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# Upper incisor morphology of the Late Miocene hominoid *Ouranopithecus macedoniensis* from Axios Valley (Macedonia, Greece)

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**Abstract** The upper incisor lingual morphology of the late Miocene Greek hominoid *Ouranopithecus macedoniensis* was almost unknown, as the described earlier maxillary remains preserve only worn incisors. During the most recent excavations in the type locality of *Ouranopithecus*, Ravin de la Pluie (RPI) of Axios Valley (Macedonia, Greece), four little-worn upper central incisors were recovered. This material and a few additional worn upper incisors, discovered recently, are described and compared in this article. Even though a morphological comparison with the old RPI material, lacking unworn or little worn incisors, is impossible, the metrical comparison and the monospecific character of the RPI hominoid sample suggest that the described incisors can be assigned to *Ouranopithecus macedoniensis*. The described upper central incisors are separated in two size-groups which in general have similar morphology except for some minor differences such as the presence of a pronounced mesial lingual pillar in the small-sized specimens. The observed significant size difference among the studied incisors is attributed to the strong sexual dimorphism of *Ouranopithecus*, which is also well expressed in the other teeth. The lingual morphology of the upper incisors of *Ouranopithecus* are not identical to those of extant great apes, though they have some similarities with those of the African great apes (*Gorilla* and *Pan*), while they are clearly different from those of the Asian great ape (*Pongo*). Even though they have some morphological similarities, the *O. macedoniensis* central incisors are probably not identical to those of the Eurasian Miocene hominoids; the most similar central incisor is that of *Ouranopithecus turkae*. Among the known African Miocene hominoids, *Nakalipithecus* upper central incisor is quite similar in morphology and size to that of *Ouranopithecus*.

**Key words:** Hominoids, *Ouranopithecus*, incisors, morphology, comparisons

## Introduction

Since the beginning of the 1970s, the late Miocene mammal locality Ravin de la Pluie (RPI) of Axios Valley (Macedonia, Greece) has been known for the presence of the hominoid *Ouranopithecus macedoniensis*. Several maxillary and mandibular remains of this taxon have been unearthed during the last 45 years, allowing a good understanding of its postcanine teeth morphology and features (Bonis and Melentis, 1977, 1978; Bonis et al., 1990; Bonis and Koufos, 1993; Bonis et al., 1998; Koufos and Bonis, 2004, 2006). In RPI, *O. macedoniensis* is associated with a rich mammalian fauna, where bovids and giraffids predominate (>60% of the fauna), either in the number of the determined specimens or the minimum number of individuals (Bonis et

al., 1992). The RPI fauna is older than the known Turolian mammal faunas of Greece and suggests a correlation with the European land mammal zone MN 10, corresponding to the late Vallesian. The magnetostratigraphic study of the Axios Valley late Miocene deposits indicates an estimated age of ~9.3 Ma for RPI. The same hominoid has also been found at the locality Xirochori 1 (XIR)—about 1.5 km from RPI—also correlated to the late Vallesian (MN 10). Magnetostratigraphic correlations suggest an estimated age of ~9.6 Ma for XIR (Sen et al., 2000; Koufos, 2013 and references therein). *O. macedoniensis* is also known from the locality Nikiti 1 (NKT), about 150 km south-west of the Axios Valley, the fauna of which indicates a terminal Vallesian age, ranging from 9.3 to 8.7 Ma [Koufos et al. (2016a) and references therein].

Despite the rich dental collection of *O. macedoniensis*, the maxillary remains are scanty and the morphology of some teeth is virtually unknown. The upper incisors of *O. macedoniensis* were only known from two previously described maxillae from RPI. However, these are heavily worn and their lingual traits are invisible (Bonis and Melentis, 1978; Bonis et al., 1998). The upper incisors of the partial skull

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XIR-1, from Xirochori 1, are also worn and cannot yield any information on their lingual morphology (Bonis and Koufos, 1993). During recent field work we recovered some isolated upper incisors, four of which are little worn and preserve well the lingual morphology. The present article describes the new incisor remains in reference to the previous material and compares them with those of the extant and Miocene hominoids.

### Materials and Methods

The described incisors are housed in the Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki (LGPOT). The material was measured with a digital caliper and the measurements are given in millimeters with an accuracy of 0.1 mm; estimated values are given in parentheses. The previously described material of *O. macedoniensis* from RPI, also housed in LGPUT, including the male maxillae RPI-128 and RPI-775 (Bonis and Melentis, 1978; Bonis et al., 1998) and the male partial skull with the maxilla XIR-1 from Xirochori 1 (Bonis and Koufos, 1993), is used as comparative material. The comparative material of the modern hominoids includes the collections of the Senckenberg Museum of Natural History, Frankfurt (SMF) and the Museum Nationale d'Histoire naturelle of Paris (MNHN); only incisors of the 1st and 2nd wear stage (see below for the definition of wear stages) are used. The studied modern hominoids belong to *Gorilla gorilla* (3 individuals), *Pan troglodytes* (7 individuals), and *Pongo pygmaeus* (5 individuals) and are all mentioned in the text with their generic name. The nomenclature for the lingual traits of incisors

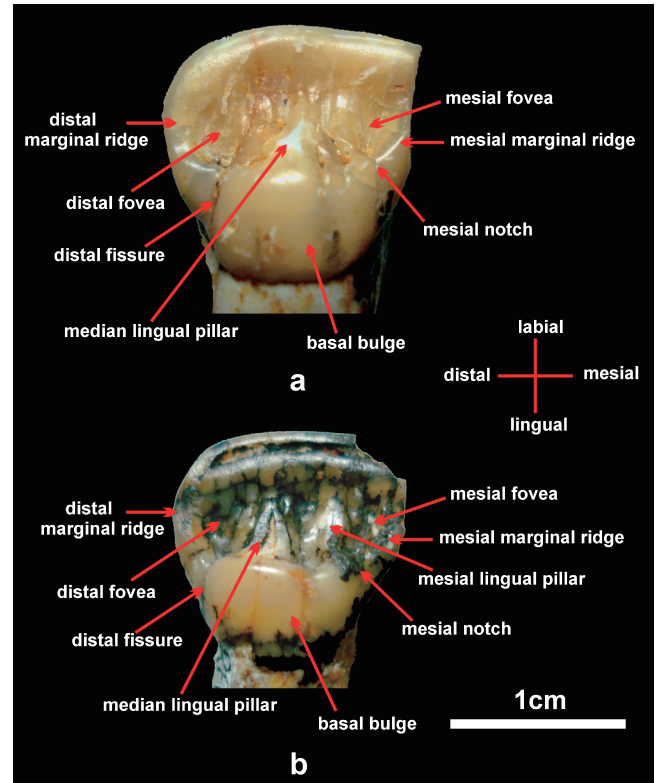


Figure 1. Nomenclature of the lingual traits of the central incisor, according to Pilbrow (2006) with minor additions. (a) *Ouranopithecus macedoniensis*, RPI-293 (size group-A). (b) *Ouranopithecus macedoniensis*, RPI-230 (size group-B).

Table 1. Measurements and indices of the studied upper incisors of *O. macedoniensis* from the late Miocene locality Ravin de la Pluie (RPI) of Axios Valley (Macedonia, Greece). Estimated values in brackets.

Collection No.	RPI-229	RPI-230	RPI-293	RPI-294	RPI-103	RPI-98	RPI-227	RPI-94
Central incisor	LI <sup>1</sup>	RI <sup>1</sup>	RI <sup>1</sup>	LI <sup>1</sup>	RI <sup>1</sup>	LI <sup>1</sup>	RI <sup>1</sup>	LI <sup>1</sup>
MD	11.4	11.5	12.7	12.5	12.2	12.8	11.4	[11]
LaL	9.4	9.5	9.7	9.9	10.8	10.4	10.5	10.4
H	10.4	10.1	10.4	9.6	—	—	6.4	[7.7]
% MD/LaL	122	120	131	126	—	—	—	—
% H/MD	91	88	82	77	—	—	—	—
MD <sub>R</sub>	—	7.4	9.5	10.0	—	—	9.1	—
LaL <sub>R</sub>	—	7.5	8.9	9.2	—	—	10.0	—
H <sub>R</sub>	—	—	[26]	—	—	—	—	19.3
H/H <sub>R</sub>	—	—	41.5	—	—	—	—	—
LaL <sub>R</sub> /MD <sub>R</sub>	—	102.0	94.0	93.0	—	—	109.0	—
Lateral incisor					RI <sup>2</sup>			RI <sup>2</sup>
MD	—	—	—	—	7.0	—	—	5.7
LaL	—	—	—	—	[7.0]	—	—	6.2
H	—	—	—	—	[7.1]	—	—	4.1
% MD/LaL	—	—	—	—	[101]	—	—	—
% H/MD	—	—	—	—	[101]	—	—	—
MD <sub>R</sub>	—	—	—	—	—	—	—	5.7
LaL <sub>R</sub>	—	—	—	—	—	—	—	4.7
H <sub>R</sub>	—	—	—	—	—	—	—	—
H/H <sub>R</sub>	—	—	—	—	—	—	—	—
LaL <sub>R</sub> /MD <sub>R</sub>	—	—	—	—	—	—	—	81.3
Wear stage	1	1	1	1	3	3	worn	worn

follows that of Pilbrow (2006) (Figure 1). Following this author, the incisors preserving lingual traits are divided in three dental wear stages: 1, a thin dentine strip exposed along the incisal margin; 2, a thick dentine strip exposed along the lingual surface. Teeth that are entirely worn are referred to as 'worn' (Table 1).

### Abbreviations

H, median labial height;  $H_R$ , median labial height of the root; LaL, labiolingual diameter;  $LaL_R$ , labiolingual diameter of the root at the cervix; MD, mesiodistal diameter;  $MD_R$ , mesiodistal diameter of the root at the cervix.

## Description of the Material

### Material

RPI-103 (maxillary fragment with the right  $I^1$ – $I^2$  and left  $I^1$ ); RPI-98 (right  $I^1$ ); RPI-227 (left  $I^1$ ); RPI-229 (left  $I^1$ ); RPI-230 (right  $I^1$ ); RPI-293 (right  $I^1$ ); RPI-294 (left  $I^1$ ); RPI-94 (right  $I^2$ ), (Figure 1, Table 1). The little-worn central incisors (1st wear stage) include RPI-229, RPI-230, RPI-293, and RPI-294; RPI-103 has quite worn incisors (3rd wear stage) and the other teeth are worn lacking the lingual morphology.

### Description

The upper central incisors RPI-293 and RPI-294 have similar size (Table 1) and morphology and probably belong to the same individual as their mesial contact facets fit well each other (Figure 1a, Figure 2a, b). RPI-293 preserves the root except its most apical part, whereas RPI-294 preserves only the cervical half of the root (Figure 2a, b). The occlusal outline of the crown is subelliptical with the labial portion longer than the lingual one. The crown is spatulate, long relative to the LaL diameter (% index  $MD/LaL > 100$  and low-crowned relative to the MD diameter (% index  $H/MD < 100$ ) (Table 1). The labial wall of the crown is smooth and mesiodistally convex, but this convexity is restricted to its incisal part. The crown is strongly swollen lingually, forming a basal bulge with no distinct lingual cingulum. There is a pronounced and triangular median lingual pillar that tapers incisally about half of the crown height; it is slightly worn, forming a triangular dentine pit. The median lingual pillar bears an elongated mesial accessory ridge, separated from it by a narrow groove. A well-expressed distal fissure separates the median lingual pillar from the distal marginal ridge (Figure 2a, b, distal view) and by a mesial notch from the mesial marginal ridge (Figure 1a). The mesial and distal foveae, separating the median lingual pillar from the marginal ridges, are nearly identical in size and shape. The almost complete root of RPI-293 is elongated, conical, and bends slightly lingually. The cross-section of the root at the cervix is more or less rounded; the % index  $LaL_R/MD_R$  ranges between 92.5 and 93.6 (Table 1). The RPI-293 and RPI-294 are morphologically and metrically overall similar, but have some minor differences such as the slightly stronger mesial lingual pillar, the slightly larger mesial fovea, and the more worn lingual traits of the latter in comparison with the former.

The other two central incisors, RPI-229 and RPI-230

(Figure 1b, Figure 2c, d), are similarly sized but are smaller than the above-described ones (Table 1); it is quite possible these are antimeres as their morphology and attrition are similar and their contact facets fit well. RPI-230 preserves well the crown, lacking only the mesiolabial enamel peel (Figure 2c, labial view) and the apical half of the root. RPI-229 lacks the distolingual part of the crown and almost the entire root; a small cervical part of the root is only preserved mesiolabially, exposing the pulp canal. The lingual morphology of these central incisors is generally similar to that of RPI-293 and RPI-294 despite minor differences. The most important difference is the presence of a second lingual pillar, situated mesially to the median one (mesial lingual pillar). The median and mesial lingual pillars of RPI-229 and RPI-230 are equally sized; the mesial one is stronger and longer than that in RPI-293 and RPI-294, separated well from the median one by a large and deep groove. Both pillars are more worn than those of RPI-293 and RPI-294, presenting triangular dentine pits. The distal marginal ridge is thinner and less convex distally than that of RPI-293 and RPI-294. The mesial fovea of RPI-229 is narrower and deeper than that of RPI-230.

The maxillary fragment RPI-103 preserves poorly the most anterior part of the premaxilla with the incisors. The central incisors are quite worn (3rd wear stage) and have lost most of their lingual morphology. The  $I^1$  is similar in size to RPI-293 and RPI-294 (Table 1; Fig. 4a); a pronounced basal bulge and a median lingual pillar can be distinguished better in the left  $I^1$ . The lateral incisor preserves the lingual incisal part of the crown; it is peg-shaped, subelliptical in occlusal view, and markedly smaller than the central incisor (Figure 2h). The labial wall is smooth and strongly convex mesiodistally. Two small lingual ridges run from the incisal margin towards the base of the crown (Figure 2h3). The thick mesial and distal marginal ridges are a continuation of the incisal margin. The central incisors RPI-98 and RPI-227 (Figure 2e, f) are heavily worn and the crown is a large dentine pit surrounded by enamel; both preserve the root. The occlusal outline of the crown is suboval. The root is like that of the above-described specimens. The lateral incisor RPI-94 (Figure 1g) preserves well the crown and the most cervical part of the root. The crown is heavily worn, showing a subtriangular occlusal outline. The root is flattened mesiodistally, having an elliptical cross-section.

## Comparisons

As the morphology of the post-canine teeth has been traditionally used for the taxonomy and phylogeny of the Miocene hominoids, the role of the incisors has long remained limited. Since the beginning of the 1990s, some scientists have started to use the incisor's lingual morphology to distinguish certain hominoid samples (e.g. Begun et al., 1990; Begun, 1992; Andrews et al., 1996; Ward et al., 1999), although they were some doubts regarding their taxonomic and/or phylogenetic significance (Harrison, 1991; Ribot et al., 1996). On the other hand the incisor's lingual morphology in the modern great apes shows great variation (Kelley et al., 1995; Benefit and McCrossin, 2000; Pilbrow, 2006). According to the last author the incisors of the extant great



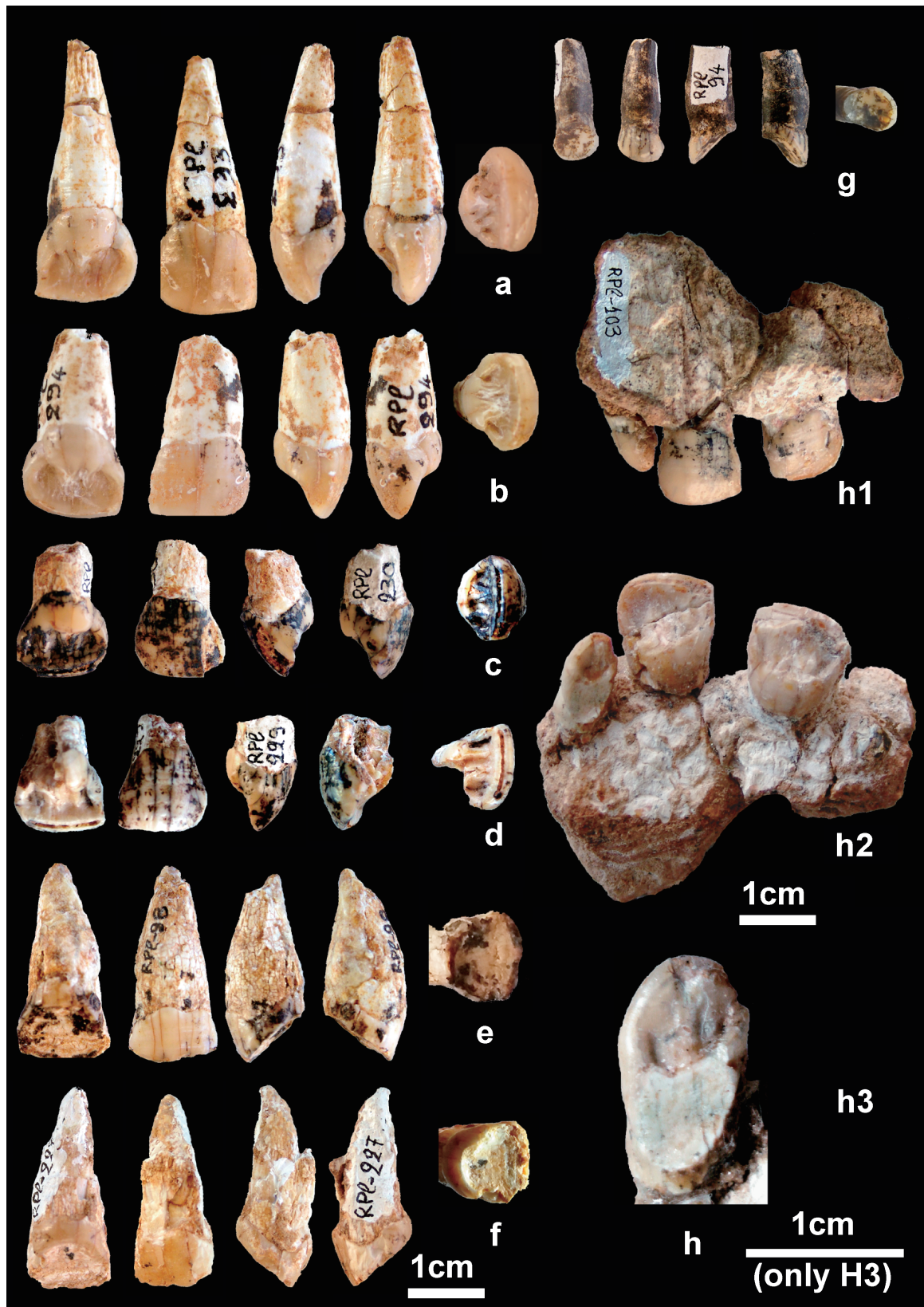


Figure 2. Upper incisors of *Ouranopithecus macedoniensis* from the late Vallesian locality Ravin de la Pluie (RPI) of Axios Valley (Macedonia, Greece): (a) right I<sup>1</sup>, RPI-293; (b) left I<sup>1</sup>, RPI-294; (c) right I<sup>1</sup>, RPI-230; (d) left I<sup>1</sup>, RPI-229; (e) right I<sup>1</sup>, RPI-98; (f) left I<sup>1</sup>, RPI-227; (g) right I<sup>2</sup>, RPI-94; (h) premaxillary fragment with I<sup>1</sup>-I<sup>2</sup> right and I<sup>1</sup> left, RPI-103; labial (h<sub>1</sub>), lingual (h<sub>2</sub>) view, and lingual morphology of the I<sup>2</sup> (h<sub>3</sub>). From left to right, lingual, lingual, labial, mesial, distal and occlusal view.

apes (gorillas, chimpanzees, orang-utans) have a high variation in their lingual morphology within the species and local populations, though it is possible in some populations to separate statistically species or subspecies based on the frequency of the lingual incisor traits (Pilbrow, 2006). In some recent publications, the incisor's lingual morphology has been used for taxonomic separation of some Miocene hominoid samples (e.g. Kelley et al., 2008; Alba et al., 2012; Pérez de los Ríos et al., 2012, 2013), but these studies did not rule out the possibility of sampling bias (as the fossil samples are small) or the presence of variation such as that observed in extant taxa (Alba et al., 2012; Pérez de los Ríos et al., 2012, 2013).

Keeping in mind all the above, we shall try to compare the *Ouranopithecus* upper incisor's lingual morphology with those of some Miocene hominoids. The comparison is restricted to the known material of each taxon and cannot be generalized, as the known incisor samples for most fossil hominoids are very poor, including a single or a few specimens, and their morphological variation is unknown. As the incisor's lingual morphology of the modern hominoids is variable (Pilbrow, 2006), the comparison with those of *O. macedoniensis* cannot give clear results; moreover, if we accept a variation in *Ouranopithecus* incisors, similar to that of the modern hominoids, then the comparison will provide more questionable results. Based on the comparison with the small samples of the modern hominoid incisors we have seen, however, we can say that the upper incisors of *O. macedoniensis* have generally more similar lingual morphology to those of *Gorilla* and *Pan* than to those of *Pongo*. The upper incisors of the last taxon, with strongly wrinkled

enamel in their lingual surface and basal bulge, are well distinguished from those of *O. macedoniensis* (Figure 3).

#### Comparison with extinct hominoids

Several Miocene hominoids are known from Turkey and the taxon closer in age to the studied one is *Ouranopithecus turkae*, known from the late Miocene locality Çorakyerler (Güleç et al., 2007). The  $I^1$  of this species has similar lingual morphology and size to that of *O. macedoniensis*, especially with RPI-293 and RPI-294 (Figure 4a, Figure 5). Two other hominoids, *Kenyapithecus kizili* and *Griphopithecus alpani*, are known from the middle Miocene locality Paşalar with a large number of upper incisors in the collection, especially from the second taxon (Kelley et al., 2008: fig. 1). The  $I^1$  of *K. kizili* differs from that of *O. macedoniensis* in displaying a triangular lingual outline with parallel mesial and distal sides over the incisal half of the crown, a strongly projected lingually basal bulge without observed median lingual pillar, a thick (hypertrophied) mesial and lingual marginal ridge, a less convex distal marginal ridge, smaller mesial and distal foveae, and smaller size (Figure 4a). The  $I^2$  of the same species (Kelley et al., 2008: fig. 4) is separated from that of *Ouranopithecus* in exhibiting a rhomboid lingual outline, more accessory ridges on the lingual surface, and probably slightly smaller size, as it is smaller than the less worn  $I^2$  of *Ouranopithecus* (RPI-103) (Figure 4b). The  $I^1$  of *Griphopithecus alpani*, the second hominoid from Paşalar (Kelley et al., 2008: fig. 1), has a rhomboid lingual outline, a pronounced median lingual pillar, a thicker and less convex distal marginal ridge, and smaller size than that of *Ouranopithecus* (Figure 4a). The  $I^2$  of *G. alpani* (Kelley

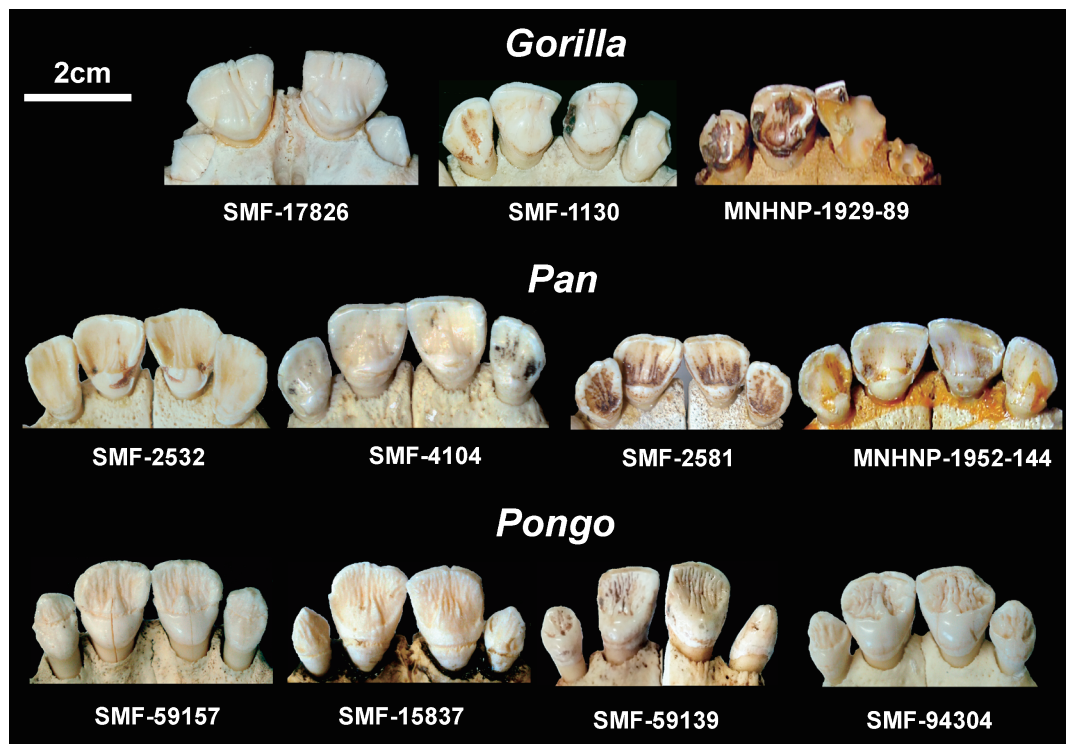


Figure 3. Upper incisors of the modern great apes, *Gorilla*, *Pan*, and *Pongo* (1st and 2nd wear stage).

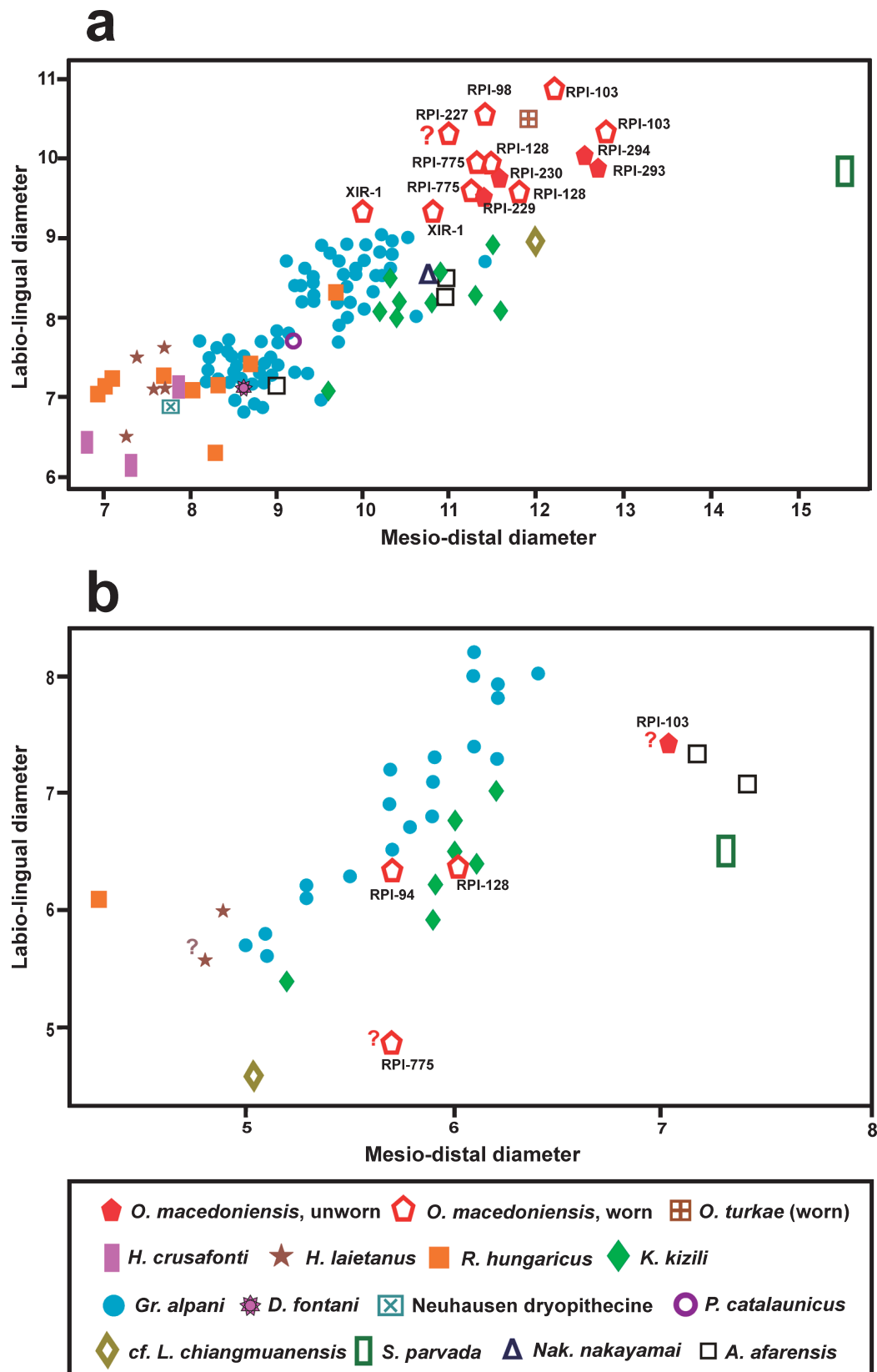


Figure 4. Scatter diagram (MD/LaL) comparing the upper central (a) and the lateral (b) incisors of *Ouranopithecus macedoniensis* with those of other hominoids. Question mark indicates estimated measurements. Figures 2 and 5 of Kelley et al. (2008) were used as the basis for these diagrams. Data sources: Alba et al. (2012), Chaimanee et al. (2003), Güleş et al. (2007), Kelley et al. (1995), Kimbel et al. (1982), Kordos and Begun (2001), Kunimatsu et al. (2007), Pérez de los Ríos et al. (2012, 2013), and Pickford (2012).



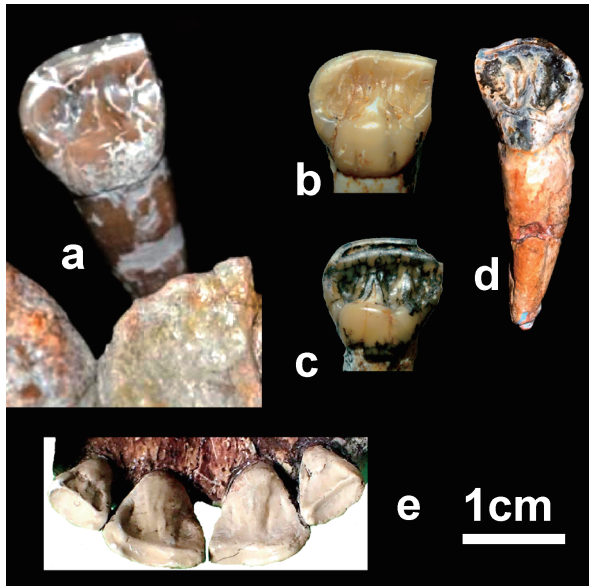


Figure 5. Lingual morphology of the upper central incisor of *Ouranopithecus* and *Nakalipithecus*. (a) *O. turkae*, Çorakyerler, Turkey, 18ÇO 2100 (photo kindly provided by A. Sevim Erol); (b, c) *O. macedoniensis*, Ravin de la Pluie, Greece, RPI-293 and RPI-230, respectively; (d) *Nakalipithecus nakayamai*, Nakali, Kenya, KNM-NA47592 (photo kindly provided by Y. Kunimatsu); (e) *Australopithecus afarensis*, Hadar-Afar, Ethiopia, A.L.200-1a (cast).

et al., 2008: fig. 4) has similar morphology to that of *Ouranopithecus* but is slightly shorter (Figure 4b).

*Rudapithecus hungaricus* is a late Miocene hominoid found in the locality Rudabánya, Hungary (Begun and Kordos, 1993; Kordos and Begun, 2001). The  $I^1$  of this taxon has a higher crown relative to MD, a shorter MD diameter relative to LaL (Table 2), and a more prominent basal bulge than that of *Ouranopithecus*. The  $I^2$  of *R. hungaricus* has high crown and triangular lingual outline (Kordos and Begun, 2001: fig. 1), differing from that of *Ouranopithecus* in having a mesiodistally shorter crown relative to LaL (Table 3) and an angular incisal margin.

The Spanish record of Miocene hominoids is rich, including several taxa. The best-known genus is *Hispanopithecus*, known with two taxa: *H. crusafonti* and *H. laietanus*. The  $I^1$  of *H. crusafonti* from the late Miocene of Vallès Penedès (Begun, 1992: fig. 8; Alba et al., 2012: fig. 4) differs from that of *O. macedoniensis* in showing a higher crown relative to MD (Table 2), a vertical groove in the mesial half of the labial surface, a triangular lingual outline, a basal bulge separated from the mesial and distal marginal ridges by deep mesial and distal vertical fissures, a strong median lingual pillar, no mesial lingual pillar, a thick mesial marginal ridge, a less convex distal marginal ridge, and remarkably smaller size (Figure 4a). The  $I^1$  of *H. laietanus* differs from that of *Ouranopithecus* in displaying a mesiodistally shorter crown relative to the LaL (Table 2), a vertical groove in the mesial

Table 2. Measurements and indices of upper central incisors of various Miocene hominoids. Data from Alba et al. (2012), Begun (1992), Chaimanee et al. (2003), Güleş et al. (2007), Kelley et al. (1995), Kimbel et al. (1982), Kordos and Begun (2001), Kunimatsu et al. (2007), Pérez de los Ríos et al. (2012, 2013), and Pickford (2012).

Species	Collection No.	MDI <sup>1</sup>	LaLI <sup>1</sup>	HI <sup>1</sup>	%MD/LaLI <sup>1</sup>	%HI <sup>1</sup> /MD
<i>Ouranopithecus macedoniensis</i>	RPI-293	12.7	9.7	10.4	131	82
	RPI-294	12.5	9.9	9.6	126	77
	RPI-229	11.4	9.4	10.4	122	91
	RPI-230	11.5	9.5	10.1	120	88
	RPI-103	12.2	10.8	—	113	—
		12.8	10.4	—	123	—
	RPI-775	11.5	9.9	—	116	—
<i>Ouranopithecus turkae</i>	CO-205	11.3	9.5	—	119	—
		11.9	10.5	—	113	—
<i>Hispanopithecus crusafonti</i>	IPS 1807	7.6	6.2	11.4	123	150
	IPS 1808	7.7	6.2	10.7	124	139
	IPS 1809	7.8	6.7	12.5	116	160
<i>Hispanopithecus laietanus</i>	IPS 61398	7.4	7.5	—	99	—
<i>Rudapithecus hungaricus</i>	RUD 121	6.9	7.0	11.1	99	161
	RUD 199	6.9	7.0	10.8	99	157
<i>Dryopithecus fontani</i>	NMB G.a.9	8.6	7.1	11.3	121	131
<i>Dryopithecine Neuhausen</i>	SMNS 47444	7.8	6.9	11.0	113	141
<i>Pierolapithecus catalaunicus</i>	IPS-21350.1	7.6	9.0	—	84	—
<i>Nakalipithecus nakayamai</i>	KNM-NA47592	10.8	8.6	11.8	126	109
cf. <i>Lufengpithecus chiangmuanensis</i>	TF 6168	12.0	8.9	—	135	—
<i>Sivapithecus parvada</i>	GSP 46460	15.5	9.8	—	158	—
<i>Australopithecus afarensis</i>	A.L. 200-1a	10.9	8.5	—	128	—
		10.9	8.3	—	131	—
	A.L. 333x-4	10.8	8.6	—	126	—

Table 3. Measurements and indices of upper lateral incisors of various Miocene hominoids. Data from Alba et al. (2012), Chaimanee et al. (2003), Güleç et al. (2007), Kelley et al. (1995), Kimbel et al. (1982), Kordos and Begun (2001), Kunitatsu et al. (2007), Pérez de los Ríos et al. (2012, 2013), and Pickford (2012). Estimated values in brackets.

Species	Collection No.	MD	LaL	H	%MD/LaL
<i>Ouranopithecus macedoniensis</i>	RPI-103	7.0	[7.0]	[7.1]	[101]
	RPI-94	5.7	6.2	4.1	93
	RPI-128	6.0	6.4	4.7	94
	RPI-775	?4.8	?5.7	—	?84
<i>Ouranopithecus turkae</i>	CO-205	6.3	7.2	—	88
<i>Hispanopithecus laietanus</i>	IPS 58331	4.8	[5.6]	—	[86]
	IPS 58333	4.9	6.0	—	82
<i>Rudapithecus hungaricus</i>	RUD-197	4.3	6.1	—	70
<i>Sivapithecus parvada</i>	GSP 46460	7.3	6.6	—	111
cf. <i>Lufengpithecus chiangmuanensis</i>	TF 6173	5.1	4.6	—	110
<i>Austarlopithecus afarensis</i>	A.L. 200-1a	7.4	7.0	—	106
		7.2	7.3	—	99

half of the labial surface, absence of median lingual pillar, a less convex distal marginal ridge (Alba et al., 2012: fig. 3G; Pérez de los Ríos et al., 2013: fig. 4F–J), and smaller size (Figure 4a). The  $I^2$  of *H. laietanus* has variable lingual morphology (Alba et al., 2012: fig. 4L–O) and differs from that of *O. macedoniensis* in having smaller size (Figure 4b) and a mesiodistally shorter crown relative to LaL (Table 3); the little-worn IPS-58333 of *H. laietanus* is distinguished from that of *O. macedoniensis* in displaying wrinkled enamel on the lingual surface.

One  $I^1$  (IPS-21350, holotype) of *Pierolapithecus catalaunicus* was described from the middle Miocene site Barranc de Can Vila (Pérez de los Ríos, 2012: fig. 1A–E). The more pronounced basal bulge, the single median lingual pillar, the less convex distal marginal ridge, the mesiodistally shorter crown relative to LaL (Table 2), and the smaller size (Figure 4a) distinguish it from *O. macedoniensis*.

The single known  $I^1$  of *Dryopithecus fontani* from the middle Miocene locality La Grive, France, was recently re-described and revised (Pérez de los Ríos et al., 2013: fig. 1A–E). Besides its markedly smaller size (Figure 4a) it differs from the central incisor of *Ouranopithecus* in displaying a large vertical groove on the mesial half of the labial crown surface, a higher crown relative to MD (Table 2), a strong median lingual pillar, no mesial lingual pillar, and a less convex distal marginal ridge. Among the dryopithecine material from the middle Miocene locality Neuhausen (Germany) there is a moderately worn  $I^1$  (Pickford, 2012: fig. 5). It differs from the *Ouranopithecus* central incisor in exhibiting a vertical groove in the mesial half of the labial crown surface, a higher crown relative to MD, a mesiodistally shorter crown relative to LaL (Table 2), a triangular lingual outline, a more linguallly projected basal bulge, wrinkled enamel on the basal bulge (Pickford, 2012: fig. 5), and remarkably smaller size (Figure 4a).

The central incisor of the Chinese late Miocene hominoid *Lufengpithecus lufengensis* differs from that of *Ouranopithecus* in having a more rounded occlusal outline of the crown (the % index MD/LaL >90 and in one case

equals 100), strongly wrinkled enamel on the basal bulge and lingual surface, a thicker mesial marginal ridge and a less convex distal marginal ridge (Xu and Lu, 2008: figs. 2.13, 4.1, 4.2). The lateral incisor of *L. lufengensis* differs from that of *Ouranopithecus* in showing an angular incisal margin, and weaker mesial and distal marginal ridges. A single  $I^1$  (TF-6168) of the hominoid cf. *L. chiangmuanensis* (Chaimanee et al., 2003: fig. 3a) differs from that of *Ouranopithecus* in displaying a basal bulge that is restricted to the cervical part of the crown, wrinkled enamel on the basal bulge and lingual surface, smaller mesial and distal foveae, and a less convex distal marginal ridge. The smaller size (Figure 4b), the mesiodistally shorter crown relative to the LaL (Table 3), and the presence of lingual cingulum (Chaimanee et al., 2003: fig. 3j) separate the  $I^2$  of cf. *L. chiangmuanensis* from that of *O. macedoniensis*.

A single  $I^1$  (GSP 46460) of *Sivapithecus parvada* from the late Miocene of Siwaliks, Pakistan differs from that of *O. macedoniensis* in having a hexagonal outline in lingual and labial aspect, a mesiodistally longer crown relative to LaL (Table 2), entirely wrinkled enamel on the basal bulge, numerous faint wrinkles on the lingual surface (Kelley, 1988: fig. 2), and a larger size (Figure 4a). The mesiodistally shorter crown relative to LaL (Table 3) and the angular incisal margin of the *S. parvada*  $I^2$  (Kelley et al., 1995: fig. 2) distinguish it from that of *Ouranopithecus*. Two other unworn upper central incisors of *Sivapithecus* from Siwaliks (GSP 6999 and YPM 16919) were described and figured by Kelley (1988: fig. 2). They differ from *Ouranopithecus*  $I^1$  in the above-mentioned features, but have smaller size; the dimensions of the unworn  $I^1$  GSP 6999 are  $10.3 \times 7.6$  mm (Pilbeam, 1969).

One isolated and little-worn upper central incisor is known from the late Miocene hominoid *Nakalipithecus nakayamai* from Nakali, Kenya (Figure 5d), described by Kunitatsu et al. (2007: fig. 3c). The subelliptical lingual outline, the mesiodistally short crown relative to LaL (Table 2), the presence of a weak lingual pillar, the few accessory lingual ridges, and the strongly curved distal



marginal ridge of its  $I^1$  agree with the morphology of RPI-293 and RPI-294 (Figure 5b, d). However, it differs from *Ouranopithecus*  $I^1$  in having slightly smaller size (Figure 4a), and a lingual cingulum continuous with the mesial and distal marginal ridges (Kunimatsu et al., 2007), a trait that is absent in *O. macedoniensis*.

The described incisors are compared with the little-worn incisors preserved in the maxilla A.L.200-1a of *Australopithecus afarensis* (Kimbel et al., 1982: fig. 4) [comparison with a cast housed in the Institut International de Paléoprimatologie, Paléontologie Humaine: Evolution et Paléoenvironnements, Université de Poitiers, France (Figure 5e)]. Apart from its smaller size, the *A. afarensis*  $I^1$  differs from *Ouranopithecus* in having a triangular lingual outline versus subelliptical in *Ouranopithecus*, a strong and lingually projected basal bulge, a strong median lingual pillar, a relatively larger mesial fovea, and no accessory lingual ridges. The  $I^2$  of *A. afarensis* is completely different from that of *Ouranopithecus* in showing a larger size relative to the  $I^1$ , a triangular lingual outline, and a mesiodistally longer crown relative to LaL (Table 3).

## Discussion

The old collection of *Ouranopithecus* from the various localities lacks unworn or little-worn incisors, a fact that prevents a direct morphological comparison with the described new incisors. Hence, the comparison is limited to a metrical one, indicating that all newly described incisors are within the variation for *O. macedoniensis* (Figure 4). The metrical similarity and the monospecific character of the RPI hominoid sample (Koufos et al., 2016b and references therein) indicate that the described new incisors belong to *O. macedoniensis*.

The lingual morphology of *Ouranopithecus* central incisors is generally consistent. Small differences among the

described specimens, such as the presence of a mesial lingual pillar in the small-sized  $I^1$ , the thicker and more convex distal marginal ridge, and the wider distal fovea of RPI-293 and RPI-294 in comparison to RPI-229 and RPI-230, can be considered intraspecific variation and cannot allow the separation of different morphs. Despite the morphological resemblance of the described central incisors, their dimensions allow them to be divided into two groups: the large-sized group-A (RPI-293, RPI-294) and the small-sized group-B (RPI-229, RPI-230) (Figure 4a). The size difference could be related to the attrition, the gradual increase of which affects the dental dimensions. However, the role of attrition is limited, as the compared teeth are more or less at the same wear stage. In order to certify this size difference, the dental dimensions of the  $I^1$  were measured in a standard point, the cervix, and plotted in a scatter diagram (Figure 6). The separation of the RPI sample in two size groups is clear, confirming that the role of attrition is limited. The attribution of the other known *Ouranopithecus* central incisors from RPI to these size groups is based on their size as they are worn and their lingual morphology has disappeared. Based on their dimensions at the cervix (Figure 6), the specimens RPI-98, RPI-103, RPI-128 and RPI-775 match with RPI-294 and RPI-294 and can be included in the large-sized group-A. The small-sized group-B includes only the specimens RPI-229 and RPI-230.

The size difference in the dentition of *O. macedoniensis* has long been recognized and was ascribed to sexual dimorphism. The species is considered as one of the most dimorphic hominoids, comparable to the extinct *Lufengpithecus lufengensis* and the extant *Pongo* (see Koufos et al., 2016a and references therein). Therefore the observed size differences of the upper central incisors can be explained by this sexual dimorphism. Consequently, the size group-A corresponds to male and the group-B to female individuals. Such size differences are also observed in both Paşalar hominoids,

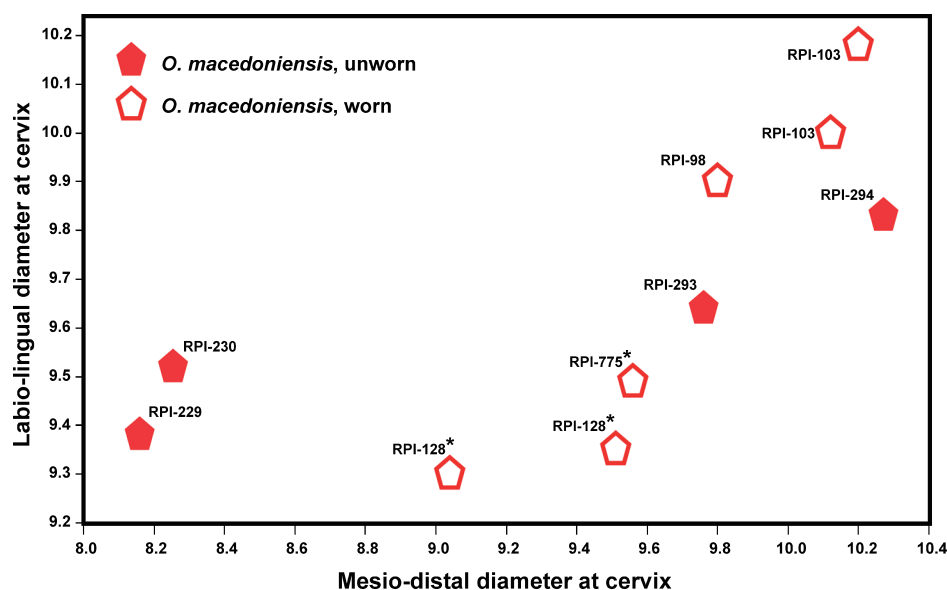


Figure 6. Scatter diagram (MD/LaL at the cervix) comparing the upper central incisor of *Ouranopithecus macedoniensis* from Ravin de la Pluie, RPI. Specimens marked with an asterisk are confidently assigned as male (associated with canines).

whose incisors are separated in two size groups corresponding to males and females (Kelley et al., 2008). However, the absence of specimens with unworn incisors in situ associated with canines cannot allow us to confirm this hypothesis for now.

The limited number of incisors in the RPI sample of *O. macedoniensis* and of the other known Miocene hominoids, combined with the possible intraspecific variation in their lingual morphology, as in the modern hominoids, does not allow confident comparisons and results for their systematic and/or phylogenetic relationships.

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### References

- Alba D.M., Casanovas-Vilar I., Almécija S., Robles J.M., Arias-Martorell J., and Moyà-Solà S. (2012) New dental remains of *Hispanopithecus laietanus* (Primates: Hominidae) from Can Llobateres 1 and the taxonomy of Late Miocene hominoids from the Vallès-Penedès Basin (NE Iberian Peninsula). *Journal of Human Evolution*, 63: 231–246.
- Andrews P., Harrison T., Delson E., Bernor R.L., and Martin L. (1996) Distribution and biochronology of European and Southwest Asian Miocene catarrhines. In: Bernor R.L., Fahlbusch V., and Mittmann H.-W. (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, pp. 168–207.
- Begun D.R. (1992) *Dryopithecus crusafonti* sp. nov., a new Miocene hominoid species from Can Ponsic (northeastern Spain). *American Journal of Physical Anthropology*, 87: 291–309.
- Begun D.R. and Kordos L. (1993) Revision of *Dryopithecus branchoi* Schlosser, 1901 based on the fossil hominoid material from Rudabánya. *Journal of Human Evolution*, 25: 271–285.
- Begun D.R., Moyà-Solà S., and Köhler M. (1990) New Miocene hominoid specimens from Can Llobateres (Vallès Penedès, Spain) and their geological and paleoecological context. *Journal of Human Evolution*, 19: 255–268.
- Benefit B.R. and McCrossin M.L. (2000) Middle Miocene hominoid origins. *Science*, 287: 2375a.
- Bonis L. de and Koufos G.D. (1993) The face and the mandible of *Ouranopithecus macedoniensis*: description of new specimens and comparisons. *Journal of Human Evolution*, 24: 469–491.
- Bonis L. de, Koufos G.D., Guy F., Peigne S., and Sylvestrou I. (1998) Nouveaux restes du primate hominoïde *Ouranopithecus* dans les dépôts du Miocène supérieur de Macédoine (Grèce). *Comptes Rendus Académie Sciences Paris*, 327: 141–146.
- Bonis L. de and Melentis J.K. (1977) Un nouveau genre de primate hominoïde dans le Vallésien (Miocène supérieur) de Macédoine (Grèce). *Comptes Rendus de l'Académie des Sciences de Paris*, 284: 1393–1396.
- Bonis L. de and Melentis J.K. (1978) Les Primates hominoïdes du Vallésien de Macédoine (Grèce). *Étude de la machoire supérieure*. *Annales de Paléontologie*, 64: 185–202.
- Bonis L. de, Bouvraïn G., Geraads D., and Koufos G.D. (1990). New hominid skull material from the late Miocene of Macedonia in Northern Greece. *Nature*, 345: 712–714.
- Bonis L. de, Bouvraïn G., Geraads D., and Koufos G.D. (1992) Diversity and palaeoecology of Greek late Miocene mammalian faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 91: 99–121.
- Bonis L. de, Koufos G.D., Guy F., Peigne S., and Sylvestrou J. (1998) Nouveaux restes du primate hominoïde *Ouranopithecus* dans les dépôts du Miocène supérieur de Macédoine (Grèce). *Comptes Rendus de l'Académie Sciences Paris*, 327: 141–146.
- Chaimanee Y., Jolly D., Benammi M., Tafforeau P., Duzer D., Moussa I., and Jaeger J.-J. (2003) A Middle Miocene hominoid from Thailand and orangutan origins. *Nature*, 422: 61–65.
- Güleç E.S., Sevim A., Pehlevan C., and Kaya F. (2007) A new great ape from the late Miocene of Turkey. *Anthropological Science*, 115: 153–158.
- Harrison T. (1991) Some observations on the Miocene hominoids from Spain. *Journal of Human Evolution*, 20: 515–520.
- Kelley J. (1988) A new large species of *Sivapithecus* from the Siwaliks of Pakistan. *Journal of Human Evolution*, 17: 305–324.
- Kelley J., Anwar M., McCollum M.A., and Ward S.C. (1995) The anterior dentition of *Sivapithecus parvada*, with comments on the phylogenetic significance of incisor heteromorphy in Hominoidea. *Journal of Human Evolution*, 28: 503–517.
- Kelley J., Andrews P., and Alpagut B. (2008) A new hominoid species from the middle Miocene site of Pasalar, Turkey. *Journal of Human Evolution*, 54: 455–479.
- Kimbel W.H., Johanson D.C., and Coppens Y. (1982) Pliocene hominid cranial remains from the Hadar Formation, Ethiopia. *American Journal of Physical Anthropology*, 57: 453–499.
- Kordos L. and Begun D.R. (2001) A new cranium of *Dryopithecus* from Rudabánya, Hungary. *Journal of Human Evolution*, 41: 689–700.
- Koufos G.D. (2013) Neogene mammal biostratigraphy and chronology of Greece. In: Wang X., Flynn L.J., and Fortelius M. (eds.), *Fossil Mammals of Asia. Neogene Biostratigraphy and Chronology*. Columbia University Press, New York, pp. 595–621.
- Koufos G.D. and Bonis L. de (2004) The deciduous lower dentition of *Ouranopithecus macedoniensis* (Primates, Hominoidea) from the late Miocene deposits of Macedonia, Greece. *Journal of Human Evolution*, 46: 699–718.
- Koufos G.D. and Bonis L. de (2006) New material of *Ouranopithecus macedoniensis* from the late Miocene of Macedonia (Greece) and study of its dental attrition. *Geobios*, 39: 223–243.
- Koufos G.D., Kostopoulos D.S., and Vlachou T.D. (2016a) Synthesis. In: Koufos G.D. and Kostopoulos D.S. (eds.), *Palaeontology of the Upper Miocene Vertebrate Localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece)*. *Geobios*, 49: 147–154.
- Koufos G.D., Bonis L. de, and Kugiumtzis D. (2016b) New material of the hominoid *Ouranopithecus macedoniensis* from the Late Miocene of Axios Valley (Macedonia, Greece) with some remarks on its sexual dimorphism. *Folia Primatologica*, 87: 94–122.
- 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., and 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 the National Academy of Sciences of the United States of America*, 104: 19220–19225.
- Pérez de los Ríos M., Alba D.M., and Moyà-Solà S. (2012) The upper central incisor of *Pierolapithecus catalaunicus* (Primates: Hominidae): description and taxonomic implications. In: Martínez-Pérez C., Furió M., Santos-Cubedo A., and Poza B. (eds.), *Paleodiversity and Paleoeecology of Iberian Ecosystems* (Book of Abstracts). X Encuentro de Jóvenes Investigadores en Paleontología, Imprenta Sichert, Valencia, pp. 149–151.
- Pérez de los Ríos M., Alba D.M., and Moyà-Solà S. (2013) Taxonomic attribution of the La Grive hominoid teeth. *American Journal of Physical Anthropology*, 151: 558–565.
- Pickford M. (2012) Hominoids from Neuhausen and other Bohnert localities, Swabian Alb, Germany: evidence for a high diversity of apes in the Late Miocene of Germany. *Estudios Geológicos*, 68: 113–147.
- Pilbeam D.R. (1969) Tertiary Pongidae of East Africa: Evolutionary Relationships and Taxonomy. *Bulletin of the Peabody Museum of Natural History, Yale University*, 31: 1–185.
- Pilbrow V. (2006) Lingual incisor traits in modern hominoids and an assessment of their utility for fossil hominoid taxonomy. *American Journal of Physical Anthropology*, 129: 323–338.
- Ribot F., Gibert J., and Harrison T. (1996) A reinterpretation of the taxonomy of *Dryopithecus* from Vallès-Penedès, Catalonia (Spain). *Journal of Human Evolution*, 31: 129–141.
- Sen S., Koufos G.D., Kondopoulou D., and Bonis L. de (2000) Magnetostratigraphy of the late Miocene continental deposits of the lower Axios Valley, Macedonia, Greece. In: Koufos G.D. and Ioakim C. (eds.), *Mediterranean Neogene Cyclostratigraphy in Marine-Continental Deposits*. *Bulletin of the Geological Society of Greece, Special Publication*, 9: 197–206.
- Ward S.C., Brown B., Hill A., Kelley J., and Downs W. (1999) *Equatorius*: A new hominoid genus from the middle Miocene of Kenya. *Science*, 285: 1382–1386.
- Xu Q. and Lu Q. (2008) *Lufengpithecus lufengensis*, an Early Member of Hominidae. *Science Press, Beijing* (in Chinese).