

Dental anatomy of the early hominid, *Orrorin tugenensis*, from the Lukeino Formation, Tugen Hills, Kenya

Brigitte SENUT^{1,*}, Martin PICKFORD² & Dominique GOMMERY³

¹ CR2P - Centre de Recherche en Paléontologie - Paris, MNHN - CNRS - Sorbonne Université, Muséum national d'Histoire naturelle, CP 38, 8, rue Buffon, F-75252 Paris cedex 05, France. E-mail: *brigitte.senut@mnhn.fr

² CR2P - Centre de Recherche en Paléontologie - Paris, MNHN - CNRS - Sorbonne Université, Muséum national d'Histoire naturelle, CP 38, 8, rue Buffon, F-75252 Paris cedex 05, France. E-mail: martin.pickford@mnhn.fr

³ CR2P - Centre de Recherche en Paléontologie - Paris, CNRS - MNHN - Sorbonne Université, Campus Pierre et Marie Curie - Jussieu, T. 46 - 56, E.5, Case 104, F-75252 Paris cedex 05, France. E-mail: dominique.gommery@upmc.fr

Abstract

Subsequent to the initial publication of the Late Miocene hominid genus and species, *Orrorin tugenensis*, in 2001, additional dental remains were discovered which comprise the subject of this paper. Detailed descriptions of all the *Orrorin* fossils are provided and comparisons are made with other late Miocene and early Pliocene hominoid fossils, in particular *Ardipithecus ramidus*, *Ardipithecus kadabba* and *Sahelanthropus tchadensis*. The Late Miocene Lukeino Formation from which the remains of *Orrorin* were collected, has yielded rare remains of a chimpanzee-like hominoid as well as a gorilla-sized ape. Although comparisons with *Ardipithecus ramidus* are difficult due to the fact that measurements of the teeth have not been published, it is concluded that *Ar. ramidus* is chimpanzee-like in several features, whereas some of the *Ardipithecus kadabba* fossils are close to *Orrorin* (others are more chimpanzee-like). This study indicates that there were at least three hominoids living in Eastern Africa during the Latest Miocene, one an early hominid, one an early chimpanzee-like ape (*Ardipithecus ramidus*) and the third a gorilla-sized ape (not yet named). Further finds are required to resolve the status of these hominoids.

Keywords

Hominidae, Hominoidea, Upper Miocene, dental anatomy, Kenya.

Résumé

Anatomie dentaire du premier hominidé, *Orrorin tugenensis*, de la Formation de Lukeino (Collines Tugen, Kenya).- Après la première publication en 2001 de l'hominidé du Miocène supérieur, *Orrorin tugenensis*, d'autres restes dentaires ont été découverts qui font l'objet de cet article. Tous les fossiles d'*Orrorin* sont décrits en détail et comparés aux autres fossiles d'hominidés du Miocène supérieur et du Pliocène inférieur, notamment *Ardipithecus kadabba*, *Ardipithecus ramidus* et *Sahelanthropus tchadensis*. La Formation Miocène supérieur de Lukeino, d'où proviennent les restes d'*Orrorin* a livré quelques rares spécimens d'un hominoïde ressemblant à un chimpanzé et un grand singe de la taille d'un gorille. Bien que les comparaisons avec *Ardipithecus ramidus* soient difficiles, car les mesures dentaires de ce dernier n'ont pas été publiées, on remarque que certains caractères d'*Ardipithecus ramidus* sont semblables à ceux du chimpanzé, certains présents chez *Ardipithecus kadabba* ressemblent à ceux d'*Orrorin* (alors que d'autres sont plus proches de ceux des chimpanzés). Cette étude montre que trois hominoïdes au moins vivaient en Afrique orientale au Miocène terminal: un hominidé ancien, un hominoïde proche du chimpanzé (*Ardipithecus ramidus*) et un de la taille d'un gorille (non encore nommé). D'autres découvertes sont nécessaires pour résoudre le statut de ces hominoïdes.

Mots-clés

Hominidae, Hominoidea, Miocène supérieur, anatomie dentaire, Kenya

1. INTRODUCTION

In 1974, an isolated lower molar was found at Cheboit in the 6 million year old Lukeino Formation in the Tugen Hills (Baringo District, Kenya) (Pickford, 1975). Its hominid status was subject to debate partly because the

tooth was rolled (Corruccini & McHenry, 1980; Hill, 1994; 1999; Hill & Ward, 1988, McHenry & Corruccini, 1980; Pickford, 1975; Ungar *et al.*, 1994; Senut, 1998), but mainly because no other specimens of comparable age had been discovered. Its status was clarified in the fall of 2000, when the Kenya Palaeontology Expedition

discovered new dental and postcranial material of a hominid in the same Formation at three sites (Kapsomin, Aragai and Kapcheberek) (Senut *et al.*, 2001; Pickford & Senut, 2001). A new taxon, *Orrorin tugenensis*, was erected for the species to which the Lukeino molar belonged and additional dental and post-cranial fossils were described which provided evidence of bipedal locomotion and climbing in this early hominid which was taller than the *Australopithecus afarensis* individual, AL 288.1 (Senut *et al.*, 2001; Pickford *et al.*, 2002; Galik *et al.*, 2004; Richmond & Jungers, 2008; Gommery & Senut, 2006; Nakatsukasa *et al.*, 2007). Since the 2001 publication, the hypodigm of *Orrorin tugenensis* has doubled and the new dental remains (Tab. 1) allow a better comparison with other Upper Miocene and Lower Pliocene hominoids such as *Ardipithecus ramidus*, *Ardipithecus kadabba* and *Sahelanthropus tchadensis*.

2. MATERIAL AND METHODS

Comparisons are made with Miocene and Pliocene hominoids from Kenya, Ethiopia and Chad. Comparisons with modern apes have been made in the collections of the African Zoology section of the Musée Royal d'Afrique Centrale (Belgium) and the Département d'Ecologie et de Gestion de la Biodiversité of the Muséum National d'Histoire Naturelle in Paris.

3. GEOLOGICAL CONTEXT AND AGE

The dental remains were collected in the Kapsomin Ravine (Fig. 1) which exposes the Kapsomin Member of the Lukeino Formation and are mostly surface finds (Senut *et al.*, 2001). The Lukeino Formation has a thickness of 110 metres of lacustrine and fluvial sediments, intruded by the trachybasaltic Rormuch Sills and it contains several tuffaceous levels. It overlies the Late Miocene Kabarnet Trachyte and is overlain by the basalts of the Early Pliocene Kaparaina Formation. Previous age estimates clustered around 6.0 Ma (Pickford, 1975; Chapman & Brook, 1978; Hill *et al.*, 1985). New age determinations employing the K/Ar method were performed on lava and tephra samples collected in a controlled stratigraphic context and the magnetic polarity of the sequence was determined. The dates obtained indicate that the Lukeino Formation is between 6.2 and 5.5 Ma (Sawada *et al.*, 2002). The Kapsomin Member is positioned between the Rormuch Sills above and the Kapsomin Basalt Member below (Fig. 2) and is dated at 5.8 to 5.9 Ma (Sawada *et al.*, 2002; Deino & Hill, 2002). This time range accords well with the faunal assemblages and the palaeomagnetism (Pickford, 1978, 1986; Pickford & Senut, 2001; Sawada *et al.*, 2002).

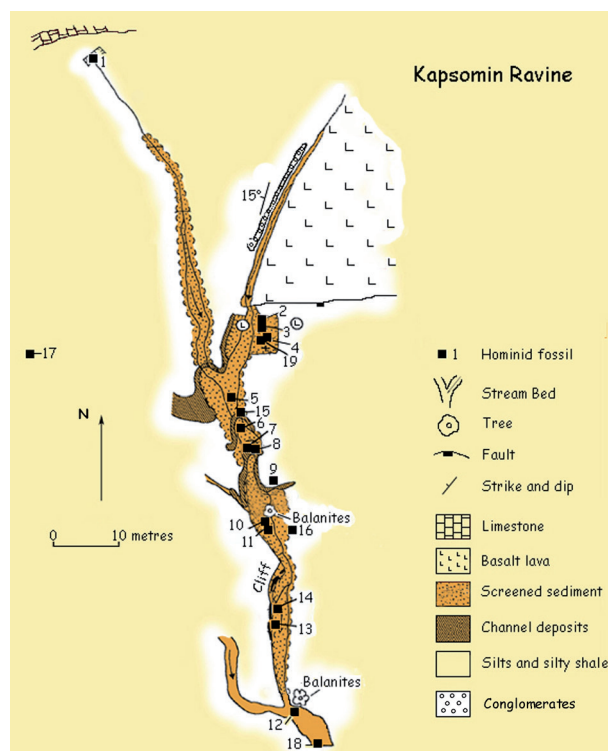


Fig. 1: Map of the Kapsomin Ravine showing the locations of the *Orrorin tugenensis* material. 1 - BAR 1002'00 Proximal femur; 2 - BAR 1004'00 Humeral shaft; 3 - BAR 1003'00 Proximal femur; 4 - BAR 1425'00 Upper canine; 5 - BAR 1001'00 Upper incisor (part of the hypodigm in Senut *et al.*, 2001 later attributed to a fossil gorilliform); 6 - BAR 1390'00 Lower p/4; 7 - BAR 1000a'00 Fragment of left mandible; 8 - BAR 1000b'00 Fragment of right mandible; 9 - BAR 210'01 Upper right M2/; 10 - BAR 1426'00 Upper M3/; 11 - BAR 1900'00 Upper M3/; 12 - BAR 200'01 Lower canine; 13 - BAR 201'01 Mandibular symphysis; 14 - BAR 202'01 Lower left i/2; 15 - BAR 380'01 Upper right M1/; 16 - BAR 400'01 Upper right P4/; 17 - BAR 521'01 Lower right p/4; 18 - BAR 1900'01 Lower right p/3; 19 - BAR 1901'01 Thumb distal phalanx.

4. DESCRIPTIONS AND COMPARISONS

Order Primates Linnæus, 1758
 Suborder Anthropeidea Mivart, 1864
 Superfamily Hominoidea Gray, 1825
 Family Hominidae Gray, 1825
 Genus *Orrorin* Senut *et al.*, 2001

Orrorin tugenensis Senut *et al.*, 2001

4.1. Mandible

The mandible is composed of three fragments (Fig. 3): BAR 1000a'00, a left mandibular fragment with the distal root of m/1, and complete but damaged m/2 and m/3; BAR 1000b'00, a right mandibular fragment with m/3

Table 1: List of the material attributed to *Orrorin tugenensis*.

N°	Locality	Identification	Collection date
KNM LU 335	Cheboit	Left m/3	1974
BAR 1000'00 a	Kapsomin	Left mandibular fragment with m/1 root, m/2 and m/3	25/10/2000
BAR 1000'00 b	Kapsomin	Right mandibular fragment with m/3	25/10/2000
BAR 1390'00	Kapsomin	Left p/4	13/11/2000
BAR 1425'00	Kapsomin	Right upper canine	16/11/2000
BAR 1426'00	Kapsomin	Left M3/	17/11/2000
BAR 1900'00	Kapsomin	Right M3/	23/11/2000
BAR 200'01	Kapsomin	Left lower canine	03/2001
BAR 201'01	Kapsomin	Mandibular symphysis (same as BAR 1000'00)	03/2001
BAR 210'01	Kapsomin	Right M2/	03/2001
BAR 380'01	Kapsomin	Right M1/	08/2001
BAR 400'01	Kapsomin	Right P4/	08/2001
BAR 521'01	Kapsomin	Right p/4	08/2001
BAR 1900'01	Kapsomin	Left p/3	08/2001
BAR 1530'02	Kapsomin	Right i/2	08/2002

and BAR 201'01, a fragment of mandibular symphysis which fits with BAR 1000a'00, despite the fact that the contact is not very good. BAR 1000b'00 has the best preserved tooth.

4.1.1. Left mandibular fragment: BAR 1000a'00

The external surface of the body is vertical and flat and shows many cracks related to taphonomic processes. The dental row (m/1-m/3) measures ca. 58 mm mesio-distally. The *corpus mandibularis* is damaged inferiorly, except below the m/3. However, the depth of the body can be measured at the level of m/3 and is estimated to be 35.4 mm, which is much deeper than in *Pan troglodytes* and *Pan paniscus*, deeper than in *Ardipithecus kadabba* (estimated at 32 mm lingually and 30 mm buccally at the m/1-m/2 level (Haile-Selassie *et al.*, 2009), slightly deeper than in *Australopithecus afarensis* (White & Johanson, 1982), and *Australopithecus anamensis* (Leakey *et al.*, 1995; Ward *et al.*, 2001) but recalls the large Miocene apes from East Africa, such as *Proconsul*, *Ekembo* and *Ugandapithecus*. It is deep relative to molar size (12.3 MD x 10.4 BL for the left m/3).

The thickness of the body, taken at the alveolar margin at the mesial break, is moderate (17.4 mm at the m/2 level), which is slightly smaller than in *Ardipithecus kadabba* (18.5 mm at the m/2), greater than in *Pan paniscus* (10.4-13.3 mm), and falls into the upper part of the range of variation of *Pan troglodytes* (12.6-18.8 mm), and less than in Pliocene hominids (24.2-28.0 mm for *Australopithecus afarensis*) (Personal data and Prat, personal communication). The mandible narrows inferiorly to 8.8 mm at the inferior border. The

base of the ascending ramus is preserved and in lateral view ends almost at the alveolar margin, slightly hiding the distal part of the m/3; the extramolar sulcus is short (approximately 6.0 mm).

The buccal surface of the mandibular ramus is remarkably flat and the lingual surface exhibits a wide depression in its lower half partly due to post-mortem compaction. There is no upper *torus mandibularis* evident in this fragment (Fig. 4).

4.1.2. Right mandibular fragment: BAR 1000b'00

The right mandibular fragment, BAR 1000b'00, is poorly preserved and does not yield additional information about mandibular morphology that is not already available from the left mandible of this individual.

4.1.3. Symphysis

A fragment of mandibular symphysis, BAR 201'01, was found in 2001 after the publication of the holotype (Senut *et al.*, 2001) (Fig. 5). Its inferior border is damaged. It preserves the roots of left central incisor, lateral incisor, canine (broken at the cervix) and the mesial root of the p/3. There is no diastema between the canine and the first premolar. The bone is broken at the level of the genioglossal fossa which is large (minimum diameter of 5.8 mm). The anterior part of the symphysis is vertical and turns infero-posteriorly in the inferior half of the bone. This morphology contrasts with that seen in chimpanzees which shows a procumbent symphysis. The mandible is high, more than 34.0 mm beneath the i/2, and probably belongs to the mandibular fragment BAR 1000'00; this is indicated by the fact that the left part of the mandibular ramus matches the infero-mesial part of

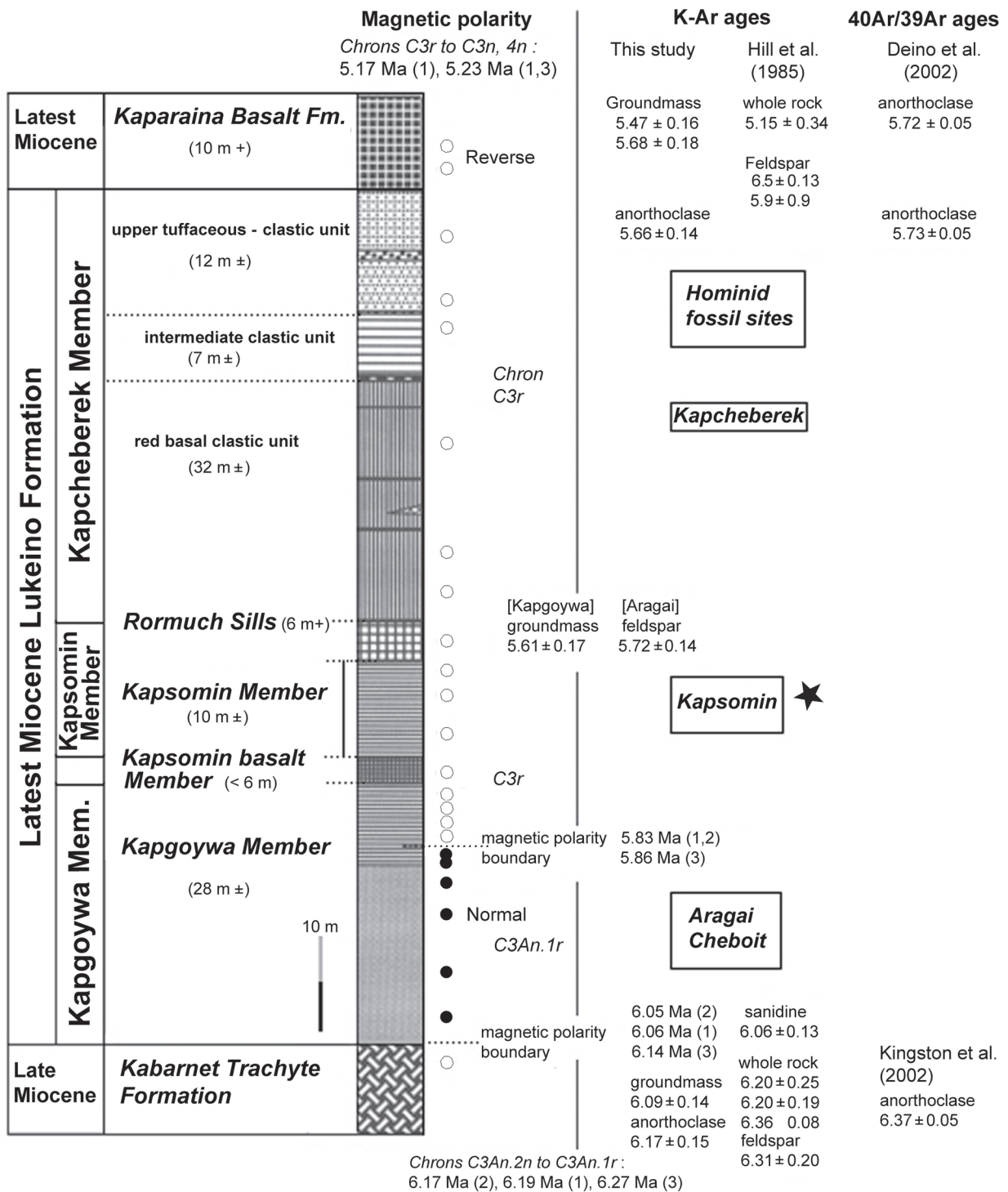


Fig. 2: Stratigraphic sequence showing the position of the hominid material. The dental remains were found at Cheboit and Kapsomin. The star shows the stratigraphic levels at which new dental material was collected (based on Sawada *et al.*, 2002; Deino & Hill, 2002).

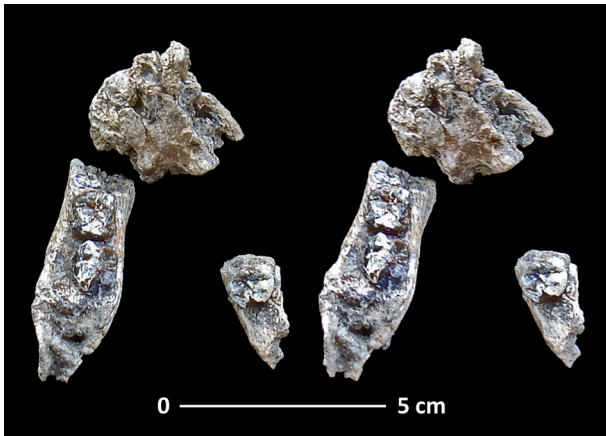


Fig. 3: Holotype mandible of *Orrorin tugenensis*, BAR 1000a'00 (left mandibular fragment), BAR 1000b'00 (right mandibular fragment), BAR 201'01 (symphysis) (stereo occlusal view) (scale = 5 cm).

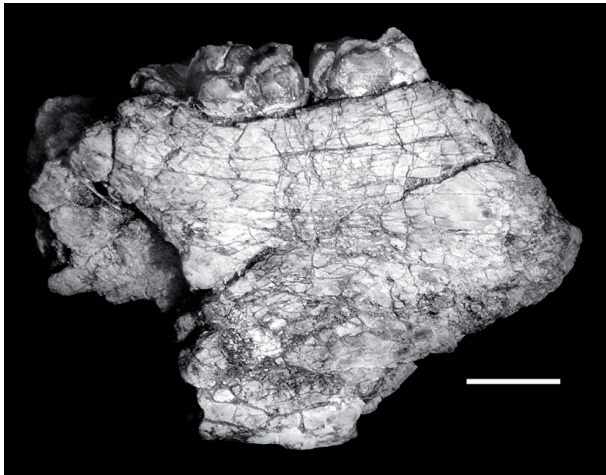


Fig. 4: Left mandibular fragment of *Orrorin tugenensis*, BAR 1000a'00 (lingual view). (Scale = 1 cm).

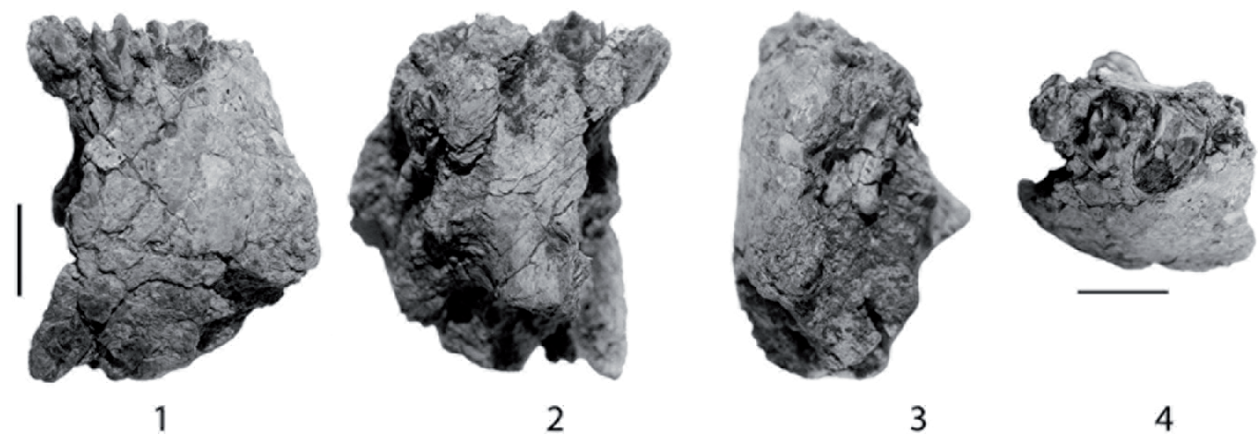


Fig. 5: Mandibular symphysis BAR 201'01 part of the holotype of *Orrorin tugenensis*. 1: labial view; 2: lingual view; 3: distal view; 4: occlusal view (Scales = 1 cm).

BAR 1000a'00 although the contact is not perfect. The roots of the incisors are mesio-distally compressed (MD/BL= 64.6% in i/1 – 5.3 mm/8.2 mm; MD/BL= 48.8% in i/2: 4.1 mm/8.4 mm) different from chimpanzees which have mesio-distally elongated lower incisor, the anterior teeth of BAR 201'01 were probably small. The alveolar planum is well preserved (length = 21.5 mm) and slopes ventro-distally moderately to a weakly developed superior transverse torus. The inclination between the anterior part of the symphysis and the planum is estimated to be 40°. Despite the difficulty of orienting the fragment, we estimate that the planum slopes at ca 35° with respect to the alveolar margin of the teeth. The canine root is small and produces a rounded aspect to the buccal surface of the mandible, which contrasts with the more angular morphology seen at the canine level in chimpanzees, related to a larger canine root. The left p/3 has two roots. In cross-section, the mesial root is triangular with rounded corners, and is smaller and mesio-buccally positioned relative to the distal one which has a slight bifurcation at its tip and which is mesio-distally compressed and bucco-lingually broad. This morphology indicates that the tooth would not have had a very asymmetrical occlusal outline and would have possessed a weakly protruding mesio-buccal slope. Despite the poor preservation of the fragment, the long axis of the distal root appears to be vertically implanted in the mandible, which contrasts with the condition seen in chimpanzees in which it is slanted. The morphology of the premolar roots shows that the C1/-p/3 honing complex would have been reduced in *Orrorin tugenensis*. Few comparisons can be made with the holotype of *Ardipithecus kadabba* (ALA-VP-2/10A) (Haile-Selassie, 2001; Haile-Selassie *et al.*, 2009), as both materials are fragmentary and the Ethiopian material was not available for comparisons. On the basis of its corpus depth and width the *Orrorin* mandible appears to be smaller than that of *Ardipithecus*.

4.2. Upper dentition

4.2.1. Upper canine

Material: BAR 1425'00 (right)

This well-preserved upper canine (Fig. 6) is a low-crowned, asymmetrical tooth which is triangular in labial view. It is not strongly mesio-distally compressed (MD = 11.0 mm; BL = 9.3 mm; height buccal = 12.7 mm). Slight wear is seen on the apex, which is smoothly pointed, and along the distal crest. The mesial shoulder is low, reaching the lower third of the crown, but is higher than the distal one. This morphology recalls *Ardipithecus ramidus* (Haile-Selassie *et al.*, 2004, 2009), *Sahelanthropus tchadensis* (Brunet *et al.*, 2002) and is also seen in female chimpanzees. In *Ardipithecus kadabba* (Haile-Selassie *et al.*, 2004), the canine (ASK-VP6-3/400, right) is broken at the cervix and thus it is not clear that the mesial shoulder is lower than in *Orrorin*, contra Haile-Selassie *et al.*, 2004.

A shallow, narrow mesial groove (which widens rootwards) runs superiorly and ends lingually at the cervix in a small cingular swelling. This groove occurs in all Miocene and modern apes, is present in *Ardipithecus kadabba*, but is absent in *Ardipithecus ramidus* and does not occur in australopithecines or *Homo*.

The labial surface is gently convex apico-cervically and mesio-distally, whereas the disto-lingual surface is concave. On its distal half, a clear but low basal swelling can be seen. This convexity differs from Miocene hominoids, but is reminiscent of female chimpanzees (Fig. 7). The lingual surface of the canine is smooth: there are no grooves, unlike *Ardipithecus kadabba* and *Australopithecus afarensis*.

Compared to *Ardipithecus kadabba*, the upper canine is shorter apico-basally and narrower labio-lingually and does not show any lingual groove.

4.2.2. Upper premolar

Material: BAR 400'01 (right P4/)

This upper P4/ is badly damaged (Fig. 8), only the buccal half of the crown is preserved (MD = 6.8 mm). The paracone is a voluminous, low, moderately worn cusp which contrasts with the small and thin one in chimpanzees. The mesial and distal fovea are preserved; the mesial one appearing to be the largest, despite the damage to the occlusal surface. Two small depressions can be seen on the buccal surface but wear has removed most of these grooves. The mesial and distal crests are present, they are incipient and short (the mesial one being shorter).

The fragmentary nature of left P4/ in *Ardipithecus kadabba* (ASK-VP-3/404) and BAR 400'01 prevents comparisons.

4.2.3. Upper molars

Material: BAR 380'01 (Right M1/), BAR 210'01 (Right M2/), BAR 1900'00 (Right M3/), BAR 1426'00 (Left M3/) (Fig. 9).

BAR 380'01: upper right first molar

This upper first molar lacks the mesial margin of the crown. It is a low-crowned, rectangular tooth broader than long (MD = 11.0 mm; BL = 12.6 mm). The buccal cusps are voluminous, deeply worn, but still possessing some relief, and the lingual ones are deeply worn exposing two lakes of dentine, the protoconal lake being the larger of the two. The crista obliqua is well marked but low. The mesial fovea is not visible as it has been obliterated by wear. The distal fovea is a small and shallow depression. There is no strong crenulation on the occlusal surface, due to advanced wear. There is no lingual cingulum. The distal interstitial facet caused by contact against the M2/ is well preserved, and matches the corresponding facet in the M2/.

BAR 210'01: upper right second molar

This upper right second molar (MD = 11.0 mm; BL = 13.2 mm) is a low-crowned tooth; the cusps are low, voluminous and internally positioned, as in the lower molars. The occlusal outline is trapezoidal and not rectangular, unlike chimpanzee specimens. The buccal cusps have slightly more relief than the lingual ones. In buccal view there is a short, shallow groove between the paracone and metacone. Crenulation of the enamel has almost been obliterated by wear leaving a small wrinkle of enamel in the short groove between the buccal cusps. The paracone is located more buccally than the metacone giving an oblique aspect to the buccal margin whereas the lingual margin runs mesio-distally. As the protocone is also more distally positioned relative to the paracone, the mesial border runs obliquely. The mesial fovea is reduced and shallow, in prolongation of the trigon basin. The distal fovea is large. The *crista obliqua* is visible, but low. The lingual cusps are worn, but dentine is not exposed. Due to the lack of cingulum and the low stature of the protocone, a mesio-lingual slope (or flare) on the protocone can be observed. It ends in the mesio-lingual corner of the tooth. This pattern differs from lower Miocene apes, *Nacholapithecus* and *Samburupithecus*, but is reminiscent of *Kenyapithecus* and *Australopithecus afarensis*. The protoconule is not expressed, but in the prolongation of the protocone, there is a low swelling in its place.

A small distal interstitial facet is present and matches the contact facet of the upper right third molar discovered in 2000 (BAR 1900'00) indicating that these two teeth belong to a single individual.

No comparisons can be made with *Ardipithecus kadabba* because no M2/ of this species is known.

BAR 1900'00: upper right third molar

The upper right third molar is lightly worn, leaving details of morphology to be observed (MD = 10.3 mm; BL = 12.9 mm). As with the M2/ the tooth shows an almost triangular occlusal outline due to the buccal protrusion of the paracone. This gives a clear oblique buccal margin.

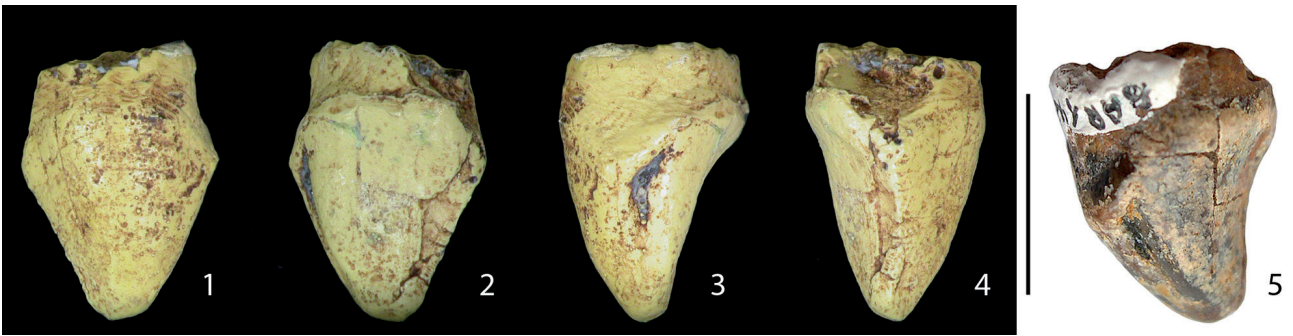


Fig. 6: *Orrorin tugenensis* upper right canine, BAR 1425'00. 1: labial view; 2: lingual view; 3: mesial view; 4: distal view; (cast) 5: mesio-lingual view (original fossil) (scale = 1 cm).



Fig. 7: Cast of *Orrorin tugenensis* upper right canine, BAR 1425'00 (left) compared with a female *Pan troglodytes* (right). 1: lingual view; 2: labial view (scale = 1 cm).



Fig. 9: *Orrorin tugenensis* right upper molars, occlusal view (M1/: BAR 380'01, M2/: BAR 210'01, M3/: BAR 1900'00) belonging to the same individual. (scale = 1 cm).

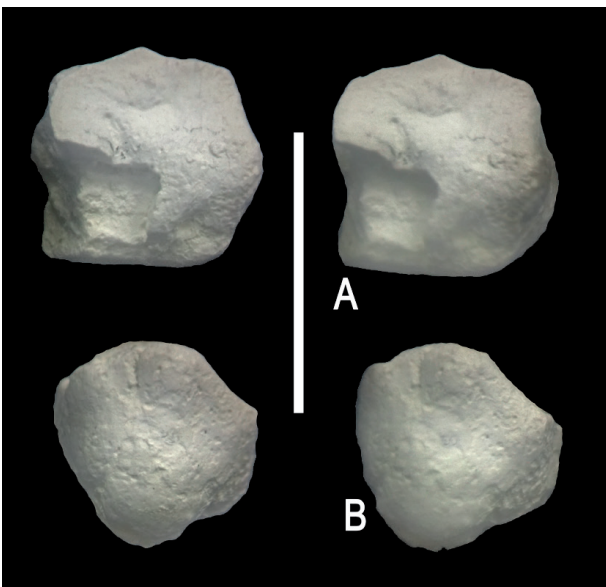


Fig. 8: *Orrorin tugenensis* right upper P4/ (cast). A: stereo occlusal view; B: stereo buccal view (scale = 1 cm).

The distal cusps of the crown are reduced and the small metacone contrasts with the enlarged protocone. There is a short and shallow buccal groove between the paracone and the metacone. The surface of the enamel is crenulated. The interstitial wear facet caused by contact with M2/ is well marked on the mesial surface and it matches the corresponding facet in molar BAR 210'01. The mesial fovea can be distinguished, but it is poorly defined and close to the paracone. The *crista obliqua* is low, but clear.

BAR 1426'00: upper left third molar

The occlusal surface is deeply worn (MD = 10.2 mm; BL = 13.1 mm) (Fig. 10). The tooth does not belong to the same individual as BAR 1900'00 as it is from an older individual. The outline of the occlusal surface is trapezoidal, almost triangular with a bucco-lingual obliquity of the buccal margin as seen in BAR 1900'00. Despite the wear, the voluminous cusps can be observed. The occlusal surface is wrinkled, especially on the lingual side of the protocone but not as much as in australopithecines. The cingulum is almost erased, only

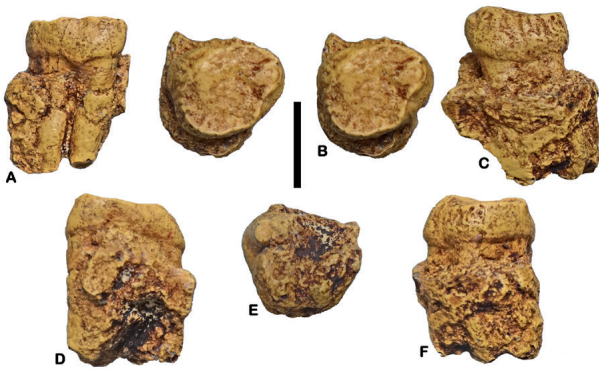


Fig. 10: *Orrorin tugenensis* upper left M3/, BAR 1426'00. A) buccal, B) stereo occlusal, C) lingual, D) mesial, E) radicular, F) distal views (scale = 1 cm).

a small remnant can be identified at the mesio-lingual corner of the protocone. As in BAR 1900'00, the distal cusps, in particular the metacone, are strongly reduced. Three roots are preserved, two buccal ones and a lingual one. The buccal roots are close to each other, the mesial one being further laterally positioned than the distal one. On the M3/, the roots are long and broad (the distal root is 13.5 mm tall on the buccal side).

The upper right molars BAR 380'01 (M1/), BAR 210'01 (M2/) and BAR 1900'00 (M3/) have interstitial facets that match each other. The wear gradient differs from those of extant chimpanzees. When the protocone and hypocone in the M1/ are strongly worn in *Orrorin* and *Pan*, the same cusps are weakly worn in *Orrorin*, but deeply worn in the M2/ of *Pan*, and the lingual cusps of the M3/ show some wear in *Pan*, whereas in *Orrorin* the dentine is still not visible (Fig. 11).

The overall morphological pattern of the molars clearly differs from those of chimpanzees by the presence of voluminous and more centrally positioned cusps of *Orrorin*, the reduction of the fovea, the reduction of the lingual cingulum and the enhanced wear gradient.

4.3. Lower dentition

4.4.1. Lower incisor

Material: BAR 1530'02 (right i/2)

BAR 1530'02 (Fig. 12) is a complete, lightly worn tooth which lacks a tiny fragment from the tip of the root. It is a long and narrow tooth (Maximal height = 27.7 mm; MD length = 7.5 mm at the occlusal level; LL width = 2.1 mm at the mesial edge of the wear surface). The root is elongated which suggests that the mandibular symphysis would have been tall which agrees with the symphyseal dimensions in Bar 201'01. The tooth is mesio-distally compressed at the cervix, the mesio-distal length is 4.9 mm and the labio-lingual width 7.7 mm. This differs from the incisors in *Pan* which are mesio-distally wider. Relative to the length of the root, the crown is taller in



Fig. 11: Comparison of the upper right molar row in *Orrorin tugenensis* (left) and an extant chimpanzee (*Pan troglodytes*) (right) (scale = 1 cm).



Fig. 12: *Orrorin tugenensis* right i/2, BAR 1530'02. 1: labial view; 2: lingual view; 3: mesial view; 4: distal view; 5: *Pan troglodytes* lower i/2 in lingual view (scale = 1 cm).

Orrorin than in chimpanzees. In lingual view, the mesial edge is slightly oblique to the long axis of the tooth and meets the apical border at an angle of just under 90°. The distal margin of the tooth is almost vertically oriented and forms a rounded junction with the apical border. On the lingual surface of the crown, a weakly developed apico-basal pillar is visible in the mid-line; from cervix to apex, the crown lengthens mesio-distally (4.9 mm at the cervix, 7.5 mm at the occlusal surface). In the superior part of the crown, slightly raised marginal ridges are visible mesially and distally. At the base of the crown lingually, there is a swelling, but not a strong tubercle as is often the case in *Pan*. There is no cingulum. In mesial view, the lingual side of the crown is strongly concave apico-basally; the labial side is slightly convex, and almost vertically oriented. This morphology contrasts with the morphology seen in most Miocene and extant African apes. A clear contact facet for the i/1 is developed superiorly. In occlusal view, the crown is 2.1 mm thick labio-lingually at the occlusal surface; the wear facet is continuous mesio-distally and slightly convex on its

labial side. As is usual in hominoids, the mesial and distal cervical lines are asymmetrical, the mesial line being more deeply v-shaped. The root is strongly compressed mesio-distally. In mesial view, it broadens gradually from the cervix inferiorly to the inferior 2/3 of its extent and then narrows rapidly towards its apex. On the distal surface of the root, a weak vertical groove is visible at its inferior end.

One $i/2$ is represented in the holotype of *Ardipithecus kadabba* (Haile-Selassie, 2001; Haile-Selassie *et al.*, 2009). Much of the occlusal part of the tooth is missing and the root is damaged. However, it differs from *Orrorin* by its prominent basal lingual tubercle and its marginal ridge structures.

4.3.2. Lower canine

Material: BAR 200'01 (left c/1)

This complete left lower canine (Fig. 13) is a slender tooth with a slightly worn apex [Total height root + crown = 38.0 mm; labial crown height = 13.4 mm; MD length at the cervix = 8.0 mm; LL breadth at the cervix = 10.4 mm; (height above the cervix = 13.4 mm)]. The crown is tall, pointed and asymmetrical in lingual and labial views. The size of the root matches the size of the left canine root preserved in the mandibular symphysis (BAR 201'01). In lingual view, the tooth is apico-basally straight. The crown is low compared to the root (11.9 mm versus 25.8 mm). The root is long (root length = 26.2 mm) and almost complete (a tiny flake is missing at its apex) and shows several hypoplastic lines along its surface (as is the case in *Ardipithecus kadabba*). On the mesio-lingual side of the root, a shallow longitudinal groove is present. In distal view, the root is straight and the crown is slightly canted lingually and is narrow. The mesial shoulder is situated approximately at midcrown (6.0 mm

from the cervix), which is relatively high compared to Miocene and modern apes, but low compared to australopithecines. It is close to the condition seen in the holotype of *Ardipithecus kadabba* ALA-VP 2/10 and STD-VP 2/61. A weak but sharp mesial crest is present and is strengthened by a small mesio-lingual groove. This pattern is different from *Ardipithecus kadabba* (STD-VP2/61) in which the mesio-lingual groove is deeper (Haile-Selassie, 2001; Haile-Selassie *et al.*, 2009). The disto-lingual crest is well-defined and runs from the apex distally down the distal edge of the crown to the basal tubercle, which is reinforced by the basal cingulum. Another small crest emerges from the basal tubercle upwards to merge with the disto-lingual crest defining a small and shallow triangular depression. In distal view, two wear facets are visible: one near the apex of the crown and one near the distal tubercle. The small apical one was caused by contact with the upper canine which suggests a non-honing C1/-p/3 complex in *Orrorin* somewhat resembling the facet in female *Pan* and many fossil hominoids (Fig. 14). The small rounded disto-buccal facet was produced by contact with the p/3, proving that there was no diastema between the two teeth, confirming the morphology seen in the mandible. Judging from the general morphology of the crown and the massive root, this tooth could represent a male individual.

Haile-Selassie (2001) report in *Ardipithecus kadabba* a bucco-lingual length smaller than the mesio-distal one (MD = 10.8 mm; LL = 7.8 mm), but the opposite is the case. Later, the terminology has changed: Haile-Selassie *et al.* (2009) use the maximum oblique diameter of the crown (11.2-10.8 mm mean for 2 specimens) and a maximum diameter perpendicular to the maximum oblique diameter (7.8 mm, same value in both specimens). The same occurs with *Sahelanthropus tchadensis* (max MD = 10.0 mm; BL = 8.0 mm). This arises from the different way of defining the mesio-distal and bucco-lingual lengths, but see Swindler (2002) for correct orientations of primate teeth.

4.3.3. Lower premolars

Material: BAR 1900'01 (left p/3), BAR 1390'00 (right p/4), BAR 521'01 (right p/4)

The lower p/3, BAR 1900'01, has two roots and is rhombohedral in occlusal outline (MD = 8.6 mm; BL = 9.7 mm) (Fig. 15). The crown is low and moderately worn: small flakes of enamel are missing at the base of the mesio-buccal slope and the mesio-lingual surface. The protoconid is a low and massive cusp which bears a slight wear facet on its apex which extends distally and disto-lingually over the distal fovea, which is thus reduced. The shortness of the fovea is related to the development of small tubercles on the distal cingulum. The metaconid is not enlarged, being represented by a swelling in the lingual cingulum. From this swelling, a small crest descends mesio-buccally to end in a cingulum



Fig. 13: *Orrorin tugenensis* lower left canine, BAR 200'01. 1-2 lingual stereo view; 3: mesial view; 4: distal view (scale = 1 cm).

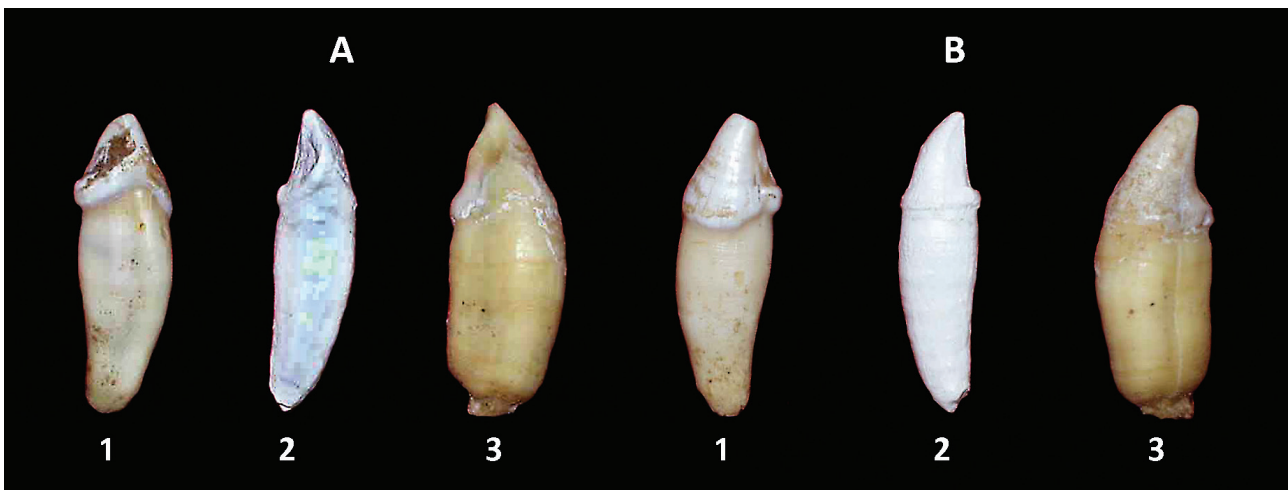


Fig. 14: Comparisons between *Orrorin tugenensis* lower canine, BAR 200'01, with male and female *Pan troglodytes*. A: mesial view; B: distal view. 1: *Pan troglodytes* female; 2: BAR 200'01; 3: *Pan troglodytes* male.

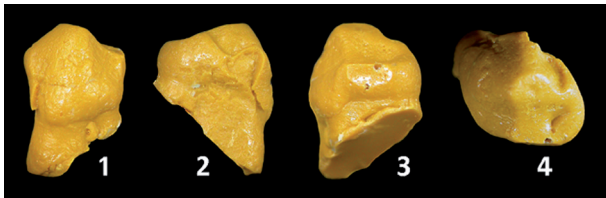


Fig. 15: *Orrorin tugenensis* left lower p/3 (cast), BAR 1900'01. 1: buccal view; 2: mesial view; 3: distal view; 4: occlusal view.

which runs on the mesial side of the tooth, but which is broken on the mesial surface of the tooth. There is a small elongated mesial fovea. On its mesial surface the fovea is bordered by a low mesial crest running down from the protoconid. The mesio-buccal groove is shallow and short, and the disto-buccal one wide, shallow and slightly concave. The two roots of the p/3 are slightly offset from one another, the mesial one sloping mesio-buccally; the distal one is bucco-lingually broadened. The extension of the enamel onto the mesial root is restricted and weaker than in chimpanzees. In distal view, a clear contact facet for the p/4 (4.0 x 2.2 mm) is present.

The weak development of the metaconid recalls the morphology seen in *Ardipithecus ramidus* (Haile-Selassie *et al.*, 2009; Suwa *et al.*, 2009). Otherwise, the *Ardipithecus* specimen being much damaged, comparisons are difficult.

BAR 1390'00 (Fig. 16), a damaged right lower fourth premolar (Senut *et al.*, 2001) is ovoid in occlusal outline and compressed mesio-distally (MD = 8 ++ mm; BL = 7.1 + mm). Enamel flakes are missing from the mesial, lingual and distal surfaces. The p/4 has two transverse roots as in *Sahelanthropus tchadensis* (Brunet *et al.*, 2002) and differs from *Ardipithecus ramidus* which possesses

a single root and *Ardipithecus kadabba* which has a Tome's root. The crown is low. The distal fovea is large as in Miocene and extant hominoids. Two main cusps are preserved: the metaconid which is small and low and a bulky protoconid which is the taller of the two cusps. A well-developed entoconid is seen on the disto-lingual corner of the crown. A distinct disto-buccal groove is preserved. From the apex of the protoconid emerge two ridges which run lingually and distally respectively. The disto-lingual aspect of the protoconid shows a wrinkled enamel surface. There is a distinct but small mesial fovea and a larger distal fovea, which is slightly lower than the mesial one. A contact facet is present on the mesial side but is not preserved on the distal side due to missing enamel. The median longitudinal fissure is deep except in the centre of the tooth. Both roots are mesio-distally compressed and exhibit a shallow longitudinal groove. The mesial root is oblique inferiorly and buccally; the distal root is vertical. The roots diverge close to the cervical level and run roughly parallel to each other. The mesial root is vertical but the distal root slants buccally. In scans two pulp canals can be observed which are blocked by some calcification (Fig. 16).

BAR 521'01 is larger than the other p/4 (MD = 7.9; BL = 9.9 mm) (Fig. 17), but is compatible in size with the lower p/3, BAR 1900'01. In its general morphology it is similar to BAR 1390'00. The tooth is quite worn and some enamel is missing on the lingual side of the crown. The protoconid is worn almost flat exposing a large area of dentine at the occlusal surface. The metaconid is visible and is smaller than the protoconid. A mesio-distal groove between the two main cusps is deeply hollowed and continuous, rising in the centre of the tooth. A short but prominent, smooth disto-buccal groove is visible, but the mesio-buccal one cannot be seen due to the heavy wear of the tooth. A clear vertical groove is present on the two roots, mesially on the anterior root and distally on the

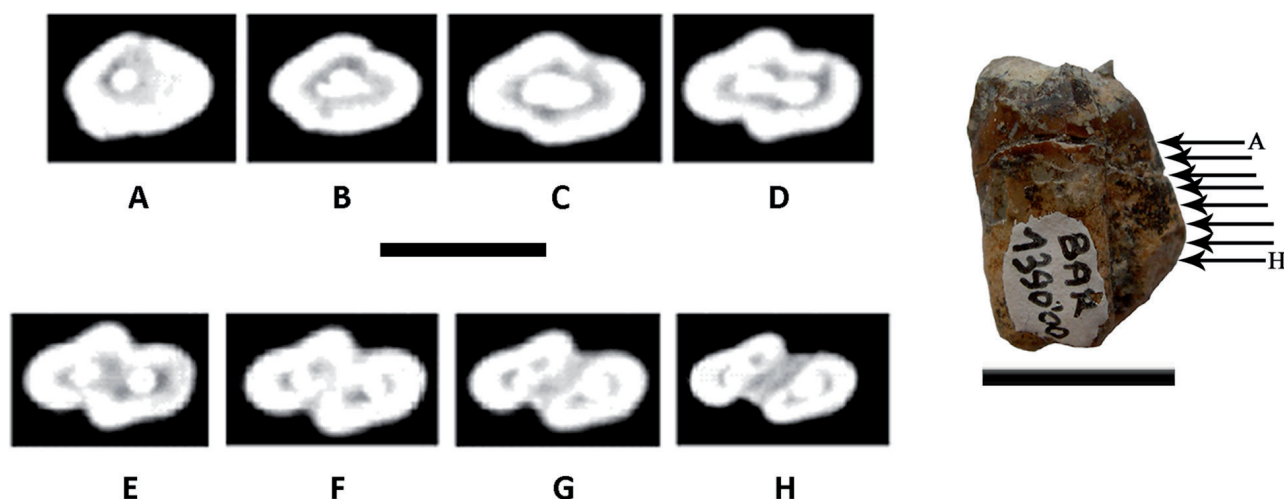


Fig. 16: Scans of the roots of the lower right p/4 of *Orrorin tugenensis* (Bar 1390'00) (Scale bars = 10 mm), A-H are scan levels shown in the accompanying image of the whole tooth. Scans are at the cervix (A), 200 microns (B) 400 microns (C) 600 microns (D) 700 microns (E) 900 microns (F) 1100 microns (H) and 1300 microns (H).

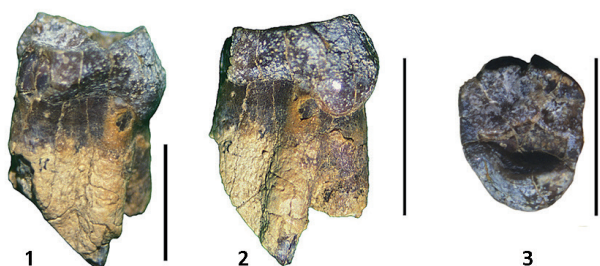


Fig. 17: *Orrorin tugenensis* right lower p/4, BAR 521'01. 1: mesial view; 2: mesio-lingual view; 3: occlusal view (scales = 1 cm).

posterior one. The roots are mesio-distally compressed, but seem less oblique than those of BAR 1390'00.

The dimensions are close to those of *Ardipithecus ramidus* (MD = 7.5-8.9 mm; BL = 9.5-9.7 mm) and fall into the range of variation of *Pan troglodytes*, they are larger than *Pan paniscus* and *Homo sapiens* and smaller than *A. anamensis* (MD = 8.2-9.7 mm; BL = 10.0-11.7 mm) and *A. afarensis* (MD = 7.7-11.1 mm; BL = 9.8-12.8 mm).

4.3.4. Lower molars

The left m/2 and m/3 and right m/3 are preserved in the holotype mandible (BAR 1000'00) (Senut *et al.*, 2001) (Fig. 3). The teeth are damaged and enamel is missing from the mesial and lingual surfaces in the left molars and from the mesial surface of the right molar which is also missing a chip of enamel distally. The occlusal outline of the m/2 is a round-cornered rectangle, being slightly elongated mesio-distally. The molars are damaged by cracks which run through the crowns, which are lightly worn. The cusps are low, bunodont,

centrally positioned and the talonid basin is restricted. In this respect, they differ from the molars of *Pan* in which the cusps are peripheralized and the talonid basin wide. The lingual cusps on the left m/3 are damaged, but are well-preserved on the right one: they are sharp and slightly higher than the buccal ones. The lingual side of the molars is more vertical than the buccal side. There is no cingulum. The distal fovea is preserved on the left m/2 and the right m/3. It is reduced and in the m/3 this reduction could be related to the mesio-distal shortness of the entoconid. The hypoconulid is well-developed and slightly buccal to the mid-line of the tooth. The trigonid and talonid show coarsely crenulated enamel, but lack the extensive wrinkling seen in chimpanzee molars. On the buccal aspect, a deep groove between the protoconid and hypoconid runs down from the occlusal surface to mid-crown height and contrasts with the weak and short disto-buccal one which separates the hypoconid from the hypoconulid.

An isolated lower left molar (KNM LU 335) was collected at Cheboit in the Lukeino Formation in 1974 (Pickford, 1975) which is lightly worn. This tooth is slightly rolled and its morphological features are not always clear. However, it is similar in morphology to the new specimens found since 2000: the crown is low and bulky, it has centrally positioned cusps; a small distal fovea and reduced talonid basin; the lingual side of the tooth is vertical and the buccal side bulbous; crenulations are present in the trigonid and talonid basins; and it has the same pattern of buccal grooves (the medial one being deeply incised whereas the distal one is shorter and shallower). The cingulum is reduced to a tiny remnant in the buccal end of the medio-buccal groove. The m/2 appears to be more elongated mesio-distally in *Ardipithecus kadabba* and *Ardipithecus ramidus* (White *et al.*, 1994; Haile-Selassie *et al.*, 2009).

5. DISCUSSION AND CONCLUSION

The new material of *Orrorin tugenensis* confirms a mixture of non-human hominoid and hominid traits. Only a few *i*/2s are known in Miocene hominoids. The *Orrorin i*/2 differs from that of *Proconsul* which has taller and narrower incisors which do not show the strong apico-basal concavity. It differs also from those of *Nakalipithecus*, *Kenyapithecus africanus*, and *Ouranopithecus* in which the crown is higher and more slender and has a strongly convex distal margin. Moreover, in *Kenyapithecus* and *Ouranopithecus* the lateral marginal ridges are more marked. In *Ouranopithecus*, the distal tubercle is well marked as are the apico-basal ridges. *Orrorin tugenensis* differs from modern apes which display a marked distal tubercle and ridges on the lingual surface of the tooth. The tooth is slightly larger than those of *Australopithecus afarensis*. The proportions of the *i*/2 are reminiscent of Plio-Pleistocene hominids.

The lower canine has slight distal apical wear and the position of its mesial shoulder differs from the condition in large Miocene apes (*Proconsul*, *Kenyapithecus*, *Nacholapithecus*). It differs from *Australopithecus anamensis* and *Australopithecus afarensis* by having the crown relatively broader labio-lingually, the morphology of the distal surface and the position of the mesial shoulder. It differs from *Ardipithecus kadabba* (Haile-Selassie *et al.*, 2001) by the presence of a weak mesial apico-basal crest bordered by a shallow groove. Its general morphology is clearly different from the canines of australopithecines and *Ardipithecus*.

The upper canine of *Orrorin* exhibits a mesial groove which is usually present in Miocene apes, but absent in later hominids (australopithecines and *Homo*). It differs from *Nakalipithecus* by the absence of a lingual cingulum, absence of a strong lingual tubercle, a more reduced mesial groove and the general morphology of the lingual surface. It differs from canines of *Ardipithecus kadabba* by the absence of lingual ridges, and a slightly weaker mesial groove (Haile-Selassie *et al.*, 2004) and it has no vertical facet caused by contact with the lower canine.

The lower premolars of *Orrorin* exhibit clearly offset roots, a feature which can be seen in scans of the mandible of *Sahelanthropus tchadensis* (Brunet *et al.*, 2005). *Ardipithecus ramidus* is characterized by single-rooted lower p/4s, an unusual pattern (Suwa *et al.*, 2009). In *Ardipithecus kadabba*, the roots of the premolars are poorly or not preserved.

The molars of *Orrorin* are thick-enamelled as in upper and middle Miocene hominoids, such as *Samburupithecus*, *Kenyapithecus* and *Nakalipithecus*. The upper molars of *Orrorin* exhibit shallow grooves between the cusps and thus differ from *Samburupithecus*, which show bulbous, inflated cusps (Ishida & Pickford, 1997). Compared with the two species of *Ardipithecus* (*A. ramidus* and *A. kadabba*), the m/2 of *Orrorin* is shorter mesio-distally for an equivalent bucco-lingual breadth. The

m/3 of *Orrorin* also differs from that of *Nakalipithecus nakayamai* in which the m/3 show massive and rather peripheralised cusps (Kunimatsu *et al.*, 2007).

Enamel thickness in molars

The enamel thickness measured on BAR 1000a'00 on the naturally broken section at the enamel-dentine junction at the apex on the metaconid is 2.1 mm (misprint in Senut *et al.*, 2001, 3.1 mm). However, the variation in modern primates as shown by Schwartz (2000) suggests that the enamel thickness in extant large-bodied hominoids does not provide valuable taxonomic information among species and can be phylogenetically uninformative, as it is not a synapomorphy. *Homo* and *Pongo* have a similar degree of enamel thickness, but do not follow the same secretion patterns of enamel. Enamel thickness is a highly functional and complex character, which varies intraspecifically and interspecifically. Differences in structure and properties of the enamel have been recorded (see references in Teaford & Ungar, 2014). Despite the presence of parallel and convergent evolution in enamel thickness, Schwartz (2000) concluded that "the success of enamel thickness patterning for discriminating among hominoid molars indicates that this feature may be used for taxonomic purposes, with some success for early fossil hominins". Many evolutionary reversals might have occurred during hominoid evolution in relation with environmental changes.

Incisor - molar relationships

Pickford (2005, 2012) showed that *Orrorin tugenensis* possessed a relationship between the length of the cutting edge of the lower incisor battery and the length of the molar row that was close to the regression for gorillas, hylobatids and many fossil hominoid primates (Fig. 18). There were five exceptions, both species of *Pan* as well as *Pongo* possess much elongated incisor cutting edges relative to their molar row length, whereas *Paranthropus* possess small incisors and huge molars. These five exceptions plot well off the regression line, *Pan* and *Pongo* to one side, and *Paranthropus* to the other. Other australopithecines plot closer to the regression line but on the same side of the line as *Paranthropus*. Fossil *Homo* plot either side of the regression line and extant *Homo* plot close to the regression line, but on the opposite side from the australopithecines.

If *Orrorin tugenensis* is considered to be an australopithecine (Richmond & Jungers, 2008) and australopithecines are considered to be ancestral to humans, then one needs to explain how and why a species, *Orrorin tugenensis*, that falls close to the regression line of the hominoid incisor - molar relationships, gave rise to a lineage that diverged more and more away from the regression line, eventually culminating in a species that is far removed from the line, but which on the way then returned to the regression line, and crossed it to give rise to *Homo*. It is more parsimonious to link *Orrorin* to *Homo*

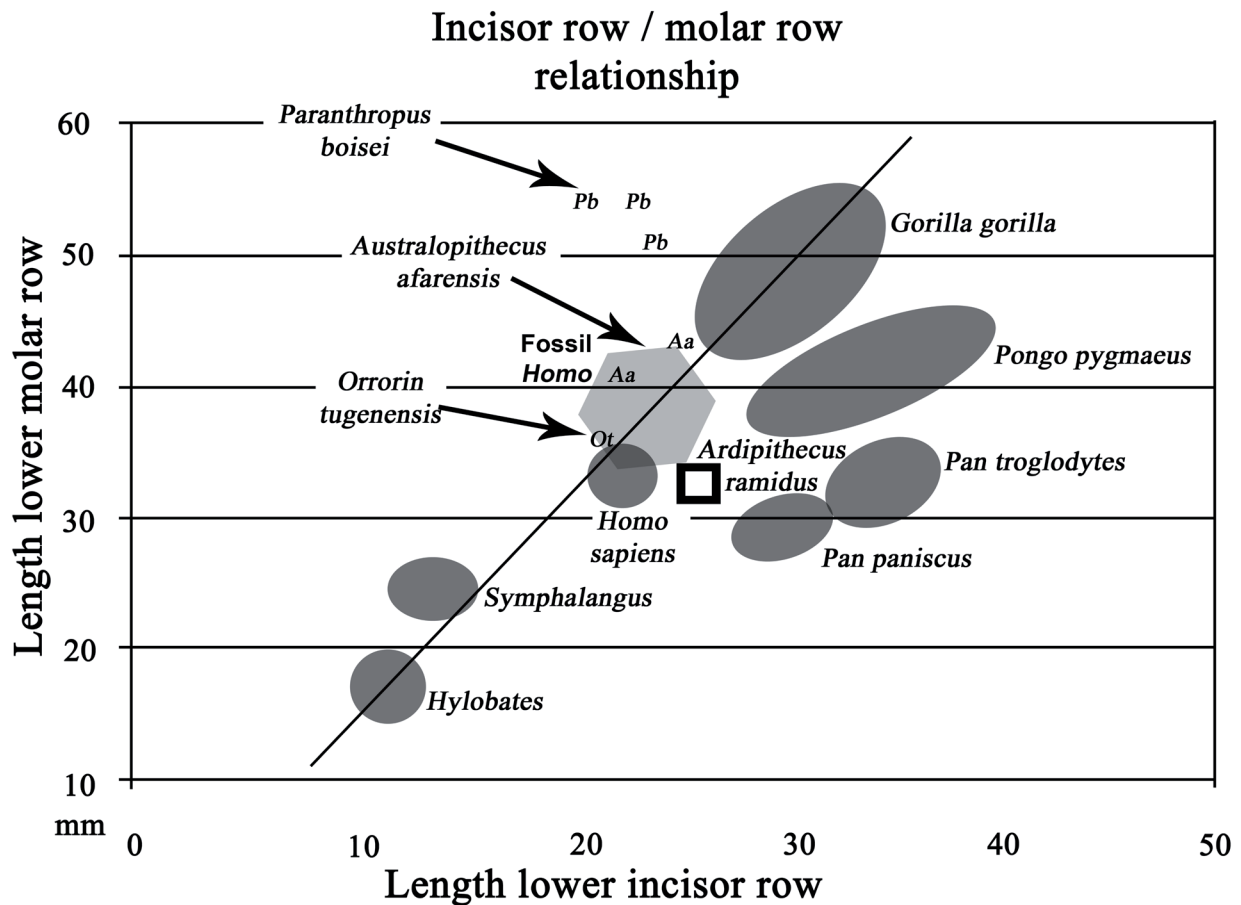


Fig. 18: Incisor - molar relationship in fossil and extant hominoids. Aa - *Australopithecus afarensis*; Ot - *Orrorin tugenensis*; Pb - *Paranthropus boisei* (visually estimated regression). The pale grey hexagon corresponds to fossil *Homo* (modified from Pickford, 2005, 2012).

without its descendants diverging from the regression in one direction, and then returning to cross over the line towards *Homo*.

Figure 18 also shows that the length of the molar row in *Orrorin* is close in dimensions to those of extant *Homo*, whereas those of *Australopithecus afarensis*, are appreciably longer, and those of *Paranthropus* much longer. If the *Orrorin* - *Australopithecus* - *Homo* (OAH) evolutionary scenario is correct, then one needs to invoke a divergence away from a *Homo*-like starting point at 6 Ma to arrive at the *A. afarensis* stage, only to return to the *Homo* situation at ca 2 Ma.

Specimens of *A. afarensis* plot not so far from the regression line. *Orrorin tugenensis* and *A. afarensis* are well within the range of variation seen in gorillas. Although *Paranthropus*, *Pongo* and *Pan* are quite different from other primates in Fig. 18, *Orrorin* and *A. afarensis* share comparable relationships.

If we now consider the relationship between body size and dentition, the awkwardness of the OAH scenario continues. *Orrorin tugenensis* has teeth that are smaller than those of *Australopithecus afarensis* (including those of small individuals such as AL 288-1, “Lucy”) and

much smaller than those of *Paranthropus*. Yet all three femoral fragments of *Orrorin* are significantly larger than that of AL 288-1 (Nakatsukasa *et al.*, 2007) indicating that its stature (and therefore its body weight) was greater than that of AL 288-1. Australopithecines are therefore more megadont than *Orrorin* was. In its body-size / dentition relationship, *Orrorin* is close to *Homo*. If the OAH scenario is valid, then we would need to invoke a change in the relationship from microdony in *Orrorin* to megadonty in *A. afarensis* and then back to microdony in *Homo*. Since the relationship between body size and dentition in hominoids and other primates is probably closely linked to nutrition and metabolism, it seems to us that it is more parsimonious to avoid invoking yet another category of evolutionary “yoyo” between *Orrorin* and *Homo*, by accepting that the megadonty of australopithecines did not revert to microdony in humans, but continued on its evolutionary trajectory towards hyper-megadonty in *Paranthropus*. We consider that there was a more direct evolutionary trajectory from *Orrorin* via Pliocene *Praeanthropus* (as defined in Senut, 1996 following the International Code of Zoological Nomenclature; unfortunately some authors use the term

as a synonym of *Australopithecus* which is not correct) towards *Homo* which remained microdont throughout. *Orrorin* could also have given rise to australopithecines, but we consider that once the latter lineage was engaged in the evolutionary strategy of megadonty, it continued along that trajectory, eventually terminating in the hyper-megadonty of *Paranthropus*. *Orrorin* therefore likely predates a dichotomy in the early hominids which gave rise to two quite distinct adaptative strategies, on the one hand, the initially highly successful australopithecine one involving increasing megadonty, and on the other, the ultimately more successful strategy of maintaining microdony. Megadonty refers to the large size of the cheek teeth relative to small body size. It is not easy to estimate body size in fossil hominids for which postcranial remains are usually fragmentary or not preserved. However, it is generally admitted that Australopithecines are megadont (McHenry, 1988, 2002), that they show a faster rate of enamel formation (Lacruz *et al.*, 2008) and that there was a trend towards hyper-megadonty from *Australopithecus* to *Paranthropus*, while in the *Homo* line there was envisaged to be a decrease in megadonty, culminating in microdony. However, early *Homo*, *H. rudolfensis* and *H. habilis* seem to be different, *H. rudolfensis* showing some degree of megadonty estimated from the roots of the upper cheek teeth. But, no postcranial bone is known for this taxon which means that the degree of megadonty will remain uncertain until fossil evidence is available. In this context, *Orrorin tugenensis*, with its small molars associated with a skeleton which is close in size to that of Pliocene Australopithecines would exhibit a body size/molar size pattern closer to later *Homo* than to Australopithecines.

Some authors suggested that *Orrorin tugenensis*, *Ardipithecus kadabba* and *Sahelanthropus tchadensis* are congeneric (Haile-Selassie *et al.*, 2004). Considering the differences between the three taxa and the variation between them, it could be suggested that *Ardipithecus kadabba* represents a mixture of different species, one like *Orrorin tugenensis*, the other more chimpanzee-like. This systematic problem will be solved only with the discovery of more complete material.

This study indicates that there were at least three hominoids living in Eastern Africa during the Latest Miocene, one an early hominid (*Orrorin tugenensis*), one an early chimpanzee-like ape (*Ardipithecus ramidus*) and the third a gorilla-sized ape (not yet named). Further finds are required to resolve the status of these hominoids.

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REFERENCES

- Brunet M., Guy F., Pilbeam D., Mackaye H., Likius A., Ahounta D., Beauvilain A., Blondel C., Bocherens H., Boisserie J.-R., De Bonis L., Coppens Y., Dejax J., Denys C., Durringer P., Eisenmann V., Fanone G., Fronty P., Geraads D., Lehmann T., Lihoreau F., Louchart A., Mahamat A., Merceron G., Mouchelin G., Otero O., Pelaez Campomanes P., Ponce De León M. S., Rage J.-C., Sapanet M., Schuster M., Sudre J., Tassy P., Valentin X., Vignaud P., Viriot L., Zazzo A. & Zollikofer C. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, 418: 145-151.
- Brunet M., Guy F., Pilbeam D., Lieberman D. E., Likius A., Mackaye H. T., Ponce De León M. S., Zollikofer C. P. E. & Vignaud P. 2005. New material of the earliest hominid from the Upper Miocene Chad. *Nature*, 434: 752-755.
- Corruccini R. S. & McHenry H. M. 1980. Cladometric analysis of Pliocene hominids. *Journal of Human Evolution*, 9: 209-221.
- Chapman G. & Brook M. 1978. Chronostratigraphy of the Baringo Basin, Kenya Rift Valley. In: Bishop W.W. (Ed.), *Geological Background to Fossil Man*. Scottish Academic Press, Edinburgh: 207-223.
- Deino A. & Hill A. 2002. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Chemeron Formation strata encompassing the site of hominid KNM-BC 1, Tugen Hills, Kenya. *Journal of Human Evolution*, 42: 141-151.
- Galik K., Senut B., Pickford M., Gommery, D., Treil J., Kuperavage A. J. & Eckhardt R. 2004. External and internal morphology of the BAR 1002'00 *Orrorin tugenensis* femur. *Science*, 305: 1450-1453.
- Gommery D. & Senut B. 2006. The terminal thumb phalanx of *Orrorin tugenensis* (Upper Miocene of Kenya). *Geobios*, 39: 372-384.
- Haile-Selassie Y. 2001. Late Miocene hominids from the Middle Awash, Ethiopia. *Nature*, 412: 178-181.
- Haile-Selassie Y., Suwa G. & White T. D. 2004. Late Miocene

- teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science*, 303: 1503-1505.
- Haile-Selassie Y., Suwa G. & White T. 2009. Hominidae. In: Haile-Selassie Y. & Wolde Gabriel G. (Eds), *Ardipithecus kadabba. Late Miocene evidence from the middle Awash, Ethiopia*. University of California Press, Berkeley: 159-236.
- Hill A. 1994. Late Miocene and Early Pliocene Hominoids from Africa. In: Corruccini R. S. & Ciochon R. L. (Eds), *Integrative Paths to the Past: Paleoanthropological Advances in Honour of F. Clark Howell*. Prentice Hall, Englewood Cliffs, NJ: 123-145.
- Hill A. 1999. The Baringo Basin, Kenya: from Bill Bishop to BPRP. In: Andrews P. & Banham P. (Eds), *Late Cenozoic Environments and Hominid Evolution: a Tribute to Bill Bishop*. Geological Society, London: 85-98.
- Hill A. & Ward S. 1988. Origin of the Hominidae: the record of African large hominoid evolution between 14 My and 4 My. *Yearbook of Physical Anthropology*, 31: 49-83.
- Hill A., Drake R., Tauxe L., Monaghan M., Barry J., Behrensmeyer K., Curtis G., Jacobs B., Jacobs L., Johnson N. & Pilbeam D. 1985. Neogene palaeontology and geochronology of the Baringo Basin, Kenya. *Journal of Human Evolution*, 14: 749-773.
- Ishida H. & Pickford M. 1997. A new late Miocene hominoid from Kenya: *Samburupithecus kiptalami* gen. et sp. nov. *Comptes Rendus de l'Académie des Sciences*, 325: 823-829.
- Kingston J.D., Jacobs B.F., Hill A. & Deino A. 2002. Stratigraphy, age and environments of the Late Miocene Mpesida Beds, Tugen Hills, Kenya. *Journal of Human Evolution*, 42: 95-116.
- Kunimatsu Y., Nakatsukasa M., Sawada Y., Sakai T., Hyodo M., Hyodo H., Itaya T., Nakaya, H., Saegusa H., Mazurier A., Saneyoshi M., Tsujikawa H., Yamamoto A. & Mbua E. 2007. A new Late Miocene great ape from Kenya and its implications for the origins of African great apes and humans. *Proceedings of National Academy of Sciences of United States of America*, 104: 19220-19225.
- Leakey M. G., Feibel C. S., McDougall I. & Walker A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature*, 376: 565-571.
- Lacruz R.S., Dean M.C., Ramirez-Rozzi F. & Bromage T.G. 2008. Megadontia, striae periodicity and patterns of enamel secretion in Plio-Pleistocene fossil hominins. *Journal of Anatomy*, 213: 148-158.
- McHenry H.M. 1988. New estimates of body weight in early hominids and their significance to encephalization and megadontia in 'robust' australopithecines. In: Grine F.F. (Ed.), *Evolutionary History of the "Robust" Australopithecines*. Aldine de Gruyter, New York: 133-148.
- McHenry H.M. 2002. Introduction to the fossil record of human ancestry. In: Hartwig W.C. (Ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge: 401-405.
- McHenry H. M. & Corruccini R. S. 1980. Late Tertiary hominoids and human origins. *Nature*, 285: 397-398.
- Nakatsukasa M., Pickford M., Egi N. & Senut B. 2007. Body weight, femoral length and stature of *Orrorin tugenensis*, a 6 Ma hominid from Kenya. *Primates*, 48: 171-178.
- Pickford M. 1975. Late Miocene sediments and fossils from the Northern Kenya Rift Valley. *Nature*, 256: 279-284.
- Pickford M. 1978. Stratigraphy and mammalian palaeontology of the late Miocene Lukeino Formation, Kenya. In: Bishop W. W. (Ed.), *Geological Background to Fossil Man*. Scottish Academic Press, Edinburgh: 263-278.
- Pickford, 1986. The geochronology of Miocene higher primate faunas of East Africa. In: Else J. G. & Lee P. C. (Eds), *Primate Evolution*. Cambridge University Press, Cambridge: 19-33.
- Pickford M. 2005. Incisor-molar relationships in chimpanzees and other hominoids: implications for diet and phylogeny. *Primates*, 46: 21-32.
- Pickford M. 2012. *Orrorin* and the African ape/hominid dichotomy. In: Reynolds S.C. & Gallagher A. (Eds), *African Genesis*. Cambridge University Press, Cambridge: 99-119.
- Pickford M. & Senut B. 2001. The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. *Comptes Rendus de l'Académie des Sciences*, 332: 145-152.
- Pickford M, Senut B., Gommery D. & Treil J. 2002. Concise review paper: Bipedalism in *Orrorin tugenensis* revealed by its femora. *Comptes rendus Palevol*, 1: 191-203.
- Richmond B. G. & Jungers W. L. 2008. *Orrorin tugenensis* femoral morphology and the evolution of Hominin bipedalism. *Science*, 319: 1662-1665.
- Sawada Y., Pickford M., Senut B., Itaya T., Hyodo M., Miura T., Kashine C., Chujo C. & Fujii H. 2002. The age of *Orrorin tugenensis*, an early hominid from the Tugen Hills, Kenya. *Comptes Rendus Palevol*, 1: 293-303.
- Schwartz G. T. 2000. Enamel thickness and the helicoidal wear plane in modern human mandibular molars. *Archives of Oral Biology*, 45: 401-409.
- Senut B. 1996. Pliocene hominid systematics and phylogeny. *South African Journal of Science*, 92(4): 165-166.
- Senut B. 1998. Les grands singes fossiles et l'origine des hominidés : mythes et réalités. *Primatologie*, 1: 93-131.
- Senut B., Pickford M., Gommery D., Mein P., Cheboi K. & Coppens Y. 2001. First hominid from the Miocene (Lukeino Formation, Kenya). *Comptes Rendus de l'Académie des Sciences*, 332: 137-144.
- Suwa G., Kono R.T., Simpson S.W., Asfaw B., Lovejoy C.O. & White T.D. 2009. Paleobiological implications of the *Ardipithecus ramidus* dentition. *Science*, 326: 96-99.
- Swindler D.R. 2002. *Primate Dentition*. Cambridge University Press, Cambridge, 296 pp.
- Teaford M.F. & Ungar P.S. 2014. Dental adaptations of African apes. In: Henke W. & Tattersall I. (Eds), *Handbook of Paleoanthropology*. Second Edition. Springer Verlag, Berlin Heidelberg: 1465-1493. DOI 10.1007/978-3-642-27800-6_36-4.
- Ungar P. S., Walker A. & Cotting K. 1994. Reanalysis of the Lukeino Molar (KNM LU 335). *American Journal of Physical Anthropology*, 94: 165-173.
- Ward C. V., Leakey M. G. & Walker A. 2001. The new hominid species *Australopithecus anamensis*. *Evolutionary Anthropology*, 7: 197-205.
- White T.D. & Johanson D.C. 1982. Pliocene hominid mandibles from the Hadar Formation, Ethiopia: 1974-1977 collections. *American Journal of Physical Anthropology*, 57: 501-544.
- White T., Suwa G. & Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature*, 371: 306-312; and 1995. Erratum. 375: 88.

