caused the caudal displacement of the TV.

From a functional perspective, the more important factor is the number of mobile presacral segments between the TV and the sacrum. The longer backed humans and hylobatids have a TV typically falling on the 6th or 7th PSV (Fig. 2). Humans and gibbons, and to a lesser extent siamangs, show a tendency toward cranially shifted TV placement. This trend is somewhat obscured in siamangs by their greater frequency of 4 lumbar vertebrae, which accounts for nearly all cases in which the TV lies on the 5th PSV (Fig. 2). Great apes are distinguished from other hominoids by typically having 5 or fewer post-transitional PSVs. In chimpanzees, bonobos, and gorillas, 10.6–36.2% of individuals have the TV at the 4th PSV, but the majority of these cases result from loss of a lumbar vertebra. Thus, there is a bias for a cranially placed TV relative to the last thoracic in 18.3–27.7% of cases. Orangutans show a different pattern in that cranial placement of the TV at the 6th PSV results from an additional lumbar vertebra and placement at the 4th PSV results mostly from caudal displacement of the TV onto the first lumbar segment. The unusual distribution of post-TV numbers in mountain gorillas continues to result from variation in TV placement and is unrelated to the length of the lumbar column. As expected, the relationship between TV placement and PSV numbers largely reflects functional demands in hominoids, yet there continues to be a bias toward cranial displacement of the TV, even in short-backed species.

From a developmental perspective, TV placement is best considered by its segment number counted from the first cervical vertebra as vertebral identity is patterned from a cranial to caudal direction during embryogenesis (Burke, 2000; Mallo et al., 2009; Pourquie, 2011). The TV of Old World monkeys is placed between the 16th and 18th PCSs (Table 1). Most hominoids locate their TV on the 19th or 20th PCS, which typically corresponds to T12 or T13 (Fig. 2). Both humans and orangutans, which have 12 thoracic vertebrae, show a modal placement of the TV on the 19th PCS. In orangutans, a few individuals even place the TV at the 18th PCS. African apes and hylobatids have the modal placement on the 20th PCS; however, there are some differences in the pattern between species. Gibbons are bimodal in TV placement at the 19th and 20th PCS corresponding to the penultimate and ultimate thoracic vertebra, whereas chimpanzees, lowland gorillas, and siamangs have a slight cranial bias in TV placement. In contrast, bonobos have a strong caudal bias in PCS TV placement, which is associated with them having an additional thoracic segment. Notably, half of the cases with an additional thoracic vertebra still maintain their TV at the 20th PCS. Mountain gorillas remain highly variable, with the TV ranging from the 19th to 23rd PCS. Thus, while most hominoid species have a modal placement of the TV at the 20th PCS, there is greater variation than can be appreciated by simply looking at the TV relative to the thoracolumbar boundary.

3.2. Spinous process morphology

If the LCA was short backed, we predict common patterns of caudal orientation of the spinous processes across the great apes or, at a minimum, the African apes. In contrast, under the long-back hypothesis, gibbons and humans would reflect the ancestral condition, and variation in spinous process angulation could occur among great apes as each converged on a caudal orientation of the lumbar spinous processes. To test these predictions, we compared the cranial and caudal angles of the spinous process in our anthropoid sample. When vertebrae are aligned to the thoracolumbar transition, baboons and colobus monkeys begin to reorient their spinous processes dorsally at T9 or T10 [Supplementary Online Material (SOM) Fig. S1]. Humans and gibbons also undergo a change in angulation between T11 and L1, but the great apes largely maintain the same caudal orientation to L3. When species are aligned by TV position, the change in spinous process angulation that occurs in monkeys, humans, and gibbons can be clearly seen to be associated with the TV, further confirming the role of spinous process orientation in facilitating lumbar dorsoventral mobility (Fig. 3). Cranial and caudal spinous process angles are similar for all species in pre-TV vertebrae, reflecting the caudal orientation of overlapping spinous processes that limits flexion and extension in primate thoracic segments. Subsequently, the caudal angle at the TV and the cranial angle at the first post-TV diverge between species. The greatest changes occur in colobus monkeys and baboons that attain perpendicular orientation, whereas the gorillas and orangutans maintain the same degree of caudal angulation throughout the pre- and post-TV spine. Gibbons and humans are similar in post-TV angulation, falling intermediate between monkeys and great apes. Chimpanzees are unique with an initial shift to a more perpendicular angulation at the TV and first post-TV. Subsequently, the chimpanzee spinous processes return to a caudal orientation to align with gorillas and orangutans.

Visual comparison of the spinous processes confirms the pattern revealed by the angulation analysis (Fig. 4). Both Old World monkeys undergo a change in spinous process shape from long, narrow, and caudally oriented to block-shaped and dorsally oriented. In colobus monkeys, lumbar spinous processes are trapezoid-shaped owing to cranial and caudal projections, a common primate pattern that may be associated with greater mobility in these acrobatic monkeys (Slijper, 1946; Shapiro, 1993). Baboon lumbar spinous processes are quadrangular with rounded distal margins (Fig. 4 and SOM Fig S2). Within hominoids, the short-backed great apes are clearly distinguished from longer backed gibbons and humans (Fig. 4). In the latter, the lumbar spinous processes are quadrangular in shape and dorsally projected generally similar to baboons (SOM Figs. S3 and S4). In contrast, each of the great apes has a strong caudal angulation that functionally mimics the thoracic spinous processes; however, each short-backed species shows a unique pattern. The chimpanzee spinous process at the TV and first post-TV attains a more rectangular shape and dorsal orientation similar to humans, gibbons, and monkeys, but subsequent vertebrae develop a caudal slant reminiscent of pre-TV processes (Fig. 4 and SOM Fig S5). Gorilla and orangutan processes undergo a slight increase in craniocaudal breadth but maintain the caudal orientation throughout the column (SOM Figs. S6 and S7). The orangutan is further distinguished by spinous processes that tend not to attain the craniocaudal breadth of other apes and retain a triangular or curved appearance in the lumbar region (Fig. 4 and SOM Fig S9).

3.3. Degree of lumbar entrapment

McCollum et al. (2010) previously determined that the frequency of lumbar entrapment varies among hominoids. Entrapment occurs in nearly 80% of gibbons and gorillas, surpassing 90% in orangutans, chimpanzees, and bonobos, and occurs in less than 20% of humans. Chimpanzees, bonobos, and orangutans also frequently entrap two lumbar vertebrae. We hypothesize that differences in lumbar entrapment will be reflected in the placement of the sacrum within the pelvis. When compared across hominoids and baboons, there is a significant difference in sacral position [ANOVA, $F(5,267) = 185.84$, $p = 9.11 \times 10^{-85}$]. Humans have the shallowest depth or highest placement of the sacrum within the pelvis (Fig. 5A). This is undoubtedly related to the reduced iliac blade height necessary for hip stabilization during obligate bipedalism (Lovejoy, 2005). Baboons have the deepest placed sacra as a result of their long iliac blades. However, their wide sacra and high number of post-transitional PSV

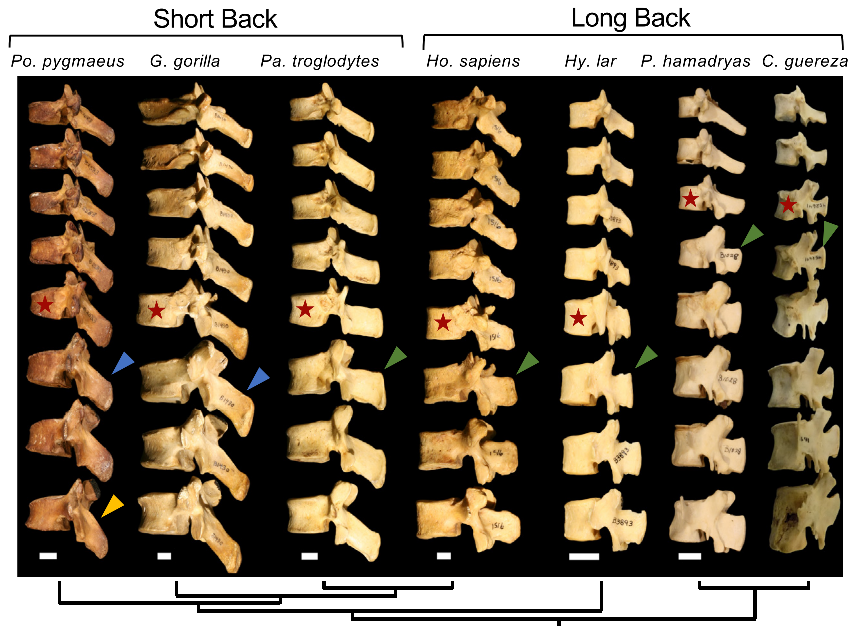

Figure 4. Representative individuals showing the last 5 thoracic and first 3 lumbar vertebrae. The TV is indicated by the red stars. Note the change in spinous process morphology between pre- and post-TV in long-backed humans, gibbons, and the two monkeys. The chimpanzee spinous process attains a morphology at the TV and 1st post-TV (green arrow) that is similar to long-backed species but resumes a caudal orientation by the 2nd lumbar (post-TV) vertebra. Orangutans and gorillas maintain the same thoracic-like caudally oriented spinous processes throughout the lumbar column including the TV and 1st post-TV (blue arrow). Orangutans are distinguished by the lack of cranial-caudal expansion and continued triangular shape of lumbar spinous processes (orange arrow). See SOM for additional representative individuals for each hominoid species and baboons. Scale bars = 1 cm (no scale for colobus monkey). Phylogeny depicted at bottom. TV = transitional vertebra. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

ensures lumbar flexibility (Machnicki et al., 2016b). Chimpanzees and gibbons have the second and third greatest sacral depth. Bonferroni post hoc tests reveal that although chimpanzees and gibbons are each significantly different from all other taxa, gorillas and orangutans are not significantly different from each other (Table 4). This indicates there is no general trend of submerging the sacrum in the stiff-backed great apes relative to hylobatids. However, the significantly deeper sacra of chimpanzees compared with those of the other apes, particularly gorillas, indicate a unique pelvic conformation.

To verify that variation in lumbar column length itself does not account for these differences, we divided the human, chimpanzee, and gorilla samples based on less than modal (4 and 4.5 for humans, 3 and 3.5 for chimpanzees and gorillas), modal (5 for humans, 4 for chimpanzees and gorillas), and greater than modal (6 for humans) number of lumbar vertebrae (Fig. 5A). All comparisons between species remained significant, indicating that chimpanzees have more deeply placed sacra regardless of the lumbar number [ANOVA, $F(6,149) = 81.90$, $p = 1.13 \times 10^{-44}$], supporting the hypothesis that chimpanzees have a specific pelvic-sacral conformation facilitating entrapment of lumbar vertebrae.

Interestingly, significant differences were detected between humans with 4/4.5 lumbar and those with 5 or 6 lumbar vertebrae [ANOVA, $F(2,62) = 11.97$, $p = 4 \times 10^{-5}$] (Table 5). However, significant differences were not observed between 3/3.5 or 4 lumbars in chimpanzees ($t = 1.428$, $df = 42$, $p = 0.161$) or gorillas ($t = 0.531$, $df = 45$, $p = 0.733$). This suggests that lumbar segment count does not alone influence sacral depth. One possibility is that the patterning of variation in lumbar numbers differentially impacts the depth of the sacrum within the pelvis. Developmentally, sacralization of the lumbar produces a change in vertebral identity independent of hind limb specification that can result in a cranial shift in sacral placement relative to the pelvis. This could account for the shallower average sacral depth in humans with 4 lumbars (as observed in Hoxa11 and Hoxd11 knockout mice) (Fig. 5B). Alternatively, an integrated pelvic shift in the craniocaudal position of the hind limb on the vertebral column (as seen with changes in Gdf11 expression) would change the number of lumbar vertebrae but not alter sacral depth within the pelvis (Fig. 5B). To explore this possibility, we returned to the large sample of vertebral counts (Williams et al., 2016). We computed the number of individuals falling at, above, or below the modal value of total precaudal segment count and the corresponding frequencies for different cervical+thoracic and sacral counts (SOM). When change in lumbar number could be attributed to a gain or loss of a cervical or thoracic vertebra, we inferred no change occurred in the lumbosacral boundary. Sacralization/lumbarization was inferred when a change in lumbar count occurred with an opposite alteration in sacral numbers, and a pelvic shift was inferred when lumbar gain/loss occurred without sacral modification. We find a significant association between the mode of lumbosacral boundary shift and species with individuals missing a lumbar vertebra (Fig. 5B). Both humans and chimpanzees have greater frequencies of sacralization (52.5% and 22.9%, respectively) than gorillas (5.3%) (comparison of 3 modes of sacral boundary shift: $\chi^2 = 37.2$, $df = 4$, $p < 0.00001$; comparison of sacralization and pelvic shift alone: $\chi^2 = 38.8$, $df = 2$, $p < 0.00001$). In addition, humans with 6 lumbars had lower frequencies of lumbarization (5.6%) ($\chi^2 = 21.0$, $df = 2$, $p = 2.7 \times 10^{-5}$). Thus, the observed differences in sacral depth in humans with a missing lumbar can be attributed to the high frequencies of sacralization. In contrast, lumbar loss in gorillas and lumbar gain in humans is overwhelmingly attributed to pelvic shifts, leaving the typical sacral depth unmodified. Interestingly, the moderate frequency of lumbar loss due to sacralization in chimpanzees (22.9%) may be reflected in our measurement data. Chimpanzees with 3/3.5 lumbars have a shallower sacral depth than those with 4 lumbars that just fails to attain significance under a directional test ($p = 0.08$). Regardless, the frequency of lumbar loss due to

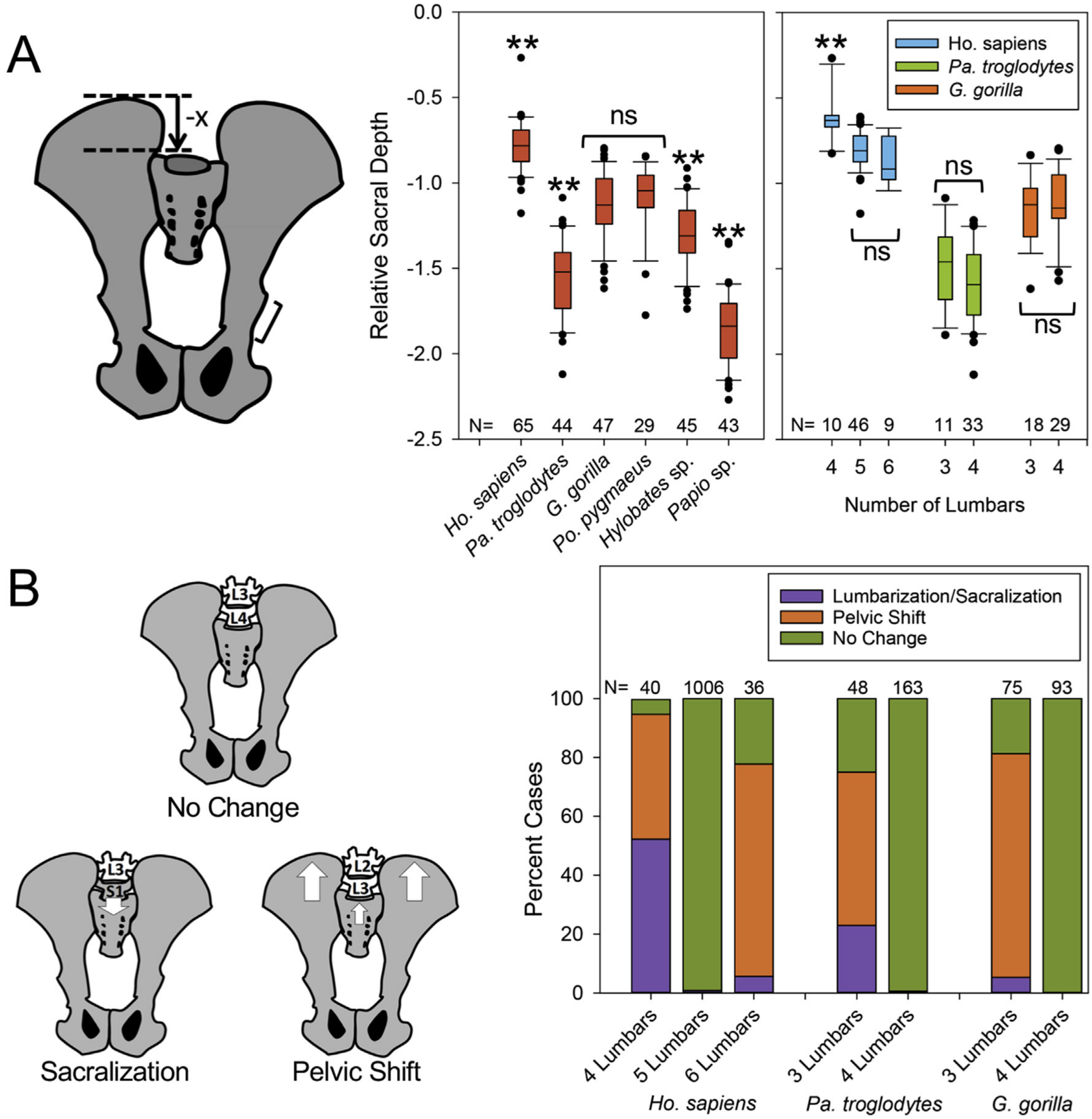

Figure 5. Impact of sacral depth on lumbar entrapment. (A) Sacral depth is measured as the distance between the iliac crest and superior margin of the auricular surface (dashed lines). Acetabular diameter is used for size correction (bracket). Depth is represented as a negative value. Box and whisker plots reveal that humans, chimpanzees, gibbons, and baboons are each significantly different from all other species, whereas no difference was detected between gorillas and orangutans. When compared within species, humans with 4 lumbar vertebrae have significantly shallower sacral depth than those with 5 or 6 lumbars (**p < 0.001, ns = nonsignificant). (B) Illustration of the different effects that sacralization of the last lumbar and pelvic shift have on sacral depth. Sacralization cranially shifts the lumbar/sacral boundary relative to the pelvis and produces a shallower sacral depth. A pelvic shift will alter the placement of the whole pelvis on the vertebral column and does not impact sacral depth. Percentages of individuals with varying lumbar counts undergoing sacralization/lumbarization, pelvic shift, or no change at the lumbosacral boundary. Note the relatively low frequencies of sacralization/lumbarization in humans with 6 lumbars and gorillas with 3 lumbars. Sample sizes for each category are included in the graphs.

Table 4
Bonferroni post hoc test corrected p values for multiple comparisons of sacral depth between species.

Species	*Pa. troglodytes*	*G. gorilla*	*Po. pygmaeus*	*Hylobates* sp.	*Papio* sp.
Ho. sapiens	*5.40×10^{-55}*	*7.72×10^{-73}*	*5.74×10^{-10}*	*5.12×10^{-31}*	*1.14×10^{-79}*
Pa. troglodytes		*2.03×10^{-20}*	*1.58×10^{-19}*	*1.57×10^{-8}*	*3.37×10^{-10}*
G. gorilla			**1.000**	*9.68×10^{-4}*	*6.45×10^{-45}*
Po. pygmaeus				*$1.13x10^{-4}$*	*$6.46 x 10^{-41}$*
Hylobates sp.					*3.43×10^{-30}*

Significant comparisons are italicized, and nonsignificant comparisons are bold.

sacralization is significantly higher in humans and chimpanzees than in gorillas. This indicates there is a difference in the developmental mechanisms governing the variation in the lumbosacral boundary and reduction of lumbar numbers between chimpanzees and gorillas, along with a difference in sacral depth that facilitates lumbar entrapment in chimpanzees.

Table 5
Bonferroni post hoc test corrected p values for multiple comparisons for sacral depth between humans with 4, 5, and 6 lumbar vertebrae.

Species by lumbar number	Human 5	Human 6
Human 4	*0.000097*	*0.00017*
Human 5		**0.753**

Significant comparisons are italicized, and nonsignificant comparisons are bold.

4. Discussion

4.1. Mechanisms of lumbar stiffening

To test hypotheses regarding the nature of the spine in the *Homo*/*Pan* LCA, we analyzed three features of lumbar stiffness: TV placement, spinous process orientation, and lumbar entrapment at the lumbosacral junction. In two of these cases, spinous process and lumbar entrapment, we found substantial variation among great apes in general, and African apes in particular, that supports the long-back model. With respect to TV placement, the evidence was more equivocal between the two models.

The short-back model [7:13(0):3-4:5-6] previously found support in the fact that all extant hominoids share a common modal placement of the TV at the ultimate thoracic, reflecting the stiff torso of the LCA (Williams, 2011a). However, from the perspective of developmental patterning, there is variation in the placement of the TV between the 19th PCS in humans and orangutans and the 20th PCS in most of the other apes. If the 20th PCS reflects the ancestral condition, humans and orangutans must have undergone a cranial shift in TV patterning, which would have the effect of increasing lumbar mobility (Fig. 2). In humans, this serves to facilitate lumbar lordosis, but the rationale in orangutans is less clear. In mice, TV positioning does not appear to be strongly associated with thoracic identity (Suemori et al., 1995) (personal observation), and the same is confirmed for orangutans as less than one-third of orangutans with a caudally placed TV at the 20th PCS have an additional (13th) thoracic vertebra. Therefore, the modal placement of the TV at the 19th PCS does not simply reflect a cranial shift in the orangutan thoracic/lumbar boundary.

This produces two distinct explanations for the unusually high frequency of caudal displacement of the orangutan TV. Under the short-back model, orangutans underwent a largely independent cranial shift in TV position coincident with the cranial shift of the ultimate thoracic; thus, individuals with caudally placed TVs are variants still maintaining the ancestral hominoid condition. However, it is difficult to understand why a cranial shift in TV placement would occur as it serves to increase the number of mobile PSVs, given the trend to stiffen the spine among great apes. In addition, the substantial variation of TV placement in mountain gorillas and the frequent occurrence of the TV at the 19th segment in chimpanzees and lowland gorillas are unexpected under the short-back model, which posits stabilizing selection to minimize the number of post-transitional PSVs.

Alternatively, the long-back model [7:13(+2):6:4] proposes parallel evolution in each hominoid lineage. Thus, the high frequency of caudal displacement of the orangutan TV reflects ongoing selection for a stiffer lumbar spine to the position observed in other large-bodied suspensory hominoids. The general absence of derived suspensory morphology in *Sivapithecus* (Madar et al., 2002; Morgan et al., 2015), which is very likely a representative of the *Pongo* clade (Pilbeam, 1982), further suggests that stiffening of the spine evolved in parallel between orangutans and African apes.

The long-back model is also more compatible with the evidence suggesting TV position was cranially positioned in Plio-Pleistocene hominins. Multiple specimens (DIK-1-1, A.L. 288-1, Sts 14, Stw 431, MH2, WT 15000) representing *Australopithecus* and early *Homo* have a TV at the penultimate (or possibly antepenultimate) thoracic vertebra (Table 2). DIK-1-1 preserves 7 cervical and 12 thoracic vertebrae; thus, the TV at T11 is positioned at the 18th PCS (Ward et al., 2017). Assuming 7 cervical vertebrae, WT-15000 is also sufficiently complete to determine that the TV is the 18th PCS (Haeusler et al., 2011). Using the large sample of vertebral counts (Williams et al., 2016), such a placement occurs commonly in humans (23.7%) and orangutans (9.9%) that have 12 thoracic vertebrae but rarely (<5%) in other hominoids with 13 or more thoracics (*Pa. troglodytes* < 1%, *G. gorilla* = 1.0%, *G. beringei* = 4.5%, *S. syndactylus* = 2.7%, and no occurrences observed in *Pa. paniscus* and *Hy. lar*). Of the humans with the TV at the 18th PCS, only 1 (0.4%) had 13 thoracic vertebrae. Furthermore, the single chimpanzee with its TV at the 18th PCS had 12 thoracic vertebrae. Thus, we accept previous inferences that other australopithecines had 12 thoracic vertebrae (Ward et al., 2017), and conclude that TV placement at the 18th PCS was modal for *Australopithecus* and early *Homo* (Table 2). The short-back model requires the TV to switch from a placement at the 20th PCS in the LCA, shift cranially to the 18th PCS in Plio-Pleistocene hominins, and revert back to a modal position at the 19th PCS in modern humans. Under the long-back scenario, the observed placement at the 18th PCS matches the position of the LCA [7:13(+2):6:4-5] (McCollum et al., 2010) (Fig. 6). Alternatively, the common placement at the 18th PCS in hominins may represent natural variation around a modal placement at the 19th PCS similar to modern humans (Haeusler et al., 2002, 2012). If so, the modal placement of the TV would be at the penultimate thoracic in our model [7:13:(+1):6:4-5]. While requiring an unlikely sampling history with respect to the hominin sample (Table 2), this model is also compatible with the long-back model as it does not require reversals from a more caudally positioned TV.

Under the long-back model, some of the shifts from a cranially placed TV at the 17th segment in early hominoids such as *Ekembo* and *Nacholapithecus* may have occurred before the split of the respective African ape/human and hylobatid lineages. Subsequent evolution from the 18th segment in the *Homo*/*Pan* LCA still requires independent caudal shifts in humans, *Pan*, and *Gorilla*. This involves a greater number of transitions than the short-back model. However, when the number of transitions is considered in conjunction with selective trends, the long-back model which proposes that each great ape lineage was subject to similar selection pressures shifting the TV from the 18th to the 20th segment has an economy of explanation that makes it difficult to favor one of the two models based on TV position alone. As such, the initial similarity of TV placement at the ultimate thoracic among hominoids does not in itself provide strong support for the short-back model.

With respect to spinous processes, the similarity among distantly related monkeys, gibbons, and humans and greater diversity between the great apes are contrary to the short-back model but conform to the predictions of the long-back model. While all of the great apes have caudally oriented spinous processes related to lumbar stiffening, they have converged on functionally similar yet distinct phenotypes. Orangutans diverge from the African apes by having relatively reduced although variable and caudally projecting spinous processes (Shapiro and Simons, 2002; Shapiro and Kemp, 2019). Particularly revealing is the chimpanzee that still retains a more dorsal orientation near the TV, which is a feature shared with non–great ape primates. This is explicable by a shared long-backed ancestor with dorsally oriented post-TV spinous processes at the *Homo*/*Pan* divergence. The short-back model can only accommodate these data if the thoracic-like morphology of cranial lumbar spinous processes in orangutans and gorillas is itself a further refinement that evolved in parallel to

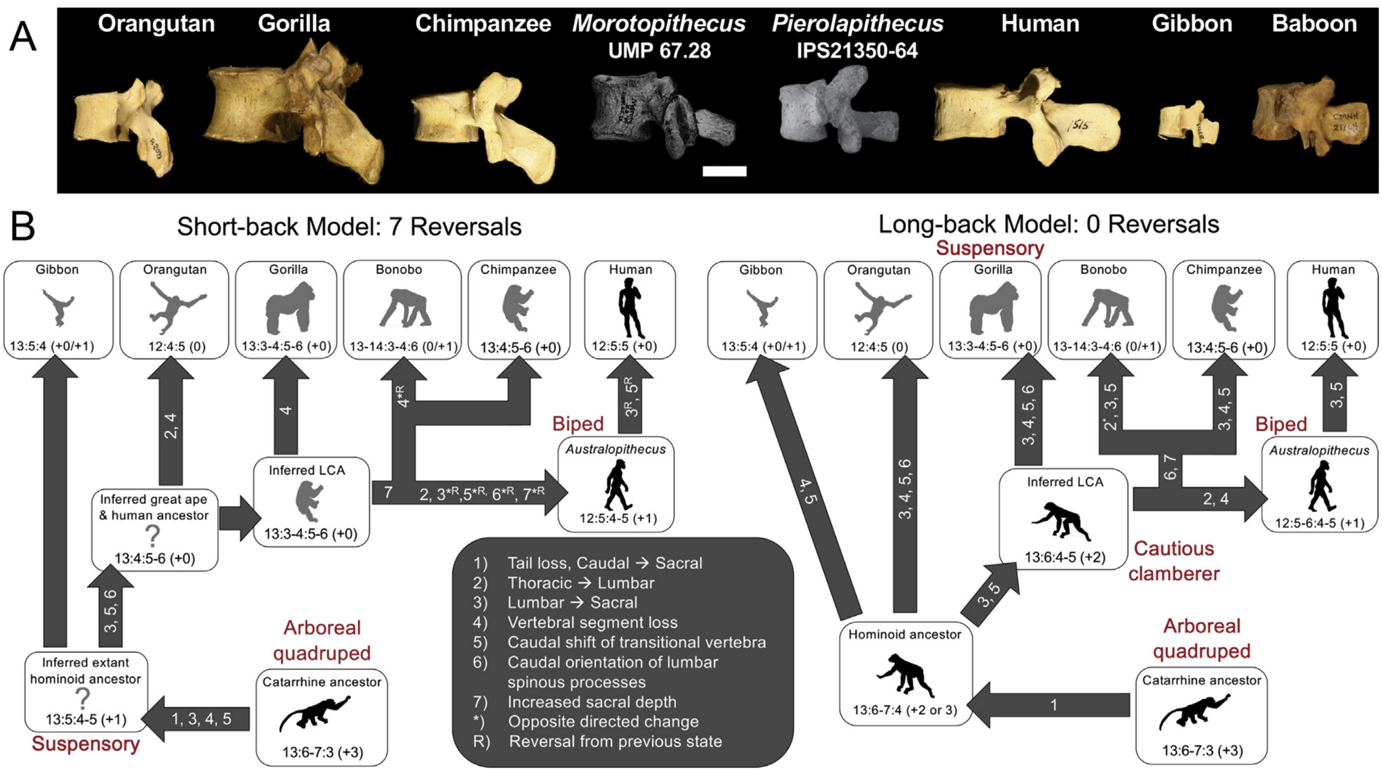

Figure 6. Evolution of the hominoid spine. (A) Third lumbar vertebrae from extant taxa compared with middle lumbar vertebrae attributed to Miocene hominoids. Note that the spinous processes of both *Morotopithecus* and *Pierolapithecus* project dorsally similar to long-backed species and are distinct from those of great apes. Scale bar = 2 cm. Fossil images are modified from (MacLatchy, 2004; Susanna et al., 2010). (B) Comparison of the short-back and long-back adaptive scenarios. Vertebral formulae show thoracic, lumbar, and sacral counts (T:L:S), and the placement of the TV relative to the ultimate thoracic is shown in parentheses. Suspensory species are gray. In the long-back model, the African ape/human inferred LCA is reconstructed with 6 lumbar vertebrae, because 5 lumbars would require a segment gain in bonobos, and a TV placed at the 18th PCS or the antepenultimate of 13 thoracics (+2). The short-back model uses fewer evolutionary transitions in features associated with lumbar stiffening; however, it requires multiple reversals of unknown functional significance and instances of nonfunctional drift in morphology to accommodate a stiff spine in the great ape ancestor. In contrast, many of the parallel steps in the long-back model occur in highly evolvable changes in vertebral number or identity. While the phylogenetic relationships for fossil taxa are unknown, the 'hominoid ancestor' and 'inferred LCA' from the long-back model are predicted to be generally analogous to *Ekembo* and *Pierolapithecus*, respectively. LCA = last common ancestor; TV = transitional vertebra; PCS = postcranial segment.

resist greater forces resulting from large body size (but see the following paragraphs) or if chimpanzees reverted to a more mobile upper post-transitional spine. Neither of these explanations account for differences in spinous process morphology between gorillas and orangutans or the similarities between gibbons and humans. Instead, evolving functional similarity through distinct morphologies in great apes is the precise prediction of the long-back model.

Data regarding spinous process orientation in Miocene hominoids are limited. *Ekembo nyanzae* and *H. laietanus* spinous process orientation are not sufficiently preserved to measure angulation, but they have been described as caudally oriented (Ward, 1993; Sanders and Bodenbender, 1994; Susanna et al., 2014). When appreciated within the range of hominoid variation identified in the present study, the spinous processes of the first (KNM-MW 13142 I), antepenultimate (KNM-MW 13142 J), and penultimate (KNM-MW 13142 K) *Ekembo* lumbars are largely dorsally oriented and do not project prominently beyond the caudal border of the vertebral body (Susanna et al., 2014). Thus, they conform to the morphology observed in longer backed humans, gibbons, and Old World monkeys. Only a small portion of *Hispanopithecus* spinous process is preserved precluding adequate assessment of its angulation (Susanna et al., 2014). The largely intact individual lumbar specimens from *Morotopithecus* and *Pierolapithecus* preserve nearly complete spinous processes (Nakatsukasa, 2008; Susanna et al., 2010). Both have been initially described as middle lumbar vertebrae (Walker and Rose, 1968; Moyà-Solà et al., 2004), although the *Morotopithecus* vertebra was later classified as a penultimate lumbar (Sanders and Bodenbender, 1994), and thus can be suitably compared with the L3 from our comparative sample (Fig. 6A). The spinous processes of the two fossils are craniocaudally short relative to vertebral body length compared with other anthropoids, potentially in part due to a greater length of the dorsal margin of the vertebral body compared with extant apes (Susanna et al., 2014). Both spinous processes have been described qualitatively as caudally inclined similar to great apes (Sanders and Bodenbender, 1994; MacLatchy, 2004; Susanna et al., 2010). While *Morotopithecus* does appear to have a slight caudal slant, *Pierolapithecus* is clearly dorsally projected similar to humans, gibbons, and baboons, and neither projects caudal to the vertebral body as in great apes. Given the short craniocaudal height of the spinous process, the cranial angle measurement is not comparable with the other taxa in our sample. Nonetheless, the caudal angle can be estimated from published photographs for both *Morotopithecus* (94°)[1] and *Pierolapithecus* (93°) and is very similar to humans and gibbons and distinct from great apes when compared

[1] While the cranial, caudal, and dorsal borders of the *Morotopithecus* spinous process are eroded, the dorsal tubercle is preserved, suggesting only a limited portion of the process is missing (Walker and Rose, 1968). The spinous process would have to deflect >5 mm caudally to approach the ±2 standard deviation range of the chimpanzee mean angulation of the 3rd post-TV.

across all post-TVs (Fig. 3). This supports a mobile lumbar column in these Miocene hominoids and suggests that spinal invagination (indicated by the placement of the transverse processes at the base of the pedicles) associated with a broader thorax and dorsally placed scapula can precede and be disassociated from shortening and stiffening the lumbar column (Nakatsukasa, 2019).

As anticipated, early hominins follow the pattern of thoracolumbar spinous process transition of longer backed hominoids (Fig. 3). The caudal angle of the spinous process can be estimated for Lucy, Sts 14, and MH2. The most complete is Sts 14, which preserves a five vertebra series from the first pre-TV to the 3rd post-TV (Robinson, 1972; Haeusler et al., 2002; Williams et al., 2016). Lucy also preserves the spinous process on her T10 and L3 (A.L. 288-1aa) (Johanson et al., 1982) which corresponds to the first pre-TV and fourth post-TV (Meyer et al., 2015). An isolated specimen consisting of the lamina and spinous process (A.L. 288-1ab) is identified as the L2 and is very similar in shape to the L3 (Meyer et al., 2015). The pre-TV spinous processes for both specimens (Sts 14h = 122° and A.L. 288-1ac = 102°) are narrow and caudally angled like those of other catarrhine vertebrae (Fig. 3). At the TV and following vertebrae of both *Au. africanus* (Sts 14g = 103°, Sts 14f = 97°, Sts 14e = 95°, Sts 14d = 95°) and *Au. afarensis* (A.L. 288-1aa = 88°), the spinous process becomes square-shaped and dorsally oriented like those of humans, gibbons, and baboons (note that the measurements for the fourth post-TV, A.L. 288-1aa, are plotted in Fig. 3 in place of the similar appearing isolated third post-TV spinous process, A.L. 288-1ab). MH2 preserves the first pre-TV (U.W. 88-114 = 112°) and TV (U.W. 88-43 = 112°) (Williams et al., 2018). In both, spinous processes are narrow and caudally oriented as in pre-TVs typical of other taxa. As the TV is cranially placed in australopithecines, these specimens correspond to the T10 and T11, respectively (Williams et al., 2018), and the more angled TV in this specimen may just represent natural variation in the alignment of the spinous process and facet orientation transitions (see SOM). Regardless, the spinous process of the individual upper lumbar vertebrae of MH1 (U.W. 88-92 = 99°, not plotted) is dorsally oriented similar to humans and gibbons (Williams et al., 2018).

The less derived spinous processes of chimpanzees correspond with previously observed differences in great ape prezygapophyseal morphology. Rosenman (2008) noted a more gradual transition between pre- and post-TV articular facets in gorillas, resulting in a unique morphology where postzygapophyses are mortised between the following prezygapophyses and mammillary processes. Subsequent analyses confirm this by showing that baboons, chimpanzees, and humans have an abrupt prezygapophyseal facet shape change between the TV and next caudal vertebra (Russo, 2010; Nalley et al., 2019). This pattern is distinct from that observed in gorillas and orangutans which continue flatter and more coronally oriented (thoracic-like) facets into the lumbar region (Rosenman, 2008; Russo, 2010).

We can understand the significance of the differences in spinous process morphology and sacral depth among great apes when features associated with stiffening of the vertebral column are considered in combination. The prediction of distinct morphologies among great apes is also met at the lumbosacral transition, where chimpanzees have a unique mechanism to facilitate lumbar entrapment. McCollum et al. (2010) had previously shown that chimpanzees have a significantly higher frequency of lumbar entrapment than gorillas. Both chimpanzees and bonobos have a high rate of entrapment of two lumbars that is facilitated by greater sacral depth. Interestingly, orangutans also have a high degree of lumbar entrapment relative to gorillas, yet they do not have a more deeply placed sacrum, suggesting a different mechanism to facilitate entrapment. The unique morphology of the chimpanzee indicates at a minimum that the *Pan* lineage attained lumbar stiffening by an independent mechanism from the other apes. Gorillas and orangutans have restricted mobility by (independently) continuing thoracic-like articular facets and spinous process morphology into the upper lumbar vertebrae. In contrast, chimpanzees (and potentially bonobos) have accentuated lower back rigidity through a greater sacral depth to entrap caudal lumbar vertebrae. Despite the differences in lumbar entrapment, the number of mobile vertebrae resulting from the combination of the absence of ribs, reoriented postzygapophyses, and lumbar entrapment is similar among great apes (orangutans: 2.4, gorillas: 2.0, chimpanzees: 2.1, and bonobos: 2.3) (McCollum et al., 2010). Therefore, the divergent morphologies do not appear to reflect differential selection on larger size per se in orangutans and gorillas, but different anatomical approaches to reaching the same functional ends. In combination with the overall increase in chimpanzee sacral depth, the morphology of the lumbosacral spine indicates the *Homo*/*Pan* LCA had a long back.

Our comparative analysis of the lumbosacral transition led us to the observation that the mechanisms of lumbar loss can impact sacral depth in humans and potentially chimpanzees. Lumbosacral patterning occurs through both intrinsic mechanisms, such as Hox expression within the somites that determines individual segment identity (Wellik, 2009), and integrative mechanisms, such as Gdf11 which signals from axial to lateral plate mesoderm to coordinate vertebral and hind limb development (Matsubara et al., 2017). When the transition from lumbar to sacral identity occurs through an intrinsic patterning change (sacralization) independent of the lateral plate derivatives (pelvis and hind limb), then relative sacral depth can be altered. Thus, the shallower sacral depth in humans with less than modal lumbar numbers is due to the relatively high rate of sacralization that explains lumbar loss. In light of the evidence suggesting independent acquisition of lumbar stiffening in chimpanzees and gorillas, the different frequencies of sacralization and the pelvic shift in those with less than modal lumbar numbers in these taxa takes on added significance by potentially indicating different developmental mechanisms underlying the independent evolution of lumbar reduction among African apes. Importantly, the fact that differences in sacral depth occur between chimpanzees and gorillas regardless of the lumbar number suggests that the mechanisms underlying a change in pelvic conformation are patterned within the lateral plate mesoderm. This will require further study. Our results further reinforce the benefits of incorporating mechanistic developmental approach to comparative morphological analyses (Lovejoy et al., 1999; Pilbeam, 2004; Reno et al., 2008; Rolian, 2014; Reno, 2016).

4.2. Long- versus short-back scenarios

The short-back model for the *Homo*/*Pan* LCA has previously been viewed as more parsimonious because it requires fewer evolutionary transitions from a great ape-like common ancestor with 4 lumbar vertebrae and a TV placed at the 20th PCS than an ancestor with 6 lumbar vertebrae and a TV at the 18th PCS (Fig. 6B). As discussed previously, a broader perspective beyond enumerating character transitions that instead incorporates function and development is needed for ancestral character state reconstruction. For instance, the short-back model does not provide a cogent rationale for the cranial shift in TV placement to the 19th PCS in the large-bodied and suspensory orangutans or a cranial shift to the 18th PCS in early hominids before a caudal reversion to the 19th PCS in humans, nor does it account for the greater precaudal segment counts in bonobos and chimpanzees relative to the other hominoids (Table 1) (McCollum et al., 2010). In contrast, the long-back model simply proposes that closely related taxa with similar bauplans (anatomy and underlying genomic and developmental structure) faced common ecological and selection pressures and thus responded in parallel ways (Figs. 2 and 6) (Reno, 2014).

When considered in total, the evolution of lumbar stiffening is most compatible with a scenario in which the *Homo*/*Pan* LCA maintained a mobile spine containing 5–6 lumbar vertebrae. While a short-back model still requires fewer morphological transitions than in the long-back model (19 versus 25, respectively), 16 of the repeated transitions in the long-back model involve simple and highly evolvable changes in vertebral identity or counts (Fig. 6B). Three additional repeated transitions result from the change in spinous process orientation for which the different morphologies of this complex trait among great apes provide direct evidence that these occurred independently. In addition, the short-back model requires reversals that run counter to the selective trends in some stiff-backed apes, such as the cranial shift of the TV (from the 20th to 19th PCS) in the orangutan and the addition of a vertebral segment in bonobos (McCollum et al., 2010). When fossil hominins are considered, further reversals are required in the human lineage [emancipation then sacralization of a lumbar vertebra (Machnicki et al., 2016a), cranial then caudal shift in the TV]. The functional benefits of any of these shifts are difficult to discern and run counter to other selective trends under the short-back model (Haeusler et al., 2002). On developmental grounds alone, reversals are presumably as likely to occur as other morphological transitions; however, when constructing a coherent evolutionary scenario, the mechanism of selection to explain these reversals should be explicitly stated. Independent selective mechanisms for reversals in orangutans, bonobos, and humans in the short-back scenario produce a decreasingly conciliative explanation compared with the long-back model.

An LCA with a long, mobile back also accords with *Ar. ramidus* which is clearly arboreal with long phalanges and a grasping hallux, but these are features that may have been inherited from a more generalized arboreal ancestor (Lovejoy et al., 2009a; White et al., 2015). Chimpanzees exhibit features directly associated with suspension and vertical climbing, including a rigid central joint complex of the wrist supported by strong ligaments, expansion of the head of the capitate, reduced mobility of the hamate and fifth metacarpal joint, marked elongation of the palm and shortened hind limbs, frequent loss of the long flexor tendon's insertion to the thumb's distal phalanx, loss of the deltopectoral crest, and lumbar entrapment (Lovejoy et al., 2009a; White et al., 2015). All of these characters are absent in *Ardipithecus*, the potential loss of which is difficult to explain in a large-bodied primate that likely used various arboreal postures including suspension, even after making its earliest forays into terrestrial bipedality. Instead, *Ardipithecus* demonstrates that each of these features likely evolved separately in chimpanzees subsequent to the LCA.

It is important to emphasize that the long-back model does not imply all shared extant hominoid features are necessarily parallelisms, particularly in African apes and humans. For example, all extant hominoids share a broadened thorax with an invaginated spine and a dorsally placed scapula (Benton, 1967). The likelihood of a more primitive postcranial skeleton in ancestral orangutans (*Sivapithecus*) suggests changes in thorax shape may have evolved independently in Asian and African hominoid lineages (Madar et al., 2002; Morgan et al., 2015). However, the reduction of the retroauricular region of the pelvis in *Ardipithecus* indicates spinal invagination and a broad thorax were already features of the earliest hominins (Lovejoy et al., 2009b). This conclusion is supported by the recently described *Rudapithecus* pelvis (Hungary, 10.0–9.7 Ma) that shows coronally oriented and flared iliac blades as seen in extant apes but lacks the long lower ilium of great apes, indicating this species may have retained a longer lumbar column (Ward et al., 2019). Similarities between the *Australopithecus* and African ape scapulae also indicate that reorganization of the thorax, shoulder, and spine is homologous in African apes and humans (Young et al., 2015). Thorax shape changes very likely occurred independently of extreme lumbar shortening in a manner similar to New World ateline monkeys (Machnicki et al., 2016b) and derived Miocene taxa such as *Morotopithecus* and *Pierolapithecus*. While *Morotopithecus* likely occurs too early in the fossil record and the phylogenetic position of *Pierolapithecus* is still uncertain (Begun, 2010; Ward, 2015; Nakatsukasa, 2019), each may at least serve as analogs for an LCA that was a generalized palmigrade cautious clamberer with a broad thorax, spinal invagination, dorsal placement of the scapulae, and long, mobile lumbar column (Figs. 3B and 6). This bauplan would serve as a pliable substrate for the evolution of bipedalism in early hominins and the parallel evolution of vertical climbing and suspension in African apes (Reno, 2014; Ward, 2015).

Conflict of interest

The authors declare no conflict of interest.

Acknowledgments

We thank Yohannes Halie-Selassie and Lyman Jellema (Cleveland Museum of Natural History), Eileen Westwig and Eleanor Hoeger (American Museum of Natural History), Bruce Patterson and Adam Ferguson (Field Museum), Judy Chupasko and Mark Omura (Museum of Comparative Zoology at Harvard University), Darrin Lunde and Nicole Edmison (Smithsonian National Museum of Natural History), and Verity Mathis (University of Florida Museum of Natural History) for access to specimens in their care and curatorial support. Linda Spurlock provided assistance with data collection at the Cleveland Museum of Natural History. Tim Ryan provided access to 3D scanning equipment. Simone Sukhdeo and Alexis Sullivan provided 3D scanner training, and Lia Gavazzi and Anna Whitaker assisted with data reconstruction. William Harcourt-Smith provided access to specimens, and Scott Williams and Robert Tague shared data. Tim Ryan, Nina Jablonski, Owen Lovejoy, Kelsey Kjosness, the associate editor, and two anonymous reviewers provided helpful comments and/or guidance throughout the project. This work is supported by the following sources: Wenner-Gren Foundation Dissertation Field Work Grant, NSF BCS-1650879, NSF IOS-1656315, and NSF BCS-1638812.

Supplementary Online Material

Supplementary online material to this article can be found online at https://doi.org/10.1016/j.jhevol.2020.102791.

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