

# 5 *Theropithecus* fossils from Africa and India and the taxonomy of the genus

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## Summary

1. The female *Theropithecus* skull from Swartkrans, South Africa, SK 561, is described for the first time after reconstruction by R. Clarke. It is closely similar to female crania from Kanjera, but the anterior dentition is better preserved. The probable male cranium SK 599 lacks a face or teeth, but is most likely referable to *Papio (Dinopithecus) ingens* on the basis of its short postglenoid processes. Several isolated teeth from Brain's recent excavations at Swartkrans demonstrate no significant size increase from members one to three; this suggests only a short span of time (perhaps less than 0.25 Ma) separated these horizons, rather than the 1+ Ma originally suggested by Brain.
2. The first fossil *Theropithecus* specimen ever published, a single lower molar from Ain Jourdel, Algeria, is described. It is a typical M<sub>1</sub> of a small species whose only distinction is the acute angle formed at the base of its median lingual notch. The distal humerus from Garaet Ichkeul, Tunisia, is probably from a macaque (rather than a *Theropithecus*, as suggested by Geraads).
3. The isolated *Theropithecus* molar from Lothagam-3, Kenya, is described. It is a slightly damaged and moderately worn tooth, probably M<sub>2</sub>, of a size comparable to several Plio-Pleistocene species of the genus. Its crown complexity and relief is high, and as it probably dates to between 4.0–3.3 Ma, it is unlikely to be a member of the *T. brumpti* lineage, whose early members have weakly complex molar crowns.
4. Two *Theropithecus* molars are described from Kanam East, Kenya. Although heavily worn, they compare most favorably with the Hadar sample of *T. darti*, which corresponds to a suggested earlier Pliocene age for the deposits.
5. Two isolated *Theropithecus* lower molars (probably M<sub>1</sub> and M<sub>2</sub>) have

- been recovered from the Senga 5A archeological site in the Semliki region of eastern Zaire. The larger, unworn tooth is comparable in size to those from a wide range of other sites, but it is most similar to populations from the Turkana Basin dating between 2.4–2.0 Ma, as suggested for other elements of the fauna. It is not possible to distinguish between isolated teeth of *T. oswaldi* and *T. brumpti* in this time range.
6. The only specimen of a *Theropithecus* ever described from outside Africa was recovered by E. Khan, not V.J. Gupta (the provenance of some of whose specimens has proven spurious). This maxilla with M<sup>2-3</sup> is also typical of the genus, but of quite large size; it probably dates to between 1.0 and 0.1 Ma.
  7. It is generally accepted that there are three main lineages within *Theropithecus*. Of these, the *T. brumpti* lineage is argued to be the sister to the *T. gelada* + *T. oswaldi* sublineages, based especially on Delson & Dean (see chapter 4). To recognize this phyletic pattern, the new subgenus *T. (Omopithecus)* is described for the *T. brumpti* lineage. Formal synonymies and diagnoses are given for the genus and the two accepted subgenera, but the subgenus *Simopithecus* is no longer recognized.
  8. Within the *T. oswaldi* lineage, the earliest site samples (from Hadar and Makapansgat) are tentatively separated as the species *T. darti*. The Ain Jourdel molar cannot be readily allocated to a known species, and the ICZN will be petitioned to suppress the nomen previously applied to it, '*Cynocephalus*' (= *Theropithecus atlanticus*, which might otherwise be a senior synonym.
  9. Within *T. oswaldi*, I follow the suggestion of M. Leakey (see chapter 3) that two African subspecies be recognized: *T. o. oswaldi* and the younger, larger *T. o. leakeyi* which presents greater reduction of the incisors, canines and P<sub>3</sub>. The subspecies time boundary is unclear but can broadly be drawn between most Turkana Basin specimens and those from Kanjera, Swartkrans, Peninj, and Olduvai Beds I–lower II on the one hand and those from Olduvai upper Bed II and above, Ologesailie, Kapthurin, Hopefield, Ternifine, and Thomas Quarries on the other. Outside Africa, the Mirzapur specimen (from India) is reduced in rank to a subspecies, *T. o. delsoni*. The questions of subspecies in modern savannah baboons and the use of this category in the fossil record are briefly discussed.

### Introduction

Since the first description of extinct *Theropithecus* from Kanjera (Andrews, 1916), numerous fossils have been reported from a great number of site units. It is useful to discuss here a variety of such specimens which have never been described sufficiently to permit colleagues to interpret or refer to them. The collection from Swartkrans, South Africa, is large

and well known, but additional specimens have become available in recent years. Isolated teeth or fragments from Ain Jourdel (Algeria), Mirzapur (India) and other sites are also in need of comparative analysis. This conference volume provides an excellent opportunity to present both the new and older material. The important sample from Ternifine, Algeria, which has never been described since its recovery in the 1950s, is discussed separately by Delson & Hoffstetter (see chapter 6).

Specimens discussed here are housed in the collections of numerous institutions, whose standard acronyms are as follows:

BM(NH) British Museum (Natural History), London (Department of Palaeontology)

IMNZ Institut des Musées nationales de Zaire, Kinshasa

KNM National Museums of Kenya, Nairobi

MNHN-P Muséum national d'Histoire Naturelle, Paris (Institut de Paléontologie)

NMT National Museum of Tanzania, Dar-Es-Salaam

PUC-GM Panjab University, Chandigarh, Geology Museum

TMP Transvaal Museum, Pretoria, South Africa (Department of Palaeontology)

UWMA University of the Witwatersrand Medical School (Department of Anatomy)

These acronyms will be employed the first time specimens are mentioned but not thereafter unless there is the possibility of confusion. Data presen-

ted in other papers in this volume will not be repeated here.

### Swartkrans, South Africa

The sample of *Theropithecus* from Swartkrans was described in some detail by Freedman (1957), with additional notes by Freedman & Brain (1977). In 1957, Freedman noted that the best preserved cranium was that of a female, SK 561, described as 'almost complete but very badly crushed' (p. 208; see Fig. 5.1). In 1980, with financial support from the Wenner-Gren Foundation, I arranged for Dr Ron Clarke to prepare a number of South African cercopithecoid fossils in the Transvaal Museum, including SK 561. Through the 1970s and 1980s, Dr C.K. Brain of that museum continued detailed excavation at Swartkrans, reinterpreting the local stratigraphy and collecting a large number of new cercopithecoid fossils (Brain *et al.*, 1988). Brain asked me to study these new specimens as part of my general work on southern African cercopithecoid palaeontology.

By way of brief review, Brain *et al.* (1988; also Brain, 1989) reported a local stratigraphy in which Member 1 at Swartkrans was heavily eroded after deposition in the chamber. The main fossiliferous patch excavated by Broom and other early workers was termed the 'Hanging Remnant', as it was emplaced high on the north wall. A second patch of Member 1 remained on the floor, separated from the former by a large gap; it was called the 'Lower Bank' or 'Orange Breccia'. All horizons above this were originally

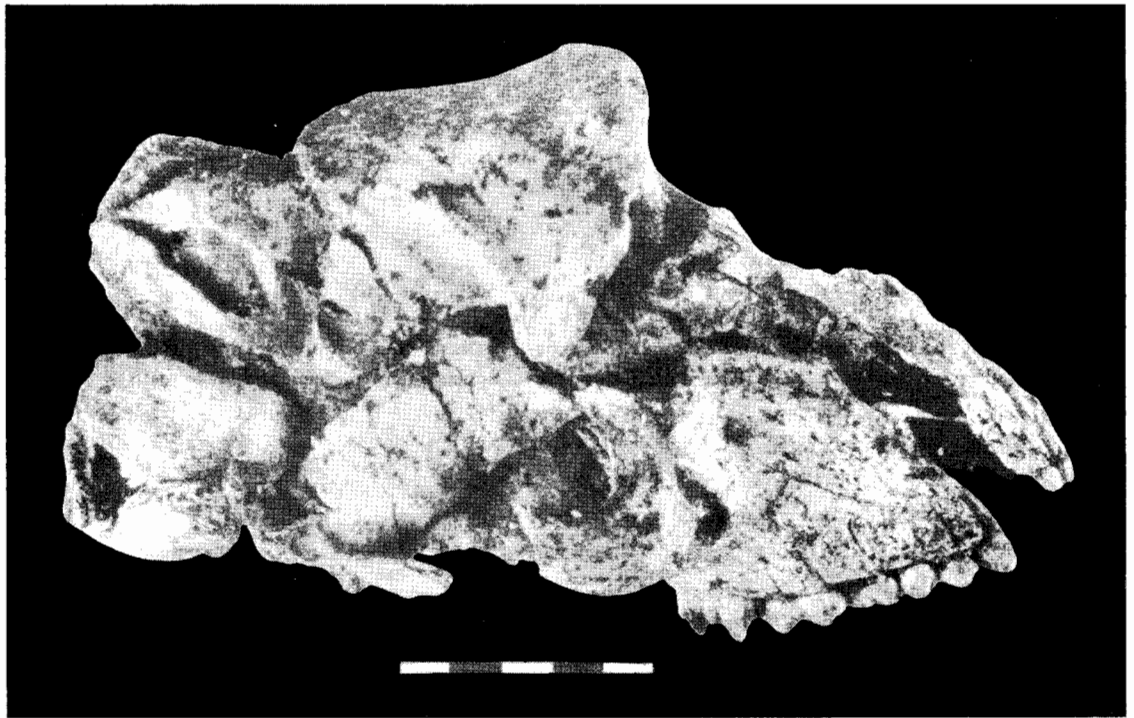


Fig. 5.1. Crushed female *Theropithecus oswaldi* cranium SK 561, before reconstruction. Scale = 5 cm.

referred to as Member 2 or b, but they have now been subdivided into four distinct Members. Member 2, termed the 'Orange' breccia, and Member 3 (the 'Black' breccia) have yielded hominid fossils and cercopithecids discussed here.

As reconstructed by Clarke, the maxilla of TMP SK 561 (from the Member 1 'Hanging Remnant') is nearly complete, lacking only a small area on the right above  $P^1-M^1$ , the base of the left orbit and the midline above the nasal aperture (Fig. 5.2). The upper dentition is complete and moderately worn, with the incisors slightly crushed together and the buccal surface of the left  $M^3$  cracked away. The middle of the palate is lacking, as is most of the sphenoid complex, although the pterygoid

plates are preserved in the basisphenoid region. The frontal bone is nearly complete and unwarped, but the internal portions of the orbits are damaged. Part of the right malar is lacking in a strip from the superior contact with the frontal down to the base of the zygomatic arch, as is the middle third of the right arch itself. The parietals were badly crushed and warped and are still missing large areas of bone, but the shape of the vault has been restored as fully as possible. The occipital and temporals are mainly complete,

Fig. 5.2. Standard views of reconstructed female *Theropithecus oswaldi* cranium SK 561, from the Swartkrans 'Hanging Remnant' of Member 1; scale bar = 5 cm.



although lacking small areas of bone on the basal surfaces, especially the middle third of the right nuchal crest and most of both postglenoid processes.

I shall use Eck's paper on *T. darti* from Hadar (see chapter 2) as the model for my comparison of the female cranium SK 561, which is in fact little different from its well-preserved counterpart from Kanjera, BM(NH) M14936. Measurements which can be taken accurately are presented in Table 5.1.

Table 5.1. *Measurements (in mm) of female Theropithecus cranium SK 561.*

Variable		Eck*
Nasion – Inion	116.0	[12]
Nasion – Basion	83.5	
Nasion – Bregma	71.0	
Nasion – Prosthion	85.5	
Nasion – Staphylion	52.6	
Basion – Inion	51.0	
Basion – Bregma	66.0	[15]
Basion – Vertex	67.5	[15]
Basion – Prosthion	126.5	
Basion – Staphylion	60.0	
Prosthion – Inion	175.0	3
Prosthion – Bregma	148.0	
Prosthion – Staphylion	65.0	[ 9]
Prosthion – Orbitale	74.0	
Prosthion – Infraorb. for.	61.0	1
Inion – Bregma	61.0	
Inion – Orbitale	117.0	4
Bi-postglenoid width	84.0	
Bizygomatic width	119.0	11
Postorbital constriction	45.0	14
Width temporal lines (min.)	2.5	
Width " at postorb. const.	49.0	
Biorbital width	83.0	
Facial height (top supra-orbital torus to alv. plane)		
Interorbital width	10.8	
Orbit height	25.0	

Table 5.1. *Contd.*

Variable		Eck*
Orbit width	28.5	
Nasal aperture max. width	18.5	
External palatal width: M <sup>2</sup>	56.0	5
External palatal width: P <sup>4</sup>	42.0	
External palatal width: C <sup>1</sup>	34.0	7
Alveolar process width: M <sup>2</sup>	15.5	
Palatal depth at M <sup>2</sup>	9.3	
Toothrow (partial) lengths:		
M <sup>3</sup> – I <sup>1</sup>	72.0	
M <sup>3</sup> – C <sup>1</sup>	67.5	
M <sup>3</sup> – P <sup>3</sup>	60.0	21
M <sup>3</sup> – M <sup>1</sup>	45.0	6
P <sup>4</sup> – C <sup>1</sup>	23.0	
P <sup>4</sup> – P <sup>3</sup>	15.0	
Alveolar width of incisors	19.0 (est.)	8

\* These measurements correspond to those described by Eck (chapter 2, this volume), under the indicated number; a number in brackets, e.g. [12], is not identical to that of Eck.

The Swartkrans skull lacks both maxillary ridges and maxillary fossae. The nasal aperture is well defined by the premaxillary wings, although the midline is damaged both superiorly and inferiorly. The aperture is rather wider than in the Kanjera specimen, but of similar height. Perhaps due to this greater width, the length of the muzzle dorsum as measured by Eck is shorter than in M14936, but the overall muzzle length and cranial length are comparable. Midcranial length is again somewhat less in the Swartkrans fossil. As Eck notes, it is not possible to determine on SK 561 whether the nasal bones were raised slightly in the midline. The curve of Spee is rather flat, as in M14936, although the premaxilla appears to rise somewhat,

perhaps resulting in the crowding of the upper incisors.

The root of the zygomatic buttress arises just distal to the mesial loph of  $M^3$ , while in M14936 it is placed just mesial to that loph. Although both specimens are damaged in the suborbital region, they appear to have been quite comparable in shape, in terms of the slope of the maxilla onto the zygoma. In both crania, the zygomatic arches are placed well out from the vault, although not strongly bowed beyond their anterolateral extent; the temporal fossae are capacious. The Kanjera specimen differs in having a much stronger inferior expansion at the anteroinferior corner of the facial surface of the zygomatic arch, while SK 561 is smoother in that area (although broken just medial to it on both sides). The posterior surfaces of the postorbital plates are damaged, so that it is difficult to discern clearly the extent of the origin of anterior temporalis, but it seems to have been similar to the condition in M14936.

Although much of the orbital margin is damaged in SK 561, the orbits appear to be quite tall, especially compared to M14936. As reconstructed, they are much larger, but there is no clear bony evidence to support this condition. The supraorbital tori are lightly constructed, as in the Kanjera and perhaps Hadar females, but somewhat more robust than in UWMA MP 222 from Makapan. In superior view, they curve convexly anteriorly and present a shallow ophryonic groove, as in M14936. The temporal lines curve sharply up and back from the posterior margin of the zygomatic processes of the frontal. They are at first a bit more obtuse than in M14936, and proj-

ect laterally over the postorbital constriction (rather than almost vertically), but as they converge toward bregma, they appear more elevated and sharper than in the Kanjera fossil. The region at bregma is damaged in SK 561, but the temporal lines appear to have met near or just posterior to that landmark, continuing as a low ridge which meets the nuchal crest at inion. The nuchal plate is strongly muscle-marked, and the crest may extend up to 7 mm beyond the vault superiorly. Basally, SK 561 is badly damaged, but the mastoid and temporomandibular joint regions appear quite similar to those of M14936, although the postglenoid processes are not as well developed; despite some damage, they appear to have been relatively small. It is worth mentioning here that the partial adult male (?) cranium TMP SK 599 was also reconstructed by Clarke and is illustrated in Delson & Dean (this volume, chapter 4, Figs. 4.9 and 4.10). That specimen appears to have been correctly identified by Freedman (1957) as a '*Dinopithecus*' rather than a *Theropithecus*, in part based upon the rather weak postglenoid processes, apparently less developed in this large male than in SK 561.

From Brain's more recent collections, seven isolated teeth and a partial mandibular corpus have been identified as *Theropithecus* (most are illustrated in Fig. 5.3). TMP Skx 9579 from the Orange Breccia of Member 1 is a partial right corpus with worn and damaged  $P_4$ - $M_3$ . The distal half of the last molar appears to identify the specimen as a *Theropithecus*. The body is reasonably well preserved and the buccinator channel small. Skx 38376 is an

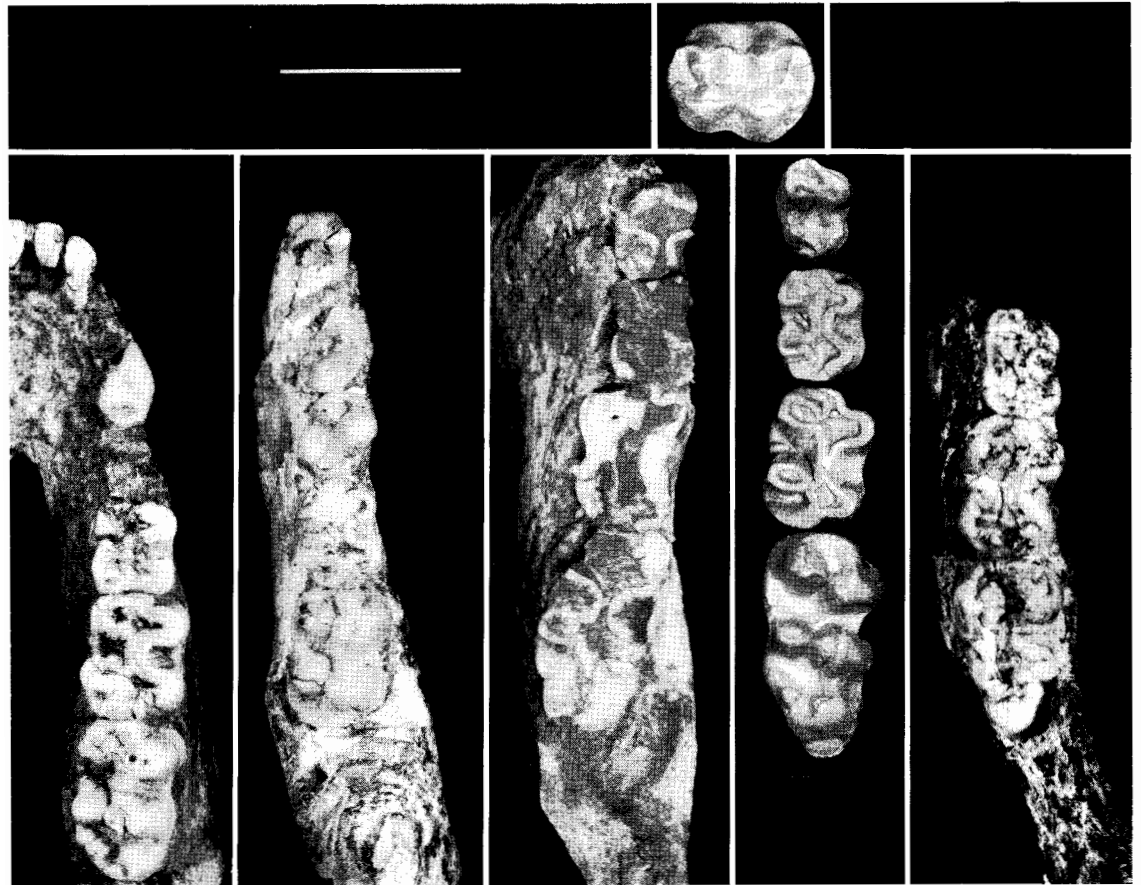


Fig. 5.3. Swartkrans dentitions in occlusal view (of *Theropithecus oswaldi* unless otherwise noted). Left to right: from 'Hanging Remnant', SK 411 (female—right  $I_{1-2}$ ,  $P_3$ ,  $M_{1-3}$ ), SK 426 (subadult male—right  $P_3$ - $M_2$ ); from Member 1, Skx 9579 (sex indeterminate—heavily worn right  $P_4$ - $M_3$ ); (top) Skx 32148 (right  $M_2^z$ , cast); casts of isolated unsexed teeth, arranged as a tooththrow: Skx 38376 (right  $P_4$ , Member 1), Skx 2996 (right  $M_{1?}$ , Member 2), Skx 28812 (right  $M_{2?}$ , Member 3), Skx 27586/27587 (left  $M_3$ , photographically reversed, Member 3); *Papio (Dinopithecus) ingens* (for comparison), from 'Hanging Remnant', SK 404 (right  $M_{1-3}$ ). Scale bar = 2 cm.

isolated, nearly unworn right  $P_4$  from the Orange Breccia which is tentatively identified as *Theropithecus*. Skx 2996, from the Brown Breccia of Member 2, is an  $M_1$  (or possibly  $M_2$ ) presenting typical *Theropithecus* trefoil wear, in a corpus fragment. From the Black Breccia of Member

3, there are a number of less worn teeth: Skx 27586/27587 is a nearly unworn, possibly unerupted rootless crown of a left  $M_3$ ; Skx 28490 is a slightly worn left  $M_3$  crown with some damage to the mesial end (so that length must be estimated); Skx 37323 is a heavily worn right  $M_3$ ; Skx



28812 is an isolated right M<sub>2</sub> (or M<sub>1</sub>); and Skx 32148 is an unworn upper molar crown, probably of a right M<sup>2</sup>, which appears referable to *Theropithecus*.

Table 5.2 presents dental data on the

new Swartkrans teeth, as well as on the original 'Hanging Remnant' sample of Member 1. The new specimens from Member 3 appear indistinguishable from the earlier sample, which suggests that there is

Table 5.2. *Measurements (in mm) of Theropithecus teeth from Swartkrans (a) Swartkrans 'Hanging Remnant' – older Member 1 finds.*

Variable	N	Minimum	Maximum	Mean	SE	CV
I <sub>1</sub> W	1			5.7		
I <sub>1</sub> LA	1			2.3		
I <sub>1</sub> L	1			2.8		
I <sub>2</sub> W	1			5.6		
I <sub>2</sub> LA	1			2.2		
I <sub>2</sub> L	1			3.8		
C <sub>1</sub> L FEMALE	1			5.2		
C <sub>1</sub> H FEMALE	1			9.9		
C <sub>1</sub> W MALE	1			8.5		
C <sub>1</sub> H MALE	1			31.5		
P <sub>3</sub> W FEMALE	1			5.9		
P <sub>3</sub> L FEMALE	1			10.2		
P <sub>3</sub> FH FEMALE	1			10.6		
P <sub>3</sub> W MALE	2	6.20	7.40	6.80	0.60	12.48
P <sub>3</sub> L MALE	2	15.10	15.40	15.25	0.15	1.39
P <sub>3</sub> FH MALE	2	21.50	24.50	23.00	1.50	9.22
P <sub>4</sub> W	4	8.00	8.80	8.38	0.19	4.61
P <sub>4</sub> L	4	9.00	11.00	10.13	0.43	8.43
M <sub>1</sub> AW	3	9.40	10.00	9.70	0.17	3.09
M <sub>1</sub> PW	3	9.60	10.50	9.97	0.27	4.74
M <sub>1</sub> L	3	11.40	12.90	11.93	0.48	7.03
M <sub>2</sub> AW	4	12.00	12.80	12.35	0.17	2.69
M <sub>2</sub> PW	4	11.50	12.40	11.90	0.20	3.29
M <sub>2</sub> L	4	14.60	17.00	15.78	0.58	7.33
M <sub>3</sub> AW	5	12.90	16.30	14.04	0.63	10.02
M <sub>3</sub> PW	4	11.80	14.80	13.08	0.63	9.62
M <sub>3</sub> L	6	18.00	26.60	21.85	1.39	15.60
dP <sub>4</sub> AW	1			7.6		
dP <sub>4</sub> PW	1			7.8		
dP <sub>4</sub> L	1			12.5		
I <sup>1</sup> W	2	6.10	6.20	6.15	0.05	1.15
I <sup>1</sup> LA	2	4.70	4.80	4.75	0.05	1.49

Table 5.2. *Contd.*

Variable	N	Minimum	Maximum	Mean	SE	CV
I <sup>1</sup> L	2	5.60	7.00	6.30	0.70	15.71
I <sup>2</sup> W	2	5.70	5.80	5.75	0.05	1.23
I <sup>2</sup> LA	2	3.40	3.90	3.65	0.25	9.69
I <sup>2</sup> L	2	5.50	5.60	5.55	0.05	1.27
C <sup>1</sup> W FEMALE	2	8.30	8.40	8.35	0.05	0.85
C <sup>1</sup> L FEMALE	2	8.40	9.00	8.70	0.30	4.88
C <sup>1</sup> H FEMALE	1			9.7		
C <sup>1</sup> W MALE	3	12.20	12.80	12.50	0.17	2.40
C <sup>1</sup> W MALE	3	16.60	17.70	17.17	0.32	3.21
P <sup>3</sup> W	5	8.50	10.30	9.34	0.32	7.59
P <sup>3</sup> L	6	7.70	9.90	8.38	0.32	9.22
P <sup>3</sup> H	6	7.10	9.00	8.23	0.34	10.15
P <sup>4</sup> W	5	9.60	10.70	10.26	0.20	4.39
P <sup>4</sup> L	7	7.90	10.40	9.21	0.36	10.42
P <sup>4</sup> H	5	7.70	11.60	9.94	0.64	14.31
M <sup>1</sup> AW	6	10.70	11.70	11.30	0.18	3.84
M <sup>1</sup> PW	6	10.00	12.00	10.93	0.28	6.33
M <sup>1</sup> L	8	11.90	15.20	13.63	0.45	9.39
M <sup>2</sup> AW	10	11.90	16.00	14.12	0.37	8.25
M <sup>2</sup> PW	7	11.10	13.70	12.69	0.34	7.17
M <sup>2</sup> L	10	14.20	20.00	17.38	0.59	10.65
M <sup>3</sup> AW	1			13.9		
M <sup>3</sup> PW	1			11.8		
M <sup>3</sup> L	1			17.2		
dP <sup>4</sup> AW	1			9.0		
dP <sup>4</sup> PW	1			8.8		
dP <sup>4</sup> L	1			9.8		

*(b) Swartkrans 'Orange' – newer Member 1 finds*

P <sub>4</sub> W	1			8.9		
P <sub>4</sub> L	2	11.50	11.70	11.60	0.11	1.34
M <sub>3</sub> PW	1			13.1		
M <sub>3</sub> L	1			23.3		

*(c) Swartkrans 'Brown' – Member 2*

M <sub>1</sub> AW	1			9.9		
M <sub>1</sub> PW	1			9.4		
M <sub>1</sub> L	1			12.7		

Table 5.2. *Contd.*

Variable	N	Minimum	Maximum	Mean	SE	CV
M <sup>2</sup> AW	1			14.3		
M <sup>2</sup> PW	1			13.2		
M <sup>2</sup> L	1			17.2		
<i>(d) Swartkrans 'Black' – Member 3</i>						
M <sub>2</sub> AW	1			12.3		
M <sub>2</sub> PW	1			12.3		
M <sub>2</sub> L	1			16.2		
M <sub>3</sub> AW	3	13.11	14.57	14.01	0.45	5.60
M <sub>3</sub> PW	3	11.53	13.76	12.62	0.64	8.85
M <sub>3</sub> L	3	22.00	26.38	24.47	1.30	9.17
M <sup>2</sup> AW	1			14.3		
M <sup>2</sup> PW	1			13.2		
M <sup>2</sup> L	1			17.2		

*Notes:* N: number of measurable specimens; SE: standard error of the mean; CV: coefficient of variation. Values are given separately by sex for canines and P<sub>3</sub>s.

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. P<sub>3</sub> FH (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 or just apical to the cervix; L, however, is taken at interdental contact points, often estimated due to wear, and decreases significantly in worn teeth.

little time difference between the lower three members (Delson, 1989). Brain (1989) originally suggested that as much as 500 Ka might have separated each of these members, based in part upon preliminary thermoluminescence dating; more recently, however (pers. comm.), he indicated that he and other faunal analysts now agreed with the shorter time frame, implying less than 250 Ka for the total

span of Member 1–3 time. The additional cercopithecids from the new Swartkrans sample, mainly *Papio* but also including a large colobine, will be described elsewhere.

### Ain Jourdel, Algeria

#### History of study

The first fossil specimen of a *Theropithecus* ever reported was described by Phil-

lippe Thomas (1884) in a monograph on the freshwater Neogene of Algeria. From the locality of Ain Jourdel, in the Constantine region, Thomas reported three lithologic units: a clayey silt, then a sandy conglomerate, and finally a molasse. In the middle conglomerate, he recovered a single tooth of a cercopithecoid, which he briefly described as follows (my translation from his French, p. 14): '... a single lower posterior molar ... This tooth, following M. Gaudry who was kind enough to examine it, indicates a monkey much larger than the modern Barbary Ape of Algeria; moreover, it presents characters which precisely recall those of *Cynocephalus porcarius*, Desm[arest], today restricted to southern Africa. We designate this monkey, provisionally at least, under the name of *Cynocephalus atlanticus*'. Plate IV included a drawing (Fig. 4) of the lateral view of this specimen at natural size; the occlusal view stated to be present also is not seen.

The horizon yielding this specimen was said to be of Pliocene age by Thomas. Arambourg (1969, 1979) discussed the site briefly (without mention of the primate tooth), indicating that it could not be relocated. Geraads (1987) has re-examined the fragmentary materials and suggested that the fauna of the conglomerate level is of later Pliocene age, perhaps about 2.5 Ma. The presence of equids and especially several bovids suggests an open-country environment.

Few researchers before 1974 commented upon the cercopithecoid specimen. Hill (1970) discussed the tooth as a lower third molar and reproduced the illustration alongside those of  $M_3$ s of a baboon and a

mandrill. Although he did not mention the clear lack of a hypoconulid (thus precluding its identification as an  $M_3$ ), Hill (p. 358) did note the relatively great height of the crown and 'deep vertical grooves between mesial and distal pairs of cusps. This suggests an allocation to the Theropithecini would be more appropriate'. Nonetheless, he listed the taxon as *Papio atlanticus*, as had Romer (1928) in a faunal list. Delson (1974) listed the material as *Theropithecus atlanticus*, but did not provide further details there or in later papers. Geraads (1980), in a report on the fauna (including *Theropithecus*) from the Thomas quarries of Morocco, mentioned that as *T. atlanticus* was the first named species of the genus, it should be considered the senior synonym of *T. oswaldi*. Later, Geraads (1987) discussed the Ain Jourdel specimen as *T. atlanticus*, while identifying the Thomas quarries finds as *T. oswaldi*, without further taxonomic evaluation.

Geraads also questioned the allocation of a partial humerus from the slightly older Tunisian locality of Garaet (or Lac) Ichkeul. Delson (1974) had mentioned the presence of *Macaca* sp. at that site, based upon the humeral fragment in the MNHN-P collections, identified as a canid by Arambourg but never published. Geraads (1987, p. 22) stated that he was 'unable to find any significant difference from *Theropithecus gelada*', but the development of the medial epicondyle closely resemble that of macaques, being far less retroflected than in any humerus of *Theropithecus*. Pickford (see chapter 8) makes the important observation that although both *Macaca* and *Theropithecus*

occur in the Pliocene and Pleistocene of the Maghreb, they do not appear to overlap at any site yet known, which probably is due to their differing environmental requirements. This observation was not made explicitly by Geraads (1987), but it is clear from his concluding table. More recently, however, Raynal *et al.* (1990) reported on a faunal assemblage from Ahl-Al Oughlam, near Casablanca (Morocco). This assemblage, estimated to date between 2.5–2.0 Ma, is said to include

*Macaca* and a *Theropithecus* whose teeth are smaller and lower-crowned than those of Ternifine.

#### Description

The Ain Jourdel specimen (see Figs 5.4 and 5.5) is a nearly unworn isolated lower molar, lacking roots and perhaps not fully erupted (but apparently completely developed). It is typical of modern and fossil *Theropithecus* teeth in almost all features,

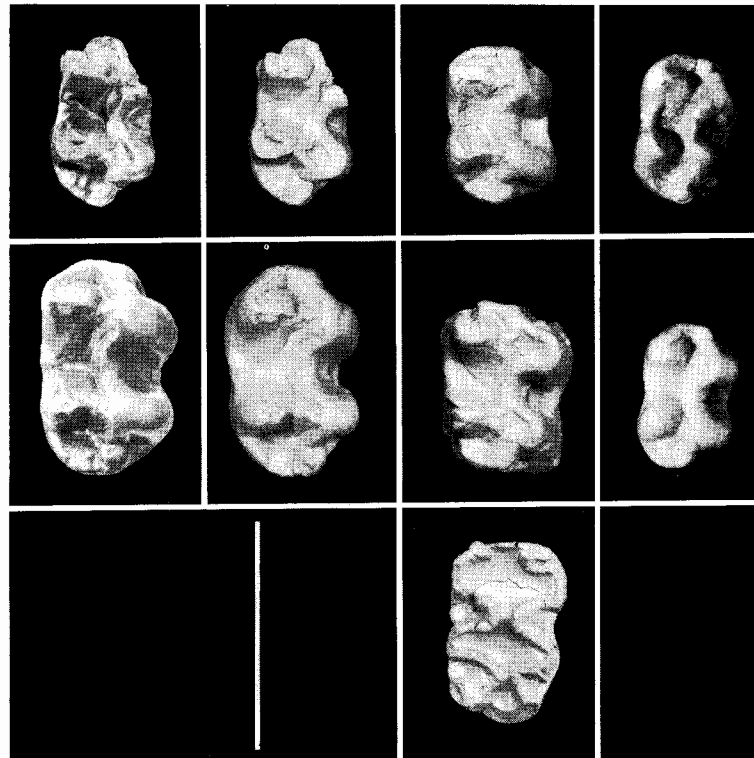


Fig. 5.4. Occlusal views of various *Theropithecus* lower molars. Top row, left to right: *T. cf. oswaldi* IMNZ Sn 5A-520, Senga 5A, right  $M_{12}$ , original and cast; MNHN-P [ΔJO 001], *T. sp. indet.* from Ain Jourdel (holotype of '*Cynocephalus atlanticus*') right  $M_{12}$ , cast and original. Middle row, left to right: *T. sp. indet.* IMNZ Sn 5A-405, Senga 5A, right  $M_{23}$ , original and cast; *T. sp. indet.*, KNM-LT 417, Lothagam-3, right  $M_{23}$ , cast; *T. gelada*, right  $M_2$ . Bottom row: *T. cf. darti*, KNM-KE 237, Kanam East (West), R  $M_3$ , cast. Scale bar = 2 cm.

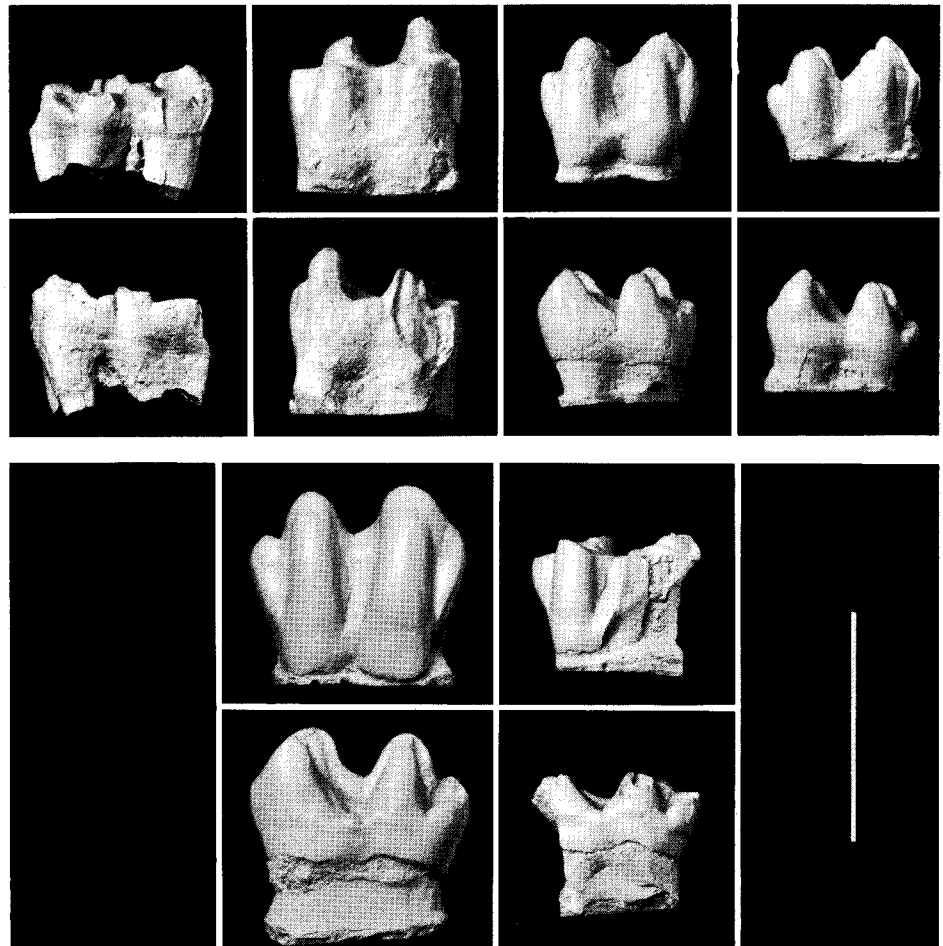


Fig. 5.5. Lateral views of various *Theropithecus* lower molars. Top two rows left to right (buccal above, lingual below): *T. cf. darti*, KNM-KE 237, Kanam East (West), R M<sub>3</sub>, cast; *T. sp. indet.*, KNM-LT 417, Lothagam-3, right M<sub>22</sub>, cast; MNHN-P [AJO 001], *T. sp. indet.*, Ain Jourdel (holotype of '*Cynocephalus atlanticus*') right M<sub>12</sub>, cast; *T. gelada*, right M<sub>2</sub>. Bottom two rows, left to right (buccal above, lingual below): *T. sp. indet.*, Senga 5A, IMNZ Sn 5A-405, right M<sub>22</sub>, cast; Sn 5A-520, right M<sub>12</sub>, cast. Scale bar = 2 cm.

such as high crown relief; deeply excavated foveas, lingual notches and buccal clefts; trigonid basin (mesial fovea) somewhat short mesiodistally; and median buccal cleft with a flattened base, rather than flowing smoothly onto the buccal surface. In addition, the lophids are angled slightly oblique to the tooth's long axis.

One distinctive feature is that the base of the median lingual notch (trigonid notch) forms an acute angle, rather than having a nearly flat base as in all other *Theropithecus*.

Measurements of this tooth are provided in Table 5.3, along with some comparative data on living and fossil material. The most

Table 5.3. Measurements (in mm) of Ain Jourdel, Senga, Lothagam and Kanam lower molars and comparative Theropithecus lower teeth.

Species/site	Source	Tooth	Note	AW	PW	Len	AW/L	Wear
Ain Jourdel	Delson	M <sub>1?</sub>		9.4	9.3	14.1	0.67	None
Senga 5A	Delson	M <sub>1?</sub>	broken	mes	10.0	15+		High
Senga 5A	Delson	M <sub>2?</sub>		12.6	12.2	19.3	0.65	None
Lothagam-3	Delson	M <sub>2?</sub>		11.3	10.6	15.1	0.75	Med
Kanam East	Delson	M <sub>3</sub>	est.	10.8	9.8	16.0		High
<i>T. gelada</i>	Delson	M <sub>2</sub>		8.6	8.6	13.3	0.65	None
	Delson	M <sub>1</sub>		6.8	7.2	10.8	0.63	Low
	Delson	M <sub>1</sub>		7.0	7.7	9.9	0.71	Med.
	Delson	M <sub>1</sub>		7.4	7.5	9.8	0.76	High
	Delson	dP <sub>4</sub>		5.3	6.0	8.2	0.65	Med.
	G. Eck, 1980 unpubl.	M <sub>1</sub>	Mean	7.4	7.6	10.6		
			Max.	8.0	8.6			
			Min.	6.8	7.1			
	Ph.D. thesis	M <sub>2</sub>	Mean	9.2	8.9	13.4		
			Max.	10.6	9.7	14.4		
		Min.	8.3	7.9	11.9			
<i>T. darti</i>	Delson	M <sub>1</sub>		8.7	8.5	12.8	0.68	Low
Hadar	Delson	M <sub>1</sub>	same	8.3	8.1	11.2	0.74	Med.
	Delson	M <sub>2</sub>	jaw	11.2	9.7	14.3	0.78	Low
	Delson	M <sub>3</sub>		9.6	8.4	15.2		Med.
	Delson	M <sub>3</sub>		10.8	10.1	15.8		High
	Delson	M <sub>3</sub>		10.8	9.1	16.6		Med.
Makapan Grey	Delson	M <sub>3</sub>	Min.	12.1	10.8	18.2		High
Kanjera	Delson	M <sub>3</sub>		11.7	10.8	19.7		High
<i>T. oswaldi</i> Okote horiz.	Leakey, chapt. 3	M <sub>1</sub>	Min.	9.9	9.7	14.2	0.70	??
		M <sub>1</sub>	Max.	10.9	11.2	14.2	0.76	??
<i>T. brumpti</i> Shung. C	Eck & Jablonski, 1987	M <sub>1</sub>		9.4	9.6	12.9	0.73	Med- High
		M <sub>1</sub>						High
" Omo 75-C40	Delson	M <sub>2</sub>	cast	13.0	12.3	18.6	0.70	Low
KF 102 (horizon?)	Delson	M <sub>1</sub>		10.3	10.2	14.4	0.72	NO ?

Notes: Delson observations are on original specimens only, unless otherwise indicated. See Table 5.2 for measurement definitions. The first four specimens are fossils whose allocation to species is still uncertain.

striking feature of the tooth metrically is its relative narrowness, even when compared to specimens which are nearly as little worn (and thus not shortened by interproximal wear). The proportions of the specimen are most comparable to an unworn  $M_2$  and little-worn  $M_1$  of *T. gelada*, but the size is greater;  $dP_4$ s are especially narrow across the protolophid, while  $M_2$ s of the other fossils are relatively wider. Overall size and proportions are comparable to those of selected  $M_1$ s of later Pliocene (and early Pleistocene?) *Theropithecus* species, but the Ain Jourdel tooth is distinguished, as noted, by the shape of its median lingual notch and to some degree its narrowness. It is compared in Fig. 5.4 with the unworn  $M_2$  of *T. gelada* and a variety of other lower molars of the fossils discussed below. It is not readily possible to allocate this single tooth to any of the known species, although it appears most similar to early *T. darti*. Perhaps when the Ahl-Al Oughlam specimens are described, they will include material closely comparable to the Ain Jourdel tooth, but until then the latter must be considered indeterminate as to species.

### Lothagam Hill, Kenya

Patterson, Behrensmeyer & Sill (1970) first reported a faunal assemblage from Lothagam Hill; *Simopithecus* sp. was included in the faunal list. Smart (1976) discussed the fauna of the lower horizon, Lothagam-1, in some detail, and Behrensmeyer (1976) provided an overview of the whole sequence, in regional context. The upper fossiliferous horizon,

Lothagam-3, which included the '*Simopithecus*', was estimated on faunal grounds to date around 4 Ma, perhaps slightly older than Ekora and equivalent to Kanapoi. A volcanic sill intruded underneath the Lothagam-3 fauna was dated to about 3.73 Ma, while the basalt apparently lying stratigraphically between Kanapoi and Ekora was dated between 2.5–4.0 Ma; the latter date (although incompletely published) was generally accepted. Hill & Ward (1988) recalculated the sill date to  $3.8 \pm 0.2$  Ma, but otherwise followed the earlier interpretation. T.D. White (pers. comm.) indicates that the fauna of Lothagam-3 appears older than that of Hadar (i.e.  $>3.35$  Ma), but is unlikely to be older than about 4 Ma.

A single isolated lower molar, catalogued as KNM-LT 417, represents *Theropithecus* from this locality. This tooth (see Figs 5.4 and 5.5) is moderately worn, the roots are damaged, and there is a large flake of enamel missing from the entoconid and a sliver of enamel from the mesial face of the metaconid. A large mesial contact facet compresses the trigonid basin, but the distal contact facet is faint if present at all. The wear pattern, deep and flattened lingual notch, and somewhat flattened base of the buccal cleft all combine to identify the tooth as belonging to a member of the genus *Theropithecus*. Its proportions (see Table 5.3) suggest that it is probably a  $M_2$ , although it is possible that it might be a  $M_1$ ; it is too broad for a  $dP_4$ . The size is roughly comparable to those of  $M_2$  from Hadar allocated to early *T. darti* (see also Eck, chapter 2), and its crown pattern is at least as complex as those. This is interesting, in light of the



low degree of crown complexity seen in the earliest members of the *T. brumpti* lineage farther north in the Turkana Basin (see Leakey, chapter 3, and discussion in Delson & Dean, chapter 4). Eck has suggested that molar size reflects age in *Theropithecus* samples, but the LT 417 basal length (Eck's variable 68) is about 15 mm, a value equalled by M<sub>2</sub>s from Pliocene through early Middle Pleistocene sites; clearly the technique is designed to work only with a sample of several teeth. Until more than a single tooth is known (and the age and even toothrow position clarified), it is not feasible to assign this specimen to a named species. Its crown complexity suggests that it does not belong to an early member of the *T. brumpti* lineage, however.

### Kanam East, Kenya

The Kanam localities in western Kenya were first discovered by Louis Leakey in the early 1930s, and their geology, faunas, and age have been the subject of much discussion since (see review in Pickford, 1987). Several cercopithecoid teeth and jaw fragments collected by Leakey were deposited in the BM(NH); they were mentioned by Szalay & Delson (1979) and Delson (1984) and are being described by Harris & Harrison (1991). In the KNM collections are several additional specimens, including two molars identified as *Theropithecus*, which M.G. Leakey has kindly permitted me to describe here. Both are catalogued as KNM KE 237, indicated as from Kanam East (West). The exact age of these deposits is still uncertain, although at Kanam West

(whose relationship to the Kanam East subsites is uncertain) Pickford (1987) indicated the presence of a late Late Pleistocene horizon (the Apoko Beds) and an earlier Pliocene one (the Kanam Beds). More recently, Plummer & Potts (1989, who also provided a good location map of the region) reported that at nearby Kanjera, the Apoko Beds may range back as far as latest Early Pleistocene, while the overlying Black Cotton Soil horizon is late Late Pleistocene. It seems most likely that the cercopithecids from Kanam East are of earlier Pliocene age, and perhaps the *Theropithecus* teeth can throw light on that question.

The two molars are heavily worn and might possibly derive from a single individual. One tooth is clearly a right M<sub>3</sub>, whose cusps have been worn down so that only large transverse 'lakes' of dentin are visible (see Fig. 5.4). The deep bases of the two lingual notches are still unworn, as is the flattened base of the median buccal cleft (Fig. 5.5). This wear has left the lingual face of the tooth much higher above the cervix than the buccal side, on which enamel has been worn away around the base of the protoconid and hypoconid, as well as from a large area at the distal base of the hypoconulid. The outline of the tooth as preserved is rather 'blocky': nearly quadrangular, rather than elongate, with no obvious narrowing of the hypoconulid heel. Some Hadar and Makapan teeth are similar in shape. Measurements are provided in Table 5.3.

The second tooth is even more worn, but I identify it as an upper ?first molar, probably of the left side (Fig. 5.6). Enamel is flaked off around most of the crown

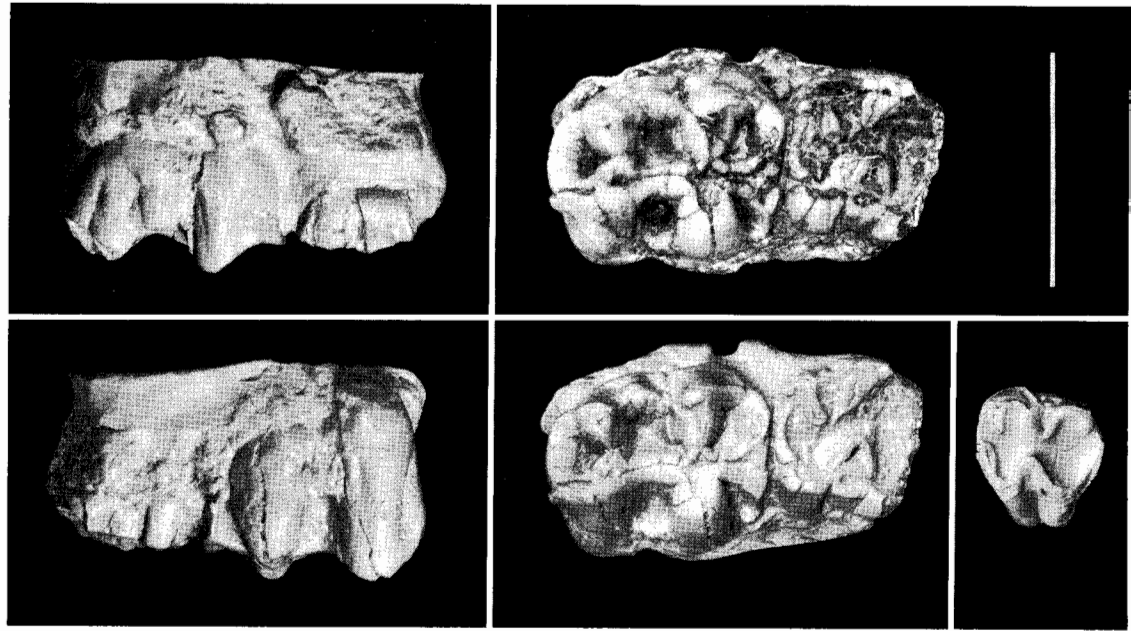


Fig. 5.6. Occlusal and lateral views of various *Theropithecus* upper molars. *T. oswaldi delsoni* from Mirzapur, India (PUC-GM A/643, holotype of '*T. delsoni*'), right  $M^{2-3}$ , buccal above lingual views of cast, occlusal view of original above cast. Lower right, *T. cf. darti* KNM-KE 237, Kanam East (West),  $R M^1$ , cast, occlusal.

base, except at the median buccal and lingual areas and buccally at the ?metacoid. This renders measurement most difficult, and only rounded estimates of width and length are provided in Table 5.4.

The overall size of the teeth is small. The  $M_3$  falls well within the range for Hadar specimens as measured by me or by Eck (see chapter 2). Makapan teeth are larger, even at a similar wear stage, as are those from Kanjera, Swartkrans, and later populations. The basal length of the tooth is about 14.7 mm, a value matched by Eck only in Hadar Sidi Hakoma (older) specimens, and still well below the mean. The upper molar is less readily placed. As seen from Table 5.4, several modern *T. gelada*

are only slightly smaller, while selected Hadar and Makapan specimens are slightly larger. It is unlikely that the specimens represent *T. gelada*, given the blocky shape of  $M_3$ , and thus an identification as *T. cf. darti* appears most reasonable. In turn, this tends to confirm the earlier Pliocene age.

#### Senga 5, Semliki, Zaire

Harris *et al.* (1987) described the geology, paleontology, and archeology of the Senga 5A site, in the Lusso Beds of the Upper Semliki Group, along the Semliki River in western Zaire. Various lines of faunal evidence suggested an age between 2.35–2.0 Ma. A more detailed analysis is

Table 5.4. Measurements (in mm) of *Theropithecus* upper molars from Kanam, Mirzapur and Comparisons.

Locality	Source	M <sup>1</sup>	AW	PW	L				
Modern	Delson		9.3	8.3	11.3				
Modern	Delson		9.6	8.3	11.3				
Kanam East	Delson	(?)	10.	10.	11.	(all estimated)			
Hadar	Delson		10.0	9.9	11.7				
Mak* Mb 4	Delson		9.8	9.5	11.9				

Locality	Source	M <sup>2</sup>	AW	PW	L	M <sup>3</sup>	AW	PW	L
Mirzapur	Delson		14.0+	13.3	14.6+		17.3	16.3	20.8
Olorge-sailie	Jolly, 1972	Min	15.0	13.5	18.7	Min	15.7	13.8	18.6
		Max	19.0	17.4	22.3	Max	18.0	15.9	22.5

\* Makapansgat Member 4 (grey breccia)

being prepared for publication by Boaz *et al.*

The original faunal list for Senga 5A included *Theropithecus* sp., and Dr Noel Boaz has recently requested that I describe the two teeth identified as that taxon. Although they are currently identified only by field numbers, they will eventually be catalogued in the collections of a museum under the authority of the IMNZ. Specimen Sn 5A 405 is a nearly complete, unworn crown of an M<sub>2</sub> (or possibly M<sub>1</sub>), lacking the roots and some of the enamel above the cervix except on the buccal side. It is of typical *Theropithecus* morphology, with high occlusal relief (tall cusps and deep basins and lingual notches), projecting mesial and distal shelves and a small cuspule tending to flatten the base of the median buccal cleft (see Figs 5.4 and 5.5). Sn 5A 520 is smaller, more worn, and more heavily damaged: the mesial quarter is broken away, and enamel is missing

buccally almost to the median cleft. Wear has exposed subcircular dentin pits on all four major cusps, but this confirms the identification of the tooth as *Theropithecus*. Neither tooth appears to be elongate enough to be identified as a dP<sub>4</sub>, and as they are from the same general horizon, it is likely that the larger specimen is an M<sub>2</sub>, while the smaller is an M<sub>1</sub>. It is conceivable that they are from the same individual, but this is not significant here. Measurements of the teeth are provided in Table 5.3.

Comparison with the data for Swartkrans teeth in Table 5.2 reveals an overall similarity of size, especially in width; the unworn Senga tooth is longer than its generally more worn Swartkrans counterparts, and both are larger overall than the Kanjera specimens summarized by Jolly (1972). Leakey (see chapter 3) reported metric data for a variety of *T. oswaldi* specimens, Delson & Hoffstetter (see chapter 6) give measurements for the

Ternifine sample and Eck (1987) provided them for the few Shungura specimens. Clearly the Middle Pleistocene samples (Olorgesailie and Ternifine, especially) average much larger than the Senga teeth, although there is some overlap with the smallest individuals. Teeth of *T. oswaldi* from the Koobi Fora Okote horizon are perhaps closest overall, but those from the KBS and Upper Burgi levels (and the correlative Omo E-G) are also similar, if not as long for their breadth. Some of this discrepancy may be due to the unworn condition of the larger Senga tooth, but it may also be slightly more elongate than those from other sites.

Eck & Jablonski (1987) and Leakey (see chapter 3) also provide data for Turkana Basin *T. brumpti*, some of which show close similarity in size to the Senga teeth. I have measured a cast of one Shungura juvenile female, tentatively identified as *T. brumpti*, which is also morphologically similar (Omo 75-C40, Table 5.3). Given the difficulties in distinguishing isolated teeth of the two species (Eck & Jablonski, 1987), no further attempt is made here. Eck (see chapter 2; also 1987) does suggest that the basal (cervical) length of lower molars can be used as a guide for comparing samples, but the value obtained for Sn 5A 405 (16.1 mm) falls into the overlap zone for all populations between Makapansgat and Olorgesailie. Overall, it is likely that a time range equivalent to the middle Shungura Formation, perhaps 2.4–2.0 Ma, would be reasonable for the Senga 5A teeth; they may be relatively elongate compared to their contemporaries.

## Mirzapur, India

### History of Study

V.J. Gupta (1977) first mentioned the possibility of *Theropithecus* from India in his description of a fragment of right maxilla with two teeth. The specimen, PUC-GM A/643, was reported to have come from 'the Lower Boulder Conglomerate Formation exposed 1.4 km WWS [sic] of Mirzapur Rest House (76° 43' 44" : 30° 54' 10"), Kharar Tehsil, Dist. Ropar, Punjab' (p. 450). Although papers by E. Khan discussing the geology of this area were cited, there was no indication as to who had actually found the fossil. Gupta identified the teeth in the maxilla as questionably  $M^{1-2}$  and indicated that they closely resembled Kenyan *Theropithecus* as described by Jolly (1972).

In 1981, Gupta & Sahni reported that the maxilla was undoubtedly of a large *Theropithecus*, which they named *T. delsoni*. The teeth were reidentified as  $M^{2-3}$ , based upon 'further examination of the maxillary fragment' (p. 70), without specifying details. The new species was diagnosed mainly as a large-sized cercopithecine, with  $M^3$  robust and slightly larger than  $M^2$ , overall size significantly larger than *T. darti* and *T. oswaldi*, approaching the dimensions of *T. brumpti*; and accessory cuspules better developed than in the African species.

Pickford (see chapter 8) has added to this history by reporting that it was he who first located the specimen in the artiodactyl collections in Chandigarh and brought it to Gupta's attention. I can further add that in 1980 Sahni visited me in New York

to discuss the fossil but was unable to show it to me because it had been packed preparatory to his return to India. On examining a number of casts of cercopithecoid dentitions, he indicated that the Indian fossil (of which I was unaware at the time) was most similar to *T. oswaldi* specimens. I was astounded by this idea but convinced by the cast he sent me on his return and much honoured by his nomenclature.

As discussed by Pickford (see chapter 8), doubt has recently been raised about the correct provenance of numerous fossils described by V.J. Gupta and a variety of international colleagues (see Talent, 1989; Krishtalka, 1989, who focused on this specimen). In the light of this problem, I contacted Prof Ashok Sahni who most graciously provided both a copy of the original catalogue entry for this specimen and the specimen itself for further study. The fossil is one of a group collected in May, 1959, by Dr Ehsanullah Khan, a respected scientist whose collections have never been questioned; the date was some six years prior to Gupta's earliest publications. The catalogue entry indicates that the maxilla (identified as a suid molar) was recovered seven-eighths of a mile west-west-south (sic) of Mirzapur Resthouse. On the same page are listed a suid ramus from half mile south and two *Equus* skulls from one mile south-east of the Resthouse. Thus, the provenance of this fossil does not appear in further doubt.

The age of the specimen however, is less clear. It is indicated as Middle Pleistocene by Gupta & Sahni, but it is not even certain what definition they are using. Azzaroli & Napoleone (1979) discussed

paleomagnetic chronology of the Chandigarh region, reporting the possible presence of the Jaramillo subchron near the Pinjor/Boulder Conglomerate 'boundary', which is poorly defined in any case. Unfortunately, the Mirzapur area is just off the map (to the west) given by Azzaroli & Napoleone and even farther away from the more eastern region mapped by Tandon *et al.* (1984), in their paleomagnetic study. Combining the magnetic and stratigraphic data suggests that the Mirzapur area might be younger than 1 Ma. If the Middle Pleistocene is accepted to begin roughly at 0.75 Ma (see Delson, 1988), this specimen is most likely of later Early Pleistocene or Middle Pleistocene age. Azzaroli (1985) discussed faunal interchange in the Siwalik sequence and noted that bovids, suids, and other taxa of African affinity appeared in India mainly after about 2.5 Ma, with movement probable in both directions. He negated later Pleistocene connections, but this specimen may serve to suggest that those were indeed possible.

#### Description

Figure 5.6 illustrates the original Mirzapur maxilla and a cast (to avoid the loss of detail due to discoloration). Measurements of the Mirzapur teeth are provided in Table 5.4, with comparative data on Olorgesailie upper teeth taken from Jolly (1972; more extensive samples from Olorgesailie could not be included because Leakey & Leakey [1973] only gave proportional width values, not raw measurements, while Leakey [this volume, chapter 3] only provided measurements of lower dentitions). There is no sign of a distal facet on the

larger tooth, which may have been the reason for Gupta & Sahni (1981) to suggest that the Mirzapur specimen likely contains  $M^{2-3}$ . The anterior tooth is heavily worn, and as they noted, the mesial margin is completely worn away, so that only a minimum estimate of both length and breadth is possible. I therefore agree with their identification.

The description of the specimen given by Gupta & Sahni is quite accurate and detailed and need not be repeated. Their suggestion that it presents more accessory cuspule development than in African *Theropithecus* does not seem however, to be valid. There are several small cracks in the enamel of both teeth which have led to some expansion in dimensions. Nonetheless, in terms of size, the Mirzapur teeth are clearly among the largest upper molars known for *Theropithecus*, within the range for Olorogésailie but larger than the few Ternifine teeth (Delson & Hoffstetter, see chapter 6) or other samples reported by Jolly (1972). They are also far larger than the teeth of *T. brumpti* reported by Eck & Jablonski (1987). Arambourg's (1947) original description of the 'type series' of *T. brumpti* from Omo gave 20 mm as the length for the incompletely erupted  $M^3$  of that Eck & Howell (1982) chose as the species lectotype, and it may be this high value to which Gupta & Sahni (1981) referred in their diagnosis (see above). In fact, however, my estimate of  $M^3$  maximum length is only 18.8 mm for this specimen, although my other measurements for it accord exactly with those given by Arambourg. The systematic position of the Mirzapur specimen will be

considered further in the final section of this paper.

## Taxonomy of *Theropithecus*

### Genus-group systematics

The problems of specific and generic taxonomy for *T. gelada* and its extinct relatives have burdened researchers for over 40 years. Jolly (1972) provided a major advance by demonstrating the generic identity of *Theropithecus* and *Simopithecus*, the name which had previously been applied to extinct species only and which Jolly relegated to subgeneric status. Szalay & Delson (1979) accepted this system, recommending that a new subgenus might prove necessary to receive the highly distinctive *T. brumpti*. Dechow & Singer (1984) also formally accepted two subgenera. On the other hand, Maier (1972; commenting upon preliminary work by Jolly) and Freedman (1976) retained *Simopithecus* and *Theropithecus* as distinct genera, citing mainly potential problems with phylogeny, rather than evaluating the set of clearly derived features shared by the two. More recently, Eck & Jablonski (1987, p. 100) argued that all of the relevant species should be included in *Theropithecus* without further genus-group subdivision, this being 'a small and tightly-knit group, ... already overburdened with taxonomic terms'. They further elaborated upon their previous arguments (Eck & Jablonski, 1984) that three phyletic lineages can be discerned within *Theropithecus*: *T. gelada*, *T. oswardi* (with *T. darti*) and

*T. brumpti* (with *T. baringensis* and *T. quadratiostris*). The generic unity of *Theropithecus* appears to have been accepted by Leakey (see chapter 3) as well, as no mention of the term *Simo-pithecus* appears in her paper.

Delson & Dean (see chapter 4) recognized the same three lineages within the genus. However, they argued that the holotype crania of *Papio baringensis* R. Leakey, 1969 and *Papio quadratiostris* Iwamoto, 1982 were essentially of conservative, *Papio*-like morphology. After considering extrinsic evidence as well, they retained Iwamoto's species in *Papio*, including it in the subgenus *P. (Dinopithecus)*. However, on the basis of dental evidence, including similarity of both the holotype and another Chemeron tooththrow to newly described jaws of early *Theropithecus* from the Turkana Basin (Leakey, see chapter 3), they accepted the possible placement of ?*T. baringensis* as an early member of the *T. brumpti* lineage. This species would still have retained a conservative *Papio*-like cranium and molars of relatively low complexity; only later *T. brumpti* developed complex, high-crowned molars, but never a relatively air-orhynch facial skeleton such as is seen in *T. oswaldi* and *T. gelada*. Such a relationship, combined with the more complete development of *Theropithecus*-like dental and cranial features in Hadar *T. darti*, implied to them that the main division within *Theropithecus* was between the *T. brumpti* lineage and all other species, including the modern form.

Delson & Dean had suggested this pattern as a working hypothesis from the out-

set, because it had been recognized earlier by Eck & Jablonski (1984, 1987). Eck (this volume, chapter 2) differentiates *T. darti* from *T. oswaldi* and that lineage from other species (see below), but he does not comment on inter-lineage relationships, nor does Leakey (see chapter 3). It is important to realize that retention of a suite of conservative features (as in the cranium of *T. gelada* or the dental similarities between *T. gelada* and *T. brumpti*) or a set of autapomorphies (as is true for each of the three lineages and their terminal species at least) does not aid in the recognition of synapomorphies between clades which can be used to determine phylogeny in a three-taxon problem (Hennig, 1966; Eldredge & Craft, 1980).

Delson & Dean further suggested that within Papionini, the closest relative of *Theropithecus* is *Papio*, including three lineages within that genus: savannah baboons (subgenus *Papio*), mandrills and drills (subgenus *Mandrillus*) and an extinct group of small-brained but relatively mandrill-like species (subgenus *Dinopithecus*). Many of the features seen in mandrills are shared also by *Theropithecus* species, and it was suggested that the former are cranially the most conservative living 'baboons', setting aside their obvious autapomorphies.

If the relationships as determined by Delson & Dean (and by Eck & Jablonski, 1987) are accepted, there are three main branching nodes within the *Theropithecus* clade: first, between a mandrill-like common ancestor and *Theropithecus*; second, between the *T. brumpti* lineage and the

two others; and third, between the *T. gelada* and *T. oswaldi* lineages. The first node would be characterized by the development of relative molar complexity and incisor reduction. The second node would document the beginning of airorhynchy and orthognathy (increasing midface height, upturned premaxilla, rounded neurocranium) in the *T. gelada/oswaldi* clade. The third node would be characterized by a 'canalization' of further anterior tooth reduction and size increase in the *T. oswaldi* lineage. The development of a reversed curve of Spee and increased molar complexity in *T. brumpti* and *T. oswaldi* (but not the earliest members of the former lineage especially) would presumably have been convergent. This hypothesis of relationships is depicted in Fig. 5.7. It can be tested in more detail through analysis of these characters and others discussed in Delson & Dean (see chapter 4), Jablonski (see chapter 7) and Eck & Jablonski (1987), but many of these characters have not been subjected to polarity analysis, and the necessary work is beyond the scope of this chapter. Other traits characteristic of each of the three main lineages are summarized by Jablonski (see chapter 7).

Either or both of the intra-*Theropithecus* nodes could be named at supra-generic level. If both are recognized, it would be best to place the *brumpti* lineage in a new genus, while recognizing *T. (Simopithecus)* for the *oswaldi* lineage. In view of most previous arguments, this would seem to be 'taxonomic overkill'. However, in order to emphasize the closer relationship between the *T. gelada* and

*T. oswaldi* lineages argued here and by Delson & Dean, I propose that a new sub-genus be recognized formally for the *T. brumpti* lineage, as originally suggested but not named by Szalay & Delson (1979). The genus-group systematics of *Theropithecus* would thus be as follows:

*Theropithecus* l. Geoffroy, 1843

(= or including *Macacus auctororum*: Rüppell, 1835, in part. *Gelada* Gray, 1843. *Simopithecus* Andrews, 1916. *Theropythecus* Vram, 1922, lapsus?. *Papio* Erxleben, 1777: Broom & Jensen, 1946; Buettner-Janusch, 1966; in part. *Dinopithecus* Broom, 1937: Arambourg, 1947; Broom & Hughes, 1949; in part. *Brachygnathopithecus* Kitching, 1952, in part. *Gorgopithecus* Broom & Robinson, 1949; Kitching, 1953, in part.)

Included subgenera: *T. (Theropithecus)* and *T. (Omopithecus)*, new.

Type species: *T. gelada* (Rüppell, 1835).

Distribution: Pliocene to later Middle Pleistocene; South Africa, East African Rift Valleys, Maghreb. ?Later Early Pleistocene or Middle Pleistocene; northern India. Modern; central Ethiopian plateau.

Diagnosis: A medium-sized to large papionin cercopithecine generally characterized by such features as: anterior union of the temporal lines and sagittal crest long, if present; marked postorbital constriction and relatively small brain size; at least some development of airorhynchy\* relative to African papionin common ancestor; inferiorly divergent lateral margins of the frontal processes of the zygomatic bones and some lateral encroachment of the malar into the orbital cone posteriorly; large temporal fossae and



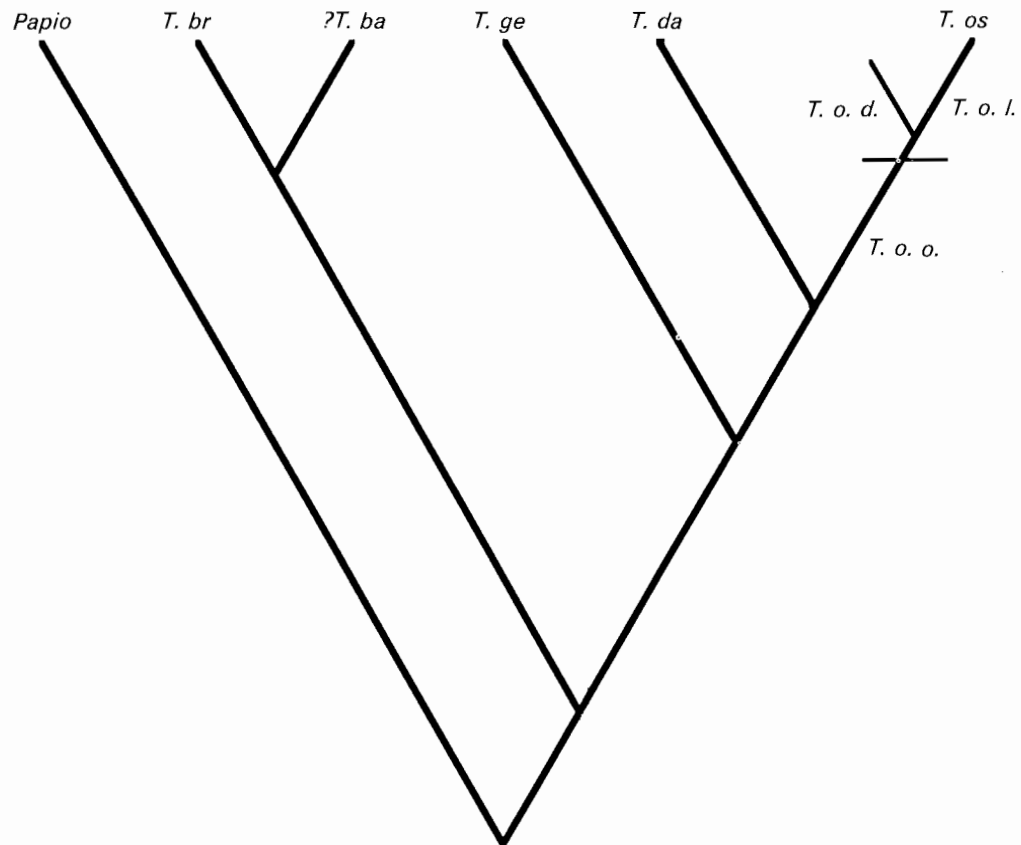


Fig. 5.7. Cladogram of relationships among the species of *Theropithecus*. *T. br* = *Theropithecus brumpti*; ?*T. ba* = ?*T. baringensis*; *T. ge* = *T. gelada*; *T. da* = *T. darti*; *T. os* = *T. oswaldi*. At upper right, thin horizontal line represents 'transition' between *T. oswaldi oswaldi* (*T. o. o.*) and *T. oswaldi leakeyi* (*T. o. l.*), while thin oblique line represents Asian *T. oswaldi delsoni* (*T. o. d.*).

bowed zygomatic arch, with the root of its maxillary buttress usually posterior to M<sup>2</sup>; rounded neurocranium; strong elevation of the temporomandibular joint above the occlusal plane, enlarged postglenoid process and a tall, upright mandibular ramus; a long mandibular symphysis, with buttressed anterior inferior margins of the ramus; relatively reduced incisors (and a shallow maxillary incisive arc); molari-

form teeth with relatively high relief\* (deep notches and clefts, tall, pinched cusps and well-developed mesial and distal foveae), trigonid basin (mesial fovea) somewhat short mesiodistally, median buccal cleft with a flattened base, rather than flowing smoothly onto the buccal surface, and M<sub>3</sub>s with consistently large hypoconulids; a reversed curve of Spee\*; delayed eruption of distal molars; and a

suite of postcranial features mainly related to increased terrestriality and manual feeding (see Jablonski and Krentz, this volume, chapters 7 and 14, respectively).

Characters marked \* not characteristic of earliest members of all lineages and may have developed convergently (or in parallel as a result of 'canalization').

*T. (Theropithecus)* I. Geoffroy, 1843

(= or including *Macacus auctorum*: Rüppell, 1835, in part. *Gelada* Gray, 1843. *Simopithecus* Andrews, 1916. *Theropythecus* Vram, 1922, lapsus?. *Papio* Erxleben, 1777: Broom & Jensen, 1946; Buettner-Janusch, 1966; in part. *Dinopithecus* Broom, 1937: Broom & Hughes, 1949; in part. *Brachygnathopithecus* Kitching, 1952, in part. *Gorgopithecus* Broom & Robinson, 1949: Kitching, 1953, in part.)

Type species: *T. gelada* (Rüppell, 1835).

Other included species: *T. oswaldi* (Andrews, 1916); *T. darti* (Broom & Jensen, 1946).

Distribution: Pliocene to later Middle Pleistocene; South Africa, East African Rift Valleys, Maghreb. ?Later Early Pleistocene or Middle Pleistocene; northern India. Modern; central Ethiopian plateau.

Diagnosis: Compared to *T. (Omopithecus)*, *T. (Theropithecus)* has: a relatively airorhynch skull; less elongate muzzle, but deep midface; weak maxillary ridge development and rounded muzzle dorsum; superior margin of supraorbital torus with shallow depression; zygomatic arch only moderately robust; neurocranium rounded, especially in posterior region.

Many of the shared features of the *T. gelada* and *T. oswaldi* lineages are con-

servative, but the relative deepening of the midface and decreased klinorhynch is an important shared derived complex linking them to the exclusion of the *T. brumpti* clade (Eck & Jablonski, 1987; see Delson & Dean, chapter 4).

*T. (Omopithecus)*, new subgenus

(= or including *Dinopithecus* Broom, 1937: Arambourg, 1947, in part. *Simopithecus* Andrews, 1916: Freedman, 1957, in part. New and unnamed subgenus: Szalay & Delson, 1979).

Type species: *T. brumpti* (Arambourg, 1947).

Other included species: ?*T. (O.) baringensis* (R. Leakey, 1969).

Distribution: Later Pliocene of Turkana and Chemeron Basins, East Africa.

Diagnosis: Compared to *T. (Theropithecus)*, *T. (Omopithecus)* has: an elongate, *Papio*-like muzzle, relatively flat muzzle dorsum, well-developed maxillary ridges and often moderately deep and extensive maxillary fossa; convex surface of the nasal aperture; generally large and broad malar with anteroinferior prolongation; robust zygomatic arch, triangular in cross-section; generally deep mandibular corpus fossa; well-developed, sinusoidal mental ridge and strongly rugose mental protuberance; and postcranial features reflecting a trend (in *T. brumpti*) to increased elbow stability but shoulder flexibility (detailed by Jablonski and Krentz, chapters 7 and 14, respectively).

The development of facial fossae is similar to that seen in *T. gelada*, while the mandibular mental protuberance is similar to that of *T. oswaldi*; other similarities and differences are discussed

by Eck & Jablonski (1984, pp. 126–7; 1987, pp. 102–4). The reversed curve of Spee and complex molars seen in later forms are not present in early members of this lineage.

#### Species and subspecies in the *T. oswaldi* clade

Eck (see chapter 2) describes the sample of *Theropithecus* from Hadar for the first time and formally includes it in *T. darti*, a species which he distinguishes from an unsubdivided *T. oswaldi*. Leakey (see chapter 3) takes a more conservative view, recognizing only one species on this clade, *T. oswaldi*, with three temporal subspecies. Earlier workers (e.g. Leakey & Whitworth, 1958; Jolly, 1972; Freedman, 1976; Szalay & Delson, 1979) grouped the species variably, often recognizing subspecies on the basis of differing combinations of morphology (especially size), time, and geography.

As a result of my own study of the Hadar (and Makapansgat) *Theropithecus*, I tend to agree with Eck that these two samples are broadly similar (and more conservative than *T. oswaldi*) in relative incisor and canine reduction, enlargement of the postglenoid process, and a number of other, less marked features. Many of these, if not all, are probably closely related to the body size increase which characterizes the history of the *T. oswaldi* lineage. From a theoretical or methodological standpoint, Leakey's argument is more valid, to unite the members of a lineage unless there is evidence of a cladogenetic speciation event, but as yet there is no overlap between the latest *T. darti* and the oldest

*T. oswaldi*. None of the alternative taxonomic possibilities – such as recognizing each sample or group of contemporaneous populations as a distinct species; separating only Hadar sample, while including the Makapansgat one in *T. oswaldi* as it already presents more derived conditions than the Hadar monkeys; or including all the fossils in a monolithic *T. oswaldi* – appear as reasonable in this case as the proposals of Eck or Leakey. For the moment, I accept the specific distinction of *T. darti*, but I realize this may be arbitrary and look forward to data on *Theropithecus oswaldi* in the 3.0–2.5 Ma time range in order to test the proposition further.

The Ain Jourdel tooth might fall near the end of this range, and the difficulties found above in allocating the specimen to one of the known taxa may suggest that some speciation occurred in the latest Pliocene. Details on the Ahl-Al Oughlam sample of apparently similar age might clarify this situation. If the Ain Jourdel specimen is referred to any of the known, named species, then Geraads' (1980) comment about the name *Theropithecus atlanticus* having priority must be evaluated. The name was originally proposed provisionally (see above), but that only makes a name unavailable if proposed after 1930, according to the International Code of Zoological Nomenclature. It seems unlikely (although conceivable) that the minor distinction of the shape of the base of the median lingual notch would be reflective of species distinction for the Ain Jourdel tooth and the population from which it was drawn. Rather than upsetting broadly accepted nomenclature, I will

request that the International Commission on Zoological Nomenclature suppress the nomen *Papio atlanticus* Thomas, 1884, for the purposes of the Law of Priority. Pursuant to the Code, current terminology may be continued pending a ruling.

In the taxonomy accepted here, *T. oswaldi* is distinguished from *T. darti* on the basis of larger size, taller post-glenoid processes, and (greater) relative reduction of incisors and canines. Within *T. oswaldi* as defined in this way, Leakey (see chapter 3) has recognized (but not diagnosed) two time-successive subspecies: *T. o. oswaldi* and the later, larger *T. o. leakeyi*. Although previous workers (see above) have recognized many more subspecies for the same group of populations, it now seems more reasonable to accept a reduction to two in Africa. Present evidence reveals that the East African representatives of *T. oswaldi* were widespread at any given time, and due to the strong similarity in morphology and size of contemporaneous populations (see also Delson & Hoffstetter, chapter 6), it is likely that the South African and North African populations were in contact with the better-known eastern forms. The distinctions (in dental size and proportions, for example) seen among such pencontemporaneous populations as those from Swartkrans and Kanjera, or those from Hopefield, Ologesailie, and Ternifine, appear to be less than those discernable today among the varieties of savannah baboons which I recognize as subspecies. Thus, the extinct gelada subspecies would seem to have had larger ranges than modern savannah baboon subspecies.

The recognition of temporal subspecies

among fossil samples always raises special problems (cf. Tattersall, 1986 and Delson, 1990, for example). I argue that such a step should proceed from a modern analogy involving closely related forms, in this case the savannah baboons. Jolly & Brett (1973) have recommended that all living baboons be classified as subspecies of the single species *Papio hamadryas*, and Szalay & Delson (1979) have gone further to recognize the small 'Rhodesian' population usually considered as a variety of the yellow baboon as the distinct *P. hamadryas kindae*. The six modern subspecies thus recognized vary in their degree of distinction from one another, but at most of the population contact areas, there is a hybrid zone. Szalay & Delson also recognized at least one extinct subspecies, the South African Plio-Pleistocene *P. hamadryas robinsoni*, reducing it from its original species rank.

More recently, Hayes, Freedman & Oxnard (1990) have reviewed this problem (although they ignored Szalay & Delson's alternative), utilizing multivariate analysis of dental measurements to seek a solution. As they argued for full species separation of at least the three studied populations (*Papio* [*h.*] *ursinus* from southern Africa, *P.* [*h.*] *cynocephalus* from Malawi and Zambia, and *P.* [*h.*] *anubis* from Kenya), a brief survey of their results is in order. In a principal components analysis, it was recognized that the strong component 1 (69 per cent of variation in males, 74.6 per cent in females) was size-dependent, with the large *anubis* and *ursinus* samples separating from the smaller *cynocephalus*, and loadings showed that other components

depended heavily on incisor and canine dimensions. A canonical variates analysis yielded less readily interpretable differences, but a dendrogram based on the intergroup distance coefficients again clustered the *ursinus* and *anubis* populations to the exclusion of *cynocephalus*. This suggests that the results were based almost entirely on size discrimination, not on tooth shape, as desired. There is no question that size may be different among the (sub)species of this group, but at what rank are such differences to be recognized. The small number of hybrids used in this study makes that portion of it less important, and their discussion of hybrid zones and interbreeding is not convincing. It is possible, and in fact likely, that at least some of these baboon populations are undergoing evolutionary change now, but the overall pattern seems to be one of partial interbreeding at the boundaries between neighbouring subspecies. Subspecies are expected to be temporary phenomena, compared to the geographic and chronological range of a species, and the modern baboon populations appear to fit that model well, as do the extinct samples of *Theropithecus*.

Leakey (see chapter 3) does not precisely diagnose the subspecies that she recognizes, but her data suggest that a division is possible roughly between (1) most Turkana Basin specimens and those from Kanjera, Swartkrans, Peninj, and Olduvai Beds I-lower II on the one hand and (2) those from Olduvai upper Bed II and above, Ologesailie, Kapthurin, Hopefield, Ternifine and Thomas Quarries on the other. The youngest reasonably extensive sample from the Turkana Basin

sequence, that from the Okote member and its correlatives, is harder to allocate to subspecies on the basis of the data presented by Leakey (see chapter 3), although it is probably referable to the earlier, smaller form. This uncertainty is especially obvious because Leakey graphed only lower molar lengths, whose variation is greatly increased by the effects of wear. Plotting molar width might not yield a clearer picture, but at least the data would all be comparable. Nonetheless, such features as overall tooth size, the ratio of canine breadth (or P<sub>3</sub> flange length) to molar length (or breadth), and estimated body mass (from long bone diameters) all suggest a similar division between the two groups of site samples listed.

The single specimen from Mirzapur discussed above appears to fit readily into the second of these groups, *T. o. leakeyi*. If the specimen had been recovered from an African locality, I would have no difficulty referring it to that subspecies. However, given its location some 5000 km from the nearest locality yielding *T. oswaldi* (more nearly 8000 km along a reasonable dispersal route), it is perhaps best not to include it in either of the named African subspecies. Instead, its specific nomen could be used at the subspecies level: *Theropithecus oswaldi delsoni*. It is of course conceivable that the population involved was a late member of the *T. brumpti* lineage (no known member of which presents such large and complex molars) or belonged to as yet unknown species or even lineage, but these alternatives are less likely and not otherwise supported at present. This leaves the *T. oswaldi* lineage with two species, of which the

younger has three temporogeographic subspecies.

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