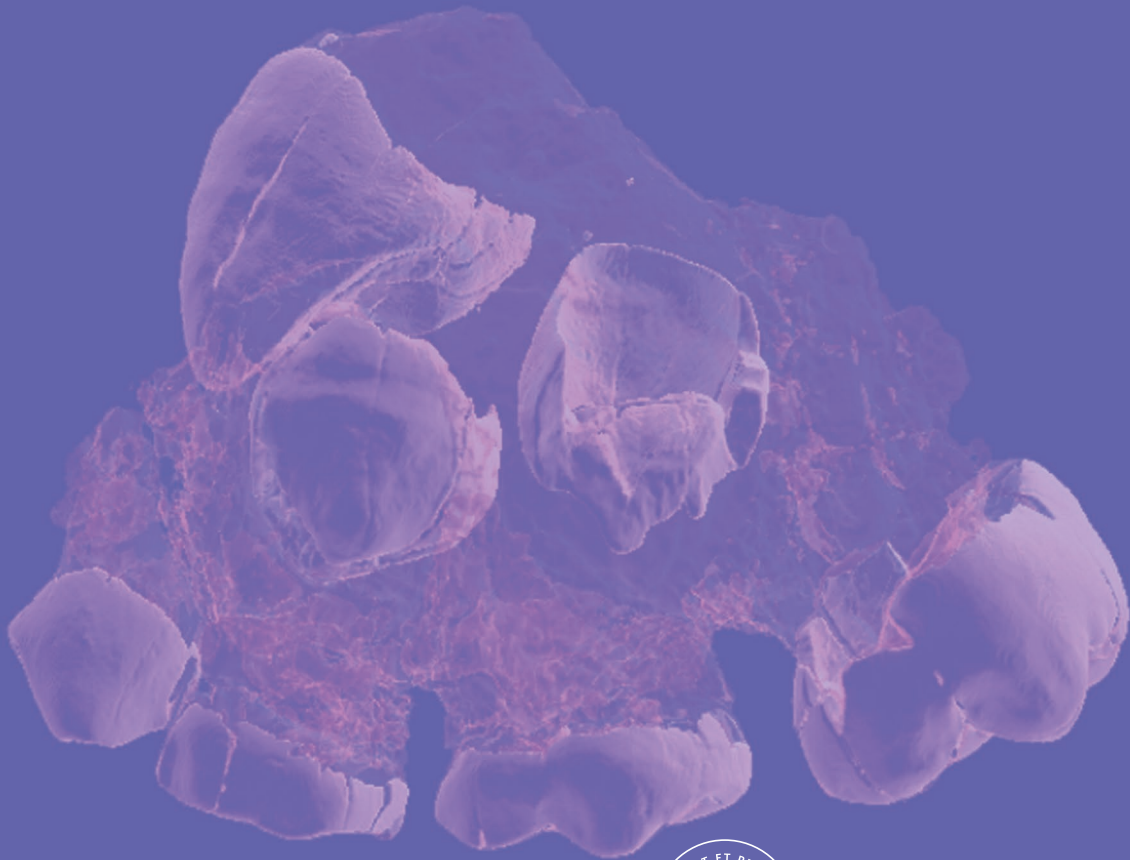


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# The Late Miocene hominoid *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974): maxillary deciduous dentition and virtual reconstruction of the unerupted permanent teeth

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## ABSTRACT

The hominoid *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) is known from three Late Miocene localities in Greece. All are correlated with late Vallesian, MN10; more precisely, they are dated between 9.6 and 8.7 Ma. During the last 50 years several fossils of this hominoid have been recovered. The present article describes the first specimen with upper deciduous teeth, recovered from the locality Ravin de la Pluie in Axios Valley (Macedonia, Greece). The upper deciduous dentition of *O. macedoniensis* is characterised by a small canine relative to the length of the deciduous premolars, with a rounded occlusal crown outline, a trapezoidal dP<sup>3</sup> with metacone and a rudimentary hypocone, a sub-squared dP<sup>4</sup>, and the absence of cingulum. The taxonomic and sexual attribution of the studied material is based on the preserved and virtually reconstructed permanent dentition, using high resolution microcomputed tomography. The morphological and metrical comparisons of the permanent dentition with the available sample of *O. macedoniensis*, as well as the monospecific character and the strong sexual dimorphism of the Ravin de la Pluie sample, allow its attribution to a female sub-adult individual of this taxon. The upper deciduous teeth of *Ouranopithecus macedoniensis* preserve some morphological features, that may have a phylogenetic value, but this hypothesis requires further investigation as the available material of all fossil taxa is poor.

## KEY WORDS

Hominoids,  
deciduous,  
description,  
comparisons,  
μCT scan,  
Greece.

## RÉSUMÉ

*L'hominoïde du Miocène supérieur Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) : dentition déciduale maxillaire et reconstruction virtuelle des dents permanentes non éruptives.

L'hominoïde *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) est connu dans trois localités du Miocène supérieur en Grèce. Toutes ces localités sont corrélées au Vallesien tardif, MN10; plus précisément, elles sont datées entre 9,6 et 8,7 Ma. Au cours des 50 dernières années, plusieurs fossiles de cet hominoïde ont été retrouvés. Cette étude décrit le premier spécimen présentant des dents déciduales supérieures, retrouvé dans la localité du Ravin de la Pluie dans la vallée d'Axios (Macédoine, Grèce). La dentition supérieure d'*O. macedoniensis* est caractérisée par une petite canine par rapport à la longueur des prémolaires dont la couronne occlusale est arrondie, une DP<sup>3</sup> trapézoïdal présentant un métacône et un hypocône rudimentaire, une DP<sup>4</sup> subcarrée, et l'absence de cingulum. L'attribution taxonomique et sexuelle du matériel étudié est basée sur la dentition permanente préservée et virtuellement reconstruite à l'aide de la tomographie microcomputée à haute résolution. Les comparaisons morphologiques et métriques de la dentition permanente avec l'échantillon disponible d'*O. macedoniensis*, ainsi que le caractère monospécifique et le fort dimorphisme sexuel de l'échantillon du Ravin de la Pluie permettent de l'attribuer à un individu subadulte femelle de ce taxon. Les dents déciduales supérieures d'*O. macedoniensis* conservent certaines caractéristiques morphologiques qui pourraient avoir une valeur phylogénétique, mais cette hypothèse nécessite des recherches plus approfondies car le matériel disponible pour tous les taxons fossiles est peu abondant.

## MOTS CLÉS

Hominoïdes,  
decidual,  
description,  
comparaisons,  
μCTscan,  
Grèce.

## INTRODUCTION

The Miocene hominoid record of the Eastern Mediterranean region is relatively poor compared to that of Central and Western Europe. Their earliest occurrence in the Eastern Mediterranean region is based on a single tooth specimen, found in the Lower Sinap (Turkey) and referred to as *Dryopithecus* sp. (Ozansoy 1965), but the exact location is still unknown. The latter can be correlated with the Turkish locality İnönü (GPTS = 16.0-15.9 Ma; Kappelman *et al.* 2003a). Furthermore, the earliest unambiguous hominoid from the Eastern Mediterranean is *Griphopithecus alpani* (Tekkaya, 1974), recorded at the Turkish localities of Çandir and Paşalar (Tekkaya 1974; Andrews & Tobien 1977), while a second hominoid, *Kenyapithecus kizili* Kelley, Andrews & Alpagut, 2008, has also been recognised at the latter fossil site. Although the age of these two fossil sites is still debated, they are most likely correlated with either MN5 or MN6 (van der Made 2003, 2005; Begun *et al.* 2003). Even if this is the case, a recent update of the Miocene hominoid bearing fossil sites in Europe suggests that Paşalar and Çandir are correlated with MN6, with the former being slightly older (Casnovas-Vilar *et al.* 2011). *Ankarapithecus meteai* (Ozansoy, 1965) was originally recovered from the Sinap Formation, Turkey (Ozansoy 1965). According to the stratigraphic correlations of Kappelman *et al.* (2003a, b), *A. meteai* is also known from the early/late Vallesian fossil sites Sinap 8A (MN9, GPTS 9.987-9.984 Ma) and Sinap 12 (MN9/MN10; GPTS 9.934-9.779/9.717-9.65 Ma). Furthermore, a fossil hominoid with similarities to *Ankarapithecus* Ozansoy, 1957 and *Sivapithecus* Pilgrim, 1910 is known from the Late Miocene locality MMTT II in Dareh Gorg (Maragheh, Iran), dated to *c.* 7.5 Ma (Suwa *et al.* 2016). *Udabnopithe-*

*cus garedziensis* (Burtschak & Gabashvili, 1945) is recorded from Udabno 1, Georgia dated to early Turolian, MN11; the palaeomagnetic evidence suggested an age ranging from 8.1-7.7 Ma (Agustí *et al.* 2020).

Two Late Miocene fossil hominoids genera *Graecopithecus* von Königswald, 1972 and *Ouranopithecus* de Bonis & Melentis, 1977a are known from the southern Balkans. The former is based on an isolated specimen, a mandible missing all teeth except the worn right m<sub>1</sub>, found at the locality Pyrgos Vassilissis (Attica, Greece). This specimen was originally assigned to *Mesopithecus pentelicus* Wagner, 1839 by K. Dietrich (von Freyberg (1951) and later described as a new hominoid under the name *Graecopithecus freybergi* von Königswald, 1972. A recent palaeomagnetic analysis suggests an estimated age of 7.18-7.17 Ma for this locality (Böhme *et al.* 2017). The synonymy of *Ouranopithecus* and *Graecopithecus* has long been debated, but more recent analyses suggest a distinct taxonomic status for this taxon (Martin & Andrews 1984; Andrews *et al.* 1996; Cameron 1997; Koufos & Bonis 2005; Fuss *et al.* 2017). More recently, an isolated premolar was found in Azmaka (Bulgaria), assigned as *cf. Graecopithecus* sp. with a possible age of 7.4 Ma (Spassov *et al.* 2012; Böhme *et al.* 2017; Fuss *et al.* 2017).

The genus *Ouranopithecus* occurs at three fossil sites in Macedonia (Greece): 1) Xirochori 1, Axios Valley (MN10; GPTS *c.* 9.6 Ma); 2) Ravin de la Pluie, Axios Valley, type locality (MN10; GPTS *c.* 9.3 Ma); and 3) Nikiti 1, Chalkidiki Peninsula (MN10; 9.3-8.7Ma), with all fossil remains assigned to *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974), (Bonis *et al.* 1990; Koufos *et al.* 1991; Koufos 1993, 1995; Bonis & Koufos 1993, 2014; Sen *et al.* 2000; Koufos & Bonis 2006). *Ouranopithecus macedoniensis* was originally found at Ravin de la Pluie in 1973

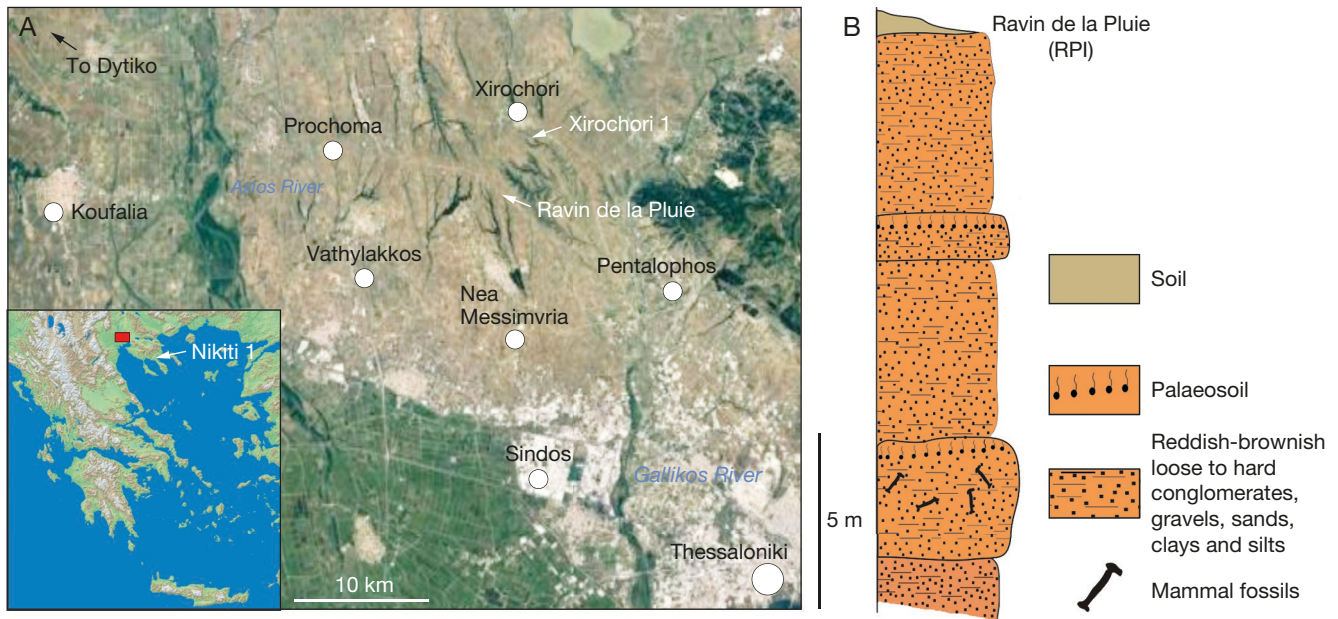


FIG. 1. — **A**, Geographical map of the Axios Valley, indicating the position of the hominoid bearing mammal localities; **B**, stratigraphic column of Ravin de la Pluie showing the position of the fossiliferous level. Credits: A, Google.

(Bonis *et al.* 1974); during the last 50 years several specimens have been recovered from this fossil site. A partial cranium with preserved face and dentition is only known from Xirochori 1 and a maxilla and a mandible from Nikiti 1 (Bonis *et al.* 1990; Koufos 1993, 1995). The sharing of some morphological features with australopithecids and *Homo* Linnaeus, 1758 has led to long discussions among researchers and several hypotheses have been expressed (Bonis & Melentis 1985; Andrews 1992; Begun 1992; Dean & Delson 1992; Bonis & Koufos 1994, 1995, 2001; Cameron 1997; Begun *et al.* 1997; Harrison 2010). Two recent papers discuss the systematic and phylogenetic position of the Miocene hominoids. The first classifies *Ouranopithecus* and *Graecopithecus* in the tribe Graecopithecini (subfamily *incertae sedis*, Hominidae Urciuoli & Alba, 2023) (Urciuoli & Alba 2023). The second is a phylogenetic analysis of the Middle-Late Miocene hominoids, suggesting that *Ouranopithecus* can be considered as a stem member of the hominin clade together with *Graecopithecus* and/or the African *Nakalipithecus* Kunimatsu, Nakatsukasa, Sakai, Hyodo, Itaya, Nakaya, Saegusa, Mazurier, Saneyoshi, Tsukijakawa, Yamamoto & Mbua, 2007 (Pugh 2022).

Some remains (maxillary fragment, mandible, partial mandible) of a hominoid have been described as *Ouranopithecus turkae* Güleç, Sevim, Pehlevan & Kaya, 2007 from the Turkish site Çorakyerler (Güleç *et al.* 2007). Recently new material from this locality indicated differences from *Ouranopithecus* allowing the erection of a new genus, named *Anadoluivius* Sevim Erol, Begun, Yavuz, Tarhan, Sönmez Sözer, Mayda, van den Hoek Ostende, Martin & Cihat Alçiçek, 2023 (Sevim-Erol *et al.* 2023). The age of the site is debated; the biochronological data suggest a correlation with either the early Turolian, MN11 (Geraads 2013), or with the Vallesian/

Turolian boundary, MN10/11 (Kostopoulos *et al.* 2020). The palaeomagnetic data gave an age ranging between 8.11–7.64 Ma (Kaya *et al.* 2016).

Ravin de la Pluie is situated in Axios Valley approximately 35 km northwest of Thessaloniki city. The fossil site is located *c.* 2 km north of the village Nea Messimvria (Fig. 1A) and has yielded several hominoid remains during a series of field campaigns over the last 50 years (Bonis *et al.* 1974; Bonis & Melentis 1977b, 1978; Koufos & Bonis 2004, 2006; Bonis & Koufos 2014; Koufos *et al.* 2016). The Late Miocene mammal localities of the Axios Valley have been known since the beginning of the 20th century (Andrews 1918; Bourcart 1919; Arambourg & Piveteau 1929).

The Late Miocene deposits of Axios Valley are divided into three formations from bottom to top: the Nea Messimvria Fm, the Vathylakkos Fm, and the Dytiko Fm (Bonis *et al.* 1988). Ravin de la Pluie is within the earliest Nea Messimvria Formation, which consists of sands, gravels, and conglomerates mixed with reddish-brown clays and silts; the fossiliferous level is in the lower part of the section (Fig. 1B). The site yielded a rich mammalian fauna including the following taxa: *Ouranopithecus macedoniensis*, *Palerinacetus* sp., *Spermophilinus* sp., *Progonomys cathalae* Schaub, 1938, *Eomellivora piveteaui* Ozansoy, 1965, *Adcrocuta eximia leptoryncha* de Bonis & Koufos, 1981, *Protictitherium thessalonikensis* Koufos, 2012, *Protictitherium* aff. *intermedium*, cf. *Hyaenictis* sp., “*Metailurus*” *parvulus* (Hensel, 1862), *Choerolophodon pentelici* (Gaudry & Lartet, 1856), *Deinotherium giganteum* Kaup, 1829, *Hipparion* cf. *sebastopolitanum*, *Hipparion macedonicum* Koufos, 1984, *Rhinocerotidae* indet., *Palaeogiraffa major* Bonis & Bouvrain, 2003, *Palaeotragus* cf. *coelophrys*, *Boblinia* cf. *attica*, *Mesembriacerus melentisi* Bouvrain, 1975, *Samotragus praecursor* Bouvrain &

TABLE 1. — Comparative material and measurements of the upper deciduous teeth used in this article. Abbreviations: **BL**, buccolingual length; **C<sup>1</sup>**, upper canine; **d**, deciduous; **ML**, mesiodistal length; **P<sup>3</sup>**, upper third premolar; **P<sup>4</sup>**, upper fourth premolar.

Specimens	MLdC <sup>1</sup>	BLdC <sup>1</sup>	MLdP <sup>3</sup>	BLdP <sup>3</sup>	MLdP <sup>4</sup>	BLdP <sup>4</sup>	Measurements
<i>Ouranopithecus macedoniensis</i> (Bonis, Bouvrain, Geraads & Melentis, 1974)							
RPL-245	7.2	7.1	8.4	8.6	10.7	9.8	GDK
<i>Gorilla gorilla</i> (Savage, 1847)							
NHMS-74698a	9.8	7.5	9.4	9.4	11.5	10.9	GDK
NHMS-74698 b	10.1	7.3	9.4	9.3	11.3	10.9	GDK
NHMS-19158a	11.7	8.8	10.4	11.1	13.3	13.5	GDK
NHMS-19158b	10.7	9.1	10.1	11.0	14.1	13.4	GDK
NHMS-7470a	11.6	7.7	11.2	10.5	12.4	12.7	GDK
NHMS-7470b	11.7	7.7	10.6	10.5	13.2	13.2	GDK
NHMS-46766a	9.3	6.7	9.6	9.2	12.4	11.3	GDK
NHMS-46766b	8.9	6.7	10.0	9.8	12.3	11.1	GDK
<i>Pan troglodytes</i> (Blumenbach, 1775)							
NHMS-6871a	7.9	5.4	6.4	6.6	8.1	8.7	GDK
NHMS-6871b	7.8	5.5	6.1	6.9	8.1	8.8	GDK
NHMS-7471a	7.9	5.0	5.8	6.4	8.7	9.0	GDK
NHMS-7471b	7.9	5.0	6.0	6.4	8.3	9.0	GDK
NHMS-7532a	8.0	4.9	5.9	7.0	8.5	9.0	GDK
NHMS-7532b	7.9	4.9	5.9	6.5	7.4	8.8	GDK
NHMS-9479a	7.8	4.9	6.1	6.4	8.0	8.5	GDK
NHMS-9479b	7.8	4.8	6.0	6.4	7.5	8.1	GDK
NHMS-46768a	8.0	5.6	6.1	6.2	7.9	8.7	GDK
NHMS-46768b	8.1	5.7	6.5	6.5	8.3	8.5	GDK
NHMS-46767a	7.8	5.2	7.0	7.0	9.1	8.8	GDK
NHMS-46767b	7.5	5.2	6.7	6.8	8.3	9.0	GDK
<i>Pongo pygmaeus</i> (Linnaeus, 1760)							
NHMS-2223a	8.6	7.4	7.6	9.3	9.8	10.3	GDK
NHMS-2223b	8.5	7.2	7.7	9.2	9.7	10.3	GDK
NHMS-7462a	10.2	7.2	8.8	9.9	10.5	11.6	GDK
NHMS-7462b	10.1	6.9	9.2	9.8	11.1	11.6	GDK
NHMS-7461a	8.9	6.7	8.1	8.4	10.3	10.5	GDK
NHMS-7461b	8.8	6.8	8.4	8.7	10.6	10.3	GDK
NHMS-1750a	10.2	7.1	8.2	9.4	9.8	9.9	GDK
NHMS-1750b	–	–	7.7	9.1	9.2	9.8	GDK
NHMS-2012a	7.7	6.7	7.5	8.3	10.3	10.0	GDK
<i>Homo sapiens</i> Linnaeus, 1758							
DPUT-SA 3	5.9	6.2	6.4	9.2	8.1	9.3	provided by M. Ioannidou
DPUT-SA 5	–	–	6.8	8.2	–	–	provided by M. Ioannidou
DPUT-SA 10	–	–	–	–	8.6	8.3	provided by M. Ioannidou
DPUT-Sa 25	–	–	6.7	7.9	8.3	9.6	provided by M. Ioannidou
DPUT-1069	–	–	7.0	7.3	8.5	8.8	provided by M. Ioannidou
DPUT-1070	–	–	7.0	7.9	9.0	9.8	provided by M. Ioannidou
DPUT-1072	–	–	6.8	8.4	9.2	8.8	provided by M. Ioannidou
DPUT-1074	–	–	6.0	8.4	8.5	9.6	provided by M. Ioannidou
NHML-nn.1dex	7.3	6.3	7.4	7.7	9.0	9.9	GDK
NHML-nn.1sin	7.6	5.7	7.6	7.4	8.6	9.7	GDK
NHML-nn.2dex	–	–	6.2	8.1	–	–	GDK
NHML-nn. 2sin	7.2	6.0	–	–	–	–	GDK
NHML-nn.3	–	–	6.8	7.9	8.6	8.9	GDK
<i>Hispanopithecus laietanus</i> Villalta Comella & Crusafont-Pairó, 1944							
IPS 1789	6.5	5.2	–	–	–	–	GDK
IPS 58330	–	–	6.4	6.2	–	–	Alba <i>et al.</i> 2012
IPS 1839	–	–	6.3	6.6	–	–	GDK
IPS 1846	–	–	–	–	7.8	8.5	GDK
<i>Rudapithecus hungaricus</i> (Kretzoi, 1969)							
RUD-126	–	–	6.3	7.8	–	–	provided by D. Begun
RUD-124	–	–	–	–	7.3	9.4	provided by D. Begun
<i>Ekembo heseloni</i> (Walker, Tedford, Martin & Andrews, 1933)							
KNM-RU 2031	5.8	4.4	–	–	–	–	Andrews 1978
KNM-RU 1919	–	–	3.9	5.4	5.4	6.0	Andrews 1978
KNM-RU 1693	–	–	–	–	7.0	8.2	Andrews 1978
KNM-RU 1803	–	–	5.8	6.5	6.8	7.6	Andrews 1978
KNM-RU 2031	–	–	6.0	7.4	7.9	9.2	Andrews 1978
<i>Proconsul meswae</i> Harrison & Andrews, 2009							
KNM-ME 11	6.9	6.3	6.8	8.4	8.1	10.1	Harrison & Andrews 2009
KNM-ME 9	6.6	6.1	6.4	7.9	7.3	8.6	Harrison & Andrews 2009

Table 1. — Continuation.

Specimens	MLdC <sup>1</sup>	BLdC <sup>1</sup>	MLdP <sup>3</sup>	BLdP <sup>3</sup>	MLdP <sup>4</sup>	BLdP <sup>4</sup>	Measurements
<i>Proconsul major</i> Le Gros Clark & Leakey, 1950							
KNM-SO 371	8.4	6.6	–	–	–	–	Andrews 1978
KNM-SO 542	8.1	5.8	7.0	7.3	9.1	9.4	Andrews 1978
KNM-SO397	–	–	–	–	8.9	9.9	Andrews 1978
KNM-SO 1101	–	–	–	–	9.1	10.3	Andrews 1978
<i>Griphopithecus alpani</i> (Tekkaya, 1974)							
NHML-D.763	–	–	6.4	7.8	–	–	GDK
NHML-D.865	–	–	6.3	7.8	–	–	GDK
NHML-L.1567	–	–	6.7	8.4	–	–	GDK
NHML-M.1874	–	–	6.0	8.3	–	–	GDK
NHML-L.1653	–	–	7.0	8.7	–	–	GDK
NHML-K.1312	–	–	6.1	7.7	–	–	GDK
NHML-K1319	–	–	6.6	8.8	–	–	GDK
NHML-K.1320	–	–	6.3	7.9	–	–	GDK
NHML-C.247	–	–	–	–	7.9	8.5	GDK
NHML-H.939	–	–	–	–	9.1	10.0	GDK
NHML-K.1374	–	–	–	–	7.8	8.9	GDK
NHML-L.1576	–	–	–	–	8.3	10.1	GDK
NHML-H.1658	–	–	–	–	9.2	10.2	GDK
NHML-H.486	–	–	–	–	7.6	8.3	GDK
NHML-M.955	–	–	–	–	7.5	9.1	GDK
NHML-K.1324	–	–	–	–	8.2	9.7	GDK
NHML-K.1392	–	–	–	–	8.7	9.6	GDK
<i>Lufengpithecus lufengensis</i> Xu, Lu, Pan, Qi, Zhan & Zheng, 1978							
ZT-299	–	–	–	–	9.0	10.2	Ji <i>et al.</i> 2013
<i>Australopithecus afarensis</i> Johanson, White & Coppens, 1978							
AL 333-86a	–	–	8.7	8.9	10.1	11.0	Johanson <i>et al.</i> 1982
AL 333-86b	–	–	8.7	8.9	10.2	10.9	Johanson <i>et al.</i> 1982
AI 333-99	7.6	6.0	–	–	–	–	Johanson <i>et al.</i> 1982
AL 333-105	–	–	8.5	9.3	10.0	10.5	Johanson <i>et al.</i> 1982
AL 333-104	7.7	6.0	–	–	–	–	Johanson <i>et al.</i> 1982
LH 21	–	–	7.9	9.3	9.7	10.7	White 1980
LH 3	–	–	–	–	10.6	12.6	White 1977
LH 3/6	6.8	5.3	9.1	9.4	–	–	White 1977
<i>Australopithecus africanus</i> Dart, 1925							
Taung skull right	6.3	6.6	7.7	9.3	9.3	10.4	GDK
Taung skull left	5.8	5.8	8.3	9.4	9.8	11.3	GDK

de Bonis, 1985, *Prostrepsiceros vallesiensis* Bouvrain, 1982, *Palaeoryx* sp. (Koufos 2006, 2012a, b; Konidaris 2013; Vlachou 2013; Valenciano *et al.* 2015; Kostopoulos 2022; Laskos & Kostopoulos 2022). As it is mentioned above, the fauna is correlated with late Vallesian (MN10), while the paleomagnetic data suggest an estimated age of *c.* 9.3 Ma (Sen *et al.* 2000; Koufos 2013).

Although the fossil record of *O. macedoniensis* is relatively rich, its deciduous dentition is poorly documented. Only two mandibular fragments with deciduous teeth are known (Koufos & Bonis 2004; Macchiarelli *et al.* 2009). Here, we report a new maxillary fragment from Ravin de la Pluie, that preserves deciduous and permanent teeth (Fig. 2). The main aim of this study is to describe the unknown morphology of the upper deciduous teeth of *O. macedoniensis*, as well as the morphology of the unerupted and unworn teeth of this hominoid after their virtual reconstruction, using high-resolution microcomputed tomography ( $\mu$ CT). Furthermore, this study also aims at comparing the upper deciduous teeth of *O. macedoniensis* with those of the extant and extinct hominoids.

## MATERIAL AND METHODS

### COMPARATIVE MATERIAL

The material and dental measurements of the deciduous teeth used for comparison are given in Tables 1 and 2. The dental measurements of the permanent teeth of the extant great apes (*Gorilla gorilla* (Savage, 1847), *Pongo pygmaeus* (Linnaeus, 1760) and *Pan troglodytes* (Blumenbach, 1775)) are taken from Mahler (1973) and for *O. macedoniensis* from Koufos *et al.* (2016). The new hominoid specimen (RPI-245) is housed in the Laboratory of Geology and Palaeontology of the University of Thessaloniki (LGPUT) and its measurements of both deciduous and permanent teeth are given in Table 3. The measurements, mesiodistal length (ML) and buccolingual length (BL) of the teeth, were measured with a digital calliper and they are given to the nearest 0.1 mm. All computations and visualisations were performed using PAST 4.05 (Hammer *et al.* 2001). The extant hominoids (*Gorilla gorilla*, *Pan troglodytes*, *Pongo pygmaeus*, *Homo sapiens* Linnaeus, 1758) are referred in the text by their scientific or common names.

TABLE 2. — Provenance, geological age, location and relevant literature of the fossil comparative material.

Specimens	Chronology	References	Sex	Site/Country	Inst./Museum	Labels
<i>Ouranopithecus macedoniensis</i> (Bonis, Bouvrain, Geraads & Melentis, 1974)						
Ravin de la Pluie	c. 9.3 Ma Sen <i>et al.</i> 2000	Present	F	Axios Valley, Greece	LGPU	RPI-245
<i>Ekembo heseloni</i> (Walker, Tedford, Martin & Andrews, 1933)						
Rusinga	17.2-16.4 Ma	Andrews 1978	?	Rusinga, Kenya	KNM	KNM-RU 2031
Rusinga	NOW 2023	Andrews 1978	?	Rusinga, Kenya	KNM	KNM-RU 1919
Rusinga		Andrews 1978	?	Rusinga, Kenya	KNM	KNM-RU 1693
Rusinga		Andrews 1978	?	Rusinga, Kenya	KNM	KNM-RU 1803
<i>Proconsul meswae</i> Harrison & Andrews, 2009						
Meswae Bridge	>20 Ma	Harrison & Andrews 2009	?	Meswae Bridge, Kenya	KNM	KNM-ME 11
Meswae Bridge	Harrison & Andrews 2009	Harrison & Andrews 2009	?	Meswae Bridge, Kenya	KNM	KNM-ME 9
<i>Proconsul major</i> Le Gros Clark & Leakey, 1950						
Songhor	20.4-19.7 Ma	Andrews 1978	?	Songhor, Kenya	KNM	KNM-SO 371
Songhor	NOW 2023	Andrews 1978	?	Songhor, Kenya	KNM	KNM-SO 542
Songhor		Andrews 1978	?	Songhor, Kenya	KNM	KNM-SO397
Songhor		Andrews 1978	?	Songhor, Kenya	KNM	KNM-SO 1101
<i>Griphopithecus alpani</i> (Tekkaya, 1974)						
Paşalar	14.2-12.85 Ma	Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-D.763
Paşalar	NOW 2023	Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-D.865
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-L.1567
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-M.1874
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-L.1653
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-K.1312
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-K1319
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-K.1320
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-C.247
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-H.939
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-K.1374
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-L.1576
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-H.1658
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-H.486
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-M.955
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-K.1324
Paşalar		Mortzou & Andrews 2008	?	Paşalar, Turkey	NHMLcast	NHML-K.1392
<i>Hispanopithecus laietanus</i> Villalta-Comella & Crusafont Pairo, 1944						
Can Llobaters	c. 9.7 Ma	Alba <i>et al.</i> 2012	?	Can Llobaters, Spain	IPS	IPS 1789
Can Llobaters	Alba <i>et al.</i> 2012	Alba <i>et al.</i> 2012	?	Can Llobaters, Spain	IPS	IPS 58330
Can Llobaters		Alba <i>et al.</i> 2012	?	Can Llobaters, Spain	IPS	IPS 1839
Can Llobaters		Alba <i>et al.</i> 2012	?	Can Llobaters, Spain	IPS	IPS 1846
<i>Rudapithecus hungaricus</i> (Kretzoi, 1969)						
Rudabanya	MN 9	NOW 2023	?	Rudabanya, Hungary	unpublished	RUD-126
Rudabanya	MN 9	NOW 2023	?	Rudabanya, Hungary	unpublished	RUD-124
<i>Lufengpithecus lufengensis</i> Xu , Lu, Pan, Qi, Zhan & Zheng, 1978						
Yuanmou Basin	6.5-6.0 Ma Ji <i>et al.</i> 2013	Ji <i>et al.</i> 2013	?	Southern China	?	ZT-299
<i>Australopithecus afarensis</i> Johanson, White & Coppens, 1978						
Hadar	3.65-2.9 Ma	Johanson <i>et al.</i> 1982	?	Ethiopia	Natural History Museum	AL 333-86a
Hadar	Walter & Aronson 1982	Johanson <i>et al.</i> 1982	?	Ethiopia		AL 333-86b
Hadar		Johanson <i>et al.</i> 1982	?	Ethiopia	–	AI 333-99
Hadar		Johanson <i>et al.</i> 1982	?	Ethiopia	–	AL 333-105
Hadar		Johanson <i>et al.</i> 1982	?	Ethiopia	–	AL 333-104
Laetoli	c. 3.85-3.63 Ma	White 1980	?	Tanzania	–	LH 21
Laetoli	Harrisson 2011	White 1977	?	Tanzania	–	LH 3
Laetoli		White 1977	?	Tanzania	–	LH 3/6
<i>Australopithecus africanus</i> Dart, 1925						
Taung skull right	3.0 and 2.6 Ma	Dart 1925	?	Taung Cave	NHML	cast n.n.
Taung skull left	Herries <i>et al.</i> 2013	Dart 1925	?	Taung Cave	MNHL	cast n.n.
<i>Gorilla gorilla</i> (Savage, 1847)						
Cranium	Recent	–	?	South Cameroun	NHMS	NHMS-7469
Cranium	Recent	–	?	Zair	NHMS	NHMS-19158
Cranium	Recent	–	?	South Cameroun	NHMS	NHMS-7470
Cranium	Recent	–	?	?	NHMS	NHMS-46766
<i>Pan troglodytes</i> (Blumenbach, 1775)						
Cranium	Recent	–	?	South Cameroun	NHMS	NHMS-6871
Cranium	Recent	–	?	?	NHMS	NHMS-7471



Table 2. — Continuation.

Specimens	Chronology	References	Sex	Site/Country	Inst./Museum	Labels
Cranium	Recent	–	?	?	NHMS	NHMS-7532
Cranium	Recent	–	?	Zoo Karlsruhe	NHMS	NHMS-9479
Cranium	Recent	–	?	?	NHMS	NHMS-46768
Cranium	Recent	–	?	?	NHMS	NHMS-46767
<i>Pongo pygmaeus</i> (Linnaeus, 1760)						
Cranium	Recent	–	?	Borneo	NHMS	NHMS-2223a
Cranium	Recent	–	?	Borneo zoo	NHMS	NHMS-7462a
Cranium	Recent	–	?	Borneo	NHMS	NHMS-7461a
Cranium	Recent	–	M	Sumatra	NHMS	NHMS-1750a
Cranium	Recent	–	F	Borneo	NHMS	NHMS-2012a
<i>Homo sapiens</i> Linnaeus, 1758						
DPUT-SA 3	Recent	–	?	–	DPUT	DPUT-SA 3
DPUT-SA 5	Recent	–	?	–	DPUT	DPUT-SA 5
DPUT-SA 10	Recent	–	?	–	DPUT	DPUT-SA 10
DPUT-Sa 25	Recent	–	?	–	DPUT	DPUT-Sa 25
DPUT-1069	Recent	–	?	–	DPUT	DPUT-1069
DPUT-1070	Recent	–	?	–	DPUT	DPUT-1070
DPUT-1072	Recent	–	?	–	DPUT	DPUT-1072
DPUT-1074	Recent	–	?	–	DPUT	DPUT-1074
NHML-nn.1	Recent	–	?	–	NHML	NHML-nn.1dex
NHML-nn.2	Recent	–	?	–	NHML	NHML-nn.2dex
NHML-nn.3	Recent	–	?	–	NHML	NHML-nn.3

TABLE 3. — *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974), RPI-245, dental dimensions of the upper deciduous and permanent teeth. The dimensions of the permanent teeth were measured on the prepared casts after their virtual reconstruction. Abbreviations: **BL**, buccolingual length; **C1**, upper canine; **d**, deciduous; **ML**, mesiodistal length; **P3**, upper third premolar; **P4**, upper fourth premolar.

Specimen	MLdC <sup>1</sup>	BLdC <sup>1</sup>	MLdP <sup>3</sup>	BLdP <sup>3</sup>	MLdP <sup>4</sup>	BLdP <sup>4</sup>	MLC <sup>1</sup>	BLC <sup>1</sup>	MLP <sup>3</sup>	BLP <sup>3</sup>	MLM <sup>1</sup>	BLM <sup>1</sup>
RPI-245	7.2	7.1	8.4	8.6	10.7	9.8	10.8	10.5	8.5	11.6	13.7	15.7

## MICROTOMOGRAPHIC DATA ACQUISITION

The microtomographic ( $\mu$ CT) data acquisition of the fossil specimen (RPI-245) was performed using a Tomoscope HV Compact 225kV Micro CT-scanner (Werth Messtechnik GmbH, Germany) installed in the Manufacturing Technology and Machine Tools Laboratory (MT-Lab) of the Mechanical Engineering Department of the International Hellenic University (IHU). The  $\mu$ CT-scanner is equipped with a 225 kV micro focal X-ray tube combined with a flat panel detector of 1024 × 1024 pixels. Scanning parameters have been adapted according to the fossil specimen's density and size, so that the best image quality can be obtained. The selected parameters might be summarized as follows: X-ray power of 22.5 W, exposure time of 500 ms, 1600 steps per revolution of the rotary table (each 0.225°), three images per step to increase the accuracy, as well as a magnification of 50L obtaining a voxel size of 49.0  $\mu$ m. Based on the  $\mu$ CT data, the reconstructed 3D geometry of the examined specimen was processed using Avizo v. 7.0 (Visualization Sciences Group 2011). First, each enamel cap was isolated from the respective dentine tissue using automatic segmentation tools. The resulting enamel cap surface was extracted using “generate surface” module with the constrained smoothing type (smoothing extent = 2). Then, we used Geomagic studio 2013 (3D Systems Inc., Rock Hill) to remove all potential artefacts (e.g. surface

spikes, small holes, intersecting triangles produced by tessellation procedure).

## ABBREVIATIONS

*Institutions*

DPUT	Department of Palaeoanthropology, University of Tübingen;
IHU	International Hellenic University;
IPS	Institut Català de Paleontologia Miquel Crusafont, Sabadell;
KNM	National Museums of Kenya;
LGPU	Laboratory of Geology and Palaeontology, University of Thessaloniki;
NHML	Natural History Museum, London;
NHMS	Natural History Museum, Stuttgart.

*Localities*

NKT	Nikiti 1, Axios Valley, Chalkidiki;
RPI	Ravin de la Pluie, Axios Valley;
XIR	Xirochori 1, Axios Valley.

*Metrical*

BL	buccolingual length;
Fm	Formation;
MD	mesiodistal length;
Index-a	(MD*100)/BL;
Index-b	(MDC <sup>1</sup> *100)/(MDdP <sup>3</sup> +BLdP <sup>4</sup> );
GPTS	geomagnetic polarity time scale.

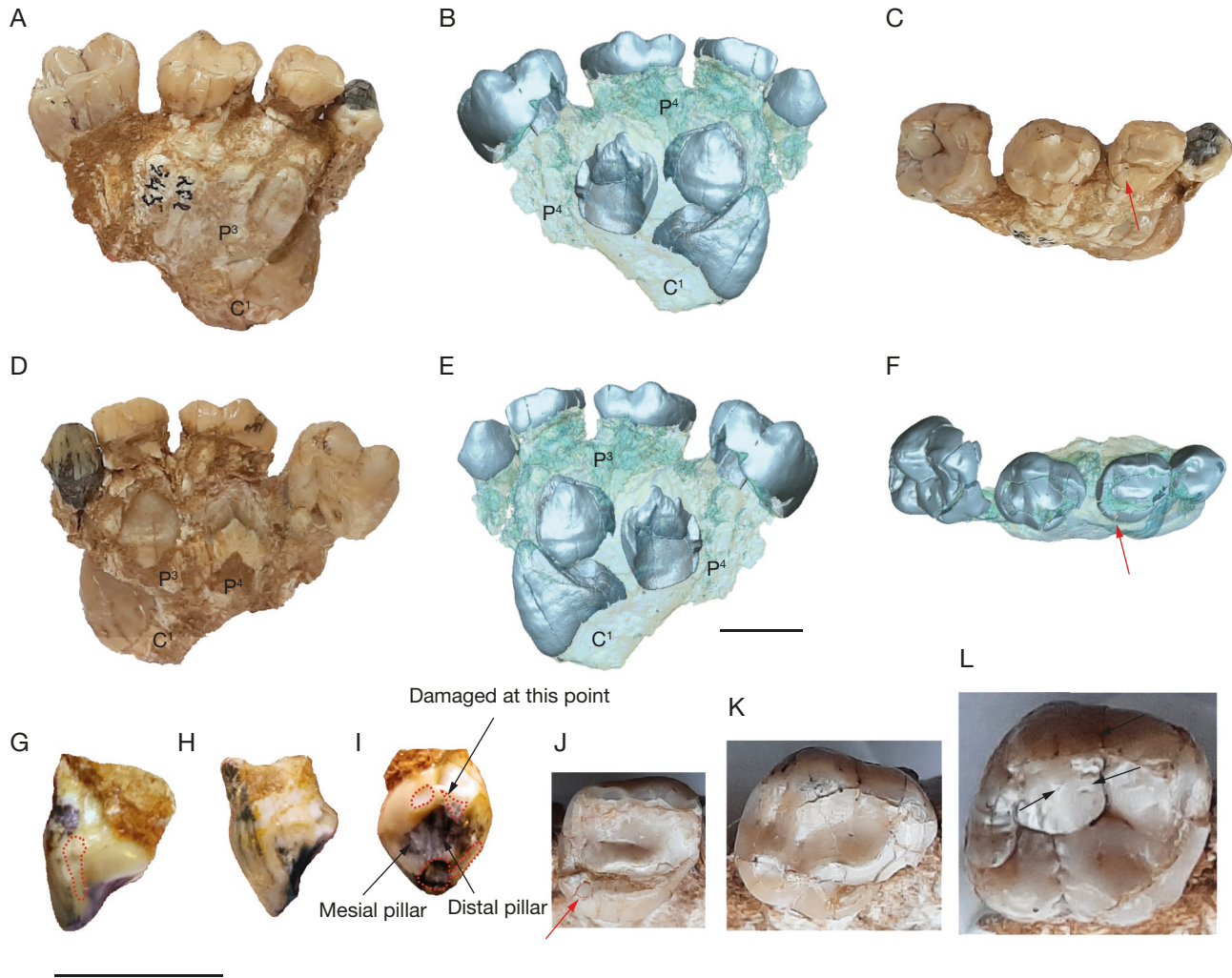


FIG. 2. — *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974), Ravin de la Pluie, Macedonia, Greece; late Vallesian, MN10, c. 9.3 Ma: **A-C**, right maxillary fragment with dC1-M1, RPI-245: **A**, lingual; **B**, labial; **C**, occlusal view; **D-F**, virtual reconstruction of RPI-245: **D**, lingual; **E**, labial; **F**, occlusal view; **G-I**, deciduous upper canine; **G**, mesial; **H**, distal; **I**, lingual view; **J**, deciduous upper third premolar, occlusal view; **K**, deciduous upper fourth premolar, occlusal view; **L**, permanent first molar, occlusal view. The **red dotted lines** indicate the dentine pits; the **red arrow** the rudimentary hypocone. Abbreviations: **C1**, upper canine; **d**, deciduous; **P3**, upper third premolar; **P4**, upper fourth premolar. Scale bars: 1 cm.

## RESULTS

### DESCRIPTION OF THE DECIDUOUS DENTITION

#### *Upper deciduous canine*

The dC1 is well preserved, missing a small part of its distolingual basal margin (Fig. 2C, F, I). It is small and low with a rounded occlusal crown outline (index-a = 101.4; Table 4). Across the mesial margin of the crown there is a stripe-like enamel wear facet from the apex to the base, where it merges with a rounded dentine pit (Fig. 2G, red dotted-line). The mesial enamel wear facet probably corresponds to a mesial crest, that wears away, and the rounded basal dentine pit to a very small mesial cingular cusplet. The distal margin of the crown is less worn; there is a narrow and short dentine pit, starting from the rounded one at the apex and extending over the distal margin (Fig. 2I, red dotted-line). The buccal wall of the crown is mesiodistally curved and featureless (Fig. 2B, E). The lingual cingulum is prominent and forms a narrow ledge across the lingual margin of the crown; it is

slightly damaged in the distal part (Fig. 2C, F, I). A weak distal pillar extends from the base towards the apex of the crown and ends almost at the middle height of the crown. The basal part of this pillar is worn and forms a dentine pit of undermined shape because the tooth is damaged in this part (the triangular-shaped pit shown in Figure 2I is not the original one). Mesial to this dentine pit there is another elliptical pit limited to the cingulum (Fig. 2I). There is also a rudimentary mesial pillar and a shallow basin between the two pillars. The poorly preserved part of the root indicates that it is elongated and less stout in relation to the crown (Fig. 2B, E). The preserved buccal height of the root is 6.8 mm and that of the crown 7.2 mm.

#### *Upper deciduous premolars*

The dP3 is well preserved and moderately worn (Fig. 2J). The outline of the occlusal crown is trapezoidal. It is truncated mesiolingually and the buccal mesiodistal length is much longer than the lingual length. Paracone and meta-

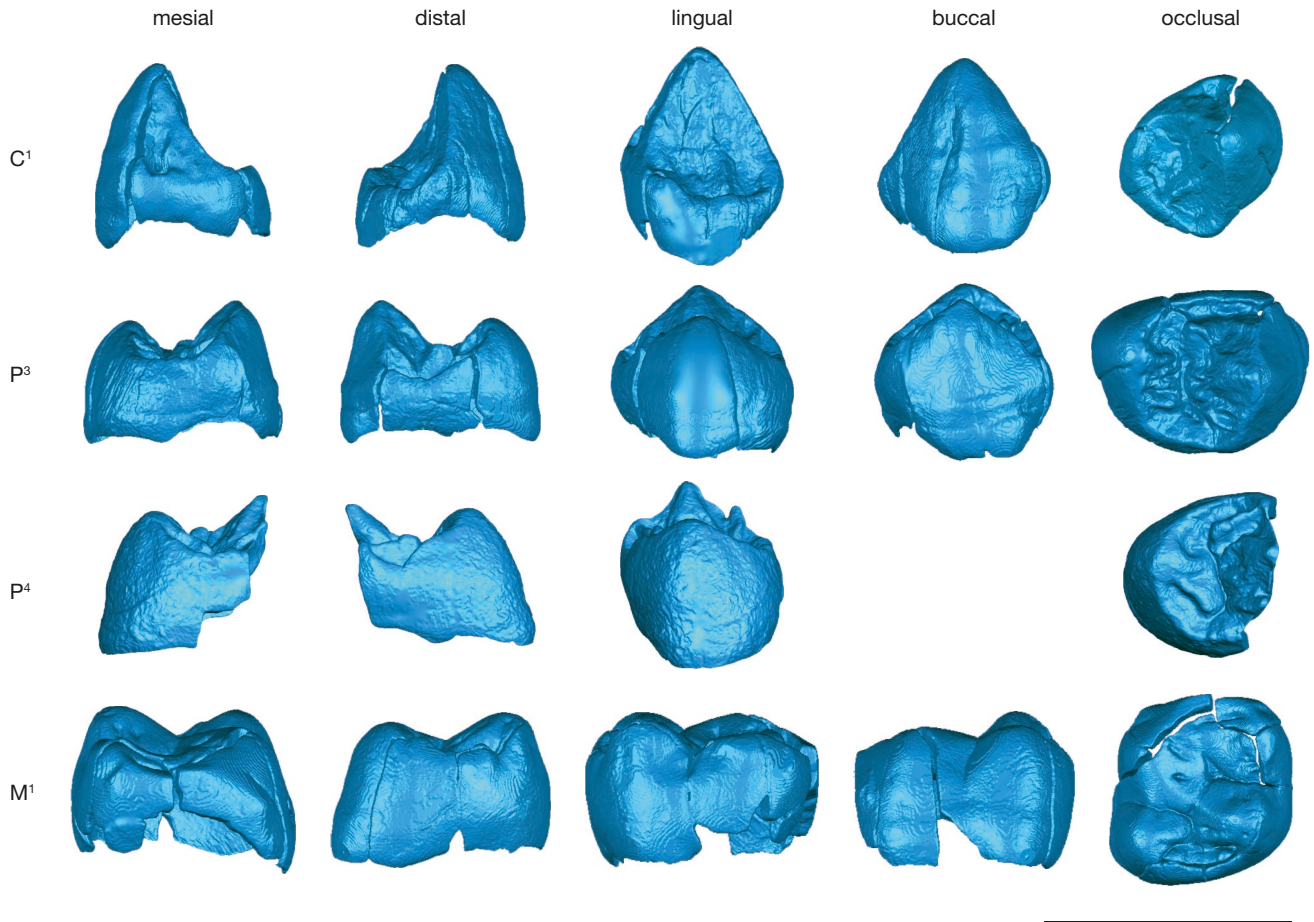


FIG. 3. — *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974), Ravin de la Pluie, Macedonia, Greece; late Vallesian, MN10; GPTS = c. 9.3 Ma. Virtual reconstruction of the unerupted upper permanent teeth; mirrored photos. Scale bar: 1 cm.

cone, although worn, are almost equal and separated by well-developed occlusal and buccal grooves. The paracone has a small and round dentine pit on its apex, while the metacone has a trace of enamel wear facet (Fig. 2J). Despite the wear, a small parastyle can be seen in the mesiobuccal corner of the crown, separated from the paracone by a faint vertical groove on the buccal wall (Fig. 2E). The protocone is worn and there is a rudimentary hypocone in the distolingual corner of the tooth, separated from the protocone by a weak lingual vertical groove; a very small dentine pit is visible at its apex (Fig. 2C, F, red arrow). A mesiodistal groove separates the buccal cusps from the lingual ones. The distal fovea is short and weak, and the cingulum is absent.

The dP<sup>4</sup> is crushed mesiolingually and lacks a small enamel peel (Fig. 2C, F, K). The occlusal outline of the crown is sub-squared and less truncated mesiolingually than dP<sup>3</sup>. The paracone and metacone are equal in size, low, and separated by an occlusal and buccal groove. There is no parastyle. The protocone is large and separated from the smaller hypocone by a deep occlusal and a distinct buccal groove. Both protocone and paracone are poorly worn and retain a small dentine pit at their apex. Two low crests run from the apex of the protocone to the paracone and metacone, forming a large trigon basin.

Another small crest connects the hypocone and the metacone. The distal fovea is short, broad, and unworn. There are no traces of cingulum.

#### DESCRIPTION OF THE PERMANENT DENTITION

The upper permanent canine and the third and fourth premolars are still into the maxillary bone. These teeth are unworn, and it is interesting to have access to their full morphology, given that unworn teeth of this species were previously unknown. They will also help in the classification and sexing of the specimens studied. They have been virtually reconstructed using a  $\mu$ CT scan (Fig. 3) and we have produced physical casts using a 3D printer. The present description of these teeth is based on their virtual reconstruction (Fig. 3) and casts. The dimensions of the permanent teeth were measured on both casts and scans.

#### *Upper permanent canine*

The C<sup>1</sup> is small with triangular external profile (Fig. 3) and almost rounded occlusal outline; the index-a is 102.8 (Table 4). The crown is low, the maximum buccal height is 12.1 mm. The buccal wall is curved mesiodistally and lacks any feature as well as the cingulum. A mesiolingual groove runs from the base to the apex, it is narrow and situated more lingually.

TABLE 4. — Indices of upper deciduous teeth of *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) and other extant and extinct hominids. Index-a. (MD\*100)/BL and index-b. (MDdC\*100)/(MDdP<sup>3</sup>+MDdP<sup>4</sup>). The indices were calculated using the mean values of the dental dimensions.

Taxa	Index-a			Index-b
	dC <sup>1</sup>	dP <sup>3</sup>	dP <sup>4</sup>	
<i>Ouranopithecus macedoniensis</i> (Bonis, Bouvrain, Geraads & Melentis, 1974)	101.4	97.2	109.2	37.5
<i>Gorilla</i> Geoffroy Saint-Hilaire, 1852	136.5	100.0	103.8	46.3
<i>Pan</i> Oken, 1816	152.0	94.3	93.9	54.6
<i>Pongo</i> Lacépède, 1799	130.7	89.3	97.0	50.0
<i>Homo sapiens</i> Linnaeus, 1758	115.7	85.6	93.5	45.4
<i>Proconsul meswae</i> Harrison & Andrews, 2009	108.9	81.0	82.5	47.2
<i>Proconsul major</i> Le Gros Clark & Leakey, 1950	133.1	95.9	91.7	51.5
<i>Ekembo heseloni</i> (Walker, Teadford, Martin & Andrews, 1933)	131.8	80.8	86.0	48.7
<i>Griphopithecus alpani</i> (Tekkaya, 1974)	—	78.7	88.1	—
<i>Hispanopithecus laietanus</i> Villalta Comella & Crusafont-Pairó, 1944	124.3	99.5	91.3	46.1
<i>Rudapithecus hungaricus</i> (Kretzoi, 1969)	—	80.8	77.7	—
<i>Lufengpithecus lufengensis</i> Xu, Lu, Pan, Qi, Zhan & Zheng, 1978	—	—	88.2	—
<i>Australopithecus afarensis</i> Johanson, White & Coppens, 1978	127.7	92.5	89.8	39.6
<i>Australopithecus africanus</i> Dart, 1925	97.7	85.6	88.1	43.4

The distal margin of the canine is more inclined distally than mesially. Lingually, the cingulum is prominent, forms a horizontal surface, like a shelf. The lingual wall of the main cusp is triangular and perpendicular to the cingulum. The distal margin of the mesiolingual groove and that of the distal margin of the tooth form a triangular basin-like feature in the distolingual part of the tooth. A small and weak pillar divides it into two smaller parts, the mesial being larger than the distal one.

#### Upper permanent premolars

The P<sup>3</sup> has an elliptical crown outline with the mesiodistal length shorter than the buccolingual one (Fig. 3). It bears two cusps separated by a mesiodistal groove; the buccal cusp is larger than the lingual one. A weak parastyle, like a small prominence, is present at the mesiobuccal corner of the tooth, giving a slight asymmetry to its occlusal crown outline. The buccal wall is curved mesiodistally and featureless. The lingual cusp is low and its base projects lingually. The mesial and distal marginal ridges are well developed. The occlusal surface is wrinkled, and the cingulum absent. The P<sup>4</sup> is broken, lacking its buccal half (Fig. 3). The preserved part bears a small lingual cusp, while the remains of the buccal one suggests that it was larger and higher. The enamel of the occlusal surface is wrinkled and the cingulum absent.

#### Upper permanent molars

The M<sup>1</sup> is well preserved and slightly worn, lacking its roots (Figs 2L; 3). The occlusal outline of the crown is squared, and the main cusps are low. The paracone and metacone are almost equal in size and height, separated by a deep groove on the occlusal crown and the buccal wall. These two cusps and the protocone form a large and deep basin. The protocone dominates the crown and it is separated from the hypocone by a weak occlusal groove and a deep lingual one. The mesial fovea is relatively long, wide, and deep. The distal fovea is smaller and less deep. Remains of enamel wrinkles are present on the cusps of the distal part of the tooth. The cingulum is absent.

#### COMPARISON WITH EXTANT HOMINIDS

The comparison with extant hominoids is based on recent material studied in NHML, NMHS, and DPUT. Unfortunately, the sample of the comparative deciduous teeth lacks sex indications. The dental measurements of the deciduous teeth used for comparison are given in Table 1.

Compared to *Gorilla* Geoffroy Saint-Hilaire, 1852, the dC<sup>1</sup> of *O. macedoniensis* is smaller, lower, less pointed, more reduced relative to the length of the deciduous premolar row and has a rounded occlusal crown outline. The dP<sup>3</sup> is smaller with a trapezoidal occlusal crown outline, a distinct metacone (absent in *Gorilla*), a smaller parastyle, and no cingulum. The dP<sup>4</sup> is smaller, has a relatively low crown with a more squared outline of the occlusal crown, smaller cusps, smaller mesial and distal foveae, and lacks a cingulum (Figs 4B, C; 5; 6; Table 4).

The dC<sup>1</sup> of *O. macedoniensis* compared to that of *Pongo* Lacépède, 1799 is shorter, but its buccolingual length is within the ranges of variation for *Pongo*; it is more reduced relative to the length of the premolar row, with more curved mesiodistally buccal wall and with a rounded occlusal crown outline. The dP<sup>3</sup> is similar in size to *Pongo*, but it differs in that it has a smaller parastyle, a trapezoidal outline of the occlusal crown, a metacone, a rudimentary hypocone and no cingulum. The size of dP<sup>4</sup> is similar to that of *Pongo*, but it differs in that it has a relatively smaller metacone and no cingulum (Figs 4B, C; 5; 6; Table 4).

Compared to *Pan*, the dC<sup>1</sup> of *O. macedoniensis* is shorter and wider, lower, more reduced relative to the length of the premolar row, with rounded occlusal crown outline. The dP<sup>3</sup> is larger and differs in having smaller parastyle, metacone, trapezoidal occlusal crown outline and absence of cingulum. The dP<sup>4</sup> is larger, with lower cusps and absence of cingulum (Figs 4B, C; 5; 6; Table 4).

The dC<sup>1</sup> of *O. macedoniensis* is larger compared to *Homo*, slightly more reduced relative to the length of the premolar row, with a more rounded occlusal crown outline, more mesiodistally curved buccal wall and more developed lingual

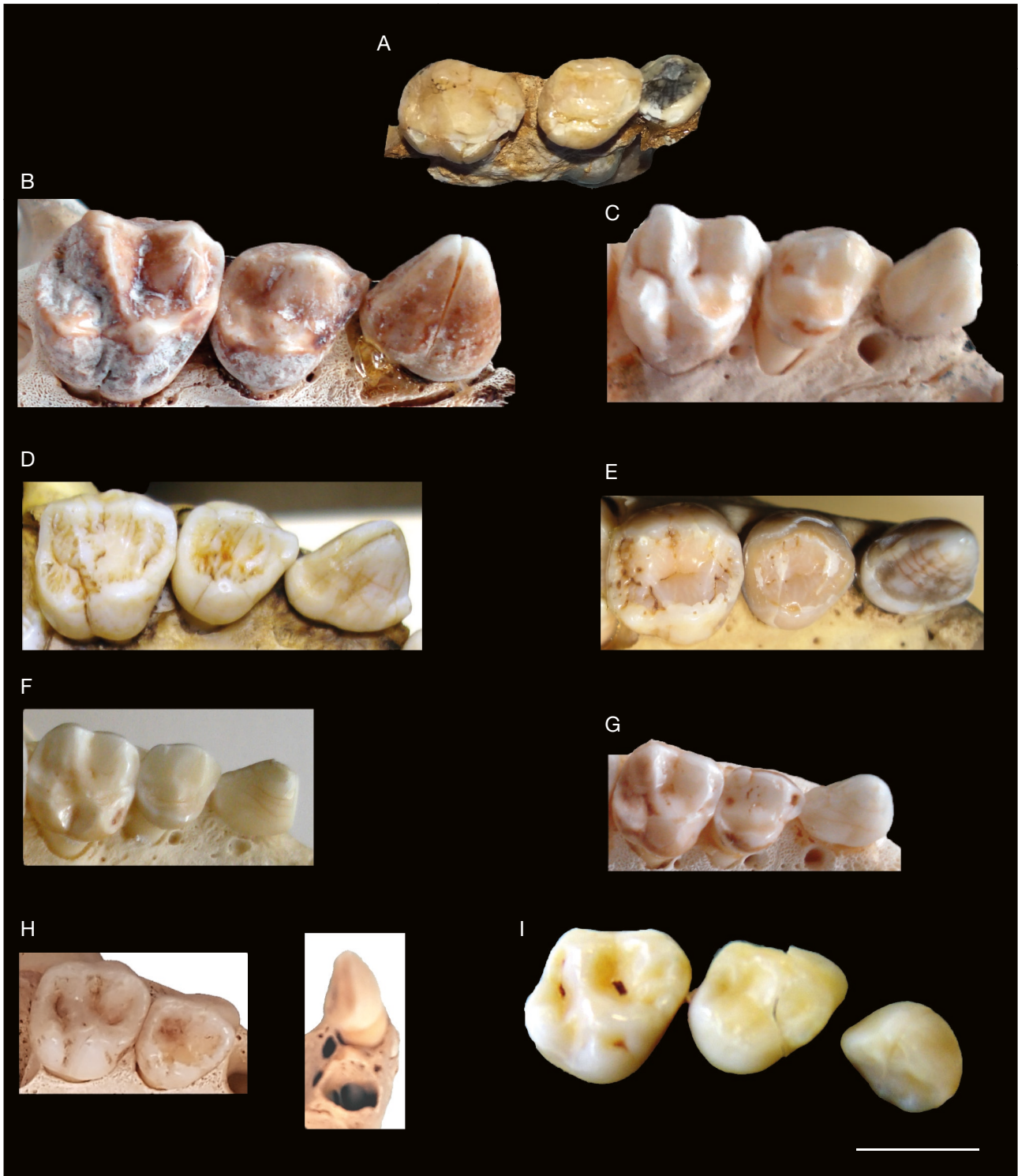


FIG. 4. — Upper deciduous dentition of *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) and some extant hominoids: **A**, *O. macedoniensis*, RPI-245 (♀); **B**, **C**, *Gorilla* Geoffroy Saint-Hilaire, 1852: **B**, NHMS 19158 (♂); **C**, NHMS 46766 (♀); **D**, **E**, *Pongo* Lacépède, 1799: **D**, MHNS 7462 (♂); **E**, NHMS 2912 (♀); **F**, **G**, *Pan* Oken, 1816: **F**, NHMS 46767 (unknown sex); **G**, MHNS 9479 (♀); **H**, **I**, *Homo* Linnaeus, 1758 (sex unknown): **H**, DPUT 1072+SA5; **I**, NHML n.n. Some tooth rows are mirrored. Scale bar: 1 cm.

cingulum. The dP<sup>3</sup> is larger with a small parastyle and it has slightly less squared occlusal crown outline. The dP<sup>4</sup> of *O. macedoniensis* has less squared occlusal crown outline and larger size (Figs 4B, C; 5; 6; Table 4).

#### COMPARISON WITH EXTINCT HOMINOIDS

*Proconsul* Hopwood, 1933 is the earliest known Miocene hominoid. The latest revision of the material referred to this genus allowed its separation into two genera, *Proconsul* and

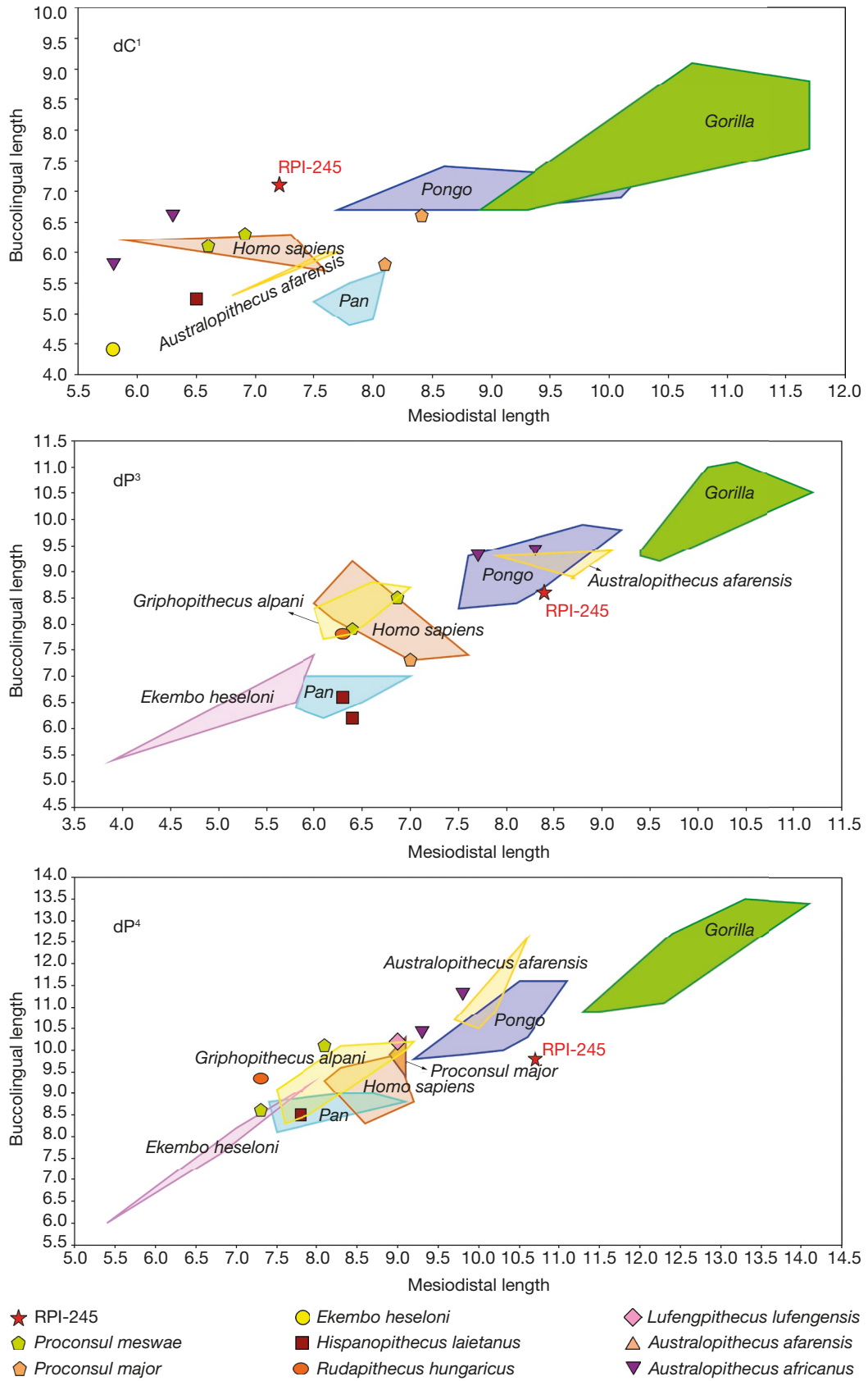


FIG. 5. — Scatter plots of the upper deciduous teeth of *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) in comparison with extant and extinct hominoids. Abbreviations: C<sup>1</sup>, upper canine; d, deciduous; P<sup>3</sup>, upper third premolar; P<sup>4</sup>, upper fourth premolar. Data source: see Table 1.

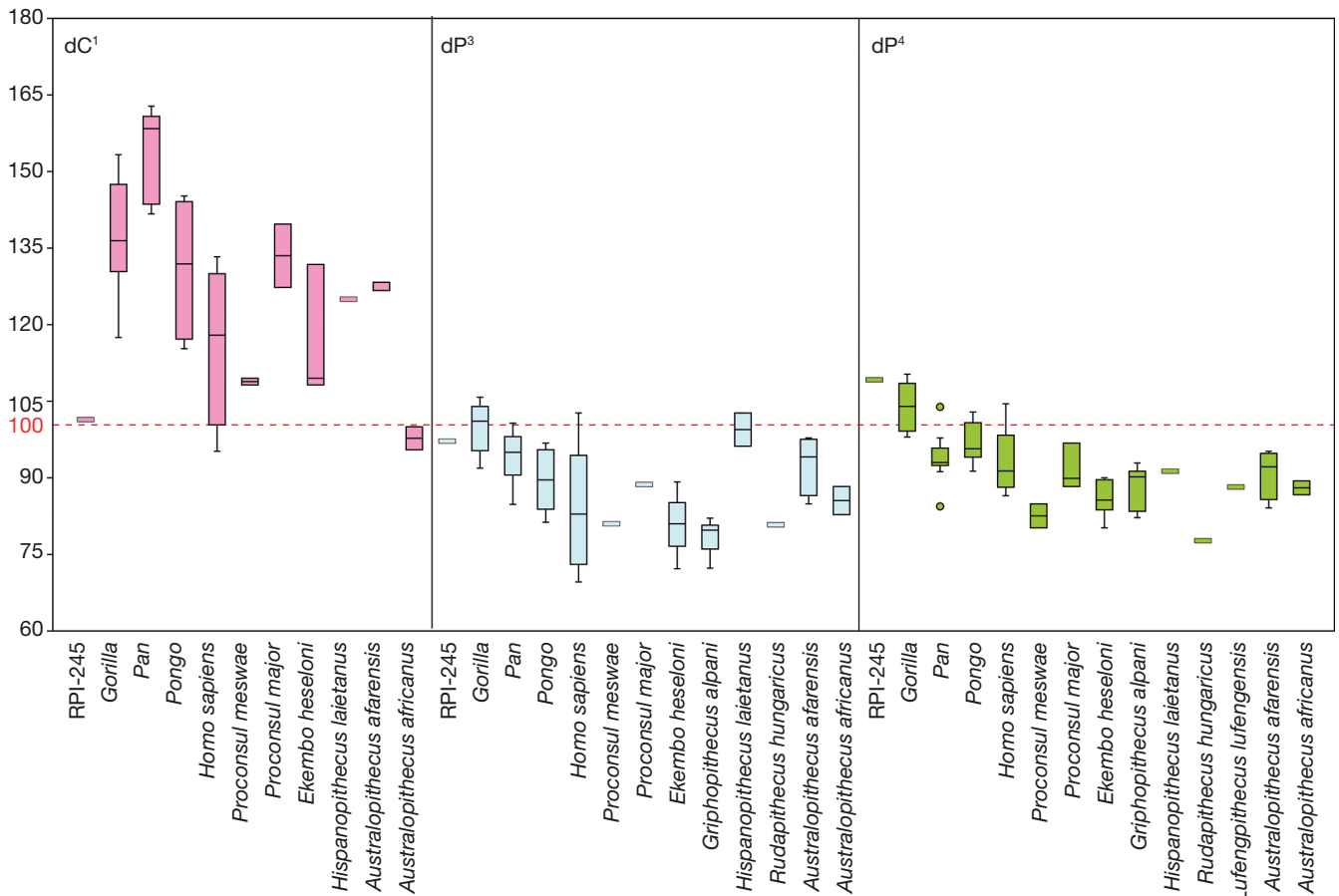


Fig. 6. — Box plots of the index-a  $[(MD \cdot 100) / BL]$  of *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) upper deciduous teeth compared to the extant and extinct hominoids; the **circles** indicate outliers. Abbreviations: **C<sup>1</sup>**, upper canine; **d**, deciduous; **P<sup>3</sup>**, upper third premolar; **P<sup>4</sup>**, upper fourth premolar. Data source: see Table 1.

*Ekembo* McNulty, Begun, Kelley, Manthi & Mbua, 2015 (McNulty *et al.* 2015). According to these authors, the material from Rusinga and Mfagano (Kenya) described by Andrews (1978) belongs to *E. heseloni* (Walker, Teadford, Martin & Andrews, 1993) and that from Songhor (Kenya) to *P. major* Le Gros Clark & Leaky, 1950, while the remaining material needs revision. Another *Proconsul* species named *P. meswae* Harisson & Andrews, 2009 is known from Meswa (Kenya). The comparison of *O. macedoniensis* is therefore based on: 1) *P. meswae* (maxillary fragment with dC<sup>1</sup>-dP<sup>4</sup>, KNM-ME 11, cast housed in NHML; Fig. 7P) and the descriptions of Andrews *et al.* (1981) and Harrison & Andrews (2009); and 2) *P. major* from the descriptions and illustrations of Andrews (1978: 102, pl. 4, fig.3).

Compared to *P. meswae*, dC<sup>1</sup> of *O. macedoniensis* is larger, lower, more reduced relatively to the length of the premolar row, with a slightly more rounded occlusal crown outline (subrounded in *P. meswae*; Table 4), a wider lingual cingulum, (narrow in *P. meswae*; Harrison & Andrews 2009) and bears two pillars on the lingual wall (one in *P. meswae*; same authors). McNulty *et al.* (2015) and Pickford *et al.* (2020) mention a “blade-like” tip or “burin-like” in both the deciduous and permanent upper canine of *Proconsul*; this feature is absent in *O. macedoniensis*. The larger size, the trapezoidal

occlusal crown outline (triangular in *P. meswae*, Fig. 7P), the presence of metacone and rudimentary hypocone, the smaller parastyle and the absence of cingulum distinguish the dP<sup>3</sup> of *O. macedoniensis* from that of *P. meswae*. The dP<sup>4</sup> is larger, has a more squared occlusal crown outline and lacks the cingulum (Figs 5-7P; Table 4). The dC<sup>1</sup> of *O. macedoniensis* is larger compared to that of *P. major* (Fig. 5) and relatively reduced compared to the length of the premolar row, with a rounded occlusal crown outline and no buccal cingulum. The smaller size, the presence of metacone and hypocone and the absence of cingulum in the dP<sup>3</sup> of *O. macedoniensis* distinguish it from *P. major*. The dP<sup>4</sup> of *O. macedoniensis* differs with a larger size, a larger hypocone, a more squared occlusal crown outline and the absence of a cingulum (Fig. 5; Table 4).

The comparison with *Ekembo* is based on the cast of *E. heseloni* (KNM-RU 1803, housed in NHML; Fig. 7Q) and the descriptions of McNulty *et al.* (2015). The dC<sup>1</sup> of *O. macedoniensis* is larger compared to that of *E. heseloni*, more reduced relatively to the length of the premolar row, and with a more rounded occlusal crown outline. The dP<sup>3</sup> is larger, has a trapezoidal outline of the occlusal crown, a metacone, a rudimentary hypocone and no cingulum. The dP<sup>4</sup> is larger, has a more squared outline of the occlusal crown and does not have a cingulum (Figs 5-7Q; Table 4).

The comparison of *O. macedoniensis* with *Griphopithecus alpani* is based on the casts of several isolated teeth from Paşalar, Turkey, housed in NHML; this sample lacks dC<sup>1</sup>. The material was studied by Mortzou & Andrews (2008), and all referred to *G. alpani*. Compared to *G. alpani*, the dP<sup>3</sup> of *O. macedoniensis* is larger with a metacone, a rudimentary hypocone and without cingulum. The dP<sup>4</sup> is larger, has a more squared occlusal crown outline and lacks the cingulum (Figs 5-7B-O; Table 4).

The comparison of *O. macedoniensis* with *Hispanopithecus laietanus* Villalta Comella & Crusafont Pairó, 1944 is based on some casts from Can Llobateres I, II, Spain (Fig. 7R-T) and the descriptions of Alba *et al.* (2012). Compared to *H. laietanus*, the dC<sup>1</sup> of *O. macedoniensis* is larger, and more reduced relative to the length of the premolar row, with a more rounded occlusal crown outline, and without the large distolingual basin-like groove of *H. laietanus*. In addition, *H. laietanus* has a strong lingual ridge extending to the middle of the canine height, which is weaker in *O. macedoniensis*. The dP<sup>3</sup> is larger and it has a trapezoidal occlusal crown outline, a metacone (in *H. laietanus* there is a crest in the position of the metacone), a rudimentary hypocone, and lacks the cingulum. The dP<sup>4</sup> is larger with a more squared occlusal crown outline and lacks the lingual cingulum (Figs 5-7R-T; Table 4).

The comparison with *Rudapithecus hungaricus* Kretzoi, 1969 is based on the photos (no permission to publish the photos) of an undescribed isolated dP<sup>3</sup> and another dP<sup>4</sup> from Rudabanya, Hungary. The dP<sup>3</sup> of *O. macedoniensis* is larger with a trapezoidal occlusal crown outline (in *R. hungaricus* is sub-rectangular, MD<BL), a smaller parastyle, a metacone, a rudimentary hypocone, and absence of the cingulum. The dP<sup>4</sup> is larger with more squared occlusal crown outline (in *R. hungaricus* is sub-rectangular, MD<BL), and without cingulum (Figs 5; 6; Table 4).

Two species of *Lufengpithecus* are known from China *L. hudienensis* Ho, 1990 and *L. lufengensis* Xu, Lu, Pan, Qi, Zhan & Zheng, 1978. A juvenile cranium of *L. hudienensis* (YV 0999) is known from the Yuanmou Basin, which preserves the deciduous dentition (Ho 1990; Kelley & Gao 2012). The mesiodistal diameter of dC<sup>1</sup> is longer than the buccolingual one in *L. hudienensis* (Ho 1990: 315), implying an elliptical occlusal crown outline, whereas it is rounded in *O. macedoniensis*. The dP<sup>3</sup> has a triangular shape (Ho 1990: fig. 4) with a prominent parastyle, unlike *O. macedoniensis*, which has trapezoidal occlusal crown outline, a very small parastyle, and a rudimentary hypocone. A juvenile cranium (ZT 299) of *L. lufengensis* is known from Southern China (Ji *et al.* 2013: fig. 5). The cranium preserves only the dP<sup>4</sup> which differs from that of *O. macedoniensis* in having a weaker hypocone, a shorter mesiodistal than buccolingual length, and a smaller size (Figs 5; 6).

The comparison with *Australopithecus afarensis* Johanson *et al.* 1978 was based on the material from Hadar (Ethiopia) and Laetoli (Tanzania), (Fig. 7U-W) and on the descriptions and illustrations of White (1977, 1980) and Johanson *et al.* (1982). The dC<sup>1</sup> of *O. macedoniensis* has similar mesiodistal length to that of *A. afarensis*, but it is wider with rounded

occlusal crown outline and more flattened mesiodistal buccal wall. The dP<sup>3</sup> of both species is of similar size, but that of *O. macedoniensis* has less squared occlusal crown outline, larger parastyle, rudimentary hypocone (in *A. afarensis* it is quite distinct and larger) and lacks a cingulum (a weak lingual cingulum is present in the dP<sup>3</sup> of KNM-AL 333-86; Fig. 7U). The dP<sup>4</sup> is slightly smaller and lacks a cingulum (a weak mesiolingual cingulum is present in the dP<sup>4</sup> of KNM-AL 333-86), (Figs 5-7U-W; Table 4).

The dC<sup>1</sup> of *O. macedoniensis* is larger compared to a cast of *Australopithecus africanus* Dart, 1925 (Taung skull; Fig. 7X), but both have similar occlusal crown outlines (rounded) and relative size compared to the length of the premolar row. The dP<sup>3</sup> has similar size, a less squared occlusal crown outline, and a more developed parastyle. The dP<sup>4</sup> of *O. macedoniensis* is slightly longer and narrower and lacks the crest connecting the hypocone with the mesial margin (Figs 5-7X; Table 4).

## DISCUSSION

The lack of upper deciduous teeth in the known collection of *O. macedoniensis* forces us to base the classification and sex determination of RPI-245 on the permanent teeth. The morphology of the upper permanent canine of RPI-245 (triangular external profile, rounded occlusal crown outline, low crown, absence of any feature in the buccal wall, presence of a mesiolingual groove, and absence of cingulum) fits quite well with the known morphology of *O. macedoniensis*. The morphology of the P<sup>3</sup> (two main cusps, weak parastyle, elliptical crown outline, presence of a metacone and a rudimentary hypocone, more symmetric shape, absence of cingulum) and P<sup>4</sup> (squared occlusal crown outline, low cusps, almost equal size of paracone and metacone, large protocone, absence of cingulum) also matches with that of *O. macedoniensis* (Bonis & Melentis 1978; Bonis & Koufos 1993; Koufos 1995; Koufos & Bonis 2006; Koufos *et al.* 2016). The size of the permanent teeth of RPI-245 is similar to that of *O. macedoniensis* (Fig. 8) except for M<sup>1</sup>, which is narrower. This is probably due to the rarity of the comparative sample; in the large samples of the extant taxa there is a large variation in the buccolingual length (Fig. 8).

The size difference observed in the *O. macedoniensis* material first found at Ravin de la Pluie was attributed to the sex of the individuals (Bonis & Melentis 1977b). This was later confirmed by the enlargement of the sample and comparison with extant hominoids. The sex determination of RPI-245 was based on the permanent teeth and in particular on the permanent canines. Previous studies have shown that male permanent canines are larger and higher than the female ones (Koufos *et al.* 2016 and references therein). This size difference is quite clear in the canines of the extant hominoids, which are divided into two groups (Fig. 8). The sample of *O. macedoniensis* follows the same pattern and is divided into two groups, corresponding to males (large size) and females (small size). The permanent canine of RPI-245 matches with the female group (Fig. 8). The size difference is less pronounced



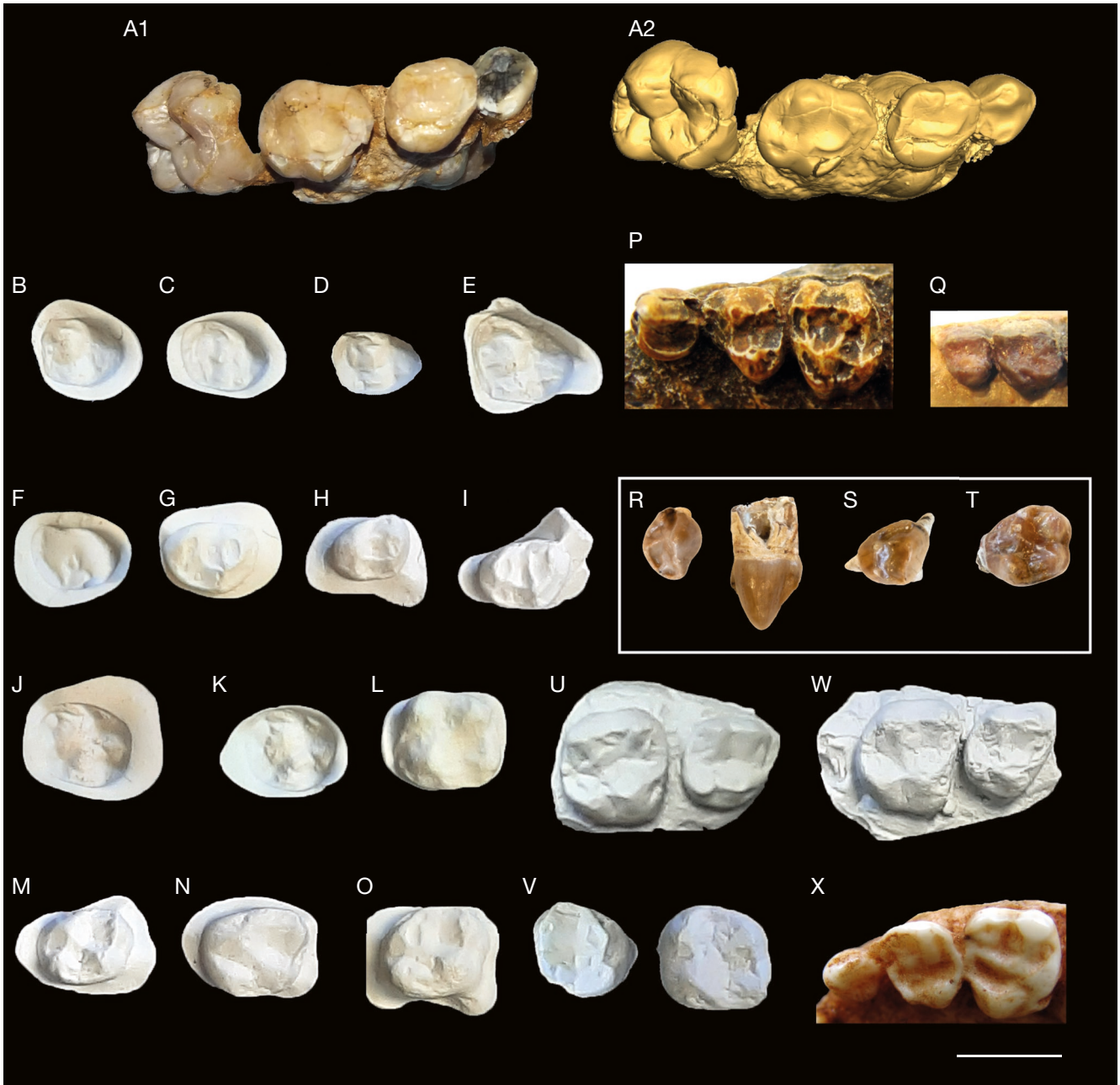


FIG. 7. — Upper deciduous teeth of various extinct hominoids: **A**, *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974), RPI-245: **A1**, original; **A2**, virtual reconstruction; **B–O**, *Griphopithecus alpani* (Tekkaya, 1974), Turkey (casts): **B–F**, right dP<sup>3</sup>s, D 763, D 865, K 1320, L 1653, M 1874; **G–I**, left dP<sup>3</sup>s, L 1567, K 1312, K 1319; **J–L**, right dP<sup>4</sup>s, C 247, H 486, H 839; **M–O**, left dP<sup>4</sup>s, K 1374, L 1576, K 1392; **P**, *Proconsul meswae* Harrison & Andrews, 2009, Kenya, KNM-ME 11 (cast); **Q**, *Ekeumbo heseloni* (Walker, Teadford, Martin & Andrews, 1933), left dP<sup>3</sup>-dP<sup>4</sup>, Kenya, KNM-RU 1803 (cast); **R–T**, *Hispanopithecus laietanus* Villalta Comella & Crusafont-Pairó, 1944, Can Llobateres, Spain; **R**, left dC<sup>1</sup>, ?Can Llobateres 2, IPS1789; **S**, left dP<sup>3</sup>, Can Llobateres 1, IPS 1839; **T**, left dP<sup>4</sup>, Can Llobateres 1, IPS 1846; **U, V**, *Australopithecus afarensis* Johanson, White & Coppens, 1978, Hadar, Ethiopia (casts): **U**, right dP<sup>3</sup>-dP<sup>4</sup>, AL 33-386; **V**, right dP<sup>3</sup> and dP<sup>4</sup>, AL 333-105 (casts); **W**, *Australopithecus afarensis*, Laetoli, Tanzania, right dP<sup>3</sup>-dP<sup>4</sup>, LH 21 (cast); **X**, *Australopithecus africanus* Dart, 1925, Taung skull, South Africa (cast). Scale bar: 1 cm.

in the postcanine teeth, because their convex hulls overlap, especially in chimpanzees. The teeth of *O. macedoniensis* follow the same pattern and separated into two groups with the RPI-245 being closer to the female group (Fig. 8). M<sup>1</sup> is slightly separated but this is possibly due to the poor sample of *O. macedoniensis*. There is probably an intraspecific variation like that observed in the extant taxa (Fig. 8). The morphology of the permanent canine of RPI-245 with a small mesiolingual

groove located more lingually also suggests a female individual (Bonis & Melentis 1978; Koufos *et al.* 2016; and references therein). All these lead to the conclusion that RPI-245 must belong to a female individual.

Most of the available bibliography on tooth eruption of the extant and fossil hominoids refers to the lower dentition (Table 5). If *O. macedoniensis* follows the same eruption pattern as extant taxa and based on the eruption of the M<sup>1</sup>

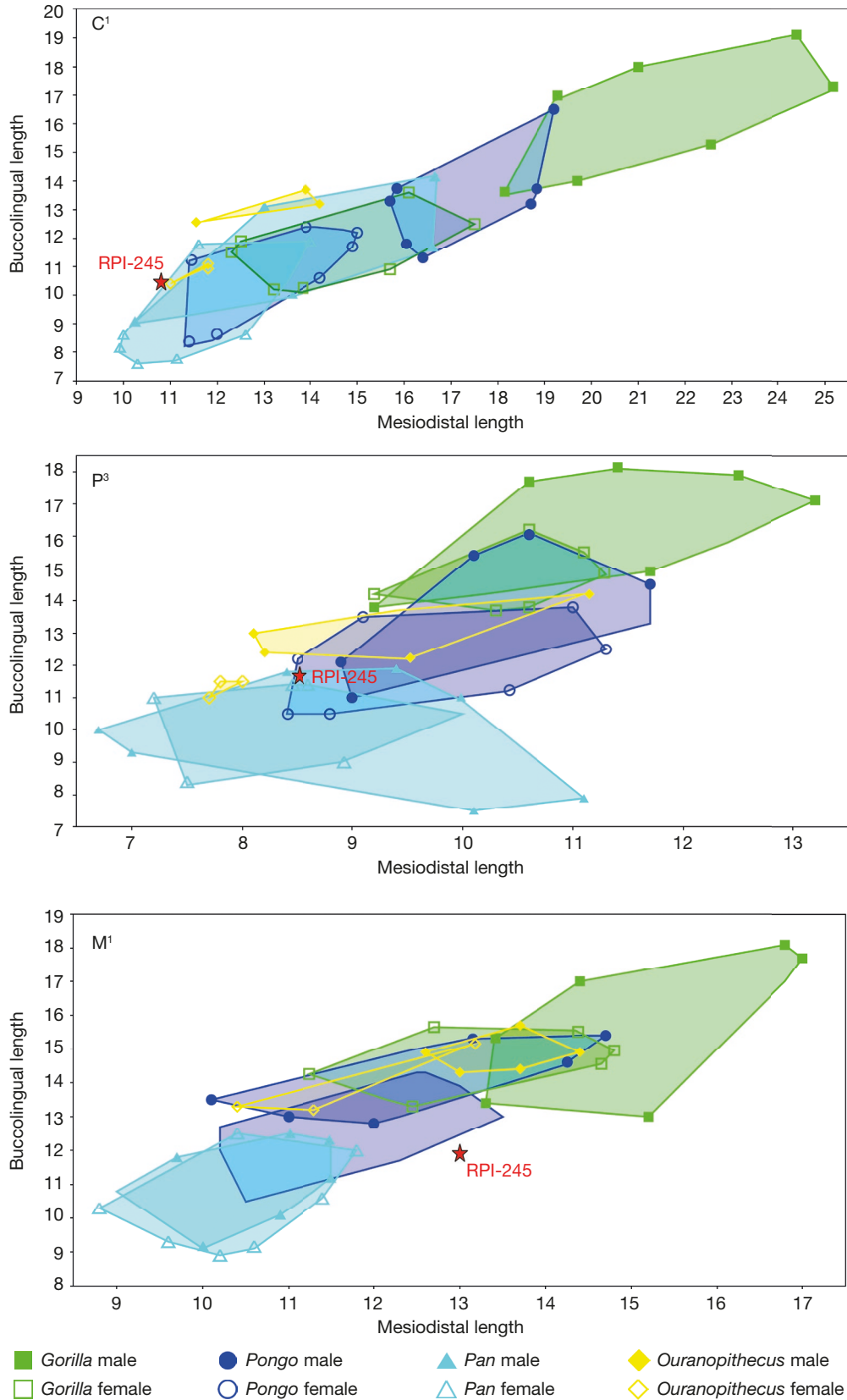


FIG. 8. — Scatter plots, comparing the upper permanent canine, third premolar and first molar of RPI-245 with the sample of *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) from Ravin de la Pluie, Xirochori 1, and Nikiti 1 and extant hominoids. Data source: Mahler (1973) for *Gorilla* Geoffroy Saint-Hilaire, 1852, *Pan* Oken, 1816 and *Pongo* Lacépède, 1799, and Koufos *et al.* (2016) for *O. macedoniensis*. Abbreviations: C<sup>1</sup>, upper canine; M<sup>1</sup>, upper first molar; P<sup>3</sup>, upper third premolar.

TABLE 5. — Age at first upper and lower molar emergence in various extant and extinct hominoids. The ages are given in years.

Species	Age at first molar emergence		Reference
	M <sup>1</sup>	m <sub>1</sub>	
<i>Afropithecus turkanensis</i> Leakey & Leakey, 1986 KNM-MO 26	–	2.4-3.6	Kelley & Smith 2003
<i>Sivapithecus parvada</i> Kelley, 1988 GSP46460	–	2.2-4.5 (3.4)	Kelley 1997
<i>Hispanopithecus laietanus</i> Villalta Comella & Crusafont Pairo, 1944 IPS-1781	3.4-3.7	–	Dean & Kelley 2012
<i>Lufengpithecus lufengensis</i> Xu, Lu, Pan, Qi, Zhan & Zheng, 1978 PA 868	–	2.1-4.4	Zhao <i>et al.</i> 2008
<i>Australopithecus afarensis</i> Johanson, White & Coppens, 1978 LH 21	–	3.3	Bromage & Dean 1985
<i>Australopithecus africanus</i> Dart, 1925 STS 24	–	3.3	Bromage & Dean 1985
<i>Pan troglodytes</i> (Blumenbach, 1775)	3.32	3.26	Dean & Wood 1981
<i>Gorilla gorilla</i> (Savage, 1847)	3.5	3.5	Dean & Wood 1981
<i>Pongo pygmaeus</i> (Linnaeus, 1760)	–	3.5	Smith <i>et al.</i> 1994
<i>Pongo pygmaeus</i>	4.6	–	Kelley & Schwartz 2005
<i>Homo sapiens</i> Linnaeus, 1758	6.31	6.07	Dean & Wood 1981

TABLE 6. — Summary of the main differences between the upper deciduous teeth of extant and extinct hominids compared to *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974).

Taxon	dC <sup>1</sup>	dP <sup>3</sup>	dP <sup>4</sup>
<i>Ouranopithecus macedoniensis</i> (Bonis, Bouvrain, Geraads & Melentis, 1974)	Small and low crowned Rounded occlusal outline Reduced relative to the length of the premolars row – Two pillars on the lingual wall No buccal cingulum	Trapezoidal occlusal outline Small parastyle Presence of metacone – Trace of a hypocone No cingulum –	Subsquared occlusal outline Low cusps Metacone is the larger cusp – No cingulum –
<i>Gorilla gorilla</i> (Savage, 1847)	Larger size High-crowned Elliptical occlusal outline Flattened buccal wall Larger relative to the length of the deciduous premolars row	Larger size Subtriangular occlusal outline Larger parastyle Absence of metacone Presence of cingulum	Larger size and higher cusps Less squared occlusal outline Strong cingulum – –
<i>Pongo pygmaeus</i> (Linnaeus, 1760)	Larger size High-crowned Elliptical occlusal outline Flattened buccal wall Larger relative to the length of the deciduous premolars row	Similar size Subtriangular occlusal outline Larger parastyle Absence of metacone and hypocone Presence of cingulum	Similar size and high-crowned Relatively smaller metacone Presence of cingulum – –
<i>Pan troglodytes</i> (Blumenbach, 1775)	Smaller size High-crowned Elliptical occlusal outline Flattened buccal wall Larger relative to the length of the deciduous premolars row	Smaller size Subtriangular occlusal outline Absence of metacone and hypocone Presence of weak cingulum –	Smaller size Higher cusps Presence of cingulum – –
<i>Homo</i> Linnaeus, 1758	Smaller size Slightly larger relative to the length of premolars row –	Smaller size No parastyle – More squared occlusal outline	Smaller size More squared occlusal outline –
<i>Proconsul meswae</i> Harrison & Andrews, 2009	Smaller size High-crowned Subrounded occlusal outline Narrow lingual cingulum One pillar on the lingual wall	Smaller size Triangular occlusal outline Absence of metacone Larger parastyle Presence of cingulum	Smaller size Less squared occlusal outline Presence of cingulum – –
<i>Ekembo heseloni</i> (Walker, Teadford, Martin & Andrews, 1933)	Smaller size Elliptical crown outline – Larger relative to the length of the deciduous premolars row –	Smaller size Subtriangular occlusal outline Absence of metacone Larger parastyle – Presence of cingulum	Smaller size Subtriangular occlusal outline – Presence of cingulum –
<i>Griphopithecus alpani</i> (Tekkaya, 1974)	– – –	Smaller size Triangular-subtriangular occlusal outline –	Smaller size Less squared occlusal outline – Presence of cingulum

Table 6. — Continuation.

Taxon	dC <sup>1</sup>	dP <sup>3</sup>	dP <sup>4</sup>
	–	Absence of metacone	–
	–	Presence of cingulum	–
<i>Hispanopithecus laietanus</i> Comella & Crusafont- Pairó, 1944	Smaller size Elliptical occlusal outline Larger relative to the length of the premolars row	Smaller size Subtriangular occlusal outline Absence of metacone	Smaller size Subtriangular occlusal outline Presence of lingual cingulum
	–	Larger parastyle	–
	Presence of a distolingual basin-like groove	Presence of cingulum	–
<i>Rudapithecus hungaricus</i> (Kretzoi, 1969)	–	Smaller size	Smaller size
	–	Subrectangular occlusal outline (MD<BL)	Subrectangular occlusal outline (MD<BL)
	–	Larger parastyle	Presence of cingulum
	–	Absence of metacone	–
	–	Presence of cingulum	–
<i>Lufengpithecus lufengensis</i> Xu, Lu, Pan, Qi, Zhan & Zheng, 1978	–	–	Smaller size
	–	–	Weaker hypocone
	–	–	Subrectangular occlusal outline (MD<BL)
	–	–	Presence of cingulum
<i>Australopithecus afarensis</i> Johanson, White & Coppens, 1978	Slightly longer and narrower Subrounded occlusal outline	Similar size More squared occlusal outline Larger hypocone Smaller parastyle	Slightly larger Similar morphology Presence of mesiolingual cingulum in KNM-AL 333-86
	–	Presence of weak lingual cingulum in KNM-AL 333-86	–
<i>Australopithecus africanus</i> Dart, 1925 (Taung skull)	Smaller Rounded occlusal outline	Similar size Smaller parastyle	Slightly smaller Presence of a crest connecting the hypocone with the mesial margin

emergence, the death age of RPI-245 is between 3.5-6.0 years (Table 5). The M<sup>1</sup> of RPI-245 is fully erupted and little worn (a rudimentary dentine pit can be seen on the apex of the paracone and there are remnants of enamel ridges on the surface) allow us to suppose an age of 3.5-5.0 years. Such an age estimate is consistent with those proposed by Dean & Wood (1981) and Dean & Kelley (2012) for gorillas, orangutans and *Hispanopithecus laietanus* (Table 5). Accepting this age would therefore imply that RPI-245 belongs to a subadult individual.

The body mass of *O. macedoniensis* is also controversial. Apart from several cranial and mandibular fossils, the postcranial skeleton is almost unknown (only two phalanges are known; Bonis & Koufos 2014). Therefore, the use of the various methods for estimating body mass based on the postcranial cannot be applied. Based on the surface of the right orbit of the male partial skull XIR-1 its body mass was estimated to be between 40-60 kg. Estimating body mass using the ratio of the occlusal surface of M<sup>1</sup> or m<sub>1</sub> to body size (Gingerich *et al.* 1982), the weight of *O. macedoniensis* ranges from 51.0-91.0 kg (mean 77.6 kg) for M<sup>1</sup> and 70.0-101.0 kg (mean 84.3 kg) for m<sub>1</sub> (Bonis & Koufos 2001). The difference in the estimated body mass between the two methods is quite clear. Considering that *O. macedoniensis* is related to gorillas (Ioannidou *et al.* 2019 and references therein), we can assume a similar body mass for male *O. macedoniensis* as for female gorillas (71.5 kg (n = 3) for *G. g. gorilla*, 97.5 kg (n = 1) for *G. b. beringei*,

and 71.0 kg (n = 2) for *G. g. gaueri*; Smith & Jungers 1997). Based on various postcranial predictors, the body mass of immature gorillas has been estimated between 1.4-46.7 kg for *G. b. beringei* and 33.0-108.0 kg for *G. g. gorilla* (Burgess *et al.* 2018). If RPI-245 is a subadult individual, then an estimated body mass of 20-50 kg is possible for it. Nevertheless, the body mass estimation of *O. macedoniensis* is a matter of speculation and the results are questionable and tentative.

Our efforts to identify features carrying a phylogenetic signal on the deciduous teeth were not successful because of the limited comparative sample of similar age fossil taxa (Table 1). We nevertheless noted that some features observed in *O. macedoniensis* may have phylogenetic significance. The dC<sup>1</sup> of *O. macedoniensis* has a rounded occlusal crown outline (index-a = 101.4; Table 4). The dC<sup>1</sup> of the younger and more derived *A. africanus* has a similar occlusal crown shape (index-a = 97.7; Table 4), but in *A. afarensis* it is elliptical (index-a = 127.7; Table 4). In the other extant and extinct hominoids, the crown outline is elliptical to oval except *P. meswae* (Table 4). The morphological characteristics of the dP<sup>3</sup> (trapezoidal occlusal crown outline, presence of metacone and a rudimentary hypocone, very small parastyle, absence of cingulum) give to it more molar-like character (high molarisation) and it is closer to the dP<sup>3</sup> of the more derived Plio-Pleistocene hominoids. In contrast, the dP<sup>3</sup> of the extant and Early-Middle Miocene hominoids are less molarised (triangular-subtriangular occlusal outline, absence of meta-

cone and hypocone, presence of cingulum or remains of it). The high molarisation is also observed in the lower deciduous premolars of *O. macedoniensis* (Koufos & Bonis 2004).

## CONCLUSION

In conclusion the morphology and dimensions of the permanent teeth (C, P<sup>3</sup>, M<sup>1</sup>) of RPI-245 are consistent with the known sample of *O. macedoniensis*. Therefore, the studied maxillary fragment with deciduous dentition from Ravin de la Pluie is attributed to a subadult female individual of this species. Although some morphological features of the deciduous teeth of *O. macedoniensis* could potentially have a phylogenetic signal, the poor sampling of the different taxa could not yet confirm this. The differences of *O. macedoniensis* from the extant and extinct hominoids are summarized in Table 6.

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