Hominoid teeth with chimpanzee- and gorilla-like features from the Miocene of Kenya: implications for the chronology of ape-human divergence and biogeography of Miocene hominoids

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Abstract One of the major lacunae in our knowledge of African hominoid evolution concerns the origins of the chimpanzee and gorilla. Several thousand specimens from the Plio–Pleistocene of Africa have been attributed to Hominidae (sensu stricto) of which only a few, including *Ardipithecus ramidus*, have been re-interpreted by some authors as possibly representing an ape rather than a hominid (Senut, 1998). Four recently discovered ape-like specimens from the late Middle Miocene (12.5 Ma) and Late Miocene (5.9 Ma) of Kenya partly fill the gap in the fossil record of African apes, and show some morphological and metric affinities with teeth of chimpanzees and gorillas. If these few specimens from Kenya are indeed more closely related to chimps and gorillas than to hominids, then this implies that the dichotomy between African apes and hominoids occurred several million years earlier than is currently estimated by most researchers. Furthermore these ape teeth from Ngorora and Lukeino suggest that extant African apes evolved in Africa, and did not immigrate into the continent from Europe or Asia.

Key words: Miocene, Kenya, *Orrorin*, *Pan*, *Gorilla*

Introduction

This paper concerns four ape-like teeth from Kenya, one from the Ngorora Formation (12.5 Ma), and three from the Lukeino Formation (5.9 Ma), collected by the Kenya Palaeontology Expedition.

In this paper we restrict the term ‘hominid’ to encompass only those hominoids that possess skeletal morphology indicative of habitual or obligate bipedal locomotion. We do not employ it in the much wider sense that has recently been used by some authors, in which even the genera *Pan* and *Gorilla* are included in the family Hominidae.

The Ngorora Lower Molar

Morphological description (Figure 1A)

Bar 91’99 is an unworn right lower molar, probably the second (11.4 mm mesiodistal × 9.4 mm buccolingual), although a case could be made for it being a third molar. The apices of the protoconid and hypoconid are buccolingually compressed and not very voluminous. They are located towards the buccal margin of the tooth and they express minor buccal flare. The apices of the protoconid and metaconid are 5.2 mm apart and the tooth is 9.2 mm broad at this level. The protoconid and metaconid have low-relief, centrally directed crests which close off a low walled mesial fovea. Anterior crests from these same cusps meet mesially to wall off the anterior side of the mesial fovea, which is buccolingually wide and mesiodistally short. The hypoconid has low crests descending from its apex mesially and distally but not crossing the grooves, which separate the cusp from its neighbors. There is a basal cingular enamel fold between the protoconid and hypoconid and a tiny fold between the hypoconid and hypoconulid. The hypoconulid has a crest descending obliquely anteriorly into the talonid basin, but it is low and does not separate the basin from the distal fovea. The postcristid reaches lingually towards the low cusplet present between the hypoconulid and the entoconid. The apices of the metaconid and entoconid are strongly buccolingually compressed and peripherally positioned, a disposition that results in a voluminous sunken talonid basin bordered by cusps that are somewhat trenchant in appearance. The posterior crest of the metaconid descends towards a low, peripherally positioned cusplet between the metaconid and entoconid. The hypoconid extends beyond the midline of the crown and reaches this small cusplet. As a consequence, the metaconid and entoconid do not touch each other. A postentoconid crest descends obliquely towards another low cusplet located between the entoconid and hypoconulid from which it is separated by narrow but short vertical grooves on the posterolingual surface. The occlusal basin is wide, deep, and long. The wall between the anterior fovea and the talonid basin is low and the posterior fovea is not clearly demarcated from it, and thus extends for almost the entire length of the tooth. The
The main differences from molars of *Pan paniscus* (Figure 1B) concern the buccal cusps, which are slightly more internally positioned in the fossil. In *P. paniscus*, the buccal cusps are even more peripherally located than they are in the Ngorora tooth. Another difference between the Ngorora tooth and *P. paniscus* lies in the height of the entoconid, which is taller and more trenchant in *P. paniscus*. The anterior fovea is bucconuligually narrower in the fossil than in *Pan*. However, these are relatively minor differences.

The Ngorora molar resembles lower molars of *Pan troglodytes* from Mahale, Tanzania (Figure 1C) more closely than it does those of *P. paniscus*. This is mainly because the buccal cusps are slightly more internally positioned in the common chimpanzee, and they thus have moderate buccal flare of the cusp walls. A minor difference is the extent of the mesial fovea, which is greater in *P. troglodytes* than it is in the Ngorora specimen, and most chimpanzee molars do not have any trace of a buccal cingulum.

**Comparison with molars of Dryopithecus**

Lower molars of the European genus *Dryopithecus* (Figure 1D–F) have peripheralized cusps, and broad but shallow occlusal basins (Begun, 2002). They also possess slight buccal cingula and some specimens have a small accessory cusplet separating the metaconid and entoconid in the lingual notch. The most significant differences between the Kenyan and European specimens are the shallower occlusal basins and the less bucconuligually compressed lingual cusps that occur in *Dryopithecus*. In particular, the Ngorora tooth resembles some of the central European *D. brancoi*, especially specimens such as those from Salmendingen, Trochtelfingen, and Ebingen (Figure 1D–F). It is not impossible that the Ngorora species is related to the genus *Dryopithecus*.

**Comparisons with Miocene African hominoids**

Comparison of the Ngorora tooth (Figure 1A) with lower molars of African fossil hominoids reveals that it does not belong to any of the described Miocene forms, none of which possess the large occlusal basin and peripheralized cusps that distinguish this tooth. The only specimen with which it accords in morphology is the Ngorora upper molar (KNM-BN 1378), which has wide occlusal fovea and a large protocone, but this tooth is appreciably larger than what would be expected to occlude with Bar 91’99.

**Implications of the Ngorora lower molar**

Until now, no fossil chimpanzees and gorillas have been reported and there has thus been a lack of evidence to test the molecular clock estimates of the dichotomy between African apes and hominids. If the derived characters of the Ngorora molar represent homologies shared with chimpanzees, then it would indicate that the *Pan* clade has its roots in the latter part of the Middle Miocene, sometime prior to 12.5 Ma.

The dichotomy between chimpanzees and humans is usually estimated by molecular biologists to be more recent than 6 Ma (Gagneux et al., 1999; Stauffer et al., 2001) and the split between chimpanzees and gorillas has been estimated at 8–9 Ma by Wrangham and Pilbeam (2001) and 7.7 Ma by Gagneux et al. (1999). The only molecular biologists who have proposed an earlier age for African ape origins are Arnason and co-workers (Arnason et al., 1996, 1998, 2000; Janke and Arnason, 2002), but their results are usually considered suspect by others who appear to favor appreciably later divergence times (Bailey et al., 1992; Adachi and
The Ngorora specimen thus runs counter to the recent ideas of Pilbeam (1996) who wrote that “the common ancestor of humans and chimpanzees was probably chimpanzee-like, a knuckle-walker with small thin-enamelled cheek teeth,” and Wrangham and Pilbeam (2001) who postulated that the “6 mybp ancestor…would have been thin-enamelled, knuckle-walking, and females would have had black body coats.” It is already known that 6 Ma hominids such as *Orrorin tugenensis* had thick-enamelled molars with restricted occlusal basins and were fully bipedal (Senut et al., 2001; Pickford et al., 2002). Instead the Ngorora fossil ape tooth accords with the scenario published by Arnason et al. (1996, 1998, 2000) based on molecular evidence, of an early divergence (ca. 13.5 Ma) between *Pan* and *Homo*.

### The Kapsomin Ape Teeth

**Bar 1757’02, upper molar**

**Description**

The Kapsomin tooth is a partial left upper molar (Figure 2A–D). It lacks the roots but the cervical line is partly preserved, allowing estimation of cusp height. Also preserved are the entire paracone and metacone, part of the hypocone and the distobuccal extremity of the protocone (the crista obliqua). The distal fovea is complete. The tooth is 14 mm mesiodistal. It is low crowned (7.3 mm from cervix to tip of metacone) and the cusps are endowed with low but broad wrinkles.

The paracone and metacone are separated from each other by a narrow slit-like buccal groove (Figure 2B). The part of the trigon basin preserved is relatively large and open, the main cusps being peripherally positioned and the cusps not bulbous. The mesial fovea is not preserved. Two low crests descend from the apex of the paracone towards the midline of the crown (i.e. towards the mesial fovea). The metacone sends a crest lingually and slightly anteriorly towards the protocone, from which it is separated by a groove. The metacone has another, smaller crest that descends obliquely distally directly towards the hypocone, bifurcating on its way down the cusp. The anterior branch of the crest forms a low wall between the trigon basin and the distal fovea. The distal cingulum reaches from the base of the metacone to the hypocone and walls off the distal fovea on the distal aspect of the tooth. The metacone and hypocone are spaced far apart, and as a consequence, the distal fovea is buccolingually wide and slightly obliquely oriented with the buccal end more...
Comparisons with Orrorin tugenensis and Pliocene hominids

Bar 1757’02 is highly divergent from the teeth in the upper tooth row of Orrorin (Figure 2F), not only in its greater dimensions, but also in its morphology. The trigon basin and distal fovea in the upper molars of Orrorin are restricted in size; the buccal cusps are more flared from apex to cervix, the buccal slit is non-existent, the main cusps are lower crowned, the dentine penetrance is low, and the enamel is less wrinkled. The Kapsomin ape tooth is closer in size and some aspects of morphology to upper molars of Australopithecus afarensis and Praeanthropus africanus. However, the higher and less-inflated cusps, the steep, flat, and unflared buccal surface, thinner enamel, and the greater dentine penetrance suggest that Bar 1757’02 is not from an australopithecine.

Comparisons with Gorilla gorilla

Upper molars of gorillas are generally longer than Bar 1757’02 but there are small individuals that overlap in size; upper M1/s of Gorilla gorilla range in mesiodistal length from 12.7 to 16.7 mm, M2/s from 13.4 to 17.9 mm, and M3/s from 12.0 to 17.0 mm (Pilbeam, 1969).

The crown morphology of Bar 1757’02 is similar in several respects to that of molars of Gorilla gorilla (Figure 2G, H). In particular the mesio-distally short but bucco-lingually wide distal fovea of the Lukeino tooth resembles that of Gorilla as does its oblique orientation. Another resemblance lies in the degree and kind of enamel wrinkling and the high dentine penetrance. In G gorilla enamel is generally considered to be thin (ranging from 0.98 to 1.63 mm on the protocone and between 0.7 and 1.33 mm on the paracone: Schwartz, 2000), and in Bar 1757’02 it is 1.6–1.7 mm on the hypocone, which falls slightly above the range of variation of Gorilla. This measure was taken on a slightly oblique natural section of the tooth (Figure 2C), and the radial thickness would be slightly less than this figure.

Comparisons with Pan

Bar 1757’02 differs markedly from molars of P. troglodytes and P. paniscus, not only in size, but also in morphology (Figure 2E). M1/s and M2/s of P. troglodytes range in mesiodistal length from 9 to 12 mm, and M3/s from 8.2 to 10.6 mm (Pilbeam, 1969). The trigon basins in molars of Pan are extensive and the crests separating the basin from the mesial and distal foveae are quite low. In any case, the distal fovea in Pan is reduced in buccolingual extent. A further difference is the greater buccolingual compression of the apices of the paracone and metacone in Pan.

Comparisons with Sahelanthropus tchadensis

Bar 1757’02 is larger than the upper molars in Sahelanthropus tchadensis (Brunet et al., 2002) (mesiodistal length is 14 mm in Bar 1757’02, compared to 10.9–11.5 mm in M1/, 13 mm in M2/, and 10.7–10.8 mm in M3/ of Sahelanthropus). Brunet et al. (2002) describe the molars as having “low rounded cusps...,” in which case they are different from the Kapsomin tooth. The enamel in the upper molars of Sahelanthropus has been reported to be 1.71 mm thick in the paracone of M3/ and 1.79 mm at the hypocone of M2/, which suggests that enamel in Sahelanthropus is approximately the same as in the Kapsomin ape in which it is 1.6–1.7 mm on the hypocone. The enamel thickness of Orrorin was originally (Senut et al., 2001) said to be 3.1 mm on the protoconid of m/2 but this was a typographical error that unfortunately carried through into both translated versions of the text. The thickness measured radially near the tip of the protoconid on the original fossil was 2.1 mm. The enamel thickness decreases towards the cervix such that it is about 1.7 mm thick about 2 mm below the apex of the cusp. Further study with a scanner is planned.

Comparisons with other Miocene hominoids

Bar 1757’02 differs in various features from most of the known medium and large hominoids from the Miocene of Africa. Molar morphology in Kenyapithecus, Nacholapithecus, Otavipithecus, and Afropithecus is quite different, these taxa possessing non-peripheralized bulbous main cusps and restricted occlusal basins (Conroy et al., 1992; Ward and Duren, 2002). In Proconsul and Ugandapithecus the cusps are not peripheralized (Harrison, 2002; Senut et al., 2000). The cusps in the upper molars of Samburupithecus are inflated, and the occlusal basins are extremely restricted (Pickford and Ishida, 1998), which makes them very divergent from the Kapsomin tooth.

Ouranopithecus and Ankarapithecus from European Late Miocene deposits have thick-enamelled molars with restricted occlusal basins and low dentine penetrance, interpreted by de Bonis et al. (1981) as features shared with Hominidae, from which we infer that the genus is markedly different from the Kapsomin ape.

Discussion

It seems clear that the fragment of upper molar from Kapsomin (Bar 1757’02) represents a species distinct from O. tugenensis. Apart from its greater dimensions, it has morphology that is different from the bunodont crown with inflated main cusps and restricted trigon basin and foveae of the latter taxon. Whereas the molars of Orrorin recall those of later hominids (Australopithecus, Praeanthropus, and even Homo) in overall crown shape, bunodonty, cusp inflation, and basin restriction, Bar 1757’02 stands out as anomalous, with its more peripheralized cusps, widely separated metacone and hypocone, wide, obliquely oriented distal...
fovea, vertical and flat buccal surface, high dentine penetration, and thinner enamel with light wrinkling. The tooth has high dentine penetration as shown by the fact that if it were worn to the same level as the M2/ in the *Orrorin* tooth row, which shows no dentine exposure, the Kapsomin ape tooth would have a large dentine exposure (the shadow at the apex of the protocone of the M2/ of *Orrorin* in Figure 2F is a small patch of chemical etching floored by enamel and is not an exposure of dentine). The morphology of the dentine-enamel junction in the Kapsomin tooth is best appreciated by examining the broken inner surface of the Kapsomin tooth where it is clearly visible, showing the dentine penetrating high into the hypocone (Figure 2C). In most of these features the tooth is closest to *G. gorilla*, yet it is by no means a perfect fit with this species.

Metrically, the Kapsomin tooth is appreciably larger than any of the *Orrorin* molars, but it falls within the range of metric variation of the gorilla. It also falls within the range of variation of Pliocene fossil hominids, including *Ardipithecus*, *Australopithecus*, and *Praeanthropus*. Its relationships to *Sahelanthropus* are not clear as published photographs of the latter do not reveal enough detail about crown morphology, but descriptions of the fossil suggest major morphological differences.

We conclude that Bar 1757′02 reveals the presence of a second hominoid in the Lukeino Formation, Kenya. Its affinities appear to lie with gorillas rather than hominids. Its dimensions fall within the range of variation of gorilla upper molars and well above that of chimpanzees, and we discount any close relationship with *Pan*, which, apart from being smaller and having peripheralized main cusps, has quite different molar crown morphology.

**Bar 1001′00, upper central incisor**

Bar 1001′00 is a right upper central incisor that has been abraded mesially and distally (Figure 3B). The preserved part of the crown is relatively low compared to root length. In lateral view the labial and lingual surfaces form a wedge-shape; the tooth is 8.7 mm thick labio-lingually near the cervix and narrows rapidly incisally. It has lightly wrinkled enamel. The crown is unlike the corresponding teeth of australopithecines and humans because there is no fossa on the lingual side (Figure 3A). In hominids the crown is higher from cervix to incisal edge and the lingual surface has a large fossa, sometimes with lingual ridges or pillars, but usually possessing a scoop-shaped profile. In gorillas, in contrast, the upper central incisors are often wedge-shaped, with no sign of a lingual fossa, or if one is developed it is not very prominent. Comparison of the Kapsomin upper incisor with those of gorillas reveals close similarities (Figure 3C) not only in size but also in shape and crown height relative to root length. Even though these similarities are enhanced by the wear stage of the Kapsomin incisor and that of the gorilla used for comparison, this is because the underlying morphology is similar. Chimpanzee and hominid teeth worn as much as the Kapsomin fossil do not develop a comparable wedge-shaped appearance in lateral view, because the lingual surface of their teeth is basin-like.

Figure 3. Kapsomin upper incisor and comparisons. (A) *Praeanthropus africanus* cast of upper central incisor from Laetoli; (A1) lingual view; (A2) distal view. (B) Bar 1001′01, cast of upper central incisor, Kapsomin large ape; (B1) lingual view; (B2) distal view. (C) *Gorilla gorilla* upper central incisor worn to the same level as Bar 1001′01; (C1) lingual view; (C2) distal view.
An anonymous referee considered that this tooth is similar to A.L. 198-17a (Johanson et al., 1982) and on this basis suggested that the Kapsomin tooth may belong to an australopithecine. However, comparison of the specimens reveals that they are divergent in morphology. The Hadar fossil has a restricted basal lingual pillar bordered mesially and distally by hollows, as in other australopithecine teeth, whereas Bar 1001’00 does not, its basal lingual part being inflated right across the preserved part of the tooth, as in gorillas with which we compared the tooth. Furthermore, the wear facet in A.L. 198-17a is apical, flat, and at right angles to the long axis of the tooth, whereas that in the Kapsomin tooth is steeply angled from incisal edge to cervix on the lingual side, again as in gorillas. In apical view the Hadar tooth is a mesiodistally elongated rectangle, slightly concave lingually with slight projection of the basal tubercle, whereas the Kapsomin tooth is much broader labiolingually. This is reflected in the dimensions of the teeth, the Kapsomin specimens measuring 8.7 mm labiolingually near cervix and the Hadar specimen only 7.1 mm. Larger upper central incisors from Hadar (A.L. 200-1a, A.L. 333x-4, and A.L. 333x-20) measure 8.5, 8.6, and 8.6 mm labiolingually, respectively.

Discussion

The upper central incisor (Bar 1001’00) was initially attributed to O. tugenensis (Senut et al., 2001) because at the time of the discovery it was assumed that only a single hominoid was represented at the site. With the discovery of Bar 1757’02, a partial upper molar, it became clear that a second, larger hominoid taxon was present at Kapsomin, leading to a re-evaluation of all the specimens from the site. Because of its dimensions (labiolingual breadth 8.7 mm) and its somewhat gorilla-like morphology and wear pattern, we now consider that the upper central incisor belongs to this second hominoid rather than to Orrorin.

Cheboit Lower Molar

Bar 2000’03 from Cheboit, Lukeino Formation, is an unworn right lower molar lacking the roots, but preserving much of the cervical line (Figure 4). The apices of the two lingual cusps are buccolingually compressed and peripherally located. The tips of the protoconid and metaconid are 5.4 mm apart and the tooth is 10.5 mm broad at this level. The two buccal cusps are slightly in advance of the lingual ones, and there is minor buccal flare. Because of the peripheral positions of the main cusps, the occlusal basin is large and elongated. The mesial fovea is wide but mesiodistally short. The hypoconulid is small and is located slightly to the lingual side of the centre line of the tooth and in a very distal position, and as a result the tooth has an elongated trapezoidal outline (Figure 4). Because of this the tooth could be a lower third molar. The distal fovea is thus small, but is not separated from the main occlusal basin by the crests from the hypoconulid or entoconid, as these do not reach each other. The tooth measures 12.7 mm mesiodistal by 11.1 mm buccolingual.

This tooth is morphologically compatible with Bar 1757’02, the upper molar from Kapsomin. We consider it likely that the two specimens belong to a single taxon.

Discussion

This lower molar differs radically from those of O. tugenensis of which it is a contemporary. The occlusal outline is long, narrow, and trapezoidal compared with a wider, more rectangular outline in Orrorin. The main occlusal basin is deep, wide, and long, compared with the shallow, narrow, and short basin in Orrorin. The distal fovea is not separated from the main basin, whereas in Orrorin it is. The buccal flare is not as marked as it is in Orrorin and the lingual cusps are more peripherally located. The main cusps are not as inflated as those of Orrorin, suggesting that the tooth has

Figure 4. Cheboit lower molar and comparisons. (A) KNM-LU 335, Orrorin tugenensis, cast of left m/3, stereo occlusal view. NB KNM-LU 335 was originally interpreted to be an m/2 (Andrews in Pickford, 1975), but comparison with teeth in the holotype mandible of O. tugenensis reveals that it is in fact an m/3. (B) Bar 2000’03, Cheboit large ape right lower molar; (B1) stereo occlusal view; (B2) mesial view.
thinner enamel and probably greater dentine penetration, but we have not yet had the opportunity to determine these parameters. In *Orrorin*, the hypoconulid is located to the buccal side of the midline, and is thus close to the hypoconid, whereas in Bar 2000’03 it is to the lingual side of midline, and far from the hypoconid. Indeed this cusp is closer to the entoconid than it is to the hypoconid, the opposite of the situation in *Orrorin*. In the latter genus, there is a clear valley buccally between the hypoconid and the entoconid, whereas in Bar 2000’02, there is not even an indentation in the distobuccal wall of the tooth. The latter tooth is also somewhat bigger than any of the *Orrorin* lower molars.

Discussion and Conclusions

Four ape-like teeth from the Miocene of Kenya reveal greater similarities to extant chimpanzee and gorilla teeth than to thick-enamelled Miocene apes and Mio-Plio-Pleistocene to recent hominids. The specimen from Ngorora (12.5 Ma) is similar in size and some morphological details to *Pan* but also has resemblances to the European Miocene genus *Dryopithecus*, with which it could be congeneric, whereas the Lukeino specimens (5.9 Ma), recall, but are not identical to, the teeth of gorillas.

The morphology of the Ngorora tooth suggests that the *Dryopithecus* lineage may have evolved in Africa and then invaded Europe about 12–12.5 Ma, rather than evolving within Europe from a thick-enamelled lineage such as *Griphopithecus* (Begun, 2002). If it is part of the *Pan* clade, then it would push back the split between hominids and African apes to the Middle Miocene. If this is so, then thick-enamelled apes such as *Kenyapithecus* possibly take on a renewed significance for throwing light on the earliest stages in the evolution of hominids, as thought by L. Leakey in the 1960s (Leakey, 1962, 1967, 1969, 1970) even though the supposedly hominid features employed by Leakey in his proposals have subsequently been interpreted as being related to sexual dimorphism and to pliosiomorphic features found in several Middle Miocene hominoids, rather than to derived morphology shared with hominids (Pickford, 1985).

It is more parsimonious to consider that thick-enamelled hominoids descended from thick-enamelled precursors rather than to hypothesize a thin-enamelled intermediate stage, as has apparently become the fashion (Wrangham and Pilbeam, 2001). What is required is a fresh look at the problem, including the relationships between diet on the one hand and enamel thickness and dentine penetration on the other.

If the Kapsomin ape teeth belong to the gorilla clade, then they would indicate that by about 6 Ma the lineage was a separate entity from the *Pan + Homo* clade. Taken together, the Ngorora and Kapsomin ape teeth, and those of the early bipedal hominid *Orrorin*, plead for considerably earlier split times between the gorilla, chimpanzee, and hominid clades than most molecular biologists have considered possible for the past three decades (Gagneux et al., 1999; Stauffer et al., 2001) but more in accord with the results of Arnason and his colleagues (Arnason et al., 1996, 1998, 2000; Janke and Arnason, 2002).

The four teeth from Baringo district, Kenya, described here reveal the presence of ape-like hominoids in East Africa during the latter part of the Middle Miocene and the Late Miocene. They thus refute the statement by Begun (2002) that “In actual fact, none of the many late Miocene African fossil localities has any hominoids...” When we add them to *Samburupithecus* from the Late Miocene of Samburu Hills, Kenya (9.5 Ma) (Ishida and Pickford, 1997), *Orrorin* from Lukeino, Kenya (6–5.7 Ma) (Senut et al., 2001), *Sahelanthropus* from Toros-Menalla, Chad (ca. 7–6 Ma) (Brunet et al., 2002), and *Ardipithecus* from Ethiopia (White et al., 1994, 1995), it is clear that Late Miocene Africa was not devoid of hominoids until they reintroduced themselves from Europe (Begun, 2002). Rather, it is more likely that chimp-sized *Dryopithecus* was originally an African lineage that invaded western Europe about 12.5–12 Ma, and while the evidence is scant, some of the large gorilla-sized hominoids from the Late Miocene of Greece and Turkey could also be of African origin rather than autochthonously evolved descendents of *Dryopithecus* or *Sivapithecus* as envisaged by Begun (2002). Despite the relative poverty of the African fossil record, the new discoveries reveal that hominoids were more diverse in the Late Miocene of Africa than they were in Europe (five genera now known in Africa compared to three or perhaps four in Europe).

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