Paléontologie / Palaeontology
(Paléontologie humaine / Human Palaeontology)

First hominid from the Miocene (Lukeino Formation, Kenya)

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Abstract – Remains of an early hominid have been recovered from four localities in the Lukeino Formation, Tugen Hills, Kenya, in sediments aged ca 6 Ma. 13 fossils are known, belonging to at least five individuals. The femora indicate that the Lukeino hominid was a biped when on the ground, whilst its humerus and manual phalanx show that it possessed some arboreal adaptations. The upper central incisor is large and robust, the upper canine is large for a hominid and retains a narrow and shallow anterior groove, the lower fourth premolar is ape-like, with offset roots and oblique crown, and the molars are relatively small, with thick enamel. A new genus and species is erected for the remains. © 2001 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Hominoidea / Hominidae / Tugen Hills / Upper Miocene / Kenya

Résumé – Premier hominidé du Miocène (formation de Lukeino, Kenya). Des restes d'hominidés, vieux de 6 Ma, ont été découverts dans quatre localités de la formation de Lukeino, dans les collines Tugen au Kenya. 13 spécimens appartenant à au moins cinq individus ont été identifiés. Les fémurs montrent que les hominidés de Lukeino étaient bipèdes sur le sol, alors que l'humérus et la phalange de la main indiquent des adaptations arboricoles. L'incisive centrale supérieure est grande et robuste, la canine supérieure grande pour un hominidé, mais de la taille de celle d'un chimpanzé femelle, conserve un sillon antérieur peu profond. La P_4 est simiesque, avec des racines décalées et une couronne oblique; les molaires sont relativement petites avec un émail épais. Un nouveau genre et une nouvelle espèce sont érigés pour ces restes. © 2001 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Hominoidea / Hominidae / collines Tugen / Miocène supérieur / Kenya

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Version abrégée

1. Introduction

Ardipithecus ramidus, publié en 1995 [28, 29], a été interprété comme étant ancestral à *Australopithecus anamensis* [13] et devenait ainsi le plus ancien hominidé connu. Toutefois, de nombreux caractères du fossile éthiopien, proches de ceux de *Pan paniscus*, suggèrent qu'il pourrait bien ne pas appartenir à un hominidé *sensu stricto*. La bipédie d'*Ardipithecus* reste à démontrer, puisque aucune étude détaillée n'a été publiée depuis 1995. De nouvelles découvertes, réalisées au Kenya à l'automne dernier par la Kenya Palaeontology Expedition (projet de coopération entre le Collège de France à Paris et le Community Museums of Kenya à Nairobi), jettent une lumière nouvelle sur le problème de la divergence entre les grands singes et l'homme et la phylogénie des hominidés. Les contextes géologique et faunique sont donnés dans la référence [17].

2. Description systématique

Ordre Primates Linnaeus, 1758
Sous-ordre Anthropoidea Mivart, 1864
Superfamille Hominoidea Gray, 1825
Famille Hominidae Gray, 1825
Genre *Orrorin* nov.

Espèce type. *Orrorin tugenensis* sp. nov.

Diagnose du genre. Hominidé aux dents jugales plus petites que celles des Australopithèques ; incisive centrale supérieure large, non en forme de pelle et à l'émail épais ; canine supérieure courte mésio-distalement portant un sillon mésial peu profond et étroit et à hauteur apicale faible ; M^3 petites et presque triangulaires ; *corpus mandibularis* relativement haut au niveau de la M$_3$; P$_4$ aux racines décalées et couronne oblique ; M$_2$ et M$_3$ petites, rectangulaires et ressemblant à celles de *Homo* ; émail épais sur les dents jugales ; incision buccale bien développée aux molaires inférieures, donnant un profil bilobé à la surface buccale ; pas de cingulum aux molaires. Fémur à tête fémorale sphérique, projetée antérieurement ; fossette digitale profonde ; col fémoral allongé et à section ovale ; humérus avec crête brachioradiale verticale ; phalange proximale de la main courbe ; dentition petite par rapport à la taille corporelle.

Diagnose différentielle. *Orrorin* se distingue d'*Australopithecus* par la morphologie des dents jugales, qui sont moins allongées mésio-distalement et plus petites, ainsi que par les caractères du fémur et, en particulier, de la tête, des trochanters et du col. Il diffère d'*Ardipithecus* par l'épaisseur plus importante de l'émail et des deux genres par la présence d'un sillon mésial à la canine supérieure.

Espèce *Orrorin tugenensis* nov.

Étymologie. Le nom générique *Orrorin* (pluriel *Ororiek*) signifie « homme originel » en Tugen. Il faut remar-quer la prononciation des deux premières syllabes semblables au mot français « aurore ». Le nom d'espèce fait référence aux collines Tugen, où fut découvert le matériel.

Localité type. Kapsomin (00°45′10,5″N : 35°52′29,9″E), formation de Lukeino, district de Baringo, Kenya.

Âge. Miocène supérieur (6 Ma).

Holotype. BAR 1000′00, mandibule fragmentaire en deux morceaux ; BAR 1000a′00 : fragment de mandibule gauche, avec M$_{2-3}$ et BAR 1000b′00 : fragment de mandibule droite avec M$_3$.

Paratypes. Les paratypes proviennent de quatre sites différents de la formation de Lukeino : Cheboit [15], Kapsomin, Kapcheberek et Aragai. La liste en est donnée dans le *tableau I*.

Description

Dents supérieures. L'incisive centrale supérieure, légèrement usée, est robuste, assez grande mésio-distalement, mais plus petite que celles d'*Australopithecus afarensis* [27], et de taille équivalente à celles d'*Ardipithecus ramidus*. La surface linguale est fortement pentue de l'apex au cervix, comme chez les chimpanzés, et diffère de celle d'*Australopithecus afarensis*, chez qui sont présentes de nettes gouttières linguales. La canine est triangulaire en vue labiale et le contour au niveau du cervix n'est pas fortement comprimé mésio-distalement. Aucune crête linguale n'est présente, mais un sillon vertical étroit et peu profond est présent mésialement. Ce sillon n'existe ni chez les Australopithèques, ni chez *Homo*, ni chez *Ardipithecus*, mais il est fréquent chez les grands singes miocènes et actuels. Les M^3 présentent un contour trapézoïdal, presque triangulaire, mais pas aussi fortement trapézoïdal que chez *Australopithecus afarensis*. Elles ont un petit métacone et un grand protocone.

Dents inférieures. Le contour occlusal de la P$_4$ est ovoïde, montrant une compression mésio-distale forte. Les racines sont décalées. La M$_2$ droite et les M$_3$ droite et gauche sont préservées dans la mandibule BAR 1000′00, mais brisées, ce qui permet de mesurer l'épaisseur de l'émail : il est épais de 3,1 mm sur le paraconide. Cette mesure est comparable à celle des autres hominidés, *Ardipithecus* exclus. La M$_1$ ou M$_2$, KNM LU 335, récoltée à Cheboit, a été au centre d'un débat [4, 5, 7, 14, 16, 26, 31], résumé dans Senut [20] et Hill [6].

Postcrânien. Les fémurs sont bien conservés, mais le *trochanter major* et la partie distale manquent. BAR 1002′00 est le plus complet, puisque 2/3 de l'os sont présents (la longueur préservée est de 215 mm environ). La tête fémorale, nettement déjetée vers l'avant, est sphérique avec une *fovea capitis* distincte. Elle regarde crânialement, mais moins que chez AL 288.1ap [8, 11]. Le col fémoral est allongé et comprimé antéro-postérieurement. Le *trochanter minor* est grand et saillant médialement. Une gouttière intertrochantérienne est visible. Les insertions des muscles vastes et fessiers sont bien marquées et la *tuberositas glutea* bien individualisée. La diaphyse fémorale est aplatie antéro-postérieurement, mais moins que chez AL 288.1ap.

Par rapport à la diaphyse, la tête est proportionnellement plus petite que chez l'homme moderne, mais plus grande que chez AL 288.1ap.

L'extrémité distale humérale est seulement représentée par la diaphyse ; elle présente un aplatissement latéral fort, avec une crête latérale brachioradiale très rectiligne, rappelant ainsi les grands singes africains [19] et *Australopithecus afarensis* de Hadar [8, 18, 21] et de Maka [30].

La phalange proximale de la main, appartenant à un jeune individu (épiphyse proximale non fusionnée), est incurvée et ressemble à celle d'*Australopithecus afarensis* et des primates arboricoles [25].

La présence, chez *Orrorin*, de molaires petites à émail épais suggère que cette combinaison de caractères [22] serait archaïque pour la lignée des Hominidae, retenue dans le genre *Homo*. Les Australopithèques ont, quant à eux, conservé un émail épais, associé à des dents orientées vers une mégadontie de plus en plus poussée au cours du temps. En revanche, la présence, chez *Ardipithecus*, de dents ju-

gales à émail fin pourrait être considérée comme un caractère dérivé de la lignée des Gorillidae, sur laquelle le spécimen éthiopien pourrait être placé. L'ancêtre commun aux grands singes africains et aux hominidés aurait donc possédé des dents jugales petites associées à un émail épais, scénario confirmé par la présence de *Samburupithecus* dans le Miocène supérieur du Kenya (9,5 Ma) [9, 10].

3. Conclusion

Orrorin confirme la présence des hominidés à 6 Ma en Afrique orientale, confortant ainsi l'*East Side Story* de Coppens [1–3]. Ses molaires sont plus petites que celles des Australopithèques, et de tailles similaires à celles d'*Ardipithecus* ; ses dents antérieures ($\underline{I}$ et $\underline{C}$) ainsi que la P_4 sont plus simiesques et rappellent les chimpanzés femelles. Les éléments postcrâniens suggèrent qu'*Orrorin* était déjà adapté à la bipédie (de manière différente et plus humaine que celle des Australopithèques), tout en étant encore agile dans les arbres.

1. Introduction

The new genus of hominid described in the mid 90's (*Ardipithecus ramidus*) [28, 29] was interpreted as being ancestral to *Australopithecus anamensis* [13] and thus the oldest known hominid. However, several features of the Ethiopian fossil suggest that it may well not be a hominid *sensu stricto*, considering the numerous features close to *Pan paniscus*, which have been described. Bipedality in *Ardipithecus* still needs to be demonstrated as no detailed studies have been published since 1995. New discoveries made in Kenya last fall by the Kenya Palaeontology Expedition, a co-operative project between the Collège de France, Paris and the Community Museums of Kenya, Nairobi shed new light on the question of ape/human divergence and the phylogeny of hominids. The geological and faunal contexts were described by Pickford and Senut [17].

2. Systematic description

Order Primates Linnaeus, 1758
Suborder Anthropoidea Mivart, 1864
Superfamily Hominoidea Gray, 1825
Family Hominidae Gray, 1825
Genus *Orrorin* nov.

2.1. Type species

Orrorin tugenensis nov. sp.

2.2. Generic diagnosis

Hominid with jugal teeth smaller than those of Australopithecines; upper central incisor large and not shovel-shaped, with thick enamel; upper canine short with a shallow and narrow vertical mesial groove, apical height low; small triangular upper M^3s; *corpus mandibularis* relatively deep below M_3; lower P_4 with offset roots and oblique crown; small *Homo*-like rectangular lower M_2 and M_3s; thick enamel on lower cheek teeth; buccal notch well developed which imparts a bilobate profile to the buccal surface; no cingulum on molars. Femur with a spherical head rotated anteriorly, neck elongated and oval in section, lesser trochanter medially salient with strong muscle insertions, deep digital fossa; humerus with a vertical brachioradialis crest; proximal manual phalanx curved; dentition small relative to body size.

2.3. Differential diagnosis

Orrorin is distinguished from *Australopithecus* by the morphology of the jugal teeth, which are smaller and less elongated mesio-distally; it differs from *Ardipithecus* by the greater thickness of enamel. It differs from both genera by the presence of a mesial groove on the upper canine. Postcranially, it differs from Australopithecines by the morphology of the proximal femur, which is more human-like than those of australopithecines or African apes.

2.4. Etymology

The generic name *Orrorin* (plural *Orroriek*) means 'original man' in Tugen. Note the pronunciation of

the first two syllables, similar to the French word 'aurore' (dawn, daybreak). The specific name refers to the Tugen Hills, where the material was found.

Species *Orrorin tugenensis* nov.

2.5. Type locality

Kapsomin (00°45′10.5″N: 35°52′29.9″E), Lukeino Formation, Baringo district, Kenya.

2.6. Age

Late Miocene (6 Ma)

2.7. Holotype

BAR 1000′00, a fragmentary mandible in two pieces; BAR 1000a′00: fragment of left mandible with M_{2-3} and BAR 1000b′00: fragment of right mandible with M_3 (*figure 1*).

2.8. Paratypes

The paratypes (*figure 1*) are from four different sites in the Lukeino Formation: Cheboit [15], Kapsomin, Kapcheberek and Aragai. *Table I* lists the holotype and paratype series.

2.9. Species diagnosis

As for the genus.

2.10. Description

2.10.1. Dental descriptions (*table II*)

2.10.1.1. Upper dentition. The lightly worn upper central incisor is robust, massive, relatively large mesio-distally, but smaller than those of Australopithecines and equivalent in size to that of *Ardipithecus ramidus*. The wear facet is inclined lingually. The labial face is almost vertical and slightly mesio-distally convex; the cervical outline is an open oval, almost circular. The lingual surface, which is planar, slopes strongly from apex to cervix as in chimpanzees and differs from *Australopithecus afarensis* [27] in which clear lingual grooves can be observed.

The upper canine is triangular in labial view, the cervical outline is not strongly mesio-distally compressed and a swelling but not a true cingulum occurs above the cervix. This swelling is clearly marked at the base of the distal and mesial crests. No lingual ridges can be observed. A shallow, narrow, vertical groove is present mesially. This groove does not occur in Australopithecines or *Homo*, nor in *Ardipithecus ramidus*, but is frequent in Miocene and modern apes. The apex of the canine is pointed (height above cervix = 13.4 mm), almost sectorial, recalling those of extant female chimpanzees. Perikymata are visible on the labial surface of the crown.

The upper M^3s are moderately to heavily worn and the details of the crowns cannot be properly seen (the left one is more worn than the right one). The teeth are trapezoidal, almost triangular in occlusal outline with small metacone and large protocone and are not strongly trapezoidal as in *Australopithecus afarensis*. The crown is low and the fovea are reduced; the distal fovea is located on the distobuccal corner of the tooth, unlike the pattern seen in Australopithecines. The occlusal surface is wrinkled but not as strongly as in Australopithecines. The roots of M_3 are long (35 mm on the distal root).

2.10.1.2. Lower dentition. The lower P_4 is ovoid in occlusal outline and compressed mesiodistally and has two offset roots. The enamel is missing from the anterior, lingual and posterior surfaces. The distal fovea is large as in extant and fossil non-human hominoids. The protoconid is higher than the metaconid and has a pointed apex from which two ridges run lingually and distally.

The lower left M_2 and right and left M^3 are preserved in BAR 1000′00. The teeth are broken and the enamel is missing from anterior and lingual surfaces of the left molars and from the mesial surface of the right molar which is also missing a chip of enamel distally. Enamel thickness at the apex on the paraconid is 3.1 mm. This is comparable to other hominids, *Ardipithecus* excluded. The occlusal outline of the M_2 is a round cornered rectangle, being slightly elongated mesiodistally. The distal fovea is not preserved except on the left M_2. The cusps are low and bunodont. The teeth are lightly worn. The lingual cusps on the lower left M_3 are damaged, but on the right M_3 the lingual cusps are pointed and slightly higher than the buccal ones. The lingual surface is vertical and there is no cingulum. The depth of the mandibular corpus below M_3 is 35.5 mm.

The lower molar (M_1 or M_2) KNM LU 335 has been the subject of a debate [4, 5, 7, 14, 16, 26, 31], which was summarised by Senut [20] and Hill [6]. Similarities to both chimpanzees and humans have been pointed out.

2.10.2. Postcranial descriptions

The two left femora (BAR 1002′00 and BAR 1003′00) are the best preserved but both lack the *trochanter major*. BAR 1002′00 is the most complete, including the femoral head, it preserves two thirds of the bone. The line of fusion of the head is visible and suggests that it belonged to a young adult. The well-defined head is spherical (33.0 mm in antero-posterior diameter and 33.0 mm perpendicular diameter) with a distinct and moderately wide *fovea capitis* and is slightly rotated anteriorly. It faces craniomedially, but less than in AL 288.1ap [11]. The proximal part of the
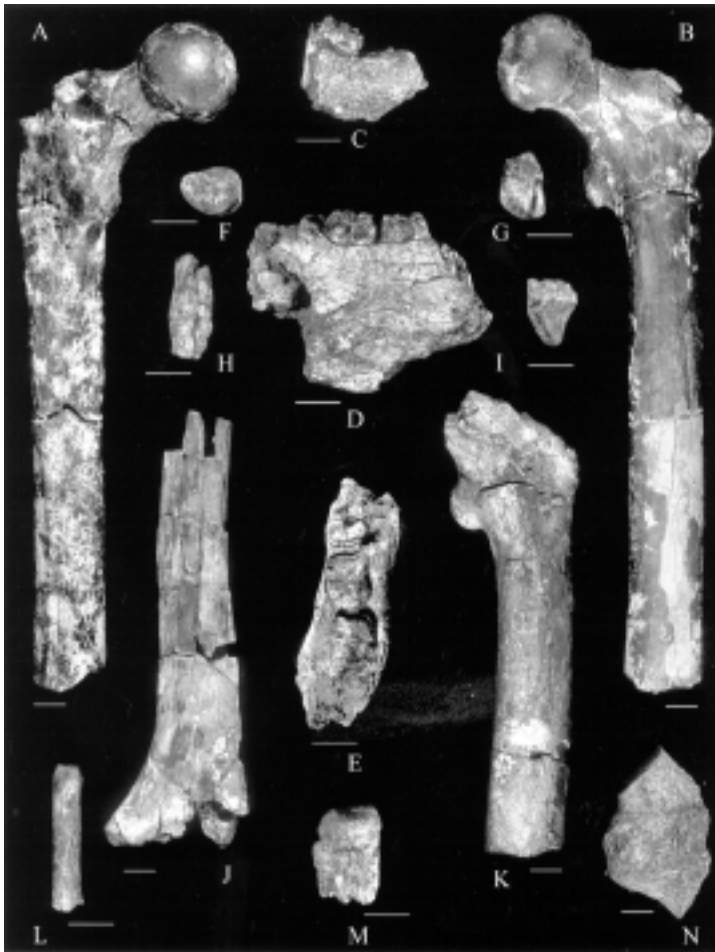
Figure 1. *Orrorin tugenensis* nov. gen. nov. sp. **A**: BAR 1002′00, left femur, posterior view; **B**: BAR 1002′00, left femur, anterior view; **C**: BAR 1000′00, right mandibular fragment with M_3, buccal view; **D**: BAR 1000′00, left mandibular fragment with M_{2-3}, lingual view; **E**: BAR 1000′00, left mandibular fragment with M_{2-3}, occlusal view; **F**: BAR 1900′00, right M^3, occlusal view; **G**: BAR 1390′00, right P_4, distal view; **H**: BAR 1001′00, upper I^1, labial view; **I**: BAR 1425′00, right $\underline{C}$, lingual view; **J**: BAR 1004′00, right distal humerus, posterior view; **K**: BAR 1003′00, proximal left femur, anterior view; **L**: BAR 349′00, manual proximal phalanx, superior view; **M**: BAR 1426′00, left M^3, distal view; **N**: BAR 1215′00, fragmentary right proximal femur, posterior view. Scale bars = 1 cm.

Figure 1. *Orrorin tugenensis* nov. gen. nov. sp. **A** : BAR 1002′00, fémur gauche, vue postérieure ; **B** : BAR 1002′00, fémur gauche, vue antérieure ; **C** : BAR 1000′00, fragment mandibulaire droit avec M_3, vue buccale ; **D** : BAR 1000′00, fragment mandibulaire gauche avec M_{2-3}, vue linguale ; **E** : BAR 1000′00, fragment mandibulaire gauche avec M_{2-3}, vue occlusale ; **F** : BAR 1900′00, M^3 droite, vue occlusale ; **G** : BAR 1390′00, P_4 droite, vue distale ; **H** : BAR 1001′00, I^1, vue labiale ; **I** : BAR 1425′00, $\underline{C}$ droite, vue linguale ; **J** : BAR 1004′00, humérus distal droit, vue postérieure ; **K** : BAR 1003′00, fémur proximal gauche, vue antérieure ; **L** : BAR 349′00, phalange proximale de la main, vue supérieure ; **M** : BAR 1426′00, M^3 gauche, vue distale ; **N** : BAR 1215′00, fémur proximal fragmentaire, vue postérieure. Chaque barre équivaut à 1 cm.

shaft is antero-posteriorly flattened; the neck is elongated and compressed antero-posteriorly (estimated length: 20.5 mm; minimal height: 20.9 mm; width: 15.9 mm), giving a flattened ovoid section. The bulky *trochanter minor* is large (18.0 mm × 12.4 mm) and medially salient. There is an intertrochanteric groove, which runs from a small and moderately deep *fossa trochanterica* to an area situated just above the *trochanter minor*. This feature has been related to frequent bipedalism [22–25]. Below the *trochanter major* runs a crest for the insertion of the *m. vastus lateralis*; the well marked *tuberositas glutea* runs distally for approximately 46 mm. A short *linea pectinea* is visible below the *trochanter minor* and runs distally as a low rugosity to meet the ridge which issues from the *tuberositas glutea* thereby forming a low and wide (9.0 mm) *linea aspera*. The general morphology of the proximal femur is clearly distinct from that of AL 288.1ap. The size of the head relative to the neck is also different. The preserved length of the femur is approximately 215 mm. The shaft is convex anteriorly and concave posteriorly, strongly flattened antero-posteriorly (below the *trochanter minor*, (antero-posterior diameter = 21.5 mm and medio-lateral di-

ameter = 29.3 mm) but less than in AL 288.1ap at the same level [8] (a-p diameter = 18.3 mm; m-l diameter = 27.0 mm). Cortical thickness at midshaft is 5.2 mm (anterior), 5.2 mm (posterior), 7.4 mm (medial) and 5.5 mm (lateral). The neck-shaft angle is estimated to be between 120° and 130° (at present there is not a very good contact between two pieces of the femur).

Compared to modern humans, the head is smaller proportionally to the shaft, but it is proportionally larger than that of AL 288.1ap.

The humerus, represented by a distal shaft, shows a straight lateral crest, onto which inserts the *m. brachioradialis*. The same feature occurs in modern chimpanzees [19] and *A. afarensis* and it has been linked with climbing adaptations [18]. The same morphology is also present at Hadar [8, 18, 21] and in the Maka specimen [30], which we consider to be a male *Australopithecus afarensis*.

In lateral view, the proximal manual phalanx (preserved length: 33.8 mm; distal breadth: 7.1 mm) is curved recalling those of extant climbing primates as well as *A. afarensis*, a feature previously linked with grasping and climbing adaptations [22–25]. From the

Table I. Hypodigm of *Orrorin tugenensis* nov. gen. nov. sp.

Tableau I. Hypodigme d'*Orrorin tugenensis* nov. gen. nov. sp.

Catalogue No	Locality	Specimen	Collector	Date
KNM LU 335	Cheboit	lower molar	Martin Pickford	1974
BAR 349′00	Kapcheberek	manual phalanx	Evalyne Kiptalam	13 October 2000
BAR 1000′00	Kapsomin	2 mandible fragments	Kiptalam Cheboi	25 October 2000
BAR 1002′00	Kapsomin	left femur	Martin Pickford	4 November 2000
BAR 1004′00	Kapsomin	right humeral shaft	Brigitte Senut	5 November 2000
BAR 1003′00	Kapsomin	proximal left femur	Dominique Gommery	5 November 2000
BAR 1001′00	Kapsomin	upper central incisor	Samuel Chetalam	10 November 2000
BAR 1215′00	Aragai	proximal right femur	Martin Pickford	11 November 2000
BAR 1390′00	Kapsomin	lower fourth premolar	Samuel Chetalam	13 November 2000
BAR 1425′00	Kapsomin	upper right canine	Kiptalam Cheboi	16 November 2000
BAR 1426′00	Kapsomin	upper left third molar	Evalyne Kiptalam	17 November 2000
BAR 1900′00	Kapsomin	upper right third molar	Joseph Chebet	23 November 2000
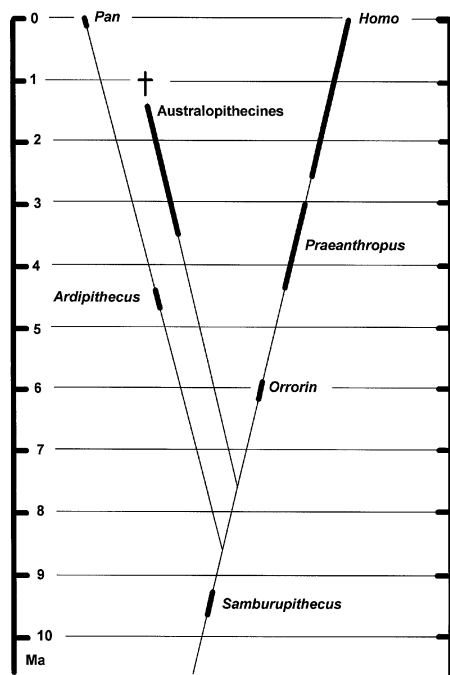
Figure 2. Phylogenetic position of *Orrorin tugenensis* nov. gen. nov. sp.

Figure 2. Position phylogénétique d'*Orrorin tugenensis* nov. gen. nov. sp.

upper limb morphology, it appears that *Orrorin* was adapted to arboreal activities.

2.11. Phylogeny

Orrorin confirms that small, thick enamelled molars are an archaic feature for the hominid lineage, which is retained in *Homo*. Australopithecines retained thick enamel but developed megadonty, which increased through time. In contrast, *Ardipithecus* has thin enamelled cheek teeth, which may be a derived trait for the Gorillidae. If so, then the common ances-

tor of hominids and gorillids would have possessed small teeth with thick enamel. This scenario is comforted by the presence of the hominoid *Samburupithecus* in the Late Miocene of Kenya (9.5 Ma) [9, 10] (*figure 2*).

2.12. *Orrorin* and the East Side story

From the point of view of the timing of the dichotomy between African apes and hominids, the presence of the hominid *Orrorin* at 6 Ma accords with the East Side story proposed by Coppens [1–3].

3. Conclusions

On the basis of dental and postcranial morphology, it appears that *Orrorin* belongs to the hominid lineage, which was already present 6 Ma ago. This confirms the hypothesis that the divergence between apes and humans took place prior to 6 Ma, and probably between 9 and 7 Ma (*figure 2*). The molars are smaller than those of Australopithecines and are closer in size to those of *Ardipithecus*. The anterior teeth, upper incisor and canine, as well as the lower P_4 are less hominid-like and more ape-like, being closer in morphology to teeth of female chimpanzees. The molar enamel is thick. Another important feature is the relatively great depth of the *corpus mandibularis*, which is an archaic feature among hominids. Compared to later hominids, it seems that small jugal teeth relative to body size would be a primitive feature, inherited from the common ancestor of African apes and hominids, and retained in the *Homo* lineage. If this is so, then Australopithecines would have progressively developed megadonty — large jugal teeth and relatively small bodies. The postcranial evidence suggests that *Orrorin tugenensis* was already adapted to habitual or perhaps even obligate bipedalism when on the ground, but that it was also a good climber. Many scholars

Table II. Dental measurements of *Orrorin tugenensis* nov. gen. nov. sp. compared to those of Pliocene hominids.

Tableau II. Mensurations dentaires d'*Orrorin tugenensis* nov. gen. nov. sp. comparées aux Hominidés pliocènes.

	n	Mesio-distal	*n*	Labio/buccolingual
I^1				
Orrorin tugenensis				
BAR 1001′00 right	1	10e	1	8.7
Ardipithecus ramidus	1	(10)	2	7.5–8.2
Australopithecus anamensis				
KNM-KP 29283 right	1	8.4	1	8.6
KNM-KP 30202 right	1	10.5	1	9.0
Australopithecus afarensis	3	10.8–11.8	5	7.1–8.6
$\underline{C}$				
Orrorin tugenensis				
BAR 1425′00 right	1	11.0	1	9.3
Ardipithecus ramidus	2	(11.2)–11.5	2	11.1–11.7
Australopithecus anamensis				
KNM-KP 29283 right	1	11.7	1	9.2
Australopithecus afarensis	9	8.9–11.6	10	9.3–12.5
M^3				
Orrorin tugenensis				
BAR 1426′00 left	1	10.2	1	13.1
BAR 1900′00 right	1	10.3	1	12.9
Ardipithecus ramidus	1	10.2	1	12.3
Australopithecus anamensis				
KNM-KP 29283 left	1	12.7	1	13.8
KNM-KP 30200 right	1	(11.0)	1	(12.0)
Australopithecus afarensis	8	10.5–14.3	8	13.0–15.5
P_4				
Orrorin tugenensis				
BAR 1390′00	1	8.0e	1	9.0e
Ardipithecus ramidus	2	7.5–8.9	2	9.5–9.7
Australopithecus anamensis				
KNM-KP 29281 right	1	8.2	1	10.6
KNM-KP 29281 left	1	8.4	1	10.0
KNM-KP 29286 right	1	9.6	1	11.6
KNM-KP 29286 left	1	9.7	1	11.7
Australopithecus afarensis	15	7.7–11.1	14	9.8–12.8
M^*				
Orrorin tugenensis				
KNM LU 335	1	11.4	1	10.6
M_2				
Orrorin tugenensis				
BAR 1000′00 left	1	11.5e	1	11.8e
Ardipithecus ramidus	1	(13.0)	1	11.9
Australopithecus anamensis				
KNM-KP 29281 right	1	13.2	1	12.5
KNM-KP 29281 left	1	13.0	1	12.7
KNM-KP 29286 right	1	14.6	1	13.6
KNM-KP 29286 left	1	14.6	1	13.7
Australopithecus afarensis	23	12.4–16.2	22	12.1–15.2
M_3				
Orrorin tugenensis				
BAR 1000′00 right	1	12.4e	1	11.2
BAR 1000′00 left	1	12.3e	1	10.4
Ardipithecus ramidus	1	12.7	1	11.0
Australopithecus anamensis				
KNM-KP 29281 right	1	14.8	1	12.3
KNM-KP 29281 left	1	14.5	1	12.4
KNM-KP 29286 right	1	13.8	1	12.3
KNM-KP 29286 left	1	14.4	1	12.8
Australopithecus afarensis	14	13.7–16.3	14	12.1–14.9

*The measurements for *Ardipithecus ramidus* and *Australopithecus afarensis* are from [28] and for *Australopithecus anamensis* from [12] (e = estimated measurement).

have considered that the earliest hominids were small animals; the femur and humerus of *Orrorin* are 1.5 times larger than those of AL 288.1, probably equivalent in size to a female common chimpanzee, indicating that the ancestor may have been larger than previously envisaged.

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