

## Femur length, body mass, and stature estimates of *Orrorin tugenensis*, a 6 Ma hominid from Kenya

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**Abstract** To understand the palaeobiology of extinct hominids it is useful to estimate their body mass and stature. Although many species of early hominid are poorly preserved, it is occasionally possible to calculate these characteristics by comparison with different extant groups, by use of regression analysis. Calculated body masses and stature determined using these models can then be compared. This approach has been applied to 6 Ma hominid femoral remains from the Tugen Hills, Kenya, attributed to *Orrorin tugenensis*. It is suggested that the best-preserved young adult individual probably weighed approximately 35–50 kg. Another fragmentary femur results in larger estimates of body mass, indicative of individual variation. The length of the femur of the young adult individual was estimated, by using anthropoid-based regression, to be a minimum of 298 mm. Because whole-femur proportions for *Orrorin* are unknown, this prediction is con-

servative and should be revised when additional specimens become available. When this predicted value was used for regression analysis of bonobos and humans it was estimated to be 1.1–1.2 m tall. This value should, however, be viewed as a lower limit.

**Keywords** *Orrorin tugenensis* · Body-mass estimate · Limb length · Femur · Bipedalism

### Introduction

Previous studies of the palaeobiology of *Orrorin tugenensis*, a 6 Ma hominid from the Tugen Hills, Kenya, concentrated on taxonomic and functional anatomical aspects of the postcranium (Senut et al. 2001, 2002; Gommery and Senut 2002; Pickford et al. 2002a; Galik et al. 2004) and on its geological context (Pickford and Senut 2001; Pickford et al. 2002b; Sawada et al. 2002).

Body size is one of the most important ecological and life-history characteristics in primate biology (Harvey and Clutton-Brock 1985; Fleagle 1986) and numerous studies have been performed to correlate body size with skeletal design and to estimate body mass in extinct animals from fossils (Jungers 1985; Damuth and MacFadden 1991; Ruff 2003). Determination of the length of the femur is also important for investigating locomotor behavior in *Orrorin*, because longer hind limbs increase energy efficiency in bipedal walking (Jungers and Stern 1983; Steudel-Numbers and Tilkens 2004; but see also Kramer and Eck 2000). Relative limb length in fossil hominids has evinced much attention of researchers (Jungers 1982, 1988; Jungers and Stern 1983; McHenry 1991, 1992; McHenry and Berger 1998). Although the adaptive

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significance of stature is not well understood, it does provide a relatively clear idea of the size of a bipedal animal. Only three partial femoral specimens of *Orrorin* have yet been collected (Senut et al. 2001; Pickford et al. 2002a, b). In this study body mass, femur length and stature in *Orrorin* have been investigated by use of these specimens.

## Methods

Three partial femora of *O. tugenensis* are known (Fig. 1). Bar 1003'00 is the proximal half of a left femur lacking the head and greater trochanter. This is the largest and most robust specimen. Bar 1002'00 is the proximal two thirds of a femur lacking part of the greater trochanter. The distal break lies at a distance of circa 215 mm from the head level (Table 1). This is the most complete specimen available. The shaft circumference at the distal break is 73 mm and the minimum circumference is 69 mm, which is measured circa 30 mm above the break and probably approximates the mid-shaft circumference. The epiphyseal line of its head has not completely disappeared, indicating this specimen is from a young adult. Longitudinal growth, however, had probably almost ceased. Bar 1215'00 is a small part of a proximal femur lacking the head and greater trochanter. This specimen is too fragmentary to be used for the purpose of this study.

We estimated the original length of the Bar 1002'00 femur and then predicted the stature of this individual from the estimated value. To estimate the original length, we obtained various allometric and isometric regressions from the literature (Table 2). For the estimator we used the femur head diameter (McHenry

1991; McHenry and Berger 1998; Köhler et al. 2002), minimum superoinferior (s-i) femur neck height (Köhler et al. 2002), and length to lesser trochanter (McHenry 1974). Reference taxa used for calculating regressions are variable: anthropoids, great apes, human. Human/non-human primates mixed models were avoided because they probably introduce a confounding error by lumping different trajectories. In accordance with a recommendation by Konigsberg et al. (1998), we adopted classical calibration when the length of Bar 1002'00 is predicted by extrapolation of the reference taxa. Otherwise, we adopted inverse calibration (femur length is regressed on the estimator). When the formula of the classical calibration model was not given in the original literature, we calculated it from the inverse calibration formula. The estimated length of the femur was examined by logarithmic scaling with the mid-shaft circumference in large-bodied catarrhines (Fig. 2).

The stature of Bar 1002'00 was estimated from the most likely femur length by using different regressions (Table 4; Olivier 1976; Jungers 1988; Konigsberg et al. 1998; Hens et al. 2000). The reference samples are either bonobo or pygmy. Whereas Olivier (1976) used the bicondylar length, other authors adopted the maximum femur length. Because the distal portion of the femur is missing in *Orrorin*, we based our comparison on the estimated femur length only. Results do not, in fact, vary substantially depending on prediction methods. Rather, different femur length predictions affect differences in stature estimate to a greater extent (see below).

For the body mass surrogate we used as many femoral measurements as possible including head, neck, and shaft dimensions (Table 3) because proportions of the femur of *Orrorin* may be different from those of modern references and it is risky to rely on a few measurements only (Ruff 1998). As for femur length prediction, classical calibration was adopted when it was relevant. We avoided human/non-human primate mixed models except for the body-mass estimate from shaft cortical area at the distal 20 and 35% levels. For this regression, only human and non-human mixed models were available from the literature (Ruff 1987).

Linear measurements were obtained by using digital sliding calipers to the nearest tenth of a millimeter or by using an osteometric board to the nearest millimeter (for longitudinal lengths). Shaft circumference at the break was measured to the nearest millimeter by use of a measuring tape in Bar 1002'00 and Bar 1003'00. Cortical area at the break was measured from digital photographs in each specimen. Each photograph was



**Fig. 1** Three femur specimens of *Orrorin*. Bar 1002'00 (a), Bar 1003'00 (b), and Bar 1215'00 (c). In each panel, the left image is the posterior view

**Table 1** Sizes of the *Orrorin tugenensis* specimens

Specimen	Average head diameter (mm)	Calculated head volume (mm <sup>3</sup> )	Neck s-i height (mm)	Length to lesser trochanter (mm)	Cortical area at the break (mm <sup>2</sup> )
Bar 1002'00	31.9	16,984.0	20.9	61.1	184
Bar 1003'00	NA <sup>a</sup>	NA	NA	NA	269

<sup>a</sup> NA: measurement not possible

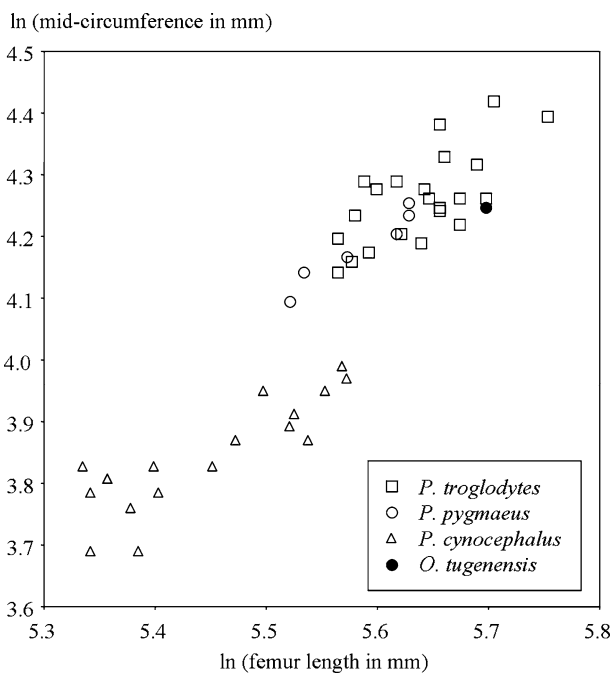
**Table 2** Femur length estimates for Bar 1002'00 (mm)

Measurement used	Source	Reference taxa	Size range	Inverse calibration <sup>a</sup>	Classical calibration <sup>a</sup>
Head diameter	Köhler et al. (2002)	Anthropoid	<i>Callithrix–Gorilla</i>	<b>313 (263–373)<sup>b</sup></b>	–
	McHenry and Berger (1998)	Great ape	<i>Pan–Gorilla</i>	286 (260–313)	<b>281 (252–309)</b>
	McHenry (1991)	Human	330–467 mm (femur length)	334 (295–379)	<b>326 (285–373)</b>
Neck s-i height	McHenry and Berger (1998)	Human	28–87 kg (body mass)	345 (294–396)	<b>298 (233–362)</b>
	Köhler et al. (2002)	Anthropoid	<i>Callithrix–Gorilla</i>	<b>298 (239–373)</b>	–
Length to lesser trochanter	McHenry (1974)	Human	Native Americans	310 (280–340)	– <sup>c</sup>

<sup>a</sup> Average with 95% confidence interval in parentheses

<sup>b</sup> Bold indicates preferred calibration

<sup>c</sup> Although classical calibration is preferred, the formula was not available



**Fig. 2** Bi-logarithmic scaling of femur mid-circumference on femur length for medium-to-large-bodied catarrhines. Note *Orrorin* (Bar 1002'00) is plotted near the periphery of the chimpanzee distribution

taken in line with the shaft axis with the break being centered in the focal area together with a scale. Edges of the cortex were traced manually and the outlined area was calculated by using the NIH image program.

**Femur length estimate**

Regressions of the femur head diameter yielded femur length estimates ranging from 281 to 326 mm (Table 2). If the 95% confident interval (CI) is included the range expands by circa 50 mm toward both sides. The regression based on the great ape model produces the lowest estimates (281 mm), because of a strong negative allometry of their hindlimb length on body size (Jungers 1985). In contrast, human-based regressions yield higher values (298–326 mm). General anthropoid regressions (reference taxa = marmoset to gorilla) on the head diameter yield intermediate values (313 mm). In addition, the s-i neck height predicts a lower value using the same reference specimens (298 mm). McHenry (1974) provides a regression formula based on the projected length to the lesser trochanter in humans. For this regression classical calibration is favored but it could not be calculated from the available data. This regression predicts a moderately large value (310 mm).

As previous studies noted (Senut et al. 2001; Pickford et al. 2002a, b), Bar 1002'00 has a larger femur head relative to other preserved parts (e.g. neck and shaft) yielding higher length estimates. The large femur head in *Orrorin* might be a derived feature because of its bipedal behavior. Alternatively, it may be a retention of a unique ancestral condition in relation to enhanced hip joint mobility for arboreal maneuvers as it is in *Pongo* (Ruff 1988) although *Pan* and extinct Miocene apes show no signs of such extreme femur head enlargement (Ruff 2002). The large articular surface of the head (particularly in anterior and superior views; Fig. 1 of Pickford et al. 2002a, b) seems to favor the latter interpretation, although the large hip joint might have been an exaptation for bearing greater stresses associated with bipedalism. Whichever is correct, it is risky to correlate the uniquely large femur head with femur length because these dimensions are probably determined by different functional demands. Thus, conservatively, we adopted 298 mm (95% CI 239–373 mm) derived from the neck s-i height using the general anthropoid regression. It should be noted, however, that the neck could be gracile, because this individual died before full maturity. This is, therefore, a conservative or modest estimate. This value is identical with that predicted from the human-based formula using the femur head size in McHenry and Berger (1998) although it is lower than that yielded by human-based regression using length to the lesser trochanter (McHenry 1974).

When an original length of 298 mm is presumed, Bar 1002'00 preserves 72% of the original length lacking the distal 83 mm. The estimation sets the mid-length 66 mm above the distal break. At the presumed mid-length, anteroposterior and mediolateral diameters are 19.3 and 24.8 mm, respectively, and the shaft circumference is 70 mm.

Figure 2 bi-logarithmically scales the femoral mid-circumference on the femur length in several medium-to-large-sized catarrhines. *Orrorin* is plotted near the periphery of the chimpanzee distribution (lower range) although it is not completely segregated from chimpanzees.

### Body-mass estimates

Bar 1002'00 (Table 3)

Body mass was estimated using the following regressions: head diameter (McHenry 1992; Grine et al. 1995; Köhler et al. 2002; Ruff 2003), head volume (Ruff

1998), neck height (Köhler et al. 2002), shaft diameters below lesser trochanter (McHenry 1992), shaft thickness at the mid-shaft (Ruff 2003), and the cortical area at the break (Ruff 1987).

General anthropoid/catarrhine regressions using the femur head size (Köhler et al. 2002; Ruff 2003) yield relatively high body-mass estimates, ranging from 45.7 to 47.4 kg. The combined 95% CI is from 32.8 to 67.7 kg. Ape-based regressions (McHenry 1992; Ruff 2003) predict slightly lower values than do general catarrhine/anthropoid regressions, although the difference is slight. Human-based regressions (McHenry 1992; Grine et al. 1995) provide lower estimates, from 30.4 to 35.8 kg (combined 95% CI from 13.2 to 50.7 kg), because of the relatively large femur head in living humans among primates (Ruff 1988).

The s-i neck height predicts 43.0 kg (95% CI 25.5–72.6 kg), which is slightly smaller than the many values predicted from femur head dimensions. In fact, it is smaller by 4.4 kg than that estimated from the femur head diameter with the same reference.

Shaft thickness below the lesser trochanter (McHenry 1992) yields rather large estimates in both human and ape-based regressions. With the ape-based regression it is 56.7 kg (95% CI 30.9–104.1 kg). Using human-based regressions it is 49.9–50.2 kg (combined 95% CI 30.2–78.3 kg). The ape-based regression predicts a higher value than human-based regressions, although the CIs overlap substantially.

When the femur length is presumed to be 298 mm, the regression using the average diameter at the mid-length (Ruff 2003) predicts relatively high values both for non-human catarrhine and ape regressions (47.7–50.1 kg, combined CI 30.1–83.5 kg).

The distal break is at the distal 28% level if the femur length is 298 mm. Although a body mass prediction formula using the cortical area at this level is not available from the literature, Ruff (1987) provides a regression formula from the cortical area at distal 20 and 35% level. Regressions for the distal 35% level yield values ranging from 30.9 to 33.0 kg (combined 95% CI 23.8–43.2 kg). Regressions for the distal 20% level yield larger values ranging from 36.7 to 37.4 kg (combined 95% CI 23.2–58.0 kg). In summary, we believe the body mass of the Bar 1002'00 individual was most probably 35–50 kg.

Bar 1003'00 (Table 3)

The body mass of Bar 1003'00 was estimated from the cortical area and external dimensions at the break. We compared this specimen with the presumed recon-

**Table 3** Body-mass estimates (kg) for *Orrorin tugenensis*

Estimator	Source	Reference group	Size range	Inverse calibration <sup>a</sup>	Classical calibration <sup>a</sup>
<i>Bar 1002'00</i>					
Head diameter	Köhler et al. (2002)	Anthropoid	<i>Callithrix–Gorilla</i>	<b>47.4 (33.1–67.7)<sup>b</sup></b>	–
	Ruff (2003)	Catarrhine	3.3–166.4 kg	<b>45.7 (32.8–63.8)</b>	–
	Ruff (2003)	Ape	5.5–166.4 kg	<b>44.3 (34.1–57.6)</b>	–
	McHenry (1992)	Ape	5.2–157.9 kg	<b>41.2 (36.1–47.0)</b>	–
	McHenry (1992) <sup>c</sup>	Human	30.4–64.9 kg	31.5 (19.2–51.4)	<b>30.4 (18.2–50.7)</b>
	McHenry (1992) <sup>d</sup>	Human	30.4–64.9 kg	31.5 (14.5–48.4)	<b>30.6 (13.2–48.0)</b>
	Grine et al. (1995)	Human	Modern Americans	35.8 (25.9–45.8)	– <sup>e</sup>
Head volume	Ruff (1988)	<i>Macaca</i> + great apes	3.3–164 kg	<b>46.6 (37.7–57.5)</b>	–
	Ruff (1988)	Great apes	36.5–164 kg	<b>43.7 (36.7–52.0)</b>	–
Neck s-i height	Ruff (1988)	Human	58.3–75.8 kg	40.9 (32.1–52.2)	<b>39.0 (30.2–50.3)</b>
	Köhler et al. (2002)	Anthropoid	<i>Callithrix–Gorilla</i>	<b>43.0 (25.5–72.6)</b>	–
ap × ml diameters below lesser trochanter	McHenry (1992)	Ape	5.2–157.9 kg	<b>56.7 (30.9–104.1)</b>	–
	McHenry (1992) <sup>c</sup>	Human	30.4–64.9 kg	<b>50.2 (32.2–78.3)</b>	–
	McHenry (1992) <sup>b</sup>	Human	30.4–64.9 kg	<b>49.9 (30.2–69.6)</b>	–
Mid-shaft average breadth <sup>f</sup>	Ruff (2003)	Catarrhine	3.3–166.4 kg	<b>47.7 (34.0–66.8)</b>	–
	Ruff (2003)	Ape	5.5–166.4 kg	<b>50.1 (30.1–83.5)</b>	–
Distal break cortical area (as distal 35%)	Ruff (1987)	<i>Macaca</i> + great apes + human	3.3–164 kg	<b>33.0 (25.3–43.2)</b>	–
	Ruff (1987)	Great apes + human	36.5–164 kg	33.9 (25.8–44.5)	<b>32.4 (24.4–42.9)</b>
	Ruff (1987)	African apes + human	40–164 kg	32.2 (24.9–41.5)	<b>30.9 (23.8–40.1)</b>
Distal break cortical area (as distal 20%)	Ruff (1987)	<i>Macaca</i> + great apes + human	3.3–164 kg	<b>37.3 (26.7–52.1)</b>	–
	Ruff (1987)	Great apes + human	36.5–164 kg	40.0 (27.7–57.6)	<b>37.4 (25.3–55.3)</b>
	Ruff (1987)	African apes + human	40–164 kg	40.0 (26.1–61.2)	<b>36.7 (23.2–58.0)</b>
<i>Bar 1003'00</i>					
Bar 1003'00 cortical area at 50%	Ruff (1987)	<i>Macaca</i> + great apes	3.3–164 kg	<b>50.2 (35.8–70.4)</b>	–
	Ruff (1987)	Great apes	36.5–164 kg	<b>69.5 (46.4–104.2)</b>	–
Mid-shaft average breadth	Ruff (2003)	Catarrhine	3.3–166.4 kg	<b>52.7 (37.6–73.8)</b>	–
	Ruff (2003)	Ape	5.5–166.4 kg	<b>55.1 (33.1–91.9)</b>	–

<sup>a</sup> Average with 95% confidence interval in parentheses

<sup>b</sup> Bold indicates preferred calibration

<sup>c</sup> Logarithmic regression

<sup>d</sup> Linear regression

<sup>e</sup> Although classical calibration is preferred, the formula was not available

<sup>f</sup> The original length is assumed to be 298 mm

struction of Bar 1002'00 and assumed that the break approximately corresponds to the 50% level. The accuracy of estimate depends on the assumption of the break level and so this should be taken into account. Macaque and great ape regression yields 50.2 kg (95% CI 35.8–70.4 kg). If the great ape model is used, it is 69.5 kg (95% CI 46.4–104.2 kg). The anteroposterior and mediolateral diameters at the break are 20.6 and 25.2 mm, respectively. These values yield a body-mass estimate of 52.7–55.1 kg (combined 95% CI 33.1–91.9 kg) using catarrhine and ape regressions. These values are greater by 4–5 kg than the values predicted for the Bar 1002'00 specimen using the same regressions (Table 3).

## Stature

Assuming the original length of Bar 1002'00 is 298 mm, the stature of the individual was estimated (Table 4). Although results from both inverse calibration and classical calibration are shown, classical calibration is appropriate, because the femur length of Bar 1002'00 is longer than for bonobos and AL 288-1 (Lucy), the femur length of which was estimated to be 281 mm (Jungers 1982) but shorter than for pygmies. The bonobo regression predicts the stature of Bar 1002'00 as 1.18 m (95% CI 1.03–1.33 m). The pygmy regression in Olivier (1976) predicts a higher stature compared with those in Jungers (1988). The estimate from the

**Table 4** Stature estimates (m) for Bar 1002'00

Femur length (mm)	Source	Reference group	Inverse calibration <sup>a</sup>	Classical calibration <sup>a</sup>
298	Jungers (1988) and Hens et al. (2000)	Bonobo	1.17 (1.05–1.29)	<b>1.18 (1.03–1.33)<sup>b</sup></b>
	Olivier (1976)	Pygmy	1.36 (1.28–1.44)	<b>1.16 (1.04–1.28)</b>
	Jungers (1988) <sup>c</sup>	Pygmy	1.14	<b>1.10</b>
	Jungers (1988) <sup>d</sup>	Pygmy	1.15	<b>1.10</b>
	Konigsberg et al. (1998) and Hens et al. (2000)	Pygmy	1.14 (1.03–1.26)	<b>1.08 (0.93–1.22)</b>

<sup>a</sup> The 95% CI is given in parentheses

<sup>b</sup> Bold indicates preferred calibration

<sup>c</sup> Logarithmic regression

<sup>d</sup> Linear regression

former is 1.16 m (95% CI 1.04–1.28 m) and that from the latter is 1.10 m (both logarithmic and linear regression). For regressions from Jungers (1988) we could not calculate 95% CI. In summary, the stature of Bar 1002'00 is likely to have been 1.1–1.2 m when this femur length is applied. This is marginally greater than the estimated stature of AL 288-1 which has an appreciably smaller femur.

Although this individual was a young adult, the stature would probably have increased only a little to reach the fully matured stage.

## Discussion

Pickford et al. (2002a, b) argued that the femora of *O. tugenensis* are characterized by many morphological features that occur in australopithecines and humans but not in extant African apes or Miocene apes. They concluded that most of these features were related to bipedal locomotion of a sort that was closer functionally to that of hominids than to that of any other hominoids, which either walked or stood bipedally in a different way (e.g. *Oreopithecus bambolii*, Köhler and Moyá-Solá 1997; Rook et al. 1999) or are only occasionally bipedal and have little or no skeletal or musculature modification for such a locomotor repertoire, including chimpanzees, orangutans, and gorillas. Determination of the length of the femur, body mass, and stature of *O. tugenensis* is intriguing for testing these conclusions. For example, for bipedalism to be energetically efficient (and thus be subject to positive selection pressures) longer legs are favored (Jungers and Stern 1983; Steudel-Numbers and Tilkens 2004; but also see Kramer and Eck 2000).

Body mass prediction for Bar 1002'00 varies depending on reference taxa and estimator (Fig. 3). Whereas human-based regressions using femur head dimension yield relatively low estimates (30.4–39.0 kg), these regressions are probably unsuitable compared

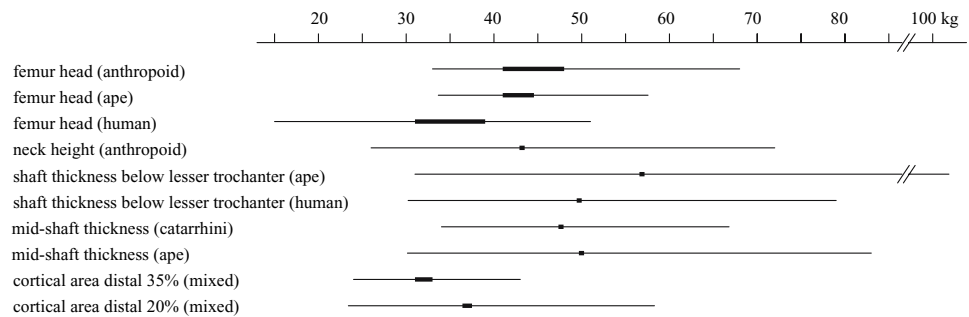
with others because modern humans have a very large femur head relative to body mass compared with living and fossil hominoids (Ruff 1988). Non-human primate regressions using the dimensions of the femur head yield relatively high body-mass estimates, ranging from 41.5 to 47.7 kg. The combined 95% CI is from 32.8 to 67.7 kg. Although ape-based regressions predict slightly lower values than general catarrhine/anthropoid regressions, the difference is slight. As is noted above, *Orrorin* has a comparatively large femur head. Therefore, predicted values obtained from head dimension, when it is large, should be treated with caution.

The s-i neck height leads to a prediction of 43.0 kg, which is smaller than the prediction from the femur head diameter using the same reference (Köhler et al. 2002), which means that Bar 1002'00 has a thin neck relative to the femur head.

Shaft thickness below the lesser trochanter, in contrast, yields rather large estimated values with both human and ape regressions. They range from 50.4 to 56.7 kg. The average diameter at the mid-length results in slightly lower predictions (47.7–50.1 kg). Because the outer cross-sectional shape is usually more irregular below the lesser trochanter than at the mid-length, we believe the latter estimates are more reliable.

In contrast, cortical area at the break yields a rather low value, irrespective of which regression (distal 20 or 35%) is used. This inconsistency is probably related to the age of the Bar 1002'00 individual. Ruff et al. (1994) noted there are age-related changes in long bone diaphyseal bone formation as a result of increased mechanical loading and that the periosteal envelope is more responsive during juvenile stages and the endosteal envelope more responsive after juvenile status. Thus, the external shaft dimension may be used to predict the body mass after Bar 1002'00 reached fully adult stage whereas the cortical cross-sectional area may be used to predict the body mass at the death of this individual.

**Fig. 3** Comparison of body-mass estimate for Bar 1002'00 by use of different surrogates and reference taxa. *Thick bar* indicates the average or the range of averages and *thin bar* indicate 95% confidence interval or combined 95% confidence intervals. For original data, see Table 3



In summary, most of the estimates fall within the range 35–50 kg for prediction of the body mass of Bar 1002'00. It seems practical to use this range as the probable body mass of this individual although it should be noted that care should be taken because these estimates are accompanied by wide CI. This range corresponds approximately to male *Pan troglodytes schweinfurthii* in Mahale and Gombe (Uehara and Nishida 1987; Morbeck and Zihlman 1989). In Mahale the mean is 42.0 kg ( $n = 6$ , 34.3–49.6 kg) and in Gombe the average is 39.5 kg ( $n = 9$ , 33.6–47.3 kg). Bar 1003'00 is larger than Bar 1002'00. By using common regression formulae the body mass of Bar 1003'00 is estimated as 5 kg greater than the latter. Because few samples are available, typical body mass of *Orrorin* remains unclear.

The stature of Bar 1002'00 was predicted as 1.1–1.2 m when a femur length of 298 mm was used. This stature is comparable with that of chimpanzees. According to Coolidge and Shea (1982) the stature of *P. troglodytes* (sex-combined) is 1.2 m (SD 0.07 m), although this predicted value is never secure. This result may have suffered from three confounding factors: prediction error, relevance of regression formula, and error of estimator. In particular, the last source of error is the most difficult to control in this case. When a general anthropoid regression is used to estimate the original length of the Bar 1200'00 femur, a large confidence interval (95% CI 239–373 mm) accompanies the value. We have no information about the shape of the whole femur of *Orrorin* and thus no idea of the accuracy of this prediction. For example, if 30 mm (= ca. 10% of 298 mm) is added to this predicted femur length (thus 328 mm), the stature estimate increases by more than 10 cm. On the basis of the data available, therefore, this stature estimate is best viewed as the lower limit (i.e. the individual was unlikely to have been shorter but could have been taller).

Four femora from Mahale (one male and three female) range from 242 to 266 mm in length and average 258.8 mm (Carlson et al. 2006). According to Morbeck and Zihlman (1989), femur length in seven

sex-combined individuals from Gombe ranges from 253 to 284 mm and the average is 264.2 mm. The modestly predicted length of *Orrorin*'s femur at circa 298 mm is somewhat greater than these values. Jungers and Stern (1983), however, cited a field record of three female bonobos whose body mass and femur length ranged from 27 to 31 kg and 281 to 291 mm, respectively. The estimated body mass of *Orrorin*, 35–50 kg, indicates this early hominid was heavier. It is, therefore, premature to conclude, solely from this predicted value, that *Orrorin* had a relatively elongated femur compared with those of living great apes. At any rate, it is likely that femur elongation in *Orrorin*, if present, is less pronounced than it is in modern humans. Attention should, however, be paid to the fact that even the cautiously predicted value taken in this study plots *Orrorin* near the periphery of the chimpanzee distribution in its scaling with the shaft circumference (Fig. 2) although *Orrorin* is not completely segregated from chimpanzees. This is a consequence not of low shaft thickness but of the femur length, because shaft thickness yields large body mass predictions (48–50 kg) for this individual. This may suggest that this femur is comparatively long for a primate in this size range. Given the large confidence interval accompanying the length prediction, however, this study neither supports nor refutes the hypothesis of femur elongation in *Orrorin*. Additional specimens preserving the distal part, or a different analytical approach, will be necessary to know precisely how long its femur was.

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