Knowledge of the evolution of African Paleogene mammals

Contribution of the Bir El Ater locality (Eocene, Algeria)

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Introduction: The Early African Paleogene mammals

The African fossil record of therians begins with the Early Cretaceous of the Middle Atlas (Morocco) (SIGOGNEAU-RUSSELL, 1991); however, the modern mammalian orders appear only during the early Tertiary in North Africa (figure 1A).

The Paleocene and Ypresian localities from the Ouarzazate Basin (Morocco) have yielded mammalian faunas with possible creodonts, « insectivores » (paleoryctids, todralestids and adapisoriculids) (GHEERBRANT, 1992, 1994, 1995), the oldest representative of euprimates (SIGÉ *et al.*, 1990) and archaic ungulates (SUDRE *et al.*, 1993). Recently, the discovery of *Phosphatherium* (Proboscidea) in

	Ypresian	Early to middle eocene				Middle eocene		Middle to late eocene	Late eocene	
	N'Tagourt 2 (Morocco)	El Kohol (Algeria)	Glib Zegdou (Algeria)	Gour Lazib (Algeria)	Chambi (Tunisia)	In Tafidet and Tamaguilelt (Mali)	M'Bodione (Senegal)	Bir el Ater (Algeria)	Dor el Talha "Evaporit Unit" (Libya)	Qasr el Sagha (Fayum, Egypt)
Metatheria					*Kasserinotherium tunisiense*					
Creodonta		*Koholia atlasense*						gen. et sp. indet		*Apterodon Hyaenodon*
Carnivora			*Glibzegdouia tabelbalaensis*							
Condylarthra	Condylarthra indet.						Condylarthra indet.			
Artiodactyla										cf. Bothriogenys sp.
Proboscidea	*Khamsaconus bulbosus*	*Numidotherium koholense*				*Moeritherium indet.*	*Moeritherium indet.*	*Moeritherium sp.*	*Barytherium grave Moeritherium lyonsi Phiomia indet.*	*Barytherium grave Moeritherium lyonsi*
HYRACOIDEA		*Seggeurius amourensis*	*Titanohyrax mongereaul*	*Megalohyrax gevini Bunohyrax or Megalohyrax indet. Microhyrax lavocati*	*Titanohyrax tantulus*			*Bunohyrax matsumotoi*	Hyracoidea indet.	Pliohyracidea indet.
Macroscelidea					*Chambius kasserinensis*			*Nementchatherium senarhense*		

	Ypresian	Early to middle eocene				Middle eocene		Middle to late eocene	Late eocene	
"Insectivora"	*Afrodon tagourtensis* *cf. Palaeoryctes minimus* *Todralestes butleri* *Didelphodontinae* *Adapisoriculidae* *?Tinerhodon disputatum*	*Garatherium mahboubi* *Insectivora indet.*	Palaeoryctes sp.	Palaeoryctes sp.	*Chambilestes foussanensis*			"Insectivora" indet.		
Rodentia			*Glibemys algeriensis* *Glibia pentalopha* *Glibia tetralopha* *Zegdoumys lavocati*		*Zegdoumys sbeitlai*			*Protophiomys algeriensis* *Nementchamys lavocati*		
Chiroptera					*Dizzya exsultans* *Rhinolophoidea indet.* *Chiroptera indet.*					
Primates			*Algeripithecus minutus* *Tabelia hammadae* *Primates indet.*	*Azibius trerki*	*Djebelemur martinezi*			*Biretia piveteaui cf. Algeripithecus* *Oligopithecidae indet.* *Primates indet.*		
Mammalia incertae sedis	Mammalia indet.		Mammalia indet.	*Heliosus insolitus*	Mammalia indet (Primates or Condylarthra?)		Mammalia indet.	Mammalia indet.	Mammalia indet.	

phosphatic deposits of the Ouled Abdoun Basin (Morocco), documents the first occurrence of modern ungulates (GHEERBRANT *et al.*, 1996).

These mammalian orders radiated during the Eocene times (table 1). New proboscideans appear, *Numidotherium* (MAHBOUBI *et al.*, 1984) at El Kohol (Algeria) and *Moeritherium* in Mali, Senegal and Libya. As for the primates, *Djebelemur* from Chambi (Tunisia) is considered as an adapiform (HARTENBERGER and MARANDAT, 1992) and *Algeripithecus* from Glib Zegdou (Algeria) as the earliest African anthropoid (GODINOT and MAHBOUBI, 1992). These Early-Middle Eocene Algerian localities and that of Chambi have also yielded new cosmopolitan orders like rodents (VIANEY-LIAUD *et al.*, 1994) or endemic ones: the oldest macroscelid is known from Chambi (HARTENBERGER, 1986), and several genera of hyraxes have been described (SUDRE, 1979; MAHBOUBI *et al.*, 1986; COURT and HARTENBERGER, 1992).

These fossils suggest the occurrence of several paleogene terrestrial interchanges between the African continent and the North-Tethyan regions (MAHBOUBI *et al.*, 1997 for an overview). The paleoryctid and adapisoriculid « insectivores » from Morocco record faunal exchanges between Europe and Africa around the K/T boundary (GHEERBRANT, 1987). GHEERBRANT (1990) considered the possible hyaenodontid creodonts and the omomyid primate from this country as strong arguments in favor of interchanges with Europe (and perhaps Asia) at the Paleocene/Eocene boundary. The zegdoumyid rodents from Gour Lazib (Algeria) (VIANEY-LIAUD *et al.*, 1994) and the macroscelid from Chambi (HARTENBERGER, 1986) indicate also North-South communications between Africa and the Holarctic continents. Then, if the Eocene period is globally characterized by an endemic evolution with the diversification of endemic lineages – such as Proboscidea and Hyracoidea –, these results suggest that the Arabo-

Table 1 *(previous page)*
Fossil terrestrial mammals known from faunas assigned to the Eocene in Africa. After ARAMBOURG *et al.* (1951), CROCHET *et al.* (this volume), GHEERBRANT *et al.* (1998), HARTENBERGER *et al.* (1997), MAHBOUBI *et al.* (1986), SUDRE (1979), VIANEY-LIAUD *et al.* (1994) and WIGHT (1980). The locality of Kpogame-Hahotoe (Togo) has yielded indeterminable remains of land mammals.

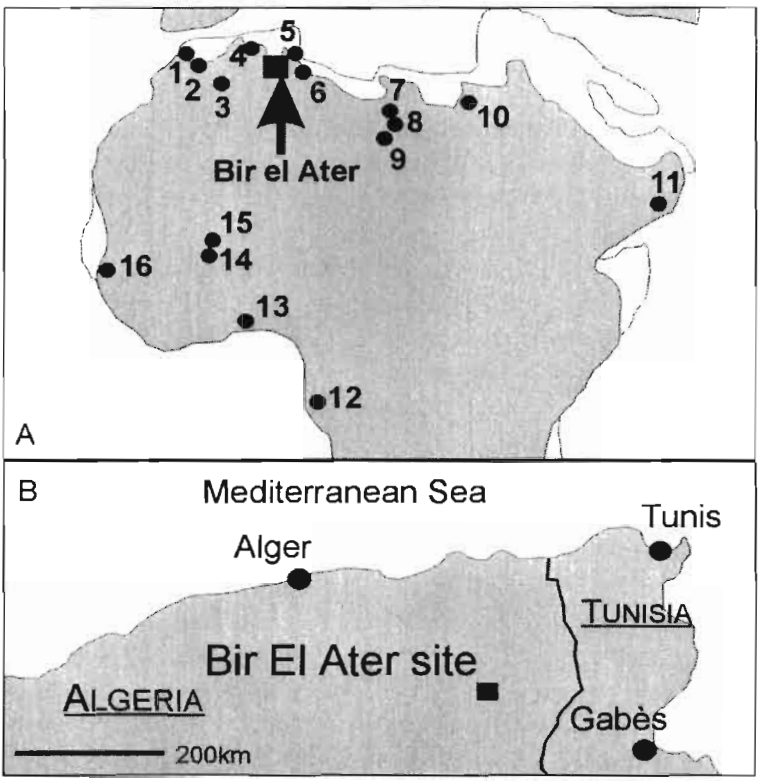

Figure 1
A, Location of the Bir El Ater site relative to the other Paleogene terrestrial mammal localities of Africa (reconstitution of the paleocoastlines during the Early Paleogene, modified from Smith *et al.* 1994): 1 Ouled Abdoun Basin (Morocco); 2 Ouarzazate Basin (Morocco); 3 Gour Lazib/Glib Zegdou (Algeria); 4 El Kohol (Algeria); 5 Chambi (Tunisia); 6 Jebel Bou Gobrine (Tunisia); 7 Zella (Libya); 8 Dor El Talha (Libya); 9 Jebel Hasanawah (Libya); 10 Fayum (Egypt); 11 Taqah and Thaytiniti (Oman); 12 Malembe (Angola); 13 Kpogame-Hahotoe (Togo); 14 In Tafidet (Mali); 15 Tamaguilelt (Mali); 16 M'bodione Dadere (Senegal).
B, Location map of the Bir El Ater site, Easthern Algeria.

African continent was not a completely isolated land mass in the Early Paleogene; it is only during the Oligocene that Africa was strictly isolated. Several localities in the Fayum depression (Egypt) (see HOLROYD, 1994) and two Oman sites (THOMAS *et al.*, 1989) document well this period.

Geological setting of Bir El Ater site

The Nementcha Mountains constitute the oriental end of the Algerian Saharan Atlas. In these massifs the Early Eocene is strictly marine and phosphatic. The presence of the continental Eocene was revealed by COIFFAIT *et al.* (1984) in deposits close to Bir El Ater in the south of the Jebel Abiod (figure 1B). These deposits yielded a composite fauna of continental and marine vertebrates in which the authors identified some rodents, several primates, a proboscidean, a hyracoid, a macroscelid as well as insectivores. Only the rodents (JAEGER *et al.*, 1985) and an anthropoid primate (de BONIS *et al.*, 1988) have been described.

In the stratigraphic section, the marine Cretaceous limestone is overlain in concordance by the Ypresian (limestone with marl intercalations) and by an other marine succession composed of marls and gypsum with mollusks and Lutetian ostracods (FAID, 1999). The vertebrate fauna was found in a detritic basal layer of a sandy fluvio-deltaic member overlaying discordantly these marine deposits. The discordance seems to represent the Lutetian tectonic Atlasic event. These Middle to Late Eocene deposits are immediately overlain by the continental Miocene.

These stratigraphic data permitted to consider the Bir El Ater locality as post Lutetian and ante Neogene in age (COIFFAIT *et al.*, 1984). The much more primitive phiomyid rodents compared to those of the Early Oligocene from the Jebel El Qatrani (Fayum, Egypt) also indicate a Middle-Late Eocene age (JAEGER *et al.*, 1985).

Comments on the mammalian fauna from Bir El Ater

This part presents the reassessment of the mammals from Bir El Ater, while insisting on the phylogenetic and paleobiogeographic conclusions. Except for the many dental remains of *Moeritherium* (Proboscidea), the whole of the material refers to small mammals (figure 2).

"Insectivora"

An « insectivore » known from only one molar trigonid is still undetermined. This specimen (figure 2A) shares with the Palaeoryctidae from the Thanetian-Ypresian of Morocco a minute, sharp and prominent trigonid with a small paraconid. But the lack of other characters, the existence of undescribed « insectivores » from the Early-Middle Eocene of Algeria (El Kohol, Gour Lazib and Glib Zegdou) and their absence (taphonomic biases?) in the Early Oligocene of the Fayum and Oman cannot allow a systematic assignment.

Macroscelidea

A new genus of elephants-shrew (Tabuce *et al.*, 2001), documented by some lower and upper cheek teeth, is attributed to the Herodotiinae. This subfamily is composed of two monospecific genera, *Chambius* from the Early-Middle Eocene of Chambi (HARTENBERGER, 1986) and *Herodotius* from the Early Oligocene of the Fayum (SIMONS *et al.*, 1991). Like these two genera (BUTLER, 1995), the new genus from Bir El Ater seems to have close relationships with the archaic ungulates ("condylarths"), and especially with one Hyopsodontidae Louisininae from the Paleogene of Europe.

Rodentia

The rodents are the most abundant fossils of the locality, with dozens of isolated teeth. When the Bir El Ater locality was found, *Nementchamys lavocati* Jaeger *et al.*, 1985 (Anomaluridae) and *Protophiomys algeriensis* Jaeger *et al.*, 1985 (Phiomyidae) were the oldest representatives of the order in Africa.

Since then, the discovery of the Zegdoumyidae permitted to reconsider the uncertain position of the Anomaluridae. It seems that this family is rooted in the zegdoumyids from the Early-Middle Eocene of Chambi and Glib Zegdou. This African group, the European Gliridae and the North American Sciuravidae would be related to the Ischyromyoids (VIANEY-LIAUD *et al.*, 1994). *Protophiomys algeriensis* remains the first occurrence of the Phiomyidae and shares several derived characters with the Asiatic Eocene Chapattimyidae (JAEGER *et al.*, 1985).

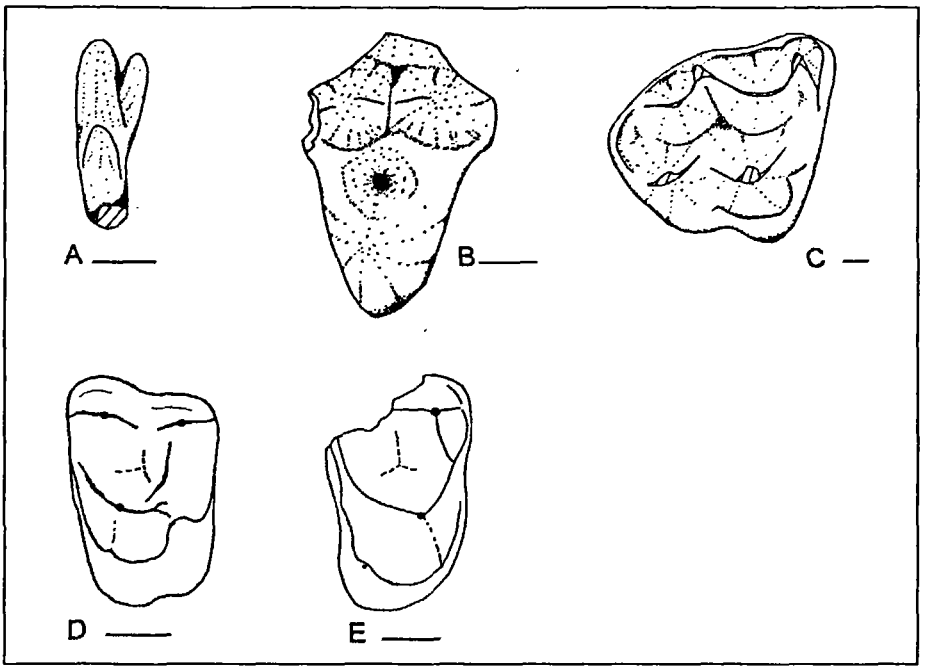

Figure 2
Mammals from Bir El Ater (scale bar 1 mm):
A, « Insectivora ». indet. UON 362, trigonid of a right lower molar in lingual view;
B, Carnivora or Creodonta indet. UON 360, right M^{1or2} in occlusal view;
C, *Bunohyrax matsumotoi* UON 372, right M^3 in occlusal view;
D, cf. *Algeripithecus* UON 364, left M^{1or2} in occlusal view;
E, Oligopithecidae indet. UON 366, right M^{1or2} in occlusal view.

Carnivora or Creodonta

Two teeth are related to a carnivore or a creodont. This assumption is supported by several characters: on the tritubercular M^{1-2} (fig. 2B), the paracone and the metacone are connected, the postmetacrista is broken but probably elongated, the parastyle is weakly cuspidate and anterior to the rest of the crown, the trigon basin is narrow with strong preprotocrista and postprotocrista, and the buccal area is well developed. This tooth shares with the creodont *Masrasector* from the Fayum

and Oman (SIMONS and GINGERICH, 1974; CROCHET *et al.*, 1990; HOLROYD, 1994) similar measurements, the mesio-distal narrowness of the protocone and the fact that the hypocone and the lingual cingulum are lacking. A tritubercular P^3 without well developed buccal cusp recalls some European forms like *Paracynohyaenodon* (hyaenodontid creodont). However, all these characters are plesiomorphic and inappropriate to relate our taxa to the creodonts rather than to the carnivores.

Hyracoidea

This order is documented by a complete upper molar and by several lower trigonids and talonids (figure 2C). COIFFAIT *et al.* (1984) attributed this hyrax to *Bunohyrax* (Pliohyracidae). This assignment is suggested by the bunodont to bunoselenodont molar morphology, the great asymmetry between the buccal and lingual cusps, the hypocristid not linked with the cristid obliqua, the parastyle and the mesostyle distally compressed, the lingual cingulid which surrounds the protocone but not the hypocone, and by a spur on the mesial base of the protocone. *Bunohyrax* is known by two species from the Jebel El Qatrani Formation (Fayum, Egypt): B. *major* and *B. fayumensis*. The small size of the Algerian fossil and the weak development of its protocone spur exclude this taxon to belong to these Egyptian species (Tabuce *et al.*, 2000). Our fossil could be related to a small size species of *Bunohyrax* distinguished by RASMUSSEN (1989) in the Green Hill Locality of the Fayum. This species was neither described nor figured, therefore it was not possible to establish detailed comparisons.

Anthropoid primates

The origin of Anthropoids is a very controversial question. The low number of known Eocene species, their fragmentary status and the importance of homoplasy make the problem very complex. The last decade has witnessed great advances in our knowledge of early anthropoidean primates in Africa and Asia (see SIMONS and RASMUSSEN, 1994 and DUCROCQ, 1998 for an overview). From Bir El Ater, three anthropoids have been discovered.

Biretia piveteaui de BONIS *et al.*, 1988

Until now, *Biretia* is the only primate described from Bir El Ater. It was considered as the oldest Catarrhini (Anthropoidea) and it could fill the gap between the Omomyid Tarsiiformes and the Catarrhini (de BONIS *et al.*, 1988). However, KAY and WILLIAMS (1994) relate *Biretia* to another anthropoid group – the Parapithecidae – and especially to the species *Quatrania wingi* from the Fayum.

cf. *Algeripithecus*

Two upper molars from Bir El Ater (figure 2D) share with *Algeripithecus* from Glib Zegdou a great degree of bunodonty, the lingual expansion of the paracone, sharpened preparacrista and postmetacrista, and the protocone-pericone link. However, our primate from Bir El Ater cannot be related to the species *A. minutus* because of its twice larger size, a paraconule-preparacrista link and a small hypocone.

Algeripithecus is considered as a primitive Parapithecidae by GODINOT (1994). According to that anthropoid assumption, cf. *Algeripithecus* from Bir El Ater would be a representative of a primitive lineage of *Algeripithecus*, contemporaneous to its sister group (the true Egyptian parapithecids). However, *A. minutus* and the other « African small bunodont simians » are rather considered by HARTENBERGER *et al.* (1997) as cercamoniine adapiforms with European affinities. Our fossil shares evident characters with these primates; anyway the Anthropoid assumption or the Adapid one could be validated only with more complete material.

suggests an Asian origin of catarrhines, and/or an ancient dichotomy between African and Asian catarrhines. This dichotomy could be the result of Eocene faunal exchanges between North Africa and Asia which are also documented by rodents (COIFFAIT *et al.*, 1984), artiodactyls (DUCROCQ, 1997) and carnivores (HOLROYD and MAAS, 1994). The discovery of a catarrhine anthropoid in the Middle-Late Eocene of Bir El Ater contributes to the debate because it is the oldest stratigraphic occurrence of the Oligopithecidae. In the current state of our knowledge, we can propose two hypothesis: either it represents the witnesses of an Asian Middle Eocene immigration, or it documents an unknown older African lineage to date.

Conclusion

The mammalian fauna from Bir El Ater appears to be one of the most diversified from the African Eocene; the majority of the terrestrial eutherian orders, known during the Paleogene in Africa, are represented. African endemic lineages are documented by Proboscidea, Hyracoidea, Macroscelidea, Anomaluridae and Phiomyidae rodents. The diversity of primates is also notable with three anthropoids and at least one undeterminate prosimiiform.

These African Paleogene fossils are important in terms of higher rank taxa systematic and phylogeny. An increased knowledge of these mammals becomes necessary, not only to identify the continent where the anthropoids originate, but also to solve the palaeontological problem of the molecular Afrotheria clade (STANHOPE *et al.*, 1998). Although the « African molecular clade » suggests a common origin for the African endemic groups (Proboscidea, Hyracoidea, Macroscelidea, Tubulidentata, Tenrecidae and Chrysochloridae), no current morphological or palaeontological data agree with that assumption.

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