

6 *Theropithecus* from Ternifine, Algeria

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Summary

1. The Ternifine *Theropithecus*, referred to *T. oswaldi leakeyi*, is here described for the first time.
2. Published analyses of the site and its fauna suggest that it may date to about 700 Ka, that the paleoenvironment was quite open and arid around the central spring-fed lake, and that the bone accumulation was partly of human cultural origin.
3. Three well-preserved specimens of the male mandible document all of the morphology of this element, revealing minor differences from described Olduvai jaws.
4. The dental sample includes 68 teeth (not counting definite antimeres), of which five are deciduous.
5. The degree of sexual dimorphism in lower canine length and width is strong, as known for other populations of this subspecies; this is one additional line of evidence supporting the interpretation of male gender for the holotype of '*Simopithecus jonathani*' from the Olduvai Masek Beds – its P₃ mesial flange was small because it received a small C¹.
6. In both cheek tooth width (length is a poor comparator because it decreases greatly with advanced wear) and canine length and width, the Ologesailie sample has the highest mean among all *T. o. leakeyi* populations, and its variation range encompasses all of them.
7. Molar size does not increase monotonically with time, but varies somewhat, with a possible decrease in the youngest fossils (e.g. Masek and Thomas Quarries).

Introduction

The largest sample of *Theropithecus* from North Africa is that collected from Ternifine (once Palikao, now Tighenif), Algeria, by Camille Arambourg and Hoffstetter in 1955–6. This sample has never been described nor illustrated in any detail (although it was analyzed by S. van den Brink in an unpublished 'mémoire de D.E.A.', 1980, Univ. Paris VI), and we thus take this opportunity to document it here,

as well as to make some comparisons with other late *Theropithecus* populations. Following M.G. Leakey and Delson (chapters 3 and 5, respectively, this volume), we include the Ternifine sample in *T. oswaldi leakeyi* Hopwood, 1934 (a mainly Middle Pleistocene subspecies typified by increased molar size and canine/premolar reduction).

Historical review of studies of Ternifine and its primates

Fossil bones were discovered outside the village of Palikao by local quarrymen as early as 1872 (and recognized as such by Tommasini). The locality was first reported in 1879 by Pomel, who described a new species of proboscidean. Tommasini (1883) was the first to report Paleolithic artifacts. In 1885, the Association française pour l'Avancement des Sciences held a meeting in Algeria, and in three abstracts Pomel (1886a, b, c) discussed the site's mammalian fauna and archaeology. These were followed by a longer report of a field trip (1888a) and then a review of the géology and fossil mammals (1888b). Camille Arambourg visited the region briefly in 1931 and recovered additional fossils.

In 1954, 1955, and 1956, Arambourg and Hoffstetter undertook extensive new excavations at Ternifine. Arambourg & Hoffstetter (1954) reported the first results of this work, and later Arambourg (1954a) described two hominid mandibles as *Atlantropus mauritanicus* (now *Homo erectus*). Specimens of *Theropithecus* were first mentioned by Arambourg (1954b) as 'a large baboon' (un grand

Cynocéphale), then as 'a large baboon similar to the giant fossil forms of eastern and southern Africa' (1955). Following the second field season, Arambourg & Hoffstetter (1955) reported the discovery of a third hominid mandible and a parietal, and included among the fauna 'a large baboon recalling certain giant forms from South Africa, as well as a cercopithece close to the macaques', but this putative second form was not mentioned again. A long monograph on the fossil hominid remains (Arambourg, 1963) was introduced by a brief review of the history of study and géology of Ternifine (Arambourg & Hoffstetter, 1963). They described the excavation techniques and stratigraphy, but did not even provide a complete faunal list, merely indicating once again the presence of a large baboon. Cooke (1963, p. 70) included '*Simopithecus* cf. *major*' in a tabulation of North African fossil mammals, but this taxon is a *lapsus*, perhaps based on a personal communication from Arambourg or a confusion with *Gorgopithecus major*, a South African large papionin previously thought related to *Theropithecus* (cf. Freedman, 1957).

In 1966, Arambourg briefly showed the Ternifine hominids and cercopithecids to Delson in Paris, and they discussed these specimens again in 1969, just weeks before Arambourg's death. In 1970, Hoffstetter permitted Delson to study the *Theropithecus* collection from Ternifine but indicated that he planned to give the fossils to a student to describe in due course. Jolly (1972) did not discuss the material in any detail in his revision of the fossil *Theropithecus*, but he tentatively included the Ternifine population in the

new Olorgesailie subspecies, *T. (S). oswaldi mariae*. Delson (1975, Fig. 19) published photographs of two mandibular fragments and nine isolated teeth, citing the taxon as *Theropithecus (Simopithecus)* aff. *oswaldi*. Szalay & Delson (1979) recognized numerous subspecies within *T. (S). oswaldi*, placing the Ternifine sample as 'subspecies indet. A' without diagnosis. S. van den Brink analyzed the Ternifine *Theropithecus* in her unpublished 1980 'mémoire de D.E.A.'. More recent studies of the locality and its fauna (see below) have discussed the cercopithecids little if at all. Delson (see chapter 5) has formally rejected the use of *Simopithecus* even as a subgenus, following the suggestions of several recent authors.

Age of the locality

The most recent overall analysis of the stratigraphy and geochronology of Ternifine is that by Geraads *et al.* (1986). They described the first results of a renewed collection effort in 1982–3, on the 110th anniversary of the finding of the site. Faunal studies summarized there, and those by Geraads (1987) and Tong (1986, 1989) concluded that Ternifine is intermediate in age between Sidi Abdallah (Morocco) or Aïn Hanech (Algeria) and the Thomas quarries (Morocco), probably closer to the latter. The former are probably Early Pleistocene and the latter later Middle Pleistocene in age, which leaves Ternifine close to the Early-Middle Pleistocene boundary, as originally suggested by Arambourg & Hoffstetter (1963) and by Jaeger (1975). Preliminary paleomagnetic

studies indicated normal polarity at the base of the section, thus either early Brunhes chron (c. 750–600 Ka) or Jaramillo subchron (c. 950 Ka). Geraads (1987) accepted the younger of these dates as most likely.

Paleoenvironment and taphonomy of Ternifine

The fauna from Ternifine includes a number of taxa which provide an indication of the paleoenvironment. The fossils themselves were recovered from a lacustrine deposit fed by artesian springs. Geraads (1981) described 11 species of ruminant artiodactyls, of which the most common were gazelles and alcelaphines, indicating a generally open and dry habitat. The small mammals (Jaeger, 1975; Tong, 1986, 1989) appear to confirm the essentially sub-desertic habitat, with gerbillids dominating the assemblage. On the other hand, the large number of hippopotamid remains and the presence of the anuran *Discoglossus* indicate that the most proximal animal community might be hydrophilous. Geraads noted that *Ursus* and *Theropithecus* also might indicate a different environment, which is supported by the common occurrence of *T. oswaldi* in localities tied to a well-watered landscape (Jolly, 1972).

In terms of the taphonomy of the Ternifine accumulation, Denys, Patou & Djemali (1984) have reported cutmarks, mainly on hippopotamid bone recovered during the 1982–3 campaign. These indications of marrow extraction and flensing, as well as a possible bone tool, led them to suggest that the assemblage was at least

partly of human origin, rather than solely a natural or carnivore accumulation. Denys *et al.* (1987) extended this work, suggesting the likelihood of a mammalian carnivore or avian raptor having been responsible for at least part of the accumulation of small mammals.

Description and comparisons

Mandible

The Ternifine fossils are housed in the Institut de Paléontologie, Muséum national d'Histoire Naturelle, Paris (MNHN-P), catalogued under the prefix TER; the museum acronym will not be repeated in the descriptions. There are three specimens of the male mandible in the Ternifine sample, which among them preserve most of the mandibular morphology. Measurements on these three specimens are given in Table 6.1.

A male symphysis preserving all the teeth from I₁–P₄ on both sides (TER 1702, Fig. 6.1) reveals more symphyseal morphology than any other male of the species yet described. There is little indication of any mandibular corpus fossa, not even as much as in Old 067/5603 (from Bed II), which is about the same size overall. Eck (see chapter 2, following Eck & Jablonski, 1987) has discussed fossa development in terms of the ratio of fossa depth (indentation) to corpus thickness. In TER 1702, this ratio is about 0.05 (difficult to determine because the indentation is so slight), which is appreciably less than in any other *T. oswaldi* and comparable only to the least excavated *T. darti* (see Eck, chapter 2, Table 2.12).

The mental ridges begin at the break below P₄, converging around a broad flattened region which extends up to the middle of the anterior symphyseal surface. About 20 mm below the anterior alveolar margin (infradentale), the ridges end in a shallow depression. The surface bulges slightly up to infradentale. The area between the ridges is not rugose or raised, as in the two large Olduvai mandibles. The planum alveolare is only slightly concave, flatter than in 067/5603. The tooth rows diverge posteriorly, with an angle of 60° from infradentale to the centers of each P₄. Presumably, the cheek tooth rows became subparallel after that point.

A left corpus (TER 1703, Figs 6.2 and 6.4), probably of an adult male, lacks the superior half of the ramus but extends forward to P₄ (below M₁ basally). This individual was slightly smaller and probably older than the preceding, as the P₄ is worn more than those in the symphysis 1702. Again, there is little indication of a mandibular corpus fossa, although the surface bone below P₄ is broken away, exposing matrix and spongy bone within. Gonion is smoothly rounded below, curving up to the point of breakage about the level of the alveolar plane. The corpus shallows slightly from M₁ to M₃, with a ratio of these two depths of 1.21, comparable to values reported by Eck (see chapter 2) for Olduvai mandibles.

A third specimen (TER 1815, Fig. 6.2) preserves most of a right ramus, whose large size suggests it may also be male. Its maximum mesiodistal length is about 58 mm, while height from the base of the notch between coronoid and condyle to

Table 6.1. Measurements (in mm) of Ternifine mandibles.

Variable (Eck number*)	TER 1702	TER 1703
Symphyseal length (infradentale–gnathion)	66.0 (est.)	
Symphyseal height (perpendicular to occlusal plane)	36.0 (est.)	
Length of planum alveolare (infradentale to inferodistal most point on superior transverse torus, 'supertorion')	39.0	
Height of planum alveolare (gnathion–'supertorion')	33.0 (est.)	
Depth of the incisive plane (26)	38.2 (est.)	
Width of the incisive plane (27)	33.9	
Alveolar width across I ₂ s (28)	16.8	
Maximum width across I ₂ s	17.7	
Alveolar width across I ₁ s	7.8	
Maximum width across I ₁ s	9.8	
External width across C ₁ s (29)	35.0	
Internal width between C ₁ s	12.5	
Internal width between P ₃ s	29.5	
Toothrow (partial) lengths:		
M ₃ – I ₁ (reconstruction, est.) 100		
M ₃ – C ₁ (reconstruction, est.) 97		
M ₃ – P ₄		64.5
M ₃ – M ₁ (30)		54.6
P ₄ – C ₁	42.2	
P ₄ – I ₁	45.3	
Alveolar thickness at M ₂		
Corpus depth, below middle of		
P ₄ (buccal side)	43.6	
M ₁ (buccal side) (24)		45.2
M ₂ (buccal side)		42.3
M ₃ (buccal side) (25)		37.4
M ₁ (lingual side)		46.9
M ₃ (lingual side)		42.3
Depth mandibular corpus fossa (22)	<1.0	
Thickness of corpus at fossa (23)	17.8	

* Numbers in parentheses correspond to measurements described by Eck (chapter 2, this volume).

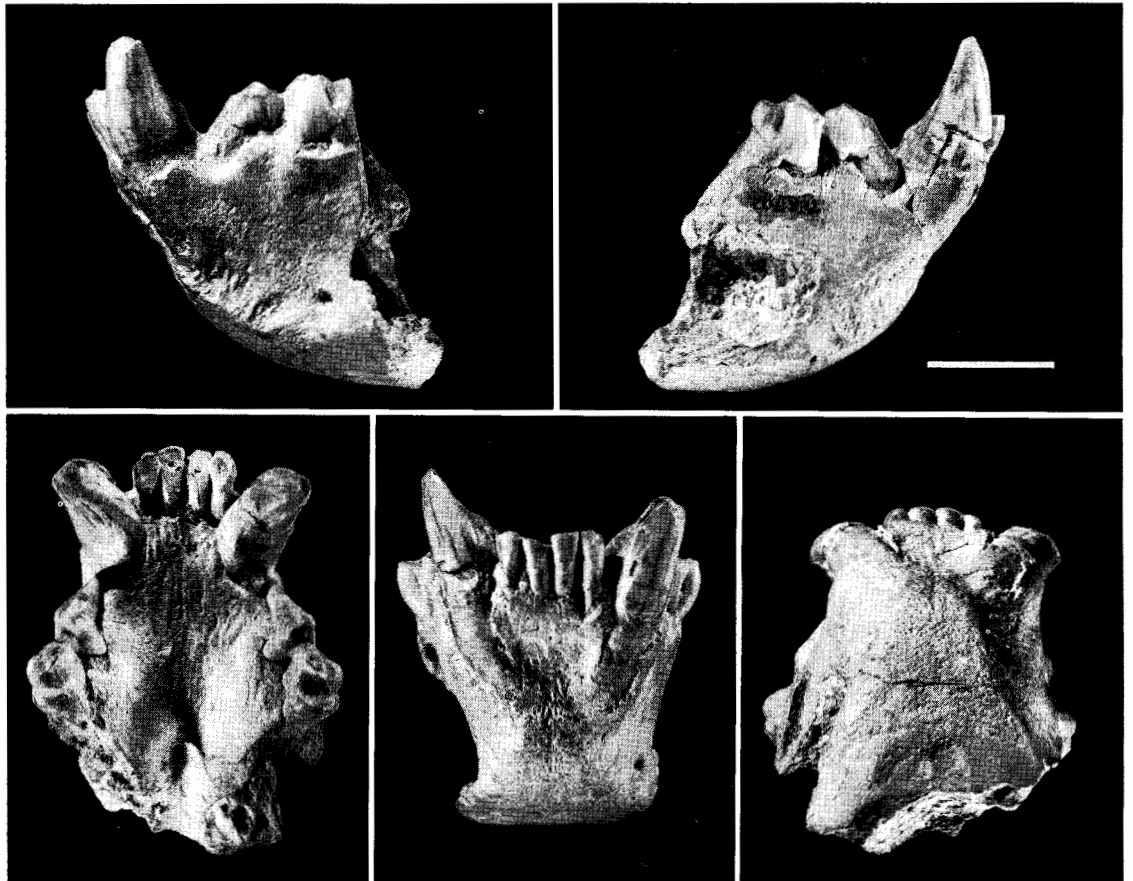


Fig. 6.1. *Theropithecus oswaldi leakeyi* from Ternifine, Algeria. Young adult male symphysis, MNHN-P TER 1702, scale bar = 2 cm. Top row, left and right lateral views; bottom row, oclusal, anterior and basal views; all in oclusal plane orientation.

the base of the ramus (anterior to gonion) is about 96 mm.

Figure 6.3 is a photographic reconstruction of the mandible based on the preceding three specimens. The symphysis is 5–10 per cent larger than the corpus fragment and was enlarged by 7 per cent to better connect with it.

Dentition

In addition to the three large fragments, 53

isolated permanent teeth were identified as *Theropithecus*. There is also a small fragment of juvenile corpus with right dP_4 - M_1 (TER 1704), as well as (one each) isolated right and left dP_4 , right dP^4 and partial left dP^3 . The teeth are in general typical of large members of the genus; measurements are presented in Table 6.2, and selected examples are illustrated in Figs 6.4–6.6. A full listing of Ternifine specimens is included in Appendix I to this volume.

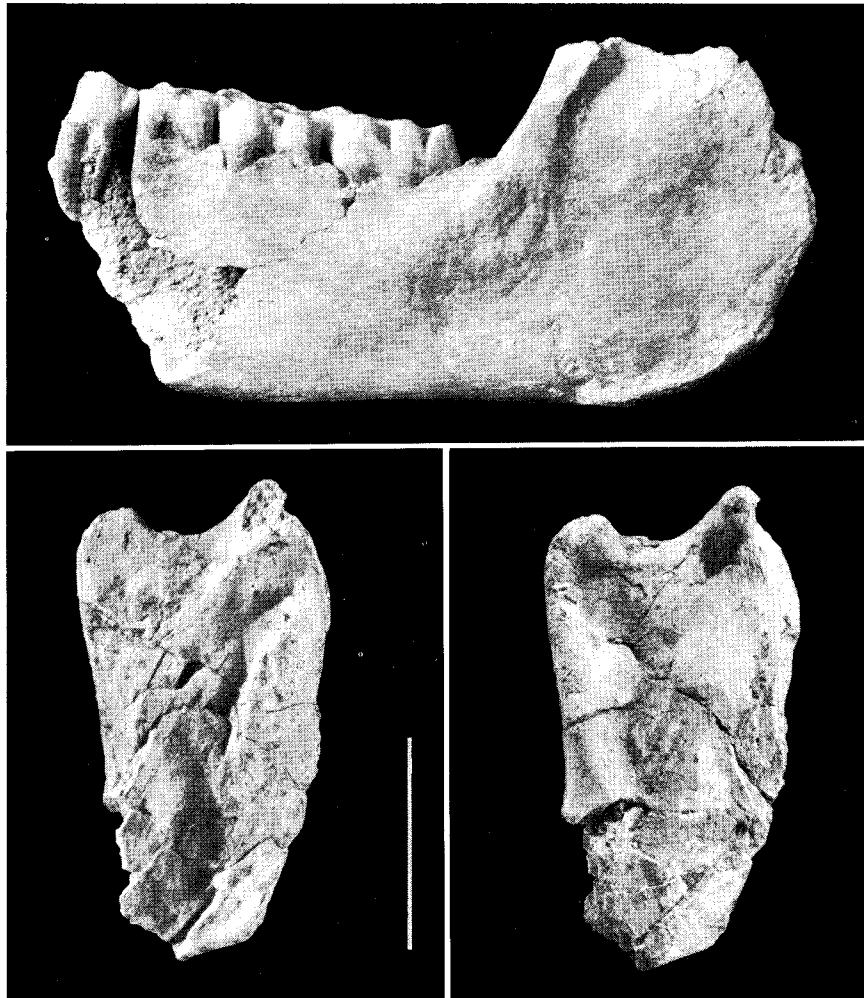


Fig. 6.2. *Theropithecus oswaldi leakeyi* from Ternifine, Algeria. Above, older adult male left mandibular corpus, MNHN-P TER 1703, lateral view; below, right partial male mandibular ramus, MNHN-P TER 1815, internal and (photographically reversed) external views; scale bar = 5 cm.

Among the most interesting of these teeth are the lower canines, which document strong sexual dimorphism in the Ternifine population. Two male lower canines (one in the symphysis, another isolated [TER 1725]) are robust in length and width, but not very tall above the cervix. A single much smaller specimen

(TER 1726) is identified as a female. It is relatively less thick mesiodistally than the male, with a lightly built root (Fig. 6.6). This degree of dimorphism is comparable to that seen in the more extensive sample of slightly larger *Theropithecus* from Olorgesailie (Jolly, 1972; Leakey & Leakey, 1973; and especially, Leakey,

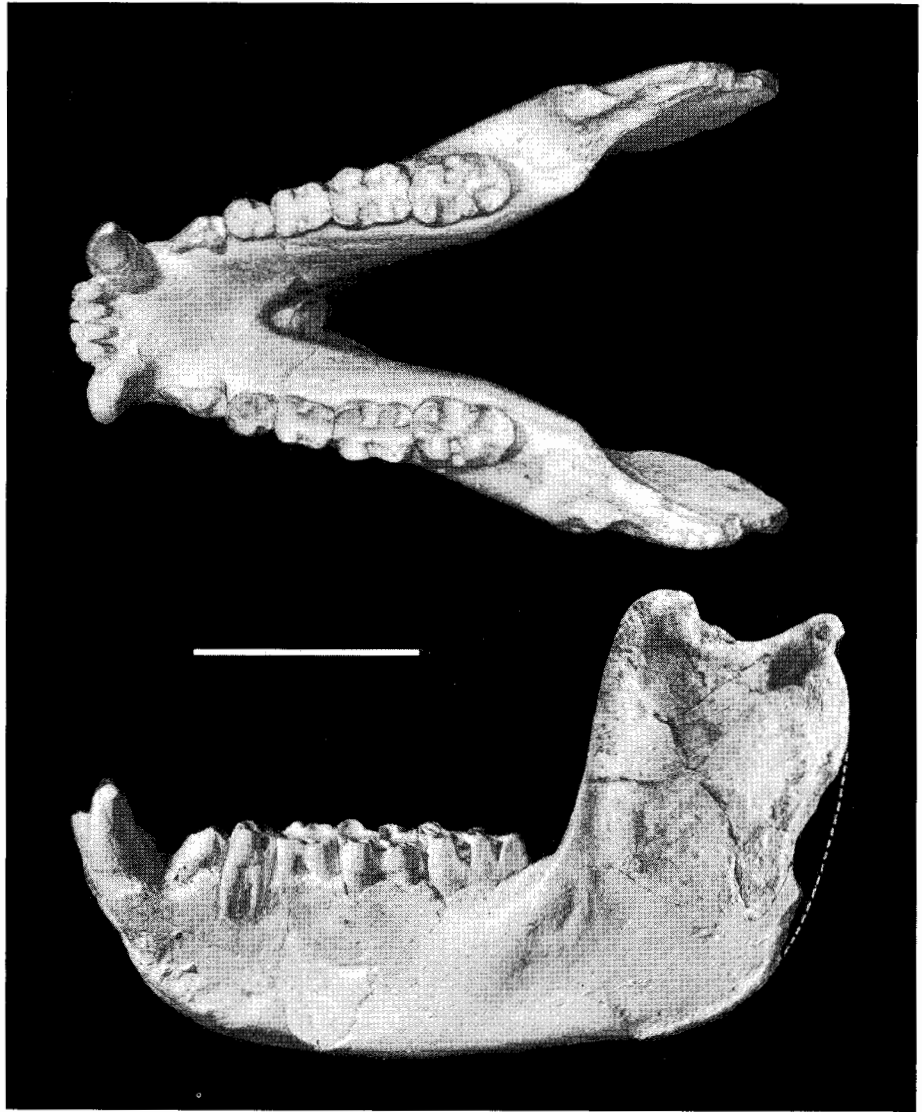


Fig. 6.3. *Theropithecus oswaldi leakeyi* from Ternifine, Algeria. Photographic reconstruction of male mandible, based on MNHN-P TER 1702, 1703 and 1815, scale bar = 5 cm.

chapter 3). Along with the clear sex difference in root length and width, this level of crown dimorphism further serves to confirm the male gender of the Olduvai Masek Beds mandible 068/6516 (previously Old. 1472, 57), as argued by

several authors. That specimen's canine roots are almost as strong as in the two Ternifine male canines, but the crown is quite low, which in turn explains the short mesiobuccal flange of the P₃; it must have received a very small upper canine crown.

Table 6.2. Measurements (in mm) of Ternifine *Theropithecus* teeth.

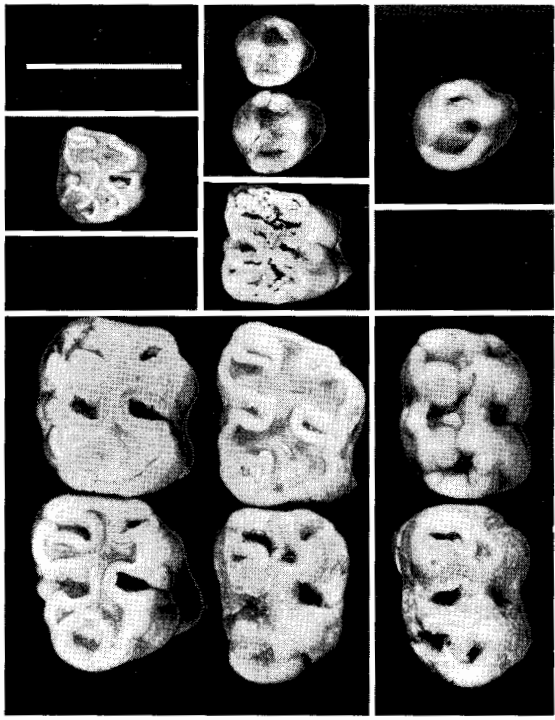
Variable	N	Minimum	Maximum	Mean	SE	CV
I ₁ W	3	6.2	8.7	7.17	0.78	
I ₁ LA	3	3.8	5.5	4.93	0.57	
I ₁ L	3	4.6	7.4	5.63	0.89	
I ₂ W	3	5.4	6.8	6.23	0.43	
I ₂ LA	3	3.5	5.2	4.10	0.55	
I ₂ L	3	4.2	6.3	5.13	0.62	
C ₁ W FEMALE	1			10.8		
C ₁ L FEMALE	1			6.0		
C ₁ II FEMALE	1			14.4		
C ₁ W MALE	2	14.3	14.7	14.50	0.20	
C ₁ L MALE	2	10.0	11.0	10.50	0.50	
C ₁ H MALE	2	20.3	23.4	21.85	1.55	
P ₃ W MALE	4	7.4	9.2	8.18	0.38	
P ₃ L MALE	3	15.3	20.4	17.87	1.47	
P ₃ FII MALE	3	15.9	20.5	17.97	1.35	
P ₄ W	7	8.9	9.8	9.53	0.13	3.62
P ₄ L	8	9.7	11.8	11.09	0.28	7.04
M ₁ AW	6	9.5	11.3	10.57	0.27	6.21
M ₁ PW	6	10.2	11.0	10.58	0.14	3.35
M ₁ L	4	12.7	16.5	15.08	0.85	
M ₂ AW	6	13.0	15.0	13.45	0.31	5.68
M ₂ PW	6	12.5	14.6	12.97	0.34	6.35
M ₂ L	6	17.0	19.8	18.10	0.39	5.28
M ₃ AW	8	14.3	16.2	15.11	0.26	4.80
M ₃ PW	8	12.7	14.5	13.33	0.22	4.74
M ₃ L	8	21.5	27.7	24.06	0.73	8.59
dP ₄ AW	3	7.5	8.3	7.97	0.24	
dP ₄ PW	3	8.2	9.0	8.57	0.23	
dP ₄ L	3	11.4	12.1	11.70	0.21	
I ² W	1			9.0		
I ² LA	1			5.4		
I ² L	1			7.5		
C ¹ W MALE	2	11.3	14.4	12.85	1.55	
C ¹ L MALE	3	15.2	17.1	15.83	0.63	
C ¹ II MALE	2	33.0	36.5	34.75	1.75	
p ²³ W	1			9.1		
p ²³ L	1			8.2		
p ²³ H	1			10.0		
p ²⁴ W	3	10.4	11.7	10.97		

Table 6.2. *Contd.*

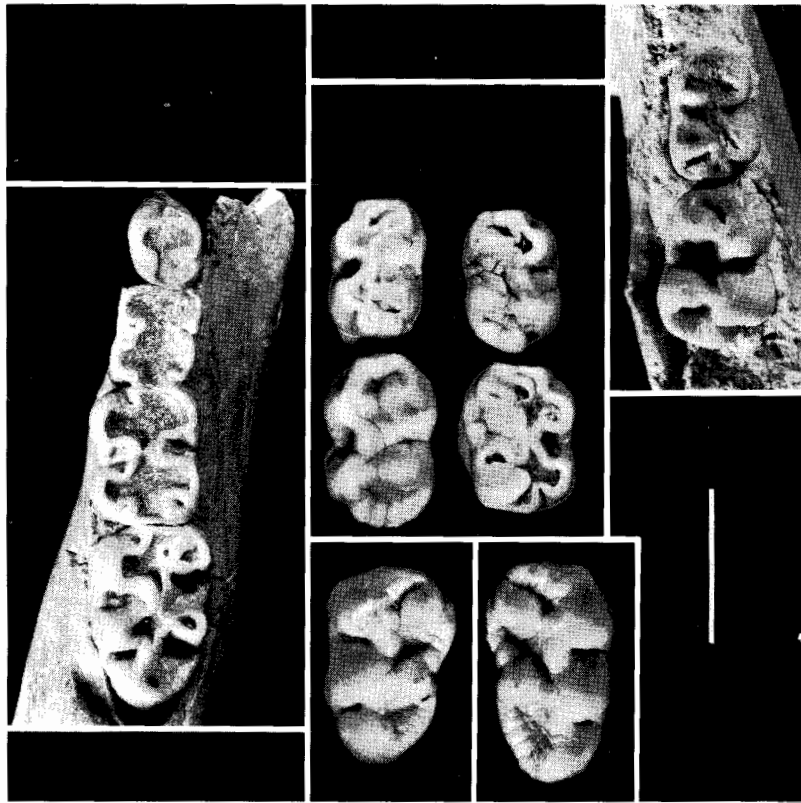
Variable	N	Minimum	Maximum	Mean	SE	CV
P ² 4L	3	9.1	10.3	9.70	0.35	
P ² 4H	3	9.4	11.2	10.57	0.58	
M ¹ AW	2	12.5	13.0	12.75	0.25	
M ¹ PW	2	11.8	13.3	12.55	0.75	
M ¹ L	2	13.2	15.9	14.55	1.35	
M ² AW	2	15.5	17.6	16.55	1.05	
M ² PW	2	14.4	16.5	15.45	1.05	
M ² L	2	19.4	19.7	19.55	0.15	
M ³ AW	4	15.5	17.6	16.50	0.55	
M ³ PW	4	13.6	16.5	14.58	0.65	
M ³ L	4	19.7	21.1	20.45	0.29	
dP ³ AW	1			7.7		
dP ⁴ AW	1			10.0		
dP ⁴ PW	1			10.4		
dP ⁴ L	1			10.9		

N: number of measureable specimens; SE: standard error of the mean; CV: coefficient of variation. Values are given separately by sex for canines and P₃s. For incisors, canines and premolars, L(ength) is always maximum mesiodistal, W(idth) is maximum buccolingual, taken perpendicular to length; therefore, for lower canines, because of their turned placement in the mandible, W is greater than L. Incisor LA is taken at the alveolar plane (=cervical level), as maximal length is only available on unworn teeth whose incisal edges have not been reduced due to attrition. P₃FII (flange height) is the distance from the cusp apex to the most mesial extent of the enamel along the mesial flange: it is equivalent to L(h) of Freedman (1957) or L of Singer (1962); L here is the maximum mesiodistal length of the tooth, as for Freedman (1957). For molariform teeth, AW and PW, respectively, are taken across the mesial and distal loph(id)s usually at the cervix; L, however, is taken at interdental contact points, often estimated due to wear, and decreases significantly in worn teeth.

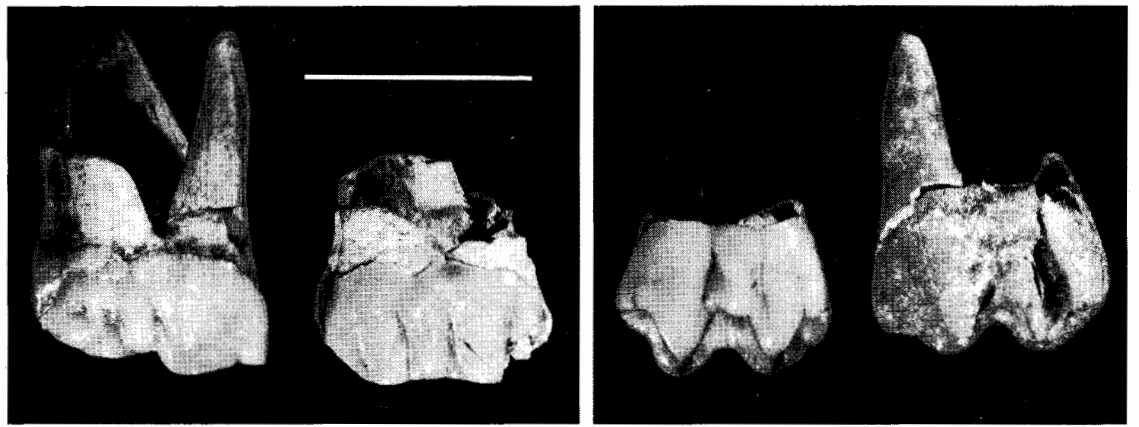
Fig. 6.4. Occlusal views of dentition of *Theropithecus oswaldi leakeyi* from Ternifine, Algeria, scale bar = 2 cm. (a) Upper teeth, left to right (and top to bottom within arranged 'toothrows'), all MNIN-P TER: left column, right dP⁴ (1733), right M²₂ (1762), right M³₂ (1758); center column, right P³ (1775), right P⁴ (1774), right M¹ (1764), right M²₂ (1761), right M³₂ (1759); right column (photographically reversed), left P⁴ (1765), left M²₂ (1763), left M³ (1760). (b) Lower teeth, left to right (and top to bottom within arranged 'toothrows'), all MNHN-P TER: 1703, left male? P₄-M₃ from corpus; left M₁₂ (1720), left M₂₂ (1757), left M₃ (1708); right M₁₂ (1715), right M₂₂ (1711), right M₃ (1707); right dP₄-M₁ (1704).



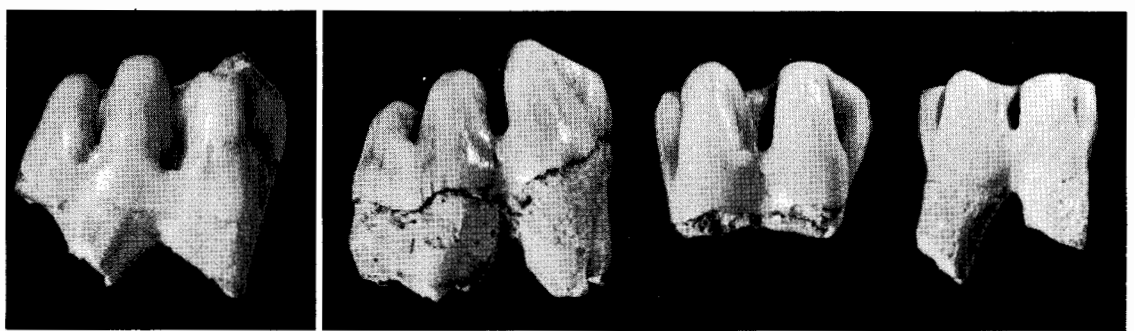
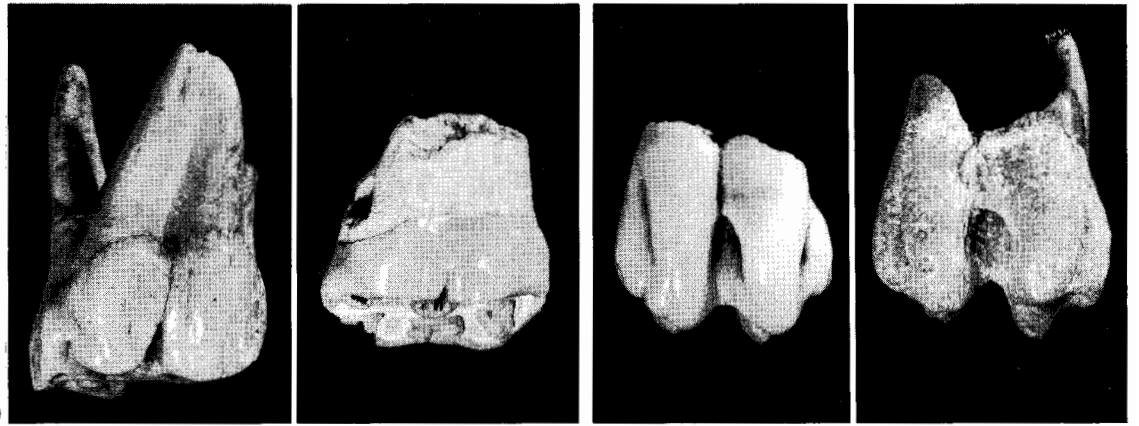
(a)



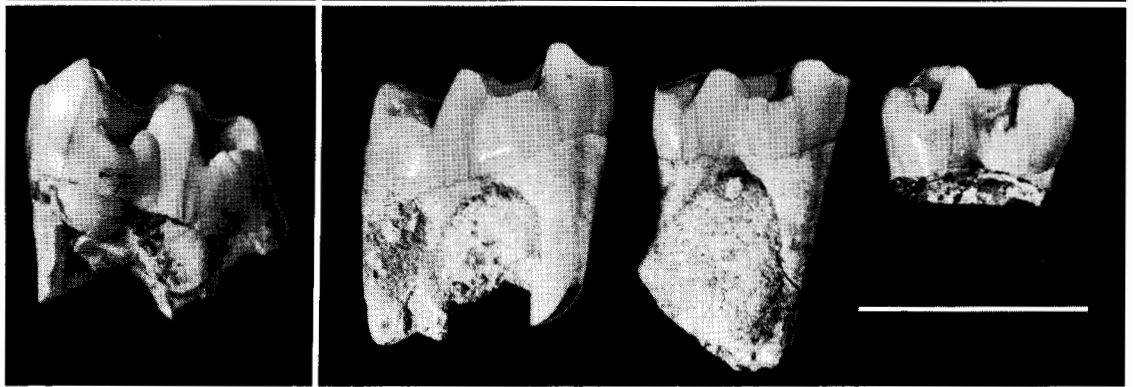
(b)



(a)



(b)



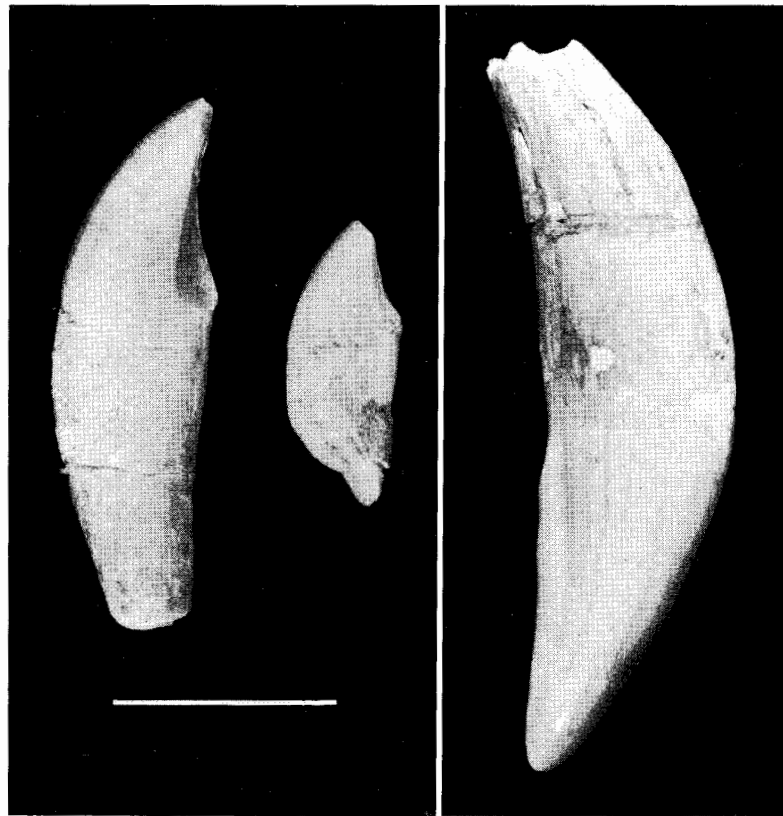


Fig. 6.6 Canines of *Theropithecus oswaldi leakeyi* from Ternifine, Algeria, in buccal view, scale bar = 2 cm. Left to right: MNHN-P TER 1725, male left C₁; 1726, female left C₁; 1780, male right C₁.

Although Eck (see chapter 2) continues to interpret this specimen as female (following Eck & Jablonski, 1984 and Leakey & Whitworth, 1958), Leakey (see chapter 3)

has provided additional evidence of its being male (see also Jolly, 1972; Leakey & Leakey, 1973; Szalay & Delson, 1979; Dechow & Singer, 1984), based on a new specimen from Kapthurin.

Fig. 6.5. Lateral views of dentitions of *Theropithecus oswaldi leakeyi* from Ternifine, Algeria, scale bar = 2 cm, all MNHN-P TER. (a) Upper teeth, top row buccal views, second row lingual views, left to right: right M^{3?} (1758), right M^{2?} (1762), left M_{2?} (1763), left M^{3?} (1760). (b) Lower teeth, top row buccal views: right M₃ (1708), right M₃ (1713), right M^{2?} (1757), right M_{1?} (1720); second row lingual views: right M₃ (1708), left M₃ (1706), left M_{2?} (1710), left M_{1?} (1715) (last three photographically reversed).

It is interesting to compare the overall dental measurements of the samples of *Theropithecus* from Ternifine, Olor-
gesailie, and Hopefield, as these localities are of comparable age and span the whole of the African continent (see Potts, 1989; Gibbons, 1990. Klein & Cruz-Urbe, 1991, suggested an age for the main Hopefield fauna between 0.7–0.4 Ma). Measure-

Table 6.3. *Measurements (in mm) of Hopfield Theropithecus teeth.*

Variable	N	Minimum	Maximum	Mean	SE	CV
P ₃ W FEMALE	3*	6.8	8.0	7.43	0.35	
P ₃ L FEMALE	1	12.1	12.1	12.10		
P ₃ FII FEMALE	3*	11.4	12.9	12.27	0.45	
C ₁ W MALE	2*	18.1	19.7	18.90	0.79	
C ₁ L MALE	2*	11.0	13.7	12.35	1.32	
C ₁ II MALE	2*	23.9	29.0	26.45	2.55	
P ₃ L MALE	1			17.8		
P ₃ FH MALE	1			25.4		
P ₄ W	4*	8.8	9.9	9.47	0.24	
P ₄ L	4*	10.1	11.1	10.67	0.23	
M ₁ AW	2*	9.7	11.8	10.75	1.05	
M ₁ PW	2*	9.9	11.6	10.75	0.83	
M ₁ L	3*	13.3	13.8	13.55	0.15	
M ₂ AW	2	14.0	14.9	14.45	0.49	
M ₂ PW	2	12.7	14.6	13.61	0.95	
M ₂ L	3	17.6	19.9	18.75	0.67	
M ₃ AW	4	15.0	18.2	16.69	0.66	
M ₃ PW	3	14.7	15.6	15.7	0.27	
M ₃ L	5	25.0	27.1	26.03	0.36	3.10
C ¹ W FEMALE	1*			10.2		
C ¹ L FEMALE	1*			9.3		
C ¹ II FEMALE	1*			18.0		

See Table 6.2 for measurement definitions.

* Indicates at least one specimen's measurements taken from Singer (1962) [SAM 6174, 6882 and 13905] or Dechow & Singer (1984) [16650 and 16680 P₃s].

ments of the Olorgesailie sample are provided by Jolly (1972), Leakey & Leakey (1973), and especially Leakey (see chapter 3), although no single published set is complete. Singer (1962) and Dechow &

Singer (1984) published measurements on the Hopfield specimens, but these differ by up to 10 per cent from measures taken by Delson¹. The latter are reported in Table 6.3 when available, along with

¹ Although Dechow & Singer (1984, p. 406) imply that their measurement techniques follow Dechow (unpublished Ph.D. Thesis, 1980), the latter did not give definitions for his dental metrics; instead, they follow Singer (1962), who in turn used the definitions of Freedman (1957), which are comparable to Delson's. It is thus unclear why there may be significant differences in values reported by these authors. Given the extensive wear on most Hopfield teeth and the uncertain condition of the Olorgesailie specimens, and in light of the great reduction in length of papionin cheek teeth with high wear, comparisons of length are less useful than those of width (although most workers emphasize the former).

published values for specimens unavailable to Delson.

In general, the Olororgesailie range of variation encompasses both Hopefield and Ternifine, with the means decreasing in that order. Various authors (e.g. Delson, 1983; Eck & Jablonski, 1987; see Eck and Leakey, chapters 2 and 3, respectively) have shown that the size of *Theropithecus* molar teeth increases through time. But attempts at more detailed correlation of size and age are not feasible – populations of comparable age vary too much both within and between samples for such precise comparisons to be meaningful. In fact, it appears that molar size may have decreased in the apparently youngest samples – Olduvai Masek Beds, Kapthurin (see Leakey, chapter 3) and Thomas Quarries (Geraads, Beriro & Roche, 1980) – but that may be due to small sample sizes.

Male canine length and width also show variation among the Middle Pleistocene samples without close correlation with age. The Hopefield specimen is extremely robust, while the Ternifine and Thomas Quarry canines are more gracile, and the Masek and Kapthurin fossils are smaller still. Once again, variation within the Olororgesailie sample appears to encompass all of the preceding individuals.

Leakey (see chapter 3, Table 3.6) also examines the relative canine-complex reduction in *T. oswaldi* by means of ratios comparing P_3 flange height and C_1 width to M_3 length in numerous specimens. Anterior teeth and M_3 do not co-occur in any Ternifine jaw, but if the two mandibles are combined, ratios of 0.65 and 0.63 are obtained. The P_3/M_3 ratio is very low, exceeded (or approached) only by the new

Kapthurin mandible. The canine ratio places Ternifine between the Kapthurin and Masek jaws and two of four from the KBS member; two other KBS specimens have higher ratios (larger canines) than a single upper Burgi jaw, however, indicating less consistency of interpretation. Based on Delson's measurements, one Hopefield specimen (South African Museum, Cape Town, No. 16680) has a premolar index of 0.74. Another Hopefield jaw (16648) preserves all three teeth in damaged condition; Delson's measurements yield premolar and canine indices of 1.02 and 0.72, respectively. Not only are the two premolar values far apart, the second is higher than for any specimen measured by Leakey. Despite potential inconsistencies, this indicates again that the Ternifine canine/ P_3 complex is reduced by comparison to the penecontemporaneous Hopefield sample.

In conclusion, the Ternifine sample of *Theropithecus oswaldi leakeyi* is reasonably typical of those populations placed in this taxon. It shows high sexual dimorphism, a reduced canine complex and a strongly buttressed mandibular corpus. Further comparison with additional specimens from younger North African localities, if they become available, might throw light on the apparent decoupling of size changes with time in different regions of Africa late in the history of this species.

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