

New material of *Ouranopithecus macedoniensis* from late Miocene of Macedonia (Greece) and study of its dental attrition

Nouveau matériel d'*Ouranopithecus macedoniensis* du Miocène supérieur de Macédoine (Grèce) et étude de l'usure des dents

George D. Koufos^{a,*}, Louis de Bonis^b

^a *Laboratory of Geology and Palaeontology, Department of Geology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece*

^b *Laboratoire de Géobiologie, Biostratigraphie et Paléontologie Humaine, Université de Poitiers, 40, Avenue du recteur-Pineau, 76022 Poitiers cedex, France*

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Abstract

During the last five years our continued excavations in the known late Miocene mammal localities of Macedonia (Greece) provided several new specimens of the hominoid primate *Ouranopithecus macedoniensis*. This new material includes maxillary and mandibular remains and it is described and compared to the old material of *Ouranopithecus* in the present article. The material of *Ouranopithecus* from the three known localities “Ravin de la Pluie” (RPI), “Xirochori 1” (XIR) and “Nikiti 1” (NKT) includes a complete series of tooth rows representing all wearing stages. Thus, the study of the dental wear of *Ouranopithecus* upper and lower teeth is studied and compared to that of the recent hominoids *Gorilla* and *Pan*, as well as to *Australopithecus afarensis*. The latter species is well known by a series of tooth rows of different wearing stages. The canine’s attrition of *Ouranopithecus* has a more derived pattern than that of the recent hominoids (*Gorilla* and *Pan*) and less derived than *A. afarensis*. The p3 of *Ouranopithecus* has similar attrition to that of *A. afarensis*, the attrition of the molars in *Ouranopithecus*, *A. afarensis* and *Pan* follows a similar pattern, while in *Gorilla* it is different.

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Résumé

Pendant les cinq dernières années, la poursuite des fouilles dans les gisements du Vallésien (Miocène supérieur) de Macédoine a permis de mettre au jour un certain nombre de nouveaux spécimens dentaires du primate hominoïde *Ouranopithecus macedoniensis*. Ce matériel comprend des éléments de mandibules ou de maxillaires qui sont décrits et comparés aux spécimens déjà connus. Les fossiles étudiés proviennent de trois localités : le « Ravin de la Pluie » (RPI), « Xirochori 1 » (XIR), « Nikiti 1 » (NKT) et comprennent des séries dentaires présentant divers stades d'usure. Cette usure, sur les dents supérieures ou inférieures, est comparée à celle des deux hominoïdes modernes *Gorilla* et *Pan*, de même qu'à celle de l'espèce *Australopithecus afarensis* connue par de nombreux spécimens représentant différents stades d'usure. L'usure des canines d'*Ouranopithecus* présente un aspect considéré comme plus dérivé que celui des grands singes modernes mais moins que celui d'*A. afarensis*. L'usure de la p₃ d'*Ouranopithecus* rappelle celle d'*A. afarensis* et diffère de celle des grands singes tandis que sur les molaires on trouve un schéma analogue chez *O. macedoniensis*, *A. afarensis* et *Pan* distinct de celui qui est présent chez le gorille.

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Keywords: Primates; Hominoidea; Late Miocene; Teeth; Attrition

Mots clés : Primates ; Hominoidea ; Miocène supérieur ; Dents ; Usure

* Corresponding author.

E-mail address: koufos@geo.auth.gr (G.D. Koufos).

1. Introduction

The hominoid primate *Ouranopithecus macedoniensis* is known from the late Miocene of Macedonia (Greece) where it was recognized in three different localities. Two of them “Ravin de la Pluie” (RPI) and “Xirochori 1” (XIR) are located in Axios valley and the third one, “Nikiti 1” (NKT), in Chalkidiki peninsula (Fig. 1). The associated fauna suggested a late Vallesian age, MN 10 (Bonis and Koufos, 1999), while the magnetostratigraphic record proposed an age between 9.6–9.3 Ma for the Axios valley material (Sen et al., 2000). The faunal data from NKT suggests a younger age than XIR and RPI; more precisely an age between 9.3–8.7 Ma is possible for the NKT fauna (Koufos, 2000). Since 1973, when the first remains of *Ouranopithecus* were found in Axios valley, some mandibular and few maxillary remains, as well as the frontal part of the skull have been recovered (Bonis et al., 1974, 1975, 1990, 1998; Bonis and Melentis, 1985; Koufos, 1993, 1995; Koufos and Bonis, 2004). During our excavations over the last 5 years in RPI some new material has been unearthed. The new material includes complete mandibles and well-preserved maxillary and mandibular remains. All this material is described and compared to the old one in this article. As the whole material includes dentitions in various wearing stages, the wearing pat-

tern of the *Ouranopithecus* dentition is studied and compared to some extant and extinct hominids.

2. Material description

2.1. Upper tooth row with P^3-M^3 dex and P^4-M^3 sin, RPI-90 (Fig. 2a, b and Table 1)

The specimen includes the right tooth row with P^3-M^3 and the left one with P^4-M^3 ; the left P^4 is broken in its lingual part. It belongs to an adult male individual and the teeth are well preserved.

P^3 . It is elongated bucco-lingually with oval occlusal outline. The mesio-distal buccal diameter is longer than the lingual one. The mesial linear contour is slightly oblique to the sagittal plane. In the mesio-buccal corner of the tooth there is a small projection of the crown. All these features give an asymmetrical outline to the tooth. The buccal wall of the P^3 is symmetrical and convex. The paracone and protocone are quite low, but the paracone is slightly higher than the protocone. As the wear starts from the protocone, the height differences are being stronger between the paracone and protocone in the worn teeth. The mesial and distal marginal crests are low and rapidly disappear by the attrition. The transverse crest of the paracone is a



Fig. 1. Map of the Axios valley and Chalkidiki peninsula indicating the geographic position of the *Ouranopithecus* bearing mammal localities. RPI = “Ravin de la Pluie”, XIR = “Xirochori 1”, and NKT = “Nikiti 1”.

Fig. 1. Carte de la Macédoine (Grèce) indiquant les gisements fossilifères ayant livré *Ouranopithecus*. RPI = « Ravin de la Pluie », XIR = « Xirochori 1 », et NKT = « Nikiti 1 ».

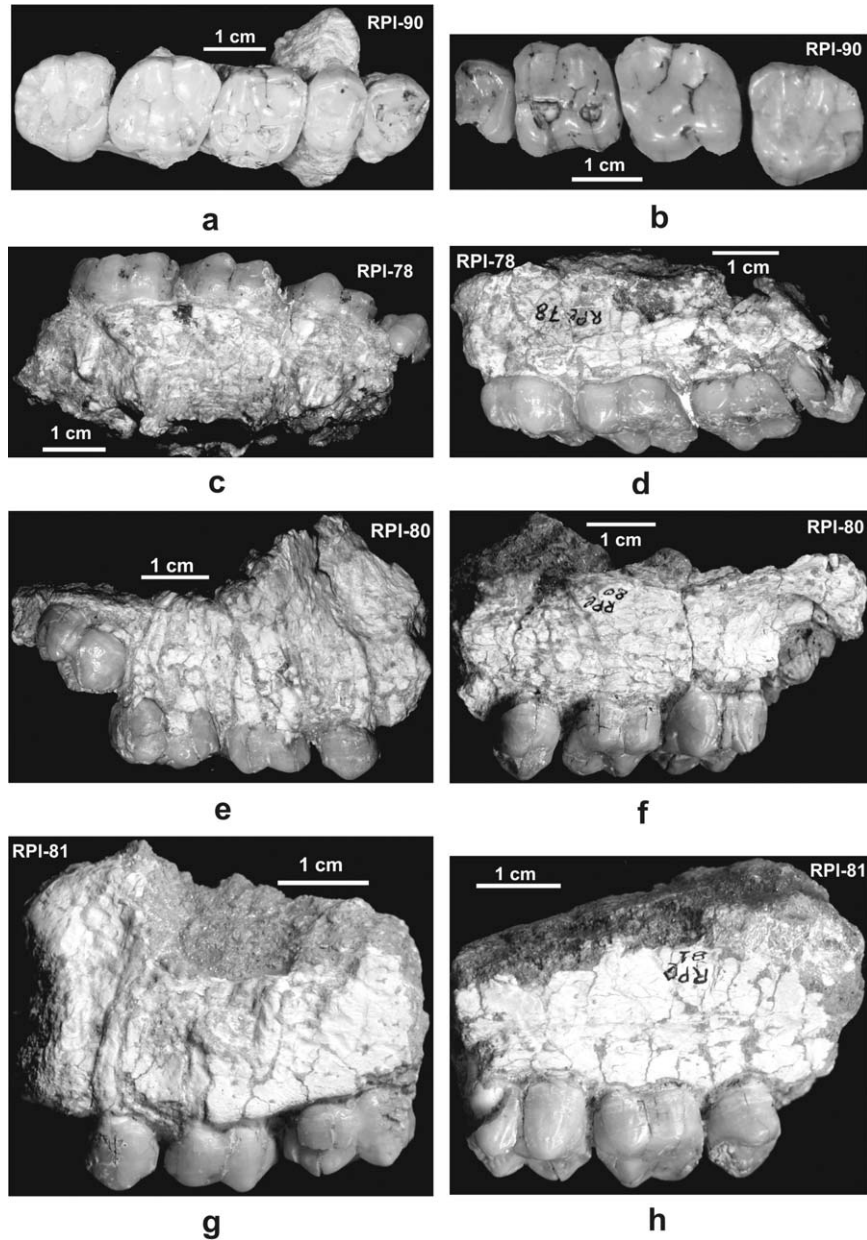


Fig. 2. *Ouranopithecus macedoniensis*, late Vallesian (MN 10), Macedonia, Greece. **a, b.** Upper tooth row with P^3 - M^3 dex and P^4 - M^3 sin RPI-90; **a.** right, and **b.** left. **c, d.** Right maxillary fragment with P^4 - M^3 , RPI-78; **c.** buccal, and **d.** lingual view. **e, f.** Right maxillary fragment with P^4 - M^3 , RPI-80; **e.** buccal, and **f.** lingual view. **g, h.** Left maxillary fragment with P^4 - M^2 , RPI-81; **g.** buccal, and **h.** lingual view.

Fig. 2. *Ouranopithecus macedoniensis*, Vallésien supérieur (MN 10), Macédoine, Grèce. **a, b.** Série dentaire supérieure avec P^3 - M^3 dex et P^4 - M^3 sin, RPI-90 ; **a.** droite, et **b.** gauche. **c, d.** Fragment de maxillaire droit avec P^4 - M^3 , RPI-78 ; **c.** vue buccale, et **d.** vue linguale. **e, f.** Fragment de maxillaire droit avec P^4 - M^3 , RPI-80 ; **e.** vue buccale, et **f.** vue linguale. **g, h.** Fragment de maxillaire gauche avec P^4 - M^2 , RPI-81 ; **g.** vue buccale, et **h.** vue linguale.

very low and swollen ridge which distinguishes a mesial faint fovea. A smaller fovea is also apparent in the distal part of the tooth. The latter is separated by a faint transverse ridge and thus a well-developed groove on the occlusal surface appears between mesial and distal fovea.

P^4 . It is similar to P^3 but more oval-shaped and symmetric. The buccal wall of the paracone is convex and symmetric while the slopes of the two crests of the paracone are similar and roughly inclined. The transverse crest of the paracone is very low and swollen. The height difference between the para-

cone and protocone is less than in P^3 . The mesial fovea is faint and smaller than the distal one. The enamel is thick.

M^1 . It is squarish, while the mesial and distal line contour is oblique to the mesio-distal axis of the tooth. Particularly, the distal line contour is oblique at its buccal part, but then it is perpendicular to the mesio-distal axis of the tooth and thus the buccal mesio-distal diameter of the tooth is smaller than the lingual one. The paracone and metacone are more or less equal-sized and they are separated by a slight groove in the buccal wall. The protocone is larger than the hypocone and

they are separated by a stronger groove on the lingual wall. There is not any trace of lingual cingulum, while a very faint one is distinguished buccally in the valley between the two cusps. There is a small talon. The enamel thickness is 2.0–2.5 mm.

M². It is larger than M¹, but of similar morphology. The talon is small and consists of two-three small cusplets. The attrition is small and there are not dentine pits.

M³. It is similar to M¹ but with larger trigon which gives a more rounded crown shape to it. The enamel is broken in the buccal half of the mesial wall. The talon is large and limited by a series of four cusplets.

2.2. Right maxillary fragment with P⁴-M³, RPI-78 (Figs. 2c,d,3 and Table 1)

It belongs to a male adult individual (Table 2). The P⁴ is broken preserving only the distal and buccal wall. The origin

Table 1
Ouranopithecus macedoniensis, late Vallesian (MN 10), Macedonia, Greece. Upper teeth measurements
Ouranopithecus macedoniensis, Vallésien supérieur (MN 10), Macédoine, Grèce. Dimensions des dents supérieures

	UPPER TEETH	RPI-78		RPI-90		RPI-80	RPI-81
		Male sin	Male dex	Male sin	Male dex	Female dex	Female Sin
I1/	M-D	–	–	–	–	–	–
	B-L	–	–	–	–	–	–
I2/	M-D	–	–	–	–	–	–
	B-L	–	–	–	–	–	–
C	M-D	–	–	–	–	–	–
	B-L	–	–	–	–	–	–
P3/	M-D	–	9.5	–	–	–	–
	B-L	–	12.2	–	–	–	–
P4/	M-D	–	8.9	9.8	9	8.7	–
	B-L	13.4	13	–	13.2	13.3	–
M1/	M-D	14.4	13.7	13.1	12.6	12.8	–
	B-L	14.9	14.4	15.1	13.9	14.0	–
M2/	M-D	15.6	15.7	15.5	15.5	14.5	–
	B-L	16.8	16.2	16.5	16.4	15.7	–
M3/	M-D	15	15.2	15.3	14.3	–	–
	B-L	16.5	16.8	16.2	16?	–	–

Tableau 2
Ouranopithecus macedoniensis, late Vallesian (MN 10), Macedonia, Greece. Mandibular measurements
Ouranopithecus macedoniensis, Vallésien supérieur (MN 10), Macédoine, Grèce. Mesures mandibulaires

MANDIBLE	RPI-89		RPI-90		RPI-80		RPI-94
	Male dex	Male sin	Female dex	Female sin	Female dex	Female sin	Male sin
Symphysial length							
Internal	–	–	40.1	–	–	–	–
External	–	–	43.0	–	–	–	–
Mandibular Height							
CBelow p3/p4	–	–	31.0	36?	–	–	35.5
Below m1/mé	41.2	42.7	30.2	32.0	30.7	–	32.6
Below m3	[38]	37.1	–	26.0	27.5	–	29
Mandibular thickness							
Below p3/p4	19.5	–	16.7	16.3	17.3	–	16.4
Below m1/m2	20.1	22.3	15.4	15.6	17.6	–	16.4
Below m3	–	25.5	–	22.4	21.5	–	20.8
Length p3-m3	–	78.0	–	63.0	[61]	[63]	59.3
Length m1-m3	–	54.1	–	43.0	[42]	[44]	40.5

of the zygomatic arch is well preserved and it seems to be quite strong, like in the known specimens of *Ouranopithecus*. It is situated above M² but it is extended backwards to the middle of M³. The M¹ has similar shape and morphology to that of RPI-90 but the talon is better developed and larger. The M^{2,3} are morphologically similar to those of RPI-90, but less worn and their enamel is wrinkled, especially in M³. There are clear accessory cusplets in the talon.

2.3. Right and left maxillary fragment with P⁴-M³ dex and P⁴-M² sin, RPI-80, 81 (Figs. 2e-h,4 and Table 1)

The two specimens possibly belong to the same individual as they were found very close to each other and they are in the same wearing stage. They belong to a young adult individual, the M³ is erupting and the teeth are little worn. In the right maxilla the anterior part of the zygomatic arch is well preserved and strong, situated above M^{1,2}. The canine fossa is well developed and deep as in the skull XIR-1 (Bonis and Koufos, 1993). The teeth have similar morphology to that described above but they are less worn. The M³ is completely unworn with wrinkled enamel. Both P⁴ are little worn keeping the wrinkled enamel.

2.4. Mandible, RPI-89 (Figs. 5a,b,6 and Tables 2 and 3)

It belongs to an adult male individual preserving i₁-m₃ sin and i₁-m₂ dex. The ascending ramus on both sides is absent, while the horizontal rami and the symphyseal area are partially missing. The mandible was found near the surface and it was broken in several pieces, arranged together. The erosion also damaged the left tooth row, while the plant roots damaged the occlusal surface of the teeth, especially that of the p₄. The horizontal ramus is strong and high with straight inferior border. The lower transverse torus is thick; in the left side the thickness is 25.3 mm. The symphysis is long and its external surface is flattened below the incisors. The rest part of the external surface of the symphysis is broken. The planum alveolare is wide and inclines roughly downwards.

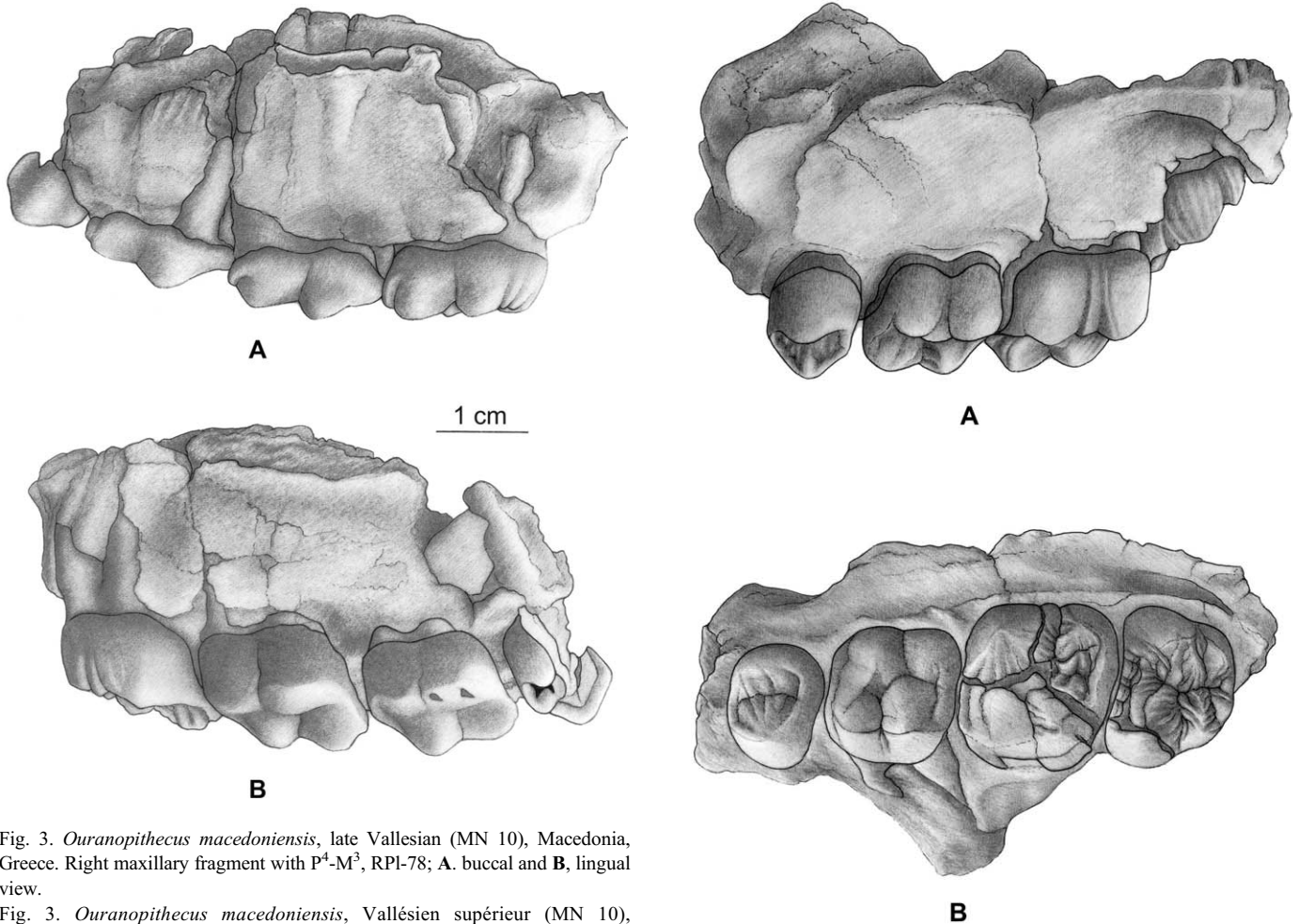


Fig. 3. *Ouranopithecus macedoniensis*, late Vallesian (MN 10), Macedonia, Greece. Right maxillary fragment with P⁴-M³, RPI-78; **A**, buccal and **B**, lingual view.

Fig. 3. *Ouranopithecus macedoniensis*, Vallésien supérieur (MN 10), Macédoine, Grèce. Portion droite de maxillaire avec P⁴-M³, RPI-78 ; **A**, vue buccale et **B**, vue linguale.

Incisors. The incisors are well preserved and spatulated. They are situated in a straight line and there is a small diastema between them and the canine. They have a strong distal cingular projection.

c. The canine is large and strong with elliptical transverse section. It has a strong and robust distal cingular projection, as well as a strong mesio-lingual and a weaker distal groove running across its height. There is not any wearing facet except on the top of the apex where the smooth enamel indicates the beginning of attrition.

p₃. Both p₃ are well preserved and they have a mesio-buccal projection. The buccal surface is somewhat convex and there is not a honing facet. There is a large buccal cuspid and a large distal fovea. The mesio-lingual cingulum is well developed and better expressed in the mesial corner of the tooth by a cingular projection. This projection is connected with the apex of the buccal cuspid by a crest. All this morphology gives the idea of the origin of an anterior fovea which is more developed and clear in *Australopithecus afarensis* (Johanson et al., 1982: Fig. 2).

p₄. The left p₄ is well preserved but the occlusal surface of the right one is strongly damaged by erosion. It is smaller and more symmetric than the p₃ with rounded occlusal aspect. It

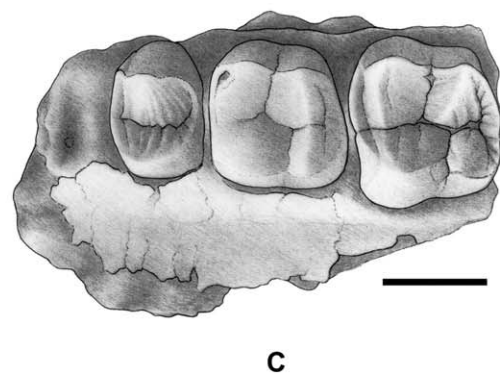


Fig. 4. *Ouranopithecus macedoniensis*, late Vallesian (MN 10), Macedonia, Greece. **A**, **B**. Right maxillary fragment with P⁴-M³, RPI-80; **A**, lingual, and **B**, occlusal view. **C**. Left maxillary fragment with P⁴-M², RPI-81, occlusal view. Fig. 4. *Ouranopithecus macedoniensis*, Vallésien supérieur (MN 10), Macédoine, Grèce. **A**, **B**. Portion droite de maxillaire avec P⁴-M³, RPI-80 ; **A**, vue linguale, et **B**, vue occlusale. **C**. Portion gauche de maxillaire avec P⁴-M², RPI-81 ; vue occlusale.

preserves two large cuspid. The lingual cuspid is slightly higher than the buccal one. There is a mesial fovea and a larger distal one which is wider lingually. No cingulum exists.

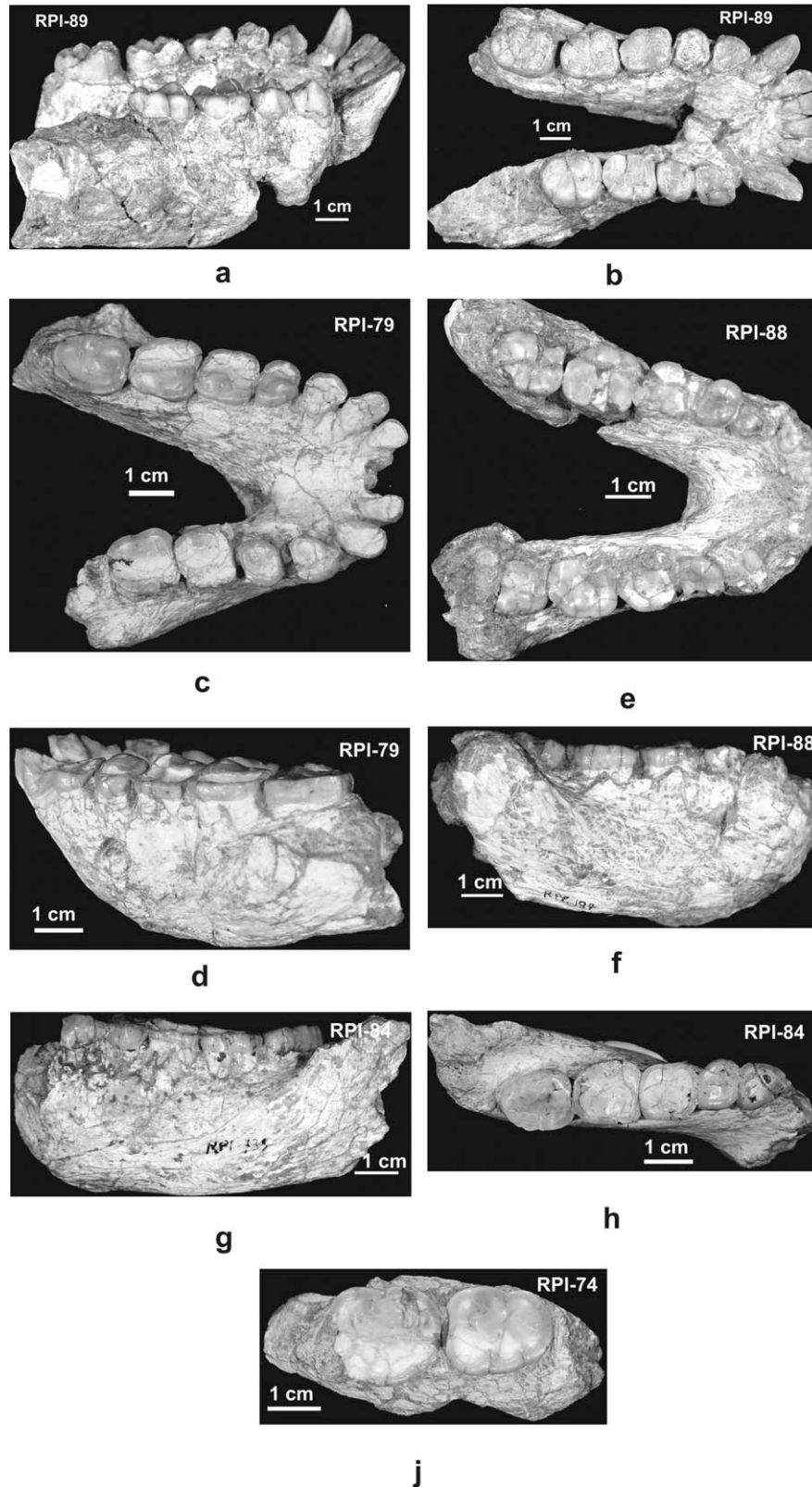


Fig. 5. *Ouranopithecus macedoniensis*, late Vallesian (MN 10), Macedonia, Greece. **a, b.** Mandible of male individual, RPI-89; **a.** left lateral, and **b.** occlusal view. **c, d.** Mandible of female individual, RPI-79; **c.** occlusal, and **d.** left lateral view. **e, f.** Mandible of female individual, RPI-88; **e.** occlusal, and **f.** right lateral view. **g, h.** Left mandibular fragment of female individual with p_3 - m_3 , RPI-84; **g.** buccal, and **h.** occlusal view. **j.** Left mandibular fragment with m_2 - m_3 sin, RPI-74; occlusal view.

Fig. 5. *Ouranopithecus macedoniensis*, Vallésien supérieur (MN 10), Macédoine, Grèce. **a, b.** Mandibule d'un individu mâle, RPI-89 ; **a.** vue latérale gauche et **b.** vue occlusale. **c, d.** Mandibule d'un individu femelle, RPI-79 ; **c.** vue occlusale et **d.** vue latérale gauche. **e, f.** Mandibule d'un individu femelle, RPI-88 ; **e.** vue occlusale et **f.** vue latérale droit. **g, h.** Fragment de mandibule d'un individu femelle, avec p_3 - m_3 , RPI-84 ; **g.** vue buccale et **h.** vue occlusale. **j.** Fragment de mandibule avec m_2 - m_3 sin, RPI-74 ; vue occlusale.

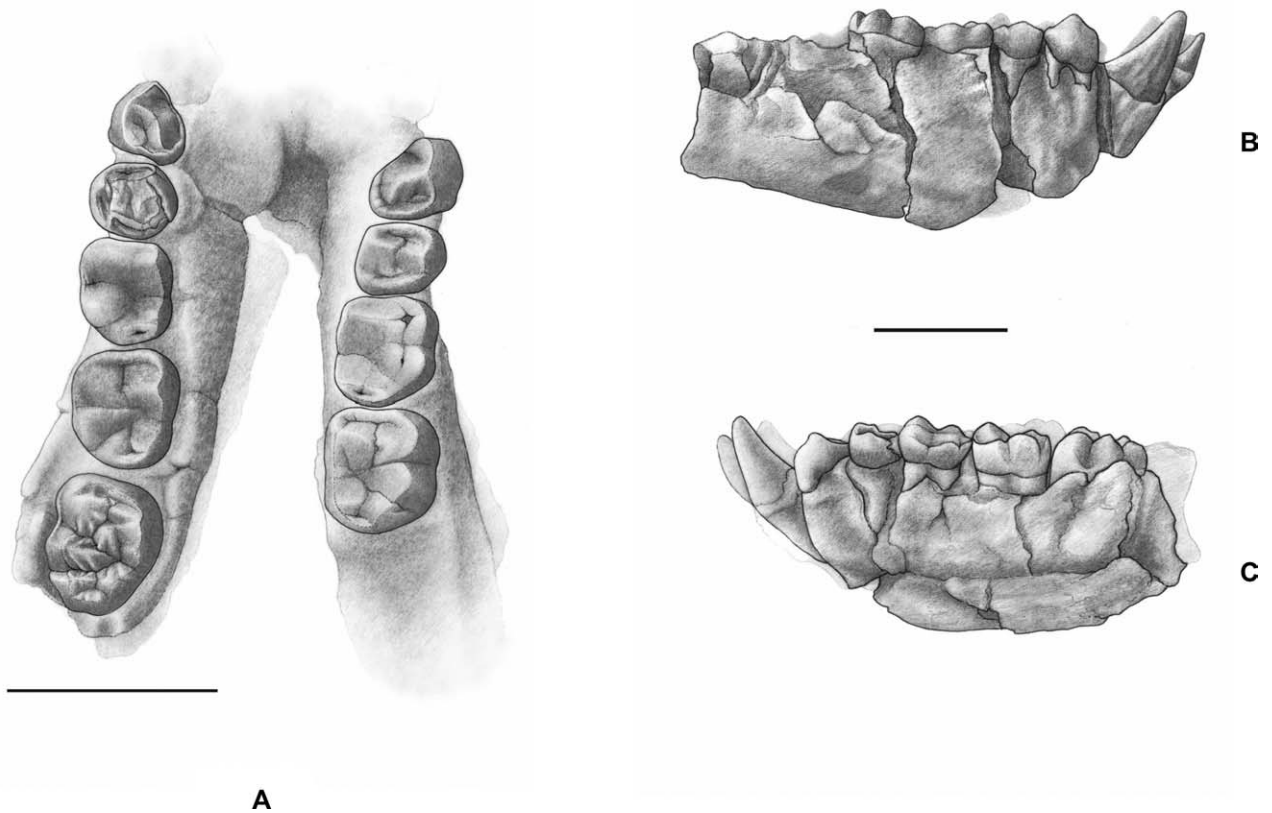


Fig. 6. *Ouranopithecus macedoniensis*, late Vallesian (MN 10), Macedonia, Greece. Mandible of male individual, RPI-89; A. Occlusal. B. Right lateral. C. Left lateral view.

Fig. 6. *Ouranopithecus macedoniensis*, Vallésien supérieur (MN 10), Macédoine, Grèce. Mandibule d'un individu mâle, RPI-89 ; A. Vue occlusale. B. Vue latérale droite. C. Vue latérale gauche.

Table 3

Ouranopithecus macedoniensis, late Vallesian (MN 10), Macedonia, Greece. Lower teeth measurements

Ouranopithecus macedoniensis, Vallésien supérieur (MN 10), Macédoine, Grèce. Dimensions des dents inférieures

LOWER		RPI-74	RPI-89		RPI-79		RPI-84	RPI-88	
TEETH		Male	Male dex	Male sin	Female Dex	Female sin	Female	Female dex	Female sin
I/1	M-D	–	9.1	9.0	–	–	–	–	–
	B-L	–	6.3	7.0	–	–	–	–	–
I/2	M-D	–	10.2	10.8	8.6	8.6	–	8.5	8.8
	B-L	–	6.3	7.0	6.0	6.3	–	5.9	6.1
Ci	M-D	–	[11.5]	11.5	7.5	7.4	–	11.0	10.7
	B-L	–	15.0	14.8	10.8	11.0	–	7.4	7.3
P/3	M-D	–	11.9	11.9	9.8	9.5	9.4	9.8	9.1
	B-L	–	12.6	11.6	10.2	10.8	9.8	10.0	9.9
P4/	M-D	–	10.5	11.4	8.5	8.6	8.5	8.1	8.5
	B-L	–	11.7	–	10.5	10.3	10.5	10.1	10.2
M/1	M-D	–	15.7	15.2	12.5	12.0	11.3	12.9	13.0
	B-L	–	14.2	13.8	13.0	12.5	11.9	12.8	12.6
M/2	M-D	–	17.5	16.9	14.2	14.2	13.7	14.5	14.1
	B-L	–	15.4	15.1	13.8	14.0	13.7	13.9	13.9
M/3	M-D	19.5	–	19.6	–	16.1	15.2	–	15.7
	B-L	16.4	–	16.6	–	13.0	13.0	–	13.1

m₁. It has low cuspids. The metaconid seems to be higher than the others. The protoconid and hypoconid are worn but the dentine is not appeared. The hypoconulid is well developed. There is not any cingulum.

m₂. It has similar morphology to m₁, but it is larger with better developed mesial fovea and hypoconulid.

m₃. It is the largest molar with similar morphology to m_{1,2}. In the disto-buccal side of the metaconid there is a small sec-

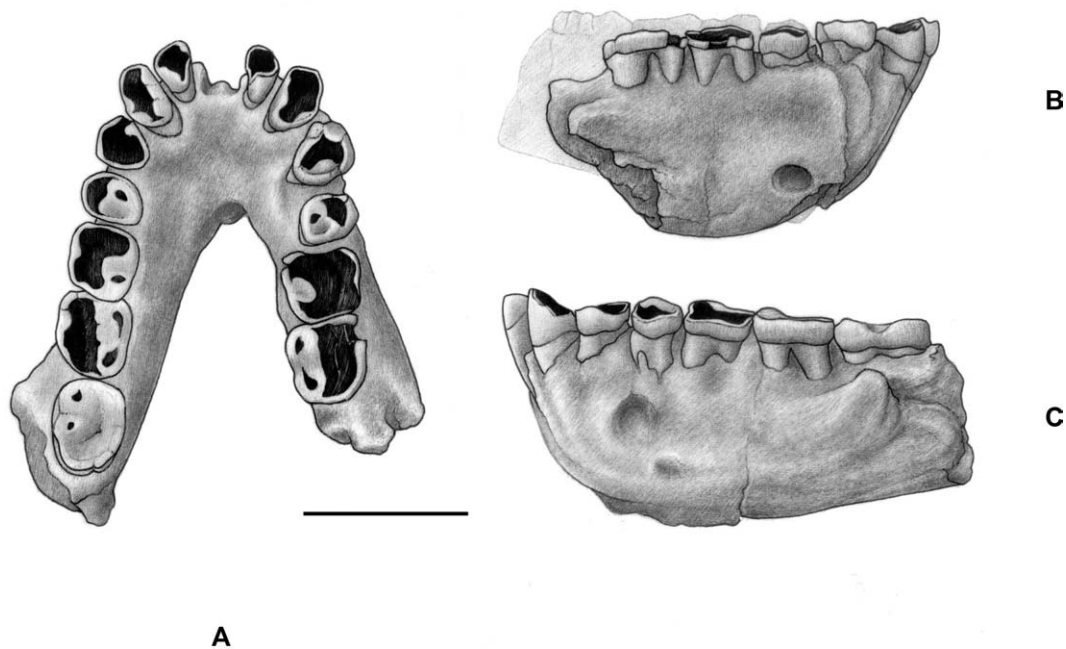


Fig. 7. *Ouranopithecus macedoniensis*, late Vallesian (MN 10), Macedonia, Greece. Mandible of female individual, RPI-79; **A**. Occlusal. **B**. Right lateral. **C**. Left lateral view.

Fig. 7. *Ouranopithecus macedoniensis*, Vallésien supérieur (MN 10), Macédoine, Grèce. Mandibule d'un individu femelle, RPI-79 ; **A**. Vue occlusale. **B**. Vue latérale droite. **C**. Vue latérale gauche.

ondary cuspid. The hypoconid is extended lingually to the mesial base outline of the entoconid. Between the metaconid and entoconid there are two small and low cusplets connecting the base of the previous cuspid. There is a small buccal cingulum restricted below the groove separating the protoconid and hypoconid.

2.5. Mandible, RPI-79 (Figs. 5c,d,7 and Tables 2 and 3)

The studied mandible with i_2 - m_3 sin and i_2 - m_2 dex belongs to an old female individual. The horizontal rami are partly preserved and the ascending rami are absent. The dentition is very worn. It was compressed from the right part and presents a slight distortion.

The horizontal rami are weaker and less high than those of the male individuals. Their inferior border is straight. There is a large mental foramen below the p_4 . In the left side there is a large hole, like a foramen situated above the mental one. It is probably the trace of a carnivore's canine. In the known specimens of *Ouranopithecus* there is only one mental foramen situated very close to the inferior border of the ramus. The inferior transverse torus is very thick; the left one is better preserved and its thickness is 23 mm. The external face of the symphysis is wide and flattened below the incisors, but from the middle of its length it is convex and inclines abruptly backwards. The planum alveolare is wide and roughly inclined downwards. The fossa genioglossa seems to be small.

i_2 . It has the typical shape of the worn ones of *Ouranopithecus*. Their upper spatulated part is totally worn. There is a

strong distal cingular projection which is partially unworn. The occlusal aspect of the crown is oval.

c. The canine is relatively small and situated with its mesio-distal axis oblique to the tooth row's axis. Both canines are worn but the right one is more worn. It has oval transverse section with distal cingular projection. In the left one a slight elongated groove is distinguished in the mesio-lingual surface of the tooth. There is a very small diastema between the canine and the incisor but no diastema between it and the p_3 .

p_3 . Both teeth are very worn having a strong mesio-buccal projection. The occlusal surface is elliptical.

p_4 . It is more symmetrical with oval occlusal contour. The buccal half of the tooth is completely worn and there is a semi-lunar dentine pit. The lingual cuspid is worn and it has a round dentine pit. The distal fovea is still preserved unworn in the disto-lingual part of the occlusal surface.

m_1 . The dentine appears in the occlusal surface of the tooth except of a small enamel islet, which remained in the lingual distal part of the tooth. The enamel is well preserved all around the worn left tooth but in the right one is broken mesially and buccally.

m_2 . Both m_2 are well preserved and extremely worn. In the buccal half of the tooth the dentine totally appears and preserves a deep mesio-distal wearing facet. The metaconid and entoconid are worn and the dentine pits are triangular-shaped. The enamel is thick in both m_1 and m_2 but it is less thick than in the males. The enamel thickness varies from 1.2–1.6 mm.

m_3 . Only the left one is preserved and it is moderately worn. The occlusal surface is almost flattened due to the advanced attrition. Nevertheless, the main cuspid are distinguished, as

well as the large hypoconulid giving a more triangular shape to the tooth.

2.6. Mandible, RPI-88 (Fig. 5e, f and Tables 2 and 3)

It is possibly a female individual with p_3 - m_3 dex and sin. The dentition is badly preserved and the teeth are cracked in several small pieces, some of which were absent. These damages possibly occurred post-mortem by weathering or during the fossilization. The anterior dentition is absent and only the roots and a small piece of the left canine are present. The left horizontal ramus is broken in its inferior border but the right one is well preserved. It is not high, with straight inferior border and thick lower transverse torus with a thickness of 23.5 mm. The external face of the symphysis is flattened below the incisors but then it is being convex, inclined abruptly backwards. The planum alveolare is wide and inclines roughly downwards. The fossa genioglossa is large and it is situated near the base of the symphysis.

p₃. Both are badly preserved and cannot be described.

p₄. The left p_4 is well preserved and worn. The buccal cuspid is worn and there is a small semilunar dentine pit in its position. The lingual cuspid is still unworn and somewhat high. The distal fovea is large and well preserved.

m₁. Both are strongly broken, but the buccal half of the right one is better preserved. There are two more or less rounded and connected dentine pits corresponding to the protoconid and hypoconid. The last dentine pit is connected with a distal one corresponding to the hypoconulid. The rest part of the tooth keeps the enamel. The enamel is relatively thick, 1.8–2.0 mm.

m₂. The left m_2 is cracked and broken in its lingual part, but the right one is more complete. The tooth is little worn. There is only a very small dentine pit in the protoconid corresponding to the beginning of its wearing facet. It has four main cuspids and a large hypoconulid. No cingulum is present.

m₃. The right one is strongly distorted while the left one is better preserved, missing several parts. The shape is triangular and besides the main cuspids and the hypoconulid seems to have secondary cusplets between the protoconid and metaconid, as well as between the entoconid and hypoconulid. A very slight buccal cingulum is developed in the groove distinguishing the protoconid and hypoconid.

2.7. Right mandibular fragment with p_3 - m_3 dex, RPI-84 (Fig. 5g, h and Tables 2 and 3)

The specimen preserves the right horizontal ramus of a female individual with the posterior dentition. The ramus is well preserved and the teeth are worn but less than in RPI-79. The ramus is relatively high but less than in the male individuals. The inferior border of the ramus is straight, while there is a small mental foramen below p_4 and near the inferior border of the ramus. The lower transverse torus has a thickness of 21 mm.

p₃: It is worn with well expressed mesio-buccal projection. The dentine appears in the projection, as well as in the mesio-lingual part of the occlusal surface. The enamel of the posterior fovea is still preserved but it is flattened.

p₄: It is worn but the enamel is preserved in its occlusal surface. There is a small dentine pit in the lingual cuspid. The buccal cuspid is totally worn and there is a large round dentine pit in its position.

m₁: It is very worn with a deep dentine pit which covers the mesial and the buccal part of the tooth. There is an enamel islet in the middle of the lingual wall and another smaller one in the disto-lingual part of the tooth. In the position of the entoconid there is a small round dentine pit. The enamel thickness is 1.1–1.7 mm.

m₂: The tooth is worn but it is clear that it has the main cuspids and a strong hypoconulid. The protoconid and hypoconid are totally worn and transformed to two connected rounded and deep dentine pits. There is an elongated dentine pit in the mesio-lingual corner of the tooth representing the beginning of its appearance in the metaconid. There is also another small dentine pit in the disto-buccal corner of the tooth.

m₃: It is larger than the other molars and less worn, having the typical shape and morphology of *Ouranopithecus*. There is a weak buccal cingulum restricted in the mesial half of the buccal line contour of the tooth, consisted of very small cusplets.

2.8. Left mandibular fragment with m_2 - m_3 sin, RPI-74 (Fig. 5j and Table 3)

It is a piece of the horizontal mandibular ramus with m_2 and m_3 . It belongs to a very old ?male individual. The m_2 is cracked post-mortem and it is very deformed. The protoconid and hypoconid are totally worn and their dentine pits are connected in a deep wearing facet covering more than the half of the transverse diameter of the tooth. There is an enamel islet in the middle of the lingual wall of the tooth. The enamel thickness is 2.1–2.3 mm. The m_3 has the morphology given above in the description of the rest specimens. There is a deep semi-circular dentine pit in the protoconid's position and another smaller and rounded in the hypoconid's one. The two dentine pits are connected at the level of the buccal groove distinguishing them. There is also a very small, rounded dentine pit in the hypoconulid's position which is in touch with the above mentioned ones. The rest occlusal surface is still covered by the enamel which thickness is 2.4–2.7 mm.

3. Wearing patterns of *Ouranopithecus* teeth

The study of the wearing patterns of *Ouranopithecus* dentition is based to the material collected from the locality Ravin de la Pluie (the majority of the material), as well as to the skull from Xirochori and the maxilla and mandible from Nikiti. The study of the wearing patterns was made separately for males and females but we did not recognize any differences and thus the description is given for both males and females.

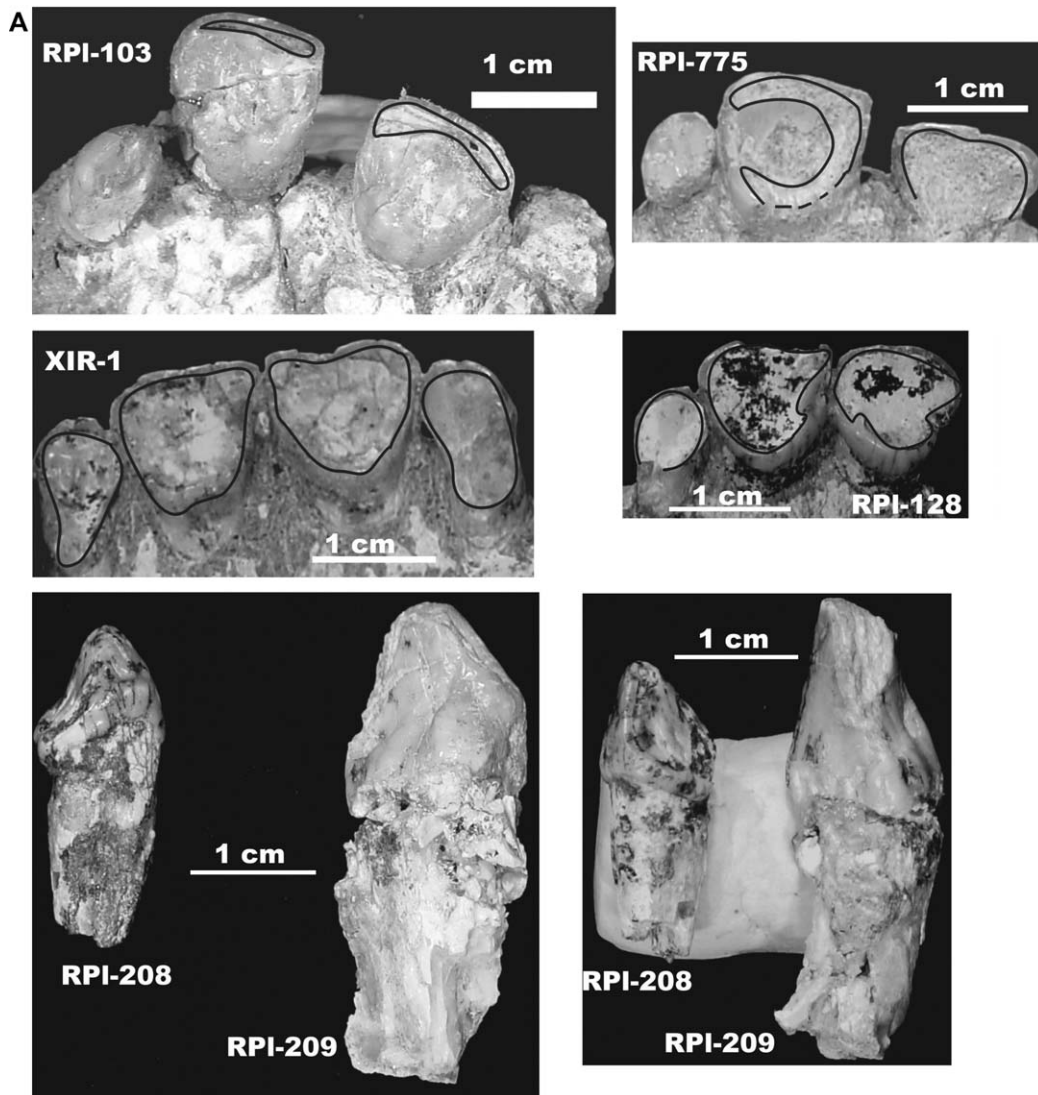


Fig. 8. Upper tooth rows of *Ouranopithecus macedoniensis* in various wearing stages. The lines indicate the borders of the wearing facets in the various teeth. The number of specimens are given in each figure.

Fig. 8. Séries dentaires supérieures d'*Ouranopithecus macedoniensis* présentant des stades d'usure variés. Les traits indiquent les bords des facettes d'usure sur chaque dent. Les nombres de spécimens sont indiqués sur chaque figure.

3.1. Upper dentition (Fig. 8)

In the little worn I^1 (RPI-103) there is a dentine zone across the upper border of the tooth and the attrition begins from its mesio-lingual corner, where the dentine zone is wider. The distal surface in the unworn or little worn I^1 is totally covered by enamel and three distal grooves are running mesio-distally. Its enamel is wrinkled, but it is gradually smoothed by the attrition. The attrition of the distal surface of the I^1 seems to begin from the middle where a very small dentine pit can be distinguished (RPI-103). In the worn I^1 the height decreases and a semilunar dentine pit appears (RPI-775). The enamel is smoothed, the grooves disappear and the attrition is directed from the mesio-lingual to the mesio-buccal wall. This is clear in the I^1 of RPI-775, where some enamel islets are preserved in its mesio-buccal corner. In the very worn teeth (RPI-128, XIR-1) the occlusal surface lacks completely the enamel. The I^1 of

RPI-128 is slightly less worn than that of XIR-1 and the traces of the buccal and lingual groove are distinguished in the peripheral enamel. The occlusal surface has triangular shape with the distal border being rounded. In the more worn I^1 of XIR-1 the occlusal surface has not enamel and its shape is more circular distally. The height of the mesial wall is reduced and in the last stages of wear all crown disappears (XIR-1).

The I^2 has a clear basal cingulum in the distal and lingual border. Its lingual wall is elevated and the attrition begins from the apex of this part (RPI-103). In the more worn teeth (RPI-775) the height of the I^2 decreases and the enamel of the occlusal surface is smoothed, but it is still possible to distinguish the grooves on its distal surface. It is worth mentioning that the grade of the attrition is higher in I^1 than in I^2 . In RPI-775 the I^1 is in an advanced stage of wear and the enamel of the occlusal surface is restricted in the mesio-buccal corner. On the contrary, in I^2 only its height decreases and there is no

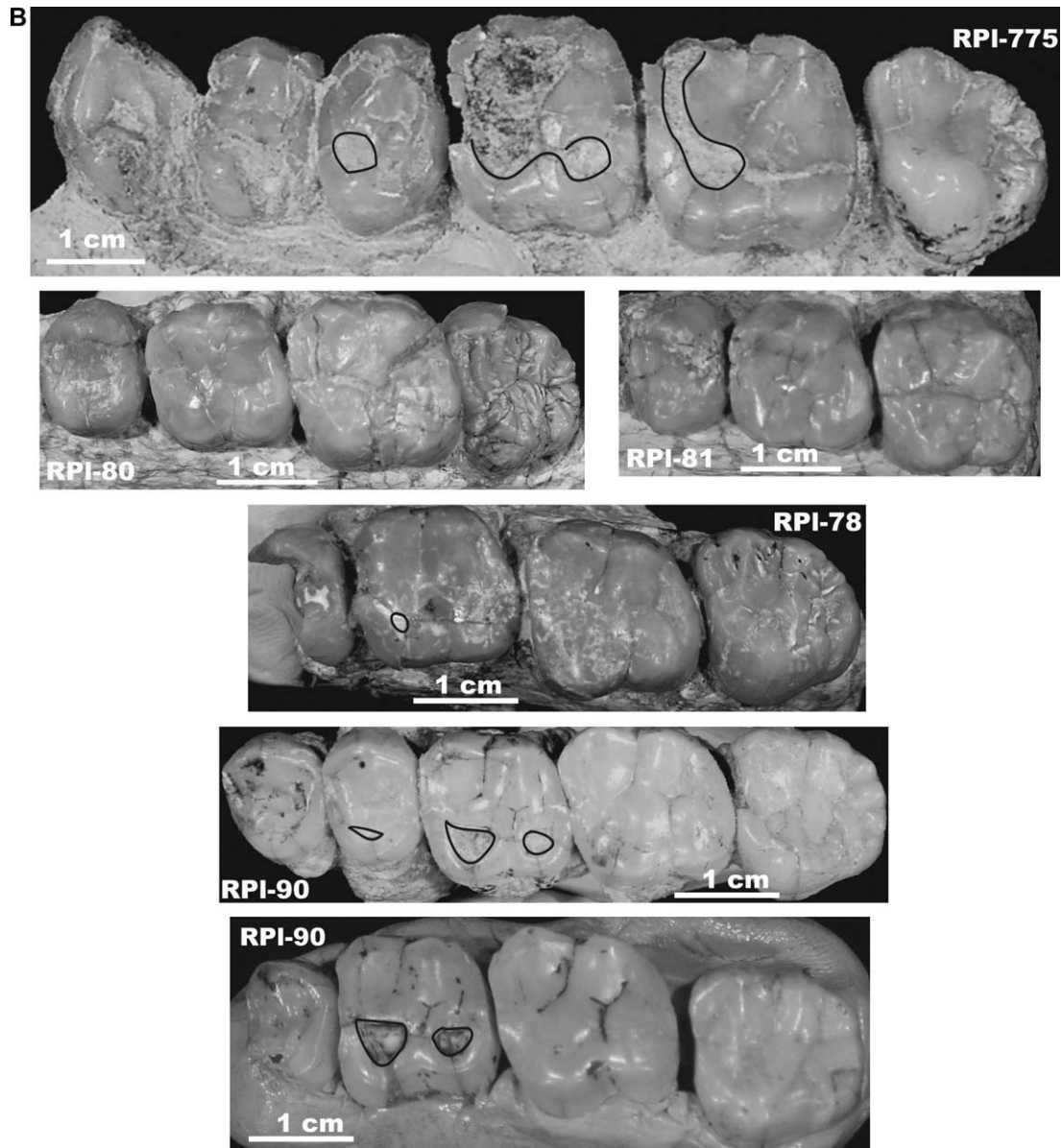


Fig. 8. (continued)

dentine pit on its occlusal surface. This is due to the remarkably smaller size of I^2 and thus its attrition begins quite later than in I^1 . In the more worn I^2 the occlusal surface has rounded shape (RPI-128) but as the wear extends to the distal cingular projection it becomes elliptical (XIR-1).

The two isolated canines RPI-208, 209 and that of the maxilla RPI-775 are little worn. The attrition begins from the mesial surface of the upper canine which is in functional contact with the distal surface of the lower canine. The mesial groove of the upper canine is preserved with its lingual border slightly worn. The tip of the upper canine is in functional contact with the distal cingular projection of the lower canine and thus its apex begins to wear. The distal surface of the upper canine is in functional contact with the protoconid's apex of the p_3 and thus a vertical wearing facet is developed. The protoconid's apex stops in the distal cingular projection of the upper canine

and a horizontal wearing facet is developed; this feature is clear in the canine of RPI-128 and XIR-1. This functional contact of the C^s with the p_3 is probably the result of the more symmetrical and rounded morphology of the latter tooth. The p_3 of *Ouranopithecus* lacks the mesial elongation of the protoconid which is in contact with the C^s , providing the honing facet of the p_3 in most of the anthropoids. In the female NKT-89 the vertical wearing facet is well developed, but although the tooth row is more worn than RPI-128 the horizontal wearing facet is not so clear. In the same wearing stage, the male canine of RPI-128 presents a wearing facet in both borders of the mesial groove which is reduced in size by the increasing of the attrition. In the more worn female canine of NKT-89 the mesial groove of the upper canine has unworn borders. All these suggest that the grade of attrition of the upper canine is higher in males than in females of *Ouranopithecus*. But, as the male ca-

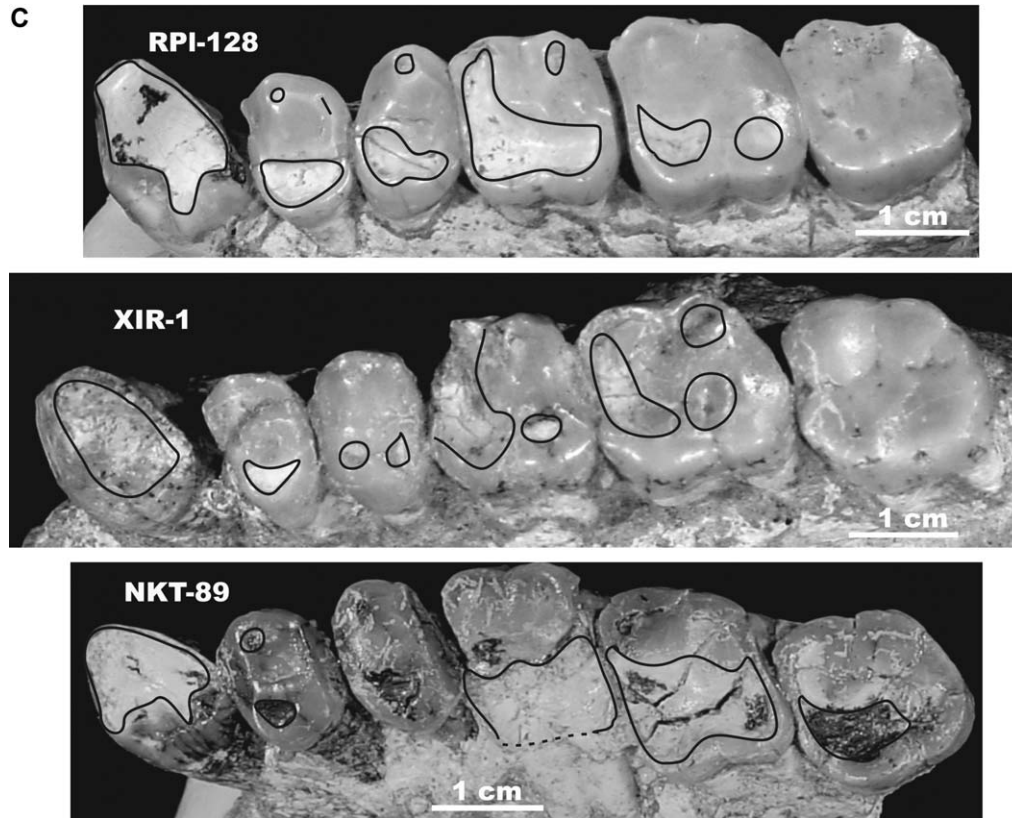


Fig. 8. (continued)

nines are larger than the female ones they still remain large even in the old individuals. In the very worn canine of the skull XIR-1 there is a large mesial wearing facet and the mesial groove is restricted in a small dot situated in the middle of the facet.

It is worth mentioning that in many cases the canines are broken during the life of the animal. In RPI-128 the left canine is broken and only its root exists. It seems that it was broken ante-mortem as a slight wear can be distinguished in the root. In RPI-775 the right canine is also broken, but this is possibly due either to water transportation or fossilization. On the contrary, the canines exist in the available mandibles. Some small post-mortem damages can be recognized only in two cases (RPI-76 56), but the canine was not broken. In fact the upper canines are larger than the lower ones and as they are used for the confronting of their enemies or digging to find roots and bulbs, they were possibly damaged more often.

In the P^3 the attrition begins from the apex and the upper mesial surface of the paracone where a small dentine pit appears. The mesial, medial and distal fovea are still well distinguished, while the enamel is smoothed (RPI-90, 775). In the more worn P^3 (RPI-128, XIR-1) a large wearing facet covers the lingual half of the tooth. In the paracone there are two small dentine pits. A slight dentine zone between them and across the distal border of the tooth, tends to connect them each other, as well as with the lingual facet. The female dentition of NKT-89 is in a more advanced wearing stage than the male RPI-128 (the M^3 of NKT-89 is worn in its lingual half, while in RPI-

128 the occlusal surface of M^3 is still covered by enamel). Although NKT-89 has higher attrition, its P^3 is less worn than that of RPI-128. The two maxillae are from different localities; the distance between them is ~120 km, but the fauna and the age from both localities are not very different (Koufos, 2000). The difference in the attrition of P^3 indicates that it is stronger in males than in females. This is possibly due to the larger size of the canines in males, which provides a different functional contact.

The unworn or little worn P^4 (RPI-80, 81) has wrinkled enamel, while the mesial and distal fovea are well distinguished. In these two maxillary fragments the attrition of P^4 seems to begin from the apex of both cusps being rounded. In the little worn P^4 of RPI-90 the paracone has worn mesial and distal border, while a small dentine pit appears in the protocone. The occlusal enamel is smoothed but the mesial and distal fovea is still distinguished. The protocone's pit enlarges (RPI-775, XIR-1) and in the more worn P^4 a small dentine pit appears in the paracone (RPI-128, NKT 89).

The little worn M^1 has partially wrinkled enamel but the majority of the occlusal enamel is smooth (RPI-78, 80, 81). The cusps begin to wear and obtain a rounded apex, while the valleys between them are flattened. The wear begins from the mesial cusps getting a dentine pit at their center (RPI-90). The protocone's pit is larger and possibly the attrition begins from this cusp (RPI-90). As the wear increases the dentine pits of the protocone and hypocone are connected (RPI-128, 775) and in the more worn teeth the lingual half of the tooth is a

large wearing facet (NKT-89). In this wearing stage the paracone and metacone have a very small dentine pit in their apex (NKT-89, XIR-1). In the more worn M^1 of RPI-128 the protocone and the paracone pit are connected through the worn mesial fovea. The occlusal enamel is restricted in the disto-buccal corner of the tooth. This pattern indicates that the attrition of M^1 begins from the protocone and it is directed to the hypocone. Then it continues from the protocone to the paracone across to the mesial border of the tooth, as well as from the protocone to the metacone diagonally. In XIR-1 the left M^1 is broken in its mesio-buccal corner ante-mortem. Thus, the attrition of both M^1 follows a slightly different pattern with an early appearance of the paracone and metacone dentine pits.

The little worn M^2 has wrinkled enamel (RPI-78, 80, 81) which is gradually smoothed by the attrition. The wear is stronger in the lingual cusps where the smoothness of the enamel is stronger. In the more worn M^2 of RPI-90 the enamel of the occlusal surface is smooth and the valley's depth between the cusps is strongly reduced. There is not any dentine pit. The worn M^2 of RPI-128 has a strong dentine pit in the protocone, which is enlarged distally to be connected with the hypocone and buccally across the mesial border to be connected with the paracone. The M^2 of XIR-1 is more worn and in the right tooth there are small dentine pits in the center of the protocone and hypocone. Another elongated dentine pit begins from the paracone and is extended across the mesial border of the tooth. Finally, in the very worn female M^2 of NKT-89 the lingual dentine pits are connected and form a large wearing facet covering the lingual half of the tooth. In the center of the paracone and metacone there is a small and rounded dentine pit.

In the left M^2 of XIR-1 the attrition is quite different. There is a deep dentine pit across the mesial border, which is deeper in the center indicating that something very acute was in contact with it. The enamel in the center of the protocone is crushed suggesting an irregular condition (Fig. 9). Behind this enamel crushing there is a hole in the enamel indicating again the action of something hard and acute. A similar hole is also present in the buccal wall of the metacone, while the paracone remains high. This pattern is different to that of RPI-128.

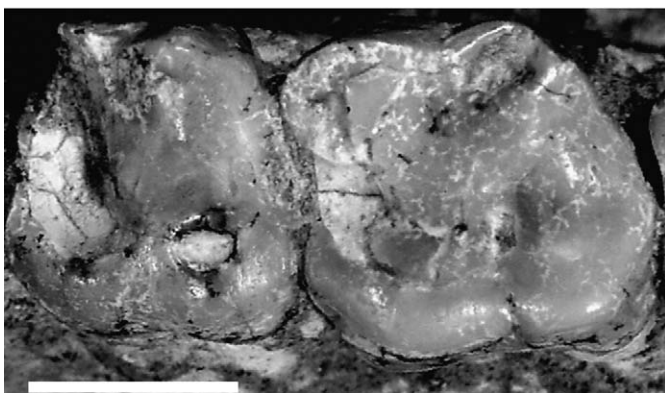


Fig. 9. The left M^1 and M^2 of the skull XIR-1 with some ante-mortem damages, which provided a different wearing pattern.

Fig. 9. M^1 et M^2 gauches du crâne XIR-1 présentant des cassures ante-mortem qui déterminent des figures d'usure particulières.

The different attrition pattern in the M^1 and M^2 of XIR-1, and the fact that the left M^1 was broken ante-mortem are evidences that the tooth row of the animal was damaged during its life. Maybe, as it was crushing something hard (nuts, roots, bulbs) or during the chewing process, a small pebble broke some teeth (M^1 , M^2 and m_1 , m_2). After that the functional contact of the upper and lower tooth row changed and consequently, the normal wearing pattern of the teeth. The holes on the occlusal surface of the M^2 indicate that either the lower m_2 had some acute parts which made these holes, or something hard made these holes during chewing. The enamel breakages in the occlusal surface provide another indication that it was damaged either by something very hard as the animal was chewing or as it was trying to break a hard nut.

The unworn or little worn M^3 has wrinkled enamel with 3–4 accessory distal cusps (RPI-78, 80, 775). The attrition smoothens the enamel, decreases the height of the cusps and flattens the occlusal surface (RPI-90, 128). In the worn M^3 of XIR-1 and RPI-128 the occlusal surface is flattened but it is still covered by enamel without dentine pits. In the very worn M^3 of NKT-89 the lingual half of the tooth is totally worn and there is a small dentine pit in the position of the paracone and metacone. All these indicate that the attrition begins from the protocone and then the dentine pits of the protocone and hypocone are connected each other. As the attrition increases the protocone's pit is directed across the mesial border of the tooth to connect with that of the paracone (NKT-89).

3.2. Lower dentition (Fig. 10)

In the little worn i_1 the dentine appears in the upper border of the tooth as a narrow wearing facet and the wear seems to begin from the lingual corner of the tooth (RPI-89, 54, 55). The wearing facet widens distally as the tooth's height decreases and the attrition is extended to the distal surface of the tooth (RPI-85, 75). The wearing facet is being gradually wider and when the attrition includes the distal cingular projection of the i_1 it becomes oval (RPI-79, NKT-21). In the very worn teeth (RPI-56) the enamel disappears and there is only the root which has an elliptical transverse section.

The available material includes a more or less complete series of i_2 allowing better study of the attrition pattern. The upper border of the unworn i_2 (RPI-83) is sharp with straight outline which slopes buccally without any wearing facet. The attrition begins from the lingual corner of the upper border and a narrow dentine zone appeared in the upper border (RPI-89, 54, 55), which is gradually extended to the slope. Consequently, the height of the tooth decreases and the wearing facet has a more triangular shape (RPI-85, 75). In the more worn teeth (RPI-196, 79, NKT-21) the wearing facet includes gradually the distal cingular projection of the tooth being more or less oval with its mesial part wider and more rounded. Finally, in the very worn teeth (RPI-56) the wearing facet has an elliptical outline with a narrow enamel zone all around the occlusal surface.

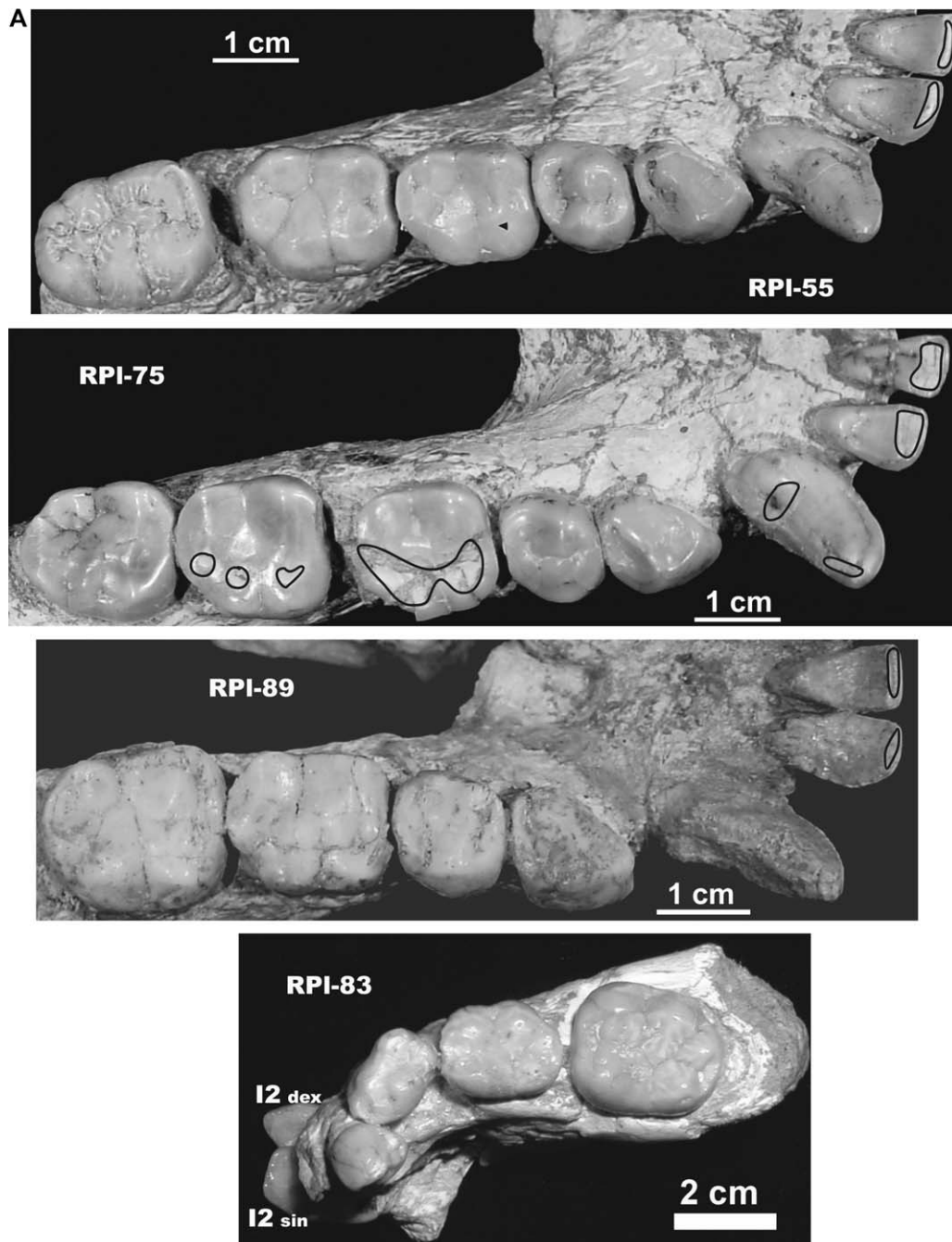


Fig. 10. Lower tooth rows of *Ouranopithecus macedoniensis* in various wearing stages. The lines indicate the borders of the wearing facets in the various teeth. The number of specimens are given in each figure.

Fig. 10. Séries dentaires inférieures d'*Ouranopithecus macedoniensis* à différents degrés d'usure. Les traits indiquent les bords des facettes d'usure sur chaque dent. Les nombres de spécimens sont indiqués sur chaque figure.

In the unworn or little worn canines (RPI-89, 54, 55) the apex is acute and the attrition begins from this point which is being rounded. The attrition of the lower canine is the result of the contact of its distal wall with the mesial wall of the upper canine. In the more worn canine of RPI-75 its height decreases and a small wearing facet begins to develop in the disto-buccal area of the tooth. The wearing facet begins from the distal cingular projection of the c_1 where the tip of the upper canine stops and it is extended upwards. In the more worn teeth

(RPI-76, 196) the wearing facet widens and covers all the tooth's height. Although the canine of RPI-76 is broken in the apex and in the distal base, we can distinguish an increase in the size of the wearing facet. In RPI-196 the attrition is more advanced and the wearing facet covers all the distal wall of the canine. In this stage the lingual border of the wearing facet is very close to the mesiolingual groove of the canine. In the canine of RPI-56 which is slightly more worn than that of RPI-196 the wearing facet is wider touching the mesiolingual

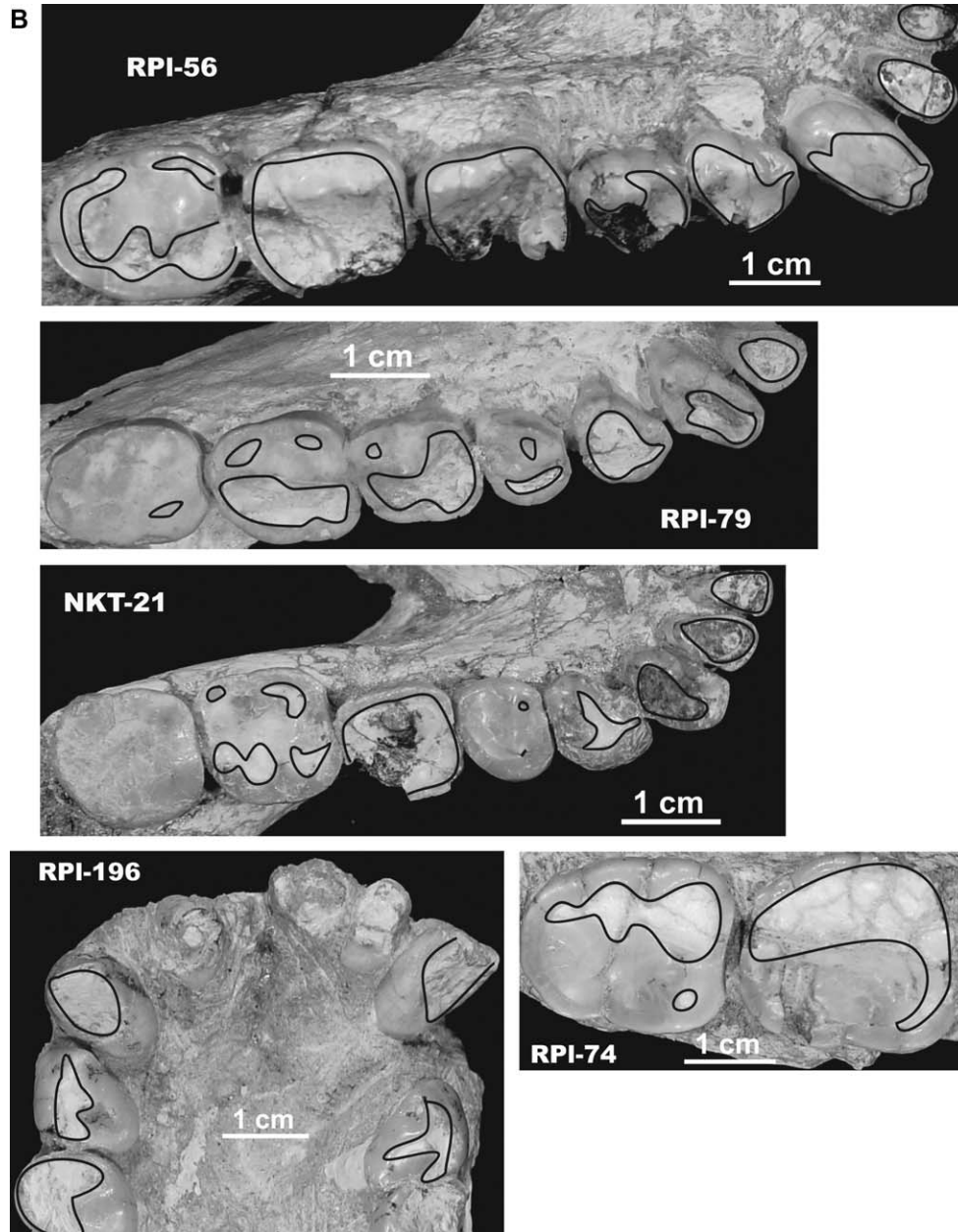


Fig. 10. (continued)

groove, while the basal part of the facet is being deeper. In the very worn canines (NKT-21, RPI-79) the wearing facet is double, one horizontal facet covering the mesio-buccal basal part of the tooth and another vertical one which corresponds to the distal wall of the c_1 .

Comparatively to the female mandible RPI-79, the male RPI-56 is less worn, as the m_3 of the previous one is almost unworn, while that of RPI-56 is worn in its buccal half. Thus, it is expected RPI-56 to have more worn canine than RPI-79. On the contrary the horizontal wearing facet of the canine in RPI-56 just begins to develop, while in RPI-79 it is quite large. This indicates that the grade of attrition in the canines is lower in males than in females. In fact, this is due to the larger size of the male canines.

The unworn p_3 (RPI-54, 55, 89) has a high buccal cuspid from the apex of which begins the attrition. No honing facet exists. As the wear increases (RPI-75, 85), the height of the buccal cuspid decreases and the enamel of the occlusal surface is smoothed, while the anterior and posterior fovea decrease in size. The dentine appears in the apex of the buccal cuspid and it forms a lambda-shaped wearing facet (right p_3 of RPI-196). One branch is extending from the apex to the base of the disto-buccal wall of the tooth, while the other is narrower and it is extending across the lingual crest of the buccal cuspid. A third wearing branch begins also from the apex and it is directed across the mesial crest of the buccal cuspid. The wearing facet covers the whole occlusal surface of the very worn teeth and it has elliptical shape (RPI-56, 79). However, the anterior fovea

is still preserved, as well as a small enamel part in the mesial wall of the tooth (RPI-56). The mesio-lingual part with the fovea remains unworn even in the very worn p_3 . The very worn stage is better preserved in NKT-21. The tip of the buccal cuspid is completely worn and the wearing facet is star-like. The three branches are following the mesial, lingual and distal crests of the buccal cuspid. The study of the p_3 attrition indicates that it begins from the distal wall, gradually extends lingually and later mesially.

In the unworn or little worn p_4 (RPI-54, 55, 85, 89) the two cuspid are more or less similar in size and there is a large distal fovea. In the more advanced stage of wear the height of the two cuspid decreases, the decreasing being stronger in the buccal cuspid. The mesial border of the mesial fovea and the distal border of the distal fovea are being worn and the enamel of the occlusal surface is smoothed (RPI-85, 89). In the worn teeth the lingual cuspid has a small dentine pit (RPI-84, 88), which is gradually extended distally (RPI-76). The mesial fovea is totally worn and it is not distinguished. The enamel at its position is flat, while the distal one is small but still distinguishable. The attrition of the occlusal enamel continues to the lingual part of the tooth more rapidly mesially than distally and the wearing facet has semilunar shape (RPI-196). The enamel remains in the disto-lingual corner of the tooth, while the disto-lingual part of the distal fovea is still distinguishable (RPI-196). In the very worn p_4 all the occlusal surface is worn except of a small enamel islet in its disto-lingual corner (RPI-56). At this stage the height of the tooth is remarkably reduced and the enamel is near its base.

The unworn m_1 (RPI-83, 54) has wrinkled enamel in the cuspid, which is being smoothed by the attrition. The wear is stronger in the buccal part of the tooth, the protoconid and hypoconid being the first worn cuspid. Thus, in the little worn teeth (RPI-89, 55) a small dentine pit appears in the apex of these two cuspid. As the wear is going on, the protoconid's and hypoconid's pits enlarge and they are connected each other, as well as with the hypoconulid's one (RPI-75). A small enamel projection is still present in the buccal groove distinguishing the two lobes of m_1 . The next wearing stage is better preserved in the m_1 of RPI-79, 84 and 88. The height of the metaconid is reduced and a dentine pit appears in the mesio-lingual corner of the tooth, connected with that of the protoconid. At the same time a dentine pit appears in the position of the entoconid. The latter extends buccally across the distal border of the tooth in order to connect with that of the hypoconulid. In the extremely worn m_1 (RPI-56, NKT-21) the enamel of the occlusal surface disappears, while in the buccal part of the tooth the wear extends to the root. In RPI-79 the enamel of the occlusal surface is restricted in the disto-lingual part of the tooth. In the right m_1 of RPI-56 and NKT-21 there is a small enamel islet in the middle of the lingual wall. The right m_1 of NKT-21 is completely worn and the attrition is deep extended to the root. It is significant that even in this very advanced wearing stage there is some enamel in the lingual wall of the tooth.

In the little worn m_2 (RPI-54, 55, 89) the valleys between the cuspid are deep, but the enamel in the surface of the cus-

pids is smoothed. The attrition decreases the height of the cuspid, especially in the protoconid and hypoconid. The first dentine pits appeared in the center of these two cuspid and in the center of the hypoconulid (RPI-75). The development of the wearing facet begins from the protoconid and it is directed backwards. In the m_2 of RPI-88 the dentine pit of the protoconid is clear, that of the hypoconid is just distinguished, while that of the hypoconulid is still covered by enamel. In the more worn m_2 (RPI-76, 84) a dentine pit appears in the metaconid and after that the attrition pattern follows that of m_1 described above.

The unworn m_3 (RPI-55, 89) has occlusal surface with deep valleys and wrinkled enamel, while in its distal margin there are some accessory cuspid. In the little worn m_3 of RPI-75 the cuspid's height is reduced, especially that of the buccal ones, while the occlusal enamel is smoothed. The lingual valley between metaconid and entoconid is still deep, while in the more worn female m_3 (RPI-84) the valley is flattened. The mesial fovea disappears in this wearing stage. In the worn m_3 the occlusal surface is flattened (RPI-79) and a small dentine pit appears in the center of the protoconid, while a trace of a pit is distinguished in the center of the hypoconid. These two dentine pits are gradually enlarged by the attrition and connected each other (RPI-76). In the more worn m_3 a dentine pit appears in the position of the hypoconulid which is also connected with the others (RPI-74). In the very worn m_3 of RPI-56 the buccal wearing facet enlarges, while a dentine pit appears in the metaconid and entoconid. The metaconid's pit extends distally to the entoconid and mesially to the protoconid.

4. Comparison of the wearing patterns with other hominoids

The wearing patterns of *Ouranopithecus* will be compared to the extant hominoids *Gorilla* and *Pan* which have more close relationships and similarities to *Ouranopithecus*. A comparison will be also given with the wearing patterns of *Australopithecus afarensis* from Hadar, as *Ouranopithecus* has close relationships to it and there is a complete series of its dentitions allowing the comparison. A comparison with the robust australopithecids or even with early *Homo* is quite difficult as there are not dentitions forming a complete series with all wearing stages. Moreover, the using prepared food by *Homo* cannot provide comparable data. The study of the wearing patterns of *Pan* and *Gorilla* is based to the collections of the Laboratory of Comparative Anatomy in the Muséum National d'Histoire Naturelle of Paris.

4.1. Gorilla

4.1.1. Upper dentition

In the upper incisors the attrition begins from the upper border forming a narrow labio-lingual wearing facet, while the enamel at the distal surface is gradually smoothed. In the advanced wearing stages the height decreases and the attrition extends to the distal surface of the teeth and in the worn ones

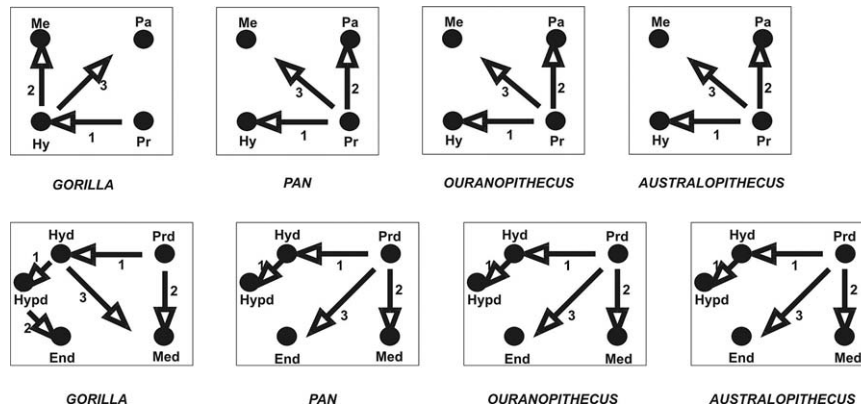


Fig. 11. Wearing pattern in the upper and lower molars of the studied hominoids. End = entoconid, Hy = hypocone, Hyd = hypoconid, Hypd = hypoconulid, Me = metacone, Med = metaconid, Pa = paracone, Pr = protocone, Prd = protoconid.

Fig. 11. Usure des molaires supérieures et inférieures des hominoïdes étudiés. End = entoconide, Hy = hypocone, Hyd = hypoconide, Hypd = hypoconulide, Me = métacone, Med = métaconide, Pa = paracone, Pr = protocone, Prd = protoconide.

to the distal cingular projection giving a triangular shape to the occlusal surface. In the very worn teeth the enamel is restricted all around the borders of the teeth. The apex of the canine is smoothed at the beginning and then a vertical wearing facet is developed in the anterior lingual surface, which is in functional contact with the posterior wearing facet of the c_1 . Another wearing facet is developed in the posterior lingual part of the canine which is in functional contact with the honing facet of the p_3 . There is not large and clear distal cingular cusp as in *Ouranopithecus*. The two wearing facets are gradually connected, as the attrition increases and the height of the canine decreases. In the very worn canines their lingual part is a large wearing facet and as the attrition increases, the enamel is restricted in the borders of the tooth. The canine's wear of *Gorilla* is different than that of *Ouranopithecus* and this due to: a. the absent or rudimentary distal cingular cusp in *Gorilla*, and b. the different functional contact of *Ouranopithecus*. In the latter the upper and lower canine are only in touch without any contact with p_3 . This is possibly due to the relatively smaller canines of *Ouranopithecus* which can allow the closing of the mouth when they are in absolute contact. On the contrary in *Gorilla* and in some other hominoids (except human) and monkeys the large size of the canines does not allow such a functional position and the upper canine is moved slightly posteriorly being in contact with the anterior surface of the p_3 . Moreover, the relatively symmetrical and with less developed mesio-buccal projection p_3 of *Ouranopithecus* does not allow the contact with the upper canine. In the little worn premolars the cusps are smoothed and a small dentine pit appears in the top of the protocone. In the more advanced wearing stages the protocone's pit extends to the distal fovea, while a small dentine pit appears in the top of the paracone. The two pits are gradually connected as the attrition is going on and the height of the tooth decreases. In the very worn teeth the occlusal surface is elliptical and few remains of enamel can be distinguished. The wear in the molars of *Gorilla* begins with a small dentine pit in the protocone and the trace of another in the hypocone. Then, as the attrition increases a dentine pit appears in the metacone and quite later in the paracone. The hypo-

cone's pit extends posteriorly and is connected with the distal fovea and then with the metacone's pit. The paracone's pit remains isolated even in the very worn molars and only in the extremely worn ones connects to the others and all the occlusal surface forms a large wearing facet. Thus, in the molars of *Gorilla* the attrition begins from the protocone and is directed posteriorly to the hypocone and then to the metacone through the distal fovea (Fig. 11). After that it is extended from the hypocone to the paracone which is the last unworn or less worn part of the tooth. This attrition pattern is quite different from that of *Ouranopithecus*.

4.1.2. Lower dentition

The attrition of the incisors is similar to that of *Ouranopithecus*. The canine's apex is smoothed in the little worn teeth but as the attrition increases a posterior vertical wearing facet appears lingually. Simultaneously, a small wearing facet appears in the buccal side of the distal cingular cuspid from the functional contact with the apex of the upper canine. In *Ouranopithecus* this facet is in the center of the distal cingular cuspid. As the attrition increases a second vertical wearing facet appears lingually near the top of the canine and gradually it extends downwards to the mid-height. The little worn premolars have smooth occlusal surface, while the honing facet and a small dentine pit develop in the top of the p_3 . In the worn p_3 the honing facet is enlarged and a small dentine pit appears in the buccal cuspid. In the p_4 the lingual cuspid is worn and connected with the mesial fovea. In the very worn p_3 a small and elongated wearing facet appears in the posterior surface of the buccal cuspid directed to the distal fovea. The buccal cuspid of the p_4 has a semicircular dentine pit and a small wearing facet in the mesial surface of the lingual cuspid. All these facets form a large one in the extremely worn teeth. The little worn molars have a dentine pit in the protoconid, hypoconid and hypoconulid. In the more worn teeth the dentine pits are enlarged, but the entoconid is only smoothed without dentine pit. In the more advanced wearing stage the dentine pits of the protoconid, hypoconid and hypoconulid are connected, while that of the hypoconulid is connected with the

distal fovea and that of the protoconid with the mesial fovea and later with the metaconid. In the very worn teeth all the pits are connected except that of the entoconid. Thus, the attrition begins from the protoconid and is directed posteriorly to the hypoconid and hypoconulid. Then it is directed to the metaconid extending simultaneously to the whole occlusal surface, the entoconid being the last area with dentine. In the very worn molars all the occlusal surface is worn and the enamel is restricted around the molars (Fig. 11).

4.2. Pan

4.2.1. Upper teeth

The attrition of the incisors and upper canine is similar to that of gorilla. The little worn premolars have smoothed enamel cusps and later a dentine pit appears in the anterior surface of the paracone and in the mesial fovea; the latter tends to connect the paracone and protocone's pits. In the more worn teeth the dentine pits of the paracone and protocone are connected to one wearing facet extending bucco-lingually, while small enamel remains are preserved in the buccal corners of the tooth. In the very worn premolars all the occlusal surface is worn and forms a more or less elliptical wearing facet. The attrition of the molars begins from the protocone and hypocone of M^1 and as the wear increases all the cusps obtain a large dentine pit. The pits of the protocone and hypocone are connected in the worn teeth; the first one extends to the mesial fovea and connects with the paracone's pit. The metacone at this stage has a double dentine pit but is still isolated. Thus, in the molars the attrition begins from the protocone and it is directed distally to the hypocone; then it is directed to the metacone diagonally extending to the whole occlusal surface of the molars (Fig. 10).

4.2.2. Lower dentition

The attrition of the incisors and canine is similar to *Gorilla*. In the little worn premolars the enamel of the cuspids is smoothed. In the more advanced wearing stage the honing facet is more developed and clear, while a dentine pit appears in the buccal cusp and later in the lingual one. These two pits are connected by the distal fovea which is being worn. In the very worn teeth the wearing facet covers all the occlusal surface which is more or less rounded. A small dentine pit appears in the protoconid, hypoconid and hypoconulid of the molars; these pits are enlarged gradually as the attrition increases. In the worn teeth the protoconid's pit is connected to those of the hypoconid and hypoconulid; those of the metaconid and entoconid are enlarged and later the first one is connected to the protoconid's pit through the dentine pit of the mesial fovea. In the more worn molars the metaconid's pit is connected to that of the entoconid, which is the last area of the tooth with enamel. Thus, the attrition is directed from the protoconid to the hypoconulid. Then it is directed from the protoconid to the metaconid through the mesial border and diagonally to the entoconid extending to the whole occlusal surface (Fig. 11).

4.3. *Australopithecus afarensis* (Figs. 12 and 13)

This australopithecine is one of the oldest and it has been fully described. It inhabited an open environment and it has thick enameled teeth like *Ouranopithecus*. The comparison is based on the drawings of the Hadar material (Kimbel et al., 1982; White and Johanson, 1982).

4.3.1. Upper dentition

The incisors are spatulated like in *Ouranopithecus* and the attrition begins from the upper border of the teeth. There is a

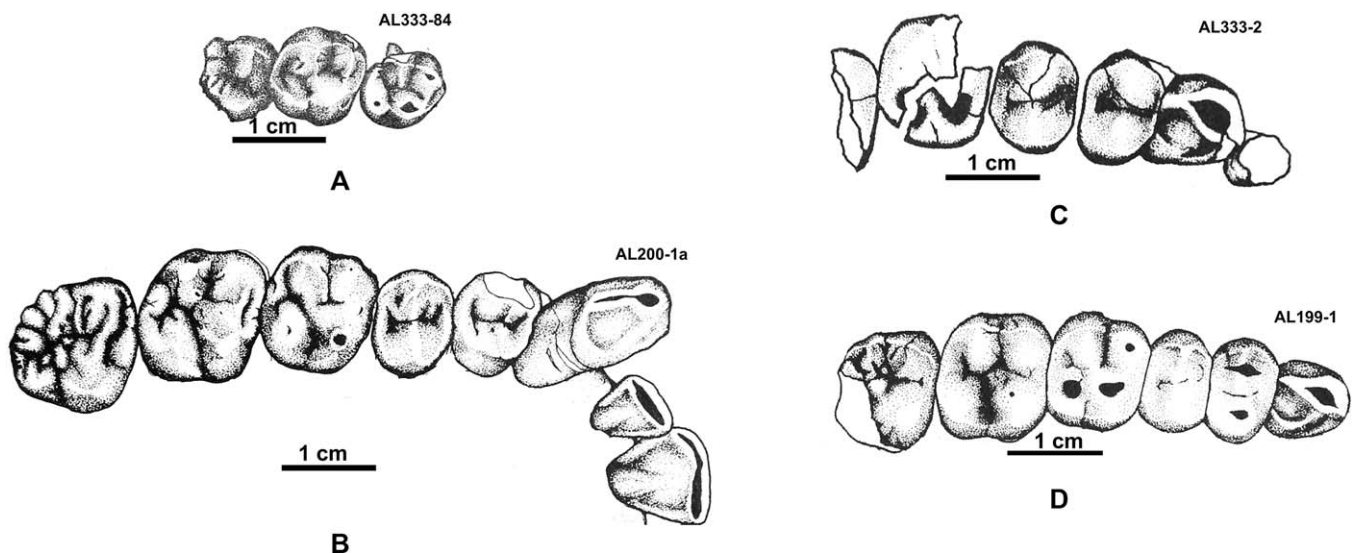


Fig. 12. Upper tooth rows of *Australopithecus afarensis* in various wearing stages. The drawings are from Kimbel et al. (1982).
Fig. 12. Séries dentaires supérieures d'*Australopithecus afarensis* à divers stades d'usure. D'après Kimbel et al. (1982).

dentine zone across this border, which is directed from the buccal to the lingual border of the tooth (Fig. 12b). The wearing pattern of *Ouranopithecus* incisors in RPI-103 is quite similar to that. The little worn canine of AL200-1a (Fig. 12b) has a wearing facet, which begins from the apex and it is directed distally. Such a pattern is observed in the little worn canine of RPI-208 of *Ouranopithecus*. In the more worn canines of *Australopithecus* the attrition is extending at a transverse level and the wearing facet has a semilunar shape (Fig. 12c, d). This pattern is different to that of *Ouranopithecus*, where there are two wearing facets, a vertical one across the distal wall and another horizontal in the distal base of the tooth. Taking into account that the wear of the lower canine in *A. afarensis* follows the same pattern we can suggest that the two teeth are in functional contact with their apexes. The canines of *A. afarensis* are less high than those of *Ouranopithecus* and it is not necessary to be the one in front of the other for the functional contact of the upper and lower tooth row. In the little worn premolars of AL200-1a the mesial and distal fovea is well distinguished, while the apex of the protocone and paracone is rounded (Fig. 12b). Such a feature is also present in RPI-80, 81, 90 of *Ouranopithecus*. In the more worn premolars of AL199-1 there are two dentine pits in the center of the protocone and paracone (Fig. 12d). It is remarkable that in the P³ of AL199-1 the paracone's pit is larger than that of the protocone's pit, indicating that the attrition begins from the previous cusp. In all available worn premolars of *Ouranopithecus* the protocone's pit is larger and more precisely in RPI-90 it is quite large, when the paracone is still covered by enamel. Thus, the attrition in the premolars of *Ouranopithecus* begins from the lingual side of the tooth. Maybe, this is due to the less high buccal cusp of *A. afarensis*. Unfortunately, the available material of *A. afarensis* does not include worn teeth in order to see the evolution of the wearing pattern. The unworn molars have wrinkled enamel like those of *Ouranopithecus* (Fig. 12a–b) which is gradually smoothed by the attrition (Fig. 12d). The attrition of the molars begins from the protocone where a small dentine pit appears and then continues to the hypocone (Fig. 12b). In the more worn teeth a dentine pit appears in the center of the paracone (Fig. 12d). Correlating these data of *A. afarensis* it seems that the attrition follows the same pattern as in *Ouranopithecus*. It begins from the lingual cusps and it is directed buccally from the mesial to the distal part of the tooth.

4.3.2. Lower dentition

The lower incisors of *A. afarensis* seem to have the same wearing pattern as *Ouranopithecus*. The only available mandible AL-400 indicates that the attrition begins from the upper border of the incisors and as their height decreases it is extended to the distal surface. It seems to be similar to the little worn teeth of *Ouranopithecus* and possibly the attrition is similar to *Ouranopithecus* in the more advanced wearing stages. The available lower canines (Fig. 13d, f, g) indicate that the attrition of the canine is restricted only on the apex of the tooth forming a transverse occlusal wearing facet. As referred

above this is in good correlation with the attrition of the upper canine and different to that of *Ouranopithecus*. In the p₃, the attrition begins from the top and continues on the anterior and posterior crests (protocristid) exactly like in *Ouranopithecus* p₃ (Bonis and Koufos, 2001: Figs. 11–3). On the p₄ it is difficult to see the order of the wear facets (Fig. 13f, g). In *Ouranopithecus* it begins from the lingual cuspid. In the molars the attrition begins from the buccal cuspid (Fig. 13b–e) in which a dentine pit appears. The protoconid's pit is stronger (Fig. 13d, e) indicating that the wear begins from this point. As the attrition is going on, the two dentine pits are connected each other and with the hypoconulid's pit forming a large wearing facet in the buccal half of the tooth (Fig. 13d, f, g). In the lingual cuspid a small dentine pit appears in the metaconid and later in the entoconid. The first one is connected to the buccal wearing facet mesially. The metaconid's pit is extended distally across the lingual border of the tooth and it is connected with that of the entoconid. This wearing pattern of the molars is similar to *Ouranopithecus*.

The *A. afarensis* wearing pattern resembles that of *Ouranopithecus* and it could indicate close relationships between the two species and a similar diet. The differences in the wearing patterns of the canines and the first premolars are possibly due to the reason that the smaller canines of *Australopithecus* are functionally contacted by their apexes, giving different functional contact in the tooth rows. In *Ouranopithecus*, because of the larger canines, the mesial surface of the upper canine is in contact with the distal one of the lower canine.

5. Conclusions

The new material of *Ouranopithecus* from RPI has enlarged the known collection of this Greek hominoid, especially with maxillary and female mandibular remains, which were very few. The material provided also a series of tooth rows in different wearing stages, which allows the study of the attrition patterns of the different teeth of *Ouranopithecus* and the comparison with other available hominoids. A series of tooth rows from two recent taxa (*Gorilla* and *Pan*) have been studied in the Laboratoire d'Anatomie Comparée (Muséum National d'Histoire Naturelle) of Paris. The attrition of *A. afarensis* has been studied from the series of illustrations and drawings given for the Hadar material (Kimbel et al., 1982; White and Johanson, 1982).

The incisor's attrition seems to be more or less similar in all studied taxa. Both upper and lower canine have different attrition pattern from those of the extant hominoids and from *A. afarensis*. The canines of *Ouranopithecus* are not in functional contact with the mesio-buccal face of the p₃ (honing facet) as it is in *Gorilla* and *Pan*. In these taxa, the large size of the canines does not allow a functional contact between them, but the upper canine is slightly moved posteriorly being in contact with the anterior part of the p₃ and the attrition of the two teeth provides the honing facet in the p₃. The mesio-buccal projection of the p₃ in the studied recent hominoids is relatively longer and it reaches the distal surface of the upper canine. In

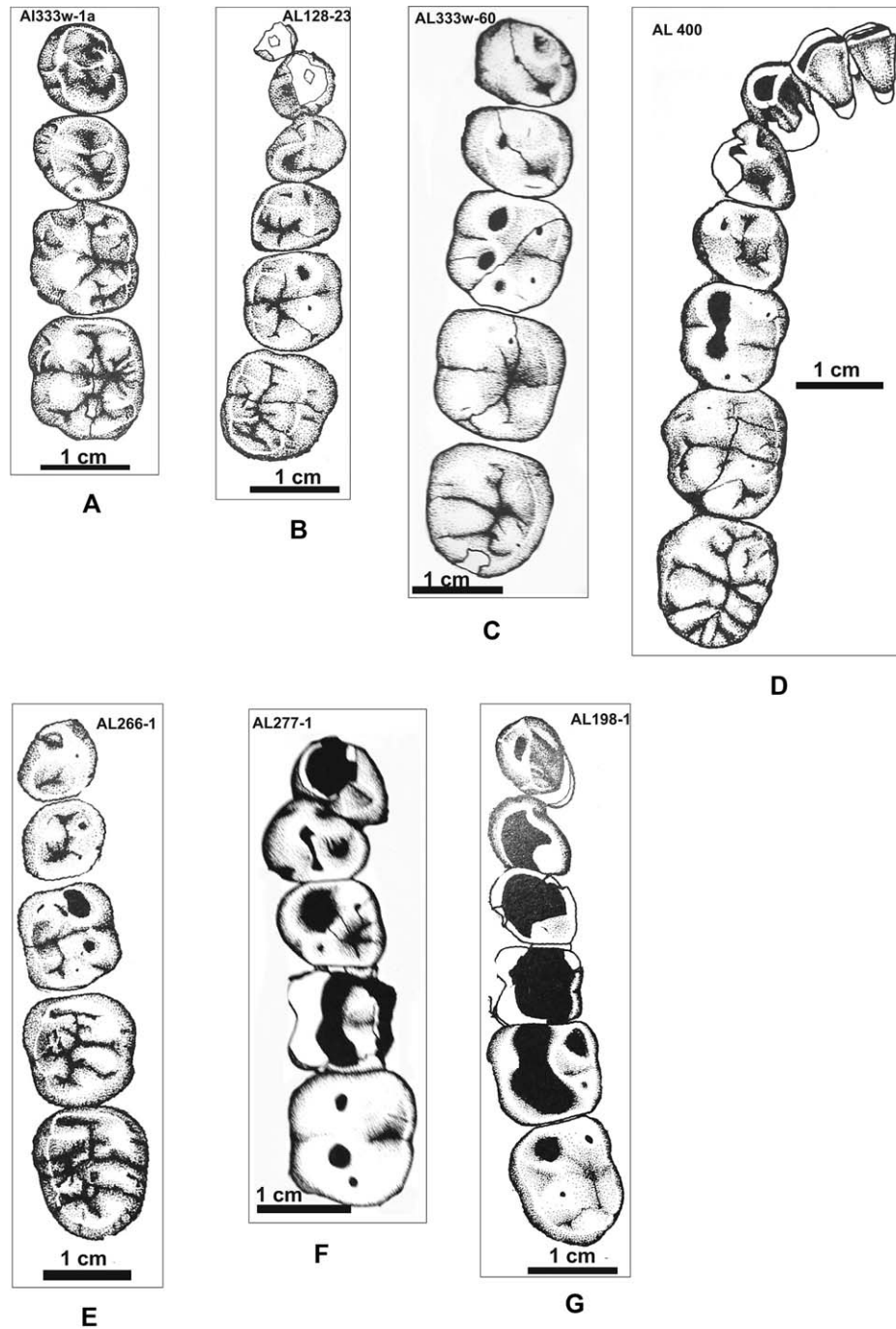


Fig. 13. Lower tooth rows of *Australopithecus afarensis* in various wearing stages. The drawings are from White and Johanson (1982).
 Fig. 13. Series dentaires inférieures d'*Australopithecus afarensis* à divers stades d'usure. D'après White et Johanson (1982).

A. afarensis the canines are relatively smaller than those of *Ouranopithecus* and they are in functional contact with their apices. The smaller canines of *Ouranopithecus* in relation to those of the extant hominoids allow an intermediate functional contact without the participation of the p_3 providing a different wearing pattern. Thus, the canine's attrition of *Ouranopithecus* indicates that its pattern is more derived than that of the recent hominoids and less derived than that of *A. afarensis*.

The molar's attrition of *Ouranopithecus* is similar to that of *A. afarensis* and *Pan*. In these hominoids the attrition of the upper molars begins from the protocone and is directed to the hypocone and then to the paracone (Fig. 11). Then it is extending diagonally to the metacone whose dentine pit remains isolated in the worn teeth, being connected to the rest in the very worn teeth. The wearing pattern of the lower molars of the above hominoids follow a similar pattern. It begins from

the protoconid and it is directed to the hypoconid and hypoconulid. In the more advanced wearing stages it is directed from the protoconid to the metaconid and then diagonally from the protoconid to the entoconid (Fig. 11). In *Gorilla* the wearing pattern seems to be different. It begins from the protocone but it is directed to the hypocone and then through the distal fovea to the metacone. Then it is directed diagonally from the hypocone to the paracone which is the last isolated dentine pit. The lower molars follow a similar pattern (Fig. 11).

It is quite possible that the different wearing pattern of *Gorilla* due to the different type of food. *Ouranopithecus* and *A. afarensis* were living in relatively open landscapes with “hard” food and they have to pulverize it. For this, they were making clock-wise cyclic movements with the lower jaw. On the contrary, *Gorilla* eats “soft” food and it is necessary to cut this in small pieces. So, its lower jaw makes mesio-distal movements providing different attrition.

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