comptes rendus palevol
2023 • 22 • 33

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

George D. KOUFOS, Christos-Alexandros PLASTIRAS, Constantine N. DAVID & Dimitrios SAGRIS

art. 22 (33) — Published on 13 November 2023
www.cr-palevol.fr

PUBLICATIONS SCIENTIFIQUES

Couverture / *Cover*:
Made from the Figures of the article.

Comptes Rendus Palevol est indexé dans / Comptes Rendus Palevol *is indexed by:*
- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par /
Articles and nomenclatural novelties published in Comptes Rendus Palevol *are registered on:*
- ZooBank® (http://zoobank.org)

Comptes Rendus Palevol est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris
Comptes Rendus Palevol *is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*
Adansonia**, **Geodiversitas**, **Zoosystema**, **Anthropozoologica**, **European Journal of Taxonomy**, **Naturae**, **Cryptogamie **sous-sections** ***Algologie**, **Bryologie**, **Mycologie.***

L'Académie des sciences publie aussi / *The Académie des sciences also publishes:*
Comptes Rendus Mathématique, Comptes Rendus Physique, Comptes Rendus Mécanique, Comptes Rendus Chimie, Comptes Rendus Géoscience, Comptes Rendus Biologies.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / https://sciencepress.mnhn.fr

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

ISSN (imprimé / *print*): 1631-0683/ ISSN (électronique / *electronic*): 1777-571X

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

George D. KOUFOS
Aristotle University of Thessaloniki, School of Geology,
Laboratory of Geology and Palaeontology, GR-54124 Thessaloniki (Greece)
koufos@geo.auth.gr (corresponding author)

Christos-Alexandros PLASTIRAS
Aristotle University of Thessaloniki, School of Geology,
Laboratory of Geology and Palaeontology, GR-54124 Thessaloniki (Greece)
and Leverhulme Centre for Human Evolutionary Studies,
Department of Archaeology and Anthropology, University of Cambridge,
Fitzwilliam Street, Cambridge CB2 1QH (United Kingdom)
chrisalexander_plastiras@yahoo.gr

Constantine N. DAVID
Dimitrios SAGRIS
International Hellenic University, School of Engineering, Manufacturing Technology
and Production Systems Laboratory (MT-Lab), GR-62124 Serres (Greece)
david@ihu.gr
dsagris@ihu.gr

Submitted on 28 February 2023 | Accepted on 6 July 2023 | Published on 13 November 2023

urn:lsid:zoobank.org:pub:81D6C4A1-7B66-41BE-8D43-8EE44214C67B

Koufos G. D., Plastiras C.-A., David C. N. & Sagris D. 2023. — The Late Miocene hominoid *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) maxillary deciduous dentition and virtual reconstruction of the unerupted permanent teeth. *Comptes Rendus Palevol* 22 (33): 667-688. https://doi.org/10.5852/cr-palevol2023v22a33

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^3 with metacone and a rudimentary hypocone, a sub-squared dP^4, 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 décidues 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^3 trapézoïdal présentant un métacône et un hypocône rudimentaire, une dP^4 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 décidues 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 Inönü (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 (Casanovas-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). *Udabnopithecus 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_1, 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 Koenigswald, 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

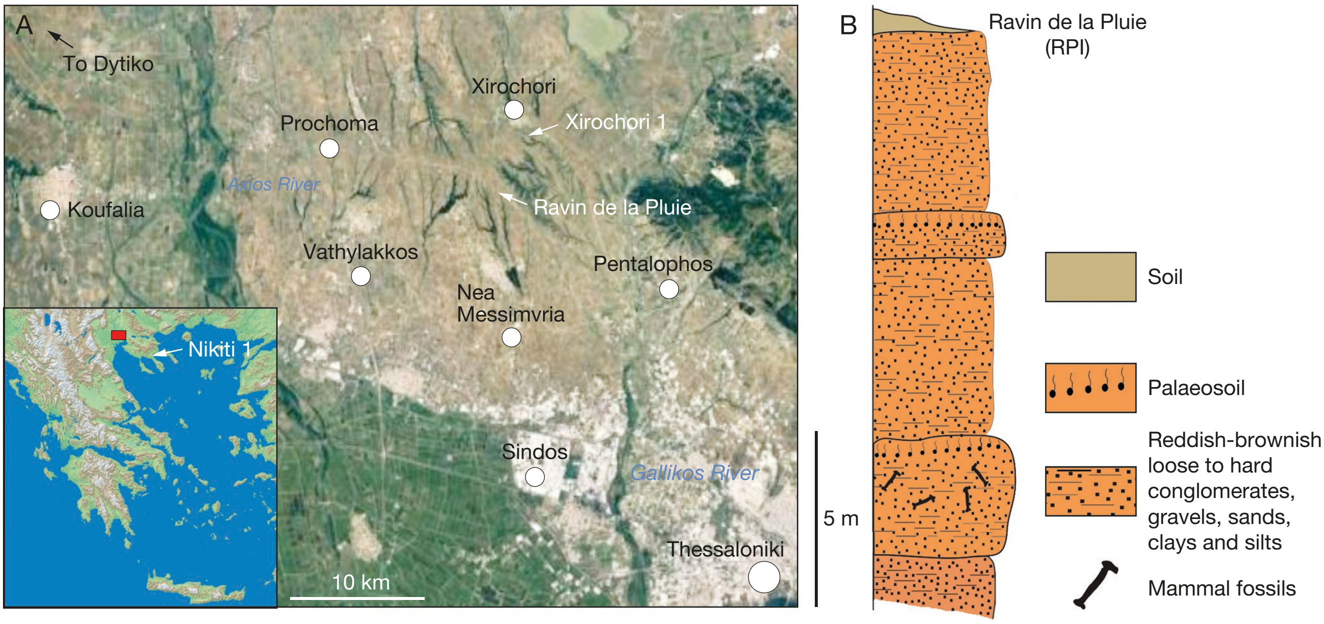

Fig. 1. — **A**, Geographical map of the Axios Valley, indicating the position of the hominoid bearing mammal localities; **B**, stratigraphic column of Ravin de la Pluie showing the position of the fossiliferous level. Credits: A, Google.

(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 australopiths 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 & Alaba 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, 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 *Anadoluvius* 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 hominoids 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*, *Palerinaceus* sp., *Spermophilinus* sp., *Progonomys cathalai* 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*, *Bohlinia* 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; **C1**, upper canine; **d**, deciduous; **ML**, mesiodistal length; **P3**, upper third premolar; **P4**, upper fourth premolar.

Specimens	MLdC1	BLdC1	MLdP3	BLdP3	MLdP4	BLdP4	Measurements
Ouranopithecus macedoniensis (Bonis, Bouvrain, Geraads & Melentis, 1974)							
RPL-245	7.2	7.1	8.4	8.6	10.7	9.8	GDK
Gorilla gorilla (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
Pan troglodytes (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
Pongo pygmaeus (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
Homo sapiens 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
Hispanopithecus laietanus Villalta Comella & Crusafont-Pairó, 1944							
IPS 1789	6.5	5.2	–	–	–	–	GDK
IPS 58330	–	–	6.4	6.2	–	–	Alba *et al.* 2012
IPS 1839	–	–	6.3	6.6	–	–	GDK
IPS 1846	–	–	–	–	7.8	8.5	GDK
Rudapithecus hungaricus (Kretzoi, 1969)							
RUD-126	–	–	6.3	7.8	–	–	provided by D. Begun
RUD-124	–	–	–	–	7.3	9.4	provided by D. Begun
Ekembo heseloni (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
Proconsul meswae 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	MLdC1	BLdC1	MLdP3	BLdP3	MLdP4	BLdP4	Measurements
Proconsul major 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
Griphopithecus alpani (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
Lufengpithecus lufengensis Xu, Lu, Pan, Qi, Zhan & Zheng, 1978							
ZT-299	–	–	–	–	9.0	10.2	Ji *et al.* 2013
Australopithecus afarensis Johanson, White & Coppens, 1978							
AL 333-86a	–	–	8.7	8.9	10.1	11.0	Johanson *et al.* 1982
AL 333-86b	–	–	8.7	8.9	10.2	10.9	Johanson *et al.* 1982
Al 333-99	7.6	6.0	–	–	–	–	Johanson *et al.* 1982
AL 333-105	–	–	8.5	9.3	10.0	10.5	Johanson *et al.* 1982
AL 333-104	7.7	6.0	–	–	–	–	Johanson *et al.* 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
Australopithecus africanus 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 (μCT). 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 (RPl-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
Ouranopithecus macedoniensis (Bonis, Bouvrain, Geraads & Melentis, 1974)						
Ravin de la Pluie	*c.* 9.3 Ma Sen *et al.* 2000	Present	F	Axios Valley, Greece	LGPUT	RPI-245
Ekembo heseloni (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
Proconsul meswae 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
Proconsul major 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
Griphopithecus alpani (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
Hispanopithecus laietanus Villalta-Comella & Crusafont Pairo, 1944						
Can Llobaters	*c.* 9.7 Ma	Alba *et al.* 2012	?	Can Llobaters, Spain	IPS	IPS 1789
Can Llobaters	Alba *et al.* 2012	Alba *et al.* 2012	?	Can Llobaters, Spain	IPS	IPS 58330
Can Llobaters		Alba *et al.* 2012	?	Can Llobaters, Spain	IPS	IPS 1839
Can Llobaters		Alba *et al.* 2012	?	Can Llobaters, Spain	IPS	IPS 1846
Rudapithecus hungaricus (Kretzoi, 1969)						
Rudabanya	MN 9	NOW 2023	?	Rudabanya, Hungary	unpublished	RUD-126
Rudabanya	MN 9	NOW 2023	?	Rudabanya, Hungary	unpublished	RUD-124
Lufengpithecus lufengensis Xu , Lu, Pan, Qi, Zhan & Zheng, 1978						
Yuanmou Basin	6.5-6.0 Ma Ji *et al.* 2013	Ji *et al.* 2013	?	Southern China	?	ZT-299
Australopithecus afarensis Johanson, White & Coppens, 1978						
Hadar	3.65-2.9 Ma	Johanson *et al.* 1982	?	Ethiopia	Natural History	AL 333-86a
Hadar	Walter & Aronson 1982	Johanson *et al.* 1982	?	Ethiopia	Museum	AL 333-86b
Hadar		Johanson *et al.* 1982	?	Ethiopia	–	Al 333-99
Hadar		Johanson *et al.* 1982	?	Ethiopia	–	AL 333-105
Hadar		Johanson *et al.* 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
Australopithecus africanus Dart, 1925						
Taung skull right	3.0 and 2.6 Ma	Dart 1925	?	Taung Cave	NHML	cast n.n.
Taung skull left	Herries *et al.* 2013	Dart 1925	?	Taung Cave	MNHL	cast n.n.
Gorilla gorilla (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
Pan troglodytes (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 Karlszuhe	NHMS	NHMS-9479
Cranium	Recent	–	?	?	NHMS	NHMS-46768
Cranium	Recent	–	?	?	NHMS	NHMS-46767
Pongo pygmaeus (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
Homo sapiens 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), RPl-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; **C^1**, upper canine; **d**, deciduous; **ML**, mesiodistal length; **P^3**, upper third premolar; **P^4**, upper fourth premolar.

Specimen	MLdC^1	BLdC^1	MLdP^3	BLdP^3	MLdP^4	BLdP^4	MLC^1	BLC^1	MLP^3	BLP^3	MLM^1	BLM^1
RPl-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 (µCT) data acquisition of the fossil specimen (RPl-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 µCT-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 µm. Based on the µCT 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;
LGPUT — 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;
RPl — 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^1*100)/(MDdP^3+BLdP^4);
GPTS — geomagnetic polarity time scale.

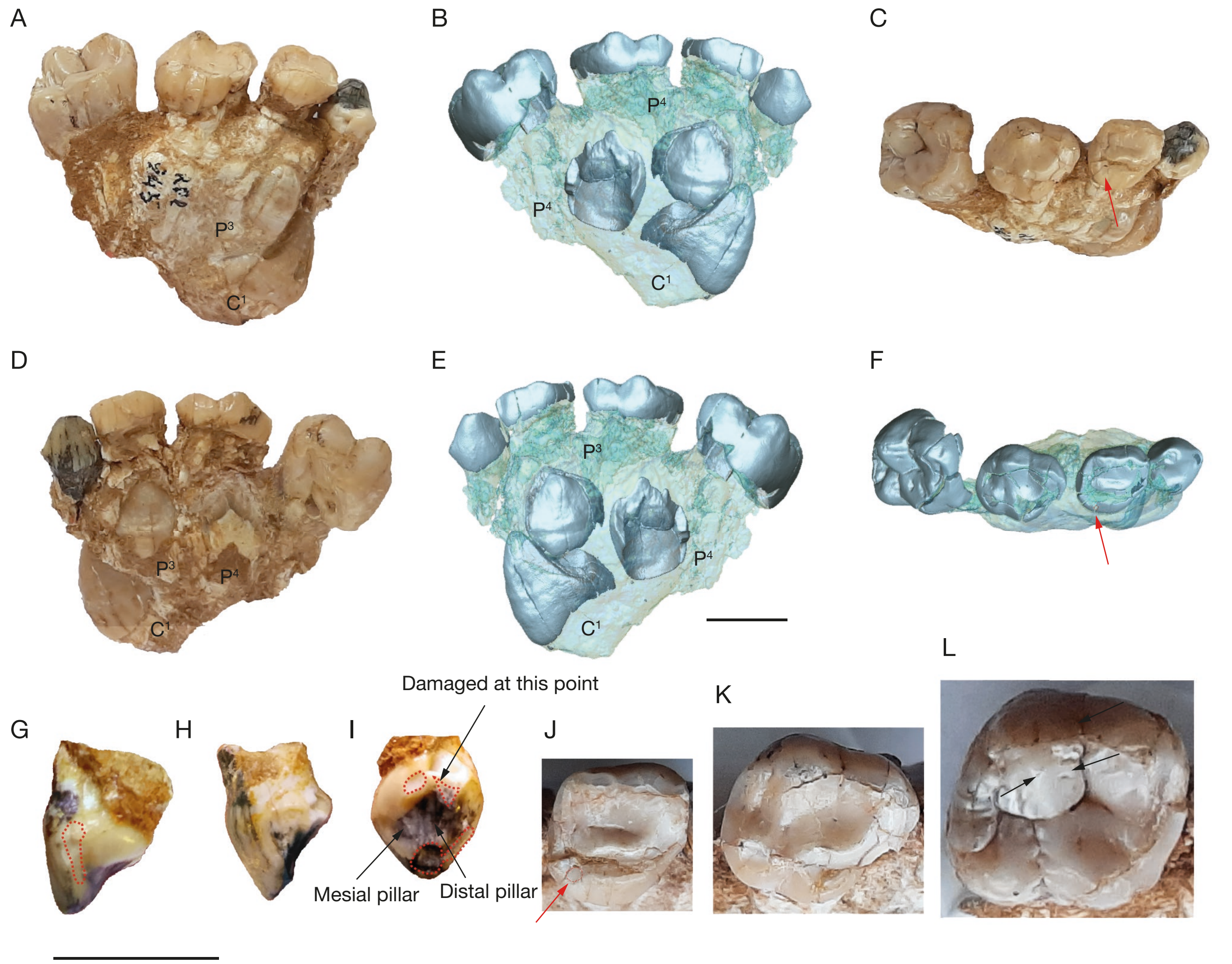

FIG. 2. — *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974), Ravin de la Pluie, Macedonia, Greece; late Vallesian, MN10, *c.* 9.3 Ma: **A-C**, right maxillary fragment with dC1-M1, RPl-245: **A**, lingual; **B**, labial; **C**, occlusal view; **D-F**, virtual reconstruction of RPl-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 disto-lingual 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-

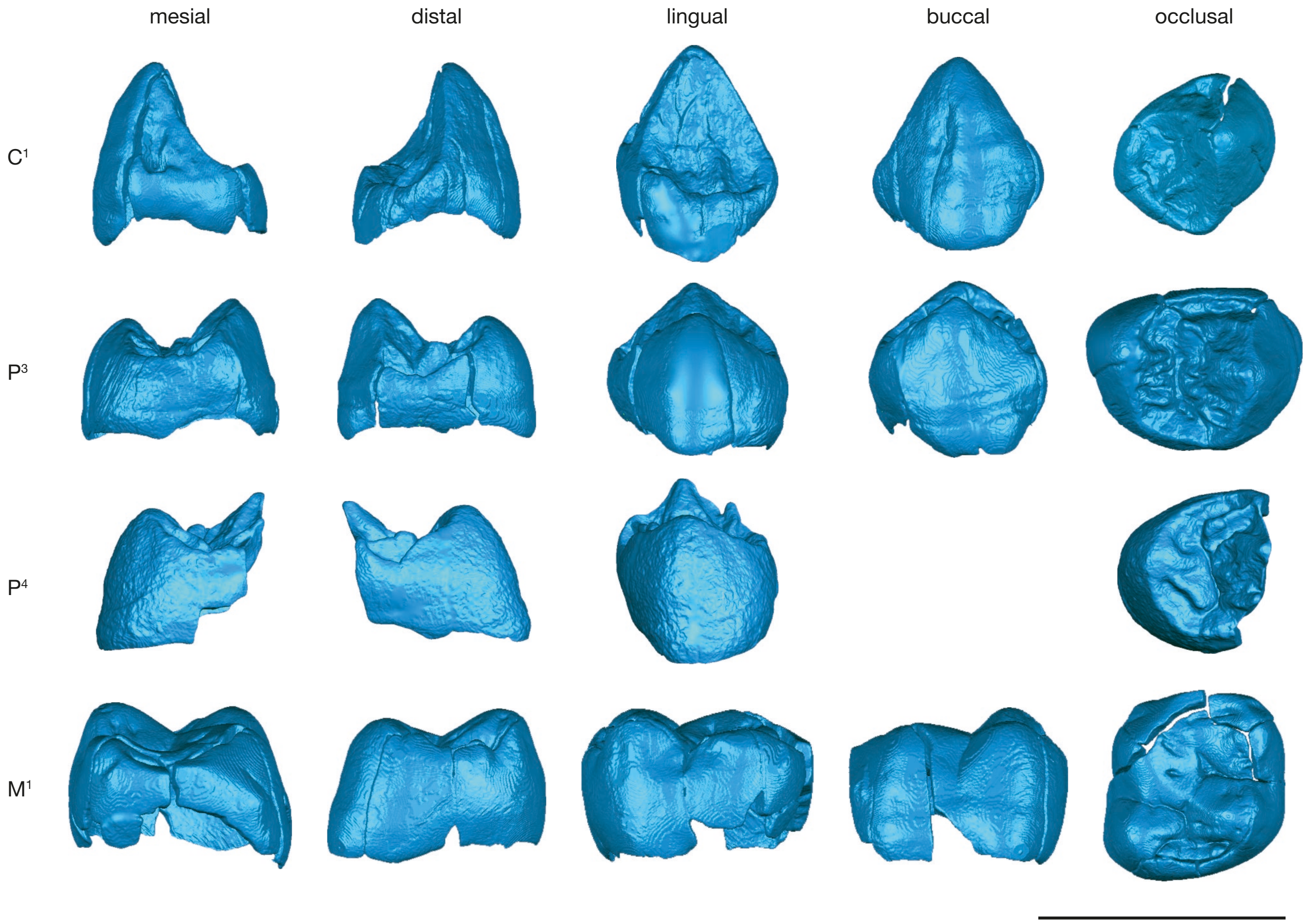

Fig. 3. — *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974), Ravin de la Pluie, Macedonia, Greece; late Vallesian, MN10; GPTS = *c.* 9.3 Ma. Virtual reconstruction of the unerupted upper permanent teeth; mirrored photos. Scale bar: 1 cm.

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^4 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^3. 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 µCT 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^1 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. (MDdC¹*100)/(MDdP³+MDdP⁴). The indices were calculated using the mean values of the dental dimensions.

	Index-a			
Taxa	dC¹	dP³	dP⁴	Index-b
Ouranopithecus macedoniensis (Bonis, Bouvrain, Geraads & Melentis, 1974)	101.4	97.2	109.2	37.5
Gorilla Geoffroy Saint-Hilaire, 1852	136.5	100.0	103.8	46.3
Pan Oken, 1816	152.0	94.3	93.9	54.6
Pongo Lacépède, 1799	130.7	89.3	97.0	50.0
Homo sapiens Linnaeus, 1758	115.7	85.6	93.5	45.4
Proconsul meswae Harrison & Andrews, 2009	108.9	81.0	82.5	47.2
Proconsul major Le Gros Clark & Leakey, 1950	133.1	95.9	91.7	51.5
Ekembo heseloni (Walker, Teadford, Martin & Andrews, 1933)	131.8	80.8	86.0	48.7
Griphopithecus alpani (Tekkaya, 1974)	–	78.7	88.1	–
Hispanopithecus laietanus Villalta Comella & Crusafont-Pairó, 1944	124.3	99.5	91.3	46.1
Rudapithecus hungaricus (Kretzoi, 1969)	–	80.8	77.7	–
Lufengpithecus lufengensis Xu, Lu, Pan, Qi, Zhan & Zheng, 1978	–	–	88.2	–
Australopithecus afarensis Johanson, White & Coppens, 1978	127.7	92.5	89.8	39.6
Australopithecus africanus 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 P³ 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 P⁴ 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 M¹ 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 hominoids

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 dC¹ 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 dP³ is smaller with a trapezoidal occlusal crown outline, a distinct metacone (absent in *Gorilla*), a smaller parastyle, and no cingulum. The dP⁴ 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 dC¹ 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 dP³ 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 dP⁴ 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 dC¹ of *O. macedoniensis* is shorter and wider, lower, more reduced relative to the length of the premolar row, with rounded occlusal crown outline. The dP³ is larger and differs in having smaller parastyle, metacone, trapezoidal occlusal crown outline and absence of cingulum. The dP⁴ is larger, with lower cusps and absence of cingulum (Figs 4B, C; 5; 6; Table 4).

The dC¹ 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

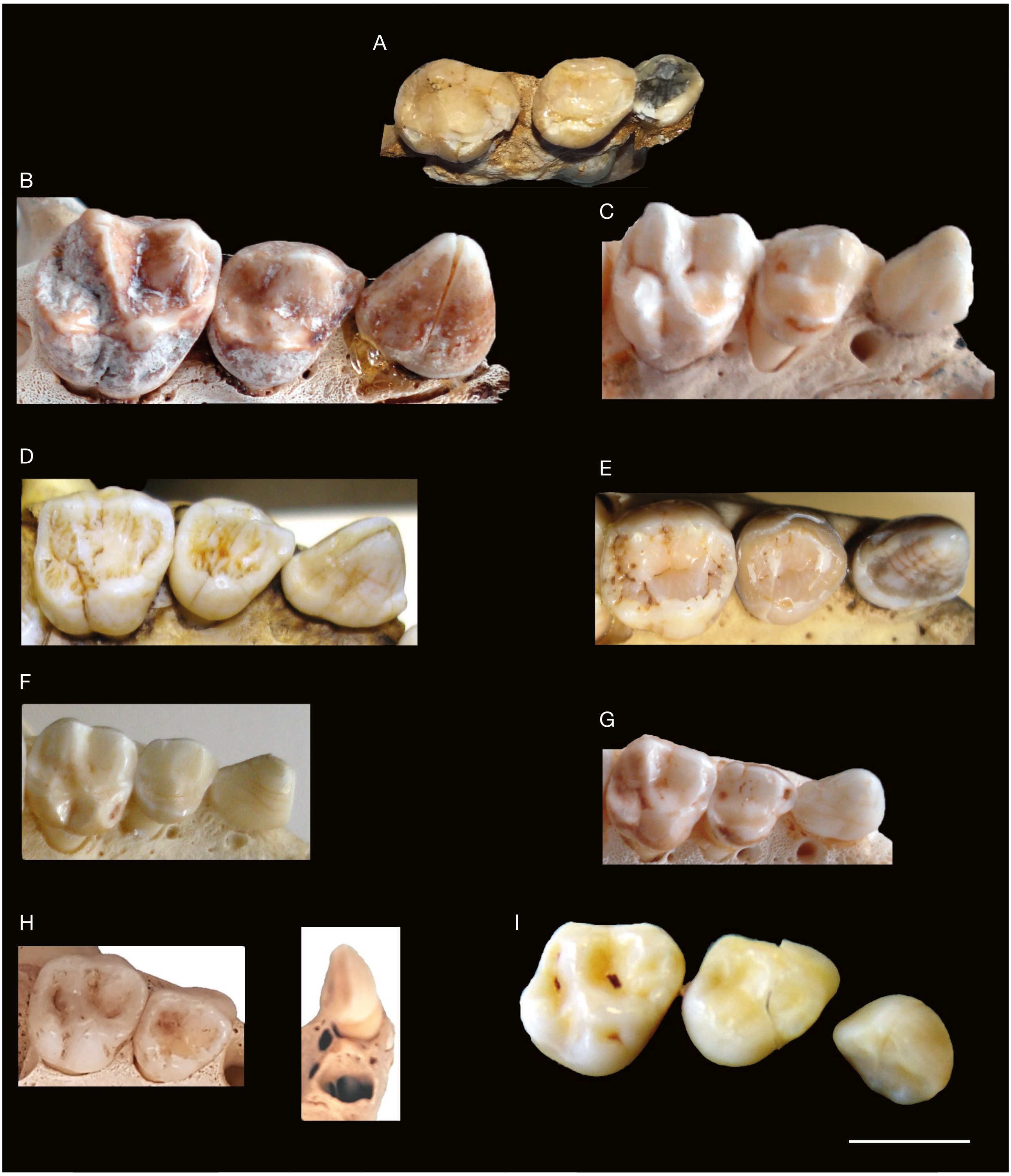

Fig. 4. — Upper deciduous dentition of *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) and some extant hominoids: **A**, *O. macedoniensis*, RPI-245 (♀); **B**, **C**, *Gorilla* Geoffroy Saint-Hilaire, 1852: **B**, NHMS 19158 (♂); **C**, NHMS 46766 (♀); **D**, **E**, *Pongo* 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 dP3 is larger with a small parastyle and it has slightly less squared occlusal crown outline. The dP4 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

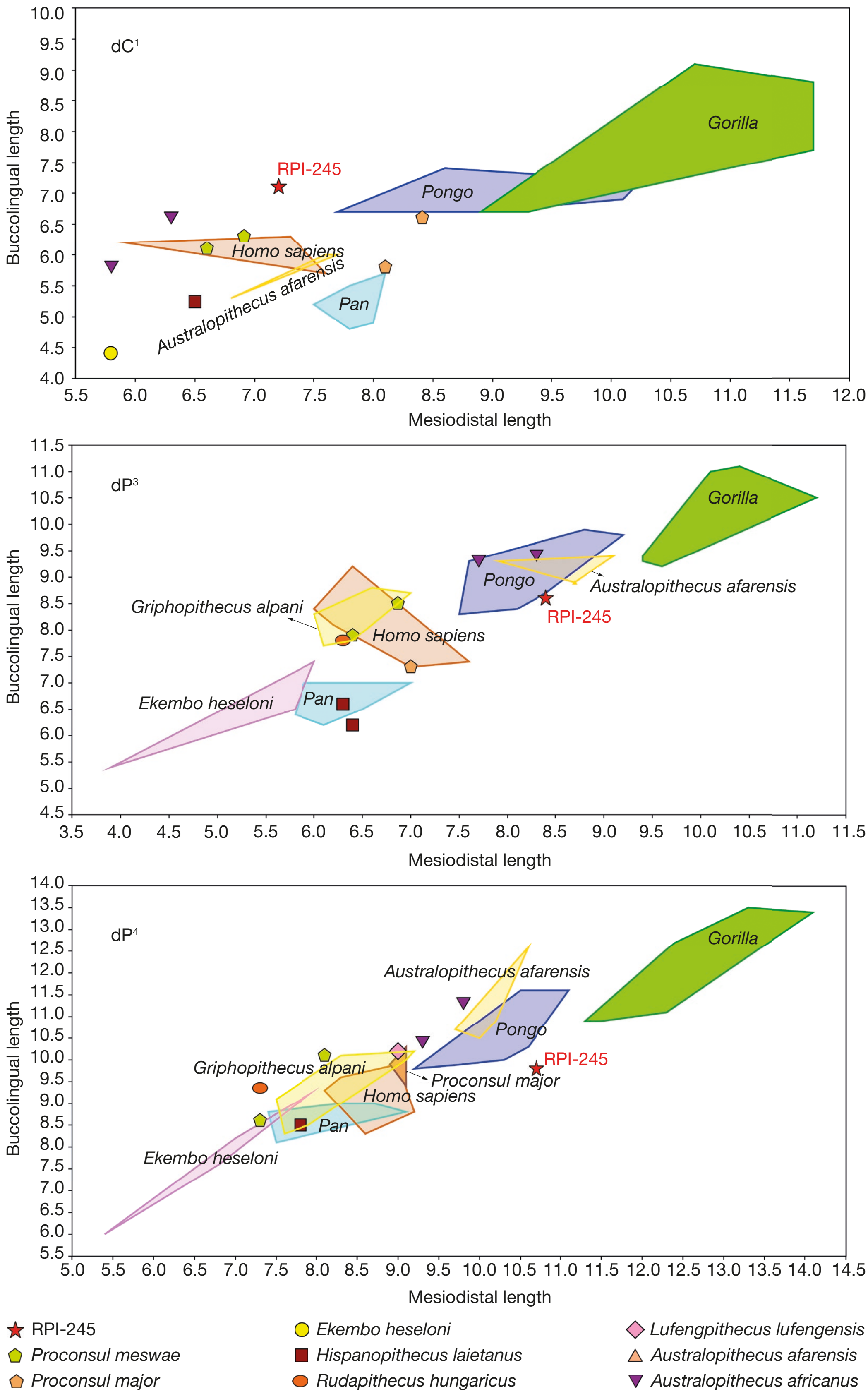

FIG. 5. — Scatter plots of the upper deciduous teeth of *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) in comparison with extant and extinct hominoids. Abbreviations: **C¹**, upper canine; **d**, deciduous; **P³**, upper third premolar; **P⁴**, upper fourth premolar. Data source: see Table 1.

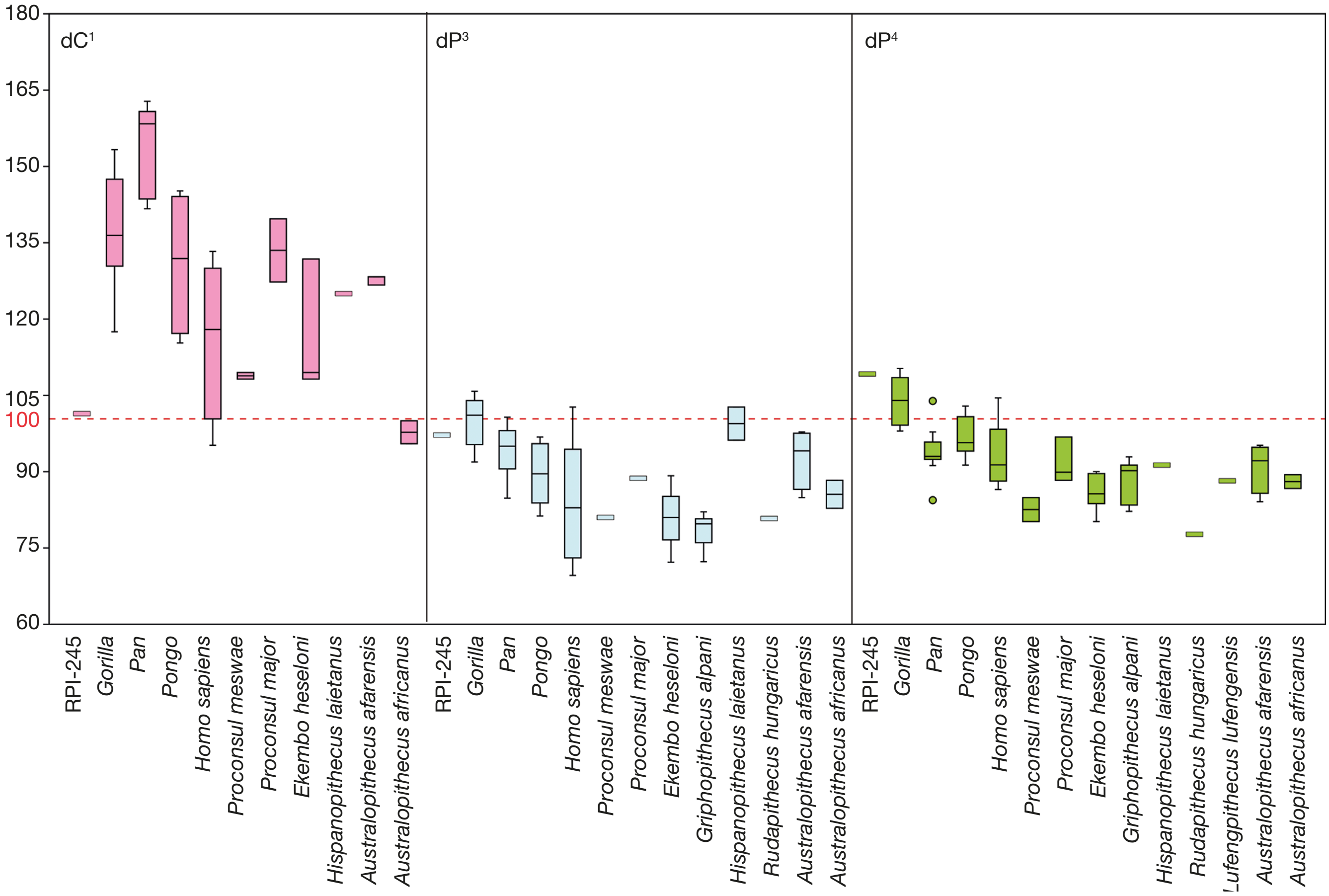

Fig. 6. — Box plots of the index-a [(MD*100)/BL] of *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) upper deciduous teeth compared to the extant and extinct hominoids; the **circles** indicate outliers. Abbreviations: **C**1, upper canine; **d**, deciduous; **P**3, upper third premolar; **P**4, 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 dC1-dP4, 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*, dC1 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 dP3 of *O. macedoniensis* from that of *P. meswae*. The dP4 is larger, has a more squared occlusal crown outline and lacks the cingulum (Figs 5-7P; Table 4). The dC1 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 dP3 of *O. macedoniensis* distinguish it from *P. major*. The dP4 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 dC1 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 dP3 is larger, has a trapezoidal outline of the occlusal crown, a metacone, a rudimentary hypocone and no cingulum. The dP4 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 dC1. The material was studied by Mortzou & Andrews (2008), and all referred to *G. alpani*. Compared to *G. alpani*, the dP3 of *O. macedoniensis* is larger with a metacone, a rudimentary hypocone and without cingulum. The dP4 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 dC1 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 dP3 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 dP4 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 dP3 and another dP4 from Rudabanya, Hungary. The dP3 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 dP4 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 dC1 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 dP3 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 dP4 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 dC1 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 dP3 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 dP3 of KNM-AL 333-86; Fig. 7U). The dP4 is slightly smaller and lacks a cingulum (a weak mesiolingual cingulum is present in the dP4 of KNM-AL 333-86), (Figs 5-7U-W; Table 4).

The dC1 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 dP3 has similar size, a less squared occlusal crown outline, and a more developed parastyle. The dP4 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 RPl-245 on the permanent teeth. The morphology of the upper permanent canine of RPl-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 P3 (two main cusps, weak parastyle, elliptical crown outline, presence of a metacone and a rudimentary hypocone, more symmetric shape, absence of cingulum) and P4 (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 RPl-245 is similar to that of *O. macedoniensis* (Fig. 8) except for M1, 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 RPl-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 RPl-245 matches with the female group (Fig. 8). The size difference is less pronounced

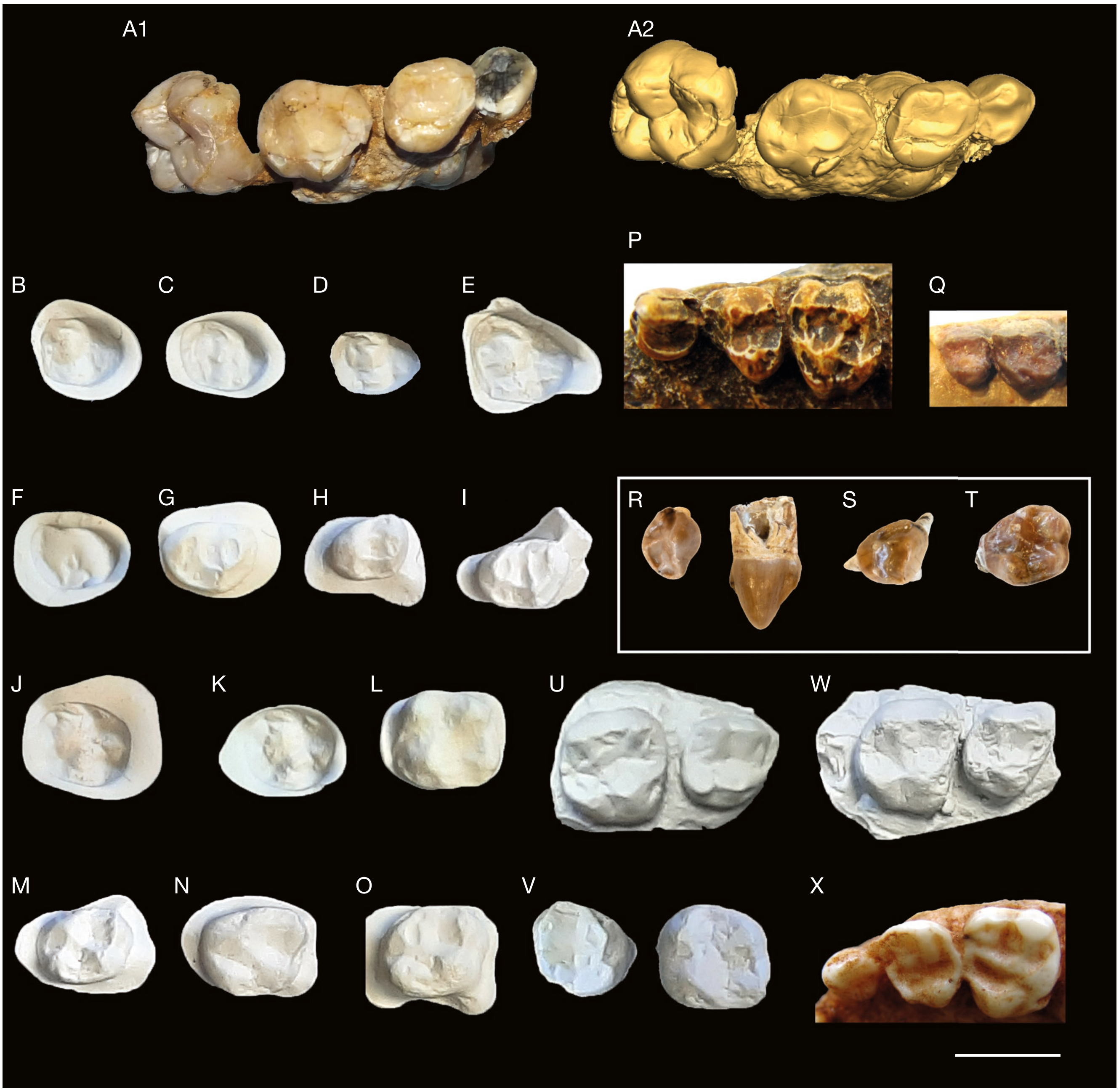

FIG. 7. — Upper deciduous teeth of various extinct hominoids: **A**, *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974), RPl-245: **A1**, original; **A2**, virtual reconstruction; **B**-**O**, *Griphopithecus alpani* (Tekkaya, 1974), Turkey (casts): **B**-**F**, right dP³'s, D 763, D 865, K 1320, L 1653, M 1874; **G**-**I**, left dP³'s, L 1567, K 1312, K 1319; **J**-**L**, right dP⁴'s, C 247, H 486, H 839; **M**-**O**, left dP⁴'s, K 1374, L 1576, K 1392; **P**, *Proconsul meswae* Harrison & Andrews, 2009, Kenya, KNM-ME 11 (cast); **Q**, *Ekembo heseloni* (Walker, Teadford, Martin & Andrews, 1933), left dP³-dP⁴, Kenya, KNM-RU 1803 (cast); **R**-**T**, *Hispanopithecus laietanus* Villalta Comella & Crusafont-Pairó, 1944, Can Llobateres, Spain; **R**, left dC¹, ?Can Llobateres 2, IPS1789; **S**, left dP³, Can Llobateres 1, IPS 1839; **T**, left dP⁴, Can Llobateres 1, IPS 1846; **U**, **V**, *Australopithecus afarensis* Johanson, White & Coppens, 1978, Hadar, Ethiopia (casts): **U**, right dP³-dP⁴, AL 33-386; **V**, right dP³ and dP⁴, Al 333-105 (casts); **W**, *Australopithecus afarensis,* Laetoli, Tanzania, right dP³-dP⁴, 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 RPl-245 being closer to the female group (Fig. 8). M¹ 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 RPl-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 RPl-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 M¹

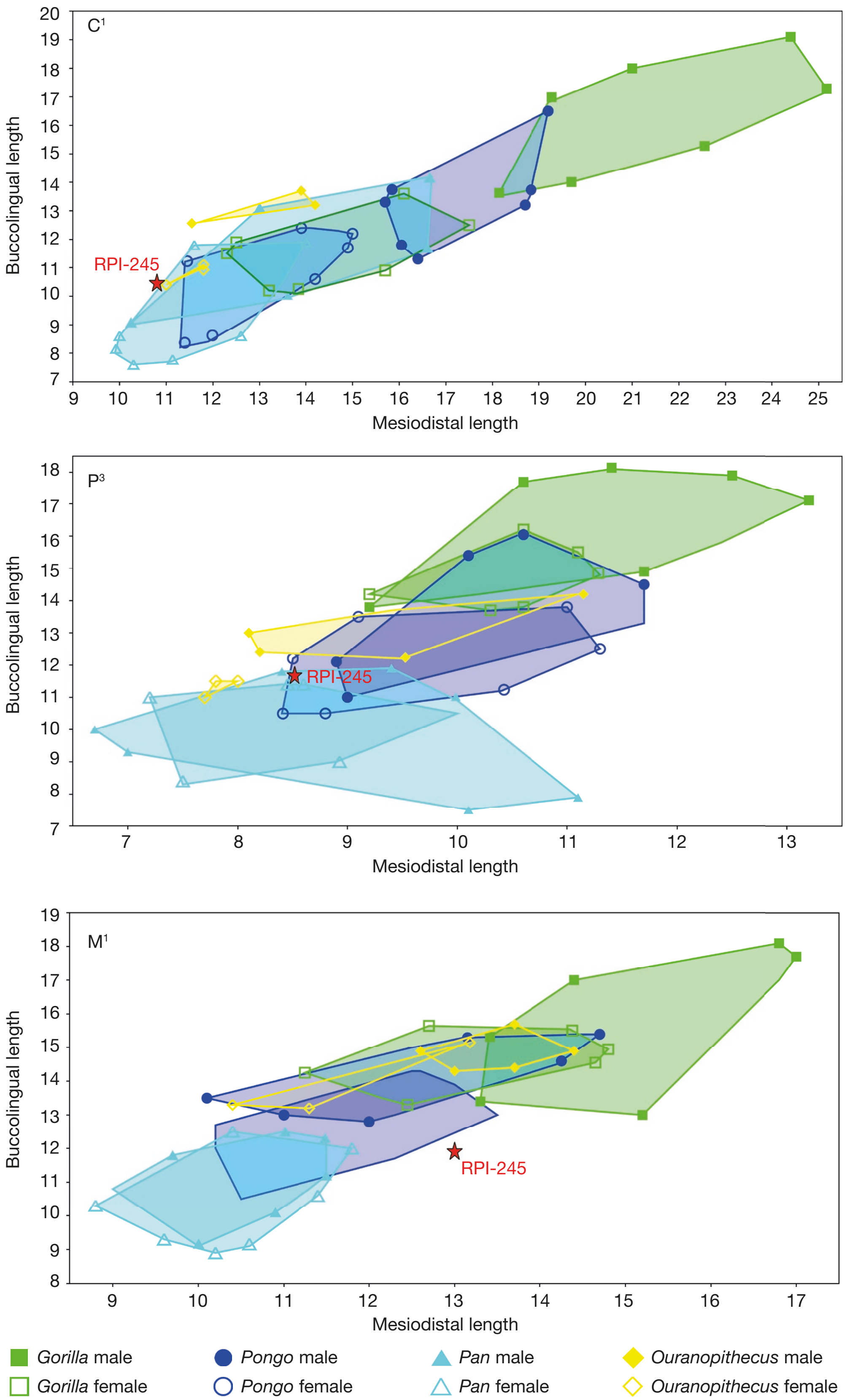

FIG. 8. — Scatter plots, comparing the upper permanent canine, third premolar and first molar of RPI-245 with the sample of *Ouranopithecus macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974) from Ravin de la Pluie, Xirochori 1, and Nikiti 1 and extant hominoids. Data source: Mahler (1973) for *Gorilla* Geoffroy Saint-Hilaire, 1852, *Pan* Oken, 1816 and *Pongo* Lacépède, 1799, and Koufos *et al.* (2016) for *O. macedoniensis*. Abbreviations: **C1**, upper canine; **M1**, upper first molar; **P3**, 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.

	Age at first molar emergence		
Species	**M1**	**m_1**	**Reference**
Afropithecus turkanensis Leakey & Leakey, 1986 KNM-MO 26	–	2.4-3.6	Kelley & Smith 2003
Sivapithecus parvada Kelley, 1988 GSP46460	–	2.2-4.5 (3.4)	Kelley 1997
Hispanopithecus laietanus Villalta Comella & Crusafont Pairo, 1944 IPS-1781	3.4-3.7	–	Dean & Kelley 2012
Lufengpithecus lufengensis Xu, Lu, Pan, Qi, Zhan & Zheng, 1978 PA 868	–	2.1-4.4	Zhao *et al.* 2008
Australopithecus afarensis Johanson, White & Coppens, 1978 LH 21	–	3.3	Bromage & Dean 1985
Australopithecus africanus Dart, 1925 STS 24	–	3.3	Bromage & Dean 1985
Pan troglodytes (Blumenbach, 1775)	3.32	3.26	Dean & Wood 1981
Gorilla gorilla (Savage, 1847)	3.5	3.5	Dean & Wood 1981
Pongo pygmaeus (Linnaeus, 1760)	–	3.5	Smith *et al.* 1994
Pongo pygmaeus	4.6	–	Kelley & Schwartz 2005
Homo sapiens 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	dC1	dP3	dP4
Ouranopithecus macedoniensis (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 – –
Gorilla gorilla (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 – –
Pongo pygmaeus (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 – –
Pan troglodytes (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 – –
Homo 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 –
Proconsul meswae 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 – –
Ekembo heseloni (Walker, Teadford, Martin & Andrews, 1933)	Smaller size Elliptical crown outline – Larger relative to the length of the deciduous premolars row –	Smaller size Subtriangular occlusal coutline Absence of metacone Larger parastyle Presence of cingulum	Smaller size Subtriangular occlusal outline – Presence of cingulum –
Griphopithecus alpani (Tekkaya, 1974)	– – –	Smaller size Triangular-subtriangular occlusal outline –	Smaller size Less squared occlusal outline Presence of cingulum

Table 6. — Continuation.

Taxon	dC¹	dP³	dP⁴
	–	Absence of metacone	–
	–	Presence of cingulum	–
Hispanopithecus laietanus Comella & Crusafont-Pairó, 1944	Smaller size	Smaller size	Smaller size
	Elliptical occlusal outline	Subtriangular occlusal coutline	Subtriangular occlusal coutline
	Larger relative to the length of the premolars row	Absence of metacone	Presence of lingual cingulum
	–	Larger parastyle	–
	Presence of a distolingual basin-like groove	Presence of cingulum	–
Rudapithecus *hungaricus* (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	–
Lufengpithecus *lufengensis* Xu, Lu, Pan, Qi, Zhan & Zheng, 1978	–	–	Smaller size
	–	–	Weaker hypocone
	–	–	Subrectangular occlusal outline (MD<BL)
	–	–	Presence of cingulum
Australopithecus afarensis Johanson, White & Coppens, 1978	Slightly longer and narrower	Similar size	Slightly larger
	Subrounded occlusal outline	More squared occlusal outline	Similar morphology
	–	Larger hypocone	Presence of mesiolingual cingulum in KNM-AL 333-86
	–	Smaller parastyle	
	–	Presence of weak lingual cingulum in KNM-AL 333-86	–
Australopithecus africanus Dart, 1925 (Taung skull)	Smaller	Similar size	Slightly smaller
	Rounded occlusal outline	Smaller parastyle	Presence of a crest connecting the hypocone with the mesial margin

emergence, the death age of RPl-245 is between 3.5-6.0 years (Table 5). The M¹ of RPl-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 RPl-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 M¹ or m1 to body size (Gingerich *et al.* 1982), the weight of *O. macedoniensis* ranges from 51.0-91.0 kg (mean 77.6 kg) for M¹ and 70.0-101.0 kg (mean 84.3 kg) for m_1 (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 RPl-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 dC¹ of *O. macedoniensis* has a rounded occlusal crown outline (index-a = 101.4; Table 4). The dC¹ 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 dP³ (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 dP³ of the more derived Plio-Pleistocene hominids. In contrast, the dP³ of the extant and Early-Middle Miocene hominoids are less molarised (triangular-subtriangular occlusal outline, absence of metacone 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^3, M^1) of RPl-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.

Acknowledgements
We would like to thank D. Alba (Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain), D. Begun (University of Toronto, Canada), and G. Suwa (University of Tokyo, Japan) for providing us with casts, useful information, and/or photographs. Thanks, are also due to M. Ioannidou (University of Tübingen, Germany) for providing us with some measurements of *Homo sapiens* deciduous teeth. The field campaigns in Northern Greece during the last 50 years have been supported by several foundations and institutes – many thanks to all of them. G.D.K. would like to thank S. Merker (Museum of Natural History, Stuttgart, Germany) and Ch. Soligo (former curator at the Natural History Museum, London) for giving access to their collections and for their hospitality. We are also indebted to the colleagues and students who helped to collect the material and prepare it in the laboratory. We would also like to thank A. Mounier and the two anonymous reviewers for their useful comments, which helped to improve the quality of the manuscript. Thanks also to Mrs Audrina Neveu for her nice work in formatting the final published text.

REFERENCES

Agustí J., Oms O., Pinero P., Chochisvili G., Bukhsianidze M. & Lordkipanidze D. 2020. — Late survival of dryopithecine hominoids in Southern Caucasus. *Journal of Human Evolution* 138: 102690. https://doi.org/10.1016/j.jhevol.2019.102690

Alba D. M., Casanovas-Vilar I., Almécija S., Robles J. M., Arias-Martorel J. & 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 (1): 231-246. https://doi.org/10.1016/j.jhevol.2012.05.009

Andrews W. C. 1918. — Note on some fossil mammals from Salonica and Imbros. *Geological Magazine* 5: 540-543.

Andrews P. 1978. — A revision of the Miocene Hominoidea of East Africa. *Bulletin British Museum (Natural History) Geology* 30: 85-225.

Andrews P. 1992. — Evolution and environment in the Hominoidea. *Nature* 360: 641-646.

Andrews P. & Tobien H. 1977. — New Miocene locality in Turkey with evidence on the origin of *Ramapithecus* and *Sivapithecus*. *Nature* 268: 699-701. https://doi.org/10.1038/268699a0

Andrews P., Harrison T., Martin L. & Pickford M. 1981. — Hominoid primates from a new Miocene locality named Meswa Bridge in Kenya. *Journal of Human Evolution* 10 (2): 123-128. https://doi.org/10.1016/S0047-2484(81)80009-7

Andrews P. J., Harrison T., Delson E., Bernor R. L. & Martin L. 1996. — Distribution and biochronology of European and South-western Asian Miocene catarrhines, *in* Bernor R. L., Fahlbusch V. & Mittmann H.-W. (eds), *The evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, 168 p.

Arambourg C. & Piveteau J. 1929. — Les Vertébrés du Pontien de Salonique. *Annales de Paléontologie* 18: 59-138.

Begun D. R. 1992. — Miocene fossil hominoids and the chimp-human clade. *Science* 257 (5078): 1929-1933. https://www.jstor.org/stable/2879797

Begun D. R., Ward C. V. & Rose M. D. 1997. — Events in the Miocene hominoid evolution, *in* Begun D. R., Ward C. V. & Rose M. D. (eds), *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York, 389 p.

Begun D. R., Güleç E. & Geraads D. 2003. — The Çandir hominoid locality: implications for the timing and pattern of hominoid dispersal events. *Courier Forschung-Institut Senckenberg* 40: 240-265.

Blumenbach F. 1775. — *De generis humani varietate native liber*. Vandenhoek et Ruprecht, Gottingae, 326 p. https://doi.org/10.5962/bhl.title.35972

Böhme M., Spassov N., Ebner M., Geraads D., Hristova L., Kirscher U., Kötter S., Linnemann U., Prieto J., Roussiakis S., Theodorou G., Uhlig G. & Winklhofer M. 2017. — Messinian age and savannah environment of the possible hominin *Graecopithecus* from Europe. *PLoS ONE* 12: e0177347. https://doi.org/10.1371/journal.pone.0177347

Bonis L. de & Melentis J. K. 1977a. — Un nouveau genre de Primate hominoide dans le Vallesien (Miocéne supérieur) de Macédoine. *Comptes Rendus de l'Acedémie des Sciences*, ser. D, 284: 1393-1396.

Bonis L. de & Melentis J. K. 1977b. — Les Primates hominoïdes du Vallésien de Macédoine (Grèce). Étude de la mâchoire inférieure. *Geobios* 10 (6): 849-885. https://doi.org/10.1016/S0016-6995(77)80081-8

Bonis L. de & Melentis J. K. 1978. — Les Primates hominoïdes du Miocène supérieur de Macédoine. Étude de la mâchoire supérieure. *Annales de Paléontologie (Vertébres)* 64: 185-202.

Bonis L. de & Koufos G. D. 1981. — A new hyaenid (Carnivora, Mammalia) in the Vallesian (late Miocene) of Northern Greece. *Scientific Annals of the faculty of Sciences of Aristotle University of Thessaloniki* 21: 79-94.

Bonis L. de & Melentis J. K. 1985. — La place du genre *Ouranopithecus* dans l'évolution des Hominidés. *Comptes Rendus Academie Sciences Paris* 300, ser. II (9): 429-432.

Bonis L. de & Koufos G. D. 1993. — The face and the mandible of *Ouranopithecus macedoniensis*: Description of new specimens and comparisons. *Journal of Human Evolution* 24 (6): 469-491. https://doi.org/10.1006/jhev.1993.1032

Bonis L. de & Koufos G. D. 1994. — Our ancestors' ancestor *Ouranopithecus* is a Greek link in human ancestry. *Evolutionary Anthropology* 3 (3): 75-83. https://doi.org/10.1002/evan.1360030303

Bonis L. de & Koufos G. D. 1995. — Phyletic relationships and taxonomic assessment of *Ouranopithecus macedoniensis* (Primates, Mammalia). *Current Primatology Ecology and Evolution* 13: 295-301.

Bonis L. de & Koufos G. D. 2001. — Phylogenetic relationships of *Ouranopithecus macedoniensis* (Mammalia, Primates, Hominoidea, Hominidae) of the Late Miocene deposits of Central Macedonia (Greece), *in* Bonis L. de, Koufos G. D. & Andrews P. (eds), *Hominoid evolution and climate change in Europe*. Vol. 2. *Phylogeny of the Neogene Hominoid Primates of Eurasia*. Cambridge University Press, Cambridge, 254 p.

Bonis L. de & Bouvrain G. 2003. — Nouveaux Giraffidae du Miocène supérieur de Macédoine (Grèce), *in* Petculescu A. & Stiuca E. (eds), *Advances in Vertebrate Paleontology "hen to Panta"*. Romanian Academy, Bucharest, 5 p.

Bonis L. de & Koufos G. D. 2014. — First discovery of postcranial bones of *Ouranopithecus macedoniensis* (Primates, Hominoidea) from the Late Miocene of Macedonia (Greece). *Journal of Human Evolution* 74: 21-36. https://doi.org/10.1016/j.jhevol.2014.05.015

Bonis L. de, Bouvrain G., Geraads D. & Melentis J. K. 1974. — Première découverte d'un primate hominoïde dans le Miocène supérieur de Macédoine (Grèce). *Comptes Rendus de l'Academie des Sciences* 278: 3063-3066.

Bonis L. de, Bouvrain G., Geraads D. & Koufos G. D. 1988. — Late Miocene mammal localities of the lower Axios valley (Macedonia, Greece) and their stratigraphical significance. *Modern Geology* 13: 141-147.

Bonis L. de, Bouvrain G., Geraads D. & Koufos G. D. 1990. — New hominid skull material from the late Miocene of Macedonia in Northern Greece. *Nature* 345: 712-714. https://doi.org/10.1038/345712a0

Bourcart J. 1919. — Note préliminaire sur les terrains sédimentaires de la région de Salonique. *Comptes Rendus Sommaire de la Société Géologique de France* 4 (19): 77-79.

Bouvrain G. 1975. — Un nouveau bovidé du Vallésien de Macédoine (Grèce). *Comptes Rendus de l'Academie des Sciences*, ser. D, 280: 1357-1359.

Bouvrain G. 1982. — Révision du genre *Prostrepsiceros* Major 1891 (Mammalia, Bovidae). *Paläontologische Zeitschrift* 56: 113-124. https://doi.org/10.1007/BF02988790

Bouvrain G. & Bonis L. de 1984. — Le genre *Mesembriacerus* (Bovidae, Artiodactyla, Mammalia) : un Oviboviné primitif du Vallésien (Miocène supérieur) de Macédoine (Grèce). *Palaeovertebrata* 14 (4): 201-223.

Bouvrain G. & Bonis L. de 1985. — Le genre *Samotragus* (Artiodactyla, Bovidae) une antilope du Miocène Supérieur de Grèce. *Annales de Paléontologie* 71: 257-299.

Bromage T. G. & Dean M. C. 1985. — Re-evaluation of the age at death of immature fossil hominids. *Nature* 317: 525-527. https://doi.org/10.1038/317525a0

Burgess M. L., McFarlin S. C., Mudakikwa A. M. R. & Ruff C. B. 2018. — Body mass estimation in hominoids: age and locomotor effects. *Journal of Human Evolution* 115: 36e46. https://doi.org/10.1016/j.jhevol.2017.07.004

Burtschak-Abramovitsch N. O. & Gabachvili E. C. 1945. — Vishaia cheloveko-obraznaiaobezianaizverkhnetretichnikh otlojenii Vostochnoi Gruzii. *Soobshenia AN Gruzzii* 6: 458-464 (in Russian).

Cameron D. W. 1997. — The taxonomic status of *Graecopithecus*. *Primates* 38 (3): 293-302.

Casanovas-Vilar I., Alba D., Garces M., Robles J. M. & Moya-Sola S. 2011. — Updated chronology for the Miocene hominoid radiation in Western Eurasia. *PNAS* 108 (14): 5554-5559. https://doi.org/10.1073/pnas.1018562108

Dart R. 1925. — *Australopithecus africanus,* the Man-Ape of South Africa. *Nature* 115: 195-199. https://doi.org/10.1038/115195a0

Dean M. C. & Wood B. A. 1981. — Developing pongid dentition and its use for ageing individual crania in comparative cross-sectional growth studies. *Folia Primatologica* 36 (1-2): 11-127. https://doi.org/10.1159/000156011

Dean D. & Delson E. 1992. — Second gorilla or third chimp? *Nature* 359 (6397): 676-677.

Dean D. & Kelley J. 2012. — Comparative dental development in *Hispanopithecus laietanus* and *Pan troglodytes*. *Journal of Human Evolution* 62 (1): 174e178. https://doi.org/10.1016/j.jhevol.2011.10.003

Fuss J., Spassov N., Begun D. R. & Böhme M. 2017. — Potential hominin affinities of *Graecopithecus* from the Late Miocene of Europe. *PLoS ONE* 12 (5): e0177127, 1-23. https://doi.org/10.1371/journal.pone.0177127

Gaudry A. & Lartet E. 1856. — Résultats des recherches paléontologiques entreprises dans l'Attique sous les auspices de l'Académie. *Comptes Rendu de l'Academie des Sciences* 43: 271-274.

Geoffroy Saint-Hilaire I. 1852. — Sur le gorille. *Comptes rendus des séances de l'Académie des Sciences* 34: 81-84

Geraads D. 2013. — Large mammals from the Late Miocene of Çorakyerler, Çankırı, Turkey. *Acta Zoologica Bulgarica* 65 (3): 381-390.

Gingerich P. D., Smith B. H. & Rosenberg K. 1982. — Allometric Scaling in the Dentition of Primates and Prediction of Body Weight from Tooth Size in Fossils. *American Journal of Physical Anthropology* 58: 81-100.

Güleç E. S., Sevim A., Pehlevan C. & Kaya F. 2007. — A new great ape from the Late Miocene of Turkey. *Anthropological Science* 115 (2): 153-158. https://doi.org/10.1537/ase.070501

Hammer C., Harper D. A. T. & Ryan P. D. 2001. — PAST: paleontological statistics software package for education and data analysis. Version 4.05. *Paleontologia Electronica* 4 (1): 1-9. http://paleoelectronica.org/2001_1/past/issue1_01.htm.

Harrison T. 2010. — Apes among the tangled branches of human origins. *Science* 327 (5965): 532-534. https://doi.org/10.1126/science.1184703

Harisson T. 2011. — Laetoli revisited: renewed paleontological and geological investigations at localities on the Eyasi Plateau in Northern Tanzania, *in* Harrison T. (ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context. Vertebrate Paleobiology and Paleoanthropology*. Springer, Dordrecht: 1-15. https://doi.org/10.1007/978-90-481-9956-3_1

Harrison T. & Andrews P. 2009. — The anatomy and systematic position of the Early Miocene proconsulid from Meswa Bridge, Kenya. *Journal of Human Evolution* 56 (5): 479-496. https://doi.org/10.1016/j.jhevol.2009.02.005

Hensel R. F. 1862. — Über die Reste einiger Säugetierarten von Pikermi in der Münchener Sammlung. *Monatsberichte der Akademie der Wissenschaften* 27: 560-569

Herries A. I. R., Pickering R., Adams J. W., Curnoe D., Warr G., Latham A. G. & Dhaw J. 2013. — A multi-disciplinary perspective on the age of *Australopithecus* in Southern Africa, *in* Reed K. E., Fleagle J. G. & Leakey R. E. (eds), *The Paleobiology of Australopithecus, Vertebrate Paleobiology and Paleoanthropology*. Springer, Dordrecht: 21-40. https://doi.org/10.1007/978-94-007-5919-0_3

Ho C. K. 1990. — A new Pliocene hominoid skull from Yuanmou, southwest China. *Human Evolution* 5: 309-318. https://doi.org/10.1007/BF02437248

Hopwood A. T. 1933. — Miocene primates from British East Africa. *Annals and Magazine of Natural History*, ser. 10, 61: 96-98. https://doi.org/10.1080/00222933308673629

Ji X., Jablonski N. G., Su D. E., Deng C. L., Flynn L. J., You Y. & Kelley J. 2013. — Juvenile hominoid cranium from the terminal Miocene of Yunnan, China. *Chinese Science Bulletin* 58: 3771-3779. https://doi.org/10.1007/s11434-013-6021-x

Johanson D. C., White T. D. & Coppens Y. 1978. — A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of eastern Africa. *Kirtlandia* 28: 1-14.

Johanson D. C., White T. D. & Coppens Y. 1982. — Dental remains from the Hadar Formation, Ethiopia: 1974-1977 collections. *American Journal of Physical Anthropology* 57 (4): 545-603. https://doi.org/10.1002/ajpa.1330570406

Ioannidou M., Koufos G. D., Bonis L. de & Harvati K. 2019. — A new three-dimensional geometric morphometrics analysis of the *Ouranopithecus macedoniensis* cranium (Late Miocene, Central Macedonia, Greece). *American Journal of Physical Anthropology* 170 (2): 295-307. https://doi.org/10.1002/ajpa.23900

Kappelman J., Duncan A., Feseba M., Lunkka J.-P., Ekart D., McDowell F., Ryan T. M. & Swisher C. C. 2003a. — Chronology, *in* Fortelius M., Kappelman J., Sen S. & Bernor R. L. (eds), *Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York, 41 p.

Kappelman J., Richmont B. G., Seiffert E. R., Maga E. M. & Ryan T. M. 2003b. — Hominoidea (Primates), *in* Fortelius M., Kappelman J., Sen S. & Bernor R. L. (eds), *Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York, 90 p.

Kaup J. 1829. — Neues Säugethiere, Deinotherium: Deinotherium giganteum. *Isis* 22 (4): 401-404.

Kaya F., Kaymakçi N., Bibi F., Eronen J. T., Pehlevan C., Erkman A. C., Langereis C. G. & Fortelius M. 2016. — Magnetostratigraphy and paleoecology of the hominid-bearing locality Çorakyerler, Tuğlu Formation (Çankırı Basin, Central Anatolia). *Journal of Vertebrate Paleontology* 36 (2): e1071710. https://doi.org/10.1080/02724634.2015.1071710

Kelley J. 1988. — A new large species of *Sivapithecus* from the Siwaliks of Pakistan. *Journal of Human Evolution* 17 (3): 305-324. https://doi.org/10.1016/0047-2484(88)90073-5

Kelley J. 1997. — Paleobiological and phylogenetic significance of life history in Miocene hominoids, *in* Begun D. R., Ward C. V. & Rose M. D. (eds), *Function, Phylogeny, Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York: 173-208.

Kelley J. & Smith T. 2003. — Age at first molar emergence in early Miocene Afropithecus turkanensis and life-history evolution in the Hominoidea. *Journal of Human Evolution* 44 (3): 307-329. https://doi.org/10.1016/S0047-2484(03)00005-8

Kelley J. & Gao F. 2012. — Juvenile homimoid cranium from the late Miocene of southern China and hominoid diversity in Asia. *PNAS* 109 (18): 6882-6885. https://doi.org/10.1073/pnas.1201330109

Kelley J. & Schwartz G. T. 2005. — Histologically-determined age at first molar emergence in *Pongo pygmaeus*. *American Journal of Physical Anthropology* 126 (S40): 128.

Kelley J., Andrews P. & Alpagut B. 2008. — A new hominoid species from the middle Miocene site of Paşalar, Turkey. *Journal of Human Evolution* 54 (4): 455-479. https://doi.org/10.1016/j.jhevol.2007.08.007

Konidaris G. E. 2013. — *Paleontological and Biostratigraphical Study of the Neogene Proboscidea from Greece*. PhD thesis, Aristotle University of Thessaloniki, *Scientific Annals School of Geology* 154, 326 p. (in Greeks).

Kostopoulos D. S. 2022. — The fossil record of Bovids (Mammalia: Artiodactyla: Pecora: Bovidae) in Greece, *in* Vlachos E. (ed.), *Fossil Vertebrates of Greece.* Vol. 2. *Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics.* Springer Nature, Switzerland, 113 p. https://doi.org/10.1007/978-3-030-68442-6_5

Kostopoulos D. S., Erol A. S., Mayda S., Yavuz A. Y. & Tarhan E. 2020. — *Qurliqnoria* (Bovidae, Mammalia) from the Upper Miocene of Çorakyerler (Central Anatolia, Turkey) and its biogeographic implications. *Paleoworld* 29 (3): 629-635. https://doi.org/10.1016/j.palwor.2019.10.003

Koufos G. D. 1984. — A new hipparion (Mammalia, Perissodactyla) from the Vallesian (Late Miocene) of Greece. *Paläontologische Zeitschrift* 58 (3/4): 307-317.

Koufos G. D. 1993. — A mandible of *Ouranopithecus macedoniensis* from a new Late Miocene locality of Macedonia (Greece). *American Journal of Physical Anthropology* 91 (2): 225-234. https://doi.org/10.1002/ajpa.1330910208

Koufos G. D. 1995. — The first female maxilla of the hominoid *Ouranopithecus macedoniensis* from the Late Miocene of Macedonia, Greece. *Journal of Human Evolution* 29 (4): 385-399. https://doi.org/10.1006/jhev.1995.1064

Koufos G. D. 2006. — The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. *Hellenic Journal of Geosciences* 41: 183-214.

Koufos G. D. 2012a. — A new protictithere from the Late Miocene hominoid locality Ravin de la Pluie of Axios Valley (Macedonia, Greece). *Paläontologische Zeitschrift* 86 (2): 219-229. https://doi.org/10.1007/s12542-011-0126-9

Koufos G. D. 2012b. — New material of Carnivora (Mammalia) from the Late Miocene of Axios Valley, Macedonia, Greece. *Comptes Rendus Palevol* 11 (1): 49-64. https://doi.org/10.1016/j.crpv.2011.09.004

Koufos G. D. 2013. — Neogene mammal biostratigraphy and chronology of Greece, *in* Wang X., Flynn L. J. & Fortelius M. (eds), *Fossil mammals of Asia. Neogene biostratigraphy and chronology*. Columbia University Press, New York, 595 p.

Koufos G. D. & 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 (6): 699-718. https://doi.org/10.1016/j.jhevol.2004.03.007

Koufos G. D. & Bonis L. de 2005. — The Late Miocene hominoids *Ouranopithecus* and *Graecopithecus*. Implications about their relationships and taxonomy. *Annales de Paléontologie* 91 (3): 227-240. https://doi.org/10.1016/j.annpal.2005.05.001

Koufos G. D. & Bonis L. de 2006. — New material of *Ouranopithecus macedoniensis* from Late Miocene of Macedonia (Greece) and study of its dental attrition. *Geobios* 39 (2): 223-243. https://doi.org/10.1016/j.geobios.2004.11.009

Koufos G. D., Syrides G. E., Koliadimou K. K. & Kostopoulos D. S. 1991. — Un nouveau gisement de Vertébrés avec hominoide dans le Miocéne supérieur de Macédoine (Grèce). *Comptes Rendus de l'Académie des Sciences de Paris*, ser. II, 313: 691-696.

Koufos G. D., Bonis L. de & Kugiumtzis D. 2016. — New material of the hominoid *Ouranopithecus macedoniensis* from the Late Miocene of the Axios Valley (Macedonia, Greece) with some remarks on its sexual dimorphism. *Folia Primatologica* 87 (2): 94-122. https://doi.org/10.1159/000446433

Kretzoi M. 1969. — Geschichte der Primaten und der Hominization. *Symposium Biologica Hungarica* 9: 3-11.

Kunimatsu Y., Nakatsukasa M., Sawada Y., Sakai T., Hyodo M., Hyodo H., Itaya T., Nakaya H., Saegusa H., Mazurier A., Saneyoshi M., Tsukijakawa H., Yamamoto A. & Mbua E. 2007. — A new Late Miocene great ape from Kenya and its implications for the origins of African great apes and humans. *Proceedings National Academy of Sciences* 104 (49): 19220-19225. https://doi.org/10.1073/pnas.0706190104

Lacépéde B. G. E. 1799. — *Mémoire sur une nouvelle table méthodique de la classe des oiseaux*. Mémoires de l'Institut national des Sciences et des Arts, Paris, 623 p.

Laskos K. & Kostopoulos D. S. 2022. — The Vallesian large *Palaeotragus* Gaudry, 1861 (Mammalia: Giraffidae) from Northern Greece. *Geodiversitas* 44 (15): 437-470. https://doi.org/10.5252/geodiversitas2022v44a15

Le Gros Clark W. E. & Leakey L. S. B. 1950. — Diagnoses of East African Miocene Hominoidea. *Quarterly Journal Geological Society London* 105: 260-263.

Linnaeus K. 1758. — *Systema naturae per egne tria naturae,secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Edition 10. Tomus 1. Salvii, Stockholm, 823 p.

Linnaeus C. 1760. — *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. *Praefactus est Ioannes Ioachimus Langivs*. Ad editionem deciman reformatum Holmiensem, 824 p.

Macchiarelli R., Mazurier A., Illerhous B. & Zanolli C. 2009. — *Ouranopithecus macedoniensis* (Mammalia, Primates, Hominoidea): virtual reconstruction and 3D analysis of a juvenile mandibular dentition (RPl-82 and RPl-83). *Geodiversitas* 31 (4): 851-863. https://doi.org/10.5252/g2009n4a851
Mahler E. P. 1973. — *Metric Variation in the Pongid Dentition*. PhD dissertation, University of Michigan, Ann Arbor, Michigan, 466 p.
Martin L. & Andrews P. 1984. — The phyletic position of *Graecopithecus freybergi* Koenigswald. *Courier Forschung-Institut Senckenberg* 69: 25-40.
McNulty K. P., Begun D. R., Kelley J., Manthi F. K. & Mbua E. N. 2015. — A systematic revision of *Proconsul* with the description of a new genus of Early Miocene hominoid. *Journal of Human Evolution* 84: 42-61. http://dx.doi.org/10.1016/j.jhevol.2015.03.009
Mortzou G. & Andrews P. 2008. — The deciduous dentition of Griphopithecus alpani from Paşalar, Turkey. *Journal of Human Evolution* 54 (4): 494-502. https://doi.org/10.1016/j.jhevol.2007.08.001
NOW 2023. — Neogene Old World (database with the Neogene localities, their fauna and age). Available at: www.helsinki.fi/science/now/database.htm
Oken L. 1816. — *Lehrbuch der naturgeschichte*. August Schmid und Companie, Jena: 1-1270.
Ozansoy F. 1957. — Faunes de mammifères du Tertiaire de Turquie et leurs révisions stratigraphiques. *Bulletin Mineral Research and Exploration Institute of Turkey* 49: 29-48.
Ozansoy F. 1965. — Study of the continental sites and the mammals from the Cenozoic of Turkey. *Mémoires de la Société géologique de France* 44: 1-92.
Pickford M., Senut B., Gommery D., Musalizi S. & Sebuyungo C. 2020. — Descriptive catalogue of large ape dento-gnathic remains from the Early and Middle Miocene of Napak, Uganda: 2010-2020 collections. *Geo-Pal Uganda* 17 (17), 61 p. https://hal.science/hal-02927082
Pilgrim G. E. 1910. — Notices of new mammalian genera and species from the territories of India. *Records of the Geological Survey of India* 60: 63-71.
Pugh K. D. 2022. — Phylogenetic analysis of Middle-Late Miocene apes. *Journal of Human Evolution* 165: 103140. https://doi.org/10.1016/j.jhevol.2021.103140
Savage T. S. 1847. — Notice of the external characters and habits of *Troglodytes gorilla*, a new species of orang from the Gaboon river. *Boston Society of Natural History* 5: 417-443.
Schaub S. 1938. — Tertiare und Quartare Murinae. *Abhandlungen Schweizerische Paläontologische Gesellschaft* 61: 1-39.
Sen S., Koufos G. D., Kondopoulou D. & Bonis L. de 2000. — Magnetostratigraphy of the Late Miocene continental deposits of the Lower Axios Valley, Macedonia, Greece, *in* Koufos G. D. & Ioakim Ch. (eds), *Mediterranean Neogene Cyslostratigraphy in Marine-Continental Paleoenvironments*. *Bulletin Geological Society of Greece* Special Publication 9: 197-206.
Sevim-Erol A., Begun D. R., Yavuz A., Tarhan E., Sönmez Sözer Ç., Mayda S., Van Den Hoek Ostende L. W., Martin R. M. G. & Cihat Alçiçek M. 2023. — A new ape from Türkiye and the radiation of late Miocene hominines. *Communications Biology* 6: 842. https://doi.org/10.1038/s42003-023-05210-5
Smith R. J. & Jungers W. L. 1997. — Body mass in comparative primatology. *Journal of Human Evolution* 32 (6): 523-559. https://doi.org/10.1006/jhev.1996.0122
Smith B. H., Crummett L. T. & Brandt L. K. 1994. — Ages of eruption of Primate teeth: a compendium for aging individuals and comparing life histories. *Yearbook of Physical Anthropology* 37 (S19): 177-231. https://doi.org/10.1002/ajpa.1330370608
Spassov N., Geraads D., Hristova L., Markov G. N., Merceron G., Tzankov T., Stoyanov K., Böhme M. & Dimitrova A. 2012. — A hominid tooth from Bulgaria: the last pre-human hominid of continental Europe. *Journal of Human Evolution* 62 (1):138-145. https://doi.org/10.1016/j.jhevol.2011.10.008
Suwa G., KunimatsuY., Ataaabadi M. M., Orak Z., Sasaki T. & Fortelius M. 2016. — The first hominoid from the Maragheh Formation, Iran. *Paleobiodiversity Paleoenviroroments* 96: 373-381. https://doi.org/10.1007/s12549-016-0234-3
Tekkaya I. 1974. — A new species of Tortonian anthropoid (Primates, Mammalia) from Anatolia. *Bulletin Mineral Research And Exploration* 83: 194-210.
Urciuoli A. & Alba D. 2023. — Systematics of Miocene apes: state of the art of a neverending controversy. *Journal of Human Evolution* 175: 103309. https://doi.org/10.1016/j.jhevol.2022.103309
Valenciano A., Abella J., Sanisidro O., Hartstone-Rose A., Alvarez-Sierra M. A. & Morales J. 2015. — Complete description of the skull and mandible of the giant mustelid *Eomellivora piveteaui* Ozansoy, 1965 (Mammalia, Carnivora, Mustelidae), from Batallones (MN10), late Miocene (Madrid, Spain). *Journal of Vertebrate Paleontology* 35 (4): e934570. https://doi.org/10.1080/02724634.2014.934570
van der Made J. 2003. — Suoidea (pigs) from the hominoid locality of Çandır in Turkey. *Courier Forschung-Institut Senckenberg* 240: 149-179.
van der Made J. 2005. — Errata and reply to guest editor's notes. *Courier Forschung-Institut Senckenberg* 254: 473-477.
Villalta Comella J. F. de & Crusafont Pairó M. 1944. — Dos nuevos antropomorfos del Mioceno español y su situación dentro de la moderna sistemática de los símidos. *Notas y Comunicaciones del Instituto Geológico y Minero de España* 13: 1-51.
Visualization Sciences Group. 2011. — Avizo® 7.0.0. *Konrad-Zuse-Zentrum für Informationstechnik*, Berlin. Available at: https://www.thermofisher.com
Vlachou T. D. 2013. — *Paleontological, biostratigraphical and paleoecological study of the Greek hipparions*. PhD thesis, Aristotle University of Thessaloniki, *Scientific Annals, School of Geology* 154, 580 p. (in Greeks).
von Freyberg B. 1951. — Die Pikermi-fauna von tour la Reine (Attica). *Annales géologique des pays helléniques* 3: 7-10.
von Koenigswald G. H. R. 1972. — Ein Unterkiefer eines fossilen Hominoiden aus dem Unterpliozän Griechenlands. *Proceedings Koniklijke Nederlandse Akademie Wetenschsppen* 75: 385-394.
Wagner A. 1839. — Fossile Ueberreste von einem Affen und einigen andern Säugethieren aus Griechenland. *Abhandlungen der Bayerische Akademie der Wissenschaften* 2: 151-172.
Walker A., Teaford M. F., Martin L. & Andrews P. 1993. — A new species of *Proconsul* from the Early Miocene of Rusinga/Mfangano Islands, Kenya. *Journal of Human Evolution* 25 (1): 43-56. https://doi.org/10.1006/jhev.1993.1037
Walter R. & Aronson J. 1982. — Revisions of K/Ar ages for the Hadar hominid site, Ethiopia. *Nature* 296: 122-127. https://doi.org/10.1038/296122a0
White T. D. 1977. — New fossil hominids from Laetoli, Tanzania. *American Journal of Physical Anthropology* 46 (2): 197-230. https://doi.org/10.1002/ajpa.1330460203
White T. D. 1980. — Additional fossil hominids from Laetoli, Tanzania: 1976-1979 specimens. *American Journal of Physical Anthropology* 53 (4): 487-504. https://doi.org/10.1002/ajpa.1330530405
Xu Q., Lu Q., Pan Y., Qi G., Zhan X. & Zheng L. 1978. — The fossil mandible of *Ramapithecus lufengensis*. *Kexue Tongbao* 23: 554-556.
Zhao L., Lu Q. & Zhang W. 2008. — Age at first molar emergence in *Lufengpithecus lufengensis* and its implications for life-history evolution. *Journal of Human Evolution* 54 (2): 251e257. https://doi.org/10.1016/j.jhevol.2007.09.019

Submitted on 28 February 2023;
accepted on 6 July 2023;
published on 13 November 2023.