

Human Palaeontology and Prehistory

Early hominid femora: The inside story

Tim D. White

*Human Evolution Research Center and Department of Integrative Biology, The University of California at Berkeley,
Berkeley, CA 94720-3160, USA*

Received 12 April 2005; accepted after revision 19 September 2005

Available online 01 December 2005

Written on invitation of the Editorial Board

Abstract

Paleontology allows exploration of evolutionary novelty in the deep past. But paleontological taxa are at risk of being inaccurately characterized by modern humans who are over-reliant on models taken from the comparatively rich but relatively evolved neontological world. The recent discovery of the earliest hominid femora from Kenya provides an opportunity to explore earliest hominid locomotion beyond the usual constraints of phylogenetic and functional models based rigidly on contemporary species. The full measure of this opportunity remains unrealized because the internal structure of the crucial fossil femora recovered has been inadequately explored and documented. One result is that phylogenetic schemes purporting to exclude all hominids except *Orrorin* from human ancestry are unsupported. Another result may be that earliest hominid locomotion has been inaccurately portrayed. **To cite this article:** *T.D. White, C. R. Palevol 5 (2006).*

© 2005 Académie des sciences. Published by Elsevier SAS. All rights reserved.

Résumé

L'histoire cachée du fémur des hominidés anciens. La paléontologie permet d'explorer dans le temps les innovations générées par l'évolution biologique, mais les taxons paléontologiques peuvent être décrits de façon inexacte par les hommes modernes. Ces derniers font trop souvent référence à des modèles basés sur des données néontologiques qui, plus abondantes que les données paléontologiques, diffèrent aussi par leur degré d'évolution, relativement plus avancé. La récente découverte au Kenya des plus anciens fémurs d'hominidés offre la possibilité d'examiner le mode de locomotion des premiers hominidés en s'affranchissant des contraintes habituelles liées aux modèles phylogénétiques et fonctionnels basés de manière rigide sur les espèces actuelles. Toutefois, il n'a pas été tiré partie de cette opportunité, la structure interne de ces spécimens cruciaux ayant été étudiée et décrite de façon inadéquate. En conséquence, les reconstructions phylogénétiques proposant d'exclure de la lignée conduisant à l'homme tous les hominidés, à l'exception d'*Orrorin*, ne sont pas étayées. De plus, il est probable que la locomotion des plus anciens hominidés ait été incorrectement appréhendée. **To cite this article:** *T.D. White, C. R. Palevol 5 (2006).*

© 2005 Académie des sciences. Published by Elsevier SAS. All rights reserved.

Keywords: Hominid; Femur; Miocene; Fossil; Paleontology; Africa, *Orrorin*; Locomotion

Mots clés : Hominidé ; Fémur ; Miocène ; Fossile ; Paléontologie ; Afrique ; *Orrorin* ; Locomotion

E-mail address: timwhite@Berkeley.edu (T.D. White).

Version française abrégée

Introduction

Le registre fossile du vivant dévoile les anatomies, les adaptations et les écologies passées. Une des contributions les plus précieuses de la paléontologie est l'utilisation de ce registre pour explorer les innovations générées par l'évolution dans des mondes aujourd'hui disparus. Toutefois, un mode alternatif d'interprétation de ce registre tyrannise la paléanthropologie tout comme d'autres sciences historiques. Ce mode se base sur la comparaison avec les données actuelles. En effet, si le présent éclaire le passé d'une multitude de façons, les riches données du monde actuel peuvent aussi compliquer la reconnaissance et l'analyse des innovations de l'évolution survenues dans le monde préhistorique. Un paléobiologiste imprudent peut facilement interpréter faussement les organismes anciens en utilisant des concepts inappropriés basés uniquement sur les formes et fonctions actuelles.

Par exemple, la dichotomie entre des locomotions « bipèdes » opposées aux locomotions « quadrupèdes » s'applique de façon satisfaisante aux hommes modernes et à leurs proches parents africains, les grands singes. Mais qu'en est-il des organismes éteints qui, situés à la base du clade hominidé, vécurent au cours du Miocène récent ? Cette dichotomie néontologique ne contribuerait-elle pas plutôt à masquer des innovations évolutives, documentées *uniquement* dans le registre fossile ? Il s'agit là d'un problème fondamental pour l'étude de l'origine et des premières phases de l'évolution des hominidés.

La mise au jour d'extrémités proximales de fémurs dans la formation de Lukeino (Tugen Hills, Kenya) en 2000 [17] était un événement crucial en paléanthropologie. Enfin, un élément clé de l'anatomie locomotrice d'un hominoïde du Miocène récent venait d'être découvert. En particulier, le fossile BAR 1002'00 était porteur de grands espoirs, étant donné l'importance du fémur proximal pour la locomotion, étant donné aussi la longue histoire des découvertes et interprétations de cet élément du squelette dans l'étude de l'évolution humaine.

Historique

L'histoire de l'analyse et de l'interprétation des fémurs d'hominidés anciens débuta en 1947 en Afrique du Sud. Dans les années 1960 et 1970, ces travaux se focalisèrent sur l'Afrique orientale. Avec les mises au jour d'un fémur d'hominidé sur le site A.L. 129 à Hadar en 1973, d'un squelette partiel (« Lucy ») à A.

L. 288 en 1974 et la découverte du site A.L. 333 l'année suivante, une mine d'informations concernant des hominidés encore plus anciens devint disponible. La publication de ces spécimens, seulement cinq années après leurs découvertes [9], fut à l'origine d'un vaste débat, toujours d'actualité, sur les aptitudes locomotrices des hominidés anciens. Le fémur proximal a une place particulièrement importante dans ce débat.

Brigitte Senut fut un des premiers chercheurs à proposer une interprétation fonctionnelle et phylogénétique des restes post-crâniens de Hadar. Senut a toujours prétendu que le genre *Homo* constituait une lignée phylogénétique ancienne. Pour elle, *Homo* était contemporain d'*Australopithecus*, tandis que, chez « Lucy », « the chimp-like elbow-joint morphology (probably convergently derived with *Hylobates*, *Pan*, and *Gorilla*, and not primitive) does not permit us to consider this hominid as a direct human ancestor » [23 (p. 193)].

En conséquence, Senut reléguait *Australopithecus* (incluant A.L. 288-1, « Lucy ») sur un rameau phylétique subsidiaire de l'évolution humaine. Cette position était celle du regretté Louis Leakey et a été défendue par son fils Richard (voir Pickford [16]). Senut s'y cramponna fermement tout au long des années 1980 et 1990. Elle ne changea pas d'avis, et au début du présent millénaire, elle proposa une « lignée *Praeanthropus-Homo* » proche de *Homo sapiens* et contemporaine d'*Australopithecus*, lignée sans descendants actuels [22].

Au cours des années 1980 et 1990, le débat sur la systématique et la locomotion des hominidés anciens se focalisa sur le matériel post-crânien de Hadar. Durant la saison de terrain 1981 dans le Moyen Aouache, un important fragment proximal de fémur fut rapporté à *A. afarensis*. Âgé d'environ 3,4 Ma, le spécimen MAK-VP-1/1 de Maka, Éthiopie, représenta jusqu'à récemment l'un des plus vieux fémurs proximaux connus. Au cours du printemps 1982, ce spécimen fut radiographié. Les résultats furent considérables. Publiées initialement en 1984 [3,26], ces données d'anatomie interne appuyaient fortement les interprétations basées auparavant sur la seule morphologie externe. À présent, pratiquement tous les chercheurs considèrent que le fémur proximal d'*Australopithecus* indique une forme de locomotion bipède.

Ardipithecus et Orrorin

Au cours des saisons de terrain 1992 et 1993, de nombreux restes crânio-dentaires et post-crâniens furent collectés à Aramis, Éthiopie, par notre équipe de recherche dans le Moyen Aouache. Ces restes, datés à environ 4,4 Ma, ont été attribués à un nouveau genre

et une nouvelle espèce d'hominidés (*Ardipithecus ramidus*), et interprétés comme étant ceux d'hominidés au sens cladistique du terme. Ils furent décrits de cette façon dans *Nature* en 1994 [27] (le nom de genre, initialement *Australopithecus*, fut modifié en *Ardipithecus* l'année suivante [28]).

Trois années plus tard, en 1997, des hominidés encore plus anciens furent découverts dans cette même région. Hailé-Sélassié et ses collègues commencèrent à collecter des restes principalement crânio-dentaires dans des dépôts du Miocène supérieur de la marge ouest du Moyen Aouache. Ils furent attribués au genre *Ardipithecus* en 2001 [7] et élevés au rang d'espèce en 2004 [8]. Au printemps 2005, le Moyen Aouache n'a toujours livré aucune tête ou col fémoral appartenant à *Ardipithecus ramidus* ou à son précurseur probable, *Ardipithecus kadabba*. En conséquence, l'ensemble de nos connaissances de l'anatomie de la tête et du col fémoraux des plus anciens hominidés provient des spécimens découverts au Kenya en 2000.

C'est en décembre 2000 que Brigitte Senut et Martin Pickford annoncèrent la découverte de ces nouveaux fossiles kenyans. Le spécimen BAR 1002'00 représentait le premier fémur proximal bien préservé d'un hominoïde fossile du Miocène récent. Pour cette raison, il était extrêmement important pour la compréhension de l'origine et des premières phases de l'évolution des hominidés. Ces fossiles furent d'abord décrits brièvement par Pickford et Senut dans le *South African Journal of Science* [17]. Ils y déclarèrent que « *the proximal femoral morphology of the Lukeino hominid is closer to that of humans than it is to that of Lucy* ». Cette conclusion était accompagnée par l'affirmation suivante : « *6 million years ago in Kenya, there was a bipedal hominid which was closer in size and morphology to extant humans than the much younger australopithecines and Ardipithecus ramidus* » [17 (p. 22)].

À la suite de ces premières annonces, les fémurs de Lukeino furent attribués à un nouveau genre et une nouvelle espèce, *Orrorin tugenensis*. En effet, ce nouveau genre fut diagnostiqué en partie sur l'allégation d'un fémur proximal « *more human-like than those of australopithecines or African apes* » [24 (p. 139)]. Dans cette publication [24], ces nouveaux fossiles kenyans du Miocène récent ont été interprétés comme ancestraux à la seule lignée du genre *Homo*. Senut et Pickford ont interprété à la fois *Australopithecus* et *Ardipithecus* comme des ramifications latérales de l'histoire de notre famille, figurant le premier comme un clade sans descendance et le second comme un chimpanzé ancestral [24 (Fig. 2, p. 142)].

Malheureusement, la description initiale de 2001 et l'analyse du genre *Orrorin* [24] est sujette à caution, à cause des nombreuses erreurs et confusions de la description de l'anatomie dentaire et post-crânienne. Étant donné ces déficiences, il était peu surprenant que de nombreux lecteurs s'avèrent peu convaincus par les premières hypothèses fonctionnelles et phylogénétiques formulées sur *Orrorin* par Senut et Pickford.

« *Orrorin* »: Questions et réponses

Dans la série de travaux et correspondances qui suivirent la découverte et l'annonce des fémurs attribués au genre *Orrorin*, j'ai fortement conseillé aux inventeurs de décrire l'anatomie interne du col fémoral. Les réponses à ces tentatives répétées visant la description de la distribution du cortex dans cette région anatomique furent décevantes et proprement ahurissantes. Toutefois, j'imaginai qu'une fois publiée par l'équipe d'inventeurs, la troisième description du spécimen révélerait ces informations.

La description et l'interprétation détaillées du fémur proximal d'*Australopithecus afarensis* de Maka, publiées en 2002 [12], constituent à ce jour l'analyse la plus exhaustive de cet élément chez un hominidé ancien. Ce travail, communiqué avant sa soumission aux inventeurs du genre *Orrorin*, montre très clairement que la distribution de l'os cortical dans le col du fémur proximal est une caractéristique cruciale pour interpréter les modes de locomotion chez les hominidés anciens [14]. En conséquence, lorsque Galik et ses collègues (incluant Senut et Pickford) publièrent *External and internal morphology of the BAR 1002'00 Orrorin tugenensis femur* dans *Science* en septembre 2004 [6], il fut extrêmement décevant de constater qu'aucune nouvelle donnée n'avait été obtenue sur la morphologie interne de ce fossile critique, et qu'aucune photographie, aucun dessin ou aucune radiographie conventionnelle n'avait été présenté(e).

De plus, bien que nous ayons invité pendant plusieurs années l'équipe découvreuse à fournir ces éléments cruciaux, l'article de *Science* offrait simplement des images scanners rectifiées – celles publiées dans les *Comptes rendus Palevol* en 2002 montraient le spécimen dans une orientation incorrecte. Comme nous l'avons signalé dans notre lettre à l'éditeur de *Science*, publiée le 11 février 2005, « *the adjusted results are still inadequate to determine whether the femoral neck's cortical thickness conforms to a human, intermediate, or chimpanzee pattern* ». Nous avons ainsi mis au défi l'équipe ayant découvert *Orrorin* de fournir « (i) *photographs, measurements, and drawings of its broken*

neck; (ii) conventional anteroposterior X-rays; and (iii) higher-resolution CT scans obtained with proper femoral orientation » [15 (p. 845)].

Les raisons pour lesquelles l'équipe ayant découvert *Orrorin* et ses collaborateurs refusent de publier une radiographie classique et une photographie classique du col fémoral re-décollé de BAR 1002'00 restent obscures, alors qu'il s'agit d'images très simples à réaliser en comparaison des images scanners, et que nous le leur avons conseillé à maintes reprises depuis 2001 (voir ci-dessus). Mystérieusement, Martin Pickford et Brigitte Senut ne faisaient pas partie des auteurs ayant répondu à notre dernière demande dans ce sens, cette fois publiée dans notre lettre de février 2005 adressée à *Science*. Leurs collègues américains ont répondu : « *it is our understanding that the initial studies were carried out under serious constraints of time and other resources...and we have made it clear that we plan to rescan and study the existing fossils if funds are made available* » [5 (p. 845)]. Cette réponse est, à nouveau, décevante, car nous espérions la publication de nouvelles données, et non pas de la réclame pour une demande de financement visant à obtenir des données attendues depuis longtemps.

L'histoire cachée du fémur des hominidés anciens... à suivre

La distribution de l'os cortical dans le col fémoral constitue une des sources d'information disponibles les plus importantes sur le mode de locomotion. Est-ce que l'hominidé ancien *Orrorin* pratiquait une bipédie similaire à celle de l'homme moderne et d'*Australopithecus*, ou une forme de locomotion originale et inconnue auparavant ? Les informations disponibles jusqu'ici plaident pour la deuxième hypothèse : la zone corticale visible au sommet du col fémoral de BAR 1002'00 sur les images scanners publiées semble différente. Mais « l'histoire cachée » de cette région anatomique clé de l'articulation pelvienne ne pourra être révélée avec précision et fiabilité sans de meilleures données. Pourquoi ces données n'ont-elles pas été rendues publiques, alors qu'il aurait simplement suffi de re-décoller le col du fémur, ou d'effectuer une simple radiographie antéro-postérieure classique ?

L'article de Galik et al. dans *Science* a été publié le 3 septembre 2004 [6]. Par un heureux hasard, la conférence interacadémique *Climats, cultures et sociétés aux temps préhistoriques, de l'apparition des Hominidés jusqu'au Néolithique* s'est déroulée à l'Académie des sciences à Paris juste dix jours après. Le Pr. Henry de Lumley m'a aimablement proposé de présenter une allo-

cution au cours de la deuxième session, intitulée : *Les premiers hominidés*. Grâce à la participation du Dr Brigitte Senut, co-découvreuse des fossiles attribués à *Orrorin*, cette session aurait pu être un forum idéal pour un échange productif de données et d'idées. Malheureusement, le Dr Senut présenta une fois de plus le même jeu de données ambigües. Ce faisant, elle laissa tous les participants dans l'expectative, sans informations sur ce que le fémur proximal des plus anciens hominidés cache en réalité.

Conclusion

La dernière décennie a été le théâtre d'avancées considérables dans la connaissance des plus anciens hominidés, grâce aux découvertes effectuées au Tchad, au Kenya et en Éthiopie. Il est clair que ces trois ensembles de fossiles représentent des hominidés cladistiques (par opposition aux chimpanzés et gorilles cladistiques). En effet, dans chacun de ces ensembles, des fossiles montrent des caractères dérivés exclusivement partagés avec des hominidés plus récents, tels qu'*Australopithecus*. Afin de savoir si les matériels provenant de ces trois pays représentent vraiment trois genres différents (*Ardipithecus*, *Orrorin* et *Sahelanthropus*), il sera nécessaire de découvrir de nouveaux fossiles [8].

Pour des raisons anatomiques et étant donné les faunes associées, il apparaît évident que ces premiers hominidés préféraient des habitats plus fermés que leurs descendants. Il est aussi clair qu'ils diffèrent de tous les grands singes actuels ou des hominidés décrits auparavant – ces plus anciens hominidés n'étaient, ni des humains, ni des chimpanzés. En conséquence, cataloguer ces fossiles dans des catégories préconçues de locomotions, d'espèces et de régimes alimentaires définies à partir du monde peu diversifié des hommes modernes et des grands singes résiduels ne peut que masquer l'originalité de ces restes de primates du Miocène récent.

L'anatomie externe des fémurs des Tugen Hills et celle de la phalange du pied du Moyen Aouache suggèrent ensembles qu'une forme de bipédie était pratiquée par ces plus anciens hominidés. S'agissait-il de la bipédie très évoluée d'*Australopithecus* ? Ce n'est en rien certain. En classant de force ces organismes dans des catégories étroitement préconçues, créées pour des organismes deux fois plus récents, et en accommodant ces nouvelles informations dans des constructions phylogénétiques vieilles de plusieurs décennies, nous sacrifions un apport que seule la paléontologie peut fournir à l'étude de nos origines et de notre évolution.

1. Paleontology's role in revealing novelty

The fossil record of life on earth reveals ancient anatomies, adaptations and ecologies. One of paleontology's most valuable contributions is the use of the fossil record to explore evolutionary novelty in all-but-vanished worlds.

Archaeologists who study prehistoric cultures know the danger of viewing the past through the prism of modern ethnohistorical observations. Archeologists call this tendency of the modern world to distort their interpretations of the past a "tyranny of the ethnographic present" [29].

A kind of parallel interpretive tyranny exists in paleoanthropology, as in other areas of historical science. Here, the rich detail of the modern world compared to the paucity of the prehistoric world can serve to obscure the recognition and analysis of evolutionary novelty. The present illuminates the past in myriad ways. However, the unwary paleobiologist can easily misinterpret past organisms by using inappropriate interpretive constructs based solely on modern form and function.

For example, the dichotomization of locomotor modes as 'bipedality' versus 'quadrupedality' works well to describe modern humans and their close African ape relatives. But what about now-extinct organisms who lived during the Upper Miocene, near the base of the hominid clade? Does this neontological dichotomization actually serve to *obscure* evolutionary novelty that is accessible *only* through the paleontological record? This is a fundamental issue for the study of hominid origins and early evolution.

The recovery of proximal femora from the Lukeino Formation in the Tugen Hills of Kenya during 2000 [17] was a milestone in paleoanthropology. At last, a key part of the locomotor anatomy from an Upper Miocene hominoid had been found. In particular, the BAR 1002'00 fossil held great promise due to the key role that the proximal femur plays in locomotion and the long history of discovery and interpretation of this skeletal element in human evolutionary studies.

2. Probing the hominid proximal femur

The first recovered proximal femoral fragment of an early African hominid was part of the Sts 14 individual. It was described in *Nature* by Broom and Robinson in 1947 [1 (p. 431)]: "The femur is much crushed, and has not yet been removed from the matrix. It is rather slender, and has a few characters not quite human." Broom and Robinson never elaborated on the nature of the novelty they initially perceived, because, as they stated in 1950: "It

seems unwise to describe this badly crushed femur in detail as the California University Expedition has found the beautifully preserved upper third of a femur apparently of an Australopithecid from a deposit at Sterkfontein, about a couple of miles from the caves where we are working. We have seen this specimen before it was cleared of matrix; but, as Prof. Camp or one of his assistants will doubtless be describing it in detail, we do not feel at liberty to say anything more about it." [2 (p. 62)].

In the next paragraph, however, Broom and Robinson asserted differences between the proximal femur of *Australopithecus* and other hominids, noting differences in the top of the greater trochanter (which they admitted was missing from the only known specimen, Sts 14), the shallowness of the trochanteric fossa, the lack of a well developed trochanteric crest, and the placement of the lesser trochanter. The femur recovered by Camp was never described, and its whereabouts remain unknown today.

The next early hominid proximal femora were found in a nearby but geologically younger breccia at Swartkrans. The deposit yielded an abundance of *Australopithecus robustus* craniodental remains, so the two proximal femora SK 82 and 96 are usually (uncritically) attributed to that species. Because of their relatively early chronological recovery and good preservation, these specimens became a comparative foundation for later studies of the proximal femur in human paleontology, and they continue to be studied today [20].

John Napier was the first to describe the Swartkrans proximal femora in 1964 [13]. This was a fact that Napier called "somewhat surprising in view of the light they throw on the walking ability of australopithecines and, hence, on certain aspects of their phylogeny" (p. 691). Napier described the novel external architectural features of the Swartkrans femora, calling particular attention to the small size of the head relative to the length of the neck. In 1972, 35 years after Sts 14 had been recovered, Robinson published definitive descriptions of the three South African proximal femora. He thereby integrated this skeletal element into his functional and phylogenetic synthesis for *A. africanus* and *A. robustus* [19].

By the time Robinson's treatise on the South African postcrania was published, the pace of fossil discovery in eastern Africa had rapidly accelerated. The first proximal femur to be added to these early hominid collections was Olduvai Hominid 20, a proximal femur without a head from Olduvai Gorge. The specimen was similar in size and morphology to preserved parts of the two Swartkrans femora. O.H. 20 was described by

Day in 1969. He noted the functional significance of the groove for the obturator externus muscle [4].

Additional discoveries in the Lake Rudolf (now Turkana) basin in the early 1970s added many new proximal femora to the early hominid fossil inventory. In 1973 Walker presented his reconstruction of an *Australopithecus* femur based on the then-available parts [25]. The same year, at the 9th International Congress of Anthropological and Ethnological Sciences in Chicago, Lovejoy presented a paper (that would be published in 1975) entitled *Biomechanical Perspectives on the Lower Limb of Early Hominids* [10]. The proximal femur played a central role in his synthesis. Lovejoy summarized research on the early hominid proximal femur to that point, itemized those anatomical features in which *Australopithecus* differed from later *Homo*, and concluded: “the lower limb skeleton of *Australopithecus* points to a long history of bipedalism among hominids” (p. 324). The next three decades witnessed the extension of that history deep into the Pliocene.

Beginning with the recovery of the A.L. 129 hominid femur from Hadar in 1973, the recovery of the partial A.L. 288 (‘Lucy’) skeleton in 1974, and the discovery of A.L. 333 the next year, a wealth of even earlier hominids became available. The publication of these materials only five years after they were found [9] generated a large and still-ongoing debate about the locomotor capabilities of early hominids. The proximal femur figured prominently in the debate.

One of the first to draw functional and phylogenetic interpretations from the Hadar postcranial remains was Brigitte Senut. Her early access to these unpublished fossils allowed her to present an analysis of the early hominid humerus and its articulations as a ‘thèse de 3^e cycle’ examined in Paris in 1978 [21]. In that and all her many subsequent works, Senut has contended that *Homo* is a phylogenetically ancient line. She concludes that *Homo* existed contemporaneously with *Australopithecus*, and that for ‘Lucy’, “the chimp-like elbow-joint morphology (probably convergently derived with *Hylobates*, *Pan*, and *Gorilla*, and not primitive) does not permit us to consider this hominid as a direct human ancestor” [23 (p. 193)].

Senut has consistently relegated *Australopithecus* (including A.L. 288-1 ‘Lucy’) to a phylogenetically peripheral side branch in human evolution. This is a stance championed by the late Louis Leakey and promoted by his son Richard (as documented by Pickford [16]). Senut held firmly to this position through the 1980s and 1990s. She has not wavered, and in the current millennium, posits a ‘*Praeanthropus*–*Homo* line-

age’ closer to *Homo sapiens*, contemporary with the dead-end lineages of *Australopithecus* [22].

Debates about early hominid systematics and locomotion during the 1980s and 1990s centered on the Hadar postcranial sample. An important proximal femoral specimen was added to *A. afarensis* during the 1981 Middle Awash field season. Dating to approximately 3.4 million years in age, the MAK-VP-1/1 specimen from Maka, Ethiopia represented, until recently, one of the oldest proximal hominid femora known. In the spring of 1982, this specimen was subjected to CT scanning. The results were dramatic. First reported in 1984 [3,26], these radiographic results provided strong internal support to interpretations formerly based solely on the external morphology. Virtually all contemporary workers now interpret the proximal femur of *Australopithecus* as indicative of some form of bipedal locomotion.

The 1990s witnessed an intensified interest in the internal structure of the early hominid proximal femur, accompanied by astonishing advances in evolutionary developmental biology, and the beginnings of an integration of this new information into studies of early hominid fossils [11]. These developments set the stage for recovery and analysis of proximal femoral remains belonging to still earlier hominids.

3. *Ardipithecus* and *Orrorin*, discovery and initial correspondence

During the 1992 and 1993 field seasons, a substantial collection of craniodental and postcranial remains was made at the Aramis site, Ethiopia by our Middle Awash research team. These remains date to approximately 4.4 Ma and represent a new genus and species of hominid (*Ardipithecus ramidus*). They are interpreted to represent cladistic hominids. They were announced as such in *Nature* in 1994 [27] (the genus name, initially *Australopithecus*, was changed to *Ardipithecus* the following year) [28].

Three years later, in 1997, even earlier hominids were discovered nearby. Haile-Selassie and colleagues began to recover largely craniodental remains from Upper Miocene deposits along the Western Margin of the Middle Awash study area. These were published in the genus *Ardipithecus* in 2001 [7] and elevated to species status in 2004 [8].

Unfortunately, as of Spring 2005, the Middle Awash has not yet yielded any head or neck of a proximal femur belonging to *Ardipithecus ramidus* or its apparent ancestral chronospecies, *Ardipithecus kadabba*. Therefore, all knowledge of the anatomy of the early

hominid femur head and neck derives from Kenyan specimens found in 2000.

I was in Ethiopia when I received the first media reports of a December 2000 press conference in which these approximately 6-Ma discoveries by Brigitte Senut and Martin Pickford were announced to the world. The BAR 1002'00 specimen represented the first well-preserved proximal femur of an Upper Miocene fossil hominoid. For this reason, it was of enormous significance for understanding hominid origins and early evolution. I immediately congratulated the authors via an e-mail to Martin Pickford on January 20, 2001.

He replied the next day, noting that the 'Millennium Ancestor' femora were more human-like than Lucy's. The fossils were initially published shortly thereafter by Pickford and Senut in the *South African Journal of Science* [17]. They claimed: "the proximal femoral morphology of the Lukeino hominid is closer to that of humans than it is to that of Lucy." This conclusion was accompanied by the statement: "6 million years ago in Kenya, there was a bipedal hominid which was closer in size and morphology to extant humans than the much younger australopithecines and *Ardipithecus ramidus*" [17 (p. 22)].

4. *Orrorin*: the first scientific publication

When the first scientific publication of the new Kenyan fossils in *Comptes rendus de l'Académie des sciences, Paris* [24] appeared later that year, Senut and colleagues assigned the proximal femora to a new genus and species, *Orrorin tugenensis*. Indeed, this new genus was differentially diagnosed, in part, with the contention that the proximal femur was "more human-like than those of australopithecines or African apes" [24 (p. 139)].

In that publication [24], these new Kenyan Upper Miocene fossils were interpreted as exclusively ancestral to the *Homo* lineage. Senut and Pickford interpreted both *Australopithecus* and *Ardipithecus* as side branches in the human family tree (they depicted *Ardipithecus* as an ancestral chimpanzee, and 'Australopithecines' as an extinct clade [24 (Fig. 2, p. 142)]. Given the historical context, it was as if their new phylogeny had been drawn by Louis Leakey himself.

Senut, of course, was being consistent with a phylogenetic interpretation about *Australopithecus* that she had held for over twenty years. At last, she was describing Upper Miocene fossils that she and the Leakeys had long predicted would represent the early human lineage. These fossils, particularly the *Orrorin* femora, were being used to support a Leakey family contention that

Australopithecus played no role in the evolution of *Homo*. But did the new fossils actually confirm Leakey's and Senut's predictions that hominids more derived than Lucy would be found in the Upper Miocene?

Unfortunately, the initial 2001 presentation and analysis of *Orrorin* [24] were flawed by a variety of confusing and inaccurate statements. Among these, enamel thickness was reported as 3.1 mm "on the apex of the paraconid" [24 (p. 140)]. This was important because the enamel thickness was one of only two characters purported to differentially diagnose *Ardipithecus* from *Orrorin*. However, since the paraconid has long been absent from the molars of all higher primates, it was unclear where the published measurement had been taken, and what it represented.

Furthermore, for some reason, the original description of the *Orrorin* proximal femur appeared to characterize the functionally critically important obturator externus groove (so important for interpreting locomotion; see above) as an "intertrochanteric groove" (p. 141), (which it is not, and whose citation, oddly, was not made to the paper by Day [4]; see earlier, but to others who emphatically disputed its significance as a marker of bipedal locomotion). Given these irregularities, it is therefore not surprising that many readers were unconvinced of the accuracy of the first functional and phylogenetic claims made by Senut and Pickford about *Orrorin*.

5. *Orrorin*: Questions and answers

After puzzling over the nomenclature and metrics presented by Senut and colleagues in their initial *Comptes rendus de l'Académie des sciences* descriptions, I e-mailed Martin Pickford on March 13, 2001, to again congratulate his team, and to ask for clarification. I also asked Pickford whether their described "intertrochanteric groove" was actually the obturator externus groove, and requested clarification of the published 3.1-mm enamel thickness value. I asked about the distribution of cortex around the femur neck as follows: "Did you photograph the femur before it was glued together, or was it found in one piece? If it wasn't broken all the way thru, do you have X-rays or CT to show what the distribution of cortex is around the neck? We have really great views of this in the Maka femur, and broken *A. afarensis* ones, and would like to compare."

Martin Pickford and colleagues replied by e-mail on April 3rd, 2001. They stated that the femur had, indeed, been found in four pieces, and that photographs, sketches and measurements of cortical thickness had been made before the specimens were glued together.

They have never been made available. They went on to say that the fossils could be unglued if necessary, and that they had a complete series of CT scans at 0.5-mm slices through the femoral neck. Their response made it clear that the obturator groove was well expressed, that the 3.1-mm enamel thickness was inaccurate, and that further studies were underway. In a follow-up e-mail on April 12th, Senut and Pickford asked us not to publish any of the observations that they had shared with us, pending a more detailed study they were preparing.

I wrote to Pickford again on August 5th, 2001, urging him to focus on the cortical distribution in the femoral neck: “Here, because of the Maka femur, we have been working intensively, particularly Owen Lovejoy. One thing we’ve learned is that broken surfaces are ALWAYS superior to CT scans in evaluating relative thicknesses. We think that great care is needed to present the relevant data both numerically and photographically, not only where the scans are, but also photographs of the unglued/broken originals with the cortex showing clearly.”

That e-mail referred to the Middle Awash team’s work on the Maka femur that we had found in 1981, scanned and X-rayed in 1982, published in 1984, and been working on ever since (see above). Pickford replied via e-mail the next day (6th August, 2001). He said that since the femur of *Orrorin* had been broken across the neck, it could be unglued and studied. Because we were about to submit the final detailed description of the Maka fossil to the *American Journal of Physical Anthropology*, we made the results of that analysis available to the *Orrorin* team by sending them an electronic pre-submission copy of the manuscript the same day.

Martin Pickford e-mailed again on September 6th, 2001 to confirm that he would unglue the femoral neck in October in order to make a direct visual assessment. Later, on November 30th (after the *Orrorin* group’s field season), I e-mailed to ask Pickford whether he had unglued the femur neck. He replied, on December 1st, that the conditions he was working under did not allow him to unglue the neck because he did not want to cause any damage. He stated that the CT scans in the team’s possession were sufficiently clear to reveal the cortical thickness.

Martin Pickford and colleagues re-described the proximal femur of *Orrorin* in *C. R. Palevol* the next year [18]. This time the anatomical descriptions were more standard and detailed. Information on the internal anatomy of the femur was presented for the first time via the CT scans they had written us about. The descriptions and illustrations of the proximal femoral anatomy

in this second publication made it clear that *Orrorin* shared several derived characters with later hominids, and thus was likely to be a cladistic hominid. Furthermore, external morphology (particularly the obturator externus groove) was in keeping with some sort of bipedal posture or locomotion.

What was missing, however, was the photographic or radiographic evidence that had, by 2002, become critical in the evaluation of locomotor mode among early hominids. The first CT scans presented by the *Orrorin* team in *C. R. Palevol* [18 (Fig. 2)] were of poor quality and nonstandard orientation. Nevertheless, despite an apparently thick inferior cortex through the neck, the poor scans appeared to show a substantial cortical thickness through the superiormost femoral neck. This is a cortex distribution not seen in *Australopithecus* or *Homo*, but more reminiscent of great apes.

Nevertheless, the text accompanying this figure claimed: “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.” The authors went on to echo their earlier phylogenetic claims as follows: “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 1981 and Senut 1980 and [18 (p. 202)]...”

On August 28th, 2002 I wrote Pickford to congratulate him on the publication of the *Palevol* article with the CT scans of the femur of *Orrorin*. I asked: “On the relative cortical thicknesses, I thought that the reviewer held you up for conventional X-rays or xeradiographs. Do you have these, and could we get a copy to compare to ours of Maka? And do you have the digital data for your CT scans? We were wondering what would happen if the actual cross-section were taken closer to the orientation that we advocate in the Maka paper. The cortical thickness through the superior neck looks very high to us, and we were wondering why this was.” Pickford replied the next day that they lacked conventional X-rays, but that they were hoping to have a detailed paper on the scans out soon.

I wrote again to Martin Pickford on October 15th of 2002, after another of his fieldwork trips to Kenya, to again inquire about whether he had been able to unglue the femur neck or get a conventional radiograph of the femur neck when he was in Nairobi. He replied the next day that he had not yet done this. My repeated attempts to ascertain the distribution of cortex in the neck of the *Orrorin* femur had proven frustrating and puzzling, but

I assumed that the discovery team's third description of the specimen, when published, would reveal it.

6. Novelty revealed, or concealed?

The detailed 2002 description and interpretation of the Maka proximal femur of *Australopithecus afarensis* [12] represents the most exhaustive analysis of the early hominid proximal femur to date. Available to the discoverers of *Orrorin* before its submission, that work makes it abundantly clear that the distribution of cortical bone in the neck of the proximal femur is a crucial feature in the interpretation of locomotor modes among early hominids [14]. So, when Galik and colleagues (including Senut and Pickford) published *External and internal morphology of the BAR 1002'00 Orrorin tugenensis femur* in *Science* during September of 2004 [6], it was extremely disappointing to realize that no new CT data had been taken from this crucial fossil, and no photographs, sketches or conventional radiographs were being presented.

Furthermore, despite *years* of our appeals to the discovery team for release of this crucial evidence, the *Science* paper presented only adjustments to the original scans, correcting for improper specimen orientation in the 2002 *C. R. Palevol* publication. As we noted in our Letter to the Editor of *Science*, published on February 11th, 2005, “the adjusted results are still inadequate to determine whether the femoral neck's cortical thickness conforms to a human, intermediate, or chimpanzee pattern.” We challenged the *Orrorin* team to provide: “(i) photographs, measurements, and drawings of its broken neck; (ii) conventional anteroposterior X-rays; and (iii) higher-resolution CT scans obtained with proper femoral orientation” [15 (p. 845)].

It is unclear why the *Orrorin* discovery team and its associates will not publish the comparatively very simple conventional radiography and conventional photography of the unglued BAR 1002'00 femoral neck that we have urged on numerous occasions (see above) since 2001. Martin Pickford and Brigitte Senut mysteriously did not join the list of authors who responded to our last, published request for these data in our February 2005 letter to *Science*. Their American colleagues responded: “it is our understanding that the initial studies were carried out under serious constraints of time and other resources [...] and we have made it clear that we plan to rescan and study the existing fossils if funds are made available” [5 (p. 845)]. We were again disappointed because we had asked for the publication of new data, not the promotion of a funding request for documentation long overdue.

7. The continuing inside story on the early hominid femur

The distribution of bony cortex in the femoral neck is among the most important available evidence for ascertaining locomotor mode. Was the bipedality that the early hominid *Orrorin* practiced like that employed by modern humans and *Australopithecus*, or was it a novel and previously unknown form of locomotion? The evidence so far made available suggests the latter. This is because of the distinctive cortex visible on the top of the BAR 1002'00 femoral neck in the published CT scans. But the ‘inside story’ from that key anatomical region of the early hominid hip cannot be accurately or reliably told without better data. Why have those data not been made available, particularly when they require only an ungluing of the femoral neck or a simple anteroposterior conventional X-ray?

The Galik et al. *Science* paper was published on the 3rd of September, 2004 [6]. Fortunately, the Inter-Academy Conference, *Climats, cultures et sociétés aux temps préhistoriques, de l'apparition des Hominiés jusqu'au Néolithique*, was held at the French Academy of Sciences a mere ten days later. Professor Henry de Lumley had graciously invited me to present a paper in the second session entitled *The First Hominids*. Because Dr. Brigitte Senut of the *Orrorin* team was a participant in the session, it represented an ideal forum for a productive exchange of data and ideas. Unfortunately, Dr. Senut once again presented the same ambiguous CT datasets. She thereby left all those in attendance wondering what really *was* the inside story on the early hominid proximal femur?

8. Conclusion

The last decade has witnessed an impressive advance in our knowledge about the earliest hominids due to discoveries in Chad, Kenya, and Ethiopia. It is clear that all three sets of fossils represent cladistic hominids (as opposed to cladistic chimpanzees or gorillas). This is because fossils in all three sets exhibit derived characters exclusively shared with later hominids such as *Australopithecus*. Whether the fossils from these three countries actually represent three separate genera (*Ardipithecus*, *Orrorin*, and *Sahelanthropus*) will necessarily require the discovery of additional fossils [8].

From associational and anatomical considerations, it is evident that these early hominids preferred more closed habitats than their descendants. It is also clear that they are different from any modern apes or previously known hominids—these earliest hominids were

neither humans nor chimpanzees. And thus, forcing them into preconceived locomotor, species, or dietary categories based on the species-poor world of modern humans and relict apes almost certainly obfuscates the novelty that these Upper Miocene fossil primate remains may reveal.

The external anatomy of the Tugen Hills femora and the Middle Awash foot phalanx both suggest that some form of bipedality was being practiced by these earliest hominids. Did they share the highly evolved bipedality of *Australopithecus*? This is not clear. By forcing these organisms into narrowly preconceived categories based on organisms half as old (or younger), and by accommodating the new evidence in decades-old phylogenetic constructs, we sacrifice the insight that only paleontology can contribute to the study of our origins and evolution.

Acknowledgements

The National Science Foundation supports fieldwork conducted in the Middle Awash study area of Ethiopia under the Ministry of Youth, Sports and Culture, with the permission of the Authority for Research and Conservation of Cultural Heritage, and the support of the Afar Regional Government. Thanks to my colleagues on the Middle Awash project for their critical comments on a draft of this contribution, and to Dr. J.R. Boisserie for translation. We dedicate this contribution to our friend and inspiration, Professor Henry de Lumley.

References

- [1] R. Broom, J.T. Robinson, Further remains of the Sterkfontein ape-man, *Plesianthropus*, *Nature* 160 (1947) 430–431.
- [2] R. Broom, J.T. Robinson, G.W.H. Schepers, Sterkfontein Ape-Man *Plesianthropus*, Transvaal Museum, Pretoria, South Africa, 1950.
- [3] J.D. Clark, Paleoanthropological discoveries in the Middle Awash Valley, Ethiopia, *Nature* 307 (1984) 423–428.
- [4] M. Day, Femoral fragment of a robust australopithecine from Olduvai Gorge, Tanzania, *Nature* 221 (1969) 230.
- [5] R.B. Eckhardt, K. Galik, A.J. Kuperavage, Questions about *Orrorin* femur, *Science* 307 (2005) 845.
- [6] K. Galik, B. Senut, M. Pickford, D. Gommery, J. Treil, A.J. Kuperavage, R.B. Eckhardt, External and internal morphology of the BAR 1003'00 *Orrorin tugenensis* femur, *Science* 305 (2004) 1450–1453.
- [7] Y. Haile-Selassie, Late Miocene hominids from the Middle Awash, Ethiopia, *Nature* 412 (2001) 178–181.
- [8] Y. Haile-Selassie, G. Suwa, T.D. White, Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution, *Nature* 303 (2004) 1503–1505.
- [9] D.C. Johanson, et al., Hadar monograph, *Am. J. Phys. Anthropol.* 57 (1982) 373–724.
- [10] C.O. Lovejoy, Biomechanical perspectives on the lower limb of early hominids, in: R. Tuttle (Ed.), *Primate Functional Morphology and Evolution*, Aldine, Chicago, 1975, pp. 291–326.
- [11] C.O. Lovejoy, M.J. Cohn, T.D. White, Morphological analysis of the mammalian postcranium: A developmental perspective, *Proc. Natl. Acad. Sci. USA* 96 (1999) 13247–13252.
- [12] C.O. Lovejoy, R.S. Meindl, C. James, Ohman, G. Kingsbury, Heiple D., Tim White, The Maka femur and its bearing on the antiquity of human walking: Applying contemporary concepts of morphogenesis to the human fossil record, *Am. J. Phys. Anthropol.* 119 (2002) 97–133.
- [13] J.R. Napier, The evolution of bipedal walking in the hominids, *Arch. Biol. (Liege)* 75 (suppl.) (1964) 673–708.
- [14] J.C. Ohman, T.J. Krochta, C.O. Lovejoy, R.P. Mensforth, B. Latimer, Cortical bone distribution in the femoral neck of hominoids: Implications for the locomotion of *Australopithecus afarensis*, *Am. J. Phys. Anthropol.* 104 (1997) 117–131.
- [15] J.C. Ohman, C.O. Lovejoy, T.D. White, Questions about *Orrorin* femur, *Science* 307 (2005) 845.
- [16] M. Pickford, Louis S.B. Leakey, *Beyond the Evidence*, Janus, London.
- [17] M. Pickford, 'Millennium Ancestor,' a 6-million-year-old bipedal hominid from Kenya, *S. Afr. J. Sci.* 97 (2001) 22.
- [18] M. Pickford, B. Senut, D. Gommery, J. Treil, Bipedalism in *Orrorin tugenensis* revealed by its femora, *C. R. Palevol* 1 (2002) 191–203.
- [19] J.T. Robinson, *Early Hominid Posture and Locomotion*, University of Chicago Press, Chicago, 1972.
- [20] C.B. Ruff, H.M. McHenry, J.F. Thackeray, Cross-sectional morphology of the SK 82 and 97 proximal femora, *Am. J. Phys. Anthropol.* 109 (1999) 509–521.
- [21] B. Senut, Contribution à l'étude des l'humérus et de ses articulations chez les Hominidés du Plio-Pleistocène, thèse présentée pour l'obtention du diplôme de docteur de 3^e cycle, Paris, 1978.
- [22] B. Senut, Palaeontological approach to the evolution of hominid bipedalism: The evidence revisited, *Cour. Forsch. Inst. Senckenberg* 243 (2003) 125–134.
- [23] B. Senut, C. Tardieu, Functional aspects of Plio-Pleistocene hominid limb bones: Implications for taxonomy and phylogeny, in: E. Delson (Ed.), *Ancestors: The Hard Evidence*, Alan R. Liss, New York, 1985, pp. 193–201.
- [24] B. Senut, M. Pickford, D. Gommery, P. Mein, K. Cheboi, Y. Coppens, First hominid from the Miocene (Lukeino Formation, Kenya), *C. R. Acad. Sci. Paris, Ser. IIA* 332 (2001) 134–144.
- [25] A.C. Walker, New *Australopithecus* femora from East Rudolf, Kenya, *J. Hum. Evol.* 2 (1973) 545–555.
- [26] T.D. White, Pliocene hominids from the Middle Awash, Ethiopia, *Cour. Forsch. Inst. Senckenb.* 69 (1984) 57–68.
- [27] T.D. White, G. Suwa, B. Asfaw, *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia, *Nature* 371 (1994) 306–312.
- [28] T.D. White, G. Suwa, B. Asfaw, Corrigendum, *Nature* 375 (1995) 88.
- [29] H.M. Wobst, The archaeo-ethnology of hunter-gatherers or the tyranny of the ethnographic record in archaeology, *Am. Antiq.* 43 (1978) 303–309.