



## Middle Miocene *Pierolapithecus* provides a first glimpse into early hominid pelvic morphology

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### ABSTRACT

Here we describe the pelvis from the holotype specimen of *Pierolapithecus catalaunicus* (IPS-21350), a middle Miocene (11.9 Ma [millions of years ago]) stem hominid from Barranc de Can Vila 1 in Abocador de Can Mata (Catalonia, Spain) for which a partial skeleton is preserved. This skeleton includes the oldest known great ape pelvic materials, which have implications for reconstructing the basal hominid body plan from which later hominids evolved. The *P. catalaunicus* pelvis is composed of a fragment from the ilium (IPS-21350.38) and one from the ischium (IPS-21350.39). Although the *P. catalaunicus* ischium consists of just a small fragment from the caudal acetabulum, the preserved morphology is consistent with the basal hominoid *Proconsul nyanzae*. The ilium is similar to *Pr. nyanzae* in its concave gluteal surface and linea arcuata form, which suggests much of the iliac and pubic form was primitive. However, the ilium was relatively more flaring than *Pr. nyanzae* and most monkeys, and could be within the range of extant lesser apes. In addition, the iliac tuberosity width was probably intermediate between extant great apes and monkeys, although maximum and minimum estimates could be accommodated within either group. The *P. catalaunicus* ilium reflects incipient modifications of the basal hominoid torso for the more frequent use of orthograde behaviors described for this taxon on the basis of other preserved anatomical regions, and also supports claims that extant ape pelvic morphology could be homoplastic given the hypothesized phylogenetic positions of *Pierolapithecus*.

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### Introduction

The pelvis is a particularly informative region of the primate skeleton for inferring locomotion and has figured into virtually all discussions of human origins (e.g., Robinson, 1972; McHenry and Corruccini, 1975; Johanson et al., 1982; Rak, 1991; Ruff, 1995; Lovejoy, 2005; Lovejoy et al., 2009c,d; Kibii et al., 2011). However, the basal hominid (great ape and human clade) pelvic morphology from which hominin pelvic morphology evolved is unknown. Two relatively complete Miocene ape pelvises are available, KNM-MW 13142 from *Proconsul nyanzae* (18 Ma [millions of years ago], Kenya) (Ward et al., 1993) and IGF11778 from *Oreopithecus bambolii* (8.25–8.10 Ma, Italy) (Hürzeler, 1958; Rook et al., 2011), although

the latter suffers from severe diagenetic compression that limits most functional assessments. *Proconsul nyanzae* has been reconstructed as an ambling arboreal quadruped that was apparently more monkey-like than great ape-like (Rose, 1994), based largely on pelvic and torso morphology similar to generalized arboreal quadrupeds such as many cercopithecoids (Ward et al., 1993; Ward, 1993, 2007). However, if the positional behaviors of early great apes differed from that of basal apes, the monkey-like pelvis of *Proconsul* might not be a good comparative analog for the morphology of the early great apes.

The middle Miocene fossil ape *Pierolapithecus catalaunicus* (Hominidae: Dryopithecinae), described from a partial skeleton and cranium from Abocador de Can Mata locality Barranc de Can Vila 1 in northeastern Spain (Moyà-Solà et al., 2004), is generally considered to be a stem hominid at 11.9 Ma (Moyà-Solà et al., 2004, 2009; Casanovas-Vilar et al., 2008, 2011), although it can be alternatively interpreted as an early crown hominid, either more closely

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related to pongines (Pérez de los Ríos et al., 2012) or hominines (Begun et al., 2012). Orthograde behaviors, such as vertical climbing, were inferred in *P. catalaunicus* from a lack of ulnocarpal contact, clavicle length and robusticity, and from rib curvature and lumbar vertebrae morphology, which were found to be intermediate in morphology between early fossil apes and the extant great apes (Moyà-Solà et al., 2004; Susanna et al., 2010). However, *P. catalaunicus* has been suggested to have rarely relied on suspensory behaviors based on hand length relative to body mass and low levels of phalangeal curvature and elongation (Moyà-Solà et al., 2004; Almécija et al., 2009; Alba et al., 2010), indicating that the locomotor adaptations of *P. catalaunicus* differed substantially from all of the extant apes (but see Begun and Ward, 2005; Deane and Begun, 2008, 2010).

Reconstructing the *Pierolapithecus catalaunicus* postcranial morphotype as well as its locomotor repertoire is important for all hypotheses as to how and when great apes evolved. The presence of many primitive and/or intermediate morphologies in the fossil great ape *P. catalaunicus* led us to conclude that the highly derived postcranial morphology of extant apes, especially related to below-branch suspension, evolved independently at least in hylobatids and great apes, and potentially independently in multiple great ape lineages as well (Moyà-Solà et al., 2004; Almécija et al., 2007, 2009; Alba, 2012). Because the hand morphology of *P. catalaunicus* suggests a non-suspensory locomotor repertoire in stem hominids, this scenario of ape evolution challenges some aspects of competing hypotheses that require a substantially derived crown hominid ancestor for hominins (e.g., Keith, 1903; Richmond and Strait, 2000). However, since the original description of *P. catalaunicus*, postcranial homoplasy among the extant great apes has been used to explain the developmental timing of wrist bone fusions (Kivell and Schmitt, 2009) and a lack of knuckle-walking features in the putative fossil hominin *Ardipithecus* (Lovejoy, 2009; Lovejoy et al., 2009a,b,c,d). If these other lines of evidence are correct, great ape-like postcranial morphology and locomotor adaptations were largely acquired independently in *Pongo*, *Gorilla*, and *Pan*.

The *Pierolapithecus catalaunicus* partial skeleton holotype (IPS-21350) preserves two undescribed pelvic fragments: the right ilium IPS-21350.38 (Fig. 1a) and the right caudal ischium IPS-21350.39 (Fig. 1b). Extant great ape pelvises are distinguished from cercopithecoid pelvises in, among other things, having laterally flaring ilia, a shallow but wide gluteal surface and a narrow iliac tuberosity (Straus, 1929; Waterman, 1929; Ward, 1993; Ward et al., 1993; Lewton, 2010). The *P. catalaunicus* ilium preserves enough of these morphologies to place it in a comparative context, providing the opportunity to evaluate pelvic morphology from a locomotor viewpoint during the critical gap between *Proconsul* and extant apes. Here we figure and formally describe both the iliac and ischial fragments from the *P. catalaunicus* skeleton, and further compare them qualitatively and quantitatively with extant hominoids, monkeys, and the basal hominoid *Proconsul nyanzae*. These analyses represent the first assessment of pelvic morphology in an early hominid, representing a significant advance in our knowledge about the early body plan and locomotor adaptations that predate the emergence of extant great apes and hominins.

## Materials and methods

Original fossil remains of *Pierolapithecus catalaunicus* (IPS-21350.38) and *Proconsul nyanzae* (KNM-MW13142) were studied and laser scanned at the Institut Català de Paleontologia Miquel Crusafont in Sabadell (Catalonia, Spain) and the National Museums of Kenya in Nairobi, respectively. Comparative pelvic materials of extant apes and monkeys were laser scanned at the American Museum of Natural History (AMNH), United States National



**Figure 1.** 1a: Dorsomedial (left) and ventrolateral (right) views of the iliac fragment IPS-21350.38. 1b: Lateral (left), cranial (middle), and ventral (right) views of the acetabulum IPS-21350.39. Scale bars equal 1 cm.

Museum (USNM), Museum of Comparative Zoology at Harvard (MCZ), Cleveland Museum of Natural History (CMNH), Naturalis Leiden (ZMA), and the Bavarian State Zoological Collections (ZSM). The comparative scan sample includes *Pongo pygmaeus* (male [m] = 5, female [f] = 5), *Gorilla gorilla* (m = 8, f = 2), *Pan troglodytes* (m = 5, f = 5), *Symphalangus syndactylus* (m = 5, f = 5), *Hylobates lar* (m = 5, f = 5), *Papio anubis* (m = 5, f = 5), *Nasalis larvatus* (m = 5, f = 5), *Ateles* sp. (m = 5, f = 2) and *Alouatta caraya* (m = 3, f = 1). Bones were laser scanned using a Next Engine Desktop 3D Scanner (NextEngine, Malibu, CA, USA). Next Engine laser scan data for each pelvis were aligned in Scanstudio (Next Engine's proprietary software), and exported as a polygonal model to PolyWorks software (Innovmetric Inc., Québec, Canada) for cleaning and refinement of the model mesh. Only high definition, high density point cloud models with few surface irregularities were included in this study.

## Measurements

**Relative iliac flare** The linea arcuata, part of the internal pelvic ring, divides the ilium into the iliac surface or true pelvis cranially and the false pelvis caudally. We quantified proportions of the iliac fossa and false pelvis using cross-sections collected from laser scan data. Cross-sections were created in PolyWorks software.

First, a vector was fit to the medial ilium using the least squares vector-fitting operation by selecting the dorsal surface, beginning below the auricular surface and ending at the mediolaterally narrowest portion (see Fig. 2). For *Pierolapithecus*, the location of the mediolaterally narrowest location was inferred based on sciatic notch morphology, which begins to flare dorsally at the caudal end of the IPS-21350.38 specimen (see Fig. 2). Because surface irregularities in scan data can affect best-fit operations (MacLatchy, 1995;

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