**Human Palaeontology and Prehistory / Paléontologie humaine et préhistoire**

## CONCISE REVIEW PAPER

### *LE POINT SUR...*

# Bipedalism in *Orrorin tugenensis* revealed by its femora

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**Abstract** – Three fragments of femora of *Orrorin tugenensis*, a 6 Ma hominid from the Lukeino Formation, Kenya, possesses a suite of derived characters that reveal that the species was habitually bipedal. Detailed anatomical comparisons with modern humans, Australopithecines and Miocene and extant African apes, reveal that *Orrorin* shares several apomorphic features with Australopithecines and *Homo*, but none with *Pan* or *Gorilla*. Within the Hominidae, the femur of *Orrorin* is closer morphologically to that of modern humans than it is to those of australopithecines. ***To cite this article: M. Pickford et al., C. R. Palevol 1 (2002) 191–203.*** © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

**bipedalism / Upper Miocene / Tugen Hills / Kenya / *Orrorin tugenensis* / femur**

**Résumé** – **La bipédie d'*Orrorin tugenensis* révélée par le fémur.** Trois fragments de fémurs d'*Orrorin tugenensis*, un hominidé de 6 Ma provenant de la Formation de Lukeino au Kenya, présentent plusieurs caractères qui suggèrent que ce dernier était bipède. Des comparaisons détaillées avec l'homme moderne, des australopithèques et de grands singes africains actuels et du Miocène révèlent qu'*Orrorin* partage plusieurs caractères dérivés avec les australopithèques et *Homo*, mais aucun avec *Pan* et *Gorilla*. Au sein des Hominidés, *Orrorin* est plus proche morphologiquement des hommes modernes que des australopithèques. ***Pour citer cet article : M. Pickford et al., C. R. Palevol 1 (2002) 191–203.*** © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

**bipédie / Miocène supérieur / Tugen Hills / Kenya / *Orrorin tugenensis* / fémur**

## Version abrégée

### 1. Introduction

Des hominidés fossiles de 6 Ma ont été découverts dans quatre localités de la Formation de Lukeino, Kenya [28,29,31,37]. Parmi ceux-ci, trois spécimens fémoraux apportent des données importantes concernant la posture, la loco-motion, la systématique et la position phylogénétique d'*Orrorin*. Le spécimen, géologiquement le plus vieux, a été récolté à Aragai à la base de la section, dans un niveau à polarité normale (intervalle C3An.1n), dont l'âge est estimé à 6,05 Ma [46], 6,06 Ma [4] ou 6,14 Ma [6]. Les deux autres fémurs proviennent de Kapsomin, de sédiments proches de la base de l'intervalle de polarité inverse succédant à la précédente [31] et dont l'âge est de 5,83 Ma [4,46] ou de 5,89 Ma [6]. Ces

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dates sont en accord avec les datations radio-isotopiques réalisées sur les trachytes sous-jacents de Kabarnet (6,09 ± 0,14 Ma) et les sills de Rormuch, intrusifs dans la Formation de Lukeino, vieux de 5,80 ± 0,22 Ma environ [28,31] et situés au-dessus des niveaux ayant livré les fémurs.

La bipédie d'*Orrorin* a été mise en doute par des auteurs qui n'avaient vu ni les moulages, ni les originaux des fossiles et mal présenté nos résultats précédents [16,18,37,38], mais d'autres, après examen des pièces, ont confirmé la bipédie d'*Orrorin* [8,16]. Nous présentons ici toute une série de caractères qui permettent d'affirmer que ce dernier était bipède.

## 2. Les spécimens

Les trois fragments fémoraux sont des parties proximales. BAR 1002'00 est un fémur gauche d'un jeune adulte presque complet, dont la tête est conservée. BAR 1003'00 est un fémur gauche dont la tête, le grand trochanter et la crête intertrochantérienne ne sont pas préservés, mais qui possède un petit trochanter. BAR 1215'00 est un fémur droit sans tête, ni grand trochanter.

## 3. Descriptions anatomiques

Le fémur BAR 1002'00 étant le plus complet, les descriptions anatomiques sont, pour la plupart, basées sur ce spécimen.

### 3.1. Vue antérieure

En raison des dommages subis par le grand trochanter sur les trois fragments fémoraux, il est difficile de préciser la forme exacte ou même le développement du tubercule fémoral. Toutefois, sur BAR 1002'00, la base de ce dernier est conservée. Le tubercule s'unit proximomédialement au grand trochanter. Sa morphologie se rapproche de celle de l'homme et diffère de celle du chimpanzé, chez qui le tubercule est généralement absent ou très faiblement développé [22,24].

La ligne intertrochantérienne est présente, mais peu marquée chez *Orrorin* (palpable et plus claire en lumière rasante), différant ainsi des grands singes miocènes et actuels chez qui elle est absente. Chez l'homme, elle reçoit le ligament ilio-fémoral très fort, stabilisateur passif de la hanche, nécessaire dans le maintien de la posture [1]. Chez BAR 1002'00, la ligne intertrochantérienne s'étend plus loin sur le col que chez l'homme ou les australopithèques (AL 288.1, AL 333.95), mais ressemble à ce que l'on observe chez les Paranthropes SK 82 et SK 97 de Swartkrans en Afrique du Sud [1,41].

Chez les trois spécimens d'*Orrorin*, le petit trochanter, bien développé, fait saillie médialement (Fig. 1A), alors que, chez les australopithèques, il est généralement projeté postérieurement et non visible en vue antérieure (Fig. 1B). Le fémur d'*Orrorin* diffère de ceux de AL 288.1 et de Maka par l'absence de gouttière au niveau de la fusion de la partie inférieure de l'apophyse trochantérienne et de la diaphyse [23,47].

Le col fémoral est long, à la différence de celui des grands singes africains actuels et miocènes [3,15,19,21,25,36,44], et ressemble à celui des australopithèques et de l'homme. Toutefois, on ne peut estimer sa longueur exacte, puisque le grand trochanter est érodé.

Par rapport à la diaphyse, la tête fémorale est plus grande chez *Orrorin* que chez les australopithèques [30] (Fig. 1), le rapprochant ainsi de la morphologie humaine.

Le grand trochanter n'étant préservé sur aucun des fémurs, on ne peut donner d'estimations très précises de la profondeur ou de la longueur de l'encoche supérieure (morphologie du bord supérieur du col fémoral), mais on peut donner des mesures minimales (longueur de 20 mm environ et profondeur de 12,5 mm à peu près) et une idée générale de sa forme. Cette encoche est allongée et peu profonde, comme chez les australopithèques et chez l'homme, alors qu'elle est profonde et étroite chez les grands singes africains actuels et fossiles.

### 3.2. Vue postérieure

La tubérosité glutéale allongée proximo-distalement s'élève dans une crête à la surface rugueuse. Elle se fusionne distalement avec une longue crête, qui se termine à la base de la diaphyse. La partie proximale de la tubérosité est beaucoup plus gonflée que ce n'est généralement le cas chez l'homme, mais se distingue de celle des chimpanzés, tout en se rapprochant de la morphologie d'*Ugandapithecus*. La disposition des attaches musculaires de cette région révèle une différence fondamentale de la musculature de la cuisse et de la hanche entre l'homme et le chimpanzé ; ainsi, chez ce dernier, on observe un renforcement spiral latéral entre les gouttières du *m. vastus lateralis* et du *m. gluteus maximus*, tandis que la tubérosité glutéale est absente [24].

Le petit trochanter est projeté médialement (Fig. 1C), plus fortement que chez les australopithèques. L'insertion du muscle ilio-psoas ne se prolonge pas sur la surface inférieure du col, comme c'est le cas chez le chimpanzé et le gibbon [3]. La ligne pectinée est nettement marquée. La ligne spirale, donnant insertion au *m. vastus medialis* est présente chez *Orrorin* ; sa morphologie est proche de celle de l'homme [14], partant bien au-dessous du petit trochanter avant de rejoindre la *linea aspera*. En revanche, chez les australopithèques, cette ligne est issue de ce dernier [24,47] (Fig. 1D).

La crête intertrochantérienne, basse, nettement visible chez BAR 1002'00, se présente comme une dépression en selle, placée entre les deux trochanters (Fig. 1C2). Une crête aussi basse est rarement observée chez l'homme ou le chimpanzé. Celle d'*Orrorin*, presque orthogonale au long axe du col fémoral, rappelle celle des australopithèques (Fig. 1C2).

La gouttière du *m. obturator externus* est bien visible chez BAR 1002'00 (Fig. 1C2) et BAR 1003'00. Le *m. obturator externus* est un adducteur, un fléchisseur et un rotateur externe de la cuisse ; la présence d'une gouttière suggère l'extension complète du fémur [10,30] et témoigne de l'extension habituelle de la hanche pendant les postures ou la locomotion bipèdes [10,22]. On la retrouve chez l'homme actuel [45] et les hominidés plio-pléistocènes [10–12,23,30,43]. Sa présence chez d'autres primates indi-

querait une bipédie fréquente [19,40,42]. Elle est générale-ment absente chez les grands singes.

### 3.3. Vue latérale

La diaphyse fémorale d'*Orrorin* est courbe, à convexité antérieure du haut vers le bas (Fig. 1E et I). Cette morpho-logie rappelle celle des hommes actuels et fossiles [12] et diffère de celle des grands singes africains, chez qui elle est rectiligne.

Sous le grand trochanter, le fémur d'*Orrorin* ne présente, ni le pilastre spiral, ni les gouttières spirales obliques (des *m. vastus lateralis* et *gluteus maximus*) qui lui sont associées et sont typiques de *Pan* [24]. Au contraire, la présence d'une tubérosité glutéale verticale, qui se prolonge dans une crête basse le long de la diaphyse, rappelle la morphologie humaine.

La fosse hypotrochantérienne se présente comme une surface plate élargie, bordée par la crête issue de la tubérosité glutéale, se rapprochant ainsi plus de la morphologie humaine (plus profonde) que de celle des chimpanzés.

### 3.4. Vue médiale

La position et l'orientation du petit trochanter sont varia-bles chez l'homme. Cette structure peut être placée plus médialement ou plus postérieurement selon les populations. Lovejoy et al. [24] indiquent que sa position chez l'homme est liée au degré d'antéversion de la diaphyse et expliquent ainsi la position postérieure observée chez les australopithè-ques. Mais rien ne prouve que la projection postérieure des australopithèques et de certains humains soit homologue, puisque certains grands singes du Miocène inférieur (*Ugan-dapithecus* et *Afropithecus*) ont un petit trochanter orienté médialement. Toutefois, chez *Orrorin*, le bord médial qui supporte le petit trochanter n'est pas perpendiculaire à la surface antérieure du fémur.

### 3.5. Vue supérieure

La fossette digitale, présente dans les trois fémurs d'*Orro-rin*, se rétrécit fortement vers l'insertion du *m. obturator externus*, tandis qu'il n'y a aucun signe d'une profonde dépression dans la diaphyse, comme c'est le cas chez les chimpanzés (Fig. 1C2 et G). Elle se rapproche des morpho-logies de l'homme et des australopithèques.

La tête fémorale est presque sphérique (32, 1 mm × 31,7 mm). Elle est décalée antérieurement par rap-port au col (Fig. 1G). Même si l'orientation de la tête est variable chez les grands singes et chez l'homme [2], le degré de torsion antérieure présent chez *Orrorin* sort largement de la variation observée chez les premiers.

Sur BAR 1002'00, la *fovea capitis* est située à la partie la plus médiale de la tête, dans le prolongement du bord supérieur du col fémoral (et juste sous la ligne moyenne du col en vue antérieure), qui est davantage comprimé antéro-postérieurement (Fig. 2) que sur AL 288.1. *Proconsul nyan-zae* présente aussi une légère compression [44], mais elle est

bien moins marquée que chez les hominidés. Cette morpho-logie est probablement liée au fait que, chez les bipèdes, le poids corporel est transféré au sol par l'articulation de la hanche, tandis que, chez les quadrupèdes, le poids est transmis à la fois par les membres antérieurs et postérieurs.

La section transversale sous le petit trochanter est presque rectangulaire chez *Orrorin*, ce qui confirme la platymérie du fémur, ce que l'on observe également chez les Paranthropes sud-africains et certains hominoïdes miocènes. La platymérie pourrait donc être considérée comme un caractère plésiomor-phe des hominoïdes et non pas comme un dérivé humain.

### 3.6. Morphologie interne

Les coupes tomodensitométriques réalisées sur les fémurs d'*Orrorin* révèlent une distribution asymétrique de la corti-cale plus épaisse à la partie inférieure qu'à la supérieure (Fig. 2). Comme l'ont montré Ohman et al. [27] dans leur étude tomodensitométrique de 35 fémurs d'hominoïdes, « tout au long du col fémoral, *H. sapiens* présente un os cortical mince à la partie supérieure et un os cortical épais à la partie inférieure qui s'épaissit distalement. En revanche, l'os corti-cal dans le col fémoral des chimpanzés montre une répari-tion plus homogène : il est plus régulièrement épais dans toutes les directions et l'épaississement de l'os cortical à la partie supérieure est encore plus marqué distalement. Comme le col fémoral se comporte comme une poutre en porte-à-faux, son ancrage à la jonction col-diaphyse est soumise aux contraintes de torsion les plus fortes ; c'est donc cette région qui est la plus intéressante biomécaniquement pour étudier les réponses aux contraintes. La distribution de l'os cortical chez les grands singes africains montre une plus grande variation des conditions de charge, en relation avec un répertoire locomoteur plus varié. La distribution d'os cortical chez les hominidés répond à un mode de charge plus stéréotypé imposé par une bipédie habituelle. » Pour ce caractère, *Orrorin* se rapproche des hommes et des austral-pithèques, et diffère fortement des grands singes africains. Ce caractère rappelle les hommes et les australopithèques.

## 4. Discussion et conclusion

Sur son fémur, *Orrorin* ne présente aucun des caractères dérivés de grand singe africain, comme la morphologie de la fosse trochantérienne. En revanche, il partage avec ces derniers des caractères plésiomorphes comme la platymérie et la position et le développement de la ligne spirale sous le petit trochanter.

En revanche, de nombreux caractères dérivés sont partagés avec les hominidés anciens et l'homme, comme la présence d'une gouttière du *m. obturator externus*, un col fémoral allongé, un col fémoral fortement aplati antéro-postérieurement, une dépression supérieure peu profonde au-dessus du col fémoral, une tubérosité glutéale bien déve-loppée, qui fusionne avec la crête qui court le long de la diaphyse postérieurement et vers le bas, et une distribution asymétrique du cortex du col fémoral.

*Orrorin* est donc un Hominidae sensu stricto qui doit avoir été bipède fréquent et orthograde, même si les différences

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mineures observées avec l'homme suggèrent qu'*Orrorin* n'ait pas été complètement humain dans sa locomotion. La morphologie de l'extrémité distale humérale et la courbure de la phalange indiquent qu'il était capable de grimper aux arbres, comme l'étaient les australopithèques [32,33].

Au sens systématique strict, *Orrorin* est un Hominidae. Pour plusieurs caractères, il est plus proche de l'homme que des Australopithèques ; ceci confirmerait l'idée que les Australopithecinae ne seraient pas des ancêtres de l'homme [9,32,37].

## 1. Introduction

Fossils of the 6 Ma hominoid *Orrorin tugenensis* were recovered from four localities in the Lukeino Formation, eastern foothills of the Tugen Hills, Baringo District, Kenya [28–29,31,37]. There are three femoral fragments in the sample that form the subject of this paper on account of their importance for understanding the posture, locomotion and systematic and phylogenetic position of *Orrorin*.

The geologically oldest femoral fragment was collected at Aragai, which is in the lowermost part of the Lukeino Formation [31], in normally magnetised sediments near the base of polarity interval C3An.1n, the base of which is estimated to be 6.05 Ma [46], 6.06 Ma [4] or 6.14 Ma [6]. The other two femoral specimens are from Kapsomin, in reversely magnetised sediments that are close to the base of the succeeding reversed polarity interval, the age of which is estimated to be 5.83 Ma [4,46] or 5.89 Ma [6]. These palaeomagnetic age estimates accord with radio-isotopic age determinations on the underlying Kabarnet Trachytes (ca 6.09 ± 0.14 Ma), and the overlying Rormuch Sills, which intruded the Lukeino Formation and which are aged ca 5.80 ± 0.22 Ma [28,31].

Haile-Selassie [18] and others [28,16], who have not seen the original fossils or casts, expressed doubts that *Orrorin tugenensis* was bipedal, but Clarke [8], having seen casts of the fossils, is in agreement with us that it was a biped.

In this paper, we compare the femora of *Orrorin* with those of fossil and extant hominids and African apes, including some Miocene forms.

## 2. The specimens

There are three fragments of hominid proximal femur from the Lukeino Formation. BAR 1002'00, a left femur, is the most complete and retains the head. The greater trochanter has been badly chewed and there is some residual distortion between the three main fragments that were slightly separated from each other prior fossilisation. The shaft is preserved for about 180 mm below the base of the greater trochanter, so it is missing approximately the distal third of the bone. BAR 1002'00

is a young adult, as revealed by visible traces of the suture between the head and the neck. Its gender is unknown.

BAR 1003'00 is a proximal left femur lacking the head, the greater trochanter and the intertrochanteric crest, but the lesser trochanter is well preserved. There are three puncture marks on the proximal surface disposed in a curved line parallel to the chewed edges of the greater trochanter. These appear to have been made by a carnivore rather than a crocodile. The shaft is preserved for a distance of 120 mm below the base of the greater trochanter, and we estimate that approximately the distal half of the bone is missing.

BAR 1215'00 is the proximal end of a right femur lacking the head and greater trochanter. The shaft is preserved for only 20 mm below the base of the greater trochanter. The surface of this specimen is roughened due to the impression of sand grains into the surface of the bone.

## 3. Anatomical descriptions

BAR 1002'00, being the most complete of the three specimens, forms the main focus of this paper, but we note that all three specimens from Lukeino are similar to each other except in size and robusticity. BAR 1003'00 is the largest and most robust, perhaps because it was a fully adult male (Fig. 1A and B).

### 3.1. Anterior view

#### 3.1.1. Femoral tubercle

Damage to the greater trochanter in all three specimens includes loss of most or all of the femoral tubercle, but in BAR 1002'00 its base is present, but nothing can be said about its shape or extent. It blends into the greater trochanter proximo-medially, in this respect being similar to other hominid femora, and different from Miocene hominoids such as *Ugandapithecus* and extant African apes, in which the tubercle is either absent or is not well developed [22,24]. This feature could be a hominid apomorphy, and is likely related to locomotion.

#### 3.1.2. Intertrochanteric line

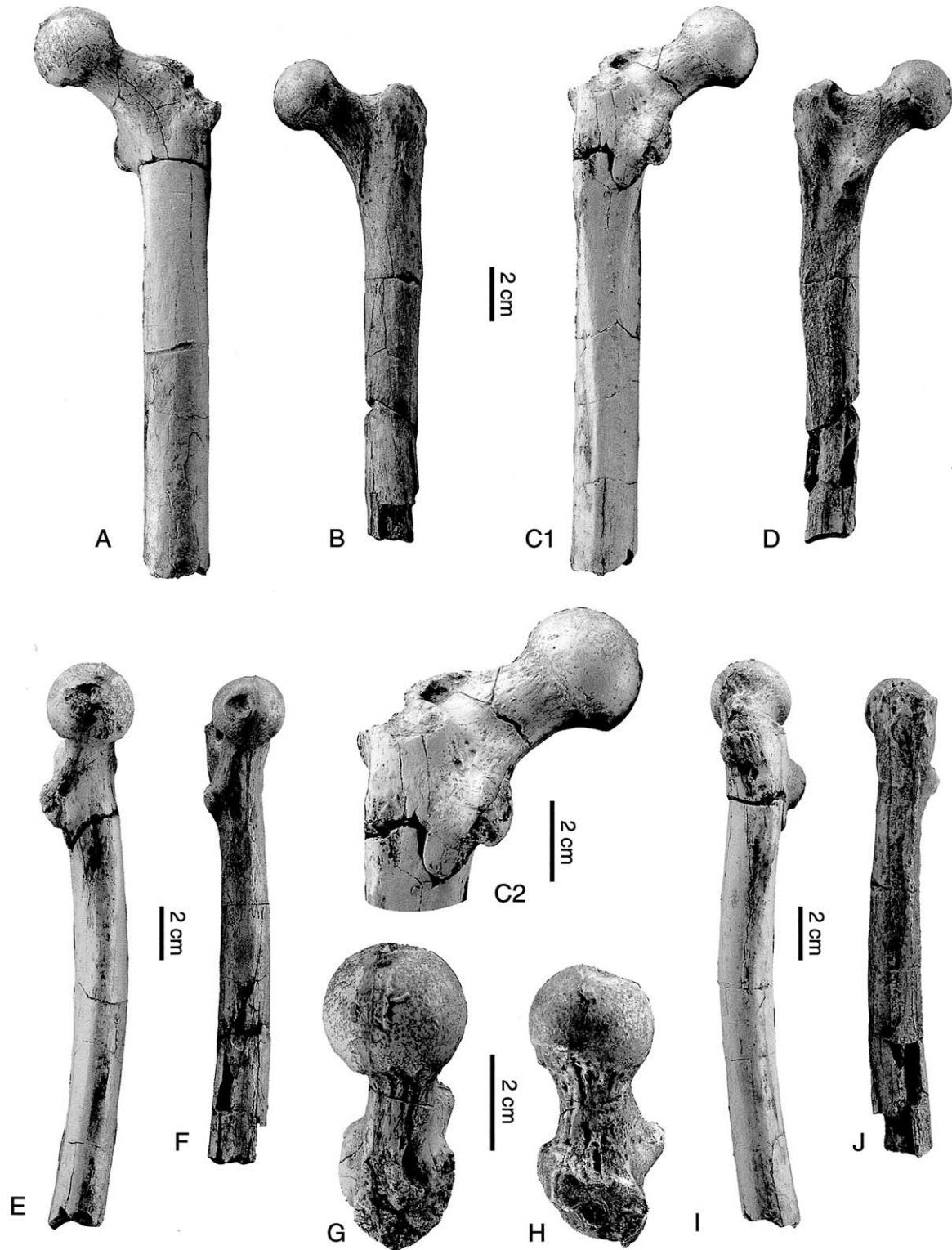The intertrochanteric line is present but has a low relief in *Orrorin*. It is palpable and clearly visible in

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Fig. 1. Vues des moulages du fémur proximal gauche de BAR 1002'00, *Orrorin tugenensis* (**A**, **C**, **E**, **G**, **I**) et AL 288.1, *Australopithecus antiquus* (**B**, **D**, **F**, **H**, **J**) montrant la morphologie externe de l'os. **A**, **B** : vue antérieure ; **C**, **D** : vue postérieure (C2 élargie pour montrer le trajet et le développement de la gouttière du *m. obturator externus*) ; **E**, **F** : vue médiale; **G**, **H** : vue supérieure ; **I**, **J** : vue latérale.

Fig. 1. Views of casts of BAR 1002'00, *Orrorin tugenensis* (**A**, **C**, **E**, **G**, **I**) and AL 288–1 *Australopithecus antiquus* (**B**, **D**, **F**, **H**, **J**), proximal left femora showing external morphology of the bone. **A**, **B**: anterior view; **C**, **D**: posterior view (C2 enlargement to show the course and extent of the *obturator externus* groove); **E**, **F**: medial view; **G**, **H**: superior view; **I**, **J**: lateral view.

slanting light. In this, it differs from extant and Miocene African apes, in which it is absent. The anterior part of the intertrochanteric line, which is the zone of insertion of the iliofemoral ligament, the function of which is to maintain the upright stance, is strongly expressed in humans [1]. In BAR 1002'00, the intertrochanteric line penetrates further onto the neck than it does in humans or australopithecines (AL 288–1), a morphology that also occurs in SK 82 and SK 97 from Swartkrans, South Africa, and in AL 333–95 [1,41].

In BAR 1002'00 and 1003'00, there is a swelling quite low on the anterior surface, which might be a continuation of the intertrochanteric line. In AL 288–1 it also extends quite low. The basal part of the intertrochanteric line is the zone of insertion of the pubofemoral ligament and part of the iliofemoral ligament. The pubofemoral ligament inserts onto the horizontal ramus of the pubis. According to Aiello and Dean [1] the superior pubic ramus in these early hominids is relatively longer than in modern humans and lies in a different angular relationship to both the ilium and the ischium [5]. This morphology suggests that *Orrorin* might have possessed a pubis in which the horizontal ramus was morphologically close to that of australopithecines. In SK 97 and SK 82, the intertrochanteric line continues as small distal crests. *Orrorin* does not possess such crests but has a low swelling which fades out distally.

### 3.1.3. Lesser trochanter position

In *Orrorin*, the lesser trochanter is medially salient in all three individuals (Fig. 1A). In australopithecines, the lesser trochanter is usually posteriorly projecting, and is not visible in anterior view (Fig. 1B). It is well developed in all the specimens from Lukeino, its extremity is smooth and the cortex appears to be dense. It is most strongly developed in BAR 1003'00, and its anterior edge forms a lip that overhangs its base. A similar lip is present in BAR 1002'00. The medial extremity of the lesser trochanter is damaged in the Aragai specimen (BAR 1215'00), but, in its preserved part, it conforms with the two specimens from Kapsomin. It differs from the Maka femur and that of AL 288–1 in not having a groove at the level of fusion between the lower part of the trochanteric apophysis and the diaphysis [23,47].

### 3.1.4. Femoral neck length

BAR 1002'00 is the only specimen with the neck entirely preserved. About half of it is preserved in BAR 1003'00 and only its base in the Aragai specimen. The neck is elongated when compared to those of recent African apes and is closer in this respect to australopithecines and humans. It is longer than in any

of the Miocene hominoids: *Ugandapithecus* [36], *Proconsul* [3,44], *Afropithecus* [15], *Nacholapithecus* [26], *Kenyapithecus africanus* [21], *Dryopithecus* [25] and *Oreopithecus* [19]. We conclude that a greatly elongated femoral neck such as occurs in *Orrorin* represents an apomorphic condition among hominoids, and that functionally it is related to bipedal locomotion and upright stance with the femur being habitually hyperextended. It is thus a defining character of Hominidae in the strict sense (i.e. excluding African and Asian apes).

### 3.1.5. Size of femoral head

The femoral head in *Orrorin* is larger relative to shaft diameter than it is in AL 288–1 and other australopithecines and great apes. In this feature, *Orrorin* is closer to the human condition than it is to the ape or australopithecine one. However, because there is some debate about the value of this character for determining relationships or locomotor repertoire in hominids [30,43], we do not give it any weight in the conclusions of this paper.

### 3.1.6. Shape and depth of superior notch

Because the greater trochanter is missing in all three Lukeino hominid femora, we cannot provide accurate estimates of the depth or length of the superior notch (above the femoral neck and between the femoral head and the greater trochanter). However, we can obtain minimum measurements (length 20+ mm, depth ca 12.5 mm), and thus an idea of its shape. The superior notch of the femur in *Orrorin* is of the hominid type, and diverges greatly from the African ape and Miocene hominoid model. This is not surprising, because the shape of the superior notch is related to the length of the femoral neck, the shallow elongated notch occurring in species in which the femoral neck is long, and a short, deep notch in species with shorter femoral necks.

## 3.2. Posterior view

See Fig. 1C1, C2 and D.

### 3.2.1. Gluteal tuberosity

The gluteal tuberosity is sometimes referred to as the third trochanter [24], but we question its homology to this structure in other primates. The gluteal tuberosity is best preserved in BAR 1002'00 (Fig. 1I), but it is also present but damaged in BAR 1003'00. In the Aragai specimen, it is not clearly expressed due to breakage, but part of it is nevertheless visible as a swelling below and posterior to the base of the greater trochanter. In the Kapsomin specimens, it is proximo-distally elongated

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and raised into a ridge with a rugose surface. Distally it coalesces with a long crest that extends to the distal extremity of the preserved part of the shaft. The proximal part of the tuberosity is swollen more than is usual in humans. In South African *Paranthropus*, this part is damaged, but appears to form a more or less vertical crest, and is thus quite similar to *Orrorin*. The distal part forms an elongated swelling.

In the morphology of the gluteal tuberosity and its coalescence with the distally leading crest, *Orrorin* is unlike any of the extant African apes and Miocene hominoids (save in some aspects *Ugandapithecus* [17]), and is closer to humans and australopithecines. In chimpanzees, for example, there is a lateral spiral pilaster between the grooves for insertion of the *vastus lateralis* and *gluteus maximus* and there is no gluteal tuberosity. As pointed out by Lovejoy et al., [24] and Stern and Larson [39], the variation in muscle attachments in this area of the femur reveals a fundamental difference between hip and thigh musculature in apes and humans, which almost certainly relate to the major postural and locomotor repertoire of the hominoids involved – quadrupedalism and semi-orthograde posture in African apes, and bipedalism and fully orthograde posture in humans and australopithecines. *Orrorin* is clearly more human-like and australopithecine-like in the morphology of the gluteal tuberosity and the regions surrounding it, from which we deduce that it was probably bipedal and orthograde, although in ways that were somewhat different from australopithecines and modern humans.

### 3.2.2. Position of lesser trochanter

In posterior view, the lesser trochanter is medially projecting (Fig. 1C), more than is usual in australopithecines (Fig. 1D) and in those extant humans that possess marked femoral shaft anteversion (mainly from the New World) in which the lesser trochanter projects posteriorly. In posterior view, the base of the lesser trochanter of *Orrorin* is seen to have several elongated but low and slightly sinuous ridges leading towards the base of the greater trochanter (i.e. supero-laterally). The extremity of the lesser trochanter is well separated from the neck, as in humans, gorillas and *Pongo*, and the insertion of the ilio-psoas muscle does not prolong onto the inferior surface of the neck as it does in chimpanzees and gibbons [3].

### 3.2.3. Lines at base of lesser trochanter (pectineal and spiral lines)

In the *Orrorin* femora, the pectineal line is clearly marked. The spiral line is the insertion of the *vastus medialis* muscle. The spiral line that departs latero-distally from the area below and medial to the lesser trochanter to join the *linea aspera* in humans is present in *Orrorin*, but it is located some distance below the base of the trochanter, as is usually the case in humans [14]. In AL 288–1 (Fig. 1D) and the Maka femur [24,47], this line cuts into the base of the lesser trochanter, forming a prominent groove in its inferior surface and this is a significant difference from *Orrorin*. A similar curved line occurs in chimpanzees, but there is no associated groove at the base of the trochanteric apophysis. The main difference between *Orrorin* and humans is that, in its distal portion, the spiral line does not closely approach the crest that descends from the third trochanter, thereby not forming a high relief *linea aspera*, as in humans. As it is, the closest approach is 6 mm in BAR 1002'00 some 100 mm below the third trochanter.

### 3.2.4. Intertrochanteric crest

In *Orrorin*, the intertrochanteric crest is clearly visible in BAR 1002'00, but between the two trochanters it has lower relief than is usually the case in humans, there being a saddle shaped depression between the bases of the greater and lesser trochanters with virtually no overhang of the intertrochanteric crest superiorly, although there are some pits in the surface of the bone immediately superior to the margin of the crest (Fig. 1C2). As a result the sub-trochanteric fossa of *Orrorin* is weak, as in South African *Paranthropus*. In humans, the crest between the two trochanters is continuous and superiorly it overhangs the sub-trochanteric fossa. This saddle shaped depression in the intertrochanteric crest is variably developed in humans and chimpanzees, but it is seldom as low as it is in *Orrorin*. Despite damage to BAR 1003'00 and BAR 1215'00, it is possible to see that the saddle shaped depression is present in all three femora from Lukeino, and it is presumably a constant feature of the species. The intertrochanteric crest of *Orrorin* is almost at a right angle relative to the long axis of the femoral neck (Fig. 1C2). This morphology recalls the pattern seen in australopithecines.

### 3.2.5. Obturator externus groove

An *obturator externus* groove is clearly visible in posterior views of BAR 1002'00 (Fig. 1C2) and BAR 1003'00. The surface of the bone in the Aragai specimen is not well enough preserved to demonstrate the presence of the groove.

In BAR 1002'00, from the fossa where the *obturator externus* attaches to the femur, the groove leads medially across the lower part of the femoral neck to terminate at its inferior margin. It is about 5 mm wide (proximo-distally) and some 25 mm long (latero-medially). There is no swelling or tubercle on the neck

superior to the groove on its medial end. The groove is highly polished where it emerges from the fossa and it diminishes slightly in depth and polish towards its medial end.

The *obturator externus* is an adductor, flexor and external rotator of the thigh. One of its functions is to shorten the distance between the pelvis and the femur thereby steadying the hip joint. Day [10] and Robinson [30] suggest that the groove is indicative of full extension of the femur. The groove is caused by pressure of the *obturator externus* tendon onto the back of the femoral neck, and has been taken to be a sign of habitual extension of the hip joint either during posture or in locomotion [10,22]. Similar grooves exist in other Plio-Pleistocene hominids such as OH 20 from Tanzania [10], SK 82 and SK 97 from South Africa [30] and other East African specimens [11–13,43], as well as AL 333–95 and AL 288–1 from Ethiopia [23], but are usually absent in apes. A similar groove occurs in a few other primates such as *Trachypithecus, Papio,* and *Ateles* [3]. Stern and Larson [39–40] and Stern and Susman [42] suggest that the groove can be indicative only of frequent bipedalism, even of a monkey-like or ape-like nature.

The presence of this groove in *Orrorin* reveals that the femur was habitually in a hyper-extended position. In humans, the *obturator externus* runs from the posterior side of the femur to insert onto the anterior part of the pelvis [45]. When the femur is hyper-extended (e.g., in a standing posture or when walking and running) the tendon presses onto the back of the femoral neck. The groove is not due to abrasion, but is caused by haversian remodelling of the bone. In humans hyper-extension of the femur occurs even in infants that are not yet walking. When the femur is flexed, as in humans sitting or in bending-over postures, the tendons do not press as much on the femoral neck. In habitually quadrupedal apes, such as chimpanzees and gorillas, there is little or no pressure from the *obturator externus* on the femoral neck, and thus no groove is produced. But even in bipedally walking chimpanzees, the femora are not as hyper-extended as they are in humans, and any pressure produced on the femoral neck by the *obturator externus* is weak compared to that in humans. The limited bipedal activity undertaken by chimpanzees is too transient to lead to remodelling of the outer contour of the bone, so no *obturator externus* groove occurs in this species.

Stern and Susman [41] considered that the grooves on AL 288–1 and AL 333–95 (*Australopithecus antiquus*) [23] were not true *obturator externus* grooves. They suggested that the presence of a small tubercle at the base of the femoral head gives the illusion of a short

obturator groove. There is no evidence of such a tubercle or bump in *Orrorin*, whereas in *Paranthropus* from South Africa there is a swelling but no tubercle between the groove and the femoral head. The occurrence of a groove in a few catarrhine and platyrrhine primates is due to convergence and not to phyletic relationship, and thus it does not weaken the value of this character for determining functional anatomy within the Hominoidea. We conclude that within the latter superfamily, the presence of a clear *obturator externus* groove is a derived character related to orthograde posture and bipedal locomotion. For this reason, the presence of an *obturator externus* groove in *Orrorin* is highly suggestive of habitually hyper-extended femora, and thus of orthograde posture and bipedal locomotion.

### 3.2.6. Quadrate tubercle

Only the inferior part of the base of the quadrate tubercle is preserved in *Orrorin*, but the tubercle itself has been damaged by carnivore chewing. We can say nothing about its morphology.

### 3.3. Lateral view

See Fig. 1I and J.

### 3.3.1. Proximo-distal curvature of the shaft

In lateral and medial views, it is evident that the femoral shaft of *Orrorin* is anteriorly convex from proximal to distal (Fig. 1E and I). Breakage accompanied by slight opening of the breaks on the anterior aspect of BAR 1002'00 exaggerates the impression of outbowing of the femoral shaft, but each undamaged segment shows distinct curvature, as does the shaft of the undamaged specimen BAR 1003'00. In *Gorilla* and *Pan*, the femoral shafts are more rectilinear in lateral view, whereas in extant and fossil *Homo* the shaft is anteriorly convex [12]. Thus, in this feature, *Orrorin* is closer morphologically to humans than to African apes.

### 3.3.2. Pilaster

In humans, the pilaster forms the anterolateral margin of the insertion for the *gluteus maximus*.

In lateral view of the *Orrorin* femora, the region below the greater trochanter shows no sign of a spiral pilaster and its associated obliquely spiral grooves for the *vastus lateralis* and *gluteus maximus* insertions that are typical of *Pan* [24]. Instead, there is a vertically oriented gluteal tuberosity, which coalesces into a low crest that descends the length of the femoral shaft. This crest starts descending the femoral shaft from the posterior part of the lateral surface just below the gluteal tuberosity and it gently curves onto the posterior surface as it descends. It is still well developed 179 mm

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below the proximal end of the gluteal tuberosity. The same morphology occurs in BAR 1003'00, but the crest is more robust and has a rugose surface. In *Orrorin*, therefore, the form and orientation of the pilaster is human-like and not at all ape-like.

### 3.3.3. Hypotrochanteric fossa

None of the *Orrorin* femora has a hypotrochanteric fossa as voluminous as those frequently developed in humans. It is more like an enlarged but low relief surface bordered by the crest that descends the shaft from the gluteal tuberosity. It is slightly excavated laterally and posteriorly, so that its border stands up as a low crest with concave sides, especially the posterior one. This morphology could well represent a precursor of the hypotrochanteric fossa that typifies human femora. In *Orrorin*, this crest is better developed than in *Pan*, and is closer to the human morphology.

## 3.4. Medial view

### Femoral anteversion

The position and orientation of the lesser trochanter is variable in humans, with some New World populations having it posteriorly oriented and Old World populations more medially located (Fig. 1E and F). Lovejoy et al. [24] suggest that the position of the lesser trochanter in humans is related to the degree of anteversion of the femoral shaft, which, according to them, relocates the lesser trochanter medialward. However, this explanation may not apply to australopithecines, and if not, then the posterior projection in australopithecines and some humans is not homologous. In the Miocene hominoids *Ugandapithecus* and *Afropithecus*, the lesser trochanter projects medially, but unlike *Ugandapithecus*, in *Orrorin* the medial border which supports the lesser trochanter does not form a right angle with the anterior surface of the femur.

## 3.5. Superior view

See Fig. 1G and H.

### 3.5.1. Position of the fovea capitis

The *fovea capitis* in BAR 1002'00 is located at the most medial part of the femoral head just below the midline of the femoral neck in anterior view and in line with the superior edge of the femoral neck in superior view (Fig. 1E and G).

### 3.5.2. Trochanteric cavity type

In *Orrorin*, the trochanteric fossa is preserved in all three femora. It narrows sharply towards the attachment of the *obturator externus* muscle and there is no sign of its deep penetration into the shaft as occurs in chimpanzees [24]. At most there is a shallow depression inferiorly (Fig. 1C2 and G). In this, *Orrorin* is close to humans and australopithecines (the fossa is as marked as it is in South African *Paranthropus*) and quite different from *Pan*. Deep penetration of the trochanteric cavity into the femoral shaft does not occur in *Gorilla* nor is it present in Miocene hominoids, and it is probable that its presence in chimpanzees represents an apomorphy of the genus. Being plesiomorphic among hominoids the morphology of the trochanteric cavity observed in *Orrorin* does not imply any special relationship between this genus and humans, but it does represent a difference from chimpanzees.

In the digital fossa, there is a slight depression anterior to the insertion of the *obturator externus*. Bacon [3] states that in humans and *Paranthropus*, the common tendon of the *obturator internus* and *gemelli* is located antero-superiorly to the *obturator externus* fossa, whereas in *Australopithecus* it is not. Even though the morphology is difficult to observe in *Orrorin*, it appears that in this feature this genus is more human-like than australopithecine-like.

### 3.5.3. Diameter of the femoral head

The femoral head is almost spherical, its greatest diameter being 32.1 mm and its least diameter 31.7 mm. The greatest diameter is proximo-distal (i.e. parallel to the shaft).

### 3.5.4. Anterior twist of femoral head

In superior view, the femoral head of *Orrorin* is posed on the femoral neck in such a way that more of the head is anterior to the neck than is posterior to it (Fig. 1G). This gives the impression that the head is deflected slightly anteriorly. For this reason, the groove round the base of the head is appreciably shallower on the posterior side than it is anteriorly. In African apes and Miocene hominoids, the head is usually posed almost symmetrically on the neck, or at least more symmetrically than in *Orrorin*. Even if the orientation of the head varies in humans and chimpanzees [2], the anterior twist in *Orrorin* is clearly outside the range of variation that occurs in the latter species. This feature may well be functionally related to bipedalism for the same reasons that the femoral neck is anteroposteriorly compressed and possesses an *obturator externus* groove, the three features comprising different parts of the same overall morphological package.

According to Jenkins [20] and Stern and Susman [41], in modern humans the articular margin of the head typically passes from antero-lateral to postero-medial, but in some specimens the margin is more or less
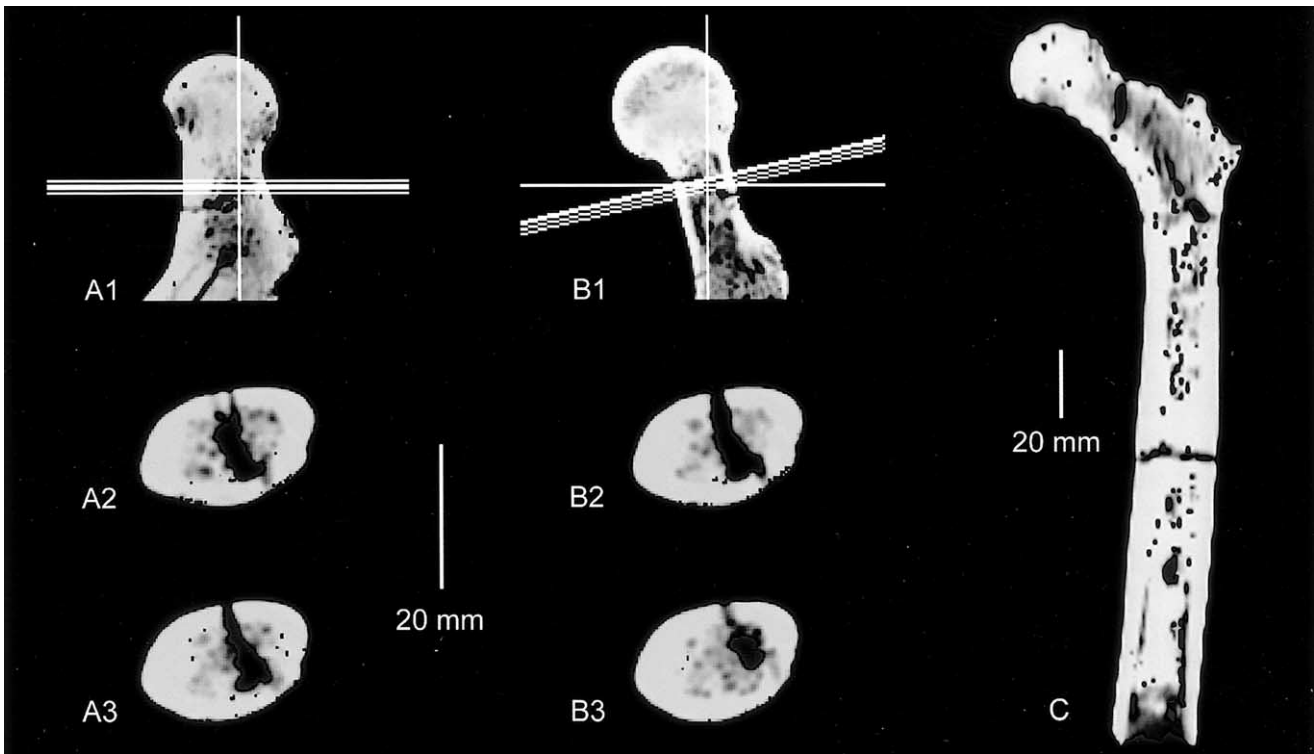
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Fig. 2. CT scans of the femoral neck of BAR 1002'00, proximal left femur, *Orrorin tugenensis*, showing the distribution of cortex in the neck and shaft. **A1**, **B1**: orientation of cross sections; **A2**, **A3**, **B2**, **B3**: cross sections of femoral neck; **C**: longitudinal section of femur.

Fig. 2. Coupes tomodensitométriques du col fémoral de BAR 1002'00, fémur proximal gauche d'*Orrorin tugenensis*, montrant la distribution de la corticale dans le col et la diaphyse. **A1**, **B1** : orientation des sections transversales; **A2**, **A3**, **B2**, **B3** : sections transversales du col fémoral; **C** : section longitudinale du fémur.

parallel to the long axis of the neck. In chimpanzees, the reverse is the case. In AL 288–1 it is less like modern humans, the articular margin of the femoral head passing from antero-medial to postero-lateral as in non-human hominoids [41] (Fig. 1H).

### 3.5.5. Femoral neck outline

The femoral neck in *Orrorin* is antero-posteriorly compressed (Fig. 2), even more so than in AL 288–1 (*Australopithecus antiquus*). In BAR 1002'00, the supero-inferior diameter is 22.5 mm compared to the antero-posterior diameter, which is 15.6 mm, whereas in BAR 1003'00 the homologous measures are 26.4+ mm by 16 mm. In BAR 1215'00 the measures are 24.6 mm by 15.2 mm. Australopithecines and humans have antero-posteriorly compressed femoral necks, but chimpanzees, gorillas, and orang-utans have almost circular or only slightly compressed femoral necks. *Proconsul nyanzae* has a slightly compressed femoral neck (anteroposterior diameter 15.2 mm, supero-inferior diameter 20.1 mm [44]) but not as greatly compressed as is usual in hominids. The functional meaning of this restructuring of the neck in

hominids is probably related to the fact that in bipeds the bulk of the body weight is transferred to the ground only through the hip joint, whereas in quadrupeds the transfer of body weight is shared between anterior and posterior limbs.

For two reasons, it is not coincidental that in hominids the presence of a flattened femoral neck correlates with the presence of a groove for the *obturator externus*. Firstly, the flattening of the neck effectively shortens the path that the *obturator externus* takes on its way from its insertion on the femur to its termination on the anterior part of the pelvis, and secondly, it reduces the effect of a convex obstacle from its path (the almost circular femoral neck that occurs in apes) that would not only impart a bend into the muscular system, but would lead to the creation of increased stresses in the *obturator externus* muscle where it passes over the femoral neck.

What it means phylogenetically, is that *Orrorin* shares with australopithecines and humans a restructured hip joint, of which antero-posterior compression of the femoral neck is just one aspect.

### 3.5.6. Transverse section below the lesser trochanter

The transverse section immediately below the lesser trochanter is medio-laterally expanded and there is a slight widening of the diaphysis linked to the flattening and to the strength of the gluteal tuberosity. In *Orrorin*, the section is rectangular with rounded corners, which makes the diaphysis platymeric (mediolateral diameter measured 3 cm below the base of the lesser trochanter is 25.5 mm, anteroposterior diameter is 21 mm) *Paranthropus* from South Africa is platymeric as are humans. Some Miocene hominoids such as *Ugandapithecus* [17] have flattened sections below the lesser trochanter. Platymeria of the femur may thus be a primitive feature within hominoids and not a derived condition of Hominidae as sometimes thought. The absence or weakness of platymeria in extant African apes may represent the derived condition among hominoids.

## 3.6. Internal morphology

### Cortex distribution in the femoral neck

CT scans of the *Orrorin* femora carried out at the Clinique Pasteur, Toulouse, reveal that the distribution of cortex in the femoral neck is asymmetric (Fig. 2). In BAR 1002'00, in which the neck is complete, the cortex is thickest inferiorly and thinnest superiorly. However, the cortex superiorly, anteriorly and posteriorly is relatively thicker than it is in humans, but appreciably thinner than it is in African apes. As shown by Ohman et al. [27] in their tomodensitometrical study of 35 hominoid femora: "Throughout the femoral neck *H. sapiens* displays thin superior cortical bone and inferior cortical bone that thickens distally. In marked contrast, cortical bone in the femoral neck of African apes is more uniformly thick in all directions, with even greater thickening of the superior cortical bone distally. Because the femoral neck acts as a cantilevered beam, its anchorage at the neck-shaft junction is subjected to the highest bending stresses and is the most biomechanically relevant region to inspect for response to stress. Cortical distribution in the African ape indicates much greater variation in loading conditions consistent with their more varied locomotor repertoire. Cortical distribution in hominids is a response to the more stereotypic loading pattern imposed by habitual bipedality." For this feature, *Orrorin* is closest to humans and australopithecines, and quite different from African apes.

In apes, the femoral neck is almost horizontal if the femur is oriented in its normal position during locomotion (i.e. with the distal femoral condyles held at the same horizontal level and the shaft almost vertical). In this configuration, body weight impinging vertically on the femoral head is transferred laterally along the neck before it passes down the almost vertical femoral shaft towards the knee. There are thus two marked angles in the bony link that transfers body weight from the pelvis to the knee, one between the femoral head and the neck, the second between the femoral neck and the shaft, the neck comprising the 'cantilever beam' of Lovejoy [22]. In this configuration, the cortex of the femoral neck has to be thick all round as tensional stresses are marked, especially along the superior surface of the neck.

In humans, in contrast, when the distal femoral condyles are oriented horizontal with respect to each other as in normal fully orthograde posture and bipedal locomotion, the femoral shaft lies at a marked angle from the vertical and the inferior part of the femoral neck is oriented almost vertically. Thus, in humans body weight is transferred from the pelvis to the femoral shaft by way of the femoral head through the neck without the two right angle bends that occurs in apes, but by a more direct path, admittedly slightly sinuous [7,27]. The biomechanical result of this is that femoral neck cortex is thickened inferiorly and reduced superiorly [22].

The pattern of distribution of femoral neck cortex in *Orrorin* is close to that of humans and australopithecines and radically different from that seen in chimpanzees and gorillas. It is not identical to that of humans and australopithecines, but is clearly much closer to these hominids than it is to that of apes. Because of the biomechanical implications, we deduce that the asymmetric distribution of femoral neck cortex in *Orrorin* provides good evidence that the femoral shaft was oriented at a marked angle in normal orthograde posture and locomotion, and thus that *Orrorin* was orthograde and that its main locomotor repertoire while on the ground consisted of bipedalism.

## 4. Discussion and conclusion

The femur of *Orrorin* shows a combination of plesiomorphic hominoid and apomorphic hominid features but no apomorphic ape-like features.

### 4.1. Ape-like features

*Orrorin* has no derived ape-like features such as the deeply penetrating trochanteric fossa that occurs in chimpanzees. Where it shares morphological features with apes, those features are plesiomorphic among hominoids, and often occur in humans and australopithecines as well. These include femoral platymeria and the position and course of the spiral line below the lesser trochanter.

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Platymeria is often taken to be a derived character in humans, because extant apes generally show little or no sign of it. However, the polarity of this character is not clear, because some Miocene apes such as *Ugandapithecus* [17] and *Proconsul nyanzae* [44] show a degree of platymeria. Whether it is homologous to that seen in humans remains to be determined. Medial projection of the lesser trochanter in *Orrorin* and Old World humans is plesiomorphic at the level of Hominoidea, as it also occurs in *Ugandapithecus* [36], *Proconsul* [3,44] and *Kenyapithecus africanus* [21] among other taxa. The posterior projection of the lesser trochanter seen in australopithecines appears to be a derived condition within Hominidae, although in humans it is part of the normal range of variation, albeit with a marked geographic distribution (Old World versus New World). A distinct gluteal tuberosity is present in *Ugandapithecus* but not in *Pan*, which indicates that its absence in the chimpanzee could represent a derived condition. What this reveals is that it is no longer permissible to study the origins of bipedalism without taking into account the functional anatomy of Miocene hominoids [34–35].

## 4.2. Human-like features

In contrast, *Orrorin* shares several apomorphic features with humans and some with australopithecines, including the presence of an *obturator externus* groove, elongated femoral neck, anteriorly twisted head (posterior twist in *Australopithecus*), antero-posteriorly compressed femoral neck, asymmetric distribution of cortex in the femoral neck, shallow superior notch, and a well developed gluteal tuberosity which coalesces vertically with the crest that descends the femoral shaft posteriorly. From this we deduce two things, firstly that *Orrorin* must be a hominid in the narrow sense of the term (i.e. excluding African apes), and secondly, that *Orrorin* must have been a habitual biped and orthograde. Comparison with australopithecines reveals that *Orrorin* had a slightly different adaptation to bipedalism from them, based on the orientation of the lesser trochanter (posterior in australopithecines, medially projecting in *Orrorin*), the orientation of the head on the neck (posterior twist in australopithecines, anterior twist in *Orrorin*), and on the size of the head relative to shaft diameter, which is greater in *Orrorin* than in australopithecines.

Considering the derived similarities between proximal femora of *Orrorin*, australopithecines and humans,

if it is argued, as some have done [38], that *Orrorin* was not a biped, and then the above listed features cannot be used to deduce bipedalism in australopithecines and humans either.

If, on the other hand, the above features are apomorphies of Hominidae and relate to locomotor functions, then the minor differences between femora of *Orrorin* and humans indicate that *Orrorin* was bipedal, but was probably not completely human-like in its locomotor pattern. However, we conclude from our study that *Orrorin* was better adapted for this kind of locomotion than any of the great apes are, be they Miocene or extant. Morphological differences from australopithecine femora are also apparent, in particular the position and orientation of the lesser trochanter and the location of the spiral line close to the lesser trochanter. *Orrorin*'s locomotion was thus not exactly like that of australopithecines either. Indeed, in its overall morphology, the femur of *Orrorin* appears to be closer to that of humans than to that of australopithecines.

From the above, we conclude that *Orrorin* was a habitual biped as shown by a suite of features in the proximal femur: moderate intertrochanteric line associated with a weak femoral tubercle, a large gluteal tuberosity and the osseous structure distal to this tuberosity, a precursor of the *linea aspera*, a shallow trochanteric fossa, the presence of a groove for the *obturator externus*, the distribution of cortex in the femoral neck, the sectional shape of the femoral neck, the size of the femoral head relative to shaft diameter, the orientation of femoral head on the neck, and the shallowness of the superior femoral notch. We infer that *Orrorin* was orthograde, even though we have no evidence of the sacrum or lower back.

Although *Orrorin* was bipedal, the morphology of its humeral shaft and the curvature of the manual phalanx, reveal that it was probably also capable of climbing trees, as were australopithecines [33].

In conclusion, from a systematic point of view *Orrorin* is a hominid sensu stricto, and in numerous features it is not chimp-like. In several features, *Orrorin* is closer to humans than australopithecines are which suggests that it may be more closely related to *Homo* than it is to *Australopithecus* and/or *Paranthropus*. If we are correct, then *Australopithecus* may represent a side branch in hominid evolution that became extinct without giving rise to *Homo*, a hypothesis that has already been suggested by Coppens [9] and Senut [32,37] among others.

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