Correction

ANTHROPOLOGY

The editors note that the affiliation for Editor Philip Reno should instead appear as Philadelphia College of Osteopathic Medicine. The corrected editor line appears below. The online version has been corrected.

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Insights into the lower torso in late Miocene hominoid \textit{Oreopithecus bambolii}

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\textit{Oreopithecus bambolii} (8.3–6.7 million years old) is the latest known hominoid from Europe, dating to approximately the divergence time of the Pan-hominin lineages. Despite being the most complete nonhominin hominoid in the fossil record, the \textit{O. bambolii} skeleton IGF 11778 has been, for decades, at the center of intense debate regarding the species’ locomotor behavior, phylogenetic position, insular paleoenvironment, and utility as a model for early hominin anatomy. Here we investigate features of the IGF 11778 pelvis and lumbar region based on torso preparations and supplemented by other \textit{O. bambolii} material. We correct several crucial interpretations relating to the IGF 11778 anterior inferior iliac spine and lumbar vertebrae structure and identifications. We find that features of the early hominin \textit{Arhipithecus ramidus} torso that are argued to have permitted both lordosis and pelvic stabilization during upright walking are not present in \textit{O. bambolii}. However, \textit{O. bambolii} also lacks the complete reorganization for torso stiffness seen in extant great apes (i.e., living members of the Hominidae), and is more similar to large hyllobatids in certain aspects of torso form. We discuss the major implications of the \textit{O. bambolii} lower torso anatomy and how \textit{O. bambolii} informs scenarios of hominoid evolution.

\textit{Oreopithecus bambolii} is an insular hominoid species from modern Tuscany and Sardinia, Italy, that is the latest recorded [8.3–6.7 Myr (1)] hominoid from Europe. \textit{O. bambolii} trunk anatomy (2–10) is understood primarily from the taphonomically flattened IGF 11778 skeleton, preliminarily described (11, 12) while embedded in a lignite slab (Fig. 1). Despite the apparently distant relationship between \textit{O. bambolii} and the chimpanzee-human clade (4, 13–16), \textit{O. bambolii} has figured prominently as a model of the chimpanzee-hominin last common ancestor (LCA) (17–20) due to features of the lower torso that have been exclusively aligned with hominins and thus assumed to reflect an adaptation to bipedal locomotion in \textit{O. bambolii} (2, 7, 8, 21, 22). Recently, guided by Miocene hominoids and early hominin \textit{Ardipithecus ramidus} (ARA-VP-6/500), some morphologies seen in early hominins (e.g., lower ilium length, proximal femoral morphology) are understood to be primitive retentions rather than functional traits linked to bipedal adaptation (23–28). Features of the \textit{Ar. ramidus} torso that are argued to have permitted both lordosis and pelvic stabilization during upright walking include a cranio-caudal approximation of the sacroiliac and acetabular joints by a reduction in the lower ilium length, a protuberant anterior inferior iliac spine (AIS) with a distinct epiphyseal origin, a sagittally oriented and greatly broadened lower iliac ischium, anterior extension of the lesser gluteals into a position favorable for hip abduction, and likely a relatively mobile lumbar vertebral column (18, 19, 23, 24). It has remained unresolved as to whether these features of \textit{Ar. ramidus} are present in \textit{O. bambolii} (17–19).

Here, we report on features of the pelvic and lumbar regions of \textit{O. bambolii} based on newly prepared elements from IGF 11778 and supplemented by other \textit{O. bambolii} fossils. The revealed pelvic and lumbar anatomy of \textit{O. bambolii} is different from all known taxa and, importantly, differs from past descriptions of the IGF 11778 specimen in key ways.

**Results**

**IGF 11778 Anatomy.** Full descriptions of IGF 11778 pelvic and vertebral elements are provided in the SI Appendix. The upper vertebral block (SI Appendix, Fig. S1) contains the last thoracic (rib-bearing) vertebra and proximal 3 lumbar vertebrae (L1–L3). The well-preserved L1–L3 laminae are proportionally short, unlike the cranio-caudally elongate lumbar laminae (and corresponding elongate vertebral bodies) seen in cercopithecoids and \textit{Ekenbo nyanzae} (KNM-MW 13142). A lower vertebral block was preserved in contact with the pelvis (Fig. 1 and SI Appendix, Fig. S2). Preparation of the lower vertebral block revealed 2 more lumbar vertebrae, likely the penultimate (L4) and ultimate (L5) lumbar vertebrae, that had been displaced from a more cranial position. The fragmentary lowermost vertebra was identified as belonging to a more recent hominoid (see SI Appendix).

**Significance**

Details of the lower torso anatomy of late Miocene \textit{Oreopithecus bambolii} show that this hominoid differed from both extant great apes (chimpanzees, gorillas, and orangutans) and early hominins (e.g., \textit{Ardipithecus}, \textit{Australopithecus}) in key ways. \textit{O. bambolii} lacked the extreme adaptations for pelvic and lumbar rigidity of extant great apes, but also lacked a hominin-like protruding anterior inferior iliac spine (AIS), short lower ilium, and abductor mechanism of the hip. The revised understanding of the \textit{O. bambolii} lower torso clarifies the phylogenetic and evolutionary scenarios for this peculiar hominid.


The authors declare no competing interest.

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Data deposition: Digital models of original \textit{O. bambolii} specimens used in this study are available on MorphoSource (http://www.morphosource.org/Detail/ProjectDetail/Show/project_id/763), with permission from the curating institutions. The MorphoSource identifier for each model is provided in the SI Appendix, Table S1. Comparative data shown herein are available on Fighrase (https://doi.org/10.6084/m9.fighrase.11301773.v2; https://doi.org/10.6084/m9.fighrase.11300978.v1).

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as lumbar based on distinct transverse processes that arise dorsal to the vertebral body, and the cranial orientation of the ultimate transverse process is consistent with being in close proximity to the iliac crest. The IGF 11778 lumbar prezygapophyses, although suffering from some distortion, suggest a medial or oblique joint orientation. Excepting the fragmentary ultimate vertebra, all of the vertebrae have a ventral keel. The sacrum of IGF 11778 is not preserved.

The pelvis itself consists of 13 fragments with significant dorsoventral compression (Fig. 1 and SI Appendix, Fig. S3). The IGF 11778 ilia are laterally flaring, culminating in a laterally directed anterior superior iliac spine (ASIS), similar to the condition seen in extant great apes and siamangs. The IGF 11778 iliac blades are at the upper limits for relative bi-ASIS breadth in anthropoids (Fig. 2) as preserved, but were most likely closer to the anthropoid average relationship prior to taphonomic flattening. The ilia do not extend as far cranially as in extant great apes, as judged by the distance between the iliac crest and the inferred possible locations of the sacroiliac joint. Although the lower ilium height cannot be exactly measured due to distortion, the range of possible estimates is relatively longer than seen in any hominin (Fig. 2). The sacroiliac joint in IGF 11778 would have been fairly narrow and coronally oriented like that in extant great apes, suggesting that the iliac blades were also coronally oriented (Fig. 2). The coronal orientation of the iliac blades precludes a hip abductor mechanism because the gluteus medius muscle would have been dorsally positioned rather than laterally positioned. The IGF 11778 AIIS (Fig. 3) is not as strongly protruding as previously inferred (2, 6, 7, 17), past inferences being misled by taphonomic crushing and rotation of the lower ilium and AIIS fragments. The pubis of IGF 11778 displays a distinctive tubercle (see SI Appendix, Fig. S5) which may be homologous to the adductor longus origin observed in some extant apes (29). The acetabulum is not directly preserved, but the acetabulum diameter can be estimated as about 32 mm based on the preserved femoral head size.

**Oreopithecus bambolii Lower Torso Morphology.** Other specimens (SI Appendix, Table S1) further clarify the *O. bambolii* bauplan. Bac 204, which appears to be the transitional vertebra based on pre- and postzygapophyseal orientation, has a demifacet for a rib preserved caudally. The transitional vertebra is thus positioned either cranial to or at the level of the last rib-bearing vertebra, likely permitting more flexion and extension of the lower spine than in most extant great apes (30). Bac 72 (9, 11, 21) preserves the lumbosacral region in articulation with a partial ilium. The Bac 72 ultimate lumbar vertebra displays a cranially inclined transverse process running along the cranial aspect of the iliac crest (Fig. 4), and the tip of the transverse process likely contacted the ilium in vivo. Whereas the ultimate lumbar would have had limited mobility due to proximity to bony structures of the pelvis, the Bac 72 penultimate lumbar was situated above the ilium and less restricted. Bac 182 (2) is an incomplete sacrum that is anteroposteriorly flattened but displays 4 distinct foramina on the left dorsal aspect (Fig. 4), arguing for at least 5 bony segments in the *O. bambolii* sacrum. A total of 5 left foramina yielding 6 segments has been proposed in Bac 182 (2), although we consider one of the foramina to be inconclusive due to state of preservation (see also ref. 31). Bac 182 and Bac 184 preserve fragmentary right iliac blades that show that the sacroiliac joint and iliac blade were paracoronally oriented (Figs. 2 and 4), and that the sacroiliac joint did not have the sharp L shape like cercopithecoids, KMN-MW 13142, and YGSP 41216. The iliac blade tip in Bac 184 does not bear a thickened ASIS. A projecting
ischiadic spine is present in Bac 182 (7) and Bac 71 (11). BA 208 preserves the broken base of the ischiadic spine and the greater sciatic notch region, which confirms that the lower ilium was not elongated as in extant great apes. Bac 71 preserves the ischiadic tuberosity which, although small for a primate of this size, is flat and bears a distinct border that is consistent with primate species bearing ischiadic callosities (Fig. 4). Bac 71 also preserves a pubic symphysis that is incomplete cranially but appears to have been short and mediolaterally broad (11). A second more public pubic symphysis, BA 208, preserves the cranial-most aspect of the symphysis, a diminutive pubic tubercle adjacent to the symphysis, and the superior aspect of a long pubic ramus. No complete acetabulum is known for O. bambolii, but all femoral heads (IGF 11778, IGF 2011V, Bac 74, Bac 75, Bac 76, and Bac 86) have a deeply excavated fovea capitis placed centrally on a highly spherical femoral head, an articular surface distribution that suggests a high level of hip joint mobility (32, 33).

Discussion

IGF 11778 has 5 lumbar vertebrae, as originally interpreted, but element identifications differ from the original descriptions (11). The bone that had been assumed to be a portion of a missing L4 vertebra (11) is actually a displaced portion of pedicle, and so what was thought to be the L5 is likely the L4 (Fig. 1 and S7 Appendix, Fig. S2). Although IGF 11778 effectively “loses” a lumbar vertebra, it gains one with the discovery of a fragmentary lumbar vertebra distally. Thus, the lower vertebral block in IGF 11778 is composed of 2 displaced lumbars that appear to represent the ultimate and penultimate lumbar vertebrae. The postmortem displacement of the lower 2 lumbar vertebrae in IGF 11778 caudally from a more cranial position is further supported by the fairly short iliac blade, which was not long enough to both articulate with the sacrum and entrap a lumbar vertebra caudal to the level of the iliac crest. This interpretation is partially guided by Bac 72, in which the ultimate vertebra’s transverse processes were in contact with the ilium but not situated fully below the cranial aspect of the iliac crest.

The spatial configuration of the IGF 11778 lower torso comes into focus when the upper lumbar block is considered along with the last rib, the lower lumbar block, and the upper ilium (Fig. 4). The distance between the last rib and the cranial rim of the iliac blade spans at least 2 vertebral levels, allowing more flexibility than in extant great apes with ribs that nearly contact the ilium. It is possible that there was a missing vertebra between the upper and lower vertebral blocks in IGF 11778, resulting in an even greater distance between the rib cage and the pelvis. However, given that most of the IGF 11778 lumbar and pelvic regions are preserved, it seems unlikely that an additional midlumbar vertebra was present but no trace of it preserved. A total of 5 non-rand-bearing lumbar vertebrae would be further supported if O. bambolii typically had a 6-segment sacrum, as surveys of modern hominoids have never found 6 lumbar vertebrae in combination with a 6-segment sacrum (34–37).

O. bambolii lacked the full suite of adaptations that limit trunk flexion-extension in large-bodied extant great apes. Multiple lines of evidence suggest that the elongate lower ilium seen in extant chimpanzees and orangutans evolved independently (23, 26, 28), so it is unsurprising that O. bambolii appears to have a moderate lower ilium length. The presence of 5 lumbar vertebrae in IGF 11778, the modal number of lumbars for humans and Symphalangus (34), suggests that the lumbar region in O. bambolii had more flexion-extension possible than that in extant great apes, with a parasagittal orientation. The curvature of the Bac 184 gluteal surface would preclude humanlike medial rotation of the anterior iliac blades into the sagittal plane, especially if combined with a narrow sacrum.

Fig. 2. Pelvic form in anthropoids. (A) Natural log-log scatterplot of lower iliac height and acetabulum diameter in extant (n = 350) and fossil anthropoids (n = 10). (B) Natural log-log scatterplot of bi-ASIS breadth measured across the anterior superior iliac spines and acetabulum diameter in extant (n = 1,494) and fossil anthropoids (n = 4). IGF 11778 preserved measurement indicated with open circle, with arrow indicating the direction of actual value. (C) Sacroiliac (SI) joint orientation indicated by red arrows; lateral iliac blade orientation indicated by black arrows. (D) The cross-section of Bac 184 (approximating the section location in ref. 41) is consistent with a coronal orientation of the sacroiliac joint and iliac blade, and inconsistent
The hominins (ARA-VP-6/500, A.L. 288-1) favor flexion-extension movements of the spine. Joint orientation that would restrict rotational movements (38) and IGF 11778 lumbar prezygapophyses suggest a medial or oblique restraint by a well-developed ventral longitudinal ligament (4). The Hammond et al. PNAS more laterally flaring (IGF 11778) than in more coronally oriented, and the iliac blade was substantially and living hominoids. The sacroiliac joint (Bac 182, Bac 184) was significant enough to necessitate O. bambolii in cercopithecoids and hylobatids. The morphology of the O. bambolii (24), and was not short and dorsally projecting like S. syndactylus —a trait widely observed in cercopithecoids and hylobatids—suggests that extension of the O. bambolii lumbar region was significant enough to necessitate restraint by a well-developed ventral longitudinal ligament (4). The IGF 11778 lumbar prezygapophyses suggest a medial or oblique joint orientation that would restrict rotational movements (38) and favor flexion-extension movements of the spine.

The lower torso in O. bambolii is unique among known fossil and living hominoids. The sacroiliac joint (Bac 182, Bac 184) was more coronally oriented, and the iliac blade was substantially more laterally flaring (IGF 11778) than in Ekombo nyanzae (39) and Sivapithecus indicus (40). Not enough of the Pierolapithecus catalaunicus ilium (41) is preserved to compare flaring, but O. bambolii exceeds Rudapithecus hungaricus (28) in the extent of lateral flare of the ilium (see also Fig. 3). The L4 transverse process origin dorsal to the vertebral body, apparently from the pedicle (see also ref. 14), suggests that the vertebral column was somewhat invaginated (23). The transverse process origin was at least as dorsally positioned as in P. catalaunicus (42, 43) and Morototipithecus bishopi (44) (SI Appendix, Fig. S4), which are intermediate between extinct great apes and E. nyanzae, Nacholapithecus kerioi, and cercopithecoids. The morphology of the O. bambolii ischium (Bac 182, IGF 11778) was long and straight like that in other Miocene hominoids (28, 40, 45) and Ar. ramidus (24), and was not short and dorsally projecting like that in hylobatids and later hominins (46). The O. bambolii ischiopubic spine (Bac 182, Bac 71) is comparable to that of modern humans in absolute size, but ischiopubic spines are known in hominins, hylobatids, and some fossil lemurs (47). One of the most intriguing interpretations raised here is the possibility of ischial callosities in O. bambolii (Fig. 4; Bac 71 and IGF 11778), a feature found only in hylobatids among extant hominoids.

Locomotor adaptation in O. bambolii has been controversial for more than half a century, with the most controversial claims being that O. bambolii either was a bipedal ape (7, 8, 10, 22, 48) or used inverted suspension (47). Although the long forelimb of O. bambolii suggests that forelimb-dominated climbing behaviors were a key part of the locomotor repertoire (2, 4, 6, 11, 49, 50), the plesiomorphic hand length proportions have a relatively balanced thumb-to-digits ratio (51, 52) that does not favor inverted suspensory behaviors per se. Regarding the bipedal hypothesis, the O. bambolii lower torso has figured prominently in the most recent arguments, with a focus on the relatively short pelvis (2, 6, 7, but note Fig. 2), a projecting AIIS region (2, 6, 7, but see Fig. 3), a short pubic symphysis (7), a long and straight pubis (7), large ischial spines (7, but see ref. 47), trabecular networks of the ilium (8), and human-like wedging and interfacet positioning of the lumbar vertebrae (7, but see ref. 9). The argument made in those studies was that O. bambolii engaged in a bizarre type of bipedal locomotion different from that of hominins. The argument made in previous studies was in close relationship to the paleoecological context: O. bambolii evolved from an unidentified ancestor in an endemic paleo-island during the late Miocene, with limited trophic resources and a lack of terrestrial predators characteristic of such environments. Following this hypothesis, O. bambolii would have developed an array of adaptations, including features of the hands and feet (see refs. 7, 8, 10, 22, 48, and 51), that allowed more efficient bipedal posture and locomotion than that reported in living apes [e.g., orangutans regularly rely on hand-assisted bipedality (53)].

Inferences about bipedal adaptation (or lack thereof) in O. bambolii are limited to a model that has been shaped by our...
understanding of bipedality in hominins specifically. The wide human sacrum positions the iliac blade more laterally relative to the midsagittal plane and allows medial rotation of the anterior blade without impinging on the abdominal cavity (54, 55). The narrow sacrum (Bac 182, Bac 72) and paracoronally oriented sacroiliac joint (Bac 182, Bac 184) in *O. bambolii* would preclude human-like medial rotation of the anterior iliac blades into the sagittal plane (Fig. 2). The paracoronal orientation of the ilium effectively eliminates the possibility of a hominin-like gluteal abductor mechanism, which is necessary for efficient single-limb support. Whereas hominins have a muscular configuration that favors abduction at the hip to maintain mediolateral trunk stability during bipedal gait, the hindlimb of *O. bambolii* would be configured to provide powerful thigh adduction during climbing based on the protuberant adductor longus muscle origin (SI Appendix, Fig. S5). Moreover, the *O. bambolii* upper ilia were not retroflexed like those of hominins, as evidenced by the shallow greater sciatic notch (Bac 182, BA 208). The *O. bambolii* femoral heads (IGF 11778, IGF 2011V, Bac 74, Bac 75, Bac 76, Bac 86) show a deeply excavated fovea capitis that greatly reduced the bone volume of the femoral head. The femoral heads and sacroiliac joint (Bac 182, Bac 184) were not adapted for the transmission of large, vertically directed loads like hominins (Fig. 4), especially genus *Homo*. The ischium in *O. bambolii* (Bac 182, IGF 11778) was fairly long and straight, which would be advantageous for vertical climbing but reduced bipedal walking economy (56). As noted elsewhere, the *O. bambolii* femur (IGF 11778) was fairly long compared not just to hominins but to extant hominoids and cercopithecoids as well (49). Although certainly more capable of bipedal positional behaviors than extant great apes, *O. bambolii* lacked features of the lower torso related to biomechanically efficient habitual and/or obligate bipedalism in hominins.

![Fig. 4. The *O. bambolii* lower torso and evolutionary scenarios.](https://www.pnas.org/cgi/doi/10.1073/pnas.1911896116 Hammond et al.)
Finally, how does a revised understanding of Oreopithecus inform evolutionary scenarios? Oreopithecus was an insular, swamp-dwelling hominoid subjected to a very different array of selective pressures than African apes and hominins, yet it provides insight into a hominoid bauplan that was not derived in the manner of extant apes and humans. The Oreopithecus lower torso shows moderate reorganization compared to early and middle Miocene hominoids, but it does not display a fully rigid lumbar region and elongate ilium like those of the extant great apes. Compared to extant taxa, Oreopithecus shares a number of affinities with Symphalangus, including 5 lumbar vertebrae, transverse processes that arose on the pedicle, an ilium that was not elongated but fairly broad, an ischial spine, and (possibly) ischial callosities. There are at least 3 evolutionary scenarios compatible with these features of the lower torso.

The first evolutionary scenario is that Oreopithecus and Symphalangus share similarities because they both retain plesiomorphic characters of crown Hominioidea (which are synapomorphic relative to stem hominoids). This scenario implies that some of the torso features associated with orthogrady evolved at the origins of the hominoid crown group at ~17 Myr (57). In this scenario, Oreopithecus could be a stem member of the Hominidae (Fig. 4). The monkey-like torso anatomy inferred for Oreopithecus (40) would require that these taxa be outside the hominoid crown group, secondarily reverted, or that they retain the plesiomorphic condition.

The second evolutionary scenario is that Oreopithecus was a member of the Hylodidae (see also ref. 58). This scenario would expand the geographical and body size ranges that are known for (extant) hylobatids. However, given that the modern hylobatid diversification began around 6.7 Myr (57), Oreopithecus would necessarily be a stem hylobatid (Fig. 4). Moreover, this scenario implies that the long and curved phalanges associated with brachiation and the reduction in body size dimorphism seen in modern hylobatids evolved later within this group. Certainly, with males larger than 30 kg (49), it would have been impossible for Oreopithecus to have crossed arboreal gaps via leaps or rickochetal brachiation like extant hylobatids.

The third evolutionary scenario is that Oreopithecus torso morphologies can be explained by convergent evolution. There is a trend within fossil hominoids for increased reliance on orthograde behaviors through time (59), and selection for orthogrady and 2R selection pressures than African apes and hominins, yet it provides insight into a hominoid bauplan that was not derived in the manner of extant apes and humans. The Oreopithecus lower torso shows moderate reorganization compared to early and middle Miocene hominoids, but it does not display a fully rigid lumbar region and elongate ilium like those of the extant great apes. Compared to extant taxa, Oreopithecus shares a number of affinities with Symphalangus, including 5 lumbar vertebrae, transverse processes that arose on the pedicle, an ilium that was not elongated but fairly broad, an ischial spine, and (possibly) ischial callosities. There are at least 3 evolutionary scenarios compatible with these features of the lower torso.

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