Zeresenay Alemseged
& Denis Geraads
*EP 1781—CNRS,
Collège de France,
30 avenue Marcelin-Berthelot,
F-92360 Meudon.
E-mail: zeray@mailtag.com
dgeraads@compuserve.com*

Received 12 May 1997
Revision received
16 January 1998
and accepted 25 January
1998

Keywords: Primates,
Cercopithecidae,
Theropithecus, late Pliocene,
Morocco.

Theropithecus atlanticus (Thomas, 1884) (Primates: Cercopithecidae) from the late Pliocene of Ahl al Oughlam, Casablanca, Morocco

The site of Ahl al Oughlam near Casablanca, Morocco, dated to ca. 2·5 Ma, has yielded a good sample of *Theropithecus atlanticus* (Thomas, 1884), a North African late Pliocene species previously known only by its holotype, a lower molar from Algeria. *Theropithecus atlanticus*, which can now be much better defined, is clearly distinct from other species of the genus, which is thus more diverse than previously thought. The mandible of *T. atlanticus* has a very characteristic deep and long post-molar sulcus and a deep and well excavated supra-lateral triangular depression of the ramus, with a sharp postero-inferior ridge. The upper and lower canines are rather large but low. The male P_3 is very wide, with well developed posterior crests; the P_4 is rounded, with a large talonid and weak notches and clefts. Median lingual notches of the lower molars form an acute angle. Although our incomplete knowledge of *T. atlanticus* precludes a detailed phylogenetic analysis, we suggest that it arose by cladogenesis from the *T. darti*–*T. oswaldi* lineage; it is replaced by the latter species in the Pleistocene.

Le gisement de Ahl al Oughlam près de Casablanca (Maroc), daté d'environ 2,5 Ma, a livré une belle collection de *Theropithecus atlanticus* (Thomas, 1884), espèce du Pliocène supérieur nord-africain qui n'était jusque là connue que par son holotype, une molaire inférieure d'Algérie. *T. atlanticus*, qui peut maintenant être bien mieux défini, se distingue bien des autres espèces du genre, dont la diversité est ainsi accrue. La mandibule de *T. atlanticus* est très caractéristique par son espace rétro-molaire vaste et profond, et sa dépression supra-latérale de la branche montante également très profonde, avec un rebord inférieur aigu. Les canines supérieures et inférieures sont grosses mais basses. La P_3 mâle est très large, avec des crêtes postérieures très développées; la P_4 est arrondie, avec un grand talonide et des sillons peu profonds. Sur les molaires inférieures, le débouché de la vallée médiane forme un angle aigu. Bien que notre connaissance imparfaite de *T. atlanticus* interdise une analyse phylétique détaillée, nous suggérons une dérivation par cladogenèse à partir de la lignée *T. darti*–*T. oswaldi*; cette dernière espèce le remplace au Pléistocène.

Journal of Human Evolution (1998) **34**, 609–621
Article No. hu980217

Introduction

The site of Ahl al Oughlam, at the south-eastern limit of Casablanca, Morocco, was discovered in 1985 by J.-P. Raynal and J.-P. Texier. Ongoing excavations have been carried out by one of us (D.G.) as part of the "Programme Casablanca" conducted by the "Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP)" of Rabat, in co-operation with the "Mission Préhistorique et Paléontologique Française au Maroc Atlantique (MPPFMA)", led by J.-P. Raynal. With almost 80 vertebrate species, of which more than 50 are micro- and macro-mammals, it is by far the richest site of the North African Neogene. It has been biochronologically dated to 2·5 Ma (Raynal *et al.*, 1990; Geraads, 1993, 1995, 1997) and is thus roughly contemporaneous with member D of the Omo Shungura Formation and the Upper Burgi member of the Koobi Fora Formation. In North Africa, it is older than Aïn Boucherit (Arambourg, 1970, 1979) but younger than Garaet Ichkeul (Arambourg, 1970) and probably contemporaneous with one of the levels of the poorly known locality of Aïn Jourdel (Thomas, 1884; Geraads, 1987).

Among the thousands of identifiable specimens from Ahl al Oughlam (AaO), two genera of Cercopithecidae were encountered: a few belong to a macaque, and about 30 to *Theropithecus*, a genus today represented only by *T. gelada* of the Ethiopian highlands, but well known in the Plio-Pleistocene of Africa, where it is represented by several species ranging in size from that of the gelada to that of a female gorilla (Jolly, 1972; Leakey & Leakey, 1973; Eck & Jablonski, 1987; Eck, 1987; Eck, 1993; Leakey, 1993; Delson, 1993; Delson & Hoffstetter, 1993).

The allocation of the specimens from Ahl al Oughlam to the genus *Theropithecus* is justified by the presence of the following characters:

—sub-vertical mandibular ramus;
—high crowned cheek teeth with cusps somewhat columnar in form with greatly increased relief giving them a distinctive wear pattern;
—foveae deeply excavated and notches deeply incised, nearly to the cervix;
—presence, on M_1 and M_2, of a large distal accessory cuspule which projects backward towards the succeeding tooth.

In short, these fossils display most of the suite of mandibular and dental morphological characters put forward by Szalay & Delson (1979) to identify the genus.

We will compare them with *T. darti* from Makapansgat in South Africa (Maier, 1972) and Hadar in Ethiopia (Eck, 1993), *T. brumpti* from Omo, in Ethiopia (Eck & Jablonski, 1987) and *T. oswaldi* from many African sites (Jolly, 1972; Leakey & Leakey, 1973; Eck, 1987; Leakey, 1993; Delson, 1993; Delson & Hoffstetter, 1993), including some in North Africa (Thomas, 1884; Geraads, 1980; Delson, 1993; Delson & Hoffstetter, 1993). The latter is probably the only species to have emigrated from Africa, into Spain (Gibert *et al.*, 1995) and India (Gupta & Sahni, 1981; Delson, 1993; Pickford, 1993).

The only *Theropithecus* fossil of similar age and geographic position to the fossils of Ahl al Oughlam is a first lower molar from the Algerian Pliocene site of Aïn Jourdel (Thomas, 1884; Geraads, 1987; Delson, 1993), housed in the MNHNP, Paris. This is the holotype of the first fossil specimen of *Theropithecus* ever named, *Cynocephalus atlanticus* Thomas, 1884, which was subsequently attributed to *Theropithecus* by Delson (1974). No morphological description was provided by Thomas (1884), but Delson (1993) pointed out that this tooth is distinctive in that the base of its median lingual notch forms an acute angle. All lower molars from Ahl al Oughlam exhibit the same morphology on their lingual side. In fact, this is the only consistent morphological difference that clearly separates lower molars of Ahl al Oughlam from those of all other species except the one from Aïn Jourdel. Accordingly we refer the Moroccan *Theropithecus* to *T. atlanticus*. The distinctiveness of this species is further confirmed by other mandibular and dental characters described below, and thanks to this new material this species can now be much better defined.

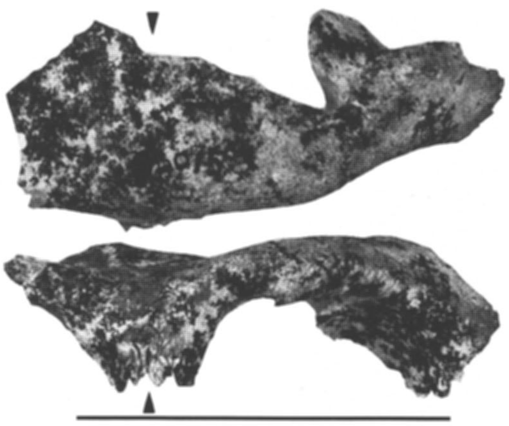

Figure 1. *Theropithecus atlanticus*, frontal bone AaO-15, superior (up) and anterior (bottom) views. Scale= 5 cm.

The material under consideration is housed in the INSAP, Rabat, Morocco. Measurements are in millimetres.

Systematic description

Skull

AaO-15 consists of a frontal bone (Figure 1), including the left brow ridge and nasion region, a left external auditory meatus, and a fragment of the cranial vault. They were found close to each other and thus probably belong to a single skull. It is more likely that they belong to *Theropithecus* than to *Macaca* because they are too large for the rather small and rare species of the *Macaca* encountered in this locality, and because the external auditory meatus is closely pressed against the postglenoid process, as in *T. oswaldi*, in contrast to all observed *Macaca*.

In frontal view, the brow ridge reaches its maximum height above the lateral border of the supra-orbital notch, which is marked by a rather strong tubercle. In the glabellar area, the outline forms a broad and deep depression. This morphology is similar to that of *T. brumpti*, while the depressed central area is narrower and shallower in *T. oswaldi* (Eck & Jablonski, 1987) (ibid.) and *T. darti* (Eck, 1993). In dorsal view, the AaO frontal differs from that of all other species of the genus in that the lateral half of the orbit is concave forward, giving the outline a distinctly sigmoid curvature, while it is more or less regularly convex, and sometimes strongly so, in other species. The preserved portion of the orbit shows that it was very broad (30–32 mm), only surpassed by a specimen from Olorgesailie (Eck & Jablonski, 1987). Finally, the fragment of the cranial vault, in the sagittal area, is remarkable for the lack of a sagittal crest; the temporal lines are well marked (thus suggesting a male specimen) but sinuous, and remain separated by several millimetres where they approach most closely, over a short distance. Even if a sagittal crest was present at the extreme rear of the skull, it was certainly very short.

Mandible

AaO-288 is an incomplete left mandible, of relatively small size, broken at the mesial limit of the first molar (Figure 2). The depth of the mandibular body below the M_1 and M_3, as well as the thickness of the body, fall within the range of the living species and are very comparable to those of *T. darti* males. The gonion and the tip of the coronoid process are lacking. The three molars are present. As is usually the case for the genus, there is a strong wear gradient on the molars: M_3 is almost untouched, M_2 is worn and M_1 is heavily worn.

Variation in the post molar sulcus within the genus *Theropithecus* has rarely been discussed. In the Ahl al Oughlam mandible it is long, deep and its lateral border ridge is high and sharp. In *T. darti* from Hadar the depth and the degree of excavation are less pronounced, the lateral ridge is low and rounded. In *T. brumpti* it is wide and well excavated but short, with a lower lateral ridge. In *T. oswaldi* it is similar to that of *T. brumpti* but relatively less excavated and has

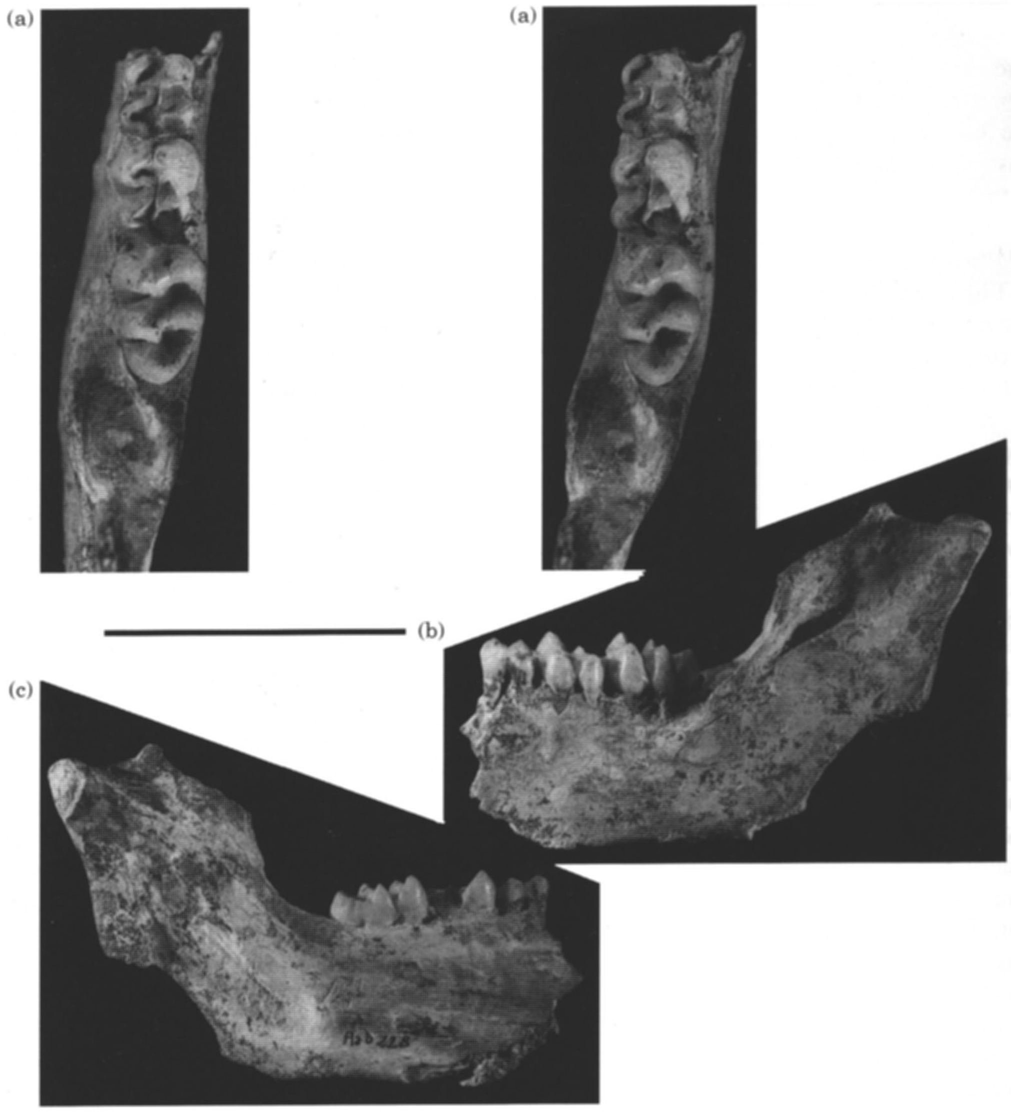

Figure 2. *Theropithecus atlanticus*, mandible AaO-288. (a) stereo view of the teeth; (b) lateral view; (c) medial view. Scale=4 cm for Figure A, 6 cm for Figures B-C.

a weak lateral ridge. In the living species this sulcus is very shallow and has a very weak lateral ridge.

The supralateral triangular depression of the ramus, which provides an attachment for fleshy fibres of the deep masseter muscle and tendon (Eck & Jablonski, 1987; Leakey, 1993), is long and deep in the Ahl al Oughlam mandible. It has a strong and sharp postero-inferior ridge, forming an angle of about 45° with the anterior border of the ramus, and is thus a bit steeper than in *T. gelada*. Compared to this, that of Hadar *T. darti* is shallow, and the postero-inferior ridge is rounded and less well defined. In *T. oswaldi* this depression is very shallow and the postero-inferior ridge is very weak. In *T. brumpti* it is deep and the postero-inferior ridge is steeply inclined, shorter and more rounded, despite the large size of the observed mandibles. In AaO-288 the postero-inferior ridge runs from near the anterior margin of the ramus (as in *T. brumpti*) but tends to lose definition (as in *T. gelada*) as it runs supero-posteriorly.

The mandible of *T. atlanticus* has a very shallow and presumably long mandibular corpus fossa of which a slight indication can be seen as far back as the mesial level of the M_3, with a very slight and progressive increase in depth up to the mesial limit of the M_1 where the mandible is broken. Though it is not completely preserved the mandibular corpus fossa of the Ahl al Oughlam specimen appears to be as shallow as that of *T. darti*. This fossa is deeper in most of the observed *T. oswaldi*, with a more anteriorly located posterior margin, and much deeper and longer in *T. brumpti*.

Although it is incomplete, the mandibular condyle of AaO-288 appears less transversely elongate than that of *T. gelada* and *T. brumpti*. The triangular depression found on the posterior surface of the condyle of both sexes of *T. oswaldi* is absent in this mandible.

Though the size and overall appearance of this mandible are close to those of male *T. darti* from Hadar, we can separate it from this and other species of *Theropithecus* by its: (1) long and deep post molar sulcus; (2) high and sharp lateral ridge of the post molar sulcus; (3) deep triangular depression of the mandibular ramus with a sharp and well developed postero-inferior ridge; (4) very shallow and long mandibular corpus fossa.

Tentatively, one might suggest the observed differences in the mandible and skull relate to a peculiar masticatory process, with perhaps greater importance of the masseter relative to the temporal muscle compared to other species.

Teeth

All permanent teeth except the incisors are represented in the collection from Ahl al Oughlam (Figure 3; Table 1). In addition, three theropith deciduous premolars (dP_3) have been recovered.

Canines. The right upper male canine AaO-303 [Figure 3(a)], moderately worn, is morphologically similar to those in males of other species of *Theropithecus* in that it is recurved and has a flat lingual surface. Its length and basal width fall within the range, but close to the lower limit, of *T. oswaldi*; its height however is very reduced, and the tooth is also much lower than those of *T. gelada*, *T. brumpti* and *T. darti* from Makapan (Figure 4). Although the tip is worn off, the original height can be estimated by comparison with that of *T. gelada*. In the latter species, upper canines taper much less quickly from base to tip: at a distance from the base equal to the antero-posterior basal length, the transversal diameter (unaffected by wear) of AaO-303 is only 62% (5·4/8·7) of the basal transversal diameter, while this ratio ranges from 80% to 90% in *T. gelada*. This allows to estimate to about 5–7 mm the height reduction by wear, and to assert that the Ahl al Oughlam tooth was really low.

Two lower canines belong to the same individual, AaO-45. As is the case for the upper canine, their length and width correspond to the smallest canines in *T. oswaldi*, but their height falls in the middle of the range for this species. Thus, the upper and lower canines are remarkably similar in size, contrasting with the strong difference displayed by other species.

Upper premolars. The single P^3 [Figure 3(b)] and one P^4, AaO-4001 [Figure 3(c)] are typical theropith teeth. However, the second P^4, AaO-3490 [Figure 3(d)], differs from almost all P^4s of *Theropithecus* species by the presence of an additional fovea at its distal

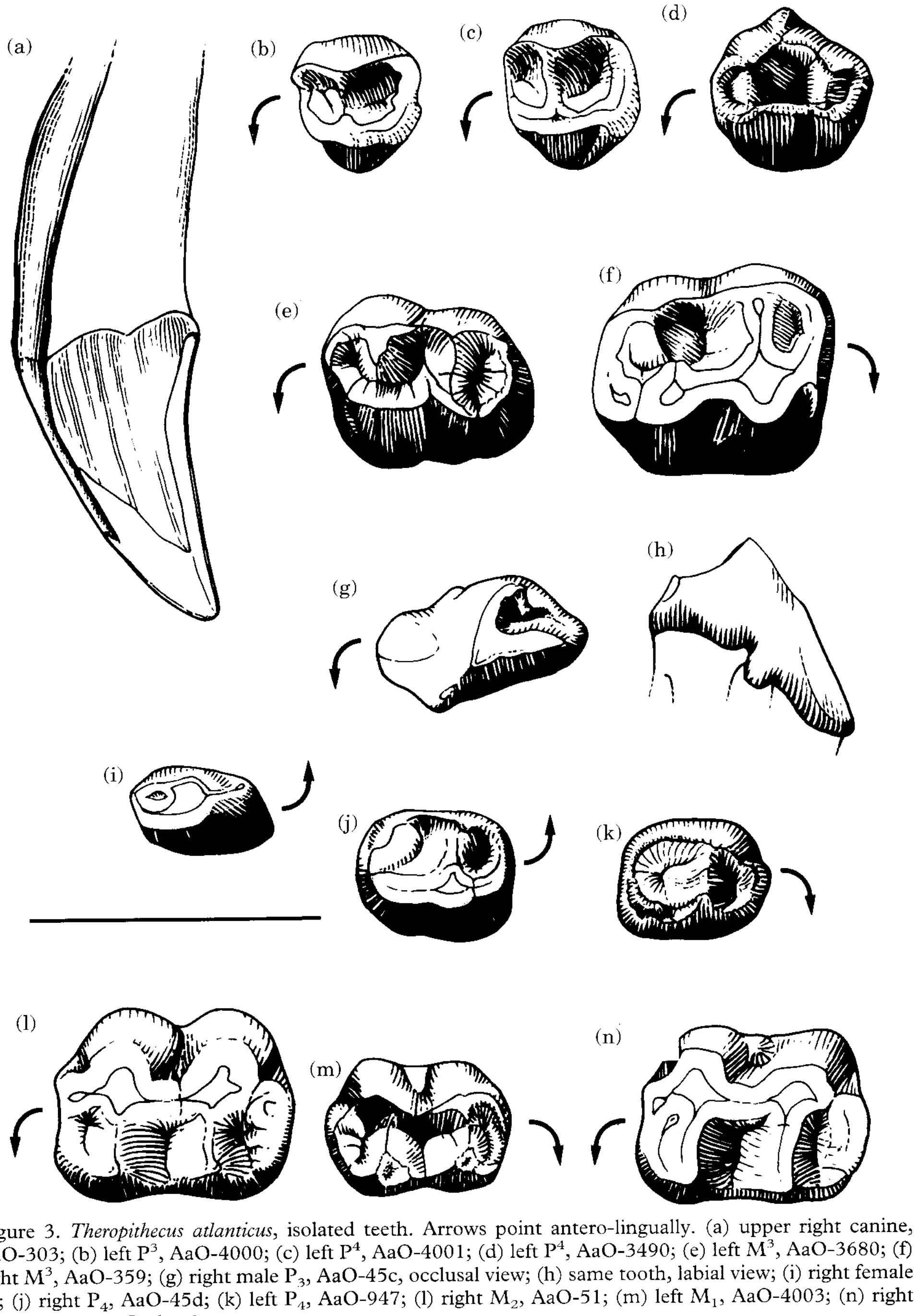

Figure 3. *Theropithecus atlanticus*, isolated teeth. Arrows point antero-lingually. (a) upper right canine, AaO-303; (b) left P^3, AaO-4000; (c) left P^4, AaO-4001; (d) left P^4, AaO-3490; (e) left M^3, AaO-3680; (f) right M^3, AaO-359; (g) right male P_3, AaO-45c, occlusal view; (h) same tooth, labial view; (i) right female P_3; (j) right P_4, AaO-45d; (k) left P_4, AaO-947; (l) right M_2, AaO-51; (m) left M_1, AaO-4003; (n) right M_2, AaO-3143. Scale=2 cm.

Table 1 Measurements (in mm) of *Theropithecus atlanticus* from Ahl al Oughlam

Upper teeth						Lower teeth					
Tooth	No.	Side	Length	Width	Height	Tooth	No.	Side	Length	Width	Height
C	AaO-303	R	13·0	8·9	23·9+	C	AaO-45a	R	13·2	8·8	23·0+
P^3	AaO-4000	L	8·6	9·4		P_3	AaO45c	R, male	16·8	8·5	
P^4	AaO-4001	L	9·2	10·0		P_3	AaO-304	R, fem.	10·3	6·0	
P^4	AaO-3490	L	11·3	11·0		P_4	AaO-45d	R	10·9	9·0	
			Length	Anterior width	Posterior width	P_4	AaO-947	L	10·5	8·3	
M^1	AaO-4002	L	11·6	9·3					Length	Anterior width	Posterior width
M^2	AaO-2042	L	13·2	11·5	10·6	M_1	AaO-4123	L	11·7	9·1	9·3
M^2	AaO-3145	R	13·0	11·7	10·8	M_1	AaO-288[1]	L	11·0	9·5	10·2
M^3	AaO-50	R	17·3	14·8	12·6	M_1	AaO-4003	L	12·7	9·0	9·5
M^3	AaO-358	L	16·6	14·4	13·7	M_2	AaO-45g	L	12·3	10·1	10·4
M^3	AaO-359	R	16·6	14·9	13·9	M_2	AaO-51	R	15·7	12·8	12·7
M^3	AaO-433	L	13·0	11·0	10·2	M_2	AaO-288[1]	L	14·1	11·9	
M^3	AaO-2041	L	14·8	13·4	11·2	M_2	AaO-3143	R	15·7	12·1	12·0
M^3	AaO-2583	R	16·1	12·4	10·8	M_3	AaO-288[1]	L	18·6	12·1	11·8
M^3	AaO-3471	L	16·0	14·2	12·4	M_3	AaO-3144	L			11·5
M^3	AaO-3489	L	16·5	13·5	13·7						
M^3	AaO-3680	L	14·3	12·1	10·4						
M^3	AaO-4125	L	17·2	13·7	12·7						

[1]Associated teeth of the mandible. Length M1–M3=44·5.

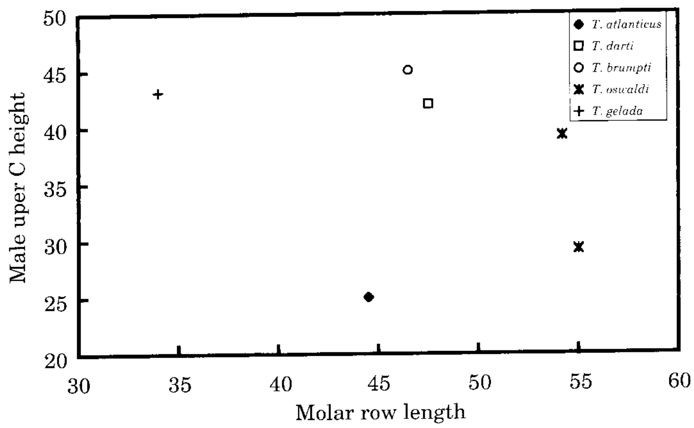

Figure 4. Plot of male upper C height *vs.* lower molar row length. All measurements are from unassociated specimens; those of the upper canines are from single individuals. In all figures, for *T. darti*, black squares are from Hadar, open ones from Makapansgat.

end and of a sharp vertical ridge on its buccal face. Moreover, unlike P^4s of all other species its length is greater than its width. A similar, but smaller fovea, exists on some teeth from Omo (for example: L338y-2257, L59-17c and L338y-23). Although AaO-3490 differs from other P^4s, the presence of a "normal" P^4 (AaO-4001) suggests that AaO-3490 is aberrant.

Upper molars. They are little different from those of other early species of *Theropithecus* in having a more primitive occlusal pattern than that of later varieties of *T. oswaldi*, with relatively lower crowns and less accentuated longitudinal and transverse ridges [Figure 3(e)–(f)]. As in *T. darti*, but in contrast to other species, the labial notch is rather shallow, though difficult to quantify.

Lower premolars. The Ahl al Oughlam male P_3s are relatively shorter than in *T. gelada* and *T. brumpti*, but comparable to *T. darti* and early *T. oswaldi* [Figure 4(g)–(h); Figure 5]. However, in contrast to the latter species, the P_3s of *T. atlanticus* are broad, both in relation to their length and to the molar row (Figures 6 & 7). The honing facet for the upper canine is wide and short. The two crests (eocristid and epicristid) descending from the eoconid are higher than in other species, and run to the postero-lingual and postero-labial corners of the tooth where they form high vertical walls, almost enclosing the distal fovea. The female P_3 [Figure 3(i)] is of course very small but it is wider than those of *T. gelada* females. The P_4s from Ahl al Oughlam have large talonids [Figure 3(j)–(k)]. The notches and clefts are shallower than in P_4s of other species, rendering the overall appearance of the teeth rather rounded. Their dimensions are comparable to those of large specimens of *T. darti* from Makapansgat (Delson, 1993) and those of *T. oswaldi* (which has much larger molars). They are clearly broader than those of *T. brumpti* (Eck & Jablonski, 1987; Leakey, 1993) and larger than those of *T. darti* from Hadar.

Lower molars. In general aspect, lower molars of *T. atlanticus* are larger but morphologically very similar to those of *T. darti* males [Figure 3(l)–(n)]. Still, these teeth can be distinguished from those of other species by the formation of an acute angle on their median lingual notch, as in the type-specimen of *T. atlanticus* (Delson, 1993). In addition, the two Ahl al Oughlam M_3s differ from those of *T. oswaldi* and *T. brumpti* by

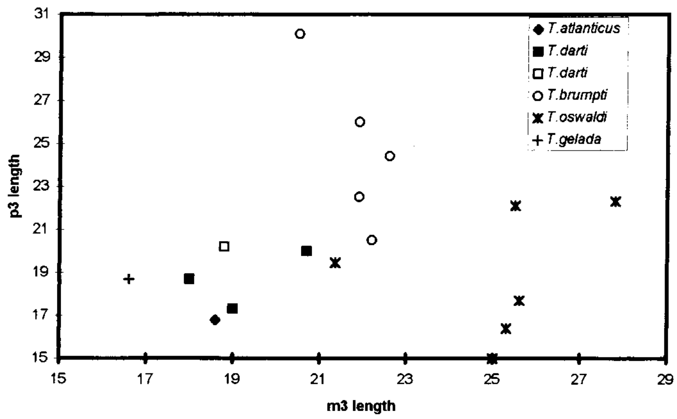

Figure 5. Plot of male P_3 length *vs.* M_3 length. All measurements are from associated specimens, except *T. darti* from Makapansgat and *T. gelada*, which are means, and *T. atlanticus*, which are from two different individuals.

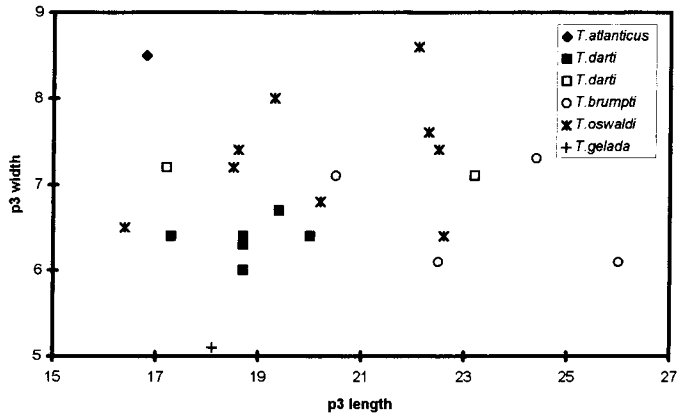

Figure 6. Plot of male P_3 width *vs.* P_3 length. All measurements are from individual specimens, except *T. gelada* (means).

the narrow and relatively shallower clefts on the labial side. The size of the Ahl al Oughlam molars is variable, but comparable to those of *T. brumpti* and *T. darti* of similar age. According to Delson (1993) the Aïn Jourdel tooth would be narrower than those of other species. It is true that the tooth is narrow (14·4 × 9·7, ratio 0·67) but there are specimens from Omo (in the National Museum, Addis Ababa) which are about as narrow, e.g., L18-23 (14·2 × 9·5, ratio 0·67), L51-8h (13·3 × 8·8, ratio 0·67), L23-53 (14·6 × 9·9, ratio 0·68), L55-1f (13·3 × 9·0, ratio 0·68), which means that this is not a unique character of this specimen. The narrowest molar at Ahl al Oughlam has a W/L ratio of 0·74 and the widest one 0·83. Pending recovery of more material from the North African late Pliocene sites, we think that the W/L ratio may vary with geologic age, since the *T. atlanticus* level of Aïn-Jourdel is slightly younger than Ahl al Oughlam (the former has *Equus*, but the latter has only *Hipparion*), but this variation has no taxonomic value.

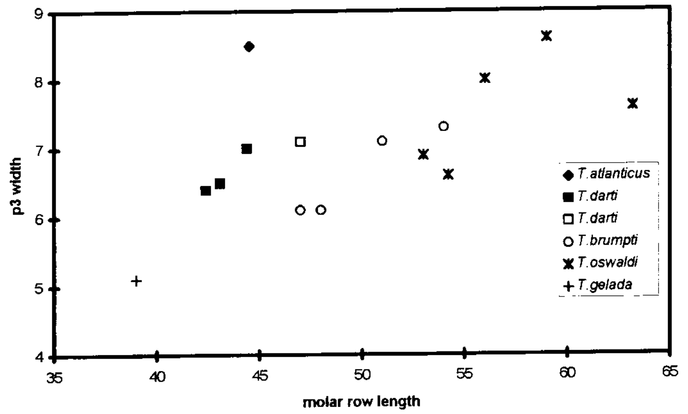

Figure 7. Plot of male P_3 width *vs.* molar row length. All measurements are from associated specimens, except *T. atlanticus* and *T. oswaldi* from Tighenif, which are unassociated, and *T. gelada*, which are means.

Table 2 Measurements (in mm) of *T. atlanticus* and *T. gelada*

T. atlanticus AaO-430 estim. length	220	distal diam.	27·6 × 22·5	mini. AP diam. shaft	15·8
T. gelada MNHNP 1945–7	223		25·5 × 20·8		14·0
Jolly, 1972	214		24 × 19		13·0
	218		24·5 × 19		13·5

Postcranium

Only five postcranial bones of *Theropithecus* have been recovered from Ahl al Oughlam: a tibia, a talus and three phalanges.

The tibia AaO-430 is about as long as that of the males of *T. gelada*, but more robust, especially the shaft (Table 2).

The tibia also differs from that of *T. gelada* in that the lower border of the medial malleolus is less steeply inclined. This is probably character 63 of Krentz (1993: 395), and it makes *T. atlanticus* more like *Papio* and *T. darti* than like other species of the genus (Krentz, 1993, Table 14.4). Another possible difference, visible both on the tibia and talus, is that the lateral articular facet between these bones is not as sharply recurved as it is in the recent species. We know nothing, however, of the variability of this feature in the living species.

Our study convinces us as to the distinctiveness of *T. atlanticus* from other species of the genus. It can be defined as follows:

Genus: *Theropithecus* (Geoffroy Saint-Hilaire, 1843)

T. atlanticus (Thomas, 1884)

Cynocephalus atlanticus Thomas, 1884

Holotype: First right lower molar housed in MNHNP, AJO-001.

Type locality: "conglomérat gréseux" of Aïn Jourdel, Algeria (Thomas, 1884)

Diagnosis: A species of *Theropithecus* of small size. The mandibular corpus fossa is very shallow as in *T. darti*. This is deeper in *T. oswaldi* and much deeper in *T. brumpti*. The post molar sulcus is long and deep, with high and large lateral border ridge. In *T. darti* the depth of the sulcus is less pronounced with a low and rounded lateral ridge. In *T. brumpti* it is well excavated but short with lower lateral ridge. In *T. oswaldi* it is similar to that of *T. brumpti* but relatively less excavated with a weak lateral ridge. The supralateral depression of the ramus is deep with a strong and sharp postero-inferior ridge. That of *T. darti* is shallow with rounded and less well defined ridge. In *T. oswaldi* this depression is very shallow with a very weak postero-inferior ridge. In *T. brumpti* it is deep but the ridge is steeply inclined, shorter and rounded. The upper canine is lower than that of any other species of the genus. The lower canines are rather large. The male P_3 is very wide with well developed posterior crests. Compared to the M_3 length it is relatively shorter than in *T. gelada* and *T. brumpti*, but comparable to that of *T. darti* and early *T. oswaldi*. However the P_3 of *T. atlanticus* is broad both in relation to its length and the molar row. The P_4 is large, rounded with large talonid, and weak notches and clefts. The median lingual notches of the lower molars form an acute angle.

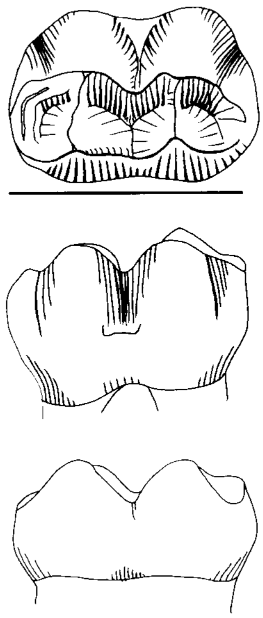

Figure 8. *Macaca sp.* second lower molar in occlusal, labial and lingual views. Scale = 1 cm.

Discussion

Theropithecus has a well documented evolutionary history in the Pliocene and Pleistocene of Africa (Jolly, 1972; Dechow & Singer, 1984; Eck, 1993; Delson & Hoffstetter, 1993). Three groups are known, one including the modern gelada, another including the *T. darti–T. oswaldi* lineage, and the third including *T. brumpti*. Among these, only *T. oswaldi* has been recognised in North Africa, as the systematic position of the Aïn Jourdel lower molar (Thomas, 1884; Delson, 1993) remained unclear. The fossils from Ahl al Oughlam solve this problem and confirm the presence of a second species of *Theropithecus* in the Late Pliocene of North Africa, thus increasing the known diversity of the genus. They also provide the first evidence of the coexistence of species of *Theropithecus* and *Macaca*. Hitherto, they were thought to be mutually exclusive (Geraads, 1987; Pickford, 1993). There are three lower molars of a macaque in the Ahl al Oughlam collection. AaO-400 is a right M_2, AaO-3991 and AaO-52 are left M_2s (Figure 8). They are very small compared to the *Theropithecus atlanticus* M_1. They would be of the right size for the dP4 of this species, but close comparison with dP_4 of *T. gelada* and *T. oswaldi* from Tighenif and Thomas-Oulad Hamida quarries make it clear that they are not milk teeth. They are rounded, without anterior and posterior expansions, and the crown is higher and the fovea and valleys are deeper. These teeth are perhaps lower crowned than those of *Macaca sylvanus*, but we would not attempt any specific identification based on isolated teeth.

The phyletic relationships of *T. atlanticus* cannot be established with certainty at this stage. As was noted earlier, however, excepting some important differences, the size and the overall appearance of the mandible and the molars of this species have more similarities with those of *T. darti* than with any other species.

—The mandible is as small as that of *T. darti*
—The depth of the mandibular corpus fossa is comparable.

—Most upper and lower molars of *T. atlanticus* have shallow and narrow clefts like those of *T. darti*.

Although this species has retained primitive features of the mandible and molars as in *T. darti*, the P_3 is remarkably small and the height of canines is reduced as in *T. oswaldi*.

It is well documented that the *T. darti*-*T. oswaldi* lineage was well established during the Plio-Pleistocene. The time range of this lineage spans the interval from approximately 3·3 Ma to probably less than 0·4 Ma. According to different authors this lineage would represent either two distinct species (Eck & Jablonski, 1987; Eck, 1993, Delson, 1993) or a single continuous chronospecies (Singer, 1962; Szalay & Delson, 1979; Dechow & Singer, 1984; Leakey, 1993). A speciation may have occurred, in this lineage, some time before 2·5 Ma, which gave rise to *T. atlanticus*. The ancestor of *T. atlanticus* would therefore be either *T. darti* or *T. oswaldi darti*. We think that the reduction in the size of canines and premolars in this species, similar to that in *T. oswaldi*, does not have phylogenetic significance, but can be explained by convergence. The faunal association of Ahl al Oughlam indicates an open environment, as many sites which yielded remains of *T. oswaldi*.

Concerning the origin of *Theropithecus*, it is worthwhile to discuss here the partial humerus from the Tunisian locality of Garaet Ichkeul. Geraads (1987) pointed out that there is no significant difference between this humerus and that of *T. gelada*. Delson (1974, 1993), however, referred it to a *Macaca*. We reassert here the former opinion. On the Ichkeul humerus, the lateral supracondylar crest is like that of the gelada, but considerably weaker than that of macaques. In both the Ichkeul humerus and that of *T. gelada* the medial epicondyle is less retroflexed than that of macaques. In addition, on the posterior portion of the distal extremity of the humerus, between the trochlea and the medial epicondyle, there is a relatively wide groove, as in the gelada, but absent in macaques. Finally, the overall slenderness of the humerus is like that of the gelada. It seems therefore that the humerus in question is closer to that of a theropith than to a macaque species. Yet, it is necessary to note that the humerus differs from both in having a shaft which is more triangular in section. If this partial humerus from Ichkeul (probably of early Pliocene age), really belongs to a *Theropithecus* species, we can imagine one more lineage of the genus with a North African origin. This suggestion remains very hypothetical, however, as the identification of postcranial parts of *Theropithecus* species remains a difficult task.

Acknowledgements

We are particularly indebted to J. Hassar Benslimane, head of the INSAP, and to J.-P. Raynal, head of the MPPFMA, for having invited D.G. to work in Morocco and allowed Z.A. to work on the theropith material. We thank Jara Hailemariam, head of the CRCCH, Muluneh Gebremariam (National Museum of Ethiopia), L. Ginsburg, M. Tranier and F. Renoult (Muséum National d'Histoire Naturelle, Paris) for their permission to work on the fossil and modern *Theropithecus* materials in their care. Thanks to Gerald G. Eck, Eric Delson and reviewers for corrections to the manuscript. We thank Alemu Admasu, Alisa Reynolds, Bill Kimbel, Eric Delson and Mario Chech for providing casts, Dominique Visset for the drawings, Maryse Delaplanche and Dorine Destable for the photos. Publication permit No. 4/97-98.

References

Arambourg, C. (1970). Les Vertébrés du Pléistocène de l'Afrique du Nord. *Arch. Mus. nat. Hist. Nat.*, sér.7 **10**, 1–126.

Arambourg, C. (1979). Vertébrés Villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux). Paris: Fondation Singer-Polignac. 1–141.

Dechow, P. C. & Singer, R. (1984). Additional fossil *Theropithecus* from Hopefield, South Africa: a comparison with other African sites and reevaluation of this taxonomic status. *Am. J. phys. Anthrop.* **163,** 405–435.

Delson, E. (1974). Preliminary review of cercopithecid distribution in the circum-Mediterranean region. *Mém. B.R.G.M.* (France) **78,** 131–5.

Delson, E. (1993). *Theropithecus* fossils from Africa and India and the taxonomy of the genus. In (N. G. Jablonski, Ed.) *Theropithecus. The Rise and Fall of a Primate Genus*, pp. 157–189. Cambridge: Cambridge University Press.

Delson, E. & Hoffstetter, R. (1993). *Theropithecus* from Ternifine, Algeria. In (N. G. Jablonski, Ed.) *Theropithecus. The Rise and Fall of a Primate Genus,* pp. 191–208. Cambridge: Cambridge University Press.

Eck, G. (1987). *Theropithecus oswaldi* from the Shungura Formation, lower Omo basin, south western Ethiopia. In: *Les faunes plio-pléistocènes de la basse vallée de l'Omo (Ethiopie)*. **3**, Cercopithecidae de la Formation de Shungura, pp. 123–139. Cahiers de Paléontologie, Travaux de Paléontologie Est-Africaine. Paris: Editions du CNRS.

Eck, G. & Jablonski, N. G. (1987). The skull of *Theropithecus brumpti* compared with those of other species of the genus *Theropithecus*. In: *Les faunes plio-pléistocènes de la basse vallée de l'Omo (Ethiopie)*, **3**, Cercopithecidae de la Formation de Shungura, pp. 11–122. Cahiers de Paléontologie, Travaux de Paléontologie Est-Africaine. Paris: Editions du CNRS.

Eck, G. (1993). *Theropithecus darti* from the Hadar Formation. Ethiopia. In (N. G. Jablonski, Ed.) *Theropithecus. The Rise and Fall of a Primate Genus,* pp. 15–83. Cambridge: Cambridge University Press.

Geraads, D. (1980). La faune des sites à *Homo erectus* des carrières Thomas (Maroc). *Quaternaria* **22,** 65–94.

Geraads, D. (1987). Dating the north African cercopithecid fossil record. *Hum. Evol.* **2,** 19–27.

Geraads, D. (1993). *Kolpochoerus phacochoeroides* (Thomas, 1884) (Suidae, Mammalia) du Pliocène supérieur de Ahl al Oughlam (Casablanca, Maroc). *Géobios* **26**(6), 731–743.

Geraads, D. (1995). Rongeurs et Insectivores (Mammalia) du Pliocène final de Ahl al Oughlam (Casablanca, Maroc). *Géobios* **28**(1), 99–115.

Geraads, D. (1997). Carnivores du Pliocène terminal de Ahl al Oughlam (Casablanca, Maroc). *Géobios* **30**(1), 127–164.

Gibert, J., Ribot, F., Gibert, L., Leakey, M., Arribas, A. & Martinez, B. (1995). Presence of the Cercopithecid genus *Theropithecus* in Cueva Victoria (Murcia, Spain). *J. hum. Evol.* **28,** 487–493.

Gupta, V. J. & Sahni, A. (1981). *Theropithecus delsoni*, a new cercopithecine species from the upper Siwaliks of India. *Bull Indian geol. Assoc.* **14,** 69–71.

Jolly, C. J. (1972). The classification and natural history of *Theropithecus* (*Simopithecus*) (Andrews, 1916), baboons of the African Plio-Pleistocene. *Bull. Br. Mus. nat. Hist. Geology* **22,** 1–123.

Krentz, H. B. (1993). Postcranial anatomy of extant and extinct species of *Theropithecus*. In (N. G. Jablonski, Ed.) *Theropithecus. The Rise and Fall of a Primate Genus*, pp. 383–422. Cambridge: Cambridge University Press.

Leakey, M. G. & Leakey, R. E. F. (1973). Further evidence of *Simopithecus*, (Mammalia, Primates) from Olduvai and Olorgesailie. In (L. S. B. Leakey, R. J. G. Savage & S. C. Coryndon, Eds) *Fossil Vert. Afr.* **3**, pp. 101–20. New York: Academic Press.

Leakey, M. G. (1993). Evolution of *Theropithecus* in the Turkana Basin. In (N. G. Jablonski, Ed.) *Theropithecus. The Rise and Fall of a Primate Genus*. pp. 85–1213. Cambridge: Cambridge University Press.

Maier, W. (1972). The first complete skull of *Simopithecus darti* from Makapansgat, South Africa, and its systematic position. *J. hum. Evol.* **1,** 395–405.

Pickford, M. (1993). Climate change, biogeography and *Theropithecus*. In (N. G. Jablonski, Ed.) *Theropithecus. The Rise and Fall of a Primate Genus*. pp. 227–243. Cambridge: Cambridge University Press.

Raynal, J.-P., Texier, J.-P., Geraads, D. & Sbihi-Alaoui, F. Z. (1990). Un nouveau gisement paléontologique plio-pléistocène en Afrique du Nord: Ahl Al Oughlam (ancienne carrière Deprez) à Casablanca (Maroc). *C. R. Acad. Sci.* Paris **310**, sér. II, 315–230.

Singer, R. (1962). *Simopithecus* from Hopefield, South Africa. *Biblioth. Primatol.* **1,** 43–70.

Szalay, F. S. & Delson, E. (1979). *Evolutionary History of the Primates*. New York, London Academic Press.

Thomas, P. (1884). Sur quelques formations d'eau douce de l'Algérie. *Mém. Soc. géol. Fr.* **3**(2), 1–53.