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Sacral vertebral remains of the Middle Miocene hominoid *Nacholapithecus kerioi* from northern Kenya

Yasuhiro Kikuchi [a, *], Masato Nakatsukasa [b], Yoshihiko Nakano [c], Yutaka Kunimatsu [d], Daisuke Shimizu [b], Naomichi Ogihara [e], Hiroshi Tsujikawa [f], Tomo Takano [g], Hidemi Ishida [h]

[a] *Division of Human Anatomy and Biological Anthropology, Department of Anatomy and Physiology, Faculty of Medicine, Saga University, Saga 849-8501, Japan*
[b] *Laboratory of Physical Anthropology, Graduate School of Science, Kyoto University, Kyoto 606-8502, Japan*
[c] *Laboratory of Biological Anthropology, Graduate School of Human Sciences, Osaka University, Osaka 565-0871, Japan*
[d] *Department of Business Administration, Faculty of Business Administration, Ryukoku University, Kyoto 612-8577, Japan*
[e] *Laboratory of Evolutionary Biomechanics, Department of Mechanical Engineering, Faculty of Science and Technology, Keio University, Kanagawa 223-8522, Japan*
[f] *Department of Rehabilitation, Faculty of Medical Science and Welfare, Tohoku Bunka Gakuen University, Miyagi 981-8551, Japan*
[g] *Japan Monkey Center, Aichi 484-0081, Japan*
[h] *Kyoto University, Kyoto 606-8502, Japan*

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ABSTRACT

This study describes two new sacral specimens of *Nacholapithecus kerioi*, KNM-BG 42753I and KNM-BG 47687A, from the Aka Aiteputh Formation in Nachola, northern Kenya, excavated in 2002. They are of roughly equal size and are considered to belong to males. When scaled by body mass, the lumbosacral articular surface area of the better preserved specimen, KNM-BG 42753I, is smaller than that in Old World monkeys but similar to that in extant great apes and New World monkeys, as well as *Proconsul nyanzae*. The relatively narrow dimensions of the first sacral vertebral body in the transverse and sagittal planes are characteristics of *N. kerioi* and *P. nyanzae* and similar to those of extant great apes. In *N. kerioi*, lumbosacral surface area relative to body mass is small. This may simply be an extension of a trend from the previously reported small thoracolumbar vertebrae to the sacrum. The first sacral vertebrae of *N. kerioi* and *Epipliopithecus vindobonensis* have a higher craniocaudal vertebral body reduction (CVR; a higher CVR indicates a wider cranial width relative to a narrower caudal width), similar to that in Old World monkeys. Old World monkeys have a higher CVR, and usually have three sacral vertebrae, fewer than seen in extant great apes, which have a lower CVR and four to six (sometimes as many as eight) sacral vertebrae. New World monkeys have a lower CVR than Old World monkeys, but generally possess only three sacral vertebrae, and have a large caudal articular surface, which may be related, at least in the Atelidae, to the grasping ability of their tails. The possibility that *N. kerioi* had only three sacral vertebrae cannot be ruled out, because *E. vindobonensis* and Old World monkeys, with higher CVRs, have sacra consisting of three sacral vertebrae.

1. Introduction

Nacholapithecus kerioi, a mid- to large-sized hominoid (with an estimated body mass of 22 kg [Rose et al., 1996; Ishida et al., 2004; Nakatsukasa et al., 2007; Kikuchi et al., 2012]), lived approximately 15 million years ago (Sawada et al., 1998). It has been found at only one site, the Aka Aiteputh Formation in Nachola in northern Kenya (Sawada et al., 1998). Sacral specimens from Miocene hominoids are rare, but in addition to the specimens described here (KNM-BG 42753I and KNM-BG 47687A), the assemblage includes a well-preserved first sacral vertebral body, KNM-BG 17822 (Rose et al., 1996). Other fossil catarrhines that have been found with partial or complete sacral elements are *Epipliopithecus vindobonensis* (Zapfe, 1958, 1960), *Proconsul heseloni* (KNM-KPS V42 [Ward et al., 1991; Walker et al., 1993]), *Proconsul nyanzae* (KNM-MW 13142M

* Corresponding author.
E-mail addresses: kikuchiy@cc.saga-u.ac.jp (Y. Kikuchi), nakatsuk@anthro.zool.kyoto-u.ac.jp (M. Nakatsukasa), nakano@hus.osaka-u.ac.jp (Y. Nakano), kunimats@biz.ryukoku.ac.jp (Y. Kunimatsu), Ishida-h@seisen.ac.jp (H. Ishida).

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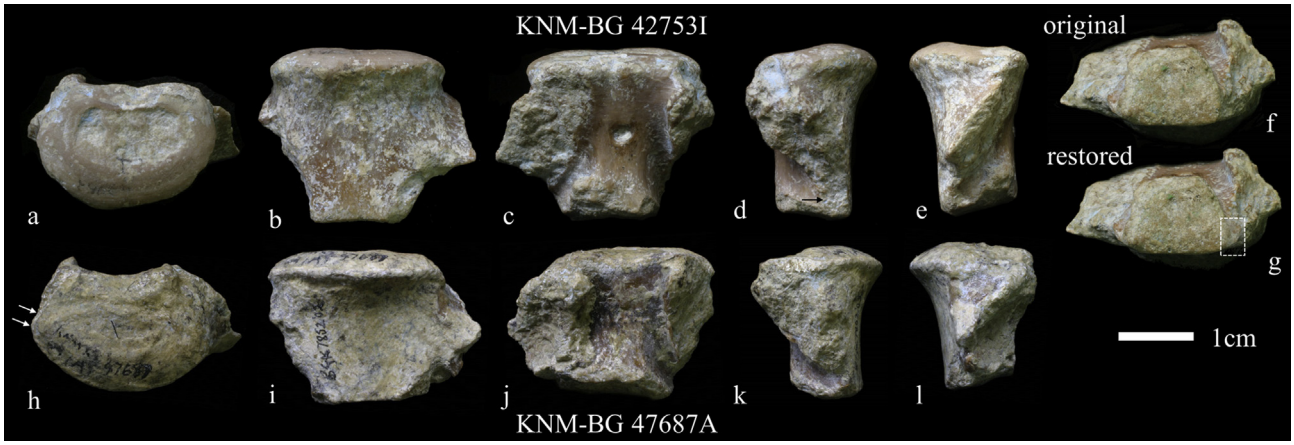

Figure 1. The two *N. kerioi* sacral specimens: KNM-BG 42753I (**a**, cranial; **b**, ventral; **c**, dorsal; **d**, right-hand; **e**, left-hand; **f** and **g**, caudal views [**f**, original; **g**, restored]) and KNM-BG 47687A (**h**, cranial; **i**, ventral; **j**, dorsal; **k**, right-hand; **l**, left-hand views). The black arrow in the right-hand view (**d**) of KNM-BG 42753I indicates erosion. The white arrows of the cranial view (**h**) in KNM-BG 47687A indicate part of the bone that is missing. The caudal view (**g**) of KNM-BG 42753I shows restoration based on the morphology of the non-deformed left-hand side (white dotted square), assuming bilateral symmetry.

and KNM-MW 13142N [Ward, 1991, 1993]), and *Oreopithecus* (BA#50 and BA#72 [Hürzeler, 1958; Straus, 1963]).

The sacrum of extant hominoids is morphologically distinct from that of non-hominoid primates. Extant hominoids generally have four to six sacral vertebrae (but may have up to eight), in contrast to extant non-hominoid primates, which generally have three sacral vertebrae (Schultz, 1930, 1938, 1961; Schultz and Straus, 1945; Ankel, 1965; Clauser, 1980; Abitbol, 1987; Pilbeam, 2004; McCollum et al., 2010; Russo and Williams, 2015). Ward (1991) indicated that the sacra of great apes generally have cranial articular surface areas and mediolateral and sagittal diameters that are relatively smaller than those of monkeys, and suggested that a relatively smaller peak load is transmitted across the lumbosacral joint in extant great apes compared to monkeys.

Relative to body mass, the cranial surface of the *P. nyanzae* (KNM-MW 13142M) sacral vertebral body is dorsoventrally and mediolaterally narrow, similar to those in extant great apes, and evidently smaller than those in monkeys (Ward, 1991). The *N. kerioi* specimen KNM-BG 17822 has a small lumbosacral joint surface, similar to that observed in extant hominoids (Rose et al., 1996). In the mediolateral narrowness of the centrum, it is also similar to the sacral vertebrae of the non-hominoid fossil catarrhine *E. vindobonensis* (Zapfe, 1960), although *N. kerioi* has a slightly lower craniocaudal vertebral body reduction (CVR; the degree of mediolateral tapering between the cranial and caudal widths of the first sacral vertebral body) than *E. vindobonensis* (Rose et al., 1996). A lower CVR is seen in extant hominoids and *Ateles*, and indicates a narrower cranial width with a wider caudal width, whereas a higher CVR, found in extant cercopithecids and *Cebus*, indicates a wider cranial width with a narrower caudal width (Rose et al., 1996). However, because of the rarity of sacral specimens from Miocene fossil hominoids, their overall morphology along with functional interpretations remain unclear.

In the present study, we describe two new sacral specimens of *N. kerioi*, confirm small lumbosacral joint surfaces in these specimens and investigate the number of sacral vertebrae in *N. kerioi*, thus attempting to elucidate evolutionary patterns in the vertebral characteristics of Early to Middle Miocene hominoids.

2. Materials and methods

Two first sacral vertebral specimens of *N. kerioi* (Fig. 1, KNM-BG 42753I and KNM-BG 47687A) were excavated in Nachola (BG-I west and BG-K fossil sites, respectively). The two specimens are of similar size and are considered to belong to males, as indicated by the size of an associated cervical vertebra (KNM-BG 42753K, adult male atlas [Kikuchi et al., 2012]). Both specimens have fairly smooth caudal articular surfaces and were not fused to the second sacral vertebra, so it is possible that these specimens may have belonged to subadults. However, some adult extant great apes (and humans [Scheuer and Black, 2000; Ríos et al., 2008]), but not monkeys, have a sacrum in which the first sacral vertebra is not completely fused to the second (Y. Kikuchi, personal observation). This state may also occur in *N. kerioi* specimens. Moreover, the fact that the epiphyseal disc (annular epiphysis) is fused to the cranial articular surface of the sacrum of KNM-BG 42753I indicates that this specimen is from an adult (Nakai, 2001). The original specimens were observed and measured at the National Museums of Kenya (NMK). Photographs of the original specimens were obtained using a digital camera (Canon Eos 5D digital single lens reflex camera with standard 50-mm macro lens; Canon Inc., Tokyo) with a macro setting. Samples were photographed alongside a clear scale, while maintaining the camera lens in a horizontal position by using a spirit level.

The better preserved specimen, KNM-BG 42753I, was compared metrically with the samples of extant primate species (37 species and 136 individuals listed in Table 1). Extant primate data were obtained from the Anthropological Institute and Museum, University of Zürich (AIMUZ, Switzerland), Museum Für Naturkunde Berlin (MFNB, Germany), and the Royal Museum for Central Africa (RMCA, Belgium). All extant samples were adult. The maturation state of these samples was noted in the specimen box, and determined by the dental eruption or epiphyseal union of the limb bones. None of the subjects exhibited any bone disease or deformation. Metric and photographic data from previously studied specimens of *N. kerioi* (KNM-BG 17822 [Rose et al., 1996], housed in NMK), *P. nyanzae* (KNM-MW 13142M [Ward, 1991, 1993], also from NMK), and *E. vindobonensis* (high quality cast of individual 2 [Zapfe, 1960], housed in AIMUZ) were also collected and compared with extant samples. The cranial surface area of KNM-BG 17822 was smaller than that of KNM-BG 42753I (Table 2). However, the coefficient of variation (CV) of these two specimens was within the male range in samples of sex-segregated extant anthropoids (Supplementary Online Material [SOM]). Thus, KNM-BG 17822 probably also belonged to a male.