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Morphology of the thoracolumbar spine of the middle Miocene hominoid *Nacholapithecus kerioi* from northern Kenya

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A B S T R A C T

A new caudal thoracic and a new lumbar vertebra of *Nacholapithecus kerioi*, a middle Miocene hominoid from northern Kenya, are reported. The caudal thoracic vertebral body of *N. kerioi* has a rounded median ventral keel and its lateral sides are moderately concave. The lumbar vertebral body has an obvious median ventral keel. Based on a comparison of vertebral body cranial articular surface size between the caudal thoracic vertebrae in the present study and one discussed in a previous study (KNM-BG 35250BO, a diaphragmatic vertebra), *N. kerioi* has at least two post-diaphragmatic vertebrae (rib-bearing lumbar-type thoracic vertebrae), unlike extant hominoids. It also has thick, rounded, and moderately long metapophyses on the lumbar vertebra that project dorsolaterally. The spinous process bases of its caudal thoracic and lumbar vertebrae originate caudally between the postzygapophyses, as described previously in the KNM-BG 35250 holotype specimen. In other words, the postzygapophyses of *N. kerioi* do not project below the caudal border of the spinous processes, similar to those of extant great apes, and unlike small apes and monkeys, which have more caudally projecting postzygapophyses. *Nacholapithecus kerioi* has a craniocaudally expanded spinous process in relation to vertebral body length, also similar to extant great apes. Both these spinous process features of *N. kerioi* differ from those of *Proconsul nyanzae*. The caudal thoracic vertebra of *N. kerioi* has a caudally-directed spinous process, whose tip is tear-drop shaped. These features resemble those of extant apes. The morphology of the spinous process tips presumably helps vertebral stability by closely stacking adjacent spinous process tips as seen in extant hominoids. The morphology of the spinous process and postzygapophyses limits the intervertebral space and contributes to the stability of the functional lumbar region as seen in extant great apes, suggesting that antipronograde activity was included in the positional behavior of *N. kerioi*.

1. Introduction

Studying the anatomy of the lumbar spine (including the functional lumbar vertebrae, i.e., the caudal thoracic vertebrae, the diaphragmatic and, when present, post-diaphragmatic vertebrae) in Miocene apes compared to extant primates is essential in understanding the evolution of hominoid posture and locomotion

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(Walker and Rose, 1968; Ward, 1991, 1993, 2007; Sanders and Bodenbender, 1994; Harrison, 1999; MacLatchy et al., 2000; MacLatchy, 2004; Moyà-Solà et al., 2004; Nakatsukasa et al., 2007; Nakatsukasa, 2008; McCollum et al., 2010). Lumbar spine anatomy has been described for the early Miocene *Proconsul heseloni* (Walker and Pickford, 1983; Kelley, 1986; Walker et al., 1993) and *Proconsul nyanzae* (Ward, 1991, 1993; Ward et al., 1993), both dated to 17–18.5 Ma (millions of years ago) (Drake et al., 1988), as well as for *Morotopithecus bishopi* (Walker and Rose, 1968; Sanders and Bodenbender, 1994; MacLatchy et al., 2000; Nakatsukasa, 2008), dated to either 20 Ma (Gebo et al., 1997) or 17 Ma (Pickford, 1998; Pickford et al., 1999, 2003). Studies have also been undertaken on the lumbar anatomy of the middle Miocene (Feibel and Brown, 1991) *Equatorius africanus* (Ward et al., 1999), as well as on the species that is the focus of the present study, *Nacholapithecus kerioi* (Ishida et al., 2004; Nakatsukasa et al., 2003, 2007), from northern Kenya, dated to around 15 Ma (Sawada et al., 1998). *Nacholapithecus kerioi* specimens have provided much information about the postcranial anatomy and diversity of middle Miocene hominoids (Nakatsukasa and Kunimatsu, 2009), and the new specimens we describe and analyze here shed further light not only on adaptations in *N. kerioi* itself but also on hominoid locomotor and postural evolution more generally.

In cercopithecoids, ventroflexion of the lower vertebrae displaces the application point of the compression from the center of the spine centra towards their ventral margins (Sanders, 1995), with the vertebral body primarily transmitting compression and extension forces, through the ventral centra (Rockwell et al., 1938; Young, 1962). If the center of the vertebral body moves the point of compression even a short distance ventrally, the vertebral body experiences longitudinal bending stress along its ventral face (Badoux, 1974). To resist such stresses, the ventral keel may be well developed (Sanders and Bodenbender, 1994). In extant hominoids, there is not the same range of flexion (Ward, 1991), and extant hominoids probably do not experience the same stresses as are found in the vertebral body of cercopithecoids (Sanders, 1995). Instead, the vertebral body is better adapted to bear loads in orthograde postures, and the lower vertebral centra of extant hominoids consequently have a more columnar appearance without hollowing, pronounced spooling, or ventral keels (Sanders and Bodenbender, 1994).

The spinous process morphology of the lumbar vertebrae discriminates extant apes from other primate species. The spinous process is one of the main subjects of the present study and has been recently discussed by Williams and Russo (2015). If the spinous process of a lumbar vertebra is oriented caudally, as seen in extant hominoids but not in cercopithecoids (Ward, 1993; Shapiro, 1993), it may be strongly related to the action of the multifidus muscle in stabilizing the lower back (Slijper, 1946; Shapiro, 1993). Moreover, this orientation may also give stability by closely approximating the adjacent vertebrae, creating bony blocks to extension, particularly when the spinous processes are tall craniocaudally (Slijper, 1946; Shapiro, 1993).

The position of the lumbar transverse processes also distinguishes extant apes from other primate species. The transverse processes in extant great apes arise from the neural arch (Ward, 1991, 1993). On the other hand, the transverse processes originate from the vertebral body in monkeys, with small apes having a state intermediate between extant great apes and monkeys (Ward, 1991, 1993). However, even in the last lumber vertebrae of cercopithecoids, the transverse processes arise from the centro-pedicular junction or begin on the pedicles (Sanders, 1995).

Diaphragmatic vertebrae are defined as rib-bearing thoracic vertebrae that have thoracic-type prezygapophyses (prezygapophyseal articular facets directed in the coronal plane) and lumbar-type postzygapophyses (postzygapophyseal articular facets directed in the sagittal plane) (Clauser, 1980). Extant apes exhibit a reduced lumbar spinal length as a result of a decreased number of lumbar vertebrae and a reduction in the craniocaudal length of each vertebral body (Schultz, 1938, 1961; Benton, 1967; Rose, 1975; Ward, 1991, 1993; Shapiro, 1993; Haeusler et al., 2002; McCollum et al., 2010; Williams, 2012a). In extant great apes, the diaphragmatic vertebral level is positioned more caudally (by one to three vertebral levels) than in cercopithecoids and platyrrhines, and is typically also the last rib-bearing vertebra (Washburn and Buettner-Janusch, 1952; Shapiro, 1993; Haeusler et al., 2002; Williams, 2011, 2012b). A reduction in the lumbar spinal length provides a greater degree of lower back stability, and reduces dorsoventral flexibility (Ward, 1993; Sanders and Bodenbender, 1994; Sanders, 1995; Johnson and Shapiro, 1998).

Concerning Miocene hominoid lumbar spine anatomy, the stem hominoid *Proconsul* has a relatively primitive lumbar anatomy for a catarrhine, for example having six or seven lumbar vertebrae (defined not by how the zygapophyses articulate but by possession of rib facets), a long vertebral body with a ventral median keel, and a more ventral position of the transverse processes relative to extant apes (Ward, 1991, 1993). These primitive characters are retained in the lumbar spine of *N. kerioi* although the transverse process origin is slightly more dorsally situated (Nakatsukasa et al., 2007). The corresponding features in a specimen of *Equatorius* (KNM-TH 28860Y caudal thoracic vertebra; Sherwood et al., 2002) are unclear because of deformation, but its relatively small and keeled vertebral body recalls those of *Proconsul* and *N. kerioi*. The lumbar vertebra of *M. bishopi* (UMP 67.28) has several derived features, such as a more dorsal position of the transverse process and a craniocaudally short vertebral body with no ventral keel formation (Walker and Rose, 1968; Sanders and Bodenbender, 1994; MacLatchy et al., 2000; Nakatsukasa, 2008). Those lumbar features could be interpreted as shared derived states of *Morotopithecus* and the extant great apes (MacLatchy et al., 2000; Young and MacLatchy, 2004).

From Europe, lumbar vertebral specimens of *Pierolapithecus catalaunicus* (12 Ma; Moyà-Solà et al., 2004), *Hispanopithecus laietanus* (9.5–10 Ma; Moyà-Solà and Köhler, 1995, 1996; Köhler et al., 1999; Susanna et al., 2014), and *Oreopithecus bambolii* (8 Ma; Harrison, 1986; Köhler and Moyà-Solà, 1997; Harrison and Rook, 1997) are known. These later European apes exhibit a more, but not yet fully, modern ape-like lumbar anatomy in terms of dorsostability and/or invagination of the lumbar spine when compared with earlier African fossil apes such as *Proconsul* and *N. kerioi*. For example, the lumbar vertebrae of *P. catalaunicus* and *H. laietanus* have more dorsally positioned transverse processes located on the pedicle (pedicular/body-junction in *P. catalaunicus*), more elliptical body articular surfaces, and no apparent ventral keel (Moyà-Solà et al., 2004; Susanna et al., 2014). *Oreopithecus bambolii* also has lumbar vertebrae with dorsally oriented transverse processes located on the pedicle (Harrison and Rook, 1997). These traits are not observed in *Proconsul* or *N. kerioi*.

As the only derived lumbar vertebral trait in *Proconsul*, both *P. nyanzae* and *P. heseloni* possess caudally oriented spinous processes, shared with extant hominoids, and not found in cercopithecoids (Ward, 1993). In *N. kerioi*, the base of the spinous process is positioned more caudally between the postzygapophyses than in cercopithecoids, suggesting that this fossil hominoid also had a caudally inclined spinous process (Nakatsukasa et al., 2007). In *P. catalaunicus*, the spinous process is nearly horizontal and slightly caudally inclined (Susanna et al., 2010). *Hispanopithecus laietanus* may have a caudally oriented spinous process, as indicated by two