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Reevaluation of the lumbosacral region of *Oreopithecus bambolii*

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ABSTRACT

Functional interpretations of the postcranium of the late Miocene ape *Oreopithecus bambolii* are controversial. The claim that *Oreopithecus* practiced habitual terrestrial bipedalism is partly based on restored postcranial remains originally recovered from Baccinello, Tuscany (Köhler and Moyà-Solà, 1997). The lower lumbar vertebrae of BA#72 were cited as evidence that *Oreopithecus* exhibits features indicative of a lordotic lumbar spine, including dorsal wedging of the vertebral bodies and a caudally progressive increase in postzygapophyseal interfacet distance. Here, we demonstrate why the dorsal wedging index value obtained by Köhler and Moyà-Solà (1997) for the BA#72 last lumbar vertebra is questionable due to distortion in that region, present a more reliable way to measure postzygapophyseal interfacet distance, and include an additional metric (laminar width) with which to examine changes in the transverse dimensions of the neural arches. We also quantify the external morphology of the BA#72 proximal sacrum, which, despite well-documented links between sacral morphology and bipedal locomotion, and excellent preservation of the sacral prezygapophyses, first sacral vertebral body, and right ala, was not evaluated by Köhler and Moyà-Solà (1997). Measures of postzygapophyseal interfacet distance and laminar width on the penultimate and last lumbar vertebrae of BA#72 reveal a pattern encompassed within the range of living nonhuman hominoids and unlike that of modern humans, suggesting that *Oreopithecus* did not possess a lordotic lumbar spine. Results further show that the BA#72 sacrum exhibits relatively small prezygapophyseal articular facet surface areas and mediolaterally narrow alae compared with modern humans, indicating that the morphology of the *Oreopithecus* sacrum is incompatible with the functional demands of habitual bipedal stance and locomotion. The *Oreopithecus* lumbosacral region does not exhibit adaptations for habitual bipedal locomotion.

Introduction

Oreopithecus bambolii is a large-bodied extinct hominoid from the late Miocene (Rook et al., 2000, 2011) of Tuscany and Sardinia, Italy. A number of *Oreopithecus* specimens have been reported (e.g., Ristori, 1890; Hürzeler, 1949, 1958; see Delson, 1986; Begun, 2002 for a review) since its initial discovery in the late nineteenth century (Gervais, 1872a,b). Although *Oreopithecus* is dentally and skeletally well represented, interpretations of its phylogenetic and morphological affinities are historically controversial (Gervais, 1872a,b; Rütimeyer, 1876; Forsyth Major, 1880; Schlosser, 1887; Schwalbe, 1915; Hürzeler, 1949, 1952, 1954, 1956, 1958, 1968; Remane, 1955; de Terra, 1956; Robinson, 1956; Straus, 1957, 1962, 1963; Schultz, 1960; Delson, 1979, 1986; Stern and Jungers, 1985; Susman, 1985, 2004, 2005; Sarmiento, 1987; Szalay and Langdon, 1987; Jungers, 1987, 1990; Harrison, 1987, 1991; Harrison and Rook, 1997; Köhler and Moyà-Solà, 1997, 2003; Wunderlich et al., 1999; Rook et al., 1999, 2004; Moyà-Solà et al., 1999, 2005, 2008; Macchiarelli et al., 2001; Moyà-Solà and Köhler, 2003; Begun, 2007; Lovejoy and McCollum, 2010). As Cartmill and Smith (2009: 127) noted, *Oreopithecus* has been "variously reconstructed as sloth-like, ape-like, and human-like, and it has been placed in almost every possible catarrhine group, from the cercopithecoids to the hominins" (see also Harrison and Rook, 1997; Begun, 2002; Pilbeam, 2002).

Discussions concerning the positional behaviors of *Oreopithecus* have been particularly contentious. *Oreopithecus* shares with extant nonhuman hominoids an extensive list of postcranial synapomorphies, including a high intermembral index (~120) (Schultz, 1960; Straus, 1963; Stern and Jungers, 1985; Susman, 1985; Harrison, 1987; Jungers, 1987, 1990), relatively mobile fore- and hind limb joints (Hürzeler, 1958; Straus, 1963; Sarmiento, 1987; Harrison, 1987, 1991; Alba et al., 2011), and a mediolaterally broad thorax

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and short lumbar region (Schultz, 1960, 1961; Straus, 1963; Hürzeler, 1968), signifying to most researchers a locomotor repertoire of vertical climbing and forelimb suspension (Schultz, 1960; Straus, 1963; Harrison, 1987, 1991; Jungers, 1987, 1988, 1990; Sarmiento, 1987; Rose, 1993, 1997; Harrison and Rook, 1997; Begun, 2007; see also Szalay and Langdon, 1987; Sarmiento and Marcus, 2000; Susman, 2004, 2005; Deane and Begun, 2008). However, in a report on restored postcranial remains from Baccinello, Tuscany, Köhler and Moyà-Solà (1997; see also Moyà-Solà et al., 1999, 2008; Rook et al., 1999; Köhler and Moyà-Solà, 2003; Moyà-Solà and Köhler, 2003) revived an alternative hypothesis that Oreopithecus may have relied on bipedal locomotion (de Terra, 1956; Straus, 1957; 1962; Kummer, 1965; Hürzeler, 1968). Köhler and Moyà-Solà (1997) argued that the ischiopubic region (BA#71) of *Oreopithecus* resembles *Australopithecus* in both size and shape, and that the overall anatomy and proportions of the foot (BA#79 and BA#83) are consistent with the human condition, though also that seen in *Gorilla*. They additionally maintained that *Oreopithecus* had hominin-like femora characterized by high bicondylar angles (see also Straus, 1963; Kummer, 1965; Hürzeler, 1968) and condyles nearly equal in size (Straus, 1963), as well as ischial spines (BA#182) larger than those of other apes and similarly sized to those of humans (Köhler and Moyà-Solà, 1997). A specimen preserving three partial lower lumbar vertebrae and the first and second sacral vertebrae (BA#72; Fig. 1) was also adduced to support the inference of bipedal locomotion (Köhler and Moyà-Solà, 1997). Köhler and Moyà-Solà (1997) claimed that the *Oreopithecus* BA#72 lower lumbar vertebrae exhibit features indicative of a lordotic spine, including dorsal wedging of the vertebral bodies and a caudally progressive increase in postzygapophyseal interfacet distance. From their observations, Köhler and Moyà-Solà (1997: 11750) concluded that, superimposed on an orthograde bauplan, the *Oreopithecus* postcranium exhibits functional adaptations specific to "habitual and not facultative terrestrial bipedal activities…"

The hypothesis that *Oreopithecus* practiced habitual bipedal locomotion has since received mixed support. Rook et al. (1999) provided additional evidence for the habitual bipedal hypothesis from their examination of the IGF 11778 ilia, which they argued exhibit well-developed sacropubic and ilioischial (and corresponding supra-acetabular) trabecular bundles like those found in modern humans, indicating that *Oreopithecus* and humans share similar patterns of pelvic weight transmission (see also Macchiarelli et al., 2001). Moyà-Solà et al. (1999, 2005) argued that the *Oreopithecus* hand (IGF 11778, BA#140) is adapted for a human-like precision grip and cited selection for this derived hand morphology as a factor that would favor habitual bipedalism (but see Susman, 2004, 2005). More recently, Moyà-Solà et al. (2008) reevaluated the BA#71 ischiopubic segment and concluded that the inferior border exhibits roughened crests for attachment of perineal musculature that are otherwise unique to humans among living primates and serve to support the pelvic viscera during habitual bipedal stance and locomotion. By contrast, Wunderlich et al. (1999) argued that several features of the *Oreopithecus* postcranium cited as adaptations to bipedalism are also found in highly suspensory extant and extinct mammals, including the presence of a well-developed ischial spine (sloths, suspensory subfossil lemurs, weakly in *Pongo*), degree and form of the bicondylar angle (*Palaeopropithecus*), and the length and robusticity of the metatarsals (*Pongo*). Susman (1985, 2004, 2005; see also Deane and Begun, 2008) reappraised the hand material (IGF 11778) and demonstrated that *Oreopithecus* emphasized an ape-like power grasp (but see Moyà-Solà et al., 2005; Pouydebat et al., 2008) and possessed curved manual phalanges, indicative of a hand morphology compatible with vertical climbing and forelimb suspension locomotor behaviors.

Although a number of *Oreopithecus* postcranial elements have been reevaluated in order to test the habitual bipedal locomotion hypothesis, the lumbosacral region has received relatively little attention. Based primarily on the IGF 11778 skeleton, it is generally agreed that *Oreopithecus* possessed a hominoid-like numerically shortened (relative to the primitive catarrhine condition) lumbar spine comprised of five vertebrae (Table 1; Schultz, 1960, 1961; Straus, 1963; Hürzeler, 1968; Harrison, 1987, 1991; Köhler and Moyà-Solà, 1997; McCollum et al., 2010). The lumbar vertebral bodies belonging to *Oreopithecus* further resemble those of living hominoids in that they are craniocaudally short (Hürzeler, 1958, 1968; Schultz, 1960; Straus, 1963; Harrison, 1987), mediolaterally broad (de Terra, 1956; Straus, 1957; Hürzeler, 1958, 1968; Harrison, 1991), and possess transverse processes that originate near the pedicle base (Harrison and Rook, 1997) (Table 1). Though the morphology of the *Oreopithecus* lumbar vertebrae is clearly

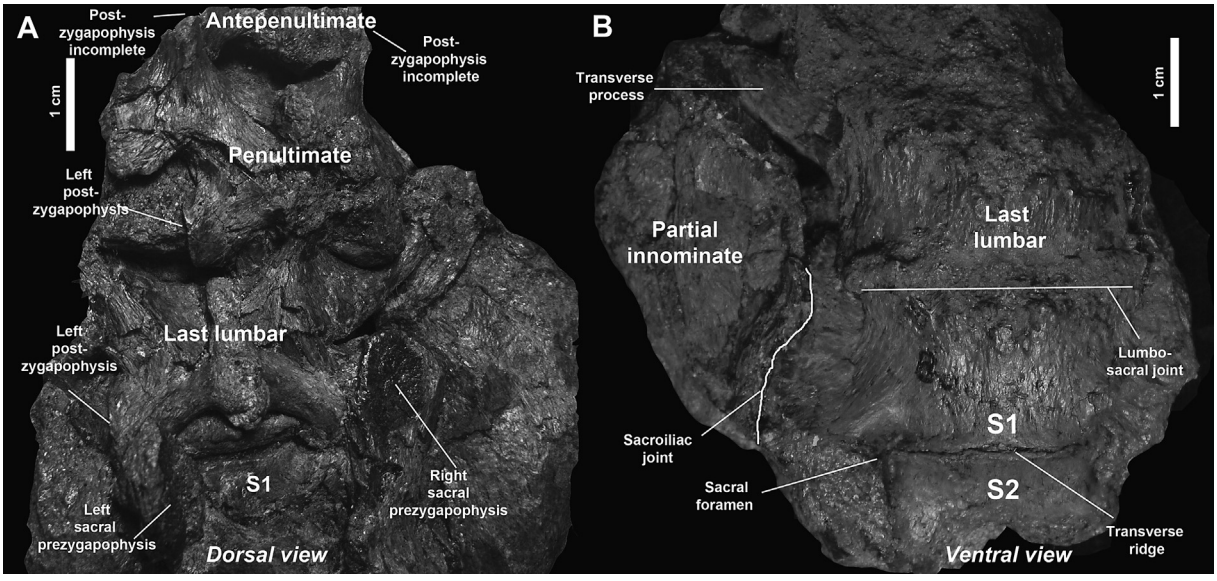

Figure 1. Photographs (by G.A.R.) of the BA#72 lumbosacral specimen in (A) dorsal and (B) ventral views.