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## Dating the Northern African cercopithecoid fossil record

The primitive cercopithecoid *Prohylobates* is known only from the (middle?) Orleanian sites of Moghara (Egypt) and Zelten (Libya). No cercopithecoid is known from north Africa during the Astarian and Vallesian periods. *Macaca* (or a closely allied form) appears in the (late?) Turolian of Sahabi (Libya) and Menacer (Algeria) where it is associated with colobines. *Macaca* persists into the Pliocene (Wadi Natrun, Egypt; Garaet Ichkeul; Ain Brimba) but apparently disappears before the end of this period, and is absent from north Africa until the middle Pleistocene (Ain Mefta). *Theropithecus* is known from a single tooth from the upper Pliocene of Ain Jourdel, and from several jaws from the middle Pleistocene of Ternifine (c. 0.7 m.y.) and Thomas Quarry III (c. 0.4 m.y.) in Algeria.

**Key words:** Biochronology,  
 Neogene, Quaternary, Primates,  
 North-Africa, Cercopithecoidea.

### Introduction

The cercopithecoid record in North-Africa is rather poor (some of the sites mentioned below have yielded only one specimen), but it is interesting because of the occurrence of some endemic taxa. The cercopithecoid-bearing localities can conveniently be arranged according to their presumed ages, into 4 groups: lower Miocene (Gebel Zelten and Moghara), Mio-Pliocene (Sahabi, Menacer, Wadi Natrun), Pliocene (Garaet Ichkeul, Ain Brimba, Ain Jourdel) and Pleistocene (Ternifine, Thomas Quarries, Ain Mefta).

### Lower Miocene

Two Lower Miocene North African sites, Gebel Zelten in Libya and the Moghara depression in Egypt, yielded a few remains of a primitive cercopithecoid, endemic in North Africa, *Prohylobates*. *P. tandyi* was described by FOURTAU in 1920, and according to SZALAY & DELSON (1979) *Dryopithecus mogharensis* of the same author belongs to the same species. From Gebel Zelten, DELSON (1979) described a different species, *P. simonsi*.

The mammalian fauna from Gebel Zelten (SAVAGE & HAMILTON, 1973; HAMILTON 1973a and b; COOKE and WILKINSON, 1978; BLACK, 1978; THOMAS, 1979; GINSBURG, 1979; PICKFORD, 1984; TASSY, 1985) is diverse enough (about 25 species) to allow the calculation of meaningful faunal distances to east African sites (PICKFORD, 1981). M. PICKFORD found that Gebel Zelten is about equally distant from his faunal sets II and III, a conclusion which is not significantly altered by more recent studies on the faunal lists. On the basis of faunal comparisons (especially the presence of several Pecora and Carnivora), THOMAS (1979) referred Gebel Zelten to the upper Burdigalian (close to Maboko around 16-17 m. y.), and the site is indeed doubtless posterior to his Neogene Dispersal Phase I (THOMAS, 1985).

However, according to HOOIJER (1978), the east African *Brachytherium heinzelini* is

more evolved than *B. snowi* of Gebel Zelten (and Moghara). The Suiformes also show that Gebel Zelten is older than the early Middle Miocene group Maboko-Nyakach-Ombo (zone IIIb of PICKFORD *et al.*, 1986b). Indeed, in these sites *Sanitherium* replaces *Diamantobius* (its probable ancestor) which is present alone at Gebel Zelten (PICKFORD, 1984). The suid *Nguruwe kijivium* was erroneously said to be present at Gebel Zelten (COOKE & WILKINSON, 1978) but it is restricted to East Africa in faunal sets I and II (PICKFORD, 1981, 1986; PICKFORD *et al.*, 1986a and b). Finally, the anthracotheres *Hyoboops* and *Brachyodus* (DINEUR, 1981) characterize set II in East Africa (PICKFORD *et al.*, 1986b). Thus, the most likely placement for Gebel Zelten is clearly near the limit between faunal sets II and III, around 17-18 m.y. given currently available faunal lists.

The site of Moghara is more difficult to correlate due to the almost complete absence of small to medium sized mammals there (neither suids, nor ruminants, nor carnivores). The occurrence of *Choerolophodon* (TASSY, 1985: 703), if it could be confirmed, would suggest a middle Miocene age, but the lower Miocene association *Hyoboops* + *Brachyodus* (DINEUR, 1981) is reported to be present but PICKFORD (in prep.) identifies two different genera. Only two species from Moghara, *Hyainailouros fourtaui* and *Prohylobates tandyi* are certainly absent from Gebel Zelten. According to DELSON (1979), *P. tandyi* differs from Gebel Zelten *P. simonsi* by its smaller size and its relatively shorter M $\bar{3}$ . Delson considers this last character to be derived, but notes however that the ratio between the lengths of M $\bar{3}$  and M $\bar{2}$  is positively allometric at least in some cercopithecids and one cannot dismiss the possibility that the Gebel Zelten *Prohylobates* is more evolved in both characters. Thus in so far as *Prohylobates* gives an indication (i.e. if the two species do not belong to different lineages), it favours an earlier age for Moghara.

## Mio-Pliocene

Sahabi, the main north African site of this period was said to have yielded cf. *Macaca* sp. and cf. *Libypithecus* sp. (BOAZ & MEIKLE, 1982) but the latter genus is probably not reliably identified (MEIKLE pers. comm.). Indeed, this latter determination is based only upon the geographic situation of the site and the occurrence at Sahabi of many taxa of eurasiatic type much weakens this argument. Thus, «cf. *Mesopithecus*» would be quite as likely a determination. Two other north african sites of comparable age have yielded primate remains: Menacer (= Marceau) in Algeria, with ?*Colobus* and ?*Macaca* (according to SZALAY & DELSON, 1979, these taxa are very similar to the more southern *Cercopithecoides* and *Parapapio* respectively) and Wadi Natrun in Egypt, the type locality of *Libypithecus markgrafi* Stromer and of *Macaca libyca* Stromer.

Sahabi is by far the richest and most thoroughly studied of these sites. It has been included in the Pliocene (post-Messinian) by DE HEINZELIN & EL ARNAUTI (1982), and BERNOR (1982) agreed with this age estimate but had to assume the late survival in this area of several taxa extinct at this time in Eurasia (but as we shall see not all of these Miocene «survivors» show northern affinities).

Sahabi being obviously close to the Mio-Pliocene boundary, its fauna may be compared to those of Mpesida (aged 7.3-6.3 m. y.; HILL *et al.*, 1985) Lukeino (between 6.3 and 5.1 m. y.; HILL *et al.*, 1985), Lothagam I (SMART, 1976; Lothagam I is usually placed at 5.5 m. y., but is probably younger than Lukeino) and Langebaanweg in South Africa (that HENDEY, 1981, puts at 5 m. y.). Table 1 shows the distribution of the most significant mammals in these sites; taxa which have been insufficiently studied or are present in all sites (*Anancus*, *Hipparion*, Hippopotamidae) or are not biochronologically

TABLE 1 - *Mio-Pliocene*.

Sahabi	Lukeino: LU Lothagam I: LT	Menacer	Langebaanweg	Wadi Natrun
cf. <i>Libypithecus</i> <i>Macaca</i>		<i>Colobus</i> <i>Macaca</i> <i>Hystrix</i>		<i>Libypithecus</i> <i>Macaca</i>
<i>Agriotherium</i>	<i>Hystrix</i> LU <i>Agriotherium</i> LT <i>Enhydriodon</i> LU, LT	cf. <i>Agriotherium</i>	<i>Hystriidae</i> <i>Agriotherium</i> <i>Enhydriodon</i>	<i>Enhydriodon</i>
<i>Adrocuta eximia</i> <i>Allohyaena</i> <i>Machairodus</i> <i>Stegotetrabelodon</i>	<i>Homotherium</i> LU <i>Stegotetrabelodon</i> LU, LT <i>Primelephas</i> LU, LT <i>Brachypotherium</i> LT	<i>Allohyaena</i> ?	<i>Ad. australis</i> <i>Palhyaena</i> <i>Homotherium</i>  <i>Mammuthus</i>	<i>Machairodus</i>
<i>Brachypotherium</i> <i>Merycopotamus</i> <i>Nyanza. syrticus</i>	<i>N. «tulotos»</i> LU, LT		<i>N. jaegeri</i> ?	
<i>N. kanamensis</i> <i>Tragoportax</i>	<i>N. kanamensis</i> LT <i>Tragoportax</i> LT <i>Tragelaphus</i> LU, LT	<i>Tragoportax</i>	<i>Tragoportax</i> <i>Tragelaphus</i> <i>Damalacra</i>	<i>N. kanamensis</i>
cf. <i>Damalacra</i> <i>Prostrepsiceros</i>	cf. <i>Damaliscus</i> LT			cf. <i>Damalacra</i>

useful have been omitted.

Despite their geographic remoteness, these faunas are sufficiently alike to be included in a single Mio-Pliocene group, within which Sahabi might be the earliest one, as COPPENS (1972) and MAGLIO (1973) suggested first. In any case, it is certainly earlier than Langebaanweg, even if the faunal lists show a number of similarities. Several taxa which no longer occur in the south african site persist in Sahabi: *Brachypotherium* (HEISSIG, 1982) *Nyanzachoerus syrticus* (cf. COOKE, 1982), *Adrocuta eximia*, *Allohyaena senyureki* (cf. HOWELL, 1982), *Prostrepsiceros* (LEHMANN & THOMAS, in press). Furthermore, the following taxa, still unknown from Sahabi, occur at Langebaanweg and many african Pliocene sites: *Mammuthus*, *Tragelaphus*, *Homotherium*, *Enhydriodon* and *Hystrix*; some of these genera may be time-transgressive (*Mammuthus* certainly is, since it does not reach North Africa until much later) but it is unlikely that all would introduce the same bias.

The differences between Sahabi and the east african sites are less clear-cut. Some of the faunal changes which distinguish the Lukeino/Lothagam I group from Mpesida distinguish it also from Sahabi: appearance of *Hystrix* (at Lukeino) and of *Primelephas*. Carnivores are unfortunately absent at Mpesida but *Enhydriodon* is present at Lukeino (PICKFORD, 1975; HILL *et al.*, 1985). The absence of *Tragelaphus* and the survival of *Prostrepsiceros* are the only (weak) arguments for putting Sahabi earlier than Mpesida, but the absence of the relatively evolved *Nyanzachoerus kanamensis* at Mpesida suggests the reverse placements. One should however note that this species is known at Sahabi by a single specimen, whose precise stratigraphic origin is unknown (COOKE, 1982).

The difference in age between Sahabi and Langebaanweg is certainly less than 2 m. y. and if the latter site is really younger than Lothagam I (HENDEY, 1981), I would suggest 6 to 6.5 m. y. for Sahabi which would put it into the Turolian, and certainly not post-Messinian.

The much poorer sites of Menacer and Wadi Natrun are difficult to fit into this

succession. HOWELL & PETTER (1985) thought that the hyaena of Menacer was the same species as that of Bou Hanifia, a lower Vallesian site, and the occurrence of an ursid (HOWELL, 1982) and a «*Miotragocerus*» (THOMAS, 1979) bring the site close to Sahabi, whereas the *Hystrix* and the (significant?) absence of *Merycopotamus* (which is common where present) suggest that it is of later age. It is difficult to give an upper age limit for Menacer, but the stratigraphy (ARAMBOURG, 1959) shows that a post Messinian age is unlikely.

At Wadi Natrun there are: *Enhydriodon* (HOWELL, 1982) a camelid (STOMER, 1902: this family appears in Africa at Laetoli, Ichkeul, Omo B, all of Pliocene age), a *Nyanzachoerus* referred to *N. kanamensis* by COOKE (1982) and a murid, *Saidomys*, similar to the one found at Hadar, Sidiha Koma member (SABATIER, 1982). This site is probably Pliocene, as THOMAS, BERNOR & JAEGER (1982) have suggested, but the occurrence of bovids akin to those of Langebaanweg are in favour of an age earlier than 4 m. y.

## Pliocene

The Algerian site of Aïn Jourdel has yielded only one cercopithecoid lower molar, the type of *Theropithecus atlanticus* (THOMAS, 1884), whereas in the Tunisian site of Aïn Brimba, only *Macaca* is present (2 molars, referred to «*Anomalopithecus bicuspidatus*» by ARAMBOURG, 1979). This macaque was referred by DELSON (1980) to *Macaca sylvanus* aff. *sylvanus*, mostly for geographical reasons. DELSON (1980) also determined a distal humerus from Garaet Ichkeul (Tunisia) as belonging to the same subspecies, but the poor state of preservation of the specimen seems to forbid such precision; I have been unable to find any significant difference from *Theropithecus gelada*.

At Aïn Jourdel, the type of *Tb. atlanticus* comes from a sandy conglomerate (conglomérat gréseux», THOMAS, 1884) which also yielded the type of a primitive member of the wildebeest lineage, *Oreonagor tournoueri* which is replaced, from Olduvai Bed I onwards, by *Connochaetes* (GENTRY & GENTRY, 1978).

In the Muséum National d'Histoire Naturelle de Paris there are also from this level an upper molar of *Equus* and a metatarsal whose dimensions are similar to those of *E. numidicus* from Aïn Boucherit (ARAMBOURG, 1970). Below the conglomerate, the «lower Pliocene» (sensu PH. THOMAS) has yielded *Hipparion* and *Kolpochoerus phacochoeroides*. The dimensions of the type of this latter species suggest a Pliocene age, but one cannot be more precise. The conglomerate is overlain by a molasse from which comes the type of «*Palaeoreas*» *gaudryi* THOMAS, a species known from Omo member E to G (GENTRY, 1986).

Unless we suppose that *Tragelaphus gaudryi*, *Oreonagor* and a primitive *Theropithecus* all persist later in Northern Africa than in the rest of the continent we must admit that Aïn Jourdel is a Pliocene site, despite the occurrence of *Equus* in its lower part. In East Africa, this genus is unknown before Omo member G/Oludvai bed I (EISENMANN, 1985), but in South Africa, it is known before 2 m. y. (VRBA, 1985) and in Europe as early as 2.5 m. y. (Roccaneyra: EISENMANN & BRUNET, 1973). Thus, the presence of *Equus* does not allow us to rule out an age of 2-2.5 m. y. for *Theropithecus atlanticus* although an earlier age is most unlikely.

The large mammals from Aïn Brimba are almost devoid of chronological meaning. The absence of elements such as *Anancus* (present at Garaet Ichkeul and Aïn Boucherit) and of any alcelaphines can be ignored, because of the shortness and ecological peculiarity of the faunal list, whereas the absence of *Equus* suggests an age earlier than 2.5 m. y., but

a lower limit within the Pliocene cannot be proposed. The same is true for Garaet Ichkeul. The absence of *Equus*, the slenderness of a humerus more reminiscent of *Ceratotherium praecox* than of *C. simum* and some (superficial?) similarity of *Redunca kbroumirensis* with *Kobus oricornus* GENTRY 1986, from Omo, are the only (weak) indications against a late placement in the Pliocene.

The rodents do not contribute much to the datation of these sites. The gerbillids from Aïn Brimba are very distinctive and unlike those from nearby localities (HAYAN TONG, pers. comm). The taxonomic and intrageneric phylogeny of the chief genus of this period and area, *Paraethomys*, is still confused (JAEGER, MICHAUX & THALER, 1975; COIFFAIT & COIFFAIT, 1981; AGUILAR, BRANDY & THALER, 1984), but it seems to point rather unambiguously toward an early upper Pliocene date for Garaet Ichkeul.

**Pleistocene**

The main north african lower Pleistocene site is Aïn Hanech in Algeria, but despite its wealth of fossils it has not yielded any Primates.

In contrast, the site of Ternifine (= Tighenif, = Palikao) also in Algeria, has yielded, apart from *Homo erectus*, an interesting sample of *Theropithecus oswaldi* (SZALAY & DELSON, 1979; VAN DEN BRINK, 1980), but no *Macaca*.

Teeth size of the Ternifine *Theropithecus* (VAN DEN BRINK, 1980, table 2-4) are smaller on average than that at Ologesailie (LEAKEY & LEAKEY, 1973) but the biochronological value of this feature has recently been seriously questioned (DECHOW & SINGER, 1984).

Some of the Ternifine taxa were already present at Aïn Hanech but they are either rare, or of poor biochronological meaning, as they persist till the upper Pleistocene (GERAADS, 1981, 1982; GERAADS *et al.*, 1986): *Ceratotherium simum* which is present from the lower Pliocene till the upper Pleistocene, *Hippopotamus sirensis* (allied to, or identical with *H. gorgops*), «*Bos*», *Crocota*, *Oryx*. On the contrary, Table 2 emphasizes the great faunal turn-over between these two sites. The elephants, equids (EISENMANN, 1980), and suids, are completely different, and undoubtedly belong to different lineages. *Sivatherium*, common at Aïn Hanech, is no longer present at Ternifine. The gazelles and alcelaphines (I believe that the specimens from Aïn Hanech determined by ARAMBOURG, 1979, as

TABLE 2 - Pleistocene.

Ain Hanech		Ternifine		Thomas Quarries
<i>Mammuthus meridionalis</i>		<i>Loxodonta atlantica</i>		<i>Elephas iolensis</i>
<i>Equus tabeti</i>		<i>Equus mauritanicus</i>	— — — — —	?
<i>Kolpochoerus</i>		<i>Metridiochoerus compactus</i>		<i>Phacochoerus</i>
<i>Sivatherium maurusium</i>				
?	— — — — —	<i>Tragelaphus algericus / maroccanus</i>		
		<i>Hippotragus cf. gigas</i>		
<i>Numidocapra crassicornis</i>	— — — — —			<i>Rabaticeras arambourgi</i>
?	— — — — —	<i>Parmularius ambiguus</i>	— — — — —	
?	— — — — —	<i>Connocbaetes taurinus prognu</i>	— — — — —	
		<i>Gazella dracula</i>		
<i>Gazella pomeli</i>	— — — — —	cf.	— — — — —	<i>Gazella atlantica</i>
?	— — — — —	<i>Theropithecus c.f. oswaldi</i>	— — — — —	
		<i>Vulpes n. sp.</i>	— — — — —	

*Connochaetes* belong in fact to *Numidocapra*) also sharpen this faunal break (GERAADS, 1981), which can only be due to a chronological gap: the large mammals show that the environments of both sites were similarly open, with Antilopini and Alcelaphini prevalent among the bovinds.

Thus, determination of the age of Ternifine depends upon that of Aïn Hanech: if the latter dates from the first half of the lower Pleistocene (which I believe to be the case (EISENMANN, 1985), Ternifine might be as old as late lower Pleistocene. On the other hand, if Aïn Hanech is late or even middle lower Pleistocene, Ternifine is certainly not earlier than middle Pleistocene. The basal clays underlying the main fossiliferous levels at Ternifine show a normal palaeomagnetic polarity (GERAADS *et al.*, 1986), which does not solve the problem as this could indicate either the Jaramillo event, or the Brunhes epoch. Comparison of Ternifine with middle Pleistocene sites leads us to favour the latter hypothesis. Most of these sites are located on the Moroccan atlantic shore. They have been referred either to the late Anfatian (a marine stage) or the continental Tensiftian, but they do not differ much in age.

The most important of these sites are:

- The Rabat sandstones, of various ages, but probably mostly Tensiftian.
- the cave fillings of Sidi Abderrahaman in which the Tensiftian overlies the Anfatian (BIBERSON, 1961).

These sites have not yielded any Primates.

- The Thomas Quarries deposits (GERAADS, BERIRO & ROCHE, 1980; GERAADS, 1980) containing *Homo erectus* are roughly contemporaneous with those of Sidi Abderrahaman. They have yielded a few teeth of *Theropithecus*, but the most complete specimen comes from fissure fillings in the Tensiftian sandstone, and it is thus younger. Such a later datation is confirmed by the metrical study of rodents, which indicate, however, an age earlier than Presoltanian (GERAADS, 1980). There is therefore no doubt that *Theropithecus* persisted in Morocco until rather late in the middle Pleistocene.

It is not yet possible to draw up a precise chronological sequence of all these sites, but as they clearly belong to the same faunal set they may be dealt with together.

There are many large mammals in common with Ternifine, in spite of a different geographic environment: *Vulpes* sp. nov., *Theropithecus* cf *oswaldi*, *Tragelaphus algericus / maroccanus* (probably a single lineage), *Connochaetes taurinus prognu*, *Equus mauritanicus* (although the specific identity, elsewhere than at Ternifine is often doubtful). The rodents are also very similar: the species of *Ellobius* and *Paraethomys* are different, but they belong to the same lineages; this is probably true also for the gerbillids (GERAADS *et al.*, 1986). Among the chief differences we may mention the disappearance of *Loxodonta atlantica* (replaced by *Elephas iolensis*), of *Metridiochoerus*, *Gazella dracula* and *Parmularius* (replaced by *Rabaticeras*, a genus also known in the Sahara at Tihodaine: THOMAS, 1977); but in North Africa these taxa are almost restricted to Ternifine.

The age of the Sidi Abderrahaman-Thomas Quarries group has recently been revised by HUBLIN (1985) who gave an estimate of 0.4 m. y., which allows us to propose an age of ca. 0.7 m. y. for Ternifine. An age of 0.5 m. y. for Ternifine, recently suggested is undoubtedly too young, but to refer Ternifine to the Jaramillo event (ca. 0.9 m. y.) would fail to explain its faunal similarities to the Moroccan sites.

None of these sites seems to have yielded *Macaca*, which reappears in the micromammal locality of Aïn Mefta (North-Western Algeria), with *M. trarensis* POMEL, 1892, which is synonymised by DELSON (1980) with *M. sylvanus*. The survival of *Ellobius* and *Arvicantibus* as well as the absence of *Lemmyscomys* led JAEGER (1975) to include this site in the late middle Pleistocene, before the Presoltanian. An age of 0.2 m. y. is a likely estimate.

**Conclusion**

The suggested chronological sequence of the north african cercopithecoid-bearing localities is therefore as follows: — (ages in million years).

Aïn Mefta	0,2	<i>Macaca</i>	
Thomas Quarries	0,4		<i>Theropithecus</i>
Ternifine	0,7		<i>Theropithecus</i>
Aïn Jourdel	2,5		<i>Theropithecus</i>
Ichkeul, Brimba	3	<i>Macaca</i>	
Wadi Natrun	4,5	<i>Macaca libyca</i>	<i>Libypithecus</i>
Menacer	5,5	? <i>Macaca</i>	? <i>Colobus</i>
Sahabi	6	cf. <i>Macaca</i>	<i>Colobinae</i>
Zelten	17,5		<i>Prohylobates simonsi</i>
Moghara	> 17,5?		<i>Prohylobates tandyi</i>

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