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Option : Stratigraphie

**LE PALEOGENE CONTINENTAL DU SUD OUEST ALGERIEN  
(Lithostratigraphie, paléontologie et sédimentologie).**

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**Volume II : Annexes (Publications)**

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**Annexe n°1**

Paléontologie systématique (Paléontologie des vertébrés)

## Nouveaux sites à vertébrés paléogènes dans la région des Gour Lazib (Sahara nord-occidental, Algérie)

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### Résumé

De récents travaux dans les terrains paléogènes de la région des Gour Lazib (Hammada du Dra, Algérie) nous ont conduits à réviser les attributions stratigraphiques et à compléter la lithostratigraphie de la formation du Glib Zegdou vers sa base. Cette série continentale repose en discontinuité sédimentaire sur un substratum paléozoïque. Les prospections systématiques dans le membre intermédiaire de la formation nous ont permis de mettre en évidence plusieurs nouveaux sites à vertébrés (dipneustes, actinoptérygiens, chéloniens et mammifères notamment), associés à des oogones de charophytes d'âge Éocène inférieur à moyen. Nous décrivons un hyracoïde (*Titanohyrax tantulus*) et un macroséolididé (?*Chambius* sp.). Nous annonçons par ailleurs la découverte de deux sites remarquables, riches en restes de mammifères. **Pour citer cet article : M. Adaci et al., C. R. Palevol 6 (2007).** © 2007 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

### Abstract

**New Palaeogene vertebrate sites from the Gour Lazib area (northwestern Sahara, Algeria).** Recent fieldworks in the Palaeogene of the Gour Lazib area (Hammada du Dra, Algeria) led us to reassess the stratigraphic allocations of the Glib Zegdou formation and to complement the lithostratigraphy of this formation. This continental series unconformably overlies a Palaeozoic substratum. The prospecting–exploration works in the middle member of the formation allowed us to discover several new vertebrate sites (with lungfish, actinopterygians, chelonians, and notably mammals), associated with Early to Middle Eocene charophyte

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oogones. We describe a hyracoid (*Titanohyrax tantulus*) and a macroscelidid (?*Chambius* sp.). We here also report the discovery of two rich mammalian sites. **To cite this article:** M. Adaci et al., C. R. Palevol 6 (2007).

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**Mots clés :** Algérie ; Éocène continental ; Vertébrés ; Mammalia

**Keywords:** Algeria; Continental Eocene; Vertebrates; Mammalia

## Abridged English version

### Introduction

The Gour Lazib area is located in the western part of the Algerian Sahara, at approximately 400 km to the southwest of Béchar (Fig. 1a) [4]. In this region, the Tertiary series form vast tabular plates or outliers ('Gour' in Arabic); they unconformably overlay the Palaeozoic substratum or the marine Cenomanian–Turonian series of the Kem Kem. The first mammals discovered in this area come from four distinct loci, the three first in Gour Lazib, the fourth on the northern side of Glib Zegdou [6,25,26]; the latter is an isolated outlier of the Gour Lazib complex. More recently, Mahboubi [16] discovered on the southern side of Glib Zegdou a fifth mammalian fossiliferous point, more fossiliferous than the others are [3,8,9,17,29,30,33]. In all loci, mammals are in association with oogones of charophytes. The biostratigraphic data resulting from these algae remains were considered by Mebrouk et al. [19,20]. These authors proposed a Ypresian to basal Lutetian age for the mammalian fauna. Since 2004, new fieldworks in this area led us to discover new mammalian sites on Glib Zegdou Formation. In this paper, the acronym HGL signifies 'Hammada Gour Lazib' and indicates a vertebrate fossiliferous level.

### Geological framework and new vertebrates from the Glib Zegdou Formation

The Glib Zegdou outlier shows the most complete continental series of the studied area. According to former authors, the lower boundary of this section was defined above a grey silicified limestone, with pink to blue blots (Fig. 1b). Without palaeontological data, this layer was correlated with the Cenomanian–Turonian of the Kem Kem [14]. In order to test this attribution, the section was improved below the grey silicified limestones where, in gypseous marls, we discovered continental vertebrate remains (HGL45 and HGL46; Fig. 1a and b). HGL45 delivered in particular a skull (Fig. 2a) and a carapace of a podocnemidid chelonian, and two possible mammalian phalanges. The

podocnemidids are documented in both Africa and South America since the Cretaceous; living forms occur in South America and Madagascar. The taxon from HGL45 is more derived than *Hamadachelys* – the unique known Cenomanian podocnemidid from the Kem Kem [32] –, but more primitive than *Dacquemys* from the Late Eocene of the Fayum [5]. By the lack of any biochronological marker, the age of the lower member of the Glib Zegdou Formation cannot be established with confidence. It seems that it could be Eocene in age, as overlying levels, but a Palaeocene age cannot be excluded. Anyway, the presumed Cenomanian–Turonian age is to be revised; in the studied area, the Cenomanian–Turonian is represented by thick marine bioclastic limestones. The upper part of the lower member of the formation yielded two other vertebrate layers; one of them corresponds to the type locality of *Titanohyrax mongereaui* (HGL49 or locus 4 of Sudre [26]; Fig. 1a and b). The middle member represents a sequence of red to yellow siltstones and sandstones where vertebrate remains, notably mammals, are abundant. The upper member consists in a thick limestone with flint pebbles. Prospecting–exploration works in the middle member of the formation allowed us to discover several new mammalian sites.

HGL04 (Fig. 1a) yielded a fragmentary mandible of *Microhyrax lavocati* bearing p1–p4 (Fig. 2e) [31] as well as rodents, a creodont, an insectivore, and a new macroscelidid ?*Chambius* sp. documented by an isolated M<sub>3</sub> (Fig. 2b and c) (Table 1). It differs from *C. kasserinensis* from the Early Eocene of Chambi, Tunisia [12], by the occurrence of a small hypoconulid and by a rather deep hypoflexid. These differences could suggest that the elephant shrew from HGL04 represents a new genus or at least a new species of *Chambius*, more primitive than *C. kasserinensis*. Nevertheless, the available material is obviously inadequate to formalize here such an assumption.

HGL10 (Fig. 1a) was discovered near to the locus 1 of Sudre [26]. Several mammals are represented (Table 1), among them an upper molar belonging to *Titanohyrax tantulus* (Fig. 2d). This specimen shows all the characters of the genus [2]: highly selenodont buccal cusps with large and salient mesostyle and parastyle; lack of

labial and lingual ribs; protocone much larger than hypocone; and prehypocrista abutting the lingually displaced metacone. The specific attribution to *T. tantulus* is supported by compatible size and brachyodonty. Up to now, *T. tantulus* was only known from Chambi [2]. A chronological correlation between Chambi and the Gour Lazib sites is however conjectural, as the stratigraphic range of *T. tantulus* is yet unknown. The charophytes association collected in HGL10 could suggest an Ypresian age rather than a Lutetian age for the middle member of the Glib Zegdou Formation (Mebrouk, in prep); the floristic association is represented by *Raskyella sahariana*, *Raskyella pecki*, *Maedleriella lavocati*, *Stephanochara acris*, *Nodosochara* aff. *jordae*, *Raskyella* sp., *Nitellopsis (Tectochara) thaleri*, *Maedleriella cristellata*, *Harrisichara* sp., *Chara* sp., and *Harrisichara* aff. *leptocera*.

In the Glib Zegdou (Fig. 1a and b), we discovered two remarkable mammalian localities (HGL50 and HGL51) just below the site of Mahboubi [16] (HGL52). HGL50 delivered more than 400 determinable mammalian remains illustrating at least 20 species (Table 1). The significance of the material consists in the discovery of fragmentary upper and lower jaws of several species. Some taxa are new. Moreover, for the previously published species from the Glib Zegdou, isolated teeth document some unknown dental loci so far. The most represented groups are rodents, hyraxes, and primates; among them, we find *Algeripithecus*, the oldest alleged anthropoid primate [8,9]. Some postcranial elements are also preserved, particularly tarsal bones (astragali and calanei) of hyraxes [31]. Fragmentary fish fossils are abundant (Table 2). In HGL51, fish remains are scarce (some large vertebrae and ganoid scales), although mammalian remains are well preserved and abundant. This level yielded several partial skulls, upper and lower jaws of at least five taxa: *Microhyrax lavocati*, *Megalohyrax gevisini*, a new hyrax, *Azibius treрки*, and *Helioseus insolitus*.

To conclude, the discovery in the Gour Lazib area of several mammalian localities in the middle member of the Glib Zegdou Formation is extremely important because of the scarcity of the Palaeogene – especially Early to Middle Eocene – mammalian sites in Africa. We can reasonably assume that our knowledge of the basal radiation of eutherian mammals in this continent will be largely updated with the study of the faunas discovered in the HGL50 and HGL51 localities.

## 1. Introduction

Dans la partie occidentale du Sahara algérien, les séries tertiaires forment de vastes plateaux désertiques

(« hammadas »), qui masquent le socle paléozoïque et quelquefois les terrains marins du Cénomano-Turonien du Kem Kem [4,15]. Les Gour Lazib, situés à environ 400 km au sud-ouest de Béchar (Fig. 1a), constituent un ensemble de buttes-témoins résultant de l'érosion des hammadas. Dans la terminologie saharienne, suivie dans cet article, le terme « gour » désigne un ensemble de « gara » (butte-témoin).

Les premiers mammifères découverts dans cette région proviennent de quatre points distincts, les trois premiers dans les Gour Lazib, le quatrième sur le flanc nord du Glib Zegdou [6,25,26]. Ce dernier est une butte-témoin isolée, appartenant au complexe des Gour Lazib. Plus récemment, Mahboubi [16] a découvert un cinquième point fossilifère sur le flanc sud du Glib Zegdou, plus riche que les précédents [3,8,9,17,29,30,33]. Les premiers fossiles découverts à proximité de la localité de Zegdou et sur le Glib Zegdou (Fig. 1a) furent des gastéropodes et des restes de poissons [1,14,15]. Ils furent datés du Sénonien. Plus tard, la découverte d'oogones de charophytes sur le flanc sud-est des Gour Lazib permit de proposer un âge Éocène moyen ou supérieur pour ces niveaux [10]. Puis, consécutivement à la découverte, associée aux mammifères, d'une flore de charophytes plus diversifiée au Glib Zegdou, Gevin et al. [6] suggèrent un âge Éocène inférieur pour la faune de mammifères. Cet âge fut discuté par Mebrouk et al. [19,20], ces auteurs n'excluant pas un âge Lutétien basal. Mahboubi [16] a donné le nom de formation du Glib Zegdou à toute cette série, d'âge Yprésien à Lutétien basal.

Depuis 2004, de nouvelles prospections nous ont permis de découvrir divers sites inédits à vertébrés dans cette formation. En janvier 2005, puis en février 2006, deux sites remarquables à mammifères ont été découverts sur le Glib Zegdou. D'autres localités, moins riches, ont également été mises au jour dans les Gour Lazib. Les deux espèces décrites dans cet article permettent de discuter l'âge relatif de la formation de Glib Zegdou par rapport aux autres sites de l'Éocène africain.

## 2. Cadre géologique et description des nouveaux sites à vertébrés

Le Glib Zegdou offre la série continentale la plus complète du secteur étudié (Fig. 1b). Les anciens auteurs ont fait débiter cette coupe à partir de calcaires gris silicifiés et massifs à taches bleues et roses, corrélés, sans arguments paléontologiques, au Cénomano-Turonien du Kem Kem [14]. Afin de tester cette hypothèse, la coupe a été complétée vers la base. De bas en haut, on distingue trois membres. Le sigle HGL correspond à « Hammada

Gour Lazib» et indique un niveau fossilifère à vertébrés.

2.1. Membre inférieur argilo-marno-gypseux

Il n'affleure qu'à la base NNW du Glib Zegdou. Il repose en discontinuité sédimentaire sur la ride paléozoïque de l'Oussada. Sa base est constituée d'une succession d'argiles silteuses rouges et de grès grossier, parfois encroûté. Affleurent ensuite un calcaire gris silicifié à taches roses, des marnes gypseuses vertes à vertébrés (HGL45 et HGL46 ; Fig. 1a), puis le calcaire silicifié et massif à taches bleues et roses signalé par les anciens auteurs.

HGL45 a livré des restes d'actinoptérygiens (écailles de polyptères et os brisés de siluriformes), ainsi qu'une dossière complète et un crâne bien conservé de chélonien

(Fig. 2a). Ces restes sont attribués à un pleurodire, de la famille des Podocnemididae (Tong, en prép.). Ceux-ci sont connus depuis le Crétacé en Afrique et Amérique du Sud, et les représentants actuels vivent en Amérique du Sud et Madagascar. Le crâne est morphologiquement plus avancé que *Hamadachelys*, le seul podocnemididé connu dans les couches cénomaniennes des Kem Kem [32] et présente des caractères de podocnemididé moderne. Le spécimen semble être différent des taxons déjà connus, et possède certains caractères qui rappellent *Dacquemys*, un podocnemididé connu dans l'Éocène supérieur de Fayoum [5]. Il est toutefois plus primitif que ce dernier, ce qui pourrait indiquer un âge plus ancien que l'Éocène supérieur. Le traitement par lavage-tamisage de quelques kilogrammes de sédiment a livré, par ailleurs, deux phalanges pouvant appartenir à un mammifère de taille moyenne. En l'absence

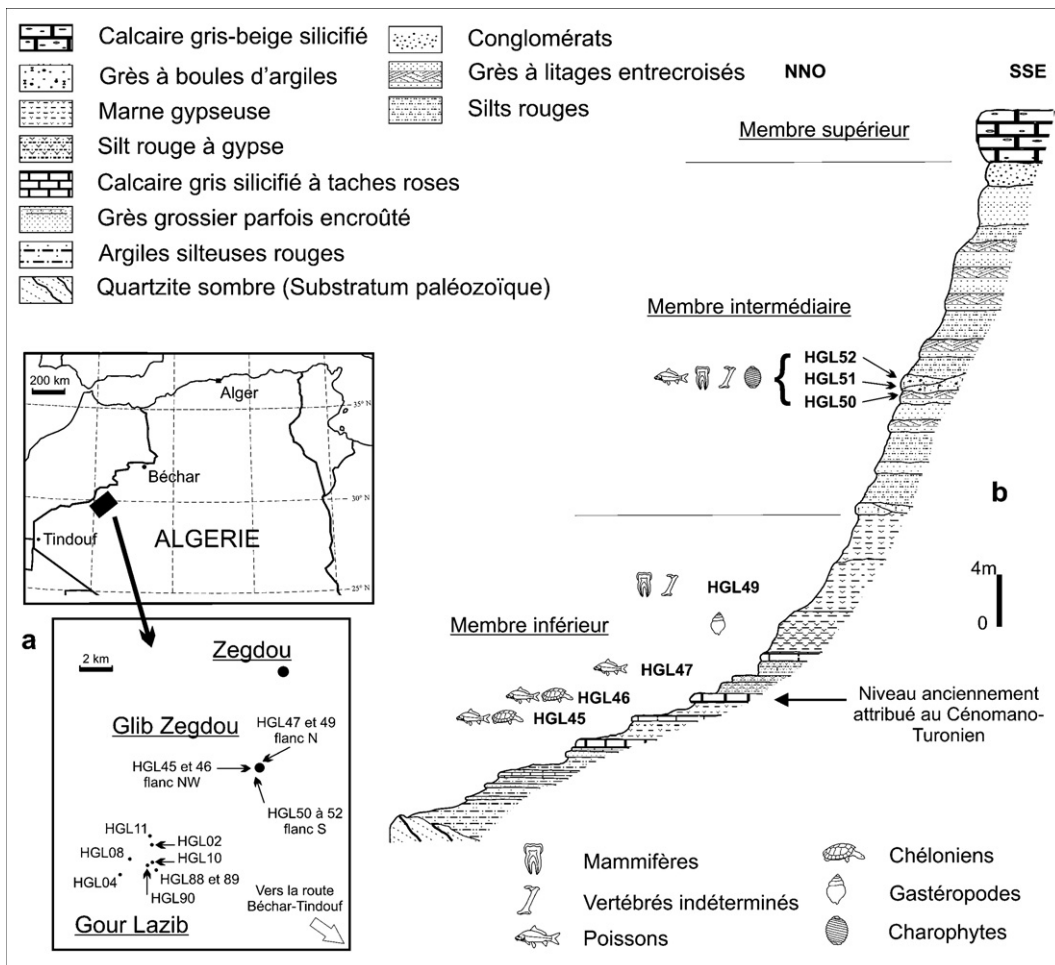


Fig. 1. a. Localisation géographique des divers loci à vertébrés découverts dans la formation du Glib Zegdou (Sahara occidental, Algérie). b. Coupe lithologique de la butte-témoin du Glib Zegdou.

Fig. 1. a. Location of the discovered vertebrate sites in the Glib Zegdou formation (western Sahara, Algeria). b. Lithological section of the Glib Zegdou outlier.

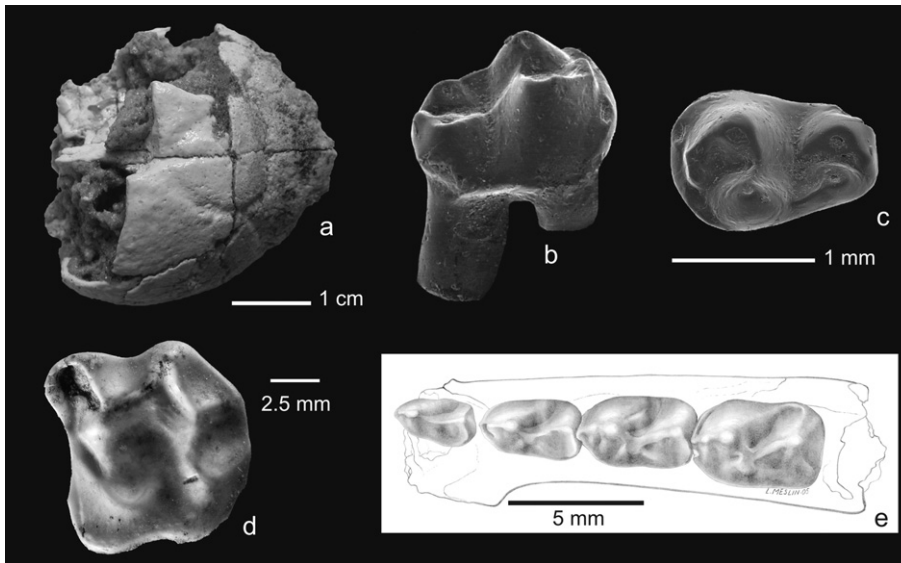


Fig. 2. Nouveaux vertébrés récoltés dans la formation du Glib Zegdou (Sahara occidental, Algérie). Podocnemididae indéterminés (Testudines, Pleurodira), UM/HGL45–01, crâne en vue dorsale **a**. ?*Chambius* sp., UM/HGL04–15, M<sub>3</sub> en vues labiale **b**. et occlusale **c**. et *Titanohyrax tantulus*, UM/HGL10–12, M<sup>1?</sup> en vue occlusale **d**. *Microhyrax lavocati*, UM/HGL04–11, P<sub>1–4</sub> en vue occlusale **e**.

Fig. 2. New vertebrates discovered in the Glib Zegdou Formation (western Sahara, Algeria). Podocnemididae indet. (Testudines, Pleurodira), UM/HGL45–01, skull in dorsal view **a**. ?*Chambius* sp., UM/HGL04–15, M<sub>3</sub> in labial **b**. and occlusal **c**. views. *Titanohyrax tantulus*, UM/HGL10–12, M<sup>1?</sup> in occlusal view **d**. *Microhyrax lavocati*, UM/HGL04–11, P<sub>1–4</sub> in occlusal view **e**.

d'éléments de datation précis, l'âge de la base du membre inférieur de la formation du Glib Zegdou ne peut être établi avec certitude. Il semble toutefois probable qu'il soit Éocène à l'instar des niveaux sus-jacents, mais on ne peut exclure un âge plus ancien (Paléocène ?). Quoiqu'il en soit, l'âge présumé Céno-mano-Turonien du petit banc de calcaire rosâtre situé au-dessus de HGL45–46 est à réviser ; dans la région, le Céno-mano-Turonien est représenté par des niveaux marins à épaisses barres calcaires bioclastiques [14].

La partie supérieure du membre montre une succession de silts rouges, de marnes à gypse, et de grès à gypse beige blanchâtre. Deux niveaux s'avèrent fossilifères (HGL47 et HGL49 ; Figs. 1a et b). Le premier n'a livré que des vertébrés indéterminables. Le second, qui correspond au locus 4 de Sudre [26], est le gisement type de *Titanohyrax mongereaui*.

## 2.2. Membre intermédiaire détritique

Il est composé d'une alternance de grès jaunes à oogones de charophytes et de silts rouges, qui passent, vers le sommet, à une alternance de grès à stratifications obliques et de silts rouges. Il renferme un horizon lenticulaire de grès jaune à rouge, à boules d'argile, très riche en charophytes. L'attaque acide d'environ 450 kg du niveau HGL50 (Fig. 1a et b) a livré de très nombreux restes de

poissons et plus de 400 restes mammaliens identifiables, documentant plus de 20 espèces d'euthériens ; certaines sont nouvelles (Tableau 1). Le traitement du sédiment se poursuit à ce jour. L'importance de ce matériel réside en la découverte, pour divers taxons, de fragments de mandibules et maxillaires. Pour les espèces précédemment publiées du Glib Zegdou, les nombreuses dents isolées permettent de documenter des loci dentaires jusqu'ici inconnus. Les groupes les plus abondamment représentés sont les rongeurs zegdoumyidés, les hyracoïdes et les primates. Des éléments postcrâniens sont présents, notamment d'hyracoïdes [31]. Le matériel ichthyologique est constitué de dents isolées, de plaques dentaires, d'écailles ganoïdes, de vertèbres, d'os du crâne et d'épines des nageoires, désarticulés et souvent brisés. Une étude préliminaire permet de reconnaître des représentants de six taxons (Tableau 2). Certains ne sont plus représentés actuellement au Maghreb. Leur association est typique de l'ichthyofaune connue à l'Éocène, à l'Oligocène et pendant une partie du Miocène dans les eaux douces, du Maghreb, à l'ouest, à la plaque arabe, à l'est, et de la région nilo-soudanienne, au sud [11,21,22].

HGL51 est un niveau gréseux friable à boulettes d'argile, situé à moins d'un mètre au-dessus de HGL50. Il a également livré des restes bien conservés de vertébrés. Les poissons sont peu abondants (écailles ganoïdes



Tableau 1

Liste faunique des mammifères identifiés dans les sites des Gour Lazib, formation du Glib Zegdou, Algérie. Les cercles noirs indiquent les localités types

Table 1

Mammalian list of the Gour Lazib sites, Glib Zegdou Formation, Algeria. The black circles indicate type localities

|  | HGL02 | HGL04 | HGL08 | HGL10 | HGL11 | HGL49 | HGL50 | HGL51 | HGL52 | HGL88 | HGL89 | HGL90 |
|--|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Rodentia                                     |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Glibemys algeriensis</i>                  |       |       |       |       |       |       |       |       | ●     |       |       |       |
| <i>Glibia pentalopha</i>                     |       |       |       |       |       |       | ○     |       | ●     |       |       |       |
| <i>Glibia tetralopha</i>                     |       |       |       |       |       |       |       |       | ●     |       |       |       |
| <i>Glibia</i> sp.                            |       |       |       |       |       |       | ○     |       |       |       |       | ○     |
| <i>Zegdoumys lavocati</i>                    |       |       |       |       |       |       | ○     |       | ●     |       |       |       |
| <i>Zegdoumys</i> sp.                         |       |       |       |       | ○     |       |       |       |       |       |       | ○     |
| Rodentia gen. et sp. nov. 1                  |       |       |       |       |       |       | ○     |       |       |       |       |       |
| Rodentia gen. et sp. nov. 2                  |       |       |       |       |       |       |       |       | ○     |       |       |       |
| Rodentia indét.                              |       | ○     | ○     | ○     |       |       | ○     |       | ○     |       |       |       |
| Carnivora                                    |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Glibzegdouia tabelbalaensis</i>           |       |       |       |       |       |       | ○     |       | ●     |       |       |       |
| Creodonta (div. sp.)                         |       | ○     | ○     |       |       |       | ○     |       |       |       |       |       |
| Lipotyphla (div. sp.)                        | ○     | ○     | ○     |       |       |       | ○     |       | ○     |       |       | ○     |
| Chiroptera                                   |       |       |       |       |       |       |       |       |       |       |       |       |
| Chiroptera gen. et sp. nov. 1                |       |       |       |       |       |       | ○     |       |       |       |       |       |
| Chiroptera gen. et sp. nov. 2                |       |       |       |       |       |       | ○     |       |       |       |       |       |
| Primates                                     |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Algeripithecus minutus</i>                |       |       | ○     | ○     |       |       | ○     |       | ●     |       |       |       |
| <i>Tabelia hammae</i>                        |       |       |       | ○     |       |       | ○     | ○     | ●     |       |       |       |
| <i>Draolestes hammaeensis</i>                |       |       | ○     | ○     |       |       | ○     |       | ●     |       |       |       |
| <i>Azibius trerki</i>                        |       |       |       | ●     |       |       | ○     | ○     | ○     |       |       |       |
| Primates gen. et sp. nov. 1                  |       |       |       |       |       |       |       |       | ○     |       |       |       |
| Primates gen. et sp. nov. 2                  |       |       |       |       |       |       | ○     |       |       |       |       |       |
| Primates gen. et sp. nov. 3                  |       |       |       |       |       |       | ○     |       |       |       |       |       |
| Primates indét.                              |       |       |       |       |       |       | ○     |       |       |       |       |       |
| Condylarthra gen. et sp. nov.                |       |       |       |       |       |       | ○     |       |       |       |       |       |
| Proboscidea                                  |       |       |       |       |       |       | ?     |       |       |       |       |       |
| Hyracoidea                                   |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Microhyrax lavocati</i>                   |       | ○     |       |       |       |       | ○     | ○     | ○     |       |       | ●     |
| <i>Titanohyrax mongereaui</i>                |       |       |       |       |       | ●     |       |       |       |       |       |       |
| <i>Titanohyrax tantulus</i>                  |       |       |       | ○     |       |       |       |       |       |       |       |       |
| <i>Megalohyrax gevini</i>                    |       |       |       | ?     |       |       |       | ○     |       |       |       | ●     |
| ? <i>Bunohyrax</i> ou <i>Megalohyrax</i> sp. |       |       |       |       |       |       |       |       |       | ○     |       |       |
| ? <i>Thyrohyrax</i> sp.                      |       |       |       |       |       |       | ○     |       |       |       |       |       |
| Hyracoidea gen. et sp. nov.                  |       |       |       |       | ?     |       | ○     | ○     | ?     |       |       |       |
| Hyracoidea indét.                            |       |       | ○     | ○     |       |       | ○     |       | ○     |       |       |       |
| Macroscelidea                                |       |       |       |       |       |       |       |       |       |       |       |       |
| ? <i>Chambius</i> sp.                        |       | ○     |       |       |       |       |       |       |       |       |       |       |
| Mammalia <i>incertae sedis</i>               |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Helioseus insolitus</i>                   |       |       |       |       |       |       | ○     | ○     | ○     |       | ○     | ●     |
| formes indéterminables                       | ○     | ○     |       | ○     |       |       | ○     |       |       | ○     | ○     |       |

et vertèbres). L'intérêt tout particulier de ce niveau consiste en la découverte de plusieurs crânes, maxillaires et mandibules de mammifères. Dans l'état actuel, cinq taxons sont représentés : *Azibius trerki*, *Helioseus insolitus*, *Microhyrax lavocati*, ? *Megalohyrax gevini* et un hyracoïde nouveau. Par-dessus vient la localité F9 de Mahboubi [16], nommée ici HGL52 (Fig. 1a-b).

Les prospections dans l'extrémité sud-ouest des Gour Lazib nous ont conduits à échantillonner d'autres niveaux détritiques dans le membre intermédiaire ; plusieurs d'entre eux ont livré des mammifères (Fig. 1a,

Tableau 1). La « butte rouge » constitue un petit affleurement ne dépassant guère les huit mètres d'épaisseur, qui correspond partiellement au membre intermédiaire détritique du Glib Zegdou. Sa partie inférieure, HGL88, est le locus 3 de Sudre [26] ; sa partie supérieure, à dominance argileuse, renferme une lentille microconglomératique à rares restes de mammifères (dont *Helioseus*) (HGL89). Le site HGL90 (= locus 2 de Sudre [26]), gisement type de *Microhyrax lavocati*, *Helioseus insolitus* et *Megalohyrax gevini*, a été rééchantillonné ; il a livré quelques dents de rongeurs et d'insectivores. La localité HGL10

Tableau 2

Liste faunique des poissons du site HGL50, formation du Glib Zegdou, Algérie  
 Table 2  
 Faunal list of the fishes from the HGL50 site, Glib Zegdou Formation, Algeria

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|                         |
|-------------------------|
| <i>Actinopterygii</i>   |
| Cladistia               |
| Polypteriformes         |
| Polypteridae            |
| Teleostei               |
| Characiformes           |
| Characiformes indéterm. |
| Siluriformes            |
| ? Clariidae             |
| Siluriformes indéterm.  |
| Perciformes             |
| <i>Dipnoi</i>           |
| Lepidosireniformes      |
| Protopteridae           |

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correspond à un niveau à empreintes végétales charbonneuses, découvert sur la gara type de *Azibius trerki* (= locus 1 de Sudre [26]). Ce site a livré des molaires mal conservées de rongeurs et de primates, ainsi que deux hyracoïdes, dont *Titanohyrax tantulus* décrit ci-dessous. Enfin, le site HGL04 a livré un créodonte et un insectivore encore indéterminés, un fragment de mandibule attribué à *Microhyrax lavocati* (Fig. 2e) [31] et une molaire isolée de macroscélididé, décrite ci-dessous.

### 2.3. Membre supérieur carbonaté

Il est constitué d'une épaisse barre de calcaire beige grisâtre à silex, dont l'examen microscopique montre un calcaire micritique renfermant des grains de quartz de petite taille. Cette barre, lorsqu'elle n'est pas érodée, coiffe la plupart des buttes-témoins des Gour Lazib, où elle a livré des sections de coquilles mal préservées d'un gastéropode continental du genre *Pseudoceratodes* sp.

## 3. Systématique

**Ordre :** Macroscelidea Butler, 1956

**Famille :** Macroscelididae Bonaparte, 1838

**Sous-famille :** Herodotiinae Simons et al., 1991

**Espèce :** ? *Chambius* sp.

**Matériel attribué :** M<sub>3</sub> droite ; UM/HGL04–15, collections de l'université Montpellier-2. Longueur = 1,6 mm ; largeur = 1,1 mm.

**Localité et âge :** HGL04, Gour Lazib, Algérie ; Yprésien à Lutétien basal.

**Description :** cette molaire est biradiculée, tétraturbulée et bunodonte. Elle est légèrement exodaeno-

donte, et présente une hypsodontie unilatérale franche (couronne haute labialement). Le trigonide est plus large et plus haut que le talonide, le protoconide et le métaconide sont de taille similaire, le paraconide est en position médiane, il est très réduit et relié au protoconide. Le cingulum antérieur est continu et marqué. Sur le talonide, l'hypoconide porte une cristide obliqua très courte, qui n'atteint pas la base postérieure du trigonide. L'hypoconulide est minuscule, en position distale et relié à l'hypoconide. L'entoconide porte une préentocristide qui remonte haut sur le flanc postérieur du métaconide.

**Comparaison :** la tétraturbulée, la bunodontie, l'exodaenodontie, la morphologie du trigonide et la simplification du talonide justifient l'attribution de cette molaire aux macroscélididés herodotiinés. Les « condylarthres » louisinins et apheliscinés, phylogénétiquement proches de ces macroscélididés primitifs [27,28,31,34], diffèrent par des tubercules moins bunodontes, un talonide plus allongé et de hauteur sensiblement égale à celle du trigonide, ainsi que par l'absence d'hypsodontie unilatérale. À ce jour, les herodotiinés sont représentés par trois espèces : *Chambius kasserinensis* de l'Yprésien à Lutétien de Chambi (Tunisie) [12], *Nementchatherium senarhense* du Bartonien à Priabonien de Bir El Ater (Algérie) [28] et *Herodotius pattersoni* du Priabonien du Fayoum, localité L41 (Égypte) [24]. Les M<sub>3</sub> de *Nementchatherium* et *Herodotius* se distinguent de la forme ici décrite par l'absence de paraconide et par une simplification plus poussée du talonide, qui confère à la couronne un contour occlusal arrondi caractéristique : perte de l'hypoconulide, disparition de l'hypoflexide, entoconide et hypoconide accolés et cristide obliqua absente. Par rapport à ces formes de la seconde partie de l'Éocène, *Chambius kasserinensis* évoque davantage la forme algérienne, en raison d'un degré moins important de simplification de la M<sub>3</sub>. On distingue, de plus, chez certains spécimens inédits de Chambi un reste de paraconide et une cristide obliqua. UM/HGL04-15 évoque également *C. kasserinensis* par une taille similaire et une forte préentocristide, qui ferme labialement le bassin du talonide, mais s'en distingue par la persistance de l'hypoconulide et d'un hypoflexide relativement profond. Ces différences pourraient suggérer l'attribution de la forme des Gour Lazib à un nouveau genre, tout au moins à une nouvelle espèce du genre *Chambius*, plus primitive que *C. kasserinensis*. Malgré tout, le matériel actuellement disponible est bien évidemment trop limité pour formaliser une telle hypothèse. Enfin, si *C. kasserinensis* est l'espèce la plus abondante à Chambi, l'unique spécimen récolté dans les divers sites du membre intermédiaire de la formation du Glib Zegdou est à signaler. Son absence à HGL50 est très signifi-



tive ; nous rappelons que ce site a livré plus de 400 restes mammaliens identifiables, essentiellement des micro-mammifères. Il faut noter ici que le macroscléridé cité par Mahboubi [16] au Glib Zegdou (HGL52) est en fait une DP d'hyracoïde. Ainsi, dans l'état actuel des données, des facteurs écologiques peuvent, mieux que des facteurs taphonomiques (nature du sédiment et conditions de dépôt), expliquer la rareté des macroscléridés dans les Gour Lazib.

**Ordre :** Hyracoidea Huxley, 1869

**Famille :** Pliohyracidae Osborn, 1899

**Sous-famille :** Saghatheriinae Andrews, 1906

**Espèce :** *Titanohyrax tantulus*

**Matériel attribué :** M<sup>1</sup> gauche ; UM/HGL10–12, collections de l'université Montpellier-2. Longueur = 10,4 mm ; largeur = 10,8 mm.

**Localité et âge :** HGL10, Gour Lazib, Algérie ; Yprésien à Lutétien basal.

**Description :** la couronne est basse et présente un contour trapézoïde. L'ectolophe est sélénodonte, il forme un W prononcé, en raison de la position très labiale des parastyle et mésostyle ; ces styles sont globuleux à leur base, et aussi puissants que le paracône et métacône. Le métastyle est réduit. Le protocône est plus étendu et lingualemment décalé par rapport à l'hypocône ; ce dernier est comprimé mésiodistalement. La préprotocrista est longue et atteint la base du parastyle ; la postprotocrista est très courte. La préhypocrista est courte, elle est dirigée vers la base du métacône ; la posthypocrista rejoint le cingulum postérieur.

**Comparaison :** Court et Hartenberger [2] ont donné une liste de caractères définissant *Titanohyrax* : forte sélénodontie (*Thyrohyrax* présente des styles moins puissants, notamment le mésostyle), absence des épérons d'émail sur l'ectolophe (lesquels sont observés chez *Saghatherium* et *Pachyhyrax*), faible développement du métastyle, protocône plus grand que l'hypocône, préprotocrista puissante, et préhypocrista rejoignant la base du métacône. Tous ces caractères définissent le taxon des Gour Lazib. Sa brachyodontie évoque les espèces *T. mongereaui* de HGL49 [26] et *T. tantulus* de Chambi [2] ; ces deux espèces se distinguent clairement par leur taille. Les mensurations d'UM/HGL10–12, semblables à celles de la M<sup>1</sup> de *T. tantulus*, justifient notre attribution spécifique.

#### 4. Discussion sur l'âge du membre intermédiaire de la formation du Glib Zegdou

La situation topographique des niveaux fossilifères du membre intermédiaire de la formation du Glib Zegdou semble indiquer qu'ils ne sont pas parfaitement syn-

chrones. Il convient cependant de rester prudent sur ce point, car il s'agit d'une formation fluvio-lacustre montrant des changements rapides de faciès et des niveaux lenticulaires. Au vu de l'hétérogénéité des cassures et les usures parfois observées sur le matériel ichtyologique et mammalien des sites HGL50 et 51, il semble qu'une partie des spécimens ait été transportée de façon différentielle. Quoiqu'il en soit, les mêmes espèces de charophytes, se retrouvant du mur au toit du membre intermédiaire, semblent attester l'homogénéité de celui-ci. À titre d'exemple, parmi les charophytes récoltées à HGL10, les espèces *Raskyella sahariana*, *Raskyella pecki*, *Maedleriella lavocati*, *Stephanochara acris* et *Nodosochara aff. jorbae* ont également été identifiées au Glib Zegdou (HGL52) ; les autres espèces reconnues à HGL10 sont *Raskyella* sp., *Nitellopsis (Tectochara) thaleri*, *Maedleriella cristellata*, *Harrisichara* sp., *Chara* sp., et *Harrisichara aff. leptocera*. Cette nouvelle association floristique pourrait suggérer un âge Yprésien, plutôt que Lutétien, pour le membre intermédiaire de la formation du Glib Zegdou (Mebrouk, travail en cours).

Concernant les mammifères, à partir d'un commentaire succinct des caractères de *Microhyrax lavocati* et *Titanohyrax mongereaui*, Rasmussen et al. [23] ont considéré que les gisements des Gour Lazib étaient contemporains de ceux du Fayoum (formation Jebel Qatrani, Fayoum Faunal Zone 2 à 4). Les arguments avancés par ces auteurs ont été réfutés par Godinot [7] ; nous n'estimons pas indispensable d'y revenir. Il semble ici plus judicieux de discuter la position relative des sites du Glib Zegdou et de Chambi, compte tenu des nouveaux mammifères découverts. À Chambi, la présence – quelques mètres sous le niveau à mammifères – de *Raskyella* cf. *sahariana*, dont l'espèce type est connue au Glib Zegdou, suggère une proximité chronologique entre les deux localités fossilifères. Pour les mammifères, seuls deux genres étaient communs jusqu'à ce jour : l'hyracoïde *Titanohyrax* et le rongeur *Zegdoumys*. Hartenberger et al. [13] signalent que la petite taille de *Titanohyrax tantulus* de Chambi, par rapport à *T. mongereaui* du Glib Zegdou, pourrait refléter l'ancienneté du site tunisien. Il nous paraît cependant que *T. mongereaui* est plus primitif que *T. tantulus*, par sa brachyodontie plus marquée, sa sélénodontie moins accentuée et des styles plus globuleux. Hartenberger et al. [13], suivant Martin [18], suggèrent, par ailleurs, que *Z. sbetlai* de Chambi – par le type paucisérié à unisérié de la microstructure d'émail de son incisive – est plus primitif que *Z. lavocati* du Glib Zegdou, qui est du type paucisérié. Vianey-Liaud et al. [33] ont toutefois insisté sur les spécialisations différentes des deux espèces et n'ont pas exclu que celles-ci puissent appartenir à deux

genres distincts. Il en est de même ici de ?*Chambius* sp., qui pourrait documenter un nouveau genre ou bien une nouvelle espèce, plus primitive que *C. kasserinensis* de Chambi. Enfin, *Titanohyrax tantulus*, seule espèce commune à la faune de Chambi et des Gour Lazib, pourrait soutenir une corrélation chronologique entre ces localités. Toutefois, ne connaissant pas l'étendue stratigraphique de *T. tantulus*, il nous paraît prématuré de répondre par l'affirmative.

## 5. Conclusion

Le prolongement de la coupe du Glib Zegdou vers le bas de la série et la mise en évidence de vertébrés continentaux à la base de la formation continentale ont permis de reconsidérer l'âge de ces niveaux. Autrefois attribués au Cénomano-Turonien sans arguments paléontologiques, ils semblent plutôt d'âge Paléogène, sans doute Éocène. La présence généralisée de restes de mammifères dans le membre intermédiaire de la formation du Glib Zegdou, daté de l'Yprésien sur la base des nouvelles charophytes récoltées, fait de la région des Gour Lazib une zone géographique d'une importance essentielle pour l'étude des mammifères africains du Paléogène ancien. Enfin, la découverte remarquable des sites HGL50 et HGL51 est d'un intérêt capital, l'étude de leurs faunes allant améliorer considérablement notre connaissance de l'évolution et de la radiation initiale des mammifères en Afrique.

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**Annexe n°2**

# DECOUPAGE LITHOSTRATIGRAPHIQUE DES HAMMADAS TERTIAIRES DE LA REGION DE BECHAR ET DE BENI ABBES (SUD-OUEST ALGERIEN)

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**Resumen:** Se presentan los últimos datos estratigráficos y sedimentológicos de las Hammadas del SW de Argelia. Se diferencian dos paleógenas superpuestas, una datada como Eoceno inferior a partir de Gasterópodos lacustres, y otra a partir de Gasterópodos Bulímidos y de Caráceas. Por encima, se describe una hammada Neógena compuesta por sedimentos continentales afectados por silicificación secundaria

**Palabras clave:** Estratigrafía, ambientes continentales, hammada, bulímidos, caráceas, Paleógeno, Neógeno, Argelia.

**Résumé:** Il s'agit de présenter les données stratigraphiques et sédimentologiques des Hamadas du Sud Ouest algérien grâce à des travaux récents. Ainsi, on distingue les hamadas paléogènes superposées, l'une datée de l'Eocène inférieur grâce à une faune de Gastéropodes lacustres continentaux, et la seconde grâce à une faune de Gastéropodes du groupe des Bulimes et à des Charophytes. Au-dessus, une hamada composée de sédiments continentaux affectés par une silicification secondaire est rapportée au Néogène.

**Mots clés:** Stratigraphie, milieux continentales, hammada, bulimes, charophytes, Paléogène, Néogène, Algérie.

Adaci, M., Bensalah, M. et Mahboubi, M. (2005): Decoupage lithostratigraphique des hammadas tertiaires de la region de Bechar et de Beni Abbes (Sud-Ouest algerien). *Revista de la Sociedad Geológica de España*, 18 (3-4): 145-149

Les terrains continentaux hammadiens paléogènes et néogènes occupent des surfaces considérables dans le Sud-Ouest algérien. Ils correspondent à de vastes plateaux désertiques et pierreux et s'étendent depuis la région de Méridja au Nord-Ouest jusqu'à Béni Abbès au Sud-Est (Fig. 1).

La présente note a pour but d'étudier cette région sur les plans lithostratigraphique et sédimentologique. Ces terrains n'ont livré aux anciens auteurs que très peu d'éléments de datation (des encroûtements d'algues et de rares restes de gastéropodes).

Les travaux menés sur ces séries, ces dernières années, nous ont conduit à subdiviser ces terrains en formations géologiques distinctes. Ainsi, la découverte de nouveaux niveaux fossilifères (Adaci, 2001) a permis d'enrichir d'une part le bilan paléontologique et d'autre part de proposer des âges à ces terrains.

## Cadre Géologique

Les séries continentales tertiaires affleurant à l'Ouest et au Sud de Béchar constituent une partie de la couverture du Sahara nord occidental. Pour désigner l'ensemble des dépôts de cette couverture, Menchikoff (1946) a utilisé pour la première fois le terme de

«Terrains post-turonien». Ces dépôts fluviaux ou fluvio-lacustres, essentiellement détritiques et pauvres en documents paléontologiques, ont été rapportés tantôt à l'Eocène, tantôt à l'Oligocène ou au Miocène (Deleau, 1952). Les Hammadas paléogènes de la région de Béchar (H. Oum Es Sebâa et H. de Méridja) occupent la partie méridionale et occidentale du «Synclinorium de Béchar» et reposent en discordance sur le Crétacé marin.

Dans la région de Béni Abbes, les terrains néogènes forment la bordure Sud-Orientale de la Hamda du Guir. Ces dépôts reposent en discordance sur les crêtes paléozoïque de la chaîne de l'Ouguarta.

## Analyse stratigraphique et sédimentologique

L'étude lithostratigraphique de ces terrains est essentiellement basée sur des données paléontologiques fournies par une flore de Charophytes et une faune de gastéropodes (*Pseudoceratodes*, *Bulimes cf. Romanella hopei*) et d'Hélicidés (*Palaeocyclotus*). Par contre, l'étude sédimentologique est basée sur l'application de l'analyse séquentielle de ces séries et par l'application de la série référentielle (naturelle) définit dans la

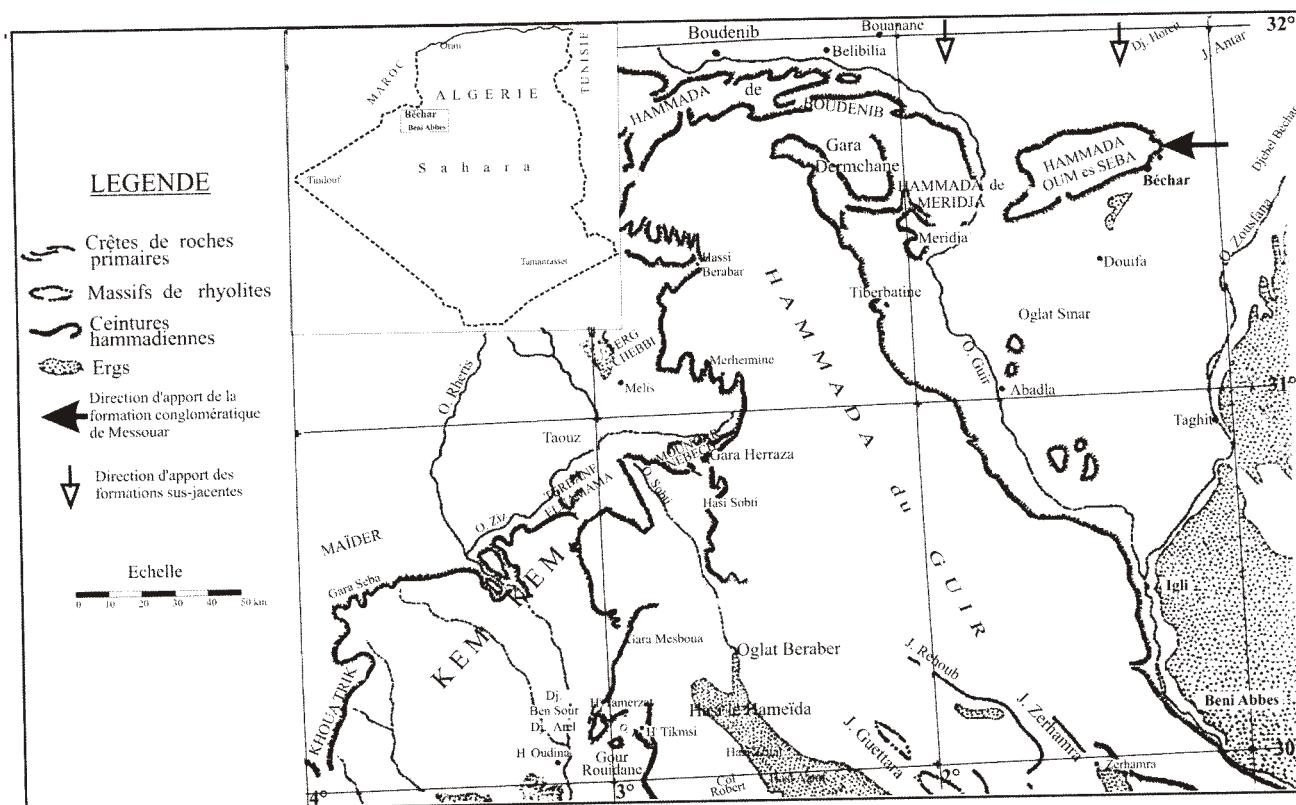


Figure 1.- Carte de localisation de la région d'étude et direction des apports.

même région par l'analyse markovienne (Nadji *et al*, 2001; Fig. 2). A partir de cette analyse, ces terrains sont subdivisés en trois hammadas d'âge différents (Fig. 3).

#### Les Hammadas paléogènes

Deux grandes Hammadas superposées sont mises en évidence et occupent le centre et la partie méridionale du bassin de Béchar.

#### Hammada inférieure : Hammada de Oum Es Sebâa

Appelée aussi «deuxième Barga», elle est constituée par trois formations distinctes:

- *Formation conglomératique de Messouar*. Mise en évidence pour la première fois à l'Ouest de Béchar (Adaci *et al*, 2001), cette formation repose en discontinuité sédimentaire, par l'intermédiaire d'une surface durcie ferrugineuse, sur les calcaires marins cénomano-turonien appelés «première Barga». Elle est constituée par des galets grossiers granodécroissants orientés Est-Ouest (3 à 50 cm) appartenant aux séries d'âge primaire. La taille, l'orientation ainsi que la forme des éléments constituant cette formation indique que la mise en place de ce faciès s'est effectuée après une forte érosion du paléorelief correspondant à une phase tectonique intense ayant affecté la région.

Guiraud (1985) décrit une instabilité tectonique durant le Santonien en invoquant l'argument sédimentaires de décharges conglomératiques dans le domaine tello-rifain et dans le constantinois. Cette

phase a débuté dans l'Afrique du Nord au Coniacien pour culminer au Santonien. La mise en place de cette formation pourrait être contemporaine ou légèrement postérieure aux événements tectoniques santoniens (Sénonien inférieur).

- *Formation évaporitique de Messouar*. Cette formation affleure à l'Est de l'Oued Guir (Messouar, Gola) où elle constitue le sous bassement de la deuxième Barga et discordant sur le conglomérat de Messouar. Elle est constituée par des marnes bariolées gypseuses intercalées de bancs décimétriques de gypse fibreux.

A l'état actuel des connaissances, cette formation n'a pas livré de fossiles. Les anciens auteurs (Menchikoff, 1946 et Lavocat, 1954) lui ont attribué un âge sénonien sans aucune preuve paléontologique. Néanmoins, l'âge paléocène n'est pas à exclure (Mahboubi, 1995).

- *Formation argilo-conglomératique de Messouar*. Elle est constituée par une succession de bancs conglomératiques à microconglomératique, de grès et d'argiles silteuses rouges. L'ensemble est coiffé par une dalle calcaire à gastéropodes (*Pseudoceratodes*). Cette formation affleure largement à l'Est de l'Oued Guir (Messouar, Gola) où elle forme la partie supérieure de la deuxième Barga. A Meridja, seul la partie supérieure de cette formation affleure et a livré quelques exemplaire de gastéropodes attribué au genre *Pseudoceratodes* associée à des encroûtements d'algues. Grâce à cette faune décrite par Jodot (1953), l'âge Éocène inférieur est attribué à cette formation).



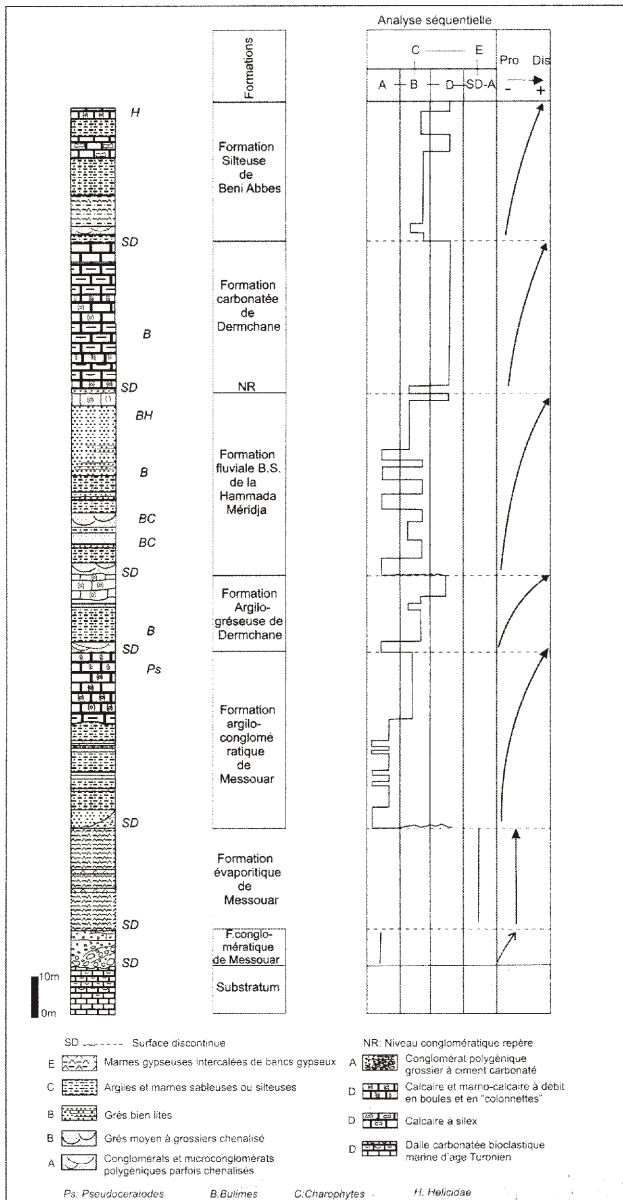


Figure 2.- Colonne lithostratigraphique synthétique des séries continentales des Hammadas paléogènes et néogène de la région de Béchar et de Béni Abbès.

**Hammada supérieure: la Hammada de Méridja**

Elle est remarquable à Méridja (à l'Ouest de Béchar), elle serait l'équivalent de la Hammada de Boudenib au Maroc. Cette Hammada comporte trois formations :

- *Formation argilo-gréseuse de Dermchane*. Elle est caractérisée par une succession de conglomérats à microconglomérats, de grès bien lités et d'argiles silteuses rouges. Cette formation est discordante sur le calcaire à *Pseudoceratodes* de Méridja par l'intermédiaire d'une épaisse décharge conglomératique qui pourrait correspondre aux événements tectoniques intra-éocène attribués dans les Nememcha par Coiffait *et al* (1984) et Mahboubi, (1995) à la base de l'Eocène supérieur.

Cette formation a livré une forme de Gastéropodes terrestres (*Bulimes*) appartenant au genre *Romanella hopei* caractéristique de l'Eocène moyen et supérieur

(Lutétien-Bartonien) du Sud de la France. Ce genre a été signalé également dans la formation de Mékaïdou (Hautes plaines oranaises) par Bensalah *et al.* (1987). La formation est ainsi, grâce à cette faune, attribuée au Lutétien-Bartonien.

- *Formation fluviale de la bordure sud de la Hammada de Méridja*. Elle est matérialisée par une succession de conglomérats à microconglomérats, de grès et d'argiles silteuses rouges. Cette ensemble est coiffé par une dalle calcaire à *Bulimes*. Ses niveaux de base nous ont fournis pour la première fois, dans cette région, une flore de charophytes associée à des *Bulime* appartenant aux genres *Romanella* et *Vicentinia* et à un *Hélicidé* du genre *Palaeocyclotus*. Selon G. Truc (Univ. Lyon1, France), l'individu de *Romanella* récolté à Méridja possède une affinité avec *Romanella hopei* de Serres 1827, espèce commune dans le Lutétien-Bartonien de Provence-Languedoc (Durand *et al*, 1984).

Le genre *Palaeocyclotus* découvert pour la première fois à Meridja (Adaci, 2001), a été signalé dans le Lutétien et le Bartonien de Provence, d'Italie septentrionale et de Tunisie (Abdeljaouad *et al*, 1984).

La flore de charophytes est constituée par trois espèces, *Peckichara sp*, *Netelopsis (T) thaleri* et *Raskyella sp*. L'âge proposé pour cette association serait Eocène moyen ou supérieur (Adaci, 2001).

La concordance entre les indications stratigraphiques fournies par les charophytes et les *Bulimes* et celle apportées par la présence du genre

| Coupes                              | Taxons   |              |            |           |         |                                      |                 |            |
|-------------------------------------|----------|--------------|------------|-----------|---------|--------------------------------------|-----------------|------------|
|                                     | Messouar | Oum Es Schââ | Garet Ziâr | Gara Gola | Méridja | Bordure sud de la Hammada de Méridja | Garet Dermchane | Béni Abbès |
| <b>Gastéropodes</b>                 |          |              |            |           |         |                                      |                 |            |
| <i>Pseudoceratodes</i>              |          |              |            |           |         |                                      |                 |            |
| - <i>Pseudoceratodes clariondii</i> | ■        | ■            |            |           | ■       |                                      |                 |            |
| <i>Bulimes:</i>                     |          |              |            |           |         |                                      |                 |            |
| - <i>Romanella hopei</i>            |          |              |            |           |         | ■                                    | ■               |            |
| - <i>Vicentinia sp.</i>             |          |              |            |           |         | ■                                    | ■               |            |
| <i>Hélicides</i>                    |          |              |            |           |         |                                      |                 |            |
| - <i>Palaeocyclotus sp.</i>         |          |              |            |           |         | ■                                    |                 |            |
| <i>Helix sp.</i>                    |          |              |            |           |         |                                      |                 | ■          |
| <b>Encroûtements d'algues</b>       |          |              |            |           |         | ■                                    |                 |            |
| <b>Charophytes</b>                  |          |              |            |           |         |                                      |                 |            |
| - <i>Reskyella sp.</i>              |          |              |            |           |         | ■                                    |                 |            |
| - <i>Netelopsis (T) thaleri</i>     |          |              |            |           |         | ■                                    |                 |            |
| - <i>Peckichara sp.</i>             |          |              |            |           |         | ■                                    |                 |            |

■ / Fossiles signalés par les anciens auteurs.  
 ■ / Fossiles découverts dans le cadre de cette étude.

Tableau I.- Faune et flore des Hammadas à l'Ouest et au Sud de Béchar.

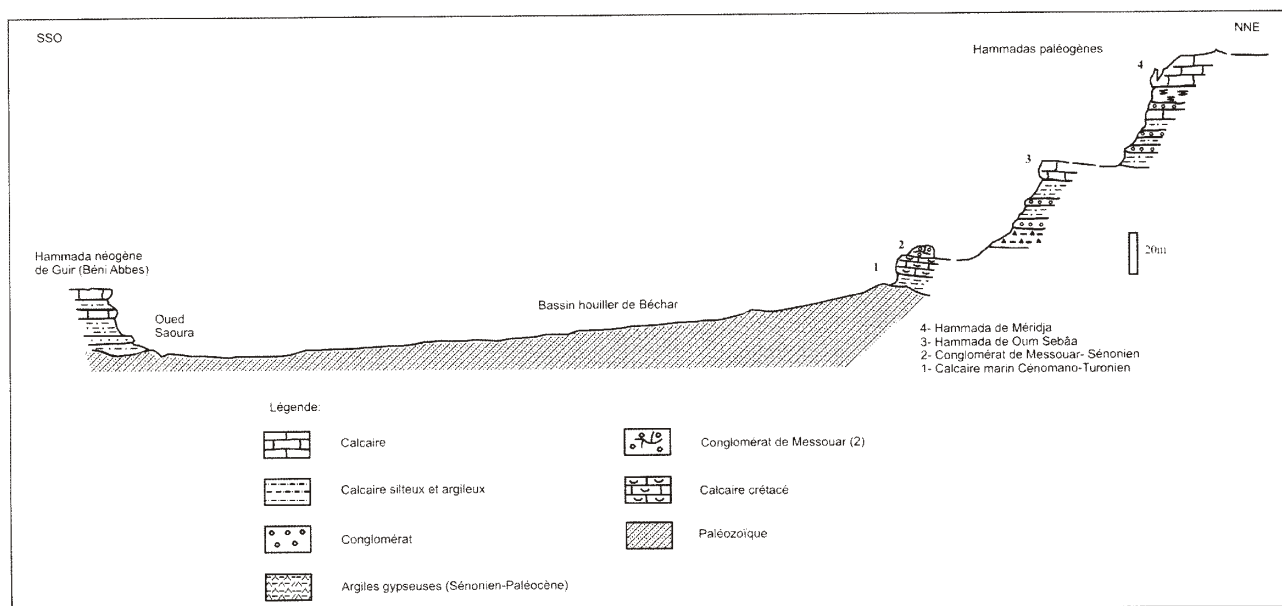


Figure 3.- Coupe schématique NNE-SSO des Hammadas tertiaires de Béchar et de Béni Abbès.

*Palaeocyclotus* mérite d'être mis en valeur. L'ensemble de ces données paléontologiques attribuent à cette formation un âge Lutétien-Bartonien (Eocène moyen-supérieur).

- *Formation carbonatée de Dermchane II*. Cette formation est représentée par une épaisse barre calcaire à *Bulimes*, caractérisée par une structure pédogénétique à débit en boules et en colonnettes verticales. Cette dalle coiffe l'ensemble des buttes témoins des Gour de Dermchane, Ziar, Gola et Oum Es Sebâa. Cette barre repose sur un niveau conglomératique correspondant à un niveau lithostratigraphique-repère dans la région d'étude (Adaci, 2001).

La présence de Gastéropodes du genre *Romanella* dans ces calcaires lui attribue un âge Eocène moyen ou supérieur.

#### La Hammada néogène

Cette Hammada a été étudiée à proximité de Béni Abbès. Elle repose en discordance sur les séries paléozoïques de la chaîne de l'Ougarta et est attribuée au Néogène sans arguments paléontologiques. Elle montre une sédimentation identique au formation décrites précédemment (Argiles silteuses à grains de gypse et quelques galets, grès et dalle calcaire) Néanmoins, la nouveauté dans cette Hammada est la silicification bien représenté par les rognons de silex dans la masse calcaire, phénomène qui n'a pas été retrouvé dans les Hammada à l'Ouest de Béchar. La dalle calcaire de cette Hammada a livré un exemplaire de gastéropode appartenant au genre *Helix* donnant un âge Miocène (?).

#### Conclusion

Les séquences, à diverses échelles, analysées à l'Ouest et au Sud de Béchar, sont souvent grano-

décroissantes. En matière de sens d'apports, deux directions d'alimentations sont mis en évidences:

- La formation conglomératique de Messouar montre une alimentation d'éléments grossier et grano-décroissant d'Est en Ouest, depuis le Dj. Béchar situé à l'Est de la région étudiée, ce qui correspondrait à la phase tectonique santonienne.

- Les formations sus-jacentes montrent que l'apport des sédiments grossiers notamment Nord-Sud, ce qui permet d'affirmer que les reliefs nourriciers sont les chaînes atlasiques situées plus au Nord.

La découvertes de nouveaux gisements fossilifères (charophytes et gastéropodes) permet d'une part de réattribué les séries continentales des Hammadas à l'Ouest de Béchar au paléogène, attribuées autrefois à l'Oligocène et au Néogène, d'autre part de faire des corrélations avec le secteur de Brézina (Piedmont Sud Atlas Saharien) et dans les Hautes Plaines oranaises (Djebel Mékaïdou) et le Sud du Tell algérois (Ksar El Boukhari).

Sur le plan tectonique, deux phases sont à signaler, d'une part la phase fini-Crétacé (mise en place des conglomérats de Messouar), d'autre part la phase d'âge éocène moyen-supérieur largement reconnue dans le Maghreb et dans le Sud de l'Europe occidentale.

Sur le plan paléoenvironnemental, les calcaires à Pseudoceratodes permettent de mettre en évidence à l'échelle du secteur d'étude deux paléolacs orientés sensiblement E-W (un à Méridja, le second à l'Est de l'Oued Guir).

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**Annexe n°3**

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## Journal of Systematic Palaeontology

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### Zegdoumyidae (Rodentia, Mammalia), stem anomaluroid rodents from the Early to Middle Eocene of Algeria (Gour Lazib, Western Sahara): new dental evidence

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## Zegdomyidae (Rodentia, Mammalia), stem anomaluroid rodents from the Early to Middle Eocene of Algeria (Gour Lazib, Western Sahara): new dental evidence

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The Palaeogene fossil record of rodents in Africa is very poor compared to that of North America or Eurasia. Despite this, Africa has long appeared to be a centre of adaptive radiation for two distinct groups of Rodentia: Hystricognathi and Anomaluroidea. The >45-million-year-old enigmatic Zegdomyidae is the oldest and only rodent family known of this age from Africa (Algeria and Tunisia). Zegdomyids have been tentatively regarded as a possible early African stem group for Anomaluridae, a link that has never been clearly established because of the highly fragmentary nature of zegdomyid fossils, as well as the major temporal and morphological gaps between zegdomyids and the first true anomaluroids from the Late Eocene. About 200 rodent teeth have been sorted after acid treatment of indurated sediments from several new localities in the Gour Lazib of western Algeria dating from the late Early or early Middle Eocene. These new fossils allow us to better describe the morphology of the Zegdomyidae (especially *Glibia* and *Zegdomyis*) and to identify a new taxon, *Lazibemys zegdouensis* gen. et sp. nov. With this material, we investigated the phylogenetic position of the Zegdomyidae in a high-level rodent phylogeny with cladistic assessment of the dental evidence. Our analyses have yielded six equally most-parsimonious trees in which zegdomyids represent the earliest offshoots (pectinately arranged) of a large clade that embraces Eocene anomaluroids plus stem and crown Anomaluridae. This phylogenetic assumption underscores the great antiquity of the Anomaluroidea clade in Africa, as expected given the high morphological divergence of the Late Eocene African anomaluroids. Zegdomyids exhibit a variety of dental morphologies and provide some suggestions on evolutionary trends within the Anomaluroidea (early stages of pentalphodonty, incisor enamel microstructure transitional from the pauciserial to the uniserial condition). The source of Zegdomyidae is still unclear inasmuch as there is no well-identified sister group among early Palaeogene rodents. Zegdomyids seem to share a common ancestry with both stem Myodonta and North American Sciuiravidae. Given the high degree of dental specialization of zegdomyids, we cannot exclude the possibility that zegdomyids are rooted in a more primitive, as yet unknown, African rodent lineage older than the Early-Middle Eocene.

**Keywords:** Rodentia; Anomaluroidea; Zegdomyidae; Africa; phylogeny; Eocene

### Introduction

The Palaeogene fossil record of rodents in Africa is remarkably scarce compared to that of North America (e.g. Korth 1994; Janis *et al.* 2008) or Eurasia (e.g. Dawson 2003), and the early evolutionary history of this mammal group here is still poorly known. Until very recently the only documentation for early Tertiary African rodents has come from a handful of localities distributed in North Africa, primarily and historically from the Oligocene of Fayum, Egypt (Osborn 1908; Wood 1968; Holroyd 1994), and then from the Eocene of Algeria-Tunisia (Jaeger *et al.* 1985; Vianey-

Liaud *et al.* 1994) and Oligocene of Libya (Fejfar 1987). Despite this poor record, Africa has long appeared to be a centre of adaptive radiation of two phylogenetically distinct groups of Rodentia, Hystricognathi and Anomaluroidea. Over the last few years several new Palaeogene localities from Egypt (earliest Late Eocene; Sallam *et al.* 2009, 2010a, b) and Libya (Late Eocene; Jaeger *et al.* 2010), as well as from Tanzania (late Early Oligocene; Stevens *et al.* 2006, 2009), Namibia (? Middle Eocene; Pickford *et al.* 2008) and Kenya (Late Oligocene; Rasmussen & Gutierrez 2009; Ducrocq *et al.* 2010), have substantially increased the species diversity, especially that of hystricognathous

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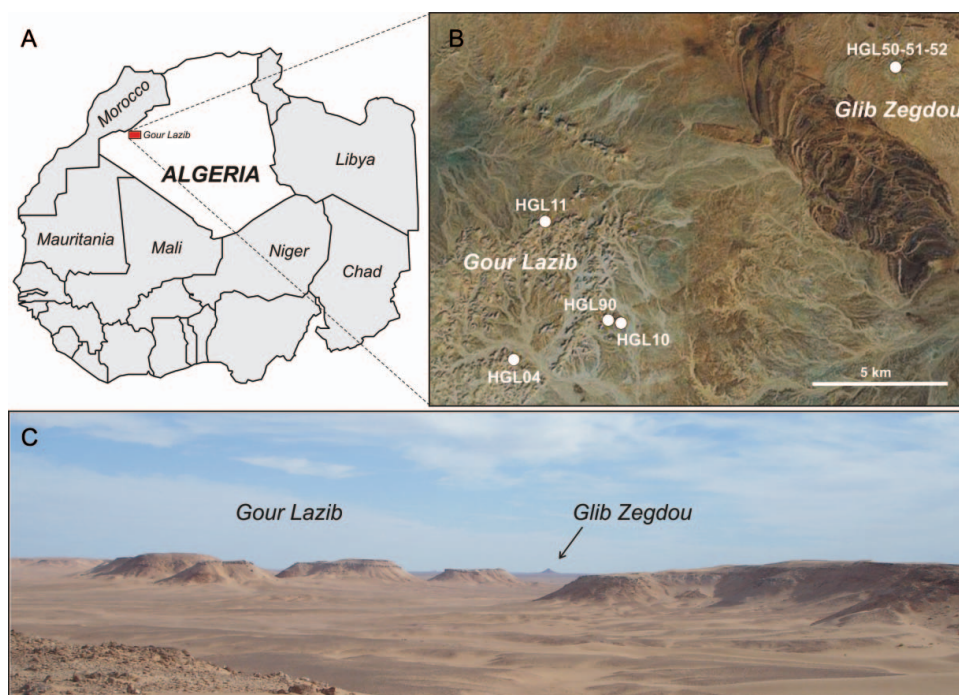
rodents, and to a lesser extent that of anomaluroids. They have not changed the pattern of diversity, however, which seems to have been limited to these two groups until the Early Miocene (e.g. Flynn & Winkler 1994; Winkler *et al.* 2010). Early African hystricognathous rodents ('Phiomorpha' *sensu* Lavocat 1962) are documented as members of the Phiomyidae (e.g. Wood 1955, 1968), an extinct family of probable Asian origin (e.g. Hussain *et al.* 1978; Jaeger *et al.* 1985, 2010; Jaeger 1988; Marivaux *et al.* 2000, 2002, 2004a; Sallam *et al.* 2009), which is considered to be the stem group of the modern African 'cane rats' (*Thryonomys*), 'dassie rats' (*Petromus*), 'mole rats' (e.g. *Bathyergus*, *Heterocephalus*...), and 'porcupines' (e.g. *Hystrix*, *Atherurus*...). The Anomaluridae is an extant family, the modern representatives of which, commonly known as the 'scaly-tailed squirrels' (*Anomalurus*, *Anomalurops*, *Idiurus* and *Zenkerella*), are endemic to western and central Africa, and practice a gliding locomotion (except *Zenkerella*). Modern African and Asian hystricognathous rodents occupy diverse habitats, ranging from open (rocky deserts, grasslands, savannas) to closed (scrub forests, rainforests) environments, while anomalurids live exclusively in dense tropical rainforests. Phiomyid rodents were among the most common members of African mammal faunas during the late Palaeogene. In contrast, anomalurids are uncommon in these faunal records, an under-representation that is most likely the result of sampling biases related to their peculiar palaeoecology and palaeohabitats that could have been similar to modern species.

The first attested occurrence in Africa of both phiomyids and anomalurids (i.e. *Protophiomys* and *Nementchamys*, respectively) dates back to the late Middle Eocene in Algeria (Bir El-Ater; Coiffait *et al.* 1984; Jaeger *et al.* 1985), although potential close relatives of anomalurids might have existed much earlier. This assumption involves the >45-million-year-old enigmatic Zegdomyidae from Maghreb (Glib Zegdou in Algeria, and Chambi in Tunisia), which are the oldest and the only rodents from this time period known in Africa thus far (Vianey-Liaud *et al.* 1994). However, the possibility of a phylogenetic link between the Anomaluridae and Zegdomyidae has never been clearly established because of the highly fragmentary nature of fossils documenting zegdomyid taxa (*Zegdomyis*, *Glibia* and *Glibemys*; Vianey-Liaud *et al.* 1994), which have so far remained limited to very few dental remains. In addition to *Nementchamys* from Algeria, the recent discovery of two morphologically divergent anomalurids from the earliest Late Eocene of Egypt (*Kabirmys* and *Shazurus*, the latter showing a degree of dental specialization otherwise found only in Miocene or modern species; Sallam *et al.* 2010a, b), has revealed that anomalurids already displayed a high morphological diversity in dental traits at that time. These strongly marked dental differences clearly reflect a more ancient diversification of the group, which must have been underway during the Middle Eocene;

a result that revives the issue of the Zegdomyidae as a possible early African stem group for Anomaluridae. This would add to the evidence of the great antiquity of the Anomaluroidea clade recently suggested by molecular estimates (e.g. Huchon *et al.* 2007; Montgelard *et al.* 2008). Indeed, a body of molecular but also morphological evidence quite confidently supports the sister group relationships of modern Anomaluridae with another family, the Pedetidae (e.g. Tullberg 1899; Bugge 1974, 1985; Meng 1990; Huchon *et al.* 2007; Montgelard *et al.* 2008; Blangakanfi *et al.* 2009; Ruf *et al.* 2009; Churakov *et al.* 2010), the unique living member of which (*Pedetes*, the 'springhare') is also endemic to Africa. Both groups make up the Anomaluromorpha (Bugge 1974). Following molecular estimates, an anomalurid–pedetid split would be expected as early as the earliest Eocene (Huchon *et al.* 2007) or even much earlier (Montgelard *et al.* 2008). However, such an early divergence is particularly difficult to assess because there is no rodent fossil record from the earliest Palaeogene of Africa, and the first occurrence of pedetids dates back only to the Early Miocene of east Africa (e.g. Lavocat 1973; Winkler *et al.* 2010). The molecular evidence for a very early divergence between Anomaluridae and Pedetidae raises, however, the critical issue of whether the common ancestor of both families is a zegdomyid-like form from Africa (Sallam *et al.* 2010b).

Despite both the morphological gap and the extensive temporal gap through the Middle Eocene separating the zegdomyids from the first attested anomalurids, zegdomyids seem to be central to discussions of the early evolutionary history of the Anomaluroidea and the Anomaluromorpha. But what are zegdomyids? They had emerged by the time of the early Palaeogene radiation of rodents, but what are their higher-level relationships among stem Rodentia? Based on dental resemblances, Vianey-Liaud *et al.* (1994) and Vianey-Liaud & Jaeger (1996) hypothesized that the ancestry of the Zegdomyidae is most likely to be found in the early Palaeogene ischyromyoid radiation rather than in the ctenodactyloid radiation (see also Marivaux *et al.* 2004a, 2005), and as such, zegdomyids could represent the African sister group of both the North American Sciuravidae and European Gliridae dating from the Early to Middle Eocene. However, this phylogenetic hypothesis and its palaeobiogeographical implications have never been properly evaluated. Recently, Dawson *et al.* (2003) argued that the Zegdomyidae and Gliridae are more closely related than they are to the Anomaluridae, and that the source of anomalurids is still unclear.

Since 2003, we have focused some of our annual field research in the Sahara of western Algeria. In particular, we have collected from the vast outcrops situated in the Gour Lazib area of the Hammada du Dra region, which includes the Glib Zegdou outlier (Fig. 1). Our surveys of the red to yellow siltstones and sandstones of the continental Glib Zegdou Formation, which date from the late



**Figure 1.** **A, B,** Location maps of the fossiliferous localities of the Gour Lazib, situated in the region of the Hammada du Dra (Sahara of western Algeria). HGL50, located on the southern flank of the Glib Zegdou outlier (**B**, satellite view from Google Earth), is the locality that has yielded most of the fossil material described in this paper. **C,** Photograph showing the typical badlands and outliers of the Gour Lazib, with the Glib Zegdou outlier in the background (picture by Rodolphe Tabuce).

Early or early Middle Eocene (between ~52 and ~46 Ma; Mebrouk & Feist, 1999; Adaci *et al.* 2007), have led to the discovery of several fossil concentrations, one yielding abundant microfossils (HGL50; Fig. 1). Intensive acid-etchings and screen-washings of the indurated sediments have provided a diverse assemblage of aquatic and terrestrial vertebrates (fishes, turtles, crocodiles, squamates), together with terrestrial mammals (such as rodents, bats, primates, creodonts, marsupials, elephant shrews, hyraxes, and ‘condylarths’; Adaci *et al.* 2007; Tabuce *et al.* 2007, 2009). More than a hundred isolated teeth of rodents have been sorted, representing only members of the Zegdoumyidae. This new material, which includes several teeth that are particularly well preserved, allows us to better describe the morphology of these early African rodents, especially *Glibia* and *Zegdoumys*, and to identify a new taxon (*Lazibemys zegdouensis* gen. et sp. nov.). These new fossils will be discussed with a special emphasis on phylogenetic and paleobiogeographical implications regarding the early evolutionary history of the Anomaluroidae.

### Dental nomenclature

Dental terminology (Fig. 2) follows that of Marivaux *et al.* (2005).

### Institutional abbreviations

**BC:** Black Crow, Namibia; **CGM:** Cairo Egyptian Geological Museum, Egypt; **DPC:** Duke Lemur Center Divi-

sion of Fossil Primates; **GZC:** Glib Zegdou level C; **HGL:** Hammada Gour Lazib; **KNM RU:** Kenya National Museum, Rusinga; **KNM SO:** Kenya National Museum, Songhor; **MNHN:** Muséum National d’Histoire Naturelle, Paris; **Pkg:** Paukkaung, Pondaung Formation, Myanmar; **Spg:** Saba Pondaung, Pondaung Formation, Myanmar; **UMC:** Université Montpellier Collections; **UMP:** Uganda Museum Paleontology; **UON:** University of Oran Nementcha, Algeria. The fossil material described in this paper is housed in the palaeontological collections of the Université Montpellier 2 (**UMC**), France.

### Systematic palaeontology

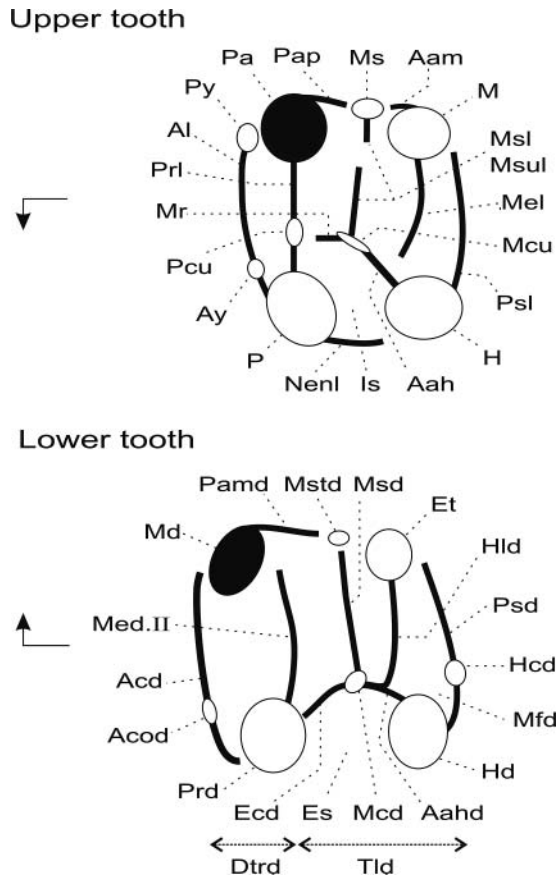
Class **Mammalia** Linnaeus, 1758  
 Order **Rodentia** Bowdich, 1821  
 Infraorder **Anomaluromorpha** Bugge, 1974  
 Superfamily **Anomaluroidea** Gervais, 1849  
 Family **Zegdoumyidae** Vianey-Liaud *et al.*, 1994

**Included genera.** *Zegdoumys* Vianey-Liaud *et al.*, 1994; *Glibia* Vianey-Liaud *et al.*, 1994; *Glibemys*, Vianey-Liaud *et al.*, 1994; *Lazibemys* gen. et sp. nov.

Genus **Zegdoumys** Vianey-Liaud *et al.*, 1994

**Type species.** *Zegdoumys lavocati* Vianey-Liaud *et al.*, 1994.





**Figure 2.** Dental terminology (modified after Wood & Wilson 1936; Marivaux *et al.* 2005). Upper tooth abbreviations: Aah, anterior arm of hypocone; Aam, anterior arm of metacone; Al, anteroloph (or anterocingulum); Ay, anterostyle; H, hypocone; Is, internal sinus; M, metacone; Mcd, metaconule; Mel, metaloph; Mr, mure; Ms, mesostyle; Msl, mesoloph; Msul, mesolophule; Nenl, neo-endoloph; P, protocone; Pa, paracone; Pap, posterior arm of paracone; Pcu, protoconule; Prl, protoloph; Psl, posteroloph (or posterocingulum); Py, parastyle. Lower tooth abbreviations: Aahd, anterior arm of hypoconid; Acd, anterocingulid (or anterolophid); Acod, anteroconid; Dtrd, distal trigonid (vestigial, there is no basin); Ecd, ectolophid; Et, entoconid; Hcd, hypoconulid; Hd, hypoconid; Hld, hypolophid; Es, external sinusid; Mcd, mesoconid; Md, metaconid; Med. II, metalophulid II (= protolophid or posterior arm of protoconid); Mfd, metafossettoid; Msd, mesolophid; Mstd, mesostylid; Pamd, posterior arm of metaconid; Prd, protoconid; Pcd, posterolophid; Tld, talonid basin.

**Referred species.** *Zegdoumys sbeitlai* Vianey-Liaud *et al.*, 1994; possibly '*Glibia namibiensis*' *sensu* Pickford *et al.* (2008).

**Emended diagnosis.** Large zegdoumyids, with submolarized premolars; differs from *Glibia* in being three times larger, in having more bulbous cusps and cuspids, in showing upper molars with a lower crested pattern, a stronger development of the neo-endoloph, which nearly closes the internal sinus lingually, a complete buccal wall but with

a smaller mesostyle, the absence of a central transverse crest, and in lacking both the mure and a posteroconule. Lower molars differ also from those of *Glibia* in showing a lesser development of the hypolophid, which can be absent, low or very short (incomplete), a lack or smaller development of mesolophid, m3 as large as the m2, and in lacking a hypoconulid. Differs from *Lazibemys* in showing lower crests, no supernumerary enamel wrinkles, upper molars with a smaller mesostyle, an oblique anterior arm of the hypocone, an absence of strong parastyle, and lower molars without ectolophid, mesolophid (or small), anterolophid, and hypolophid (or small). Differs from *Glibemys* in showing lower molars without strong mesolophid, anterolophid, mesostylid and distal ectolophid, the absence of connection between the posterolophid and the entoconid, and a lesser development of the hypolophid.

**Remarks.** Given that the dental material documenting *Z. sbeitlai* is very scarce (only two teeth), the generic diagnosis is essentially based on the material referred to *Z. lavocati*.

*Zegdoumys lavocati* Vianey-Liaud *et al.*, 1994  
(Fig. 3A–R)

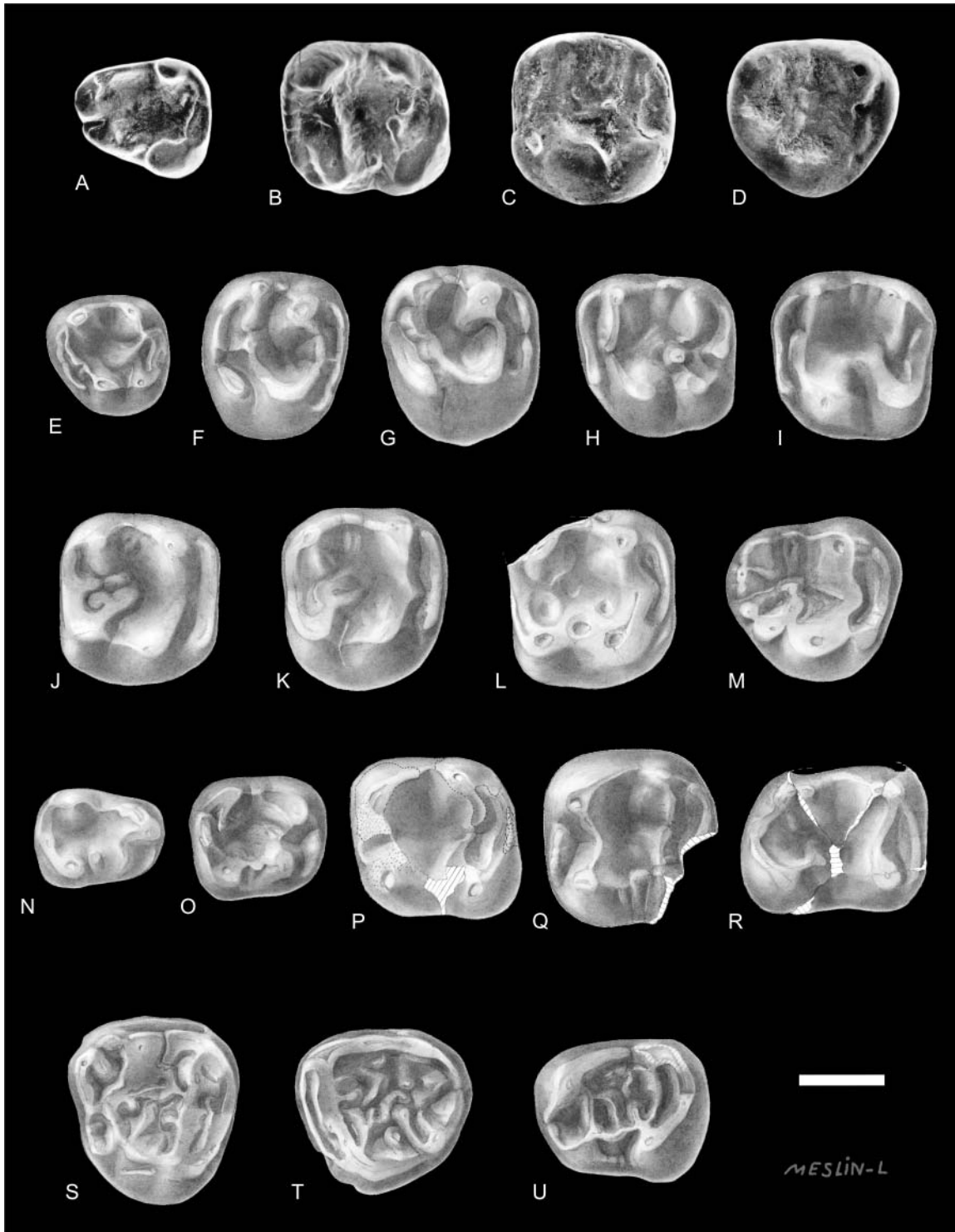
**Differential diagnosis.** Differs from *Zegdoumys sbeitlai* in showing less lophodont lower molars, which are characterized by a lesser development of the hypolophid and the absence of mesolophid and ectolophid.

**Material.** Two left DP4 (HGL50-01-02), two right P4 (HGL50-03-04), three right M1 (HGL50-05-07), five left M1 (HGL50-08-09, HGL90-01, HGL04-01, HGL52-GZC14), one right M2 (HGL50-10, buccally broken), three right M3 (HGL50-11-12, HGL52-GZC15), two left dp4 (HGL50-74, HGL52-GZC13), one right dp4 (HGL50-13), two right p4 (HGL50-73, HGL11-01), two right m1 (HGL50-14-13, very worn), three left m1 (HGL50-16, HGL52-GZC11 (holotype), HGL52-GZC12), one left m2 (HGL50-17, distally broken), one right m3 (HGL90-02, lingually broken). Dental measurements are reported in Table 1.

**Occurrence.** Intermediate member of the Glib Zegdou Formation, late Early or early Middle Eocene (Adaci *et al.* 2007): HGL50 (Glib Zegdou outlier), HGL52, HGL04, HGL11, and HGL90 situated in the Gour Lazib (Hammada du Dra), Algeria (Fig. 1).

**Description.** The original material referred to *Zegdoumys* was limited to five teeth documenting few dental loci for this genus (Vianey-Liaud *et al.* 1994). The new material includes practically all dental loci, thereby allowing a better description and characterization of this taxon.

**Upper dentition.** Among the new loci, the documentation of the upper deciduous and permanent premolars



**Figure 3.** Isolated teeth of the large bodied Zegdoumyidae from the Gour Lazib. **A–R**, *Zegdoumys lavocati* Vianey-Liaud *et al.*, 1994; **A**, HGL52-GZC13, left dp4; **B**, HGL52-GZC11, left m1; **C**, HGL52-GZC14; **D**, HGL52-GZC14, right M3; **E**, HGL50-01, left DP4; **F**, HGL50-04, right P4; **G**, HGL50-03, right P4; **H**, HGL04-01, left M1; **I**, HGL50-08, left M1; **J**, HGL50-06, right M1; **K**, HGL50-05, right M1; **L**, HGL50-10, right M2; **M**, HGL50-11, right M3; **N**, HGL50-13, right dp4; **O**, HGL11-01, right p4; **P**, HGL50-16, left m1; **Q**, HGL50-17, left m2; **R**, HGL90-02, right m3. **S–U**, *Lazibemys zegdouensis* gen. et sp. nov.; **S**, HGL50-70, left M1; **T**, HGL50-71, left M3; **U**, HGL50-72, left p4. Scale bar = 1 mm. Original artwork (E–U) by Laurence Meslin.



**Table 1.** Dental measurements (in mm) of *Zegdoumys lavocati* (MD, maximum mesiodistal length; BL, maximum buccolingual width).

| Tooth | Specimen                        | Length MD | Width BL |
|-------|---------------------------------|-----------|----------|
| DP4   | HGL50-01                        | 1.405     | 1.395    |
| DP4   | HGL50-02                        | 1.393     | 1.318    |
| P4    | HGL50-03                        | 1.718     | 2.095    |
| P4    | HGL50-04                        | 2.095     | 1.992    |
| M1    | HGL50-05                        | 1.84      | 2.096    |
| M1    | HGL50-06                        | 1.796     | 2.001    |
| M1    | HGL50-07 (worn)                 | 1.704     | 1.901    |
| M1    | HGL50-08                        | 1.836     | 2.033    |
| M1    | HGL50-09 (buccally broken)      | 1.729     | —        |
| M1    | HGL04-01                        | 1.739     | 1.844    |
| M2    | HGL50-10 (distobuccally broken) | 1.882     | 2.161    |
| M3    | HGL50-11                        | 1.929     | 1.845    |
| M3    | HGL50-12                        | 1.797     | 1.754    |
| dp4   | HGL50-74                        | 1.423     | 1.245    |
| dp4   | HGL50-13                        | 1.378     | 1.131    |
| p4    | HGL11-01                        | 1.566     | 1.418    |
| p4    | HGL50-73                        | 1.758     | 1.703    |
| m1    | HGL50-14                        | 1.863     | 1.665    |
| m1    | HGL50-15                        | 1.892     | 1.609    |
| m1    | HGL50-16                        | 1.883     | 1.849    |
| m2    | HGL50-17 (distobuccally broken) | 1.948     | 1.993    |
| m3    | HGL90-02 (lingually broken)     | 2.119     | 1.602    |

is important. DP4 (Fig. 3E) displays a triangular outline and is markedly smaller ( $\sim$  twice) than P4, which is more oval-shaped (Fig. 3F, G). The triangular shape of the deciduous teeth is linked to the development of a strong parastyle that appears as a distinct cusp situated mesiobuccally on a low and mesiodistally enlarged anterocingulum. P4 bears only a minute parastyle on a very low anterocingulum, which remains unconnected to both the protocone and paracone. The hypocone on DP4 is distinct and is twinned to the protocone. It is barely visible on P4, just appearing as a lingual swelling on a strong posteroloph, and is close to but separated from the protocone. As in P4, the paracone, metacone and protocone in DP4 are bulbous and equally sized. Both categories of teeth bear a minute metaconule that is entirely submerged in the buccal metaloph. DP4 differs substantially from P4 in showing a metaconule–hypocone connection via a strong development of the anterior arm of the hypocone, while P4 is characterized by a metaconule–protocone (lingual metaloph) connection and the absence of anterior arm of the hypocone. P4 is also characterized by a mesiodistal compression of the tooth that makes the crown oval in shape with the paracone and metacone close together, only separated by a strong mesostyle. DP4 has no mesiodistal compression. P4 is three rooted, but shows the distal roots partially or entirely merged together.

As on premolars, upper molars display bulbous cusps, and the crests are moderately developed and low. M1 (Fig. 3H–K) and M2 (Fig. 3L) are quadrangular with

rounded lingual and buccal margins, while M3 (Fig. 3D, M) is heart-shaped with a smaller hypocone, which is much more buccal in position than those of M1–2. The metacone on M3 is a distinct cusp but reduced with respect to the paracone. On M1 and M2, the hypocone is strongly developed, and is as large as the protocone, paracone and metacone. M2 is larger than M1, and shows its hypocone slightly buccal to the protocone. On the three molars of the tooththrow, the mesial borders of the crowns show a low anterocingulum that is isolated from both the protocone and paracone. On M3, the anterocingulum bears a moderately developed anterostyle. On the other molars, an anterostyle is barely visible on the anterocingulum (a small enamel swelling). A minute metaconule is present on all teeth, and is located at mid-distance between the metacone and the protocone. However, this metaconule is not connected to the protocone as in P4, but to a strong, long, and oblique anterior arm of the hypocone as in DP4. In fact, there is no lingual metaloph on the molars, and the buccal metaloph is discontinuous (interrupted by narrow notches) between the metacone and the metaconule. In contrast, the protoloph is continuous and connects the lingual aspect of the paracone to the mesiobuccal aspect of the protocone. The protoloph bears a minute swelling in midcourse that could be the rest of a protoconule. The posteroloph is strong and links the hypocone to the metacone. Buccally, the trigon basin is closed (walled-off) by the development of a mesostyle, which is mesiodistally elongated, thereby connecting the metacone and a strong but short posterior arm of the paracone. The mesostyle, although well developed, is inferior to the main buccal cusps. Lingually, the bulbous protocone has a short outgrowth (neo-endoloph), which extends distally toward the hypocone and closes the trigon basin. Only a narrow and very shallow notch separates the protocone from the hypocone.

**Lower dentition.** The lower deciduous premolars (dp4) are clearly distinguishable from their permanent counterparts (p4) in showing a vestigial trigonid that is much narrower (labiolingually pinched) than the talonid. The dp4 are also clearly smaller than p4. The trigonid of dp4 (Fig. 3A, N) is characterized by a prominent metaconid, which is the main cuspid of the teeth, and a minute protoconid, which is labiolingually close to the metaconid but displaced far distally. On p4 (Fig. 3O), the protoconid is well marked, as it is as large as the entoconid and the hypoconid and located far buccally from the metaconid, thereby making the p4 outline more quadrangular. Both cuspid (metaconid and protoconid) are linked by a thin, curved, but complete metalophulid II. The occlusal pattern of both teeth is very simple, characterized by a vast talonid basin without an internal transverse crest, except on p4 where a very short and low hypolophid connects the entoconid. The external sinusid of both teeth is closed by the presence of a distinct and mesiodistally elongated mesoconid, which is isolated on dp4, and connected to a short

anterior arm of the hypoconid on p4. Lingually, the talonid basin is also closed on both teeth by the presence of a well-developed mesostylid, which is connected to a strong and long posterior arm of the metaconid. Distally, the posterolophid is long and massive, and links the hypoconid to the entoconid on dp4, and only the hypoconid on p4. Mesially, p4 differs from dp4 in showing a short, low but wide anterior cingulid situated between the metaconid and the protoconid.

The new material documenting the lower molars is not as well preserved as the holotype (HGL52-GZC11, a left m1 [formerly considered as a m2]; Fig. 3B; Vianey-Liaud *et al.* 1994). From the scarce material currently available, the m2 (Fig. 3Q), like its upper counterparts, is the largest tooth of the lower tooththrow. This tooth is square shaped without the difference between trigonid and talonid breadth observed on m1. The m3 (Fig. 3R), in contrast, is longer than it is wide, and is slightly smaller than the m2. The three molars (m1-3) are characterized by bulbous cuspids (metaconid, protoconid, hypoconid, and entoconid), and show a weak development of the internal transverse crests. The metaconid is the strongest cuspid of the teeth, and has a strong posterior arm that ends at the base of the mesial aspect of the entoconid. There is practically no difference in elevation between the trigonids and the talonids. As in the premolars, the posterolophid connects the entoconid from the hypoconid and appears as the strongest transverse crest of the teeth. There is no hypoconulid. A well-marked anterocingulid is developed on nearly all the breadth of the mesial margin of teeth, but remains unconnected to both the protoconid and metaconid. The posterior arm of the protoconid is thin but long, and reaches the buccal aspect of the metaconid, thus forming a complete metalophid II on the three teeth. A hypolophid is variably developed, and in all cases is low, short, and connected to the entoconid but not to the hypoconid. The anterior arm of the hypoconid is either absent or weakly developed (m3). A minute and isolated mesoconid is present between the protoconid and the hypoconid. There is neither ectolophid nor mesolophid.

Genus *Glibia* Vianey-Liaud *et al.*, 1994

**Type and only species.** *Glibia pentalopha* Vianey-Liaud *et al.*, 1994.

**Diagnosis.** As for the type and only species (below).

*Glibia pentalopha* Vianey-Liaud *et al.*, 1994  
(Fig. 4A–A’)

1994 *Glibia tetralopha* Vianey-Liaud *et al.*: 106, fig. 6,  
fig. 8, pl. 1, figs 8, 9.

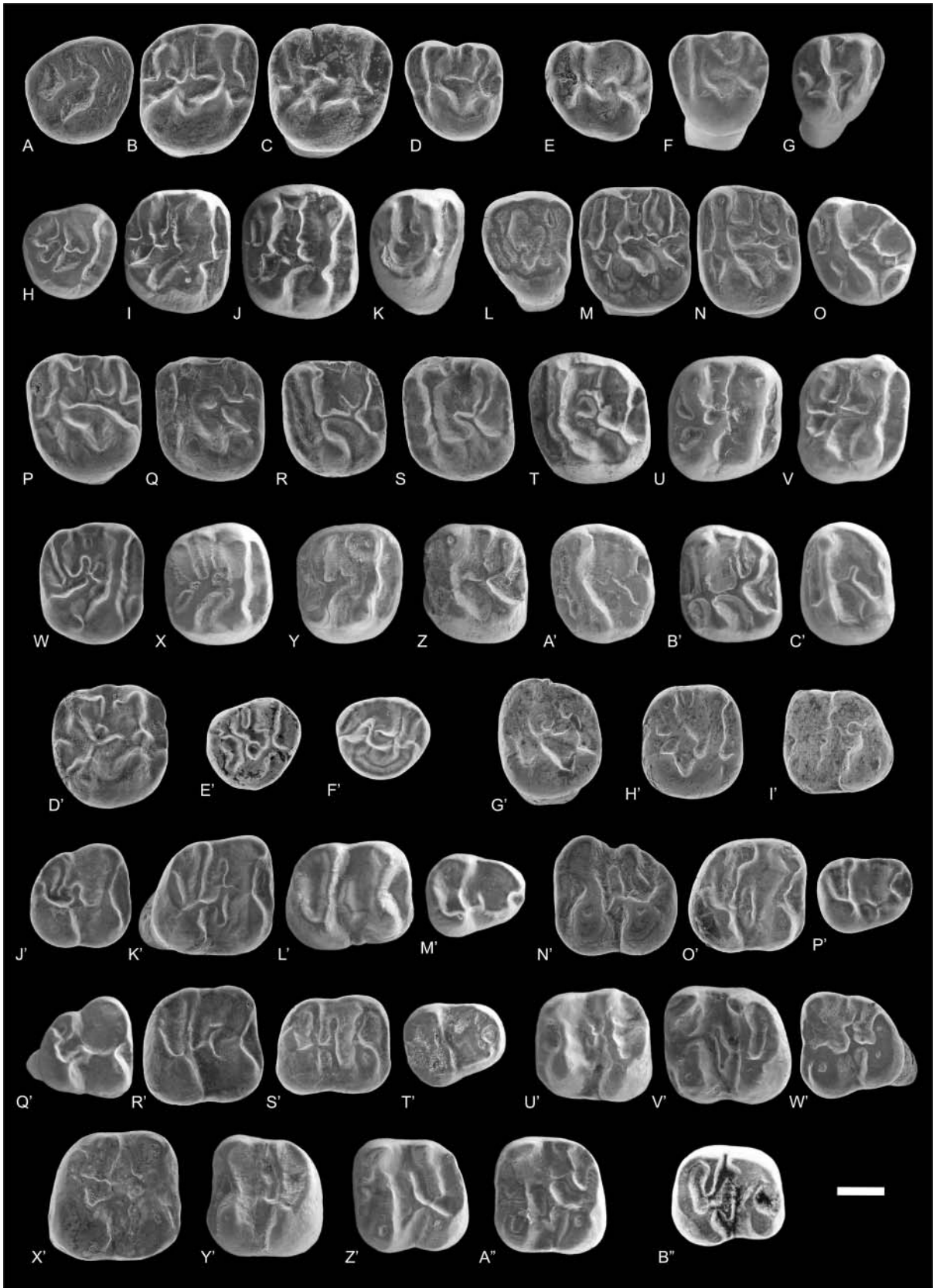
**Emended diagnosis.** Tiny zegdoumyid characterized by upper and lower teeth tetra- or pentalophodont, depending on the highly variable development of the central transverse crests (mesolophule and mesolophid, respectively), and by

less bulbous cusps and cuspids than in *Zegdoumys*, *Glibemys* and *Lazibemys*. Differs from *Zegdoumys* and *Glibemys* in showing a strong and complete hypolophid on lower molars. Upper molars differ from those of *Zegdoumys* and *Lazibemys* in showing a frequent development of a central crest, which is a composite of a mesolophule and a mesoloph; the presence of a protoconule, a minute metaconule centrally displaced; the presence of a posteroconule, lesser development of the neo-endoloph; and in showing a tendency to close the internal sinus by the development (in only few cases) of a thin mure. The metaloph is generally connected to the mesial extremity of the anterior arm of the hypocone, but can develop secondary connections via thin enamel crestules either to the posterocingulum or even to the mesolophule.

**Material.** Two right DP4 (HGL50-18, HGL52-GZC17), one left DP4 (HGL50-19), two right P4 (HGL50-20-21), seven right M1 (HGL50-32-36, HGL52-GZC20, HGL52-GZC34), 10 left M1 (HGL50-22-31), six right M2 (HGL50-37-40, HGL52-GZC19 and 21), six left M2 (HGL50-41-46), three right M3 (HGL50-47, HGL52-GZC39, HGL90-03), one left M3 (HGL50-48), four right p4 (HGL50-49-51, HGL52-GZC16), three right m1 (HGL50-52-54), two left m1 (HGL50-55 and 57), seven right m2 (HGL50-58-61, HGL50-79, HGL52-GZC27-28), eight left m2 (HGL50-56, HGL50-62-66, HGL52-GZC26 (holotype), HGL52-GZC33), two right m3 (HGL50-67-68), one left m3 (HGL50-69), a very worn fragment of left mandible (HGL51-01) bearing m2 and the alveoli of I2, p4 and m1. Dental measurements are reported in Table 2.

**Table 2.** Dental measurements (in mm) of *Glibia pentalopha* (L, maximum mesiodistal length; W, maximum buccolingual width BL; n, number of specimens; x, mean; SD, standard deviation; OR, observed range).

| Tooth | n  | Measurement | x    | SD   | OR        |
|-------|----|-------------|------|------|-----------|
| DP4   | 2  | L           | 1.05 | 0.01 | 1.04–1.06 |
|       |    | W           | 1.04 | 0.06 | 1.00–1.08 |
| P4    | 2  | L           | 1.01 | 0.02 | 1.00–1.02 |
|       |    | W           | 1.2  | 0.04 | 1.17–1.22 |
| M1    | 14 | L           | 1.18 | 0.06 | 1.05–1.27 |
|       |    | W           | 1.34 | 0.07 | 1.17–1.42 |
| M2    | 10 | L           | 1.08 | 0.05 | 0.99–1.14 |
|       |    | W           | 1.3  | 0.04 | 1.24–1.39 |
| M3    | 2  | L           | 1.09 | 0.11 | 1.01–1.16 |
|       |    | W           | 1.02 | 0.09 | 0.96–1.09 |
| p4    | 3  | L           | 1.07 | 0.01 | 1.06–1.08 |
|       |    | W           | 0.9  | 0.03 | 0.88–0.93 |
| m1    | 5  | L           | 1.25 | 0.08 | 1.17–1.39 |
|       |    | W           | 1.12 | 0.06 | 1.06–1.19 |
| m2    | 10 | L           | 1.24 | 0.05 | 1.17–1.31 |
|       |    | W           | 1.23 | 0.05 | 1.11–1.30 |
| m3    | 3  | L           | 1.06 | 0.04 | 1.02–1.10 |
|       |    | W           | 1.09 | 0.04 | 1.05–1.13 |



**Occurrence.** Intermediate member of the Glib Zegdou Formation, late Early or early Middle Eocene (Adaci *et al.* 2007): HGL50, HGL51 and HGL52 (Glib Zegdou outlier), and HGL90 situated in the Gour Lazib (Hammada du Dra), Algeria (Fig. 1).

**Remarks on *Glibia tetralopha* Vianey-Liaud *et al.*, 1994.**

The dental material referable to *Glibia* is the most abundant among the new collections, allowing for a better description of this taxon. More importantly, this new material provides a glimpse into the range of morphological variations observed in the occlusal dental pattern of this genus, which led us to consider *G. tetralopha* (HGL52-GZC18, HGL52-GZC23, HGL52-GZC25, and HGL52-GZC29) as a variant of *G. pentalopha*. However, one tooth originally described by Vianey-Liaud *et al.* (1994) as a M1 or M2 (HGL52-GZC22; Fig. 4H') of '*G. tetralopha*', exhibits a dental pattern that is somewhat distinct and out of the range of variations of the diagnostic characters for *G. pentalopha*. Indeed, this tooth displays a strong metaconule, a protocone–metaconule connection (lingual metaloph), and has no anterior arm of the hypocone (no metaconule–hypocone connection); a suite of dental traits, which is otherwise never found in *Glibia*. As such, this tooth could represent an upper molar of a rare species, and most likely another genus.

**Remarks on *Glibia namibiensis* Pickford *et al.*, 2008.**

This species was recently described by Pickford *et al.* (2008) on the basis of a single isolated right upper molar (BC 1'08), found in fossiliferous carbonate deposits (Black Crow) from Sperrgebiet, Namibia, that are considered to be Lutetian in age. This tooth exhibits an occlusal pattern that is characterized by several anatomical details, which are of undoubted zegdoumyid affinity. This is particularly shown in the development of a strong hypocone, which is nearly equal in size to the metacone and slightly more buccal in position to the protocone. More significant in this tooth is the buccal closure of the trigon basin that, as on upper teeth of *Glibia* and *Zegdoumys*, is the result of the important development of a mesostyle, which appears elevated and enlarged mesiodistally. More generally, BC 1'08 differs

from teeth of *Glibia pentalopha* and *Zegdoumys lavocati* in the absence of conules, and in showing a stronger development of the transverse crests (especially the protoloph and the metaloph), which are thicker and higher. The anterior and posterior cingula are also slightly more developed, with the anterior cingulum connected lingually to the protocone, thereby forming an anteroloph. The protocone of BC 1'08 displays a strong posterior outgrowth, which forms a sub-complete neo-endoloph that closes the internal sinus lingually. This longitudinal lingual crest joins the hypocone via a thin and short enamel connection. Such a lingual structure better characterizes upper molars of *Z. lavocati* rather than molars of *G. pentalopha*. *Glibia*'s teeth show a rather lower and often very short posterior outgrowth of the protocone, which never closes the internal sinus, while in *Zegdoumys*, the protocone outgrowth is much more developed and in some cases closes the internal sinus as in BC 1'08. In overall morphology, this unique specimen from Sperrgebiet, Namibia, exhibits a dental pattern that appears evolutionarily advanced over that characterizing *G. pentalopha* and *Z. lavocati* from the Gour Lazib. This tooth, which is nearly twice as big as the upper molars of *Z. lavocati*, undoubtedly belongs to a distinct species ('*Glibia namibiensis*'), as suggested by Pickford *et al.* (2008). However, owing to the new dental evidence assembled from the Gour Lazib, we think that the dental morphology of this Namibian species better matches the diagnosis of the genus *Zegdoumys*. As such, we propose that this species could be preferably referred to the genus *Zegdoumys* than *Glibia* (i.e. *Zegdoumys namibiensis*).

**Description.**

**Upper dentition.** Deciduous (DP4) and permanent (P4) premolars are sampled for this species. P4 (Fig. 4K, L) is slightly larger than DP4 (Fig. 4D–G), and differs in several points. P4 is oval, while DP4 is rather triangular in shape due to a stronger development of both the anterocingula and posterocingula, and to a buccal displacement of the protocone with respect to the hypocone. Mesiobuccally, both teeth show a small parastyle. On DP4, the hypocone develops an oblique anterior arm (mesiobuccally directed), which connects both the metaloph and a small and

**Figure 4.** Isolated teeth of the small bodied Zegdoumyidae from the Gour Lazib. A–A'', *Glibia pentalopha* Vianey-Liaud *et al.*, 1994; A, HGL52-GZC39, right M3; B, HGL52-GZC20, right M1; C, HGL52-GZC34, right M1; D, HGL52-GZC18, left DP4; E, HGL07-1, left DP4; F, HGL50-19, left DP4; G, HGL50-18, right DP4; H, HGL50-47, right M3; I, HGL50-38, right M2; J, HGL50-35, right M1; K, HGL50-20, right P4; L, HGL50-21, left P4; M, HGL50-25, left M1; N, HGL50-43, left M2; O, HGL50-48, left M3; P, HGL50-26, left M1; Q, HGL50-29, left M1; R, HGL50-30, left M1; S, HGL50-28, left M1; T, HGL50-24, left M1; U, HGL50-34, right M1; V, HGL50-33, right M1; W, HGL50-37, right M2; X, HGL50-39, right M2; Y, HGL50-40, right M2; Z, HGL50-27, left M2; A', HGL50-42, left M2; B', HGL50-45, left M2; C', HGL50-46, left M2; D', HGL50-32, right M1; E', HGL22-1, right M3; F', HGL09-2, right M3; G', HGL52-GZC22, left M2; H', HGL52-GZC23, right M1 (sp *tetralopha*, other genus); I', HGL52-GZC29, left m3; J', HGL50-68, right m3; K', HGL50-61, right m2; L', HGL50-53, right m1; M', HGL50-51, right p4; N', HGL52-GZC26, left m2; O', HGL52-GZC27, right m2; P', HGL52-GZC16, right p4; Q', HGL50-67, right m3; R', HGL50-60, right m2; S', HGL50-54, right m1; T', HGL50-49, right p4; U', HGL50-55, left m1; V', HGL50-56, left m2; W', HGL50-69, left m3; X', HGL50-73, right m2; Y', HGL50-62, left m2; Z', HGL50-63, left m2; A'', HGL50-65, left m2; B'', *Glibemys algeriensis* Vianey-Liaud *et al.*, 1994, HGL52-GZC32, right m1. Scale bar = 0.5 mm.

mesiodistally elongated enamel swelling. This swelling occupies a central position in the trigon basin and could be a minute metaconule that is mesially displaced. On one specimen (HGL50-18; Fig. 4G), a very thin crest extends mesially from this 'metaconule' and reaches the protoloph, thus forming a mure. The hypocone on P4 does not develop an anterior arm, and the metaloph extends lingually to the hypocone. A tiny and very low enamel swelling (? metaconule) can be also observed on P4. A minute and isolated mesostyle is observed only on DP4. P4 differs also from DP4 in showing a development of a low but long neo-endoloph from the protocone that joins the hypocone, thereby closing the internal sinus lingually.

M1 and M2 exhibit similar cusp and crest arrangements (Fig. 4). These two teeth differ simply in overall proportion, with M1 larger and more quadrangular in shape than M2, which is narrower and rectangular. On M2, the metacone is reduced (in some cases crestiform; Fig. 4C'), and slightly more lingual in position with respect to the paracone. Both molars display a low but long anterocingulum that occupies all the breadth of the crown. On M1, the anterocingulum is more extensively developed buccally, and reaches the paracone on its buccal aspect, while on M2 it reaches the paracone on its mesial aspect. Whatever the buccal terminus, the anterocingulum does not meet the paracone. The same is true lingually with the protocone. Mesial to the protocone, the anterocingulum bears a small enamel swelling corresponding to a minute anterostyle. The degree of development of this style is highly variable on M1 or M2. The protoloph is complete, slightly curved mesially, and links the protocone to the paracone. In mid course, it bears a small but distinct protoconule. This conule is sometimes connected to the anterocingulum by a thin enamel crestule (Fig. 4N, P, B'). Distally, there is no posteroloph but a simple and low posterocingulum, which is more extensively developed buccally on M1. As for the anterocingulum, this posterocingulum is neither connected to the hypocone nor to the metacone. Just distobuccally to the hypocone, the posterocingulum bears a small but distinct tubercle that we name here the posteroconule; a character which is unusual among rodents, and seemingly autapomorphic of *Glibia*. As on DP4, the hypocone develops a strong and long anterior arm, which is oblique, mesiobuccally directed. This arm joins a small and crestiform (mesiodistally elongated) central conule, which is most likely a metaconule that is mesially displaced. In some teeth, this metaconule is clearly distinct, while in some others it is indistinct, entirely merged with the distal extremity of the anterior arm of the hypocone. In several teeth (about 75% of M1-2), a thin crest extends mesially from the metaconule, and reaches in some cases the protoloph or the protoconule, thus forming a complete mure (e.g. Fig. 4P, R, V, B'). The lingual protoloph associated with the anterior arm of the hypocone plus the mure generates a deep internal sinus. When the mure is absent or short (not connected to

the protoloph), the internal sinus remains open transversally (e.g. Fig. 4S-U, X-A'). A thin crestule, buccally directed, emerges from the metaconule. This central crestule, which is a mesolophule, is generally very limited in length (incipient), but in some cases extends buccally (Fig. 4B, I, J, M, N). In fact, in this specific case, can be observed another crestule (mesolophe) that extends lingually from a strong mesostyle to reach the mesolophule. The resulting apparent transverse crest linking the metaconule to the mesostyle is in fact a composite central crest. This dental trait is highly variable in *Glibia*, with some teeth showing only either the mesolophule or the mesoloph, while some others display both crests, but short and not linked together. The metaloph also displays different types of arrangements. It is generally connected to the mesial extremity of the anterior arm of the hypocone, but can develop secondary connections either to the posterocingulum (Fig. 4B, C, I, J, M, N, P, Q, U) or even to the mesolophule (Fig. 4N, Q, W), via thin enamel crestules. Buccally, practically all teeth show a mesostyle, which can be strongly developed (i.e. elevated and mesiodistally elongated) in some specimens. In these cases, the external sinus is obstructed, and the teeth appear with a buccal wall. Lingually, the protocone has a posterior outgrowth, which can be slightly, moderately or strongly developed. The hypocone can also develop a short anterior outgrowth. When both outgrowths are present (Fig. 4B, I, P, T), the internal sinus is closed by a low neo-endoloph. Few supernumerary enamel wrinkles can be observed on the occlusal surface in some teeth, but they are arranged stochastically.

The M3 (Fig. 4A, E, F, H, O) is heart-shaped and smaller than M2. The protocone and the paracone are equal in size, but the paracone is salient and dominates the other cusps. The hypocone is half the size of the protocone and the metacone is crestiform, virtually indistinct. As on M1 and M2, there is a posteroconule on the posteroloph. The protocone and the hypocone are linked by a strong neo-endoloph. The hypocone develops an anterior arm, which connects a small metaconule. A central crest links the metaconule to the mesostyle. There is no metaloph. The anterocingulum is long and connects the protocone mesiolingually. The protoloph is well developed and curved mesially. One specimen (HGL50-47; Fig. 4H) shows a thin mure, which links the mesial extremity of the anterior arm of the hypocone to the protoloph. Buccally, the crown is characterized by a wall, which consists of a junction between the metacone, a strong mesostyle and the posterior arm of the paracone.

**Lower dentition.** Only permanent premolars (p4) have been identified (Fig. 4M', P', T'). These lower premolars show the trigonid narrower than the talonid. The cuspids are salient and equally sized, and the few crests present are low. The metaconid occupies a mesiolingual position, while the protoconid appears more distal and well separated from the metaconid. Both cuspids are distally linked by a complete metalophulid II. Mesially, the crown bears a

low and short anterocingulid between the metaconid and the protoconid. There is no anteroconid. In the talonid basin, the entoconid and the hypoconid are labiolingually opposed and linked together by a low hypolophid and a strong posterolophid. A hypoconulid is barely visible on the posterolophid, just distolingual to the hypoconid. A minute mesoconid is located between the hypoconid and the protoconid. There is neither ectolophid nor anterior arm of the hypoconid, and the mesoconid remains isolated as a result. A short mesolophid emerging from the mesoconid can be observed on some specimens. Lingually, a strong mesostylid seems to be present but it is entirely submerged in a strong and long posterior arm of the metaconid. There is no anterior arm of the entoconid, and the internal sinusid remains open lingually between the entoconid and the mesostylid.

The dental structure of m1 and m2 is similar to that of p4 except for some details, which are more developed or accentuated in molars. From the material available, which consists of isolated teeth, we identify the largest molars showing a quadrangular outline as m2 (Fig. 4K', N', O', R', V', X'-A''). The m1s are smaller, and otherwise longer than they are wide (rectangular outline) (Fig. 4L', S', U'). In contrast, m3s are clearly distinguishable from m1-2s as they are much smaller and characterized by a triangular outline with a talonid narrower than the trigonid (Fig. 4J', Q', W'). The three lower molars show the development of an anterocingulid. This cingulid is generally low and not extensively developed labiolingually, rather limited in length and located between the metaconid and the protoconid. It is practically never connected to both the protoconid and metaconid, but few teeth show a connection with the metaconid. On two specimens (HGL50-55 and HGL50-62; Fig. 4U', Y'), this anterocingulid extends mesiobuccally around the protoconid. The main cuspids are salient, notably the metaconid, which is stronger and dominant. The protoconid is slightly more distally positioned with respect to the metaconid. Both cuspids are linked by a strong metalophid II, which connects the metaconid mesiobuccally. There is practically no difference in elevation between the trigonid and talonid basins. On the talonid, the entoconid is slightly mesial to the hypoconid. A strong and transverse hypolophid links both cuspids. On m3, the hypolophid is incomplete, buccally interrupted, and often backwardly directed (HGL50-68; Fig. 4J'). In HGL50-67, it connects the posterolophid (Fig. 4Q'), while in HGL50-69 it is short and connects the mesolophid (Fig. 4W'). The anterior arm of the hypoconid is thin and lingually directed. Distally, the posterolophid is low, and links the entoconid to the hypoconid. On some teeth, the posterolophid ends lingually at the base of the entoconid. On the posterolophid, just distolingual to the hypoconid, a crestiform hypoconulid can be observed on several specimens. Centrobuccally, there is a well-developed and transversally elongated mesoconid. This central cuspid can be either connected to the

hypolophid by a thin distal ectolophid or be isolated, free of connection. There is no (or barely visible) mesial ectolophid joining the mesoconid to the protoconid. A mesolophid is developed from the mesoconid, but it does not reach the lingual margin of the crown. An ectomesolophid is also observable in few specimens (HGL50-61, HGL52-GZC26, HGL-50-54; Fig. 4K', N', S'). Lingually, there is no mesostylid, but the metaconid develops a long and moderately elevated posterior arm, which partially closes the lingual margin of the crowns.

Genus *Lazibemys* gen. nov.

**Type species.** *Lazibemys zegdouensis* sp. nov.

**Diagnosis.** As for the type species.

**Etymology.** Combination of *Lazib*, in reference to the 'Gour Lazib', and *mys*, Greek for mouse.

*Lazibemys zegdouensis* sp. nov.  
(Fig. 3S-U)

**Diagnosis.** Zegdoumyid of the size of *Zegdoumys lavocati*, characterized by complex occlusal surfaces, with supernumerary enamel wrinkles. Differs from *Zegdoumys* and *Glibia* in showing upper molars with complete lingual, distal and buccal walls, reflecting the strong developments of the neo-endoloph and posteroloph, and the connection between the parastyle, paracone, mesostyle and metacone. Differs also in showing a strong parastyle, and in developing a labiolingually oriented anterior arm of the hypocone connected to a long metaloph. The lower premolar is highly molariform, showing a pentalophodont pattern including a strong development of the anterocingulid (anterolophid), posterolophid and metalophid II, and the presence of a short and low mesolophid, and a complete but low hypolophid. Differs from *Zegdoumys* and *Glibia* in showing a strong lingual wall, an anterolophid, and a complete ectolophid. Differs from *Glibemys* and *Zegdoumys* in developing a complete hypolophid and a strong ectolophid.

**Etymology.** The species name refers to 'Zegdou', the unique water well in the vast rocky desert region of the Gour Lazib.

**Material.** Holotype: a left M1, HGL50-70 (Fig. 3S). Paratypes: a left M3, HGL50-71 (Fig. 3T); a left p4, HGL50-72 (Fig. 3U). Dental measurements are reported in Table 3.

**Occurrence.** Intermediate member of the Glib Zegdou Formation, late Early or early Middle Eocene (Adaci *et al.* 2007): HGL50, Glib Zegdou outlier of the Gour Lazib (Hammada du Dra), Algeria (Fig. 1).

**Table 3.** Dental measurements (in mm) of *Lazibemys zegdouensis* gen et sp. nov. (MD, maximum mesiodistal length; BL, maximum buccolingual width).

| Tooth | Specimen  | Length MD | Width BL |
|-------|-----------|-----------|----------|
| M1    | HGL50-70  | 1.90      | 2.17     |
| M3    | HGL50-71  | 1.98      | 1.87     |
| p4    | HGL-50-72 | 1.97      | 1.68     |

**Description.** Among the hundred isolated teeth recovered, only two upper molars and one lower premolar from HGL50 exhibit a peculiar dental morphology. The occlusal pattern is clearly distinct from *Zegdoumys*, *Glibia* and *Glibemys*, justifying the recognition of a new genus and species among the Zegdoumyidae.

**Upper teeth.** The dental pattern of the two upper molars (M1 and M3) is somewhat complex due to the presence of supernumerary enamel wrinkles on the occlusal surface. However, the main cusps and crests are still recognizable. We identify a nearly triangular tooth as an M1 (the holotype; Fig. 3S); it is characterized by a paracone that appears to be offset distally with respect to the protocone, and by the development of a strong parastyle on the mesiobuccal border of the crown. This parastyle appears to be as large as the paracone, metacone and protocone, and is connected both to a strong and elevated anterocingulum (# anteroloph) and to the paracone via its strong anterior arm. Lingually, the anterocingulum is not connected to the protocone. The metacone is slightly more lingual in position to the paracone. A strong, elevated and mesiodistally elongated mesostyle makes a junction between these two main buccal cusps. In fact, the anterostyle–paracone–mesostyle–metacone complex forms a complete buccal wall of the crown. Lingually, the protocone and the hypocone are mesiodistally opposed. The protocone is mesially canted and develops a strong and long distal outgrowth (neo-endoloph) that reaches the mesiolingual aspect of the hypocone. As such, the internal sinus is entirely closed. Distally, a thin and elevated posteroloph connects the hypocone to the metacone. The hypocone displays a strong and transverse anterior arm, which extends buccally via the metaloph. There is a small but distinct enamel swelling situated at the junction between the metaloph and the anterior arm of the hypocone that could be the trace of a metaconule. There is no well-identified transverse internal crest (mesolophule or mesoloph), but several enamel wrinkles, which show otherwise a buccolingual orientation, occur within the trigon basin. Mesially, the protoloph is complex, as it is a composite crest made by the association of a short lingual outgrowth of the paracone with the anterior arm of the protocone, which is mesiobuccally oriented and shows a hook-like termination in its buccal extremity. Neither transverse arms are aligned labiolingually given the distal displacement of

the paracone with respect to the protocone, but they connect together via the hook-like structure of the anterior arm of the protocone.

The M3 (Fig. 3T) is slightly smaller than the M1 (Fig. 3S) and is characterized by its more or less heart-shaped outline due to the buccal position of the hypocone. As in M1, the trigon basin of M3 lacks an internal transverse crest but displays a net of supernumerary enamel wrinkles. The main cusps are equally sized and appear less bulbous than those in M1, notably the metacone, which is crestiform on M3. Mesially, this tooth displays a long anterocingulum situated at the base of the crown. This anterocingulum is connected neither to the protocone nor to the paracone, and appears somewhat relatively lower than that developed on M1. Mesiobuccally, there is no parastyle and the metacone is not offset distally with respect to the protocone. The paracone and metacone are widely spaced but linked by a crest formed by the posterior arm of the paracone, a mesiodistally elongated mesostyle and a strong anterior arm of the metacone, which are interconnected. As on M1, this complex forms a complete buccal wall. Lingually, the protocone is V-shaped and connects the hypocone via a strong neo-endoloph. The hypocone is linked to the metacone by a strong posteroloph, and the protocone to the paracone by a strong and transverse protoloph. These transverse and horizontal crests form a complete rimmed crown. Distolingually, the hypocone displays a thin, short and buccally directed anterior arm, which connects a very thin and curved metaloph. There is no trace of conules.

**Lower tooth.** The unique lower tooth referred to in this new genus is a permanent premolar (p4), which is highly molariform (Fig. 3U). This tooth is characterized by a bulbous metaconid, entoconid and hypoconid, among which the metaconid is very prominent. In contrast, the protoconid is minute but well separated from the metaconid, making the trigonid of this tooth slightly narrower than the talonid. There is no difference in elevation between the trigonid and the talonid. The entoconid and hypoconid are labiolingually opposed and linked distally by a trenchant posterolophid, which forms a massive distal wall. Inside the talonid basin, there is also a low and curved hypolophid that joins the entoconid to the anterior arm of the hypoconid, which is short, thin and lingually oriented. Mesiolingually, the metaconid extends distally in developing a very strong, long and high posterior arm that ends just before the short and elevated anterior arm of the entoconid. This arrangement forms a massive lingual wall that is interrupted by a narrow and shallow notch due to the lack of junction between both arms. Mesially, the metaconid and the protoconid are linked by a short anterolophid. The posterior arm of the protoconid is well developed and joins the metaconid on its distobuccal aspect, thereby forming a complete metalophulid II. The anterocingulid and metalophulid II isolate a small but deep fossa on the vestigial trigonid. Buccally, there is a distinct mesoconid, which

connects both the protoconid and the anterior arm of the hypoconid via a complete ectolophid. From the mesoconid, a low mesolophid extends lingually but does not reach the lingual wall of the crown. The mesoconid and the bulbous hypoconid delimit a narrow and shallow external sinusid. Supernumerary enamel wrinkles occur in the talonid basin.

### Comparisons and discussion of *Lazibemys*

The three teeth referred to a new genus and species show a dental structure that is much more complex than that characterizing the other zegdoumyid species. This complexity relies on the addition of enamel wrinkles, notably in the trigon basin of upper molars, and in addition a better development of the transverse and longitudinal crestids on the unique lower tooth. Teeth are also characterized by the development of a wall of enamel running at the periphery of the occlusal surface. This wall is constituted by the connection of the mesial, buccal, distal and lingual crests (-ids). Basically, the structural organization of these three teeth is consistent with that of the teeth of *Zegdoumys* and *Glibia*, with similar crest connections and cusp arrangement. The main difference concerns the degree of development, which appears to be much more advanced in *Lazibemys* than in *Zegdoumys* and *Glibia*. The lower premolar of *Lazibemys* is molariform, showing a pentalophodont pattern, but with internal transverse crestids moderately developed and still low. To some extent, the dental pattern of this tooth could be compared to that of the unique lower molar of *Glibemys*, but it differs substantially by showing a better development of the transverse (complete hypolophid) and longitudinal (i.e. complete ectolophid) crestids. Interestingly, such an advanced degree of dental development is much more comparable to that of more recent anomaluroids such as *Nementchamys*, *Kabirmys* and *Pondaungimys* that are found in coeval localities dating from the end of the Eocene (see Jaeger *et al.* 1985; Dawson *et al.* 2003; Marivaux *et al.* 2005; Sallam *et al.* 2010b). These taxa have molarized premolars, which exhibit a fully accomplished pentalophodont pattern, with strong and elevated transverse crestids. The upper teeth in *Lazibemys* are characterized by the addition of supernumerary enamel wrinkles, which occur on the whole occlusal surface. This intricate net of crenulations (vermiform) makes the occlusal surface of *Lazibemys*' teeth more complex than that of *Zegdoumys* or *Glibia*'s teeth. A crenulated pattern on the occlusal surface is particularly characteristic of the upper cheek teeth of *Nementchamys lavocati* (late Middle Eocene; Jaeger *et al.* 1985; Marivaux *et al.* 2005). However, in this taxon, the degree of complexity of the crenulations is somewhat extreme compared with that developed in *Lazibemys*, and certainly reflected a specific dietary specialization. *Lazibemys zegdouensis* was certainly not as specialized as *Nementchamys*, but probably had different feeding habits from *Zegdoumys* and *Glibia*. This new taxon is therefore particularly interesting in showing a dental pattern resembling

that of *Nementchamys*. The potential phylogenetic links between *Lazibemys* and *Nementchamys* could be envisaged. However, deciphering the nature of these relationships requires more morphological support than current data allow.

### Incisor enamel microstructure

Among the isolated teeth sorted from the residues of HGL50 are several lower and upper rodent incisors. Some of these incisors, as well as fragments of incisors, were embedded in resin and polished longitudinally. The polished sections were then etched for 30 s with H<sub>3</sub>PO<sub>4</sub> (37%) to make the microstructural details visible. There are two main categories of incisors that are clearly distinguishable by the size (small versus large). Given the small size of *Glibia* and the abundance of the material referred to this taxa, it is most likely that the small isolated incisors are those of *Glibia* rather than *Glibemys*, which is otherwise known from only one isolated lower molar (Vianey-Liaud *et al.* 1994). Concerning the large incisors, they can be either attributed to *Zegdoumys* or *Lazibemys*, although the material referred to *Zegdoumys* is more abundant. The specimens were examined by scanning electron microscope at different magnifications.

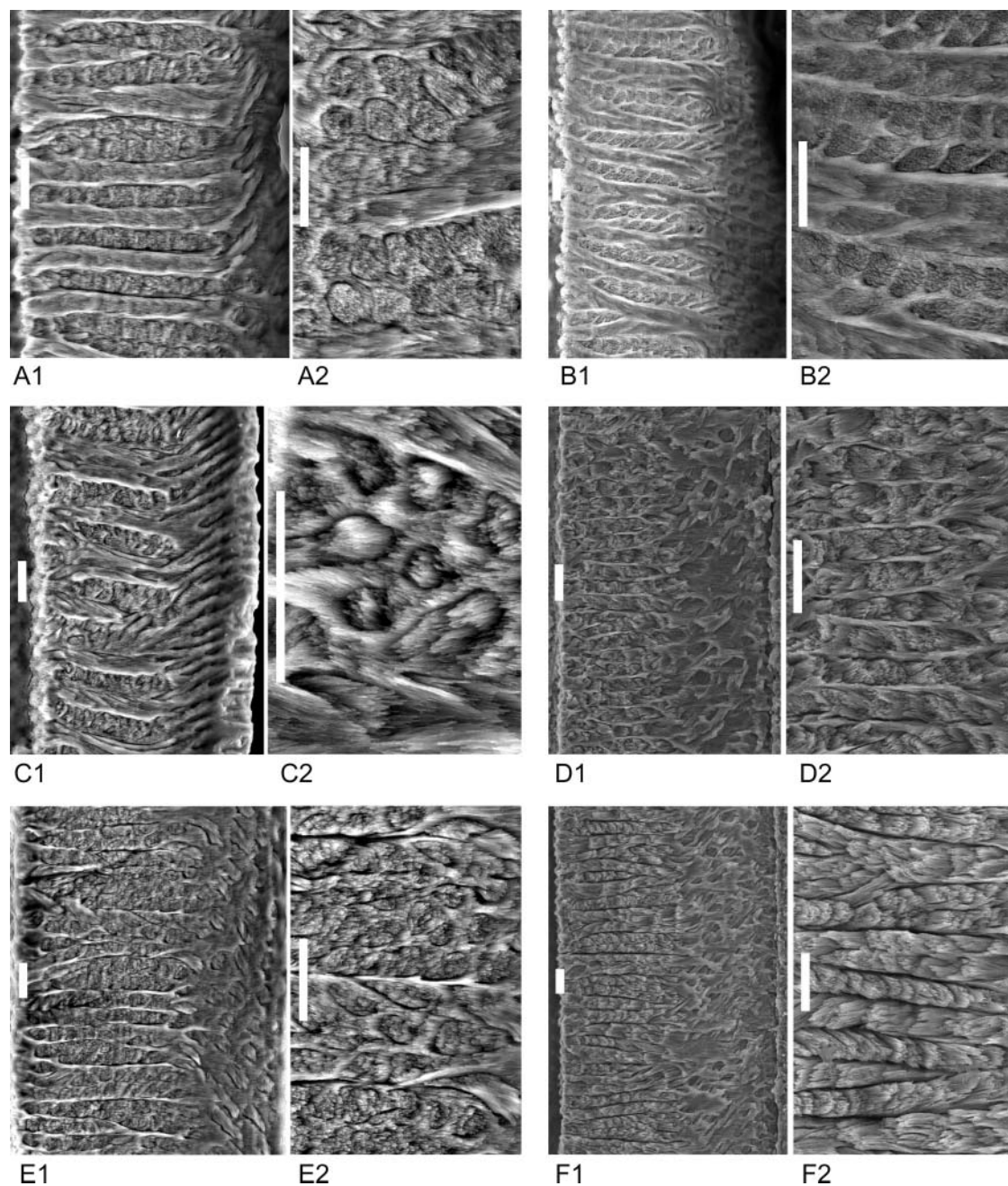
#### Small incisors

In longitudinal section, the total enamel thickness of each specimen measured (Table 4) is about 60  $\mu$ m with two distinct layers: the *portio interna* (PI) and the *portio externa* (PE). The thickness of PE ranges from 25 to 50% of total enamel thickness, and has radial enamel with apically inclined prisms. The PI consists of decussating prisms appearing as Hunter–Schreger bands (HSB), generally 1–2 prisms wide per band, except in HGL50-77 (Fig. 5C), which bears 2–3 prisms per band. The HSB are straight and exhibit little (max. 10°) or no inclination to the enamel dentine junction (EDJ). The prisms are mostly rounded in cross section, except in HGL50-76 (Fig. 5B), which seems to show slightly flattened prisms (oval). The interprismatic matrix (IPM) in the PI is rather thick, with the crystallites completely surrounding the prisms, forming a prism sheath as a result (parallel to the prism direction). With 2–3 prisms per band and an IPM forming a prism sheath, the enamel microstructure of the HGL50-77 incisor (Fig. 5C) has a pauciserial Schmelzmuster (e.g. Martin 1993). In contrast, the enamel microstructure of the HGL50-75, 76 and 78 incisors (Fig. 5A, B, D) show a tendency toward thinning of HSB, with 1–2 prisms per bands. Besides, more than 50% of their HSB have only one prism per band (uniserial). This pattern of crystallite arrangement in PI, associated with a reduction of the number of prisms per HSB, typifies a Schmelzmuster transitional from the pauciserial to the uniserial condition (e.g. Martin 1993). Although HGL50-78



**Table 4.** Incisor enamel features on the rodent specimens from the Gour Lazib.

| Specimen | Fig. 5 | Incisor         | Size       | Prisms per HSB | Prism cross section           | Inclination of HSB (°) | Enamel thickness (µm) PE + PI | Percentage of PE | IPM in PI   | Schmelzmuster                         | Percentage of uniserial HSB |
|----------|--------|-----------------|------------|----------------|-------------------------------|------------------------|-------------------------------|------------------|---|---------------------------------------|-----------------------------|
| HGL50-75 | A1-2   | Lower           | Small      | 1-2            | Rounded                       | 0                      | 62                            | 25%              | Thick and surrounds prisms (sheath)                   | Transitional pauciserial to uniserial | 60%                         |
| HGL50-76 | B1-2   | Lower           | Small      | 1-2            | Rounded to flattened (oval)   | 10                     | 67                            | 35%              | Thick and surrounds prisms (sheath)                   | Transitional pauciserial to uniserial | 50%                         |
| HGL50-77 | C1-2   | Lower           | Very small | 2-3            | Rounded                       | 10                     | 56                            | 35%              | Thick and surrounds prisms (sheath)                   | Pauciserial                           | 0%                          |
| HGL50-78 | D1-2   | Lower or upper? | Small      | 1-2            | Rounded                       | 0                      | 60                            | 50%              | Thick and surrounds prisms (sheath)                   | Transitional pauciserial to uniserial | 70%                         |
| HGL50-74 | E1-2   | Lower           | Large      | 1-3            | Rounded                       | 0                      | 76                            | 35%              | Thick and surrounds prisms (sheath)                   | Transitional pauciserial to uniserial | 50%                         |
| HGL10-01 | F1-2   | Upper           | Large      | 1-2            | Rounded to slightly flattened | 0-5                    | 90-93                         | 35%              | Moderately thick, crystallites run parallel to prisms | Transitional pauciserial to uniserial | 65%                         |



**Figure 5.** Scanning electron photomicrographs of the incisor enamel microstructure in longitudinal section. For each specimen (A–F), images labelled ‘1’ show the total enamel thickness, and ‘2’ are magnifications. **A**, HGL50-75, small lower incisor with transitional paucio-uniserial (TPU) Schmelzmuster; **B**, HGL50-76, small lower incisor with TPU Schmelzmuster; **C**, HGL50-77, very small lower incisor with pauciserial Schmelzmuster; **D**, HGL50-78, small upper or lower incisor with TPU Schmelzmuster; **E**, HGL50-74, large lower incisor with TPU Schmelzmuster; **F**, HGL10-01, large upper incisor with TPU Schmelzmuster. Measurements for the different specimens are reported in Table 4. Scale bars = 10  $\mu\text{m}$ .

(Fig. 5D) is a very small fragment, the pronounced curvature of this specimen suggests that this tooth could be an upper incisor. This incisor differs from the lower small incisors in being characterized by a more important number of uniserial HSB (70%).

### Large incisors

In longitudinal section, the total enamel thickness (PI + PE) of the two specimens measured (Table 4) reaches about 80  $\mu\text{m}$  (90  $\mu\text{m}$  in HGL10-01), with PE in both cases representing 35%. PE has radial enamel with apically

inclined prisms. In HGL50-74 (Fig. 5E), the Schmelzmuster is mainly pauciserial (1–3 prisms per HSB in PI, with a thick IPM forming a prism sheath), but it shows a tendency toward thinning of HSB. Indeed, in this specimen, about 50% of the HSB are uniserial, thereby typifying a Schmelzmuster transitional from the pauciserial to the uniserial condition. The HSB are straight and not inclined to the EDJ. HGL10-01 seems to be an upper incisor, which shows a greater number of uniserial HSB (Fig. 5F), a condition that is similar to that described above on the small upper incisor.

## Phylogenetic analysis

### The problem of the Zegdoumyidae

The Zegdoumyidae is the oldest and the only rodent family known from the Early or earliest Middle Eocene in Africa. In the absence of a comprehensive African fossil record predating and postdating the first occurrence of this family, and because of the highly fragmentary nature of fossils from which the taxa were originally documented, the phylogenetic and geographical origins of the Zegdoumyidae, as well as its subsequent evolution, remain a matter of speculation (Vianey-Liaud *et al.* 1994; Vianey-Liaud & Jaeger 1996; Dawson *et al.* 2003; Marivaux *et al.* 2004a, 2005). Furthermore, even if it is regarded as a possible early African stem group for Anomaluridae (Vianey-Liaud *et al.* 1994; Vianey-Liaud & Jaeger, 1996), there is a morphological gap between zegdoumyids and the first unequivocal anomaluroids (*Nementchamys*, *Kabirmys*, *Shazurus* and *Pondaungimys*), associated with a major sampling gap through nearly the entire Middle Eocene. From the new fossil material described here, our focus is therefore to highlight the higher-level relationships of the Zegdoumyidae, and to assess its role in the early evolutionary history of the Anomaluroidea (Zegdoumyidae – Anomaluridae) or even of the Anomaluromorpha (Zegdoumyidae – Anomaluridae – Pedetidae).

### Material and methods

We investigated the phylogenetic position of the Zegdoumyidae in a high-level rodent phylogeny with a cladistic assessment of the dental evidence. Our analysis is primarily based on dental characters inasmuch as several fossil taxa (especially zegdoumyids) are known only by isolated teeth. We mainly employed the dental characters listed in Marivaux *et al.* (2004a, 2005), but added and reinterpreted several dental characters and character states as a means to describe better the variety of dental morphologies observed among zegdoumyids, anomaluroids and other stem groups. All the selected characters are equally weighted. Multistate characters were considered as ordered if changes from one state to another required passing through intermediate states (Slowinski 1993). With such

an *ad hoc* assumption, character state assignments do not convey a priori judgments about character polarity (unconstrained parsimony). In this analysis, we constrained the taxonomic sample by selecting taxa that existed in a time period corresponding to the early Palaeogene radiation of rodents (during which zegdoumyids emerged), and that are included within the ‘Ischyromyiformes’ clade (*sensu* Marivaux *et al.* 2004a). This sample includes members of the Ischyromyidae (*Acritoparamys*, *Reithoparamys*), Sciuravidae (*Knightomys*, *Prolapsus*, *Pauromys*), Sciuridae (*Paleosciurus*), Aplodontidae (*Prosciurus*), Gliridae (*Eoglivivus*, *Glamys*, *Bransatoglis*), Theridomorpha (*Pantrogna*, *Hartenbergeromys*, *Protadelomys*), Cricetidae (*Pappocricetodon*, *Atavocricetodon*), Dipodidae (*Plesiosminthus*, *Aksyromys*) and Zelomyidae (*Andersomys*). All anomaluroid taxa known in the Palaeogene of Africa (*Nementchamys lavocati*, *Kabirmys qarunensis*, *Shazurus minutus*; Jaeger *et al.* 1985; Sallam *et al.* 2010a, b) and South Asia (*Pondaungimys anomaluropsis*; Dawson *et al.* 2003; Marivaux *et al.* 2005), as well as those known in the Miocene of Africa (*Paranomalurus walkeri*, *P. bishopi*, *P. soniae*; Lavocat 1973) and at the present day (*Anomalurus peli*, *A. derbianus*, *A. beecrofti* (*Anomalurops beecrofti*), *Idiurus macrotis*, and *Zenkerella insignis*) were scored for investigating the nature of the possible Zegdoumyidae–Anomaluridae link. In addition to *Zegdoumys lavocati*, *Glibia pentalopha* and *Lazibemys zegdouensis* gen. et sp. nov., we have included *Glibemys algeriensis* from Zegdou (Vianey-Liaud *et al.* 1994), which is known from only one tooth. The living *Pedetes capensis* was also added at a later stage for assessing the Anomaluromorpha clade and the critical issue of whether the common ancestor of Anomaluridae and Pedetidae might trace back in Africa to a zegdoumyid-like form. Characters were polarized via the out-group comparison method (Watrous & Wheeler 1981), using stem Rodentia and basal members of the Ctenohystrica (*sensu* Marivaux *et al.* 2004a) (*Tribosphenomys*, *Archetypomys*, *Cocomys* and *Birbalomys*). The final data matrix includes 150 characters and 42 taxa. The description of characters (character states) and the data matrix are provided in Appendices 1 and 2, respectively.

The data matrix was managed using NDE (Nexus Data Editor v. 0.5.0; Page 2001) and Mesquite (v.2.72; Maddison & Maddison 2009), and phylogenetic reconstruction was performed with PAUP\* v.4.0 beta 10 Win (Swofford 2002). As the dataset of the matrix contained too many taxa to execute an exact search, a Heuristic search using random step-wise addition (1000 replications with randomized input order of taxa) and tree-bisection-reconnection (TBR) branch swapping options was undertaken. Clade robustness was measured by the Bremer Index (Bremer 1988) and the Bootstrap percentages (BP) in equally weighted maximum-parsimony (after 1000 iterations comprising two replications with randomized input order of taxa).

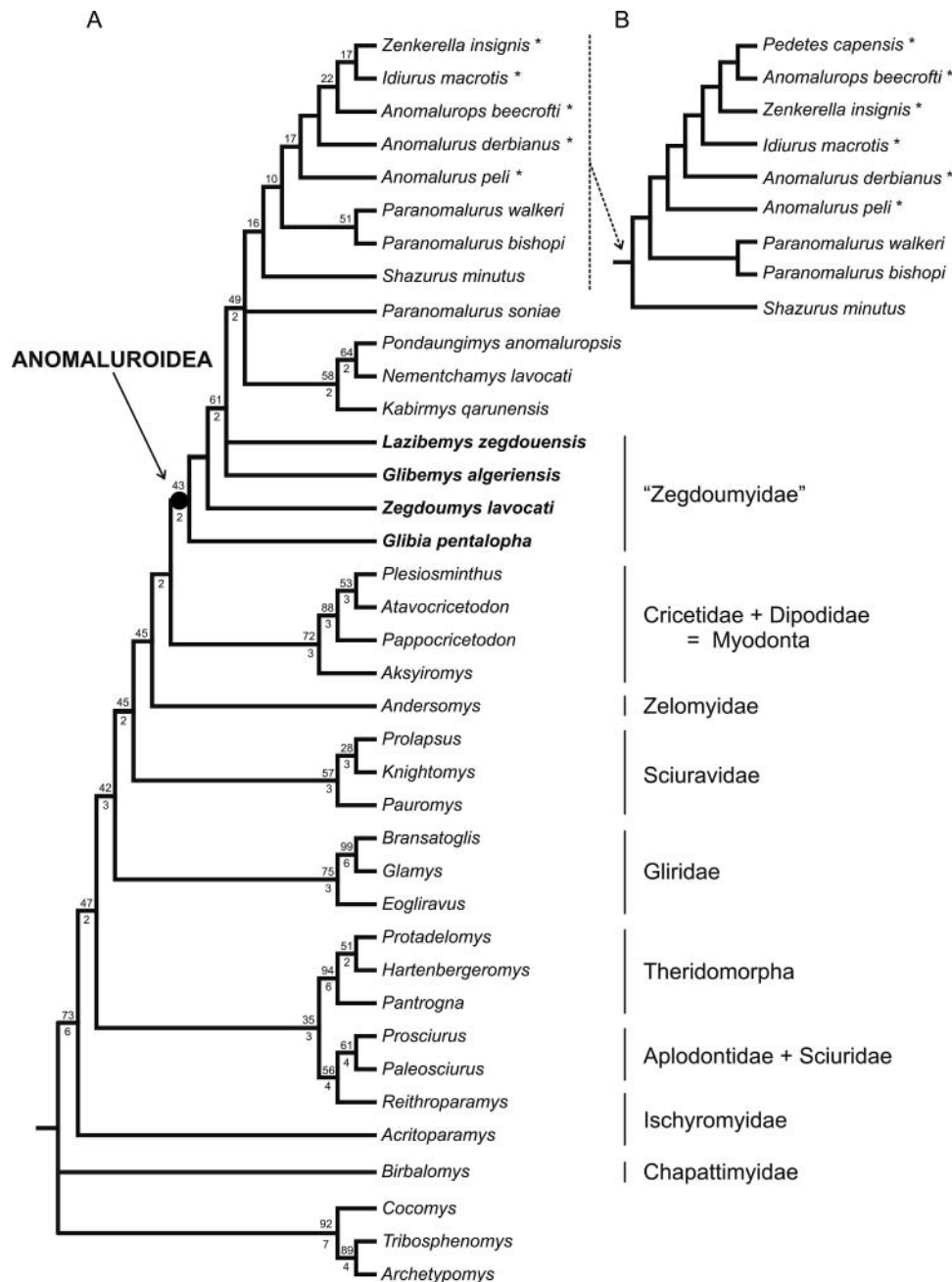
## Results and discussion

### Phylogenetic results and dental character discussion

**The phylogenetic position of the Zegdoumyidae.** Heuristic searches performed on our dataset yielded six equally most parsimonious trees. Each tree has a total length of 848 steps; consistency index (CI) = 0.29, retention index (RI) = 0.64. The alternative topologies generated mainly reflect inadequate resolution of species that are poorly sampled, such as *Lazibemys zegdouensis* gen. et sp. nov., which is documented by three teeth, and *Glibemys algeriensis*, which is known from only one tooth. Alternative topologies also occur regarding the phylogenetic position of the Miocene *Paranomalous soniae*, which is set apart from the other Miocene species of the genus (*P. walkeri* and *P. bishopi*), and is more closely related to the Late Eocene anomaluroid forms. A strict consensus tree (Fig. 6A) has been transposed onto a chronostratigraphical context (Fig. 7) as a means of assessing the ghost lineages implied by this branching pattern. These phylogenetic results, based on dental characters, point towards the monophyly of a large clade that embraces all zegdoumyid taxa (*Zegdoumys*, *Glibia*, *Lazibemys*, and *Glibemys*), the Palaeogene (*Pondaungimys*, *Nementchamys*, *Kabirmys*, and *Shazurus*) and Neogene (*Paranomalous*) anomaluroid taxa, and the crown Anomaluridae (*Anomalurus*, *Anomalurops*, *Idiurus*, and *Zenkerella*). Such a topology clearly sets the Zegdoumyidae apart from the Gliridae and/or the Sciuravidae, but supports the idea of a phylogenetic link between the Zegdoumyidae and the Anomaluridae. Assuming this large clade to be the Anomaluroidea clade (the black solid circle labelled on the strict consensus tree; Fig. 6A), zegdoumyids appear here as the earliest offshoots of this clade. Zegdoumyid taxa exhibit a variety of dental morphologies, which have different but phylogenetically significant degrees of similarity to subsequent anomaluroids. This is shown especially in the development of early stages of pentalphodonty (i.e. development of the anterior arm of the hypocone associated with the development of a third central loph on upper molars (short mesolophule + short mesoloph, especially on *Glibia*); development of a low anterolophid, a nearly complete hypolophid and a short mesolophid on lower molars (especially in *Glibia*); some development of buccal and lingual walls on upper teeth (i.e. development of a large mesostyle and short neo-endoloph (strong and complete in *Lazibemys*)) and a lingual wall on lower teeth (i.e. development of the posterior arm of the metaconid); and multiplication of accessory enamel wrinkles (especially in *Lazibemys* and to a lesser extent in *Glibia*). Therefore, despite the major morphological and temporal (nearly the entire Middle Eocene; Fig. 7) gaps separating zegdoumyids from the first true anomaluroids formerly recognized as such (*Nementchamys*, *Pondaungimys*, *Kabirmys*, and *Shazurus*),

these early African rodents can now be viewed, ‘*faute de mieux*’, as stem Anomaluroidea. There is, however, no support for the monophyly of the family Zegdoumyidae inasmuch as zegdoumyid taxa do not form a clade but appear pectinately arranged at the base of the Anomaluroidea clade (Fig. 6A). From a phylogenetic systematic point of view, given the apparent paraphyly of the Zegdoumyidae, *Zegdoumys*, *Glibia*, *Glibemys* and *Lazibemys* should be considered here as Anomaluroidea *incertae sedis*. However, the basal branching pattern of the Anomaluroidea clade relies on limited morphological evidence, especially for some taxa. For this reason, here we will keep the name ‘Zegdoumyidae’ for this paraphyletic basal taxon pending further fossil data substantiating its monophyly.

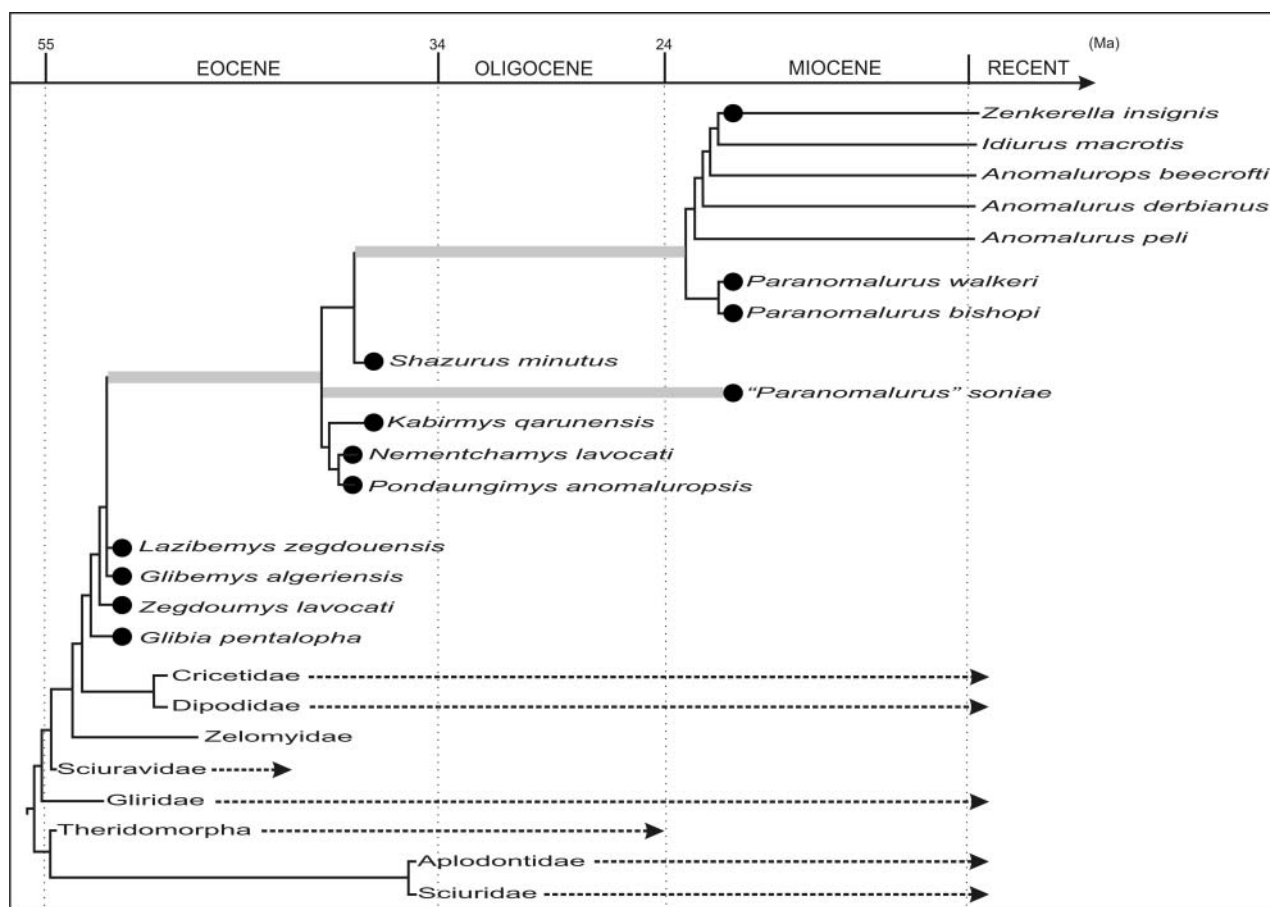
**The phylogenetic position of the Late Eocene anomaluroids.** Subsequent nodes within the Anomaluroidea clade highlight the relationships among and between Palaeogene and Neogene anomaluroids and extant anomalurids. Interesting is the position of most of the latest Middle and earliest Late Eocene anomaluroids (*Pondaungimys*, *Nementchamys*, *Kabirmys*), which form a clade that is sister to all other extinct and extant anomalurids (other than the ‘zegdoumyids’). These Late Eocene taxa (except *Shazurus*) appear to be evolutionarily intermediate in dental morphology (Fig. 8A–F) between the Early–Middle Eocene ‘zegdoumyids’ and the Early Miocene anomalurids (Fig. 8I–L). This is particularly shown in the degree of development of the transverse and longitudinal crests and crestids, which are generally longer, thicker and higher than in ‘zegdoumyid’ teeth. In addition, the trigonids (vestigial) and talonids of lower teeth are at the same elevation, while the trigonids (vestigial) are slightly more elevated in ‘zegdoumyids’. Upper and lower teeth in these taxa are fully pentalphodont, with lower molars having long and complete anterolophid, metalophid II, mesolophid, hypolophid and posterolophid, and upper molars showing long and complete anteroloph, protoloph, mesolophule–mesoloph complex, metaloph and posteroloph (Fig. 8A–F). Lower molars also develop a strong and complete ectolophid (absent or short in ‘zegdoumyids’), which links the hypolophid to the protoconid, and isolates a deep external sinusid. The lingual margin of the lower teeth bears a strong mesostylid, which is generally connected (or not, e.g. *Kabirmys*; Fig. 8F) to a long and elevated posterior arm of the metaconid, thereby closing the talonid basin lingually. There is no more trace of hypoconulid on the posterolophid. These Late Eocene anomaluroids also appear to be advanced compared to ‘zegdoumyids’ in several characters of the upper dentition. The structure of their upper molars is basically similar to that observed in ‘zegdoumyids’, but it differs substantially in showing several much more pronounced features. This is particularly true for the anterior and posterior cingula, which become much stronger



**Figure 6.** Assessment of the phylogenetic position of the Zegdomyidae in a high-level rodent phylogeny. **A**, strict consensus of six equally most-parsimonious trees of 848 steps each (consistency index, CI = 0.29; retention index, RI = 0.64), showing the position of the zegdomyid taxa at the base of the Anomaluroidea clade. Bremer (B) and Bootstrap (BP) values are indicated by the numbers labelled under and above internal branches, respectively (B > 1; BP > 5). **B**, strict consensus of six equally most-parsimonious trees of 867 steps each (CI = 0.29; RI = 0.64), generated from the same dataset as A, but with the addition of *Pedetes capensis*. Given that the branching pattern of the stem groups in the cladogram B is strictly similar to that of the cladogram A, we have only reproduced the branching pattern of the crown groups of the cladogram B, showing the position of *Pedetes*. In both cladograms, extant species are labelled by an asterisk. Description of characters and the data matrix are in Appendices 1 and 2, respectively.

and elevated (i.e. anteroloph and posteroloph), connecting both the buccal and lingual cusps (paracone–protocone and metacone–hypocone, respectively). Lingually, the protocone displays a very strong and long posterior outgrowth

(neo-endoloph), which runs toward the hypocone. This outgrowth forms a massive lingual wall that can close the internal sinus entirely (*Pondaungimys* and *Nementchamys*) or nearly entirely (*Kabirmys*) (Fig. 8).



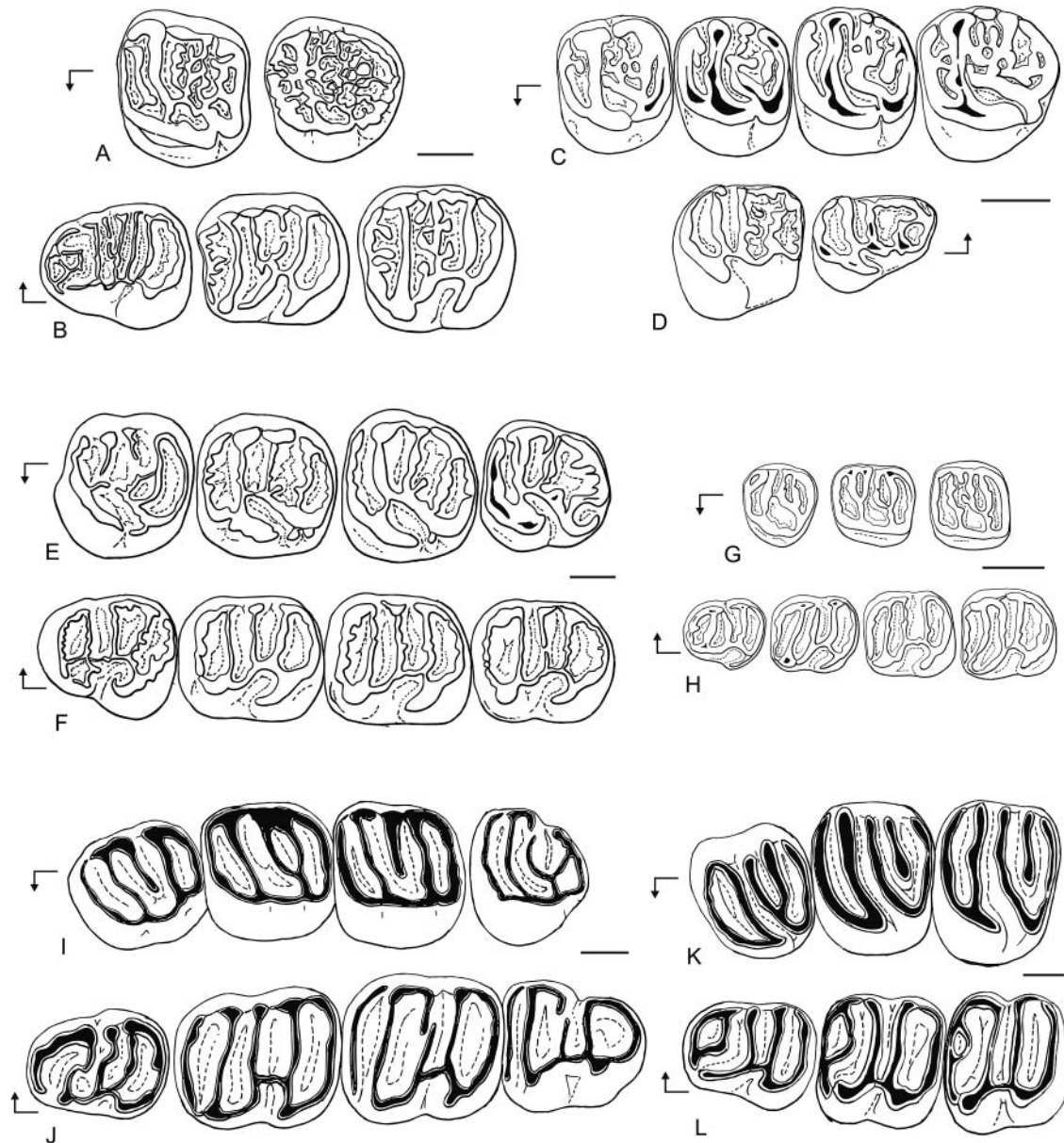
**Figure 7.** Strict consensus tree of six equally most-parsimonious trees (Fig. 6A) transposed onto a chronostratigraphical context. The black solid circles indicate the stratigraphic occurrence of the fossil taxa. The grey branches indicate the phylogenetically implied ghost lineages within the Anomaluroidea clade. The dotted arrows correspond to the stratigraphic extension of some fossil and extant families sampled for this phylogenetic analysis. The position of the family names indicates the first occurrence of these families.

### The phylogenetic position of *Shazurus* and the Neogene forms.

*Shazurus minutus* from the Late Eocene of Egypt (BQ2, Fayum) has been recently described by Sallam *et al.* (2010a) as a highly derived anomalurid (Fig. 8G, H). This taxon is indeed surprisingly specialized given its age, i.e. showing a dental pattern modified in a direction somewhat similar to that of some Early Miocene species of *Paranomalous* (especially *P. bishopi* and *P. walkeri*; Lavocat 1973) (Fig. 8I–L), or even to extant species of *Anomalurus* (*A. peli*, *A. derbianus*, *A. pusillus*) (Fig. 9A, B). As such, *Shazurus* is radically distinct from *Kabirmys* found in the same Fayum locality (BQ2; Sallam *et al.* 2010b), or from the roughly coeval *Nementchamys* and *Pondaungimys* (Fig. 8). With such an advanced degree of dental specialization, *Shazurus* appears more apically positioned in our phylogeny of Anomaluroidea as a result, and nested within Miocene Anomaluridae (Fig. 6A). Accordingly, this phylogenetic position makes the Miocene genus *Paranomalous* polyphyletic. The two species *P. walkeri* and *P. bishopi* form a clade (*Paranomalous* Clade (PC)), which is

the sister group to crown Anomaluridae (Crown Clade (CC)). *P. soniae* is set apart (Fig. 6A), appearing with *Shazurus* at the base of the clade PC + CC, or in some alternative topology (3/6), more closely related to the Late Eocene anomaluroid taxa (*Kabirmys*, *Nementchamys* and *Pondaungimys*). As for *P. walkeri* and *P. bishopi*, the upper and lower teeth of *P. soniae* display a pentalophodont pattern that is fully developed, with thick and elevated transverse crests, which underscores the advanced condition of their dental pattern compared to that of Palaeogene forms (i.e. *Kabirmys*, *Nementchamys*, *Pondaungimys* and ‘zegdoumyids’, except *Shazurus*). *P. walkeri* and *P. bishopi* are generally considered to be Miocene Anomaluridae of modern aspect (Fig. 8I–L), inasmuch as their dental pattern (as for *Shazurus*) is specialized in a direction comparable to that of extant species of *Anomalurus*. *Paranomalous soniae* (Fig. 8K, L) lacks some of these advanced dental specializations (e.g. upper teeth not square shaped (hypocone still slightly buccal to the protocone on M1-2), absence of strong development of lingual and buccal

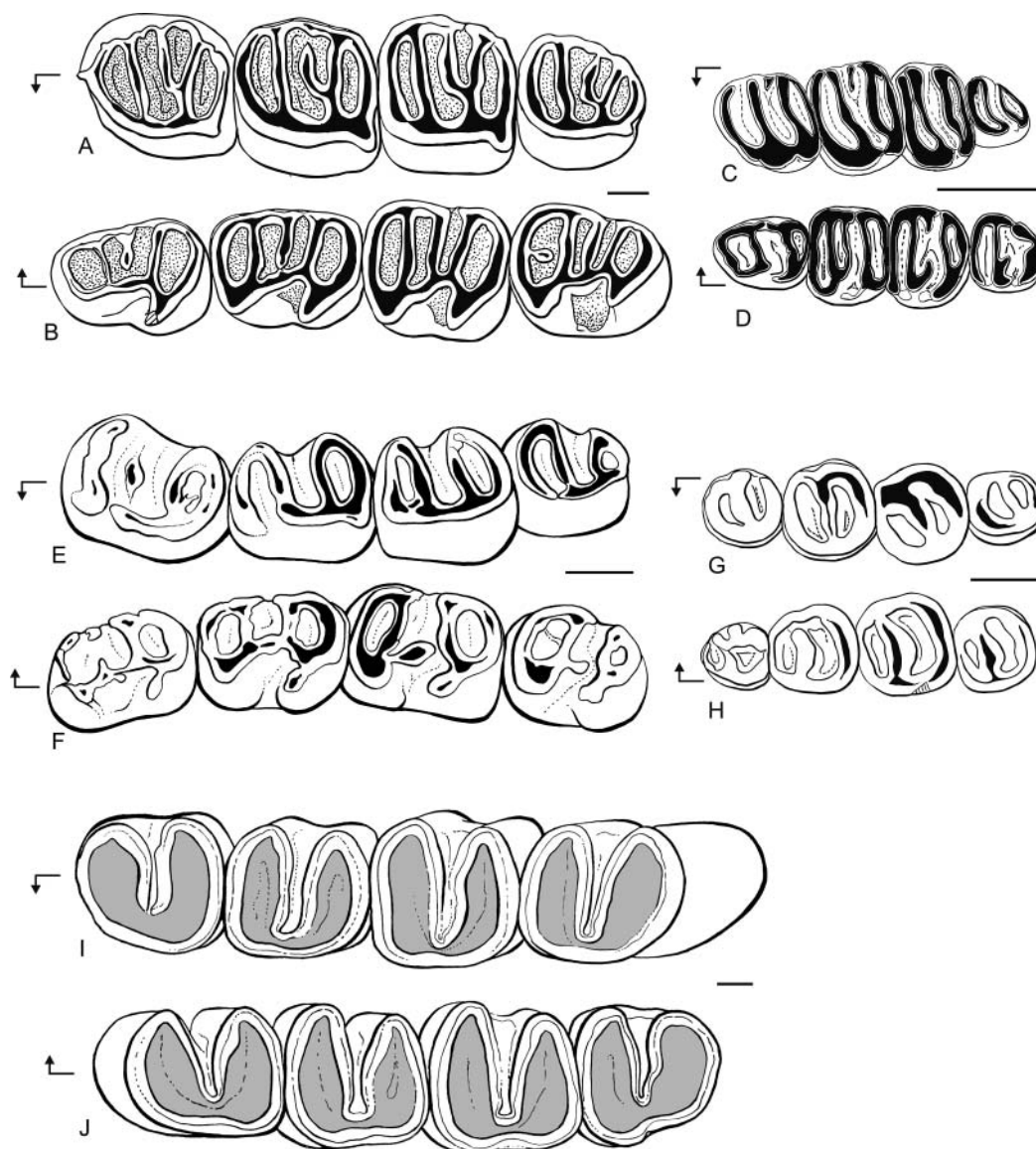




**Figure 8.** Upper and lower dentitions of extinct Anomaluroidea. **A, B**, *Nementchamys lavocati*, M2-3 (**A**, UON 84-30 and UON 84-29) and p4-m2 (**B**, UON 84-26, UON 84-25 (reversed) and UON 84-27). **C, D**, *Pondaungimys anomaluropsis*, P4-M3 (**C**, Pkg 157) and p4-m1 (**D**, Spg 14); **E, F**, *Kabirmys qarunensis*, P4-M3 (**E**, DPC 21294E (reversed), DPC 21488F, DPC 22442J and DPC 21488G) and p4-m3 (**F**, DPC 21839B, DPC 21221C, DPC 21221D and DPC 23305E); **G, H**, *Shazurus minutus*, P4-M2 (**G**, DPC 23305B, CGM 83701 and DPC 21221A (reversed)) and p4-m3 (**H**, DPC 23305A, DPC 21488B, DPC 21296A (reversed) and DPC 21358A); **I, J**, *Paranomalous bishopi*, P4-M3 (**I**, UMP 7060 (reversed)) and p4-m3 (**J**: KNM SO 744); **K, L**, *Paranomalous soniae*, P4-M2 (**K**, KNM SO 788) and p4-m2 (**L**, KNM RU 2338 (reversed)). Scale bars: 1 mm. Arrows in front of the premolars indicate the orientation of the tooth rows (mesiolingual). Original drawings by Monique Vianey-Liaud and Laurent Marivaux.

walls on upper molars (i.e. strong but incomplete neo-endoloph; smaller mesostyle; weak development of the posterior and anterior arms of the paracone and metacone, respectively; anteroloph and posteroloph not connected to the paracone and metacone, respectively), and deep internal sinus remaining transversally open), and as such appears divergent from the two other species of the genus. In fact,

*P. soniae* exhibits a mosaic of derived (shared with the other *Paranomalous* species) and primitive (shared with *Kabirmys*, *Nementchamys* and *Pondaungimys*) dental characters that convey to this taxon an intermediary evolutionary stage. Given the position of *P. soniae* in our phylogenetic tree (Fig. 6A), which reflects its peculiar dental pattern, this species could be referred to a new genus.



**Figure 9.** Upper and lower dentitions of modern anomalurids and pedetids. **A, B**, *Anomalurus peli* (MNHN 1984-1160), P4-M3 (A) and p4-m3 (B); **C, D**, *Idiurus macrotis* (MNHN 1985-220), P4-M3 (C) and p4-m3 (D); **E, F**, *Anomalurops beecrofti* (MNHN 1886-85), P4-M3 (E) and p4-m3 (F); **G, H**, *Zenkerella insignis* (MNHN 1970-112), P4-M3 (G) and p4-m3 (H); **I, J**, *Pedetes capensis* (UMC-V820). Scale bars: 1 mm. The arrows situated in front of the premolars indicate the orientation of the tooth rows (mesiolingual). Original drawings by Monique Vianey-Liaud (A–D, G, H) and Laurence Meslin (E, F, I, J).

### The problem of the Pedetidae

**The phylogenetic position of *Pedetes*.** Heuristic searches performed on our matrix including *Pedetes capensis* yielded again six most parsimonious trees. Each tree has a total length of 867 steps; consistency index (CI) = 0.29, retention index (RI) = 0.64. A strict consensus tree is presented in Figure 6B. The structure of this cladogram is basically similar to the previous one, except within the crown group Anomaluridae. *Pedetes capensis* is, indeed, nested within the Anomaluridae clade, appearing as a terminal taxon, which is the sister group of *Anomalurops*.

Considering *Pedetes* as the sole extant representative of the distinct family Pedetidae, its position within the crown Anomaluroidae makes here the family Anomaluridae paraphyletic. A body of molecular and morphological evidence quite confidently supports close relationships between *Anomalurus* and *Pedetes* (e.g. Tullberg 1899; Bugge 1974, 1985; Meng 1990; Huchon *et al.* 2007; Montgelard *et al.* 2008; Blanga-Kanfi *et al.* 2009; Ruf *et al.* 2009; Churakov *et al.* 2010). Accordingly, Pedetidae is regarded as the sister group of Anomaluridae (Anomaluromorpha), but not as a group nested within the Anomaluridae as we

found here. *Pedetes* exhibits a highly specialized dental pattern, being considerably simplified (Fig. 9I, J). Upper and lower teeth are high-crowned, and their occlusal structure is rapidly erased by natural wear, giving rise to a simple bilobed pattern, for which it remains difficult to identify homologous structures with other taxa (e.g. Wood 1965; Lavocat & Michaux 1966). In *Pedetes*, the two transverse lobes of the upper teeth are linked lingually by a longitudinal crest, which forms a lingual wall (there is no internal sinus; Fig. 9I). Is such a lingual crested structure homologous to the long neo-endoloph characterizing most of anomaluroids?

The lower molars of *Pedetes* (Fig. 9J) also have a longitudinal crest, which links the two transverse lobes buccally (there is no external sinusid), but not lingually as it does in some anomaluroids. The upper dentition of *Anomalurops* (Fig. 9E) is strikingly reminiscent of that of *Pedetes* in showing a pattern somewhat bilobed. In the upper teeth of this taxon, the mesial lobe is formed by the double buccolingual connection of the anteroloph with the protoloph, and the distal lobe, by the double buccolingual connection of the metaloph with the posteroloph. The two lobes are lingually linked by a strong neo-endoloph, which connects the protocone to the hypocone (internal sinus closed lingually). In contrast, the lobes are widely separated buccally. There are neither mesostyle nor posterior and anterior arms of paracone and metacone, respectively (there is no buccal wall). This buccal condition in upper teeth of *Anomalurops* is even unusual among anomaluroids, but matches that observed in upper teeth of *Pedetes*. Are these apparent similar dental structures (on upper teeth) between *Anomalurops* and *Pedetes* the result of a possible recent common ancestry?

Unfortunately, the evolutionary history of Pedetidae in Africa is poorly documented. The first occurrence of the group dates only from the Early Miocene with the genus *Megapedetes*, a taxon which already exhibited an advanced stage of the bilobed dental pattern (Lavocat 1973). Molecular data would suggest a very ancient divergence between anomalurids and pedetids, dating back to the earliest Eocene (Huchon *et al.* 2007) or even earlier (Montgelard *et al.* 2008), although there is no trace of rodent in Africa before the late Early Eocene. Therefore, the close phylogenetic relationship between *Pedetes* and *Anomalurops* revealed by our analysis is probably incorrect and is likely to be due to a high degree of a global dental resemblance that was achieved by convergence. In fact pedetids and anomalurids show many distinctive cranial features, especially regarding the morphology of their zygomatic region (e.g. Hautier *et al.* 2008). Even if both families show a hystricomorphous condition, they differ substantially from each other in the origin of the masseteric musculature and in the morphology of the infraorbital foramen. In *Pedetes*, the medial masseter spreads far anteriorly from the medial side of the zygomatic arch through a greatly enlarged infraorbital foramen onto

the whole lateral surface of the rostrum (Offermans & de Vree 1989). The condition found in anomalurids is clearly distinct, by associating a low development of the infraorbital part of the medial masseter to a small foramen (Tullberg 1899; Hautier *et al.* 2008). Given that both groups were already extremely specialized by the Early Miocene, an ancient anomalurid–pedetid split seems more conceivable. Considering the sister group relationship between Anomaluridae and Pedetidae, the presence of stem anomaluroids in Africa as early as the late Early Eocene (i.e. ‘zegdoumyids’) would suggest the existence of stem pedetids at the same time.

**‘Zegdomyidae’ and Pedetidae.** The question as to whether the common ancestor of Anomaluridae and Pedetidae might trace back to a zegdomyid-like form, as suggested by Sallam *et al.* (2010b), is interesting but receives no answer from the new ‘zegdoumyid’ dental material we describe here. If Anomaluridae and ‘Zegdomyidae’ are closely related, a potential relationship between Pedetidae and ‘Zegdomyidae’ is far from obvious. Furthermore, this phylogenetic affiliation would be inconsistent with the evolutionary pattern of the incisor enamel microstructure. ‘Zegdomyids’ as well as other early anomaluroids (such as *Nementchamys* and *Pondaungimys*) display incisor enamel with transitional pauci- to uniserial Schmelzmuster (Martin 1993; Marivaux *et al.* 2005; this paper). Such a transitional condition represents an early and primitive stage of microstructural complexity toward the more derived uniserial condition, which characterizes extant anomalurids (Martin 1993, 1995) as well as several other extant groups of rodents, notably those included among the ‘mouse-related clade’ and the ‘squirrel-related clade’ (e.g. Huchon *et al.* 2007; Blanga-Kanfi *et al.* 2009), or the ‘Ischyromyiformes’ (*sensu* Marivaux *et al.* 2004a). In contrast, Miocene (*Megapedetes*) and extant (*Pedetes*) pedetids exhibit a highly divergent incisor enamel microstructure, which is characterized by a Schmelzmuster with a multiserial condition (Martin 1995). This derived condition of the Schmelzmuster is exclusively found in extinct and extant Ctenodactylidae (Martin 1992, 1995), Diatomyidae (Martin 1995; Marivaux *et al.* 2004b; Dawson *et al.* 2006) and hystricognathous rodents (Martin 1992, 1994; Marivaux *et al.* 2004a), which make up the Ctenohystrica clade (Huchon *et al.* 2000, 2007; Marivaux *et al.* 2004a). From the ‘zegdoumyid’ incisors analysed here, no Schmelzmuster transitional from the pauciserial to the multiserial condition has been observed. For all these reasons (dental and microstructural), it seems quite unlikely that the origin of pedetids can be traced back to a zegdomyid-like form.

In the absence of a comprehensive fossil record documenting the pedetid lineage during the Palaeogene, the origin of this family will remain a matter of speculation. Why do two closely related extant families (Anomaluridae – Pedetidae) display two highly divergent incisor enamel

microstructures (uniseriate versus multiseriate), which represent different pathways of evolution? This interesting and critical question remains open. Pedetids exhibit a masseteric configuration very close to that found in the Ctenohystrica, which are characterized by a greatly enlarged anterior part (i.e. *pars infraorbitalis*) of the masseter muscle extending through a wide infraorbital foramen (Offermans & de Vree 1989). The striking convergent evolution of enamel microstructure between the Pedetidae and the Ctenohystrica could also be due to similar biomechanical requirements of higher stress and wear resistance (Martin 1999).

### Macroevolutionary and palaeobiogeographical implications

Our phylogenetic results clearly show that 'zegdoumyids' are basal members of the Anomaluroidea clade. This phylogenetic assumption underscores, therefore, the great antiquity of the Anomaluroidea clade in Africa, as expected given the high morphological disparity of the Late Eocene African forms (i.e. *Kabirmys* versus *Shazurus*; Sallam *et al.* 2010a, b). The fossil record of Anomaluroidea in Africa is still remarkably poor, notably regarding the Middle Eocene, Oligocene and Neogene. The few localities from Algeria (Bir El Ater and Gour Lazib; Jaeger *et al.* 1985; Vianey-Liaud *et al.* 1994; this paper), Egypt (Birket Qarun-Fayum; Sallam *et al.* 2010a, b), Namibia (Sperrgebiet; Pickford *et al.* 2008), Kenya (Rusinga and Songhor; Lavocat 1973) and Uganda (Napak; Lavocat 1973) provide only scattered snapshots regarding the evolutionary history of this fascinating rodent group. We lack a good idea about both the palaeodiversity and palaeoecology of anomaluroids, but the few fossil species available (only about 13) through the Tertiary and the extant forms demonstrate that this group was successful. From the morphology of a proximal extremity of an ulna (KNM SO 806 from Songhor, Kenya), which shows functional attributes comparable to those observed in modern gliding anomalurids (Lavocat 1973), we can be sure that a least one of the Early Miocene anomaluroid species already exhibited a gliding locomotion. But, when and how did they achieve this peculiar gliding adaptation? And, why does a living *Zenkerella* not glide? In the absence of a comprehensive cranial and postcranial bone record documenting Palaeogene forms, these interesting questions remain open.

Compared to some other modern rodent groups with a similar antiquity (e.g. muroids, hystricognaths, etc.), living anomalurids are poorly diversified (only seven species) and limited to tropical to subtropical forests of western and central Africa (e.g. Dieterlen 1993; Julliot *et al.* 1998; Dial 2003). However, from a historical biogeographical point of view, judging from the location of some fossil species, it is clear that the modern geographical restriction of the group is a relict distribution. The Palaeogene anomaluroid record reveals that the group had a much more widespread distri-

bution, which extended from Africa (northern and southern latitudes) into tropical South Asia. The presence of anomaluroids outside Africa was recently demonstrated with the discovery of *Pondaungimys anomaluroopsis* from the late Middle Eocene Pondaung Formation of Myanmar (Dawson *et al.* 2003; Marivaux *et al.* 2005). Some other anomaluroids are listed as a component of South Asian Palaeogene faunas (e.g. Chaimanee *et al.* 1997; Marivaux 2000; Marivaux & Welcomme 2003), but are not yet published (i.e. Krabi, Thailand (latest Eocene); Bugti Hills, Pakistan (Early Oligocene); Marivaux, unpublished).

The occurrence of closely related anomaluroids in Africa and South Asia during the Palaeogene (*Nementchamys* and *Pondaungimys*) has been regarded as another indication of faunal exchanges between both landmasses in the Middle to Late Eocene (Dawson *et al.* 2003; Marivaux *et al.* 2005). For the two past decades, the existence of palaeobiogeographical links between Asia and the Afro-Arabian landmass during the Palaeogene has been documented among other rodents (hystricognathous), primates (anthropoids), artiodactyls (anthracotheres), and proboscideans (e.g. Ducrocq 1995, 1997, 2001; Chaimanee *et al.* 1997; Antoine *et al.* 2003; Dawson *et al.* 2003; Marivaux *et al.* 2000, 2002, 2005; Tabuce & Marivaux 2005; Gheerbrant & Rage 2006; Sallam *et al.* 2009; Jaeger *et al.* 2010). Most of these aforementioned mammalian groups (except proboscideans; see Antoine *et al.* 2003) are interpreted as having invaded Afro-Arabia from Asia, although the mode, the precise timing, and the pathways by which dispersals occurred remain unknown. For anomaluroid rodents, the demonstration that 'zegdoumyids' are basal members of this group gives emphasis to the role of Africa as the ancestral homeland of the Anomaluroidea clade. Therefore Palaeogene anomaluroids from South Asia (*Pondaungimys*) have an African origin, indicating that the group migrated to Asia from Afro-Arabia.

Finally, from a high-level phylogenetic perspective, the source of the 'Zegdoumyidae' remains unclear inasmuch as there is no well-identified sister group among early Palaeogene rodents. 'Zegdoumyids' seem to share a common ancestry with both stem Myodonta, Asian Zelomyidae and North American Sciuravidae (Fig. 6A). Given the high degree of dental specialization of 'zegdoumyids', we cannot exclude the possibility that 'zegdoumyids' are rooted in a more primitive, yet unknown, African rodent lineage older than the Early-Middle Eocene. Only the discovery of pre-zegdoumyid forms in Africa will provide new insights into the high-level phylogenetic and geographic origins of this early African rodent group.

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## Online supplementary material

### Appendix 1

List of morphological characters and character states employed in the phylogenetic analyses.

Characters followed by an asterisk are considered ‘ordered’.

### Appendix 2

Matrix of the 150 morphological characters used in the phylogenetic analyses. Characters were coded ‘0’, ‘1’, ‘2’, ‘3’ or ‘4’ (polymorph character states: 0 + 1, 1 + 2, 2 + 3...; uncertain character states: 0/1, 1/2, 2/3...); missing data were coded ‘?’; non-applicable character states were coded ‘-’.

**Annexe n°4**

# Early Tertiary mammals from North Africa reinforce the molecular Afrotheria clade

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The phylogenetic pattern and timing of the radiation of mammals, especially the geographical origins of major crown clades, are areas of controversy among molecular biologists, morphologists and palaeontologists. Molecular phylogeneticists have identified an Afrotheria clade, which includes several taxa as different as tenrecs (Tenrecidae), golden moles (Chrysochloridae), elephant-shrews (Macroscelididae), aardvarks (Tubulidentata) and paenungulates (elephants, sea cows and hyracoids). Molecular data also suggest a Cretaceous African origin for Afrotheria within Placentalia followed by a long period of endemic evolution on the Afro-Arabian continent after the mid-Cretaceous Gondwanan breakup (approx. 105–25 Myr ago). However, there was no morphological support for such a natural grouping so far. Here, we report new dental and postcranial evidence of Eocene stem hyrax and macroscelidid from North Africa that, for the first time, provides a congruent phylogenetic view with the molecular Afrotheria clade. These new fossils imply, however, substantial changes regarding the historical biogeography of afrotheres. Their long period of isolation in Africa, as assumed by molecular inferences, is now to be reconsidered inasmuch as Eocene paenungulates and elephant-shrews are here found to be related to some Early Tertiary Euramerican 'hyposodontid condylarths' (archaic hoofed mammals). As a result, stem members of afrotherian clades are not strictly African but also include some Early Paleogene Holarctic mammals.

**Keywords:** molecules versus fossils; Afrotheria; Africa; Eocene; hyrax; elephant shrew

## 1. INTRODUCTION

Recent molecular analyses have proposed well-resolved higher level phylogenies for living eutherian mammals in recognizing four superordinal clades: Laurasiatheria (shrews, moles, hedgehogs, bats, cetaceans, even- and odd-toed ungulates, carnivorans and pangolins), Euarchontoglires (rodents, rabbits, primates, flying lemurs and tree shrews), Xenarthra (anteaters, sloths and armadillos) and Afrotheria, which includes tenrecs (Tenrecidae), golden moles (Chrysochloridae), elephant-shrews (Macroscelididae), aardvarks (Tubulidentata) and elephants, sea cows and hyraxes (Paenungulata; Murphy *et al.* 2001a,b; Springer *et al.* 2003, 2004). For Afrotheria, there is a broad molecular consensus for its monophyly deriving from various nuclear and mitochondrial genes as well as from rare genomic changes that constitute probable

synapomorphies (Madsen *et al.* 2001). In contrast, morphological data have until now failed to provide strong support for Afrotheria (Shoshani & McKenna 1998; Archibald 2003; Robinson & Seiffert 2004; Zack *et al.* 2005). In the absence of a comprehensive fossil record for stem members of crown Afrotheria, most high-level phylogenetic analyses have been based primarily on the morphology of extant afrotheres (Asher *et al.* 2003). However, modern afrotheres seem inadequate for reconstructing morphological phylogenies because their long period of endemism in Africa favoured the emergence of morphological convergences with laurasiatherian mammals due to similar selection pressures. Stem members of Afrotheria are thus highly critical for resolution of this phylogenetic issue because they exhibit morphological patterns that have not been overwritten by subsequent evolution and further specializations.

Intensive palaeontological work in Early to Middle Eocene North African localities in Algeria (Gour Lazib) and Tunisia (Chambi) have led to the recovery of several new fossils of mammals. Based on biostratigraphic studies,

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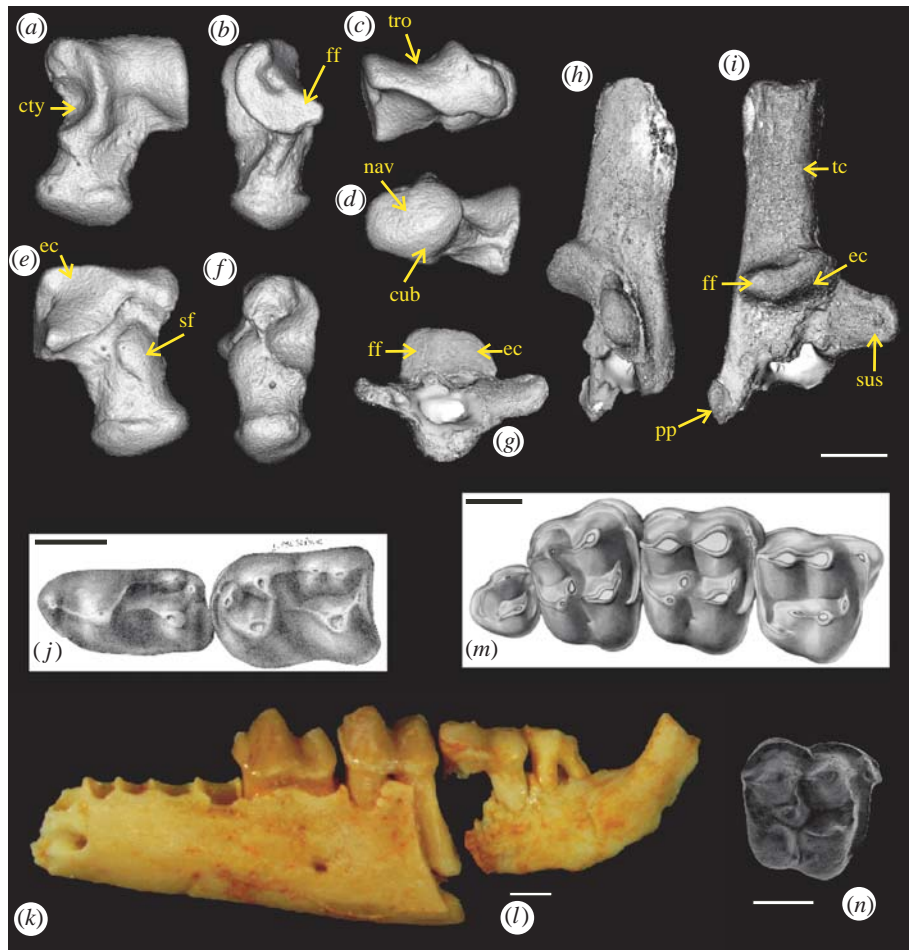


Figure 1. Stem macroselid *Chambius kasserinensis*, early Eocene, Chambi, Tunisia. Left astragalus UM/CB77 in (a) dorsal, (b) lateral, (c) proximal, (d) distal, (e) plantar and (f) medial views; these three-dimensional renderings have been generated from microtomographic data obtained on the ID19 beamline of the European Synchrotron Radiation Facility (Grenoble, France). Right calcaneus UM/CB79 in (g) distal, (h) medial and (i) dorsal views. Left dentary UM/CB74 preserving premolar (P)<sub>4</sub>-molar (M)<sub>1</sub> in (j) occlusal and (k) labial views. Left dentary UM/CB74 preserving M<sub>2</sub>-M<sub>3</sub> in (l) labial view. Right upper maxillary holotype UM/CB6 preserving P<sup>4</sup>-M<sup>3</sup> in (m) occlusal view. Right M2 UM/CB71 in (n) occlusal view. Scale bars, 1 mm. ctv, cotylar fossa; cub, cuboid facet; ec, ectal facet; ff, fibular facet; nav, navicular facet; pp, peroneal process; sf, sustentacular facet; sus, sustentaculum; tc, tuber calcanei; tro, astragalular trochlea.

the Gour Lazib formation has been assigned either a late Ypresian or Early Lutetian age (Tabuce *et al.* 2004) and the Chambi locality an Ypresian age (Hartenberger *et al.* 2001). The newly discovered Algerian fossils document rodents, primates (particularly assigned to *Algeripithecus*, the oldest alleged anthropoid), creodonts, chiropterans, insectivores and hyraxes. For the last clade, we have recovered several fragmentary upper and lower jaws as well as tarsal bones of *Microhyrax lavocati* (Sudre 1979; Tabuce *et al.* 2001a), which considerably improves our knowledge of this basal hyrax. From Chambi, we collected additional remains (teeth and tarsal bones) of *Chambius kasserinensis* (Hartenberger 1986), the oldest known and most primitive elephant-shrew, whose postcranial anatomy was so far unknown. These fossils extend back the date of the oldest macroselidean records with associated dental and postcranial remains by *ca* 30–40 Myr.

## 2. RESULTS

### (a) Description and comparisons

*Chambius* is a small mammal with an estimated body weight of 13 g according to the equation of Legendre (1989). Its upper molars appear to be more primitive than those of more recent *Nemantchatherium* (Tabuce *et al.* 2001b) and

*Herodotius* (Simons *et al.* 1991) in having a robust metaconule, a more prominent parastyle and a comparatively more reduced hypocone (figure 1). On the basis of their tooth characters, basal elephant-shrews have been compared with ‘hyposodontid condylarths’, notably with the North American *Haplomyllus* and the European louisianine *Microhyus*, and these studies suggested ‘condylarth’ affinities for basal elephant-shrews. This hypothesis was recently strengthened on tarsal characters shared between *Haplomyllus* (Zack *et al.* 2005), *Microhyus* (Tabuce *et al.* 2006) and extant elephant-shrews. *Chambius* tarsal bones reveal specializations for rapid running and/or jumping terrestrial locomotion. The pulley-shaped and the semi-circular crests of the astragalular trochlea are indicative of lateral stability and dynamic movements (Lewis 1989); the tibio-astragalular motion was certainly limited to flexion–extension. The calcaneus of *Chambius* is long both proximally and distally to subtarsal joints, a morphology also characteristic of cursorial and/or saltatorial mammals (Tabuce *et al.* 2006). The calcaneus bears an ectal facet oriented at nearly 90° to the long axis of the bone. This character, observed in both living elephant-shrews and *Haplomyllus*, constitutes a derived condition within eutherians (Zack *et al.* 2005). *Microhyus* differs in having a

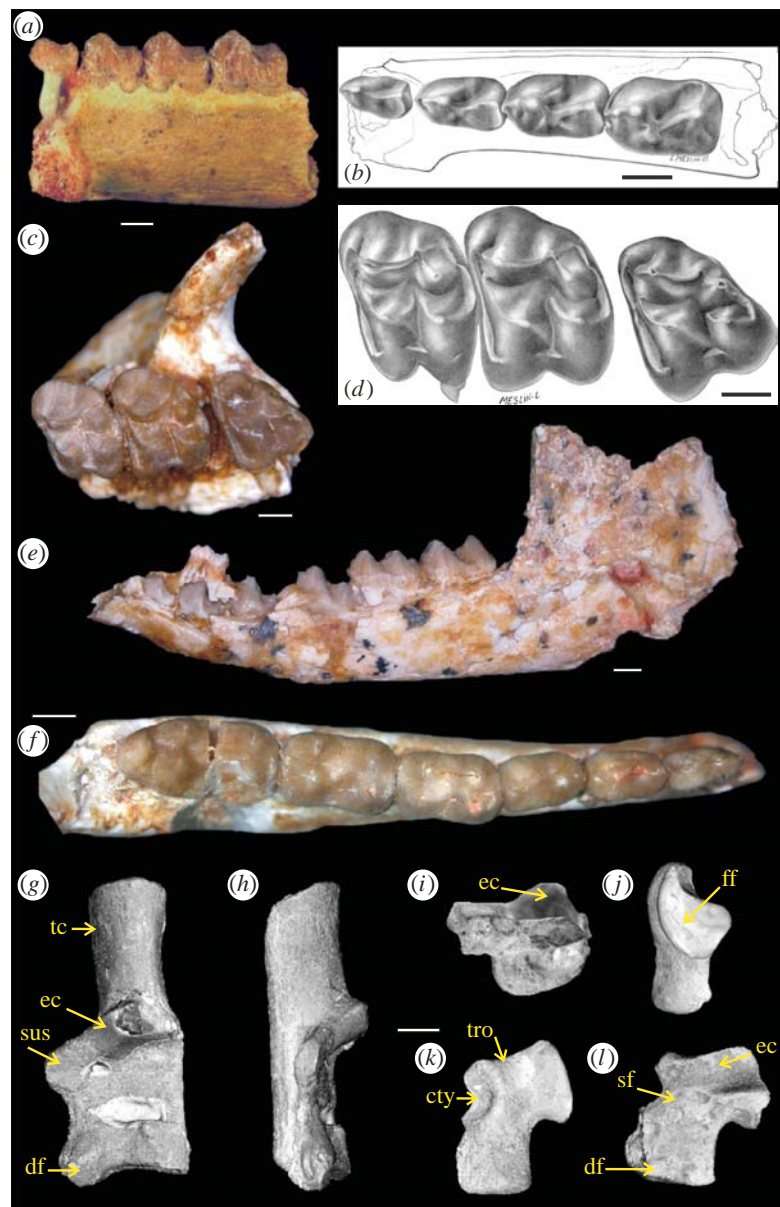


Figure 2. Stem hyrax *Microhyrax lavocati*, early to middle Eocene, Gour Lazib, Algeria. Right dentary UM/HGL04-11 preserving  $P_1$ – $P_4$  in (a) lingual and (b) occlusal views. Left upper maxillary UM/HGL50-101 preserving  $M^1$ – $M^3$  in occlusal views (c and d). Right dentary UM/HGL50-102 preserving  $P_1$ – $M_2$  and deciduous premolar (DP) $_2$  in (e) lingual view. Right dentary UM/HGL50-108 preserving  $P_2$ – $M_3$  in (f) occlusal view. Left calcaneus UM/HGL90-11 in (g) dorsal, (h) medial, and (i) distal views. Left astragalus UM/HGL50-103 in (j) lateral and (k) plantar views. Right astragalus UM/HGL51-11 in (l) distal view. Scale bars, 2 mm. cty, cotylar fossa; df, distal facet; ec, ectal facet; ff, fibular facet; sf, sustentacular facet; sus, sustentaculum; tc, tuber calcanei; tro, astragalar trochlea.

proximodistally elongated crestentic ectal facet. *Microhyrax* differs also from *Chambius*, *Haplomylus* and modern elephant-shrews in the lack of a fibular facet. *Chambius* and *Microhyrax* share a large peroneal process. This plesiomorphic condition (Szalay & Decker 1974; Hooker 2001) sets apart *Chambius* from both modern macroscelids and *Haplomylus*. The astragalus of *Chambius* is, nevertheless, typically macroscelidid in showing a sustentacular facet shifted to the medioplantar side of the bone. This character occurs only in the living elephant-shrews *Petrodromus*, *Elephantulus*, *Rhynchocyon* (unknown in *Macroscelides*), as well as in Scandentia (Meng *et al.* 2003). *Chambius* presents a cuboid facet on the astragalus as in living elephant-shrews. In addition, as in modern macroscelids, the *Chambius* astragalus displays a large concave depression, called a cotylar fossa, for articulation with the medial malleolus of the

tibia. This character also occurs in some ‘condylarths’, notably in the lousinine (Tabuce *et al.* 2006) and apheliscine (Zack *et al.* 2005) ‘hyopsodontids’. Following these comparisons, it appears that *Chambius* tarsal bones represent a morphological intermediate between *Haplomylus* and living elephant-shrews, thus reinforcing the relationships between some archaic Euramerican ‘ungulates’ and members of Afrotheria.

Hyraxes have been classified among the ‘ungulates’ by morphologists since the end of the nineteenth century but recently assigned to Afrotheria by molecular biologists. They represented, during the Paleogene, the most diverse group of terrestrial ‘ungulates’ in Africa (Rasmussen 1989; Schwartz *et al.* 1995). *Microhyrax*, from the early-middle Eocene of Gour Lazib (Algeria), is one of the smallest known hyraxes with a body mass estimated



around 3 kg (Schwartz *et al.* 1995). *Microhyrax* displays a mosaic of primitive and derived dental characters (Tabuce *et al.* 2001a; figure 2). On one hand, lower premolars are simple relative to other Paleogene hyraxes: the metaconid is small on premolar (P)<sub>2-4</sub>, and the talonid is reduced bearing only a strong hypoconid and a salient cristid obliqua. On the other hand, lower molars are reminiscent to those of *Megalohyrax*, *Titanohyrax*, *Antilohyrax*, *Saghattherium*, *Thyrohyrax* and *Selenohyrax* from the Eocene/Oligocene of the Fayum (Egypt) in showing derived structures such as the interrupted protocristid and hypocristid (Rasmussen 1989). *Microhyrax* is, however, clearly distinct from these taxa in its simple premolars and the morphological pattern of upper molars. Molar (M)<sup>1-3</sup> display evident primitive characters such as small parastyle and mesostyle, weakly W-shaped ectoloph and paraconular swelling (Tabuce *et al.* 2001a). *Microhyrax* is also unique by the increasing reduction of the metacone from M<sup>1</sup> to M<sup>3</sup>.

Functionally, the tarsal bones of *Microhyrax* show no cursorial adaptations given the short tuber calcanei and moderately grooved astragalar trochlea, which indicates little flexion–extension. But, as the living *Dendrohyrax*, *Microhyrax* might display some arboreal capacity according to its mobile midtarsal joint (Fischer 1986). Basal perissodactyls differ from *Microhyrax* in having a saddle-shaped navicular facet. The peculiar combination of all tarsal characters strongly supports a relationship between *Microhyrax* and tethytheres (proboscideans and sirenians). The head of the astragalus in *Microhyrax* is characterized by a navicular facet with no trace of cuboid facet. This serial arrangement, called taxepody, differs from the diplarthral or alternating arrangement observed in perissodactyls. Taxepody characterizes Proboscidea, Sirenia, Embrithopoda (putative tethytheres), more derived hyraxes (Rasmussen *et al.* 1990) and several ‘condylarths’ such as *Meniscotherium*, a North American phenacodont and European ‘hyopsodontid’ louisinines (*Microhyus* and *Paschatherium*; Godinot *et al.* 1996; Tabuce *et al.* 2006). The astragalus of *Microhyrax* is typically hyracoid by the combination of a spiral articulation for the fibular malleolus and a deep cotylar fossa (Rasmussen *et al.* 1990). This latter trait is thus a key astragalar character shared by basal hyraxes (*Microhyrax*) and elephant-shrews (*Chambius*). Moreover, it characterizes *Numidotherium koholense*, a basal proboscidean from the early Eocene of northwestern Africa (Mahboubi *et al.* 1984). The Eocene Asian tethythere ‘anthracobunids’ (Gingerich *et al.* 1990), the tubulidentates and their possible extinct relative *Plesiorycteropus* (MacPhee 1994), plus the louisinine (Tabuce *et al.* 2006) and apheliscine (Zack *et al.* 2005) ‘condylarths’, also display the cotylar fossa. Considering that this peculiar astragalar feature occurred among several groups having different modes of locomotion (hyraxes are terrestrial to scansorial or even cursorial; elephant-shrews, louisinines and apheliscines are cursorial to saltatorial; tubulidentates show fossorial capacities; and modern proboscideans are characterized by their graviportal stance), this character is seemingly not strictly functional and, therefore, it could be interpreted as the result of shared ancestry (see also Zack *et al.* 2005). Consequently, the cotylar fossa observed here in stem members of Hyracoidea, Proboscidea, Tubulidentata and Macroscelidea, represents a reliable afrotherian synapomorphy. However, living golden moles and tenrecs, both

crown members of Afrotheria, do not show this tarsal evidence (Salton & Szalay 2004). The lack of paleontological data for stem tenrecs and golden moles is a critical issue for assessing if this astragalar feature has never been developed in both groups or if it has been subsequently lost. This character also needs to be checked on the Eocene quadrupedal sirenian *Pezosiren* (other sirenians have no hindlimbs) (Domning 2001). Anyway, the cotylar fossa could not be a strict afrotherian synapomorphy as it is also present in some other eutherian mammals: cercopithecoid primates (e.g. *Macaca*, *Colobus*; MacPhee 1994), ‘condylarths’ (e.g. *Meniscotherium*, *Ancodon*), creodonts (e.g. *Oxyaena*; Gunnell & Gingerich 1991) and archaic South American ‘ungulates’ (Cifelli 1983).

#### (b) Phylogenetic analysis

On the basis of a recent phylogenetic analysis, including the tarsal anatomy of modern hyraxes and elephant-shrews, the monophyly of Afrotheria was not supported (Zack *et al.* 2005). Zack *et al.* (2005) scored the operational taxonomic units (OTU) Macroscelidea as a chimera based on the tarsal characters of the living *Rhynchocyon* with the dental features of the Eocene *Chambius*. The OTU Hyracoidea was also established on a composite morphology based on several Eocene, Oligocene and modern hyraxes. We modified the analysis of Zack *et al.* (2005) in removing these taxonomic chimeras and in scoring the tarsal and dental morphology of *Microhyrax* (hyrax) and *Chambius* (macroscelidid) from new paleontological evidence of both taxa. Other macroscelidids are represented by *Rhynchocyon* (Pliocene to Holocene) and *Myohyrax* (Miocene; Butler 1995). In addition to hyracoids and macroscelidids, we supplemented the analysis by sampling the afrotherian orders known since the Eocene: proboscideans (*N. koholense*) and sirenians (*Protosiren*). The phylogenetic relationships within the paenungulate clade (see Gheerbrant *et al.* (2005a) for an overview of paenungulate classification and history) were assessed in coding *Anthracobune* (‘Anthracobunidae’ from the early-middle Eocene of Indo-Pakistan), *Arsinoitherium* (Embrithopoda from the late Eocene?, early Oligocene of Africa) and *Phenacolophus* (a putative archaic embrithopod from the late Palaeocene of China and Mongolia). Other representatives of modern ‘ungulates’ are *Diacodexis* (Cetartiodactyla) and *Hyracotherium* (Perissodactyla). As for archaic ‘ungulates’, the matrix includes at least one representative of each of the ‘condylarth’ families: two arctocyonids (*Molinosodus* and *Chriacus*), a mesonychid (*Dissacus*), a periprychid (*Mithrandir*), a mioclaenid (*Claenodon*), a phenacodontid (*Ectocion*), five ‘hyopsodontids’ (*Hyopsodus*, *Apheliscus*, *Haplomyilus*, *Paschatherium* and *Microhyus*) and *Protungulatum* (‘condylarth’ *incertae sedis*, specified as outgroup).

In order to minimize homoplasy, the taxonomic dataset exemplifies only groups that existed in the time period corresponding to the early palaeontological record of ‘ungulates’ and afrotheres. Despite their incomplete fossil record, early ‘ungulates’ and afrotheres present a major phylogenetic advantage as they are expected to provide morphological patterns that have not been overwritten by subsequent evolution (our primary assumption). Except for *Numidotherium* and *Protosiren*, for which cranial remains are documented, most selected afrotheres, especially *Chambius* and *Microhyrax*, are only known by dental and tarsal remains. In this context, we have limited



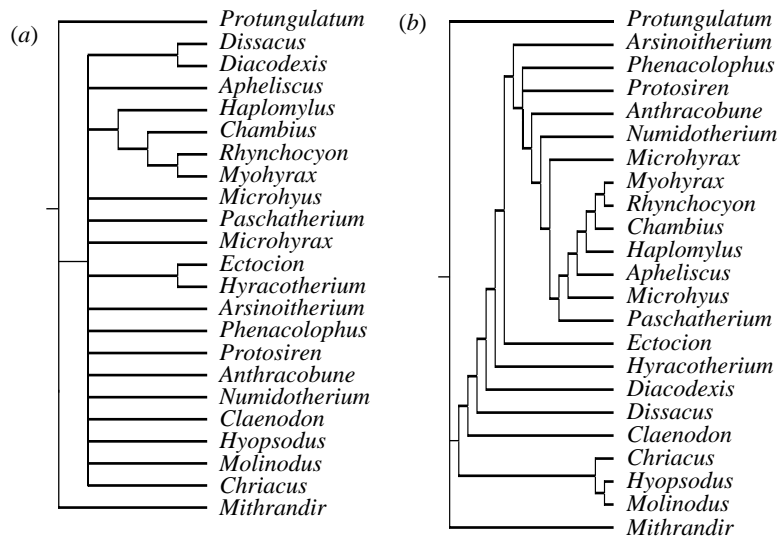


Figure 3. (a) Strict consensus tree of 105 equally parsimonious trees recovered from a parsimony analysis of 52 morphological characters, all characters are unordered. Tree length = 225 steps, consistency index = 0.33, retention index = 0.54. (b) Strict consensus tree of 3 equally parsimonious trees recovered after an *a posteriori* reweighting of the characters according to their rescaled consistency index, consistency index = 0.43, retention index = 0.67.

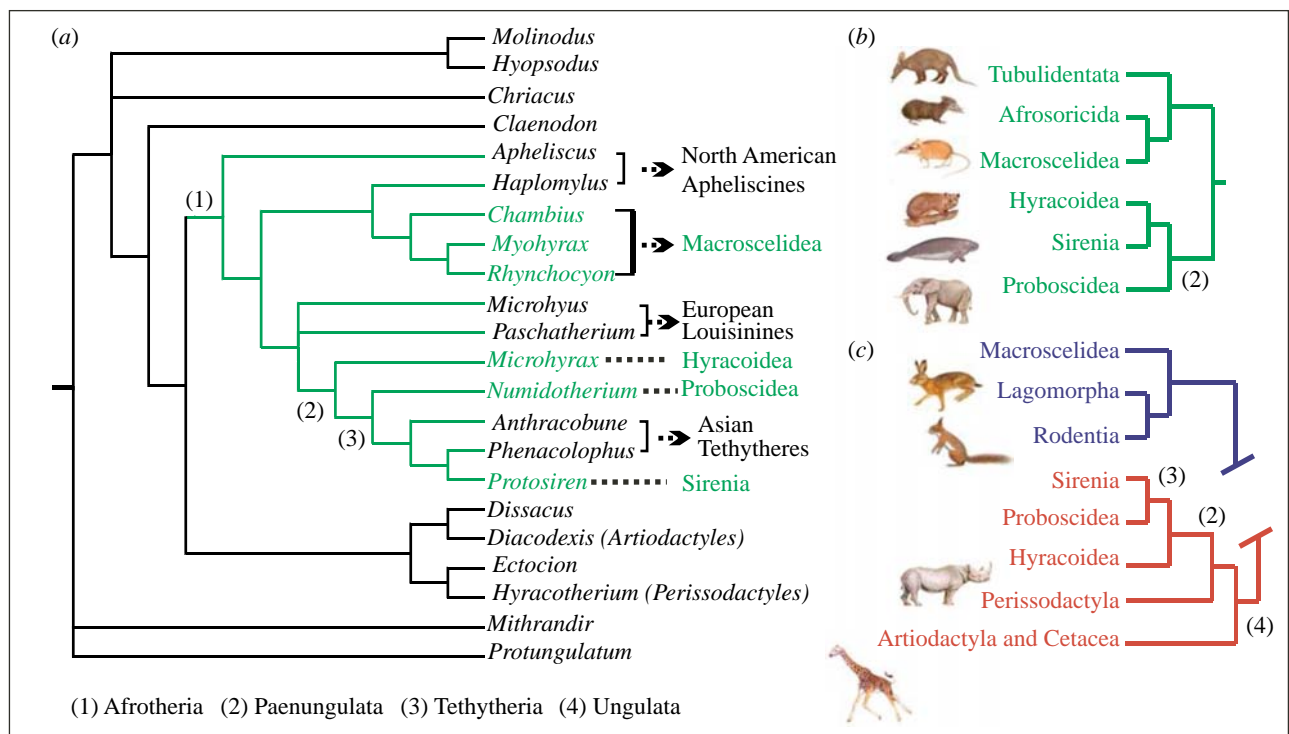


Figure 4. (a) Strict consensus of 4 equally parsimonious trees recovered from a parsimony analysis of 52 morphological characters, all characters are unordered. Tree length = 214 steps, consistency index = 0.35, retention index = 0.55. (b) molecular phylogeny of afrotheres resulting from Springer *et al.* (2004). (c) morphological phylogenetic position of selected afrotheres resulting from Shoshani & McKenna (1998); the majority of morphological studies consider Afrotheria to be polyphyletic: Macroscelidea are allied with Glires (Lagomorpha and Rodentia) among Anagalida; and Paenungulata (hyraxes, sirenians and proboscideans) are included in the super-order Ungulata. Green colour indicates, in (a) and (b), members of living afrotherian orders; in (c), blue colour indicates Anagalida, and red colour indicates Ungulata.

the analysis to dental and tarsal features as a means of minimizing the effect of missing data.

The data matrix contains 52 characters and 23 taxa (electronic supplementary material). We analysed the matrix using heuristic search option in PAUP v. 4.0b10 software (Swofford 2003) with the tree-bisection-reconnection branch-swapping algorithm, a random addition sequence and 1000 replications. An initial analysis of the dataset generated 105 equally most parsimonious trees of

225 steps each. The strict consensus tree is unresolved (figure 3a). A successive approximations reweighting by the method of Farris (1969) was performed, reweighting characters according to their rescaled consistency index, as a means of reducing the misleading effect of homoplasious characters. This analysis yielded three equally most parsimonious trees. The strict consensus presented in figure 3b shows the monophyly of an Afrotheria clade. In that topology, paenungulates,

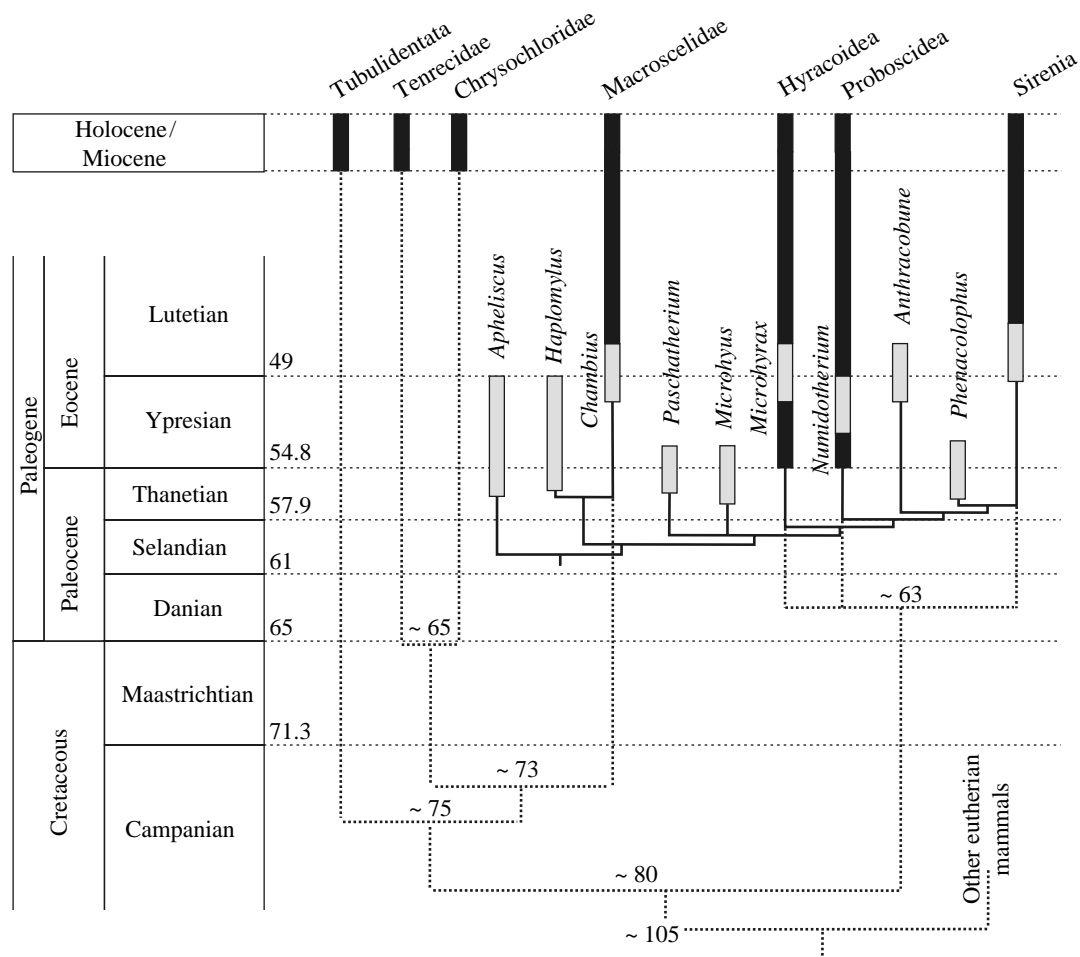


Figure 5. Phylogeny, fossil record and molecular inferences for Afrotheria. Solid lines show phylogenetic relationships of afrotheres resulting from a parsimony analysis of 52 morphological characters (figure 4). Geological ranges of the selected early Paleogene afrotheres are indicated by grey bold lines. Known stratigraphic distribution of modern afrotherian orders are indicated by black bold lines. Dashed lines represent the molecular phylogeny and divergence times for afrotheres estimated by Springer *et al.* (2003).

lousinines, aspheliscines and macroscelidids appear to be pectinately arranged. Among the paraphyletic paenungulates, *Arsinoitherium* occupies a basal position. Since its original description, the systematics and phylogenetic position of *Arsinoitherium* is disputed: Andrews (1906) related this genus to hyraxes, while, more recently, Court (1992a) and Gheerbrant *et al.* (2005b) considered *Arsinoitherium* as the sister group of proboscideans or tethytheres, respectively. *Arsinoitherium* exhibits an autopomorphic dental morphology. As such, it differs substantially from basal tethytheres in showing an unusual case of hypsodonty and in having a very peculiar bilophodonty of its cheek teeth. Court (1992b) hypothesized that this morphological dental pattern could derive from a hyper-specialized dilambdodonty. It seems to us that the homology of selected dental characters scored in *Arsinoitherium* with respect to the other ingroup taxa is not attested, thereby we excluded that genus from the phylogenetic analysis.

In that new phylogenetic framework, heuristic searches generated four equally most parsimonious trees of 214 steps each. The strict consensus presented in figure 4a is much more resolved than the previous analysis. The paenungulate, tethythere and macroscelid clades appear monophyletic, while lousinines and aspheliscines are polyphyletic. These results (figure 4a) are particularly interesting since they are consistent with current molecular phylogenies on high-level

relationships within Afrotheria (figure 4b). For the first time, morpho-paleontological analyses recover undemonstrated relationships between some stem afrotheres: paenungulates are allied with macroscelids and far from the clade including Perissodactyla (here *Hyracotherium*) and Cetartiodactyla (here *Diacodexis*; figure 4c). The paenungulate clade is composed of hyraxes plus tethytheres: proboscideans, ‘anthracobunids’, *Phenacolophus* and sirenians. In addition, European lousinines are related to paenungulates, and the North American aspheliscine *Haplomyllus* appears as the sister group of macroscelids (figure 4a).

### 3. PALEOBIOGEOGRAPHIC IMPLICATIONS

In view of our results, and considering the strong molecular evidence for the monophyly of Afrotheria, the early biogeography history of this super-order must be amended since stem afrotheres are not only restricted to Africa but also include some Euramerican ‘hypsodontids’ and Asian tethytheres. The occurrence in Asia of afrotheres during the Early Paleogene was already suspected in as much as ‘anthracobunids’ from the Indian subcontinent and *Phenacolophus* from central Asia were described as Tethytheria (see Gheerbrant *et al.* (2005a) for a summary). Therefore, stem afrotherians appeared both in Africa and in Holarctic area, which substantially changes the paleobiogeographic scenario derived from molecular inferences. Molecular phylogenies argue for an unusual case of endemism in Africa

of Afrotheria from the Cretaceous to the Miocene (approx. 105–20 Myr ago; Madsen *et al.* 2001; Springer *et al.* 2003), while our results suggest the existence of dispersal events between Africa, Euramerica and Asia. According to the fossil record (figure 5), such events might have occurred around the Palaeocene/Eocene (P/E) boundary during which numerous intercontinental mammalian dispersals occurred (Bowen *et al.* 2002; Tabuce & Marivaux 2005; Gingerich 2006; Gheerbrant & Rage 2006). A question then arises about the direction of these afrotherian migrations, which depend on the geographical location considered wherein afrotherians were likely to have originated. Two scenarios are conceivable. The first one suggests Palaeocene Laurasian origins for Afrotheria, as expected by both our phylogenetic and current biostratigraphic datasets. Nevertheless, this scenario fails if we consider a Cretaceous origin for afrotheres as molecular studies suggest (figure 5). If these molecular estimates are valid, the second scenario implies a Cretaceous African origin for Afrotheria, followed by dispersal to Euramerica (apheliscines and lousinines) and Asia ('anthracobunids' and *Phenacolophus*) before the P/E boundary. However, the Cretaceous and Palaeocene fossil record of African mammals is too poorly documented to test this scenario and Late Cretaceous fossil mammals are urgently needed. Therefore, only a more complete African fossil record will allow a relevant morphological versus molecular debate regarding the origin, evolution and subsequent migrations of afrotherians.

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**Annexe n°5**



## **Anthropoid versus strepsirhine status of the African Eocene primates *Algeripithecus* and *Azibius*: craniodental evidence**

Rodolphe Tabuce, Laurent Marivaux, Renaud Lebrun, Mohammed Adaci, Mustapha Bensalah, Pierre-Henri Fabre, Emmanuel Fara, Helder Gomes Rodrigues, Lionel Hautier, Jean-Jacques Jaeger, Vincent Lazzari, Fateh Mebrouk, Stéphane Peigné, Jean Sudre, Paul Tafforeau, Xavier Valentin and Mahammed Mahboubi

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# Anthropoid versus strepsirhine status of the African Eocene primates *Algeripithecus* and *Azibius*: craniodental evidence

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Recent fossil discoveries have demonstrated that Africa and Asia were epicentres for the origin and/or early diversification of the major living primate lineages, including both anthropoids (monkeys, apes and humans) and crown strepsirhine primates (lemurs, lorises and galagos). Competing hypotheses favouring either an African or Asian origin for anthropoids rank among the most hotly contested issues in paleoprimateology. The Afrocentric model for anthropoid origins rests heavily on the >45 Myr old fossil *Algeripithecus minutus* from Algeria, which is widely acknowledged to be one of the oldest known anthropoids. However, the phylogenetic position of *Algeripithecus* with respect to other primates has been tenuous because of the highly fragmentary fossils that have documented this primate until now. Recently recovered and more nearly complete fossils of *Algeripithecus* and contemporaneous relatives reveal that they are not anthropoids. New data support the idea that *Algeripithecus* and its sister genus *Azibius* are the earliest offshoots of an Afro–Arabian strepsirhine clade that embraces extant toothcombed primates and their fossil relatives. *Azibius* exhibits anatomical evidence for nocturnality. *Algeripithecus* has a long, thin and forwardly inclined lower canine alveolus, a feature that is entirely compatible with the long and procumbent lower canine included in the toothcomb of crown strepsirhines. These results strengthen an ancient African origin for crown strepsirhines and, in turn, strongly challenge the role of Africa as the ancestral homeland for anthropoids.

**Keywords:** Algeria; primate evolution; toothcombed primates; activity pattern

## 1. INTRODUCTION

Among the few early Paleogene continental sites from Afro–Arabia that have yielded a diverse mammalian fauna, the Glib Zegdou and Gour Lazib localities in

Hammada du Dra, southwestern Algeria, are famous for their fossil primates dating from the early or early middle Eocene (between approx. 52 and 46 Ma). These primates document an important but poorly known phase of the early Paleogene primate radiation in Africa. *Azibius* and *Draolestes* were tentatively thought to be related to the 'plesiadapiforms' (= 'archaic' primates) (Sudre 1975; Tabuce *et al.* 2004) and *Algeripithecus* plus *Tabelia* (Godinot & Mahboubi 1992, 1994; Godinot 1994)

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were considered as basal anthropoids, closely related to the much later Eocene–Oligocene forms documented from the Fayum in Egypt (Simons 1992, 1995, 1997a; Seiffert *et al.* 2005a; Seiffert *et al.* in press); a fossil record that has engendered the hypothesis that Africa is the homeland of the Anthropoidea clade (Simons & Rasmussen 1994b). Simultaneously, discoveries of basal anthropoids in the Eocene of southern and eastern Asia have demonstrated that Asia has also played a critical role in the origin and early radiation of anthropoid primates (Beard *et al.* 1994, 1996, 2004; Kay *et al.* 1997; Jaeger & Marivaux 2005; Bajpai *et al.* 2008). The various geographical scenarios for our basal history thus depend on the putative anthropoid status of *Algeripithecus* and *Tabelia*, these critical issues being linked to the fragmentary nature of their fossil remains.

In the framework of our paleontological project in the early Tertiary of North Africa, since 2003, we have focused our yearly field researches on the vast outcrops situated in the Gour Lazib area, including the Glib Zegdou outlier. Intensive survey of the red to yellow siltstones and sandstones of fluvial origin of the continental Glib Zegdou Formation has allowed the discovery of well-preserved craniodental remains of at least 30 eutherian species documenting several primates, hyraxes, rodents, elephant-shrews, insectivoran-grade mammals, chiropterans, creodonts and ‘condylarths’ (Adaci *et al.* 2007; Tabuce *et al.* 2007). The mammalian fauna from the Glib Zegdou Formation is currently the most diverse from the entire Afro–Arabian Eocene. The new fossil primates demonstrate that *Azibius* is a senior synonym of *Tabelia* and that *Draolestes* is invalid because its hypodigm includes specimens of both *Azibius* and *Algeripithecus*. Our study reveals a close relationship between *Azibius* and *Algeripithecus*, which are now the only known valid genera within the Azibiidae. The phylogenetic study of azibiids highlights their strepsirhine affinities and rejects the anthropoid status of *Algeripithecus* as a result.

## 2. SYSTEMATIC PALEONTOLOGY

Order Primates, Linnaeus, 1758

Suborder Strepsirhini, Geoffroy, 1812

Family Azibiidae, Gingerich, 1976

### (a) *Included genera*

*Azibius* Sudre, 1975 and *Algeripithecus* Godinot & Mahboubi, 1992.

### (b) *Emended diagnosis*

Azibiids (figures 1 and 2) differ from all other primates in having high, mesio-distally aligned  $P_{3-4}$  cusps, forming a blade-like structure;  $P_{3-4}$  also present a degree of overlapping and a mesial crown elevation associated with an inclination of the lingual cingulid. On  $M_{1-2}$ , azibiid traits are the distally offset metaconid, the absence of hypoconulid, and the narrow sub-circular talonid basin, which is open lingually by a deep notch in front of the entoconid. The  $P^{3-4}$  have a peak-shaped lateral profile resulting from the labially inclined protocone and the very high and vertical sharp edge aspect of the ectoloph. The bunodont  $M^{1-2}$  have a large hypocone, a thick lingual cingulum, and lack a distinct metaconule.

### (c) *Remarks*

*Algeripithecus* is smaller than *Azibius* (table S2 in the electronic supplementary material). Based on the various available equations, deriving from the regressions of  $M_1$  area against body mass of living primates (e.g. Conroy 1987; Bajpai *et al.* 2008), the estimated body mass of *Algeripithecus* ranges from 65 to 85 g and *Azibius* from 115 to 160 g. *Algeripithecus* differs also from *Azibius* by rather less bunodont teeth, a higher metaconid (or possibly protostylid) on  $P_{3-4}$ , a longer trigonid and shorter talonid on  $M_1$ , a smaller third lobe on  $M_3$ , the lack of both paraconule and parastyle on  $P^4$ , and by a more reduced  $M^3$ . Azibiids are only known from the late early or early middle Eocene (Mahboubi 1995; Mebrouk & Feist 1999; Adaci *et al.* 2007) of the Glib Zegdou Formation, Gour Lazib area, Algeria. However, another taxon, close to *Algeripithecus*, could also be present in the contemporaneous site of Chambi, Tunisia (Seiffert *et al.* in press).

## 3. RESULTS AND DISCUSSION

### (a) *The euprimate affinities of Azibiidae*

Sudre (1975) described *Azibius* as a possible ‘paromomyiform’ (=‘Plesiadapiformes’). Later, Gingerich (1976) suggested *Azibius* is a euprimate (primates of modern aspect), and erected the Azibiinae, a new subfamily of Adapidae. He thereby rejected the assumption proposed by Szalay (1975) according to which *Azibius* was a hypodontid-like condylarth. More recently, Holroyd & Simons (1991) have reinforced the adapid status of *Azibius*, while Hartenberger *et al.* (1997) have suggested a macroselidid affinity. Finally, after the discovery of *Draolestes*, which was considered to be the sister taxon of *Azibius*, Tabuce *et al.* (2004) suggested that azibiids are related to carpolestid plesiadapiforms, reviving Sudre’s initial attribution. This hypothesis was criticized by Godinot (2006) and Silcox (2008), who favoured euprimate affinities for azibiids. The abundant new material reveals that *Draolestes* is invalid because its hypodigm contains specimens of both *Azibius* and *Algeripithecus* (table S1 in the electronic supplementary material). The supposed carpolestid affinities of *Azibius* relied on the morphology of the  $P_4$ , which are enlarged in both taxa compared to the molars, exodaenodont (a lobe of enamel overhangs the labial side of the roots), and show apical cusps aligned anteroposteriorly in a blade-like structure. However, from a detailed comparison, Silcox (2008) suggested that this blade-like morphology is non-homologous between *Azibius* and carpolestids. We agree with her opinion because the  $P_3$  of azibiids, previously unknown, are also enlarged, exodaenodont, high-crowned and have a similar shearing morphology as the  $P_4$ , while the  $P_3$  of carpolestids is reduced and lacks the blade-like morphology. Most importantly, the new material reveals that the upper tooth originally thought to be the  $M^2$  of ‘*Draolestes*’ (GZC-41, holotype) is in fact a  $P^4$  of *Azibius*. This new dental allocation clearly precludes any carpolestid affinities for azibiids. The bona fide upper and lower molars of *Azibius* show, as do those of *Algeripithecus*, a euprimate morphology.

### (b) *Testing the anthropoid status of Algeripithecus and Azibius*

*Algeripithecus* was successively considered as a propithecoid, a proteopithecoid or a parapathecoid anthropoid

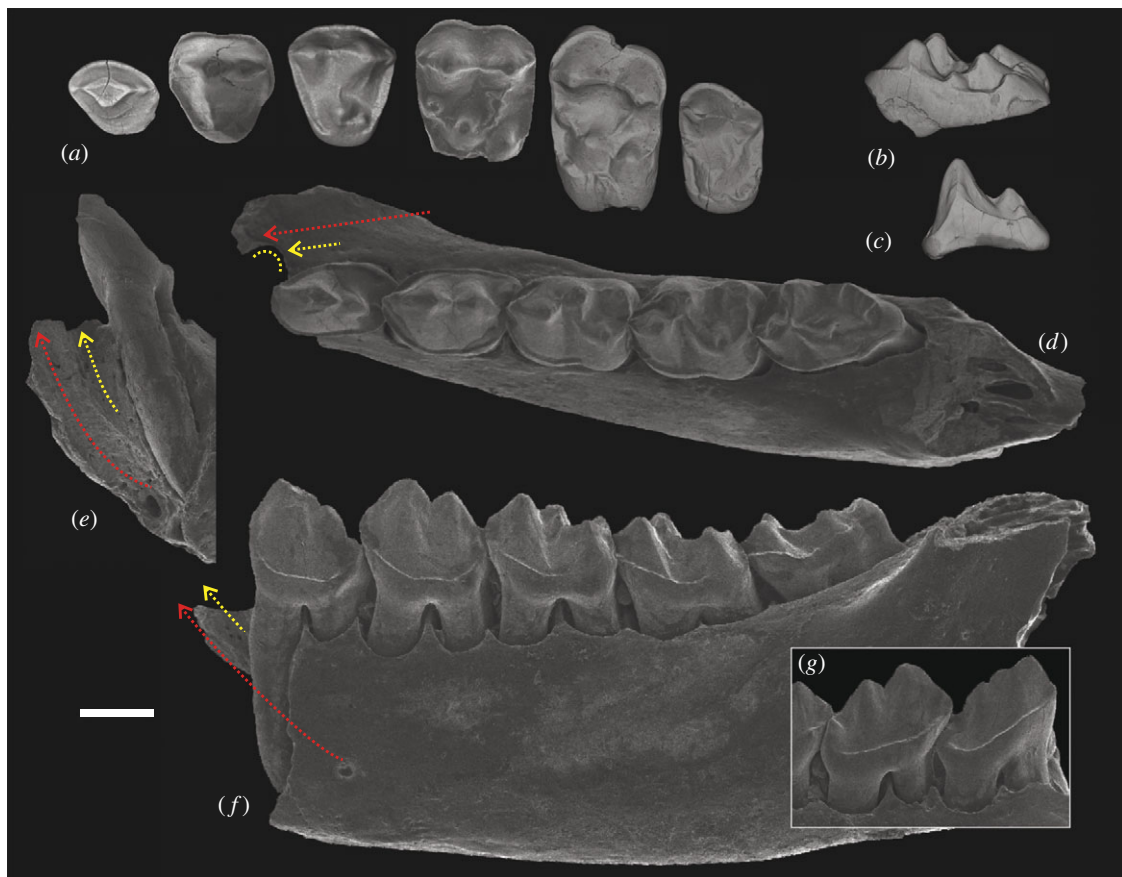


Figure 1. *Algeripithecus minutus*. (a) Composite of isolated P<sup>2</sup> (HGL50/297, reversed), P<sup>3</sup> (HGL50/298, reversed), P<sup>4</sup> (HGL50/299, reversed), M<sup>1</sup> (GZC7), M<sup>2</sup> (GZC1) and M<sup>3</sup> (HGL50-321) in occlusal views. (b) M<sup>2</sup> (GZC1). (c) P<sup>4</sup> (HGL50/299) in mesial and distal views, respectively. (d–f) Mandible with P<sub>3</sub>–M<sub>3</sub> and alveoli for C–P<sub>2</sub> (denoted by red and yellow arrows, respectively) (HGL50/397) (d) in occlusal, (e) mesial and (f) labial views. (g) P<sub>3–4</sub> (HGL50/397) in lingual view. Scale bar, 1 mm.

(Godinot & Mahboubi 1992; Godinot 1994; Seiffert *et al.* 2005a, *in press*). Its upper molars strongly resemble those of *Biretia*, a primitive parapithecoid from the late middle Eocene of Algeria and the early late Eocene of Egypt (de Bonis *et al.* 1988; Seiffert *et al.* 2005a). Common traits include a similar degree of bunodonty, the same occlusal outline, the robustness and the postero-lingual position of the hypocone, and the important development of the lingual cingulum (figure 1a). Upper molars of *Biretia* differ in having an uninterrupted lingual cingulum and enlarged conules. Further differences that are evident on premolars and molars clearly distinguish parapithecoids from azibiids: P<sup>2</sup> of *Biretia* is three-rooted, P<sup>4</sup> is less molariform due to the absence of the metacone, the roots of P<sub>3–4</sub> are oblique in orientation, their crown is low, their metaconid is offset lingually and the entoconid is present on P<sub>4</sub>; the paraconid occurs on M<sub>1</sub>, the metaconid is transverse to the protoconid on M<sub>2–3</sub>, the cristid obliqua reaches the trigonid wall at a more labial point, the hypoconulid is enlarged and central on the postcristid of M<sub>1–2</sub>, and M<sub>3</sub> is reduced. Azibiids also lack some dental features of later parapithecoids (*Abuqatrania*, *Apidium* and *Parapithecus*; Seiffert *et al.* *in press*) such as the bulbous conules on upper molars and the absence of lower molar protoconids. Other basal anthropoid families such as proteopithecids and eosimiids are also distinct from azibiids, and all dental resemblances represent only primitive

retentions or convergences (see text 2 in the electronic supplementary material). Azibiids also differ from most omomyiforms by their large hypocone and the loss of the paraconid. Some superficial similarities on lower premolars with microchoerines and anaptomorphines are the anterior elevation of the thick basal cingulid and the pronounced overlapping of P<sub>3–4</sub> (Godinot 2006). However, the buccolingually enlarged and molariform P<sub>4</sub> of omomyiforms are clearly distinct from the mesiolingually elongated and blade-like P<sub>4</sub> of azibiids.

In addition to this purely dental evidence, the newly recovered fossils of *Algeripithecus* and *Azibius* include dentary and maxilla, which are decisive in reconstructing the affinities of azibiids. The maxilla of *Azibius* lacks P<sup>1</sup> and shows above P<sup>2–3</sup> a very anterior position of the infraorbital foramina (IOF) (figure 2a–c). In occlusal view, the lateral maxillary broadening starts at the level of the P<sup>2</sup>. By comparisons with extant and extinct primates, these characters indicate that *Azibius* possesses a short rostrum. The pronounced curve and the thickening of the mandible under P<sub>4</sub> in *Algeripithecus* are also indicative of a short jaw (figure 1d). Besides, *Azibius* presents a reduced suborbital depth of the maxilla above P<sup>4</sup>. This feature is also observed in the omomyid *Necrolemur*, in the platyrrhine *Aotus*, as well as in most small and medium-sized modern strepsirhines (e.g. *Loris*, *Galago*, *Microcebus*). *Tarsius* and *Biretia megalopsis* show an extreme compression of the suborbital region in having a complete

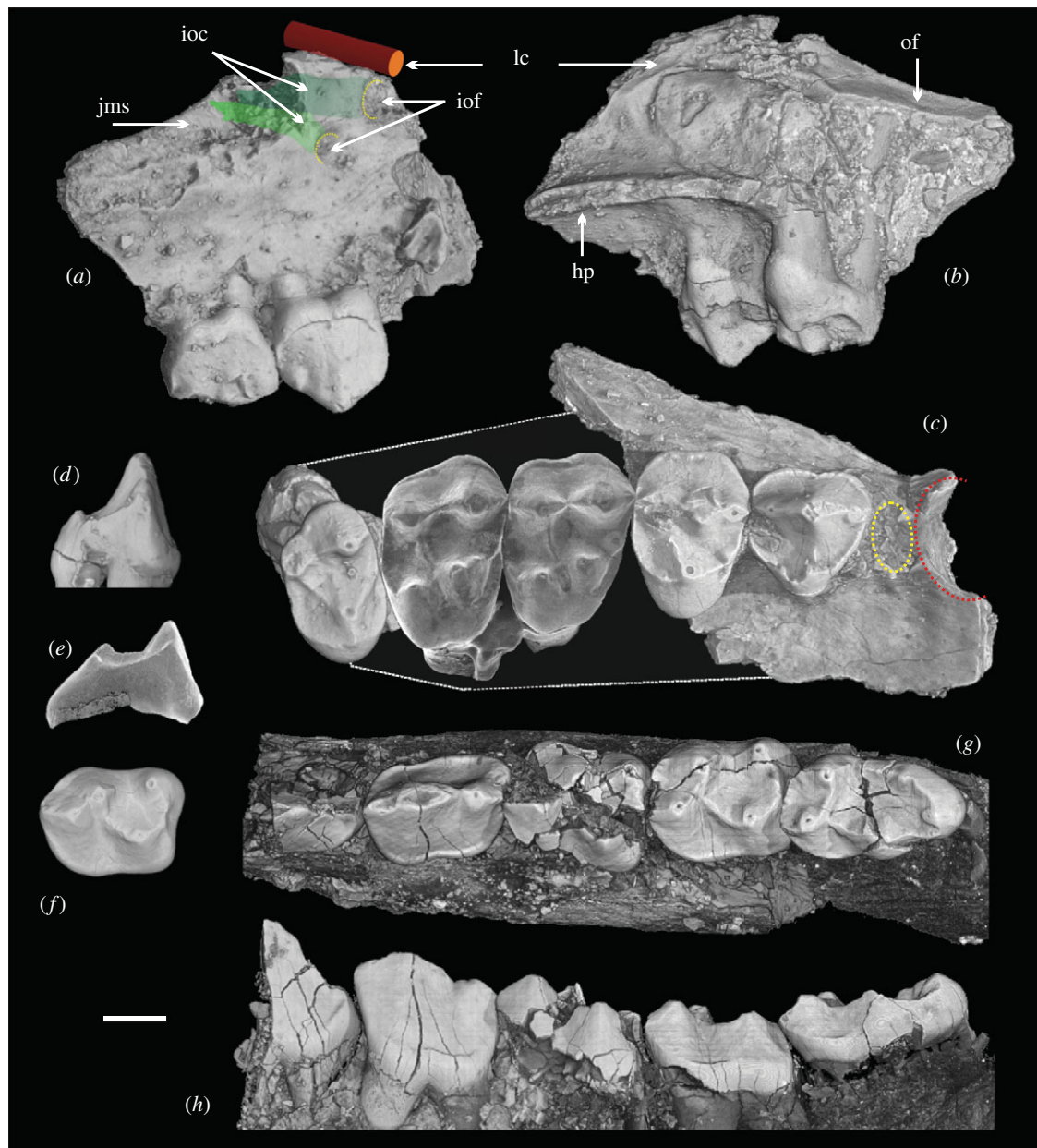


Figure 2. *Azibius trerki*. (a,b) Maxilla with P<sup>3-4</sup> (HGL51/46) in labial (a) and disto-lingual (b) views. (c) Composite of maxilla with M<sup>1-2</sup> (HGL50/396, reversed), P<sup>3-4</sup> and M<sup>3</sup> with alveoli for C–P<sup>2</sup> (denoted by red and yellow circles, respectively) (HGL51/46) in occlusal view. (d) P<sup>3</sup> (HGL51/46) and (e) P<sup>4</sup> (GZC41) in distal view. (f) M<sub>1</sub> (HGL50/248, reversed) in occlusal view. (g,h) Mandible with P<sub>3</sub>–M<sub>3</sub> (HGL50/256) in occlusal (g) and labial (h) views. Abbreviations: hard palate, hp; infra-orbital canals, ioc; infra-orbital foramina, iof; jugo-maxillary suture, jms; lacrimal canal, lc; orbital floor, of. Scale bar, 1 mm.

orbitopalatal fusion and an exposure of the lingual roots of molars in the orbit floor (Seiffert *et al.* 2005a). The reduced suborbital depth of the maxilla and the orbitopalatal fusion are observed in primates having large orbits and a nocturnal activity pattern. Comparative scans performed using conventional and synchrotron microtomography (see text 3 in the electronic supplementary material) of the maxilla through the lingual P<sup>4</sup> root of some of these primates (see figure S1 in the electronic supplementary material) show that *Azibius* is comparable to *Aotus* and intermediate in condition between *Tarsius* and *Loris*, thereby suggesting very large orbits in *Azibius* probably associated with a nocturnal activity pattern. The cumulative area (0.74 mm<sup>2</sup>) of the two IOFs in *Azibius* is greater than it is in *Tarsius*, most small anthropoids and living strepsirrhines of equivalent weight (e.g.

*Galago senegalensis*, *Loris tardigradus*; Muchlinsky 2008; Rossie *et al.* 2006). Several omomyiforms (e.g. *Shoshonius*, *Necrolemur*) have a large IOF, like *Azibius*. In mammals, the IOF transmits the infraorbital nerve and a small artery to the maxillary region; a large IOF is correlated with an increase in vibrissa number, which is characteristic of nocturnal species (Muchlinsky 2008). The large IOF in *Azibius* thus indicates a fine sensory acuity of the face, and strengthens the hypothesis of a nocturnal activity pattern. Comparative three-dimensional microtomographic reconstructions show that the course of the lacrimal canals in *Azibius* is oblique rostroventrally (figure 2a–b) as in all living strepsirrhines, adapiforms (e.g. *Adapis*) and omomyiforms (e.g. *Microchoerus*; figure 3). In contrast, *Tarsius* and all anthropoids (Rossie *et al.* 2006), including taxa with long snouts such



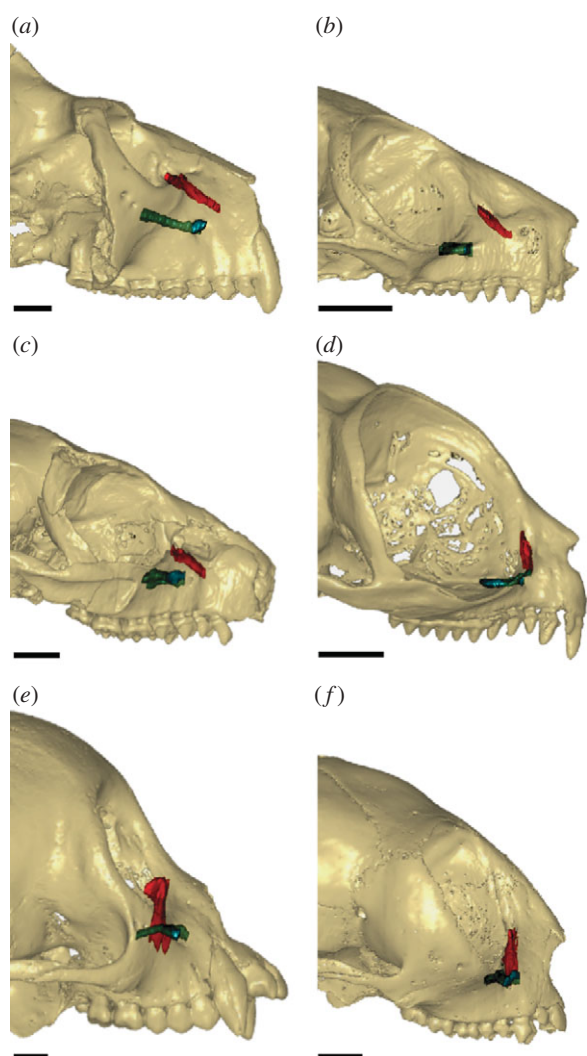


Figure 3. Variability in the configuration of the lacrimal and infraorbital canal in extant and extinct primates (virtual three-dimensional surfaces derived from  $\mu$ CT image data; see text 3 and table S3 in the electronic supplementary material). (a) *Adapis* sp., (b) *Microcebus murinus*, (c) *Microchoerus erinaceus*, (d) *Tarsius syrigha*, (e) *Cebus apella* and (f) *Aotus trivirgatus*. Note how these canals tend to be perpendicular in anthropoids and *Tarsius*, but form a narrower angle in *Azibius trerki* (figure 2), crown and stem strepsirhines and *Microchoerus*, an extinct omomyiform primate. Scale bar, 5 mm.

as *Theropithecus*, show a lacrimal canal that is vertical and oriented perpendicular to the infraorbital canal (figure 3). The maxilla of *Azibius*, although partially preserved, thus reveals distinctive cranial traits that allow us to exclude anthropoid affinities for azibiids.

Consequently, the first unquestionable occurrence of anthropoids in Afro–Arabia is the parapithecoid *Biretia* from the late middle to early late Eocene of Algeria (Bir El Ater) and Egypt (Birket Qarun Locality 2) (de Bonis *et al.* 1988; Seiffert *et al.* 2005a). This result, along with the recent discovery of a putative early Eocene eosimiid in India (Bajpai *et al.* 2008; see also Rose *et al.* 2009) and the well-supported basal position of this primate family within the anthropoids (Kay *et al.* 1997; Jaeger & Marivaux 2005; Bajpai *et al.* 2008), seems to support a South Asian origin for anthropoids (Beard 2004, 2006) and a subsequent dispersal into Africa during the

middle Eocene. Such a mammalian dispersal event between Africa and South Asia has also been proposed for several groups including anthracotheriid artiodactyls, and anomaluroid and hystricognathous rodents (Tabuce & Marivaux 2005; Gheerbrant & Rage 2006).

However, this paleobiogeographical issue for the early evolution of anthropoids is complicated by (i) the morphological gap between African parapithecoids and Asian eosimiids and (ii) the poorly documented omomyiform *Altiatlasius* from the late Paleocene of Morocco (Sigé *et al.* 1990), which was recently reconsidered either as a stem primate (Tabuce *et al.* 2004; Marivaux 2006; Silcox 2008) or a possible eosimiid-like anthropoid (Beard 2004, 2006; Seiffert *et al.* 2005a; Marivaux 2006; Bajpai *et al.* 2008; our phylogenetic results, see figure S2 in the electronic supplementary material). As such, *Altiatlasius* could be the earliest anthropoid, a record that equivocally supports an African origin of anthropoids during the late Paleocene, or their early dispersal into Africa from Asia, at least during the Paleocene (Beard 2006). This would extend the root of the Anthropoidea clade back to the Paleocene. In the absence of any undisputed *Altiatlasius* descendant in Africa during the early to middle Eocene (with the exception of two half-teeth, putatively related to *Altiatlasius*, from the Lutetian of Morocco (Tabuce *et al.* 2005), a Paleocene African origin of anthropoids would imply a big gap of about 20 Myr in the anthropoid fossil record in Africa, pre-dating the first appearance of the earliest parapithecoids. The existence of such a long ghost lineage seems speculative given the debate surrounding the phylogenetic affinities of *Altiatlasius*. Indeed, the extremely fragmentary nature of *Altiatlasius* cautions against over-interpreting its affinities, especially in light of the example of *Algeripithecus*.

#### (c) Higher-level affinities of the Azibiidae

Phylogenetic analyses of primates based on craniodental and postcranial characters show that azibiids are nested within the Strepsirhini clade, setting *Algeripithecus* clearly apart from the Anthropoidea clade. The analysis reveals two major groups within Strepsirhini (figure 4): (i) the paraphyletic adapiforms mainly known from the Eocene of Europe, North America and Asia (Godinot 1998; Marivaux *et al.* 2006); and (ii) an Eocene–Oligocene Afro–Arabian clade that gave rise to living crown strepsirhines (lemurs, lorises, galagos) (Seiffert *et al.* 2003, 2005b; Godinot 2006). Within this Afro–Arabian clade, azibiids are successive sister taxa of djebelemurines (*Djebelemur*, Hartenberger & Marandat 1992; ‘*Anchomomys*’ *milleri*, Simons 1997b) and a group that embraces *Plesiopithecus* (Simons 1992; Simons & Rasmussen 1994a) and crown strepsirhines, including their late Eocene–Oligocene fossil representatives from the Fayum, that is, *Wadilemur*, *Saharagalago* and *Karamisia* (Seiffert *et al.* 2003, 2005b; figure 4), and possibly *Omanodon* and *Shizarodon* from the Oligocene of Oman (Gheerbrant *et al.* 1993; Godinot 2006). Also, noteworthy is the putative lemuriform *Bugtilemur* from the Asian Oligocene, which is now regarded as a peculiar adapiform without direct affinities with crown strepsirhines (Marivaux *et al.* 2006). Within the paraphyletic adapiforms, the European cercamoniine *Anchomomys* appears to be the sister taxa of the Afro–Arabian strepsirhine clade.

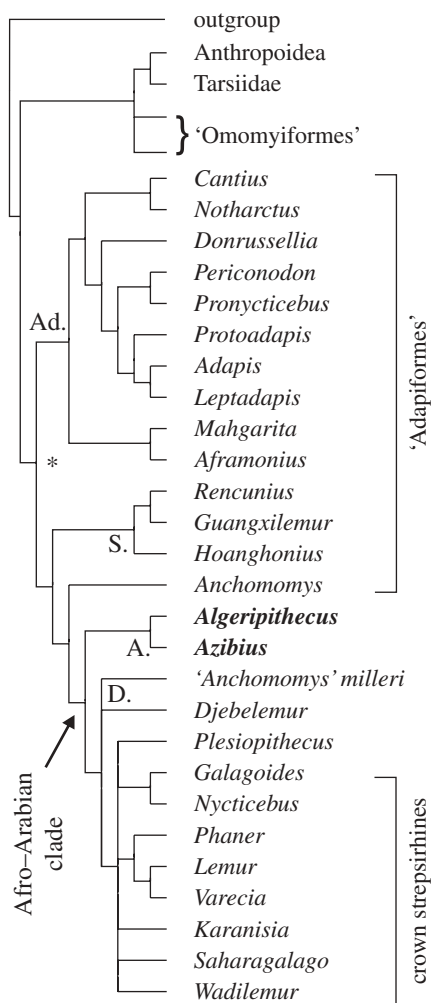


Figure 4. Phylogenetic position of the azibiids *Algeripithecus* and *Azibius* (in bold) within the Strepsirhini clade (denoted by the asterisk). This topology results from an analysis, including 83 primate taxa and 341 dental, cranial and postcranial characters, having generated 369 equally most parsimonious trees of 2851 steps each (consistency index, CI = 0.1887; retention index, RI = 0.5335) (see text 2 and figure S2 in the electronic supplementary material). Abbreviations: Azibiidae, A.; Adapidae, Ad.; Djebelemurinae, D.; Sivaladapidae, S.

*Anchomomys* does not present, however, the derived characters of the Paleogene Afro–Arabian taxa, notably the overlapping and the anterior coronal elevation of lower premolars. The tree topology could be explained by some convergences on molars between *Anchomomys* species and '*Anchomomys*' *milleri*, hence the initial name given to this Fayum primate (see also Seiffert *et al.* 2005b). Considering the middle Eocene age of the oldest *Anchomomys* and the much earlier age of both azibiids and *Djebelemur*, it is difficult to conceive that a European 'anchomomyine' lineage, having developed a hypocone, gave rise to the Afro–Arabian strepsirhine clade.

Within this group, the djebelemurines and crown strepsirhines have more derived lower molars than the azibiids by the development of a mesial fovea built by the connection of the long curved paracristid with the premetacristid. Except on the  $M_3$  of *Azibius*, where this mesial fovea occurs, azibiids show instead a short premetacristid on  $M_{2-3}$  (generally absent on  $M_1$ ), which is usually isolated from the paracristid. Lower molars of *Omanodon*

and *Plesiopithecus* also display this incomplete mesial fovea. Furthermore, azibiids along with *Djebelemur*, *Plesiopithecus* and *Wadilemur* differ from *Karanisia*, *Saharagalago* and '*Anchomomys*' *milleri* by the absence of the posterolingually protruding entoconid lobe on lower molars; in *Azibius* the entoconid is moderately expanded posteriorly on the  $M_1$ . On upper molars, azibiids are more primitive than crown strepsirhines by the association of a larger paraconule, a symmetrical crown without waisting of the distal border, and by the absence of the connection between the mesiolingually directed hypometaconulecrista and the postprotocrista (except on some  $M^1$  of *Algeripithecus*). *Azibius* and *Plesiopithecus* differ in numerous premolar and molar traits but they share bunodont molars and, more importantly, a cranium with a short rostrum and very large orbits indicative of a nocturnal activity pattern. As many adapiforms are diurnal according to their rather small orbit sizes, they appear much more distant from crown strepsirhines than azibiids. This is critical regarding the ancestry of crown strepsirhines as this group was indeed considered as emerging from a nocturnal lineage (e.g. Godinot 2006). However, recent results based on opsin genes have shown that ancestral strepsirhines were diurnal or cathemeral, and that nocturnality has evolved several times within crown strepsirhines and haplorhines as well (Tan *et al.* 2005; Ankel-Simons & Rasmussen 2008). Despite the apparent lability of nocturnality, it is worth pointing out that some stem strepsirhines, such as *Azibius*, have already achieved this trait early in the Tertiary.

#### (d) *The early diversity of 'pre-toothcombed' primates in Africa*

The lower toothrow of crown strepsirhines is characterized by an unusual incisor–canine toothcomb, in which the incisiform canine is reduced and strongly procumbent (Rosenberger & Strasser 1985). *Wadilemur* and *Karanisia* provide the earliest fossil evidence for such a lower dental structure (Seiffert *et al.* 2003, 2005b). Djebelemurines are considered to be stem strepsirhines because they do not develop the toothcomb, their canine being only moderately reduced. The anterior dentition of azibiids is unknown, but the alveoli in front of  $P_3$  in the mandible of *Algeripithecus* show that the canine alveolus is long, thin and forwardly inclined, suggesting that this tooth would be incisiform and procumbent (figure 1d–f). Such a canine may indicate that azibiids were toothcombed primates. The broadening of the maxilla at the level of the large canine in *Azibius* is also characteristic of the dental arcade morphology of some extant strepsirhines. However, as azibiids seem to diverge cladistically before djebelemurines (figure 4), a group without the toothcomb, this implies either the absence of a 'true' toothcomb in azibiids or its secondary loss in djebelemurines, a hypothesis that appears unlikely. Even if further evidence is required to ascertain the presence of a 'true' toothcomb in azibiids, it appears that *Algeripithecus* is unique among early Paleogene African primates documented to date in having a long and procumbent lower canine. This morphology seems compatible with the incisor–canine functional unit that pre-dates the toothcomb of crown strepsirhines. The toothcomb of crown strepsirhines is coupled with a  $P_2$ , which is often

caniniform and commonly higher and/or larger than the other premolars. These derived traits, observed in Miocene and Recent strepsirrhines (Fleagle 1999), are achieved as early as the late Eocene in *Wadilemur* (Seiffert *et al.* 2005b). The tall and sub-caniniform P<sub>2</sub>, along with the loss of P<sub>1</sub> and the reduced and procumbent canine, were proposed as synapomorphies of crown strepsirrhines (Rasmussen & Nekaris 1998). Therefore, even if *Algeripithecus* possesses the two latter traits, its reduced P<sub>2</sub> seems to preclude direct relationships between azibiids and crown strepsirrhines. However, this character is not as definite as *Karanisia* (a crown strepsirrhine or even a stem lorisiform based on molar characters) and seems also to present a reduced P<sub>2</sub>, thereby suggesting that the toothcomb could pre-date the specialization of the P<sub>2</sub> within Paleogene Afro–Arabian strepsirrhines.

Thus, the question of whether azibiids are stem or crown strepsirrhines is unresolved based on the known morphology of their front dentition. However, the phylogenetic analysis assessed on the global morphological evidence suggests that azibiids are the earliest offshoot of stem strepsirrhines to the exclusion of adapiforms. Azibiids are furthermore characterized by numerous autapomorphic features such as a pronounced bunodonty of molars, a large hypocone, a loss of paraconid and high-crowned posterior premolars forming a blade-like structure. As *Plesiopithecus* does by its very large procumbent lower canine, azibiids exemplify, therefore, an aberrant group of stem strepsirrhines, reinforcing the diversity, unsuspected for a long time, of Afro–Arabian Paleogene strepsirrhines. The apparent high degree of specialization of the azibiid family, associated with its late early or early middle Eocene age reveals the antiquity of this Afro–Arabian clade. As a result, we cannot exclude the possibility that this clade is rooted in a primitive, yet unknown, African lineage older than the earliest Eocene. This working hypothesis is tantalizing, especially in view of the age of *Altiatlasius*, testifying to the presence of primates as early as the late Paleocene in Africa. The divergence time of crown strepsirrhines, estimated by recent molecular analysis as between 67 and 84 Ma (Horvath *et al.* 2008), and the possibility that *Algeripithecus* displays a true toothcomb are two interesting arguments in favour of the great antiquity of ‘pre-toothcombed’ primates in Africa.

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**Annexe n°6**



**LES MICROVERTEBRES PLEISTOCENES ET HOLOCENES D'EL HARHOURA 2 (RABAT-TEMARA, MAROC)**

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Les petits vertébrés (rongeurs, insectivores, amphibiens, reptiles) retrouvés en contexte archéologique peuvent nous renseigner sur l'évolution de la biodiversité et fournissent souvent des informations paléoenvironnementales plus précises que les grands mammifères. Ils sont peu étudiés en Afrique du Nord, notamment en ce qui concerne la fin du Quaternaire. Parmi les quelques sites nord-africains de cette période on trouve la grotte d'El Harhoura 2 (Rabat-Témara, Maroc) remarquable tant par la richesse spécifique des petits vertébrés terrestres (plus d'une trentaine de taxons) que l'abondance des restes identifiables (une concentration allant jusqu'à 250 000 éléments par m<sup>3</sup> de sédiments). Ce site a livré plusieurs couches archéologiques qui permettent de suivre l'évolution des faunes et des environnements au cours de la transition Pléistocène supérieur - Holocène.

L'analyse taphonomique montre des différences de prédateurs entre les différents niveaux (rapaces nocturnes vs petits carnivores ou rapaces diurnes) et des altérations post-prédatons qui indiquent l'absence de tri, une faible météorisation, mais beaucoup de traces de racines et une éventuelle bioturbation. L'étude paléoécologique montre des paysages en mosaïques tout au long de la séquence, avec cependant des épisodes plus ouverts au cours du Pléistocène supérieur, et une ultime période plus boisée à l'Holocène moyen. La nature locale (modifications du paysage, proximité des points d'eau, prédateurs ayant des régimes alimentaires différents) ou globale (climat, aridité/humidité) de ces changements est discutée dans le contexte archéologique et paléoclimatique. Ces données nous permettent d'améliorer nos connaissances sur le cadre environnemental dans lequel l'Homme moderne est apparu et a évolué dans cette région.

**Mots clés :** Microvertébrés, Afrique du Nord, Maroc, Pléistocène, Holocène, Systématique, Taphonomie, Paléoécologie, Homme moderne.

**THE REMARKABLE DIVERSITY OF THE MAMMALIAN ORDER HYRACOIDEA IN THE EOCENE OF THE GOUR LAZIB, ALGERIA**

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Living hyraxes are poorly diversified with only three small-sized genera restricted to Africa and Middle East. They represented, on the contrary, the dominant 'ungulate' group during the Paleogene on the Arabo-African continent. Late Eocene to Oligocene sites of the Fayum in Egypt are particularly famous for their hyrax fossil record. The beginning of the hyrax radiation is however less documented yet, since rare fragmentary remains are known from few Early to Middle Eocene sites in North Africa. Among them, the Glib Zegdou and Gour Lazib localities in the Algerian Sahara have yielded, until recently, four



species mainly documented by dental remains only. Since 2003, paleontological expeditions in this area have led to the recovery of numerous new craniodental and postcranial remains of, at least, five other species, making the Gour Lazib sites the richest localities documenting the early stage of the hyrax radiation. The taxa are ecologically differentiated from each other by diverse dental morphologies that indicate several dietary specializations from omnivory to folivory; their estimated body-mass ranges from 3kg to over 1000kg; and several types of astragalus indicate generalist, arboreal and cursorial adaptations. This remarkable diversity, comparable to that found in the Fayum, is surprising at such an early date and reveals the great antiquity of the order Hyracoidea and its rapid diversification during the early Eocene.

## **SHARK AND RAY REMAINS FROM THE MIDDLE AND LATE EOCENE OF THE WESTERN DESERT OF EGYPT**

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The Fayum of Egypt is well known by vertebrate palaeontologists for its rich marine mammal faunas. Less well known are the equally rich and diverse shark and ray faunas based on isolated and occasionally associated teeth.

Over the last 20 years, large collections of fossil fish remains have been collected from the Middle and Late Eocene sediments at Wadi AL Hitan World Heritage Site (Zeuglodon Valley) and its surroundings by fieldworkers from the universities of Michigan and London and the Rangers of the EEAA (Egyptian Environmental Affairs Agency). Surface collecting was complemented by bulk sampling from geographically and stratigraphically defined sections from sediments representing palaeoenvironments ranging from offshore to lagoonal.

Although some of the larger teeth have been described and figured over the last century, the bulk of the fauna, those with teeth under 5mm in size, has previously remained undescribed.

This talk focuses on the sharks and rays that were collected from the sediment around a large skeleton of †*Basilosaurus isis*, collected in 2006 and prepared in the Museum of Paleontology, University of Michigan, Ann Arbor in 2007 and 2008. Large numbers of shark and ray teeth were obtained, and represent a high diversity assemblage from a probable inner shelf setting. Possible direct association between the whale remains and some of the sharks and rays will be discussed.



**EXTENSION GEOGRAPHIQUE DE LA FORMATION CONTINENTALE EOCENE DU GLIB ZEGDOU ET RECONSTITUTION PALEOENVIRONNEMENTALE DE SA FAUNE DE MAMMIFERES (EOCENE INFERIEUR A MOYEN, ALGERIE)**

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Des prospections géologiques et paléontologiques ainsi que le levé d'une dizaine de coupes lithologiques, sur les affleurements continentaux paléogènes de la région des Gour de la Hammada du Dra (Algérie) nous ont permis de mettre en évidence plusieurs sites à vertébrés, sur une étendue de plus de quarante kilomètres.

La faune de vertébrés est constituée de dipneustes, d'actinoptérygiens, de chéloniens et plus particulièrement de mammifères associés à des oogones de charophytes indiquant un âge Éocène inférieur à moyen.

Les nombreux mammifères récoltés ont une préservation exceptionnelle pour le Paléogène ancien arabo-africain et permettent une reconstitution paléoenvironnementale réalisée par la méthode des cénogrammes et par l'analyse de la diversité écologique.

L'abondance des espèces de petite taille (insectivores, primates, rongeurs), la présence d'espèces de taille intermédiaire (hyracoïdes) et la rareté des grandes espèces (hyracoïdes) mettent en évidence un milieu forestier fermé. Par ailleurs, les données sédimentologiques indiquent un milieu fluvio- (lacustre). L'analyse de la diversité écologique va à l'appui de l'hypothèse d'un milieu fermé mais ne permet pas de rejeter l'hypothèse de milieux plus ouverts sous climat tropical à saisons sèches en présence d'un système fluvial (et lacustre) où auraient pu proliférer les charophytes qui apparaissent particulièrement abondantes dans certains niveaux.

**Mots clés:** Eocène, Gour Lazib, Algérie, Mammifères, Cénogramme, Analyse de la Diversité, Ecologique, Paléoenvironnements.

**LES FAUNES QUATERNAIRES DE GUENFOUDA, (MAROC ORIENTAL)**

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Les fouilles menées depuis 2004 dans la grotte de Guenfouda, située dans les Monts d'Oujda, ont permis de mettre en évidence un matériel faunique riche et varié, associé à une industrie lithique abondante.

Les amphibiens sont représentés par 4 taxons : *Discoglossus pictus*, *Bufo mauritanicus*, *Bufo viridis* et *Rana* sp.. Parmi les reptiles au moins 13 taxons semblent être présents : *Testudo* sp. et *Emys* ou *Mauremys* parmi les chéloniens ; *Trogonophis wiegmanni* parmi les amphibéniens, et les squamates *Chamaeleo chamaeleon*, *Agama* cf. *bibronii*, cf. *Eumeces*, *Chalcides* sp., *Malpolon* sp., *Coronella* cf. *girondica* et *Natrix maura*, ainsi que des éléments appartenant aux familles Geckonidae et Lacertidae non déterminés.

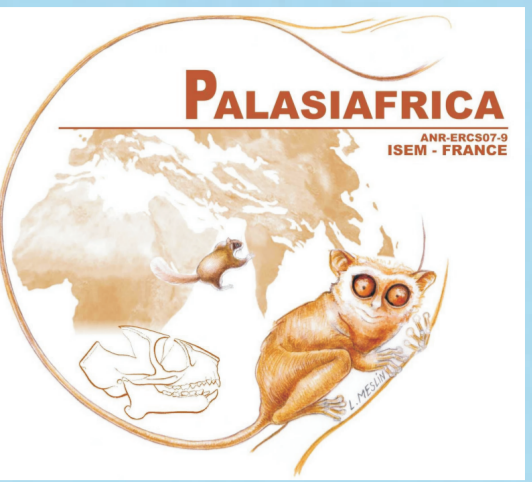
Les carnivores sont représentés par : *Canis familiaris* et *Vulpes vulpes*. Les herbivores sont très abondants et représentés par : *Equus* sp. (*mauritanicus* ?) et *Equus asinus*, *Sus scrofa* ou *Sus scrofa* cf. *domestica*, *Bos primigenius*, *Alcelaphus buselaphus*, *Ammotragus lervia*, *Ovis aries*, *Capra hircus* et au moins deux espèces de *Gazella*.



# Extension géographique de la formation continentale éocène du Glib Zegdou et reconstitution paléoenvironnementale de sa faune de mammifères (Sahara nord occidental - Algérie)

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La région des Gour de la Hammada du Dra (Glib Zegdou, Gour Lazib et Gour Idergane) est située dans la partie occidentale du Sahara algérien (Fig.1). Elle est constituée d'un ensemble de buttes témoins au sommets tabulaires, parfois isolées, résultant de l'érosion des hammada. Mahboubi (1995) a donné le nom de formation de Glib Zegdou à cette série continentale. Cette dernière masque souvent le socle paléozoïque et quelques fois les terrains marins du Cénozoïque du Kem Kem (Adaci et al., 2007). Depuis février 2004, de nouvelles prospections paléontologiques annuelles dans cette région, nous ont conduit à la découverte de plusieurs sites remarquables à vertébrés (mammifères, poissons, chéloniens, oiseaux) associés à un nombre parfois impressionnant de gyrogonites de charophytes.

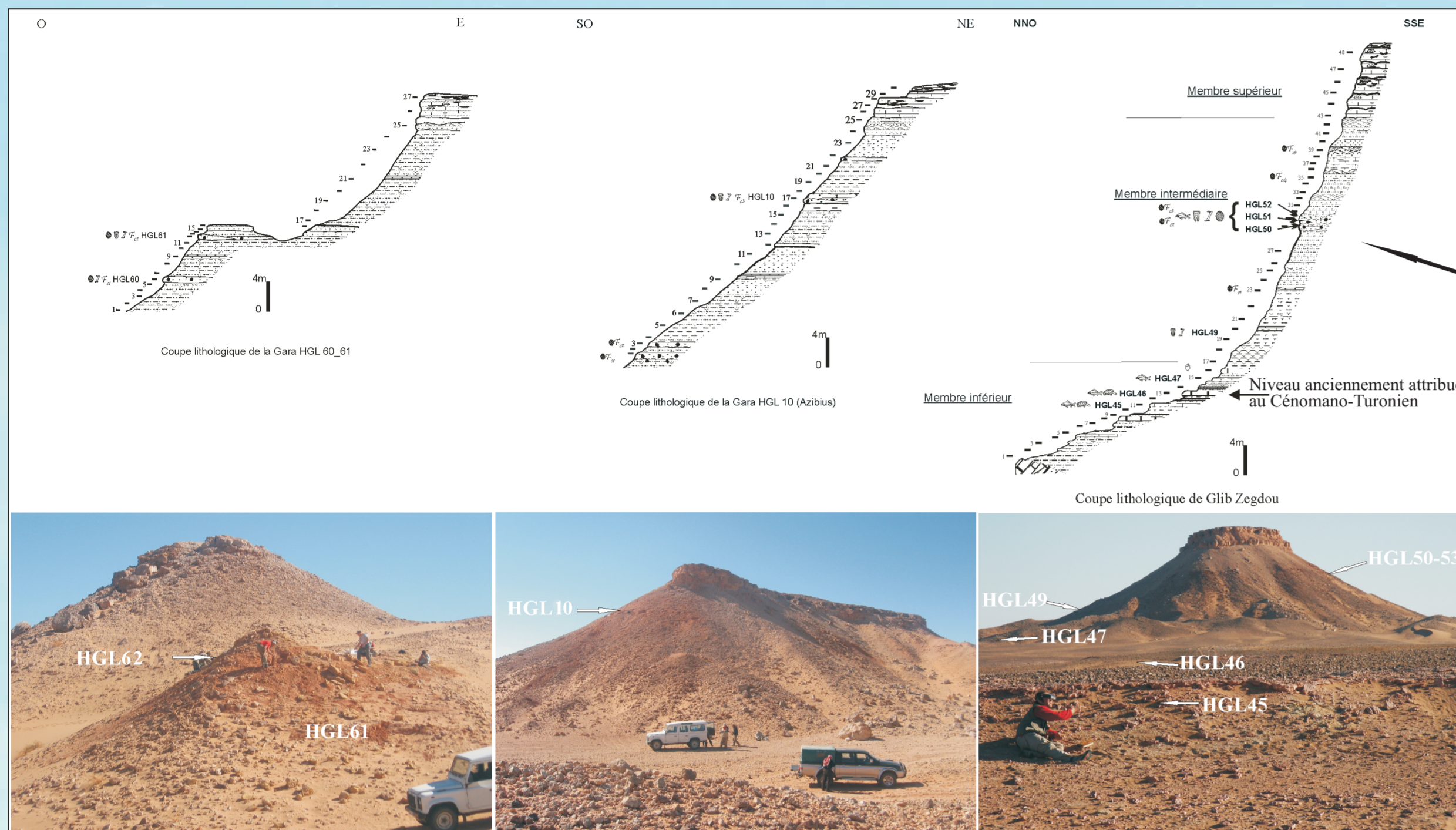


Fig. 2: Coupes lithostratigraphiques de référence des Gour Lazib.

Sur le plan biostratigraphique, les mammifères découverts sont pour la plupart endémiques (Tabuce et Marivaux 2005) ; et par conséquent leur intérêt biostratigraphique est limité. Cependant, l'étude des oogones de charophytes permet de proposer un âge Yprésien à Lutétien basal pour le membre intermédiaire de la formation du Glib Zegdou (Mebrouk et al., 1997 et 2004). Afin d'apporter d'autres éléments de datation, des analyses magnétostratigraphiques sont en cours.

## Reconstitution paléoenvironnementale

Grâce à son bon état de préservation et sa grande diversité spécifique (plus de 27 espèces), la faune de mammifères des Gour Lazib est unique à l'échelle du continent africain pour l'Eocène inférieur (Tab.1). Elle nous assure une bonne application de la méthode des scénogrammes et d'analyse de la diversité écologique pour reconstituer le paléohabitat de cette communauté mammalienne. Une méthode complémentaire au scénogramme (présence de taxons arboricoles), utile pour reconstituer les couvertures de végétations des localités

**Lithostratigraphie:** Les affleurements étudiés s'étendent sur plus de 40 km, du Glib Zegdou à l'Est jusqu'aux Gour Idergane à l'Ouest (Fig.1). La formation continentale du Glib Zegdou est subdivisée en 3 membres sédimentaires (Fig. 2). Un membre inférieur argilo-marno-gypseux recouvrant un substratum paléozoïque surmonté par un membre intermédiaire argilo-silto-gréseux très fossilifère. L'ensemble est coiffé par un membre supérieur grés-carbonaté souvent silicifié.

**Vue détaillée des niveaux HGL50 - HGL53**

|                                      | HGL02 | HGL04 | HGL08 | HGL10 | HGL11 | HGL49 | HGL50 | HGL52 | HGL53 | HGL88 | HGL89 | HGL90 |
|--------------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| <b>Rodentia</b>                      |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Gilbertomyia algierensis</i>      |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Gilbertomyia pentaplocha</i>      |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Gilbertomyia tetralopha</i>       |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Gilbertomyia sp.</i>              |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Zegdourmys lavocati</i>           |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Zegdourmys sp.</i>                |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Rodentia gen. et sp. nov. 1</i>   |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Rodentia gen. et sp. nov. 2</i>   |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Rodentia indet.</i>               |       |       |       |       |       |       |       |       |       |       |       |       |
| <b>Carnivora</b>                     |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Gilbertomyia tabellataensis</i>   |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Cretodonta (div. sp.)</i>         |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Lipotyphla (div. sp.)</i>         |       |       |       |       |       |       |       |       |       |       |       |       |
| <b>Chiroptera</b>                    |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Chiroptera gen. et sp. nov. 1</i> |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Chiroptera gen. et sp. nov. 2</i> |       |       |       |       |       |       |       |       |       |       |       |       |
| <b>Primates</b>                      |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Allogopithecus minutus</i>        |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Tabella hammadae</i>              |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Draïstella hammadaensis</i>       |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Azibus trekri</i>                 |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Azibus sp. nov.</i>               |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Primates gen. et sp. nov. 1</i>   |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Primates gen. et sp. nov. 2</i>   |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Primates gen. et sp. nov. 3</i>   |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Primates indet.</i>               |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Condylarthra gen. et sp. nov.</i> |       |       |       |       |       |       |       |       |       |       |       |       |
| <b>Hyacoïdes</b>                     |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Microhyrax lavocati</i>           |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Titanohyrax mongeraui</i>         |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Titanohyrax tantulus</i>          |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Megalohyrax geveni</i>            |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Titanohyrax sp.</i>               |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Hyacoïdes gen. et sp. nov.</i>    |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Hyacoïdes indet.</i>              |       |       |       |       |       |       |       |       |       |       |       |       |
| <b>Macroscélides</b>                 |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Chambius sp.</i>                  |       |       |       |       |       |       |       |       |       |       |       |       |
| <b>Mammalia incertae sedis</b>       |       |       |       |       |       |       |       |       |       |       |       |       |
| <i>Heliocoeus insolitus</i>          |       |       |       |       |       |       |       |       |       |       |       |       |
| formes indéterminables               |       |       |       |       |       |       |       |       |       |       |       |       |

Tableau 1: Liste faunique des mammifères des Gour Lazib



Vue panoramique des Gour Lazib

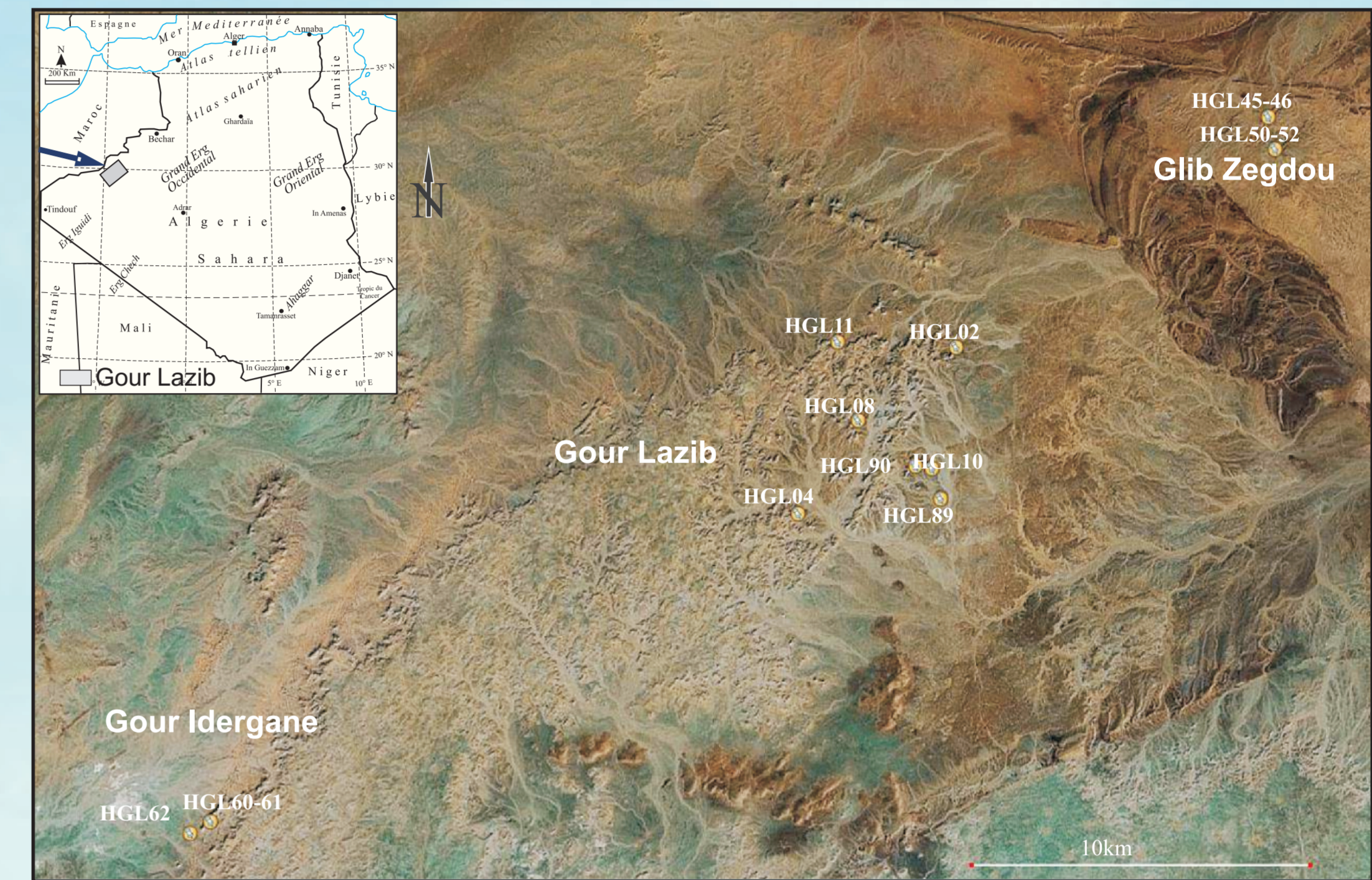


Fig. 1: Localisation géographique de la région d'étude et des sites à vertébrés des Gour Lazib

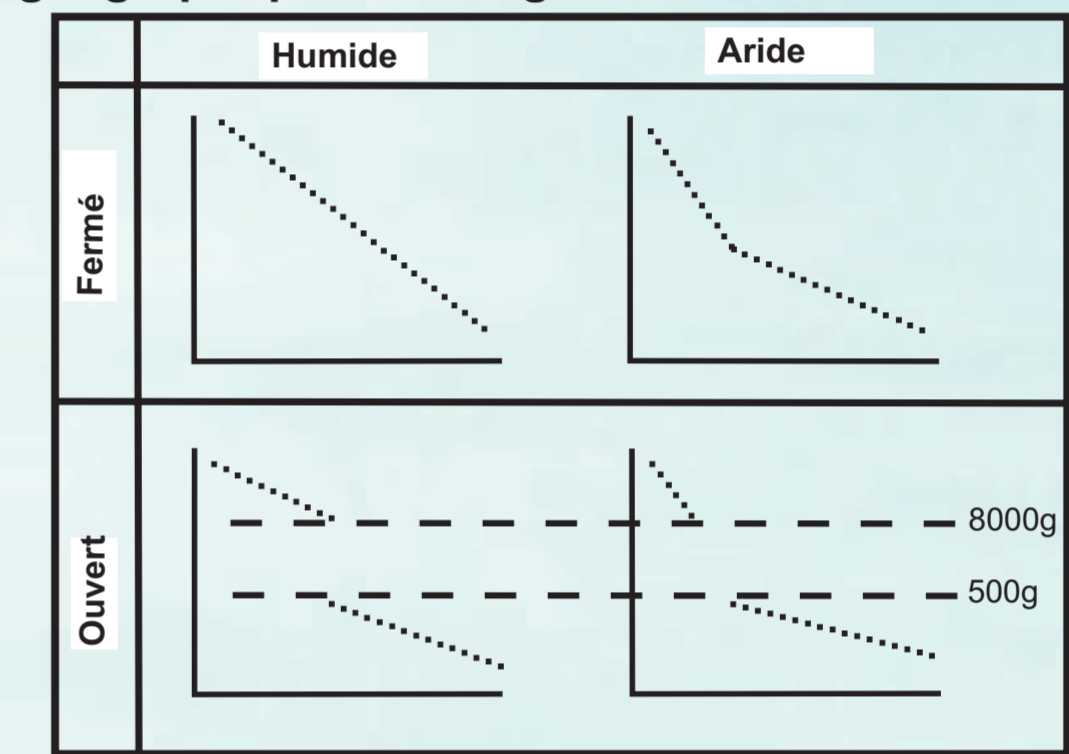


Fig. 3: Modèles de scénogrammes identifiés par Legendre (1989) et Travouillon et Legendre (2009)

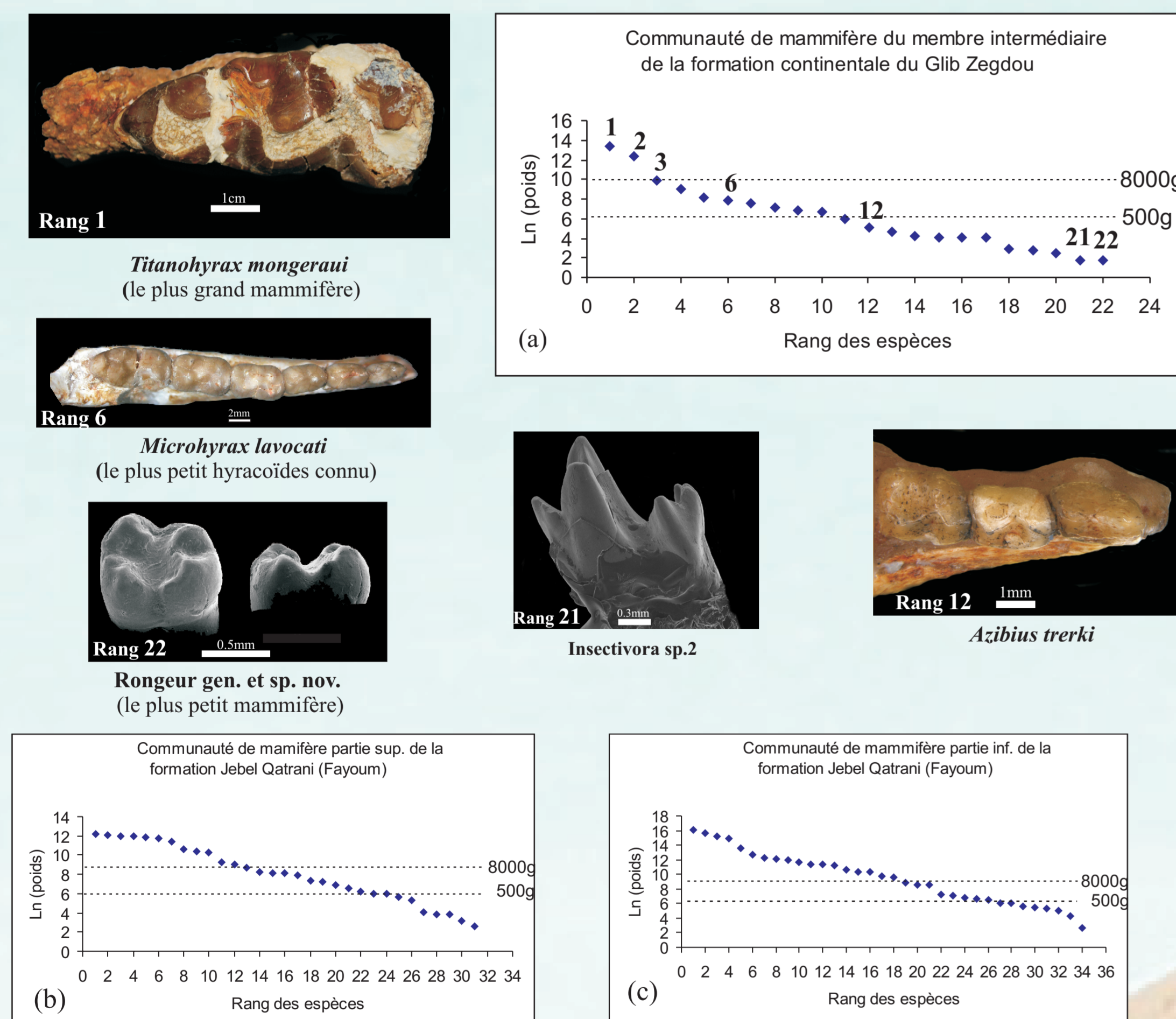


Fig. 4: Scénogrammes: Communautés de mammifères (a) du membre intermédiaire de la formation continentale des Gour Lazib; (b) de la partie supérieure de Jebel Qatrani; (c) de la partie inférieure de Jebel Qatrani (Ducrocq, 1997).

**3- Analyses de la diversité écologique:** La méthode utilisée ici est celle appliquée par Gagnon (1997) à la faune du Fayoum, elle même dérivée des travaux de Fleming (1973) puis Andrews et Evans (1979).

**Le spectre taxonomique,** de la faune des Gour Lazib, montre la prédominance de trois groupes, respectivement les rongeurs, les ongulés qui sont représentés essentiellement par des hyacoïdes, viennent ensuite les primates. Les insectivores et les carnivores sont minoritaires. Globalement, cette prédominance en pourcentage est comparable à celle des quatre zones du Fayoum et notamment à FFZ1 (Fig. 6.a).

**4- Concernant le régime alimentaire** (Fig.6.b), les herbivores « browser » présentent une richesse dominante devant les insectivores et les frugivores. Viennent ensuite les carnivores et les omnivores. Ce spectre évoque une affinité avec les milieux forestiers.

**5- L'examen des distributions pondérales** (Fig.6.c) de la faune des Gour Lazib évoque un milieu fermé caractérisé par une abondance des espèces de moins de 1 kg et par une décroissance rapide de la diversité spécifique, montrant ainsi un déséquilibre entre la distribution des espèces de petites tailles et les autres catégories. Ces résultats confirment ceux du scénogramme.

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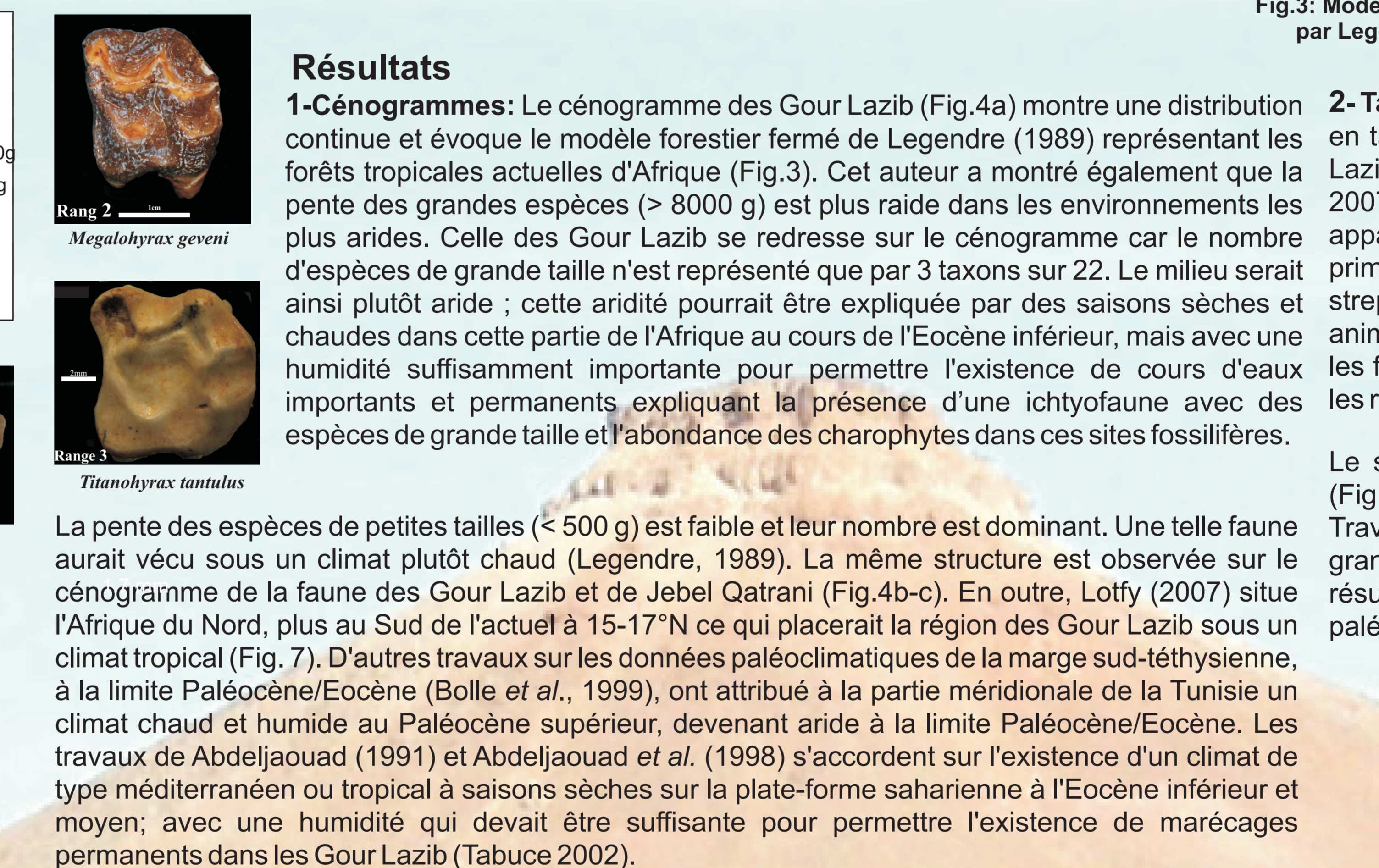


Fig. 6: Analyse de la diversité écologique des Gour Lazib (en gris) et comparaison avec le niveau fossilifère FFZ1 de Jebel Qatrani (en blanc) au Fayoum (Gagnon, 1997).

**6- En terme de diversité générique et spécifique** (Fig. 8a-d), la faune des Gour Lazib évoque les environnements fermés et ressemble à celle du Fayoum. Sa diversité d'ongulés est nettement inférieure à celle des communautés de milieux ouverts et avoisine celle des milieux forestiers actuels. Les hyacoïdes sont les seuls représentants des ongulés dans ces sites et représentent ainsi les plus grands mammifères. L'absence des proboscidiens est à signaler dans ces assemblages. Enfin, la diversité des primates est légèrement supérieure à celles des milieux ouverts et approche celles des milieux forestiers.

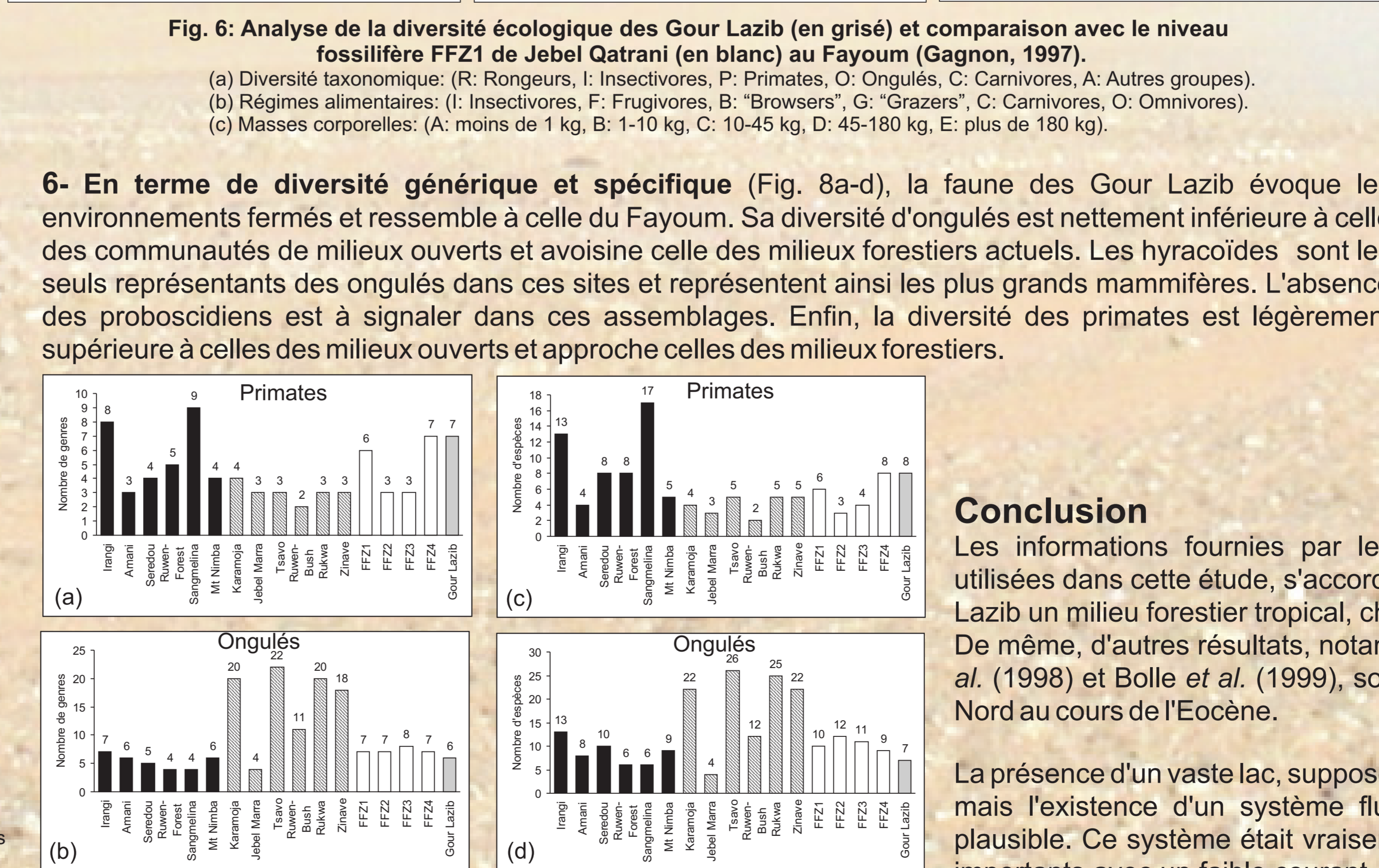


Fig. 8: Diversité générique (a, b) et spécifique (c, d) des primates et des ongulés. En noir, les environnements forestiers africains actuels. En hachuré, les environnements ouverts africains actuels. En blanc, les niveaux de Jebel Qatrani. En gris, 17-Gour Lazib.

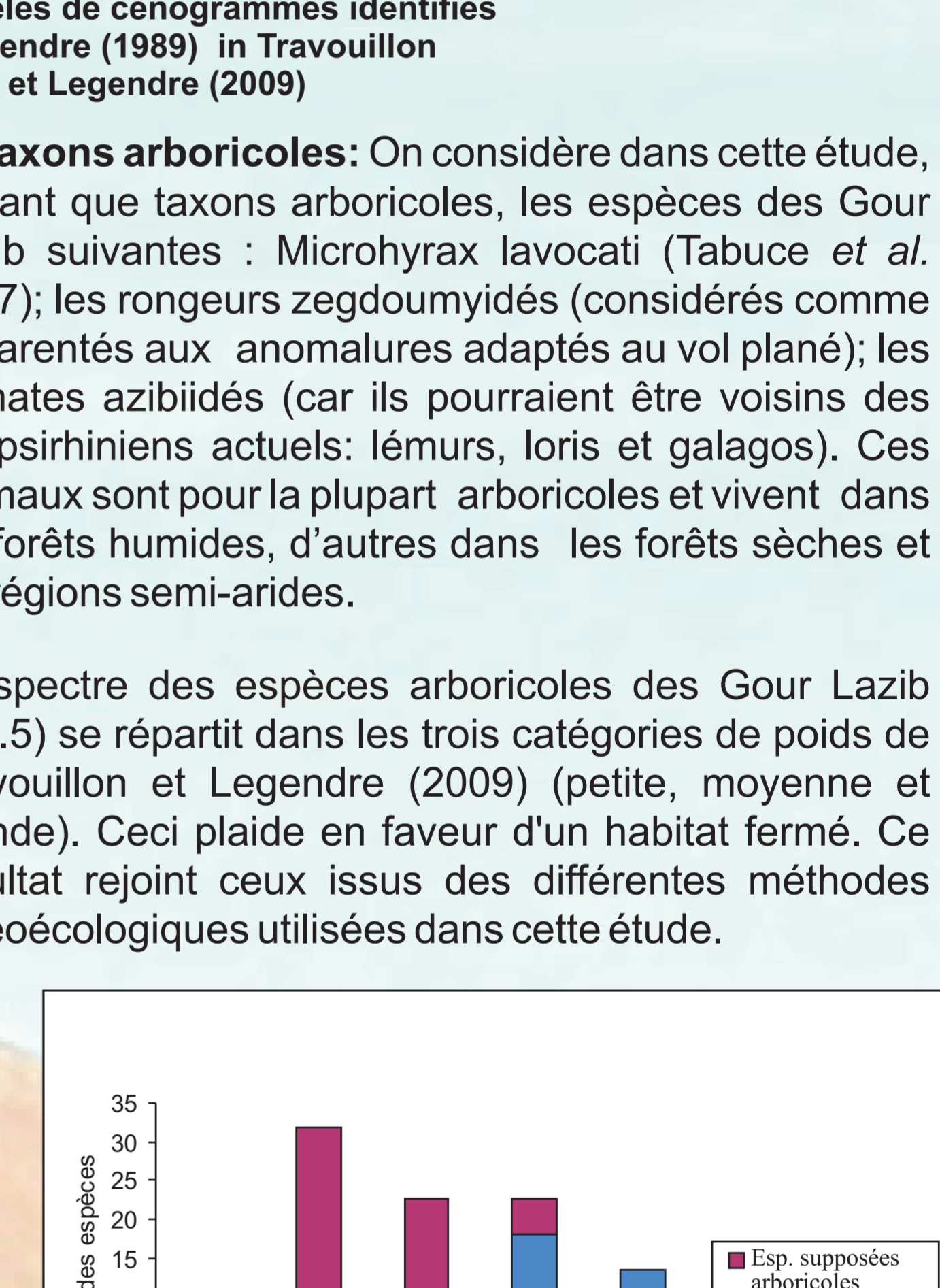


Fig. 5: Pourcentages des taxons dans chacune des catégories de poids choisies avec les espèces supposées arboricoles de la faune mammalienne des Gour Lazib.

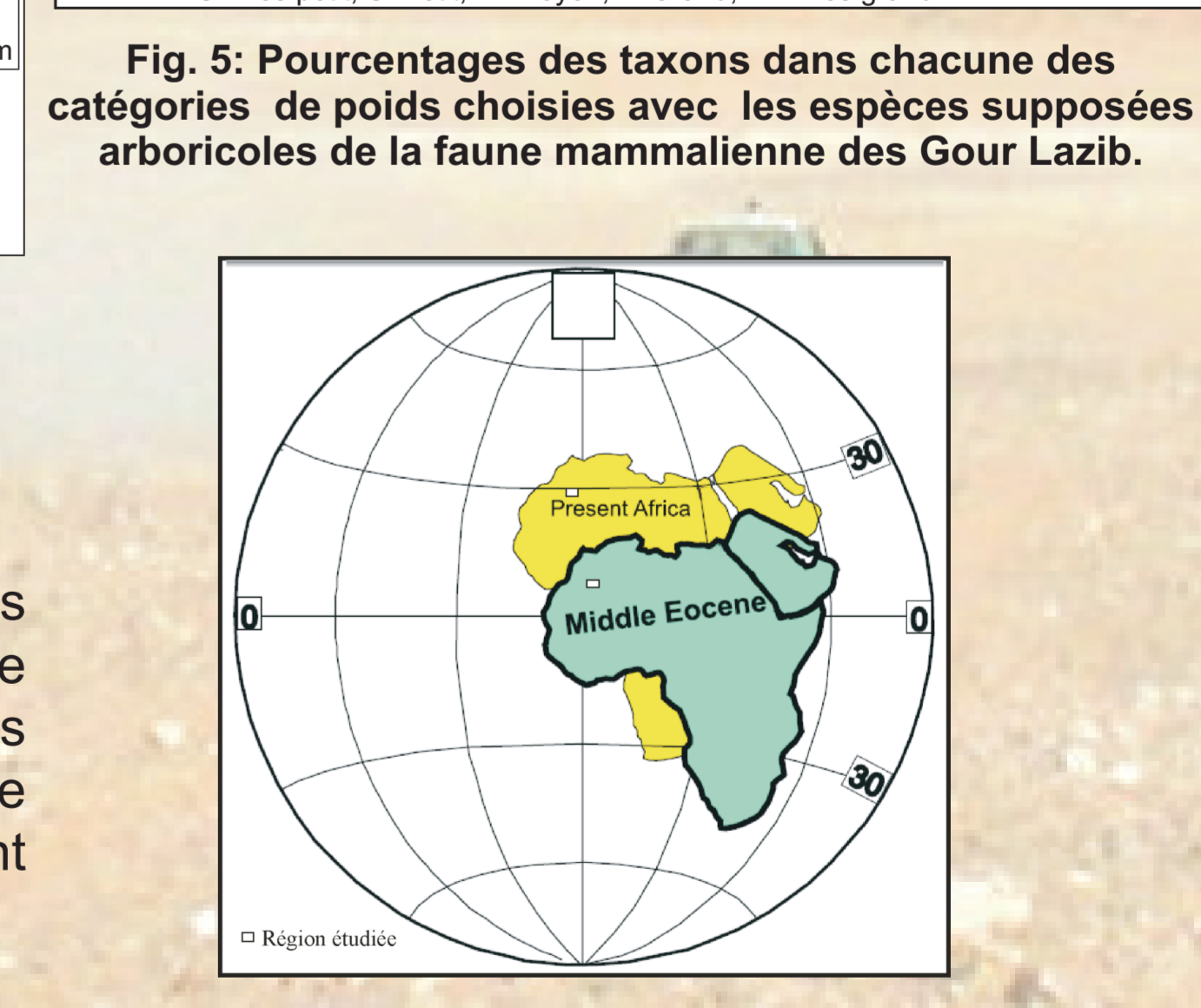


Fig. 7: Paléogéographie du continent africain à l'Eocène moyen-Oligocène inférieur (Lotfy 2007)

## Conclusion

Les informations fournies par les différentes méthodes paléoenvironnementales, utilisées dans cette étude, s'accordent pour inférer à la faune mammalienne des Gour Lazib un milieu forestier tropical, chaud et humide, soumis à une saisonnalité marquée. De même, d'autres résultats, notamment ceux obtenus en Tunisie par Abdeljaoued et al. (1998) et Bolle et al. (1999), soutiennent la présence d'un tel climat en Afrique du Nord au cours de l'Eocène.

La présence d'un vaste lac, supposé par Gevin (1975b) et Tabuce (2002) reste possible, mais l'existence d'un système fluvial avec méandres reste l'hypothèse la plus plausible. Ce système était vraisemblablement représenté par des cours d'eau très importants avec un faible courant, probablement bordé d'une forêt-galerie où vivaient les primates et rongeurs, puis de milieux ouverts en périphérie dans lesquels les hyacoïdes de grandes tailles devaient évoluer.

**Remerciements:** Nous remercions vivement le recteur de l'Université de Tlemcen pour son aide précieuse. Nous remercions également les autorités civiles et militaires des Wilayates de Bechar et Tindouf qui ont donné l'autorisation de prospection et qui nous ont assistés au cours de nos missions. Enfin, Monsieur Yahiaoui et sa famille sont remerciés pour leur accueil chaleureux et assistance.





**DEUX NOUVEAUX TELEOSTEENS DES GISEMENTS DES PHOSPHATES DU MAROC  
(BASSIN DES OULED ABDOUN, EOCENE) : ANATOMIE ET SYSTEMATIQUE**

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Le bassin des Ouled Abdoun, au Maroc, est constitué d'une série phosphatée continue du Maastrichtien à l'Yprésien, documentant ainsi une période de plus de 25 millions d'années. Parmi les nombreux vertébrés fossiles des gisements des phosphates, les Actinoptérygiens y présentent une importante composante faunique constituée par au moins 11 familles appartenant aux Pycnodontes et aux téléostéens Aulopiformes, Ichthyodectiformes, Albuliformes, Osteoglossiformes et Perciformes. Cette diversité est sans cesse augmentée par les nombreux travaux de terrains effectués dans le cadre d'un projet de coopération franco-marocaine. Les deux nouveaux taxons décrits ici en sont une illustration.

Le premier taxon est représenté par un spécimen : un toit crânien subcomplet, écrasé latéralement. Il provient de l'intercalaire Thanétien-Yprésien et partage de nombreuses synapomorphies avec *Phosphichthys thomasi* (Perciformes, Serranidae de l'Eocène inférieur de Metlaoui, Tunisie), telles des crêtes pariétales courtes, un prootique bien développé. Le taxon marocain se distingue par son neurocrâne moins large et l'ornementation moins prononcée de ses frontaux.

Le second taxon est représenté par deux neurocrânes bien préservés, qui proviennent du Danien. Il est attribué ici aux Megalopidae (Elopiformes, Elopomorpha) et présente de nombreux points communs avec les genres *Protarpon* et *Promegalops* (Yprésien, London Clay, Angleterre) : pariétaux unis par une ligne médiane, ptérotiques et fosses post-temporales bien développés. La comparaison avec le Megalopidae actuel, *Megalops atlanticus*, est également proposée.

Il s'agit de la première mention de Megalopidae dans les Phosphates d'Afrique du Nord et du premier Serranidae dans les Phosphates du Maroc.

**Mots clés.** Anatomie crânienne, Megalopidae, Serranidae, Systématique, Eocène, Bassin des Oulad Abdoun.

**THE DISCOVERY OF AVIAN EGG AND BONE REMAINS FROM THE GOUR LAZIB,  
(EOCENE, ALGERIA)**

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Numerous avian eggshells and one well-preserved small ovoid-shaped egg (32 x 28 mm) were collected in the Gour Lazib area from three localities (HGL10, 51 and 62); these sites are dated from the early to early middle Eocene by both the charophyte assemblages and associated mammalian fauna (e.g., primates, rodents and hyraxes) (Adaci et al. 2007). The scanning electron microscopy (SEM) study of the eggshells led to attribute them to neognathous birds. These eggshells are characterized by a thin shell (less than 0.5 mm thick) with a prismatic microstructure composed of three structural layers. Moreover, the richest mammalian site HGL50, which is located one meter below the eggshells found on HGL51, yielded



an avian carpometacarpus belonging to the Presbyornithidae. This discovery suggests that the egg remains found on the Gour Lazib area may be referred to this bird family, which is so far unknown in the Paleogene deposits of the Afro-Arabian continent.

ADACI M., TABUCE R., MEBROUK F., BENSALAH M., FABRE P.-H., HAUTIER L., JAEGER J.-J., LAZZARI V., MAHBOUDI M., MARIVAUS L., OTERO O., PEIGNE & TONG H. 2007. Nouveaux sites à vertébrés paléogènes dans la région des Gour Lazib (Sahara nord-occidental, Algérie). *C.R. Palevol* 6: 535-544.

### **FOSSIL AGAMID LIZARD REMAINS FROM THE EARLIEST OLIGOCENE OF EGYPT**

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Agamid lizards, a group of 54 genera in two subfamilies, are found in Africa, Asia, and Australia. Together with the Chamaeleontidae and some extinct basal forms, they comprise the Acrodontia, lizards with acrodont dentition. The Acrodontia have been suggested to have a Gondwanan origin, with the oldest members found in the Triassic of India. Early agamids are known from the Late Cretaceous of Asia.

Few agamid lizard remains have been recovered from Africa. A single jaw fragment bearing acrodont dentition, possibly attributable to Agamidae, has been reported from the Palaeogene of Morocco, and material identified as agamid was reported from the Oligocene of Oman. We here add to the African record several agamid jaws with attached teeth from earliest Oligocene deposits of the Jebel Qatrani Formation in the Fayum Depression, Egypt. The teeth are in the form of short cylinders, with a very rounded labial surface; shearing edges are concave lingually and the shearing tip is crescentic; accessory cusps are absent. In these characteristics, they most closely resemble the teeth of *Uromastyx*. Species of *Uromastyx* currently inhabit the Saharan and Somalian regions of Africa and adjacent Arabia.

Living agamids are diurnal lizards generally found in terrestrial and arboreal habitats, with only a few species being semi-aquatic. If the Fayum fossil agamid had similar habitat preferences it might explain the paucity of remains found in the predominantly fluvial sediments of the Fayum deposits.

### **NEW RODENT ASSEMBLAGES FROM THE EOCENE DUR AT-TALAH ESCARPMENT (SAHARA OF CENTRAL LIBYA): SYSTEMATIC, BIOCHRONOLOGIC AND PALEOBIOGEOGRAPHIC IMPLICATIONS**

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In the framework of a Franco-Libyan paleontological project, surveys in the Idam Unit of the Dur At-Talah escarpment (Sahara of Central Libya) have led to the discovery of several microfossil concentrations. Screen washings have yielded diverse assemblages of aquatic and terrestrial vertebrates, together with terrestrial mammals (rodents, bats, creodonts, marsupials, elephant shrews, hyraxes, primates). From isolated teeth, five rodent taxa belonging to the Phiomyidae (Hystricognathi) have been identified, being distributed among three genera (*Phiomys*, *Protophiomys*, and *Talahphiomys* gen. nov.) with three new species. These rodent assemblages suggest a late middle Eocene age for the Idam deposits. Other mammals, especially Proboscidea, which occur in the same sedimentological unit, substantiate this age hypothesis. Interestingly, the dental patterns of *Protophiomys* and *Talahphiomys* have somewhat stronger affinities with South Asian hystricognath baluchimyines than with Fayum phiomyids. It is clear that baluchimyines and phiomyids have a common ancestry, and that dispersal occurred between Asia and



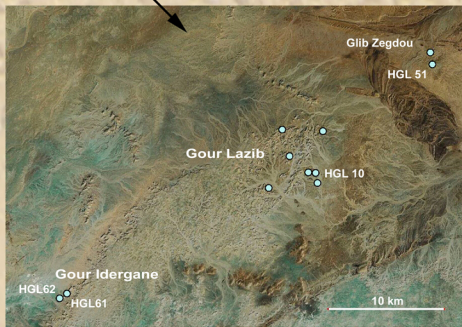
# THE DISCOVERY OF AVIAN EGG AND BONE REMAINS FROM THE GOUR LAZIB, (EOCENE, ALGERIA)

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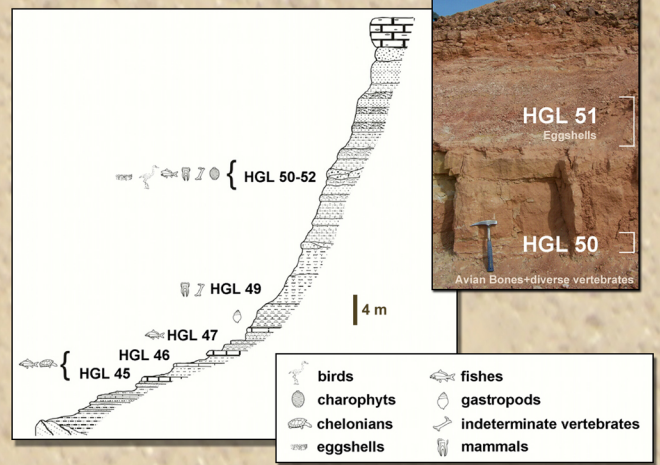
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Numerous avian eggshells and one well-preserved small ovoid-shaped egg (32 x 28 mm) were collected in the Gour Lazib area from three localities (HGL10, 51 and 62 Fig. 1a); these sites are dated from the early to early middle Eocene by both the charophyte assemblages and associated mammalian fauna (e.g., primates, rodents and hyraxes Adaci *et al.* 2007). Moreover, the richest mammalian site HGL50, which is located one meter below the eggshells found on HGL51, yielded an avian carpometacarpus (Fig. 1b).

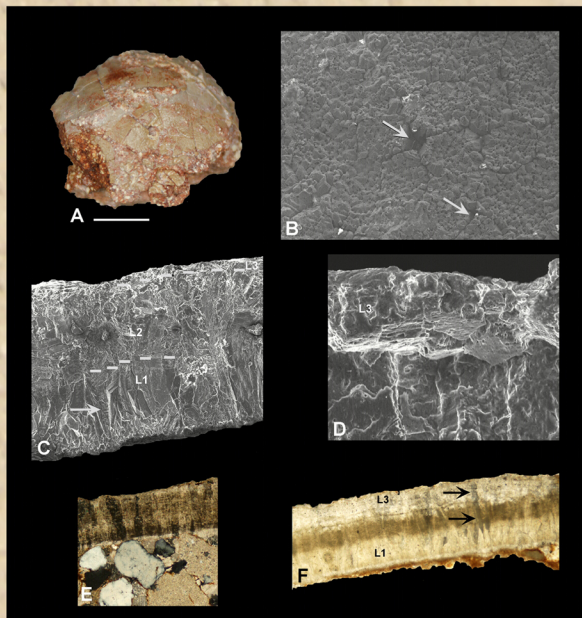


**Figure 1b.** Lithological synthetic section of the Glib Zegdou with photograph of the levels having yielded avian remains, HGL 50 and HGL 51.



**Figure 1a.** Location of the discovered vertebrates sites in the Glib Zegdou Formation (western Sahara, Algeria).

The eggshells, which are in variable proportions according to the sites have been collected directly in situ or in screen-washing the sediments. We have used scanning electron and polarizing light microscopes (SEM and PLM) to study the radial sections and the outer surfaces.



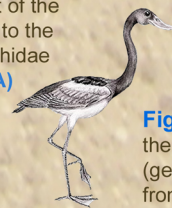
The microstructural study of the eggshells led to attribute them to neognathous birds. They are composed by a trilaminar arrangement of calcite crystals: at the base an inner mammillary layer (L1) which evolves gradually into interlocking shell columns (L2) overlaying by a thin external layer (L3). Their thicknesses are less than 0.5 mm, depending on their preservation. Their pore openings are isolated and their outer surface is not ornamented.

**Figure 2.** A. n° HGL10A, a nearly complete egg with an ovoid shape. B-D. SEM micrograph images of eggshells. B. n° HGL10-4a Circular pore orifices on the outer surface (arrows) x 180. C. n° HGL10B eggshell exhibits a typical neognathous microstructure with three prismatic structural layers (L1-L3), radial view SEM x 150. Wedges of the L1 grade into prisms. The boundary between L1 and L2 is gradational. D. n° HGL62A Detail of the smallest L3 which is a synapomorphic feature of the crown clade Aves, SEM x 550. E and F. Polarizing light micrographs of thin sections. E. n° HGL10A-1 Eggshell fragment from the specimen HGL10A. Note the prismatic structure with well distinct columns x 40. F. n°HGL10B The mammillae are underlined by alterations and a possible canal pore is observable (arrows) x 100.

This discovery suggests that the egg remains found in the Gour Lazib area may be referred to the Presbyornithidae, a family so far unknown in the Paleogene deposits of the Afro-Arabian continent. This extinct waterfowl family, typical of lacustrine environments (bones sometimes associated with eggshell fragments, Leggitt and Buchheim 1997, Leggitt *et al.* 1998) has been discovered in the Upper Cretaceous to Paleogene deposits from both North America and Eurasia (Hope 2002, Kurochkin *et al.* 2002, Ericson 2000, Dyke 2001, Mayr 2005).



**Figure 3.** Avian carpometacarpus (n° HGL50-115) attributed according to morphological characteristics (position and extension of dorsal/ventral crests of the trochlea, a conspicuous rim along the outline of the dorsal crest of the trochlea...) to the Presbyornithidae in ventral (A) and dorsal (B) views.



**Figure 4.** Reconstitution of the presbyornithid bird (genus *Presbyornis* from USA)



**Annexe n°7**

# MAGNETIC POLARITY STRATIGRAPHY AND AGE OF THE EARLYMIDDLE CONTINENTAL EOCENE DEPOSITS OF EL KOHOL AND GOUR LAZIB (ALGERIA)

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## 1. INTRODUCTION

The Paleogene continental deposits of Africa have witnessed major events in early Tertiary mammalian history. This continent has been a centre of evolution for some important groups, such as Afrotheria, and has been also a secondary diversification centre for anthropoid primates and hystricognath rodents. Knowledge of early evolutionary history of African mammals has been considerably improved during the last past decades. Nevertheless, the Paleogene fossil record of terrestrial mammals in Africa is still scarce and poorly dated. Recognition of Eocene-Oligocene African fauna is limited to several localities, mainly dispersed along the southern paleo-coastline of the Tethys Sea.

During most of the Paleogene, Africa was geographically relatively isolated from other landmasses. Although several limited terrestrial faunal interchanges between Africa and the North Tethyan landmass and/or Asia have been documented through these times (e. g. Tabuce and Marivaux 2005; Gheerbrant and Rage 2006), the significant degree of endemism of the vertebrate fauna of Paleogene African fossiliferous localities have impeded biostratigraphic correlations with non African fossil assemblages. The low ordinal diversity of vertebrate taxa, the absence of absolute dating, the lack of good marine invertebrate record and the long ranging taxa characterizing the flora and lower vertebrate fauna, have been causes of the poorly constrained ages of these Eocene-Oligocene mammalian localities.

The numerous localities of the Fayum Depression in Northern Egypt have yielded so far the richest collections of Paleogene faunas, including diversified fossil primates (e.g. Simons and Kay 1983; Simons and Bown 1985; Simons 1989, 1997; Seiffert et al. 2005, 2010). Paleontological field research began in the Fayum depression by the end of the 19<sup>th</sup> century (Dames 1883; Schweinfurth 1886; Andrews 1901). Since over 40 years, Simons and his team, considerably expanded Fayum fossil collections. Remains of Anthropoid primates collected from the Jebel Qatrani Formation constitute actually the richest African record of early anthropoids. The Fayum is recognized as the best documented Paleogene site in Africa but the age of these deposits has been a long-standing controversy. Over the years, the Jebel Qatrani Formation has

been believed to be entirely late Eocene (Van Couvering and Harris 1991), purely Oligocene (Bown and Kraus 1988; Gingerich 1993) or latest Eocene to early Oligocene in age (Rasmussen et al. 1992; Kappelman et al. 1992; Seiffert et al. 2005; Seiffert 2006).

The significant degree of endemism of the Fayum fauna, the restricted number of comparable faunal assemblages and the lack of good biostratigraphic marine invertebrate have made relative dating arduous. A minimum age of late Oligocene was obtained by radiometric dating ( $^{40}\text{Ar}/^{39}\text{Ar}$  method) of the Widan el Faras Basalt, which unconformably overlies the Jebel Qatrani Upper sequence (Kappelman et al. 1992). A time-stratigraphic framework for the deposits of the Fayum depression was further provided by reversal magnetic polarity (Kappelman, 1992; Kappelman et al. 1992). However, several different potential correlations to the Geological Polarity Time Scale, based on mammalian biostratigraphic and sequence stratigraphic studies, were proposed during the past decades (Kappelman et al. 1992; Gingerich 1993; Seiffert et al. 2005). Seiffert (2006) proposed the last revised reinterpretation of Fayum magnetic polarity sequence on the basis of mammalian biostratigraphy and his preferred magnetostratigraphic correlation of the Fayum deposits supports that the Jebel Qatrani Formation contains both late Eocene and early Oligocene components. These deposits are believed to span a great time period, ranging from the earliest late Eocene (~37 Ma) to latest early Oligocene (~29Ma).

The most complete late Paleogene afro-arabian mammal assemblages outside of Egypt has been reported from Thaytiniti and Taqah sites in the Dhofar province of Sultanate of Oman (Thomas et al. 1989, 1991, 1992; Pickford et al. 1994). Both sites, at the base of the transgressive marine unit of the Ashawq Formation, have been relatively well dated. Chronological constraints of these terrestrial mammalian localities have been mainly based on the presence of marine invertebrates. The foraminiferal assemblages, described from the Ashawq Formation, are characteristic of earliest Oligocene time and the lacustrine and the paludal deposits of Zalumah Formation, underlying the Ashawq Formation, have yielded charophytes characteristic of late Priabonian (Thomas et al. 1989). The Dhofar sites have yielded rich mammal assemblages somewhat close to those of Jebel El Qatrani Formation (Thomas et al. 1989, 1991, 1992; Roger et al. 1993; Pickford et al. 1994; Gheerbrant 1995; Seiffert 2006). Seiffert's (2006) reinterpretation of the correlation of Taqah and Thaytiniti magnetic polarity sequences suggest an earliest Oligocene age for the Omani fossiliferous strata.

Revised correlation of the Fayum and Dhofar magnetostratigraphies provides so far the most reliable continental references for the late Paleogene of Africa but the chronology of African localities which record older time than Fayum sequence is still poorly constrained. The oldest quarry of Fayum deposits, Birket Qarun Locality-2, which has yielded an abundant Paleogene mammal assemblage including creodonts, chiropterans, proboscideans, primates, hyracoids, macroscelidids, ptolemaiids, anomaluroid and hystricognathous rodents, is considered as earliest Priabonian (~37 Ma.) in age (Seiffert et al. 2008). Its mammalian fauna is close to that described from Bir El Ater in the Nementcha Mountains, Algeria and from Dur At-Talah, Central Libya. These localities have yielded the oldest known genus of hystricognathous phiomyid rodent *Protophiomys* (Jaeger et al. 1985; Sallam et al. 2009; Jaeger et al. 2010a), species of primitive proboscidean *Moeritherium* (Andrews 1901; Tassy 1981; Delmer et al. 2006) and the parapithecoid anthropoid *Biretia* (de Bonis et al. 1988; Seiffert et al. 2005; Jaeger et al. 2010b) which substantiate the hypothesis that these sites are roughly similar in age.

Other African Eocene fossiliferous localities from Morocco (Ouarzazate basin, Ouled Abdoun basin), Algeria (Gour Lazib, El Kohol), and Tunisia (Chambi) fall outside the time sequence represented by the Fayum deposits and appear to be significantly older than the oldest quarries of Fayum. In Morocco, the near shore marine deposits from Ouarzazate basin (Adrar Mgorn 1, Adrar Mgorn 1bis, N'Tagourt 2, and Aznag localities) (Cappetta et al. 1978; Sigé et al. 1990; Sudre et al. 1993; Gheerbrant 1992, 1993, 1994, 1995, Gheerbrant et al. 1998a; Tabuce et al. 2005) and the phosphate deposits of Ouled Abdoun basin (Cappetta 1981, 1983, 1984, 1985, 1986; Gheerbrant et al. 1998b; 2001; Cavin et al. 1999; Gheerbrant et al. 2003; Bourdon 2006) document the oldest known placental mammals of Africa including the oldest known proboscidean *Eritherium azzouorum* (Gheerbrant 2009). The mammal localities of the Ouarzazate basin have been well dated as late Thanetian (Adrar Mgorn 1 and Adrar Mgorn 1 bis), early Ypresian (N'Tagourt 2), and middle Lutetian (Aznag) on the basis of the nannofossils (Gheerbrant et al. 1998a; Tabuce et al. 2005), the selachians (Cappetta et al. 1987; Cappetta 1993; Gheerbrant 1993; Gheerbrant et al. 1998a) and magnetostratigraphic studies (Gheerbrant et al. 1998a). Based on the foraminifera and selachian assemblages, the phosphate fossiliferous horizons of Ouled Abdoun basin have been dated as Thanetian to Ypresian in age (Gheerbrant et al. 1998a, 2003, 2005).

The Eocene Maghrebi sites of Algeria (Gour Lazib and El Kohol) and Tunisia (Chambi) display mammalian assemblages lacking the presence of immigrant genera of mammals which have entered Africa during middle Eocene faunal exchanges between Asia and North Africa (e.g., Tabuce and Marivaux 2005; Gheerbrant and Rage 2006). Anthracotheriid artiodactyles, anthropoid primates and hystricognathous rodents, which are believed to derive from Asiatic immigrants (Marivaux et al. 2002, 2004; Beard et al. 1994, 1996; Ducrocq 1997, 1999; Jaeger et al. 1999; Ducrocq et al. 2000; Beard and Wang 2004; Jaeger and Marivaux 2005; Tabuce and Marivaux 2005; Bajpai et al. 2008), are first documented in the late middle-late Eocene deposits of Africa (Jaeger et al. 1985; de Bonis et al. 1988; Mahboubi et al. 2003; Seiffert et al. 2005; Sallam et al. 2009; Jaeger et al. 2010a, b). The localities of Chambi and Gour Lazib have yielded peculiar fauna assemblages comprising Zegdomyidae (Vianey-Liaud et al. 1994), a poorly known group of primitive rodents considered by Marivaux et al. (2010) as a possible early African stem group for Anomaluridae, earliest offshoots of an endemic Afro–Arabian strepsirrhine clade including *Azibius*, *Algeripithecus* (Godinot and Mahboubi 1992; 1994; Tabuce et al. 2009) and *Djebelemur* (Hartenberger and Marandat 1992), and a primitive representative of the macroselidid *Chambius* (Hartenberger 1986; Tabuce et al. 2007; Adaci et al. 2007), without any evidence of the previously mentioned Asian immigrants.

To sum up roughly, the main fossiliferous Eocene sites which document the early evolutionary history of North African mammals, may be placed in two categories based on faunal assemblage comparison: the localities which pre-dates the middle Eocene dispersal event and arrival of invading anthracotheriid artiodactyls, hystricognathous rodents and anthropoids from Asia (Adrar Mgorn 1, N'Tagourt 2, El Kohol, Hammada du Dra, Chambi localities) and those which are thought to be late middle to early late Eocene in age, approximately equivalent in age to Birket Qarun Locality-2 of Fayum (Dur At-Talah, Bir El Ater). A third cluster would include the middle Eocene localities of M'Bodione Dadere in Senegal (Gorodiski and Lavocat 1953), In Tafidet in Mali (Arambourg et al. 1951 Gheerbrant et al. 1998a), Mahenge in Tanzania (Harrison et al. 2001; Gunnell et al. 2003; Kaiser et al. 2006), Aznag in Morocco (Tabuce et al. 2005) and Sperrgebiet in Namibia (Pickford et al. 2008) which are thought to be Lutetian in age,

but mammalian remains from these localities are very scarce and poorly preserved. The age of the sparse mammal fossils from Tamaguélelt, Mali, has been controversial, being considered either early Eocene or middle Eocene in age (Lavocat 1953; Radier 1959; Savage 1969; Mahboubi et al. 1986; Patterson and Longbottom 1989; Moody and Sutcliffe 1993; Tapanila et al. 2004). However, studies of benthic foraminifera, bivalves, shark and ray teeth and the pycnodont fish, actually support an early Eocene age for Tamaguélelt phosphate conglomerate (O'Leary et al. 2006). The Mahenge locality in Tanzania has been well-dated by U/Pb absolute age of ~ 45–46 Ma (Harrison et al. 2001) and the age of the Aznag locality in the Ouarzazate Basin of Morocco, has been well constrained by correlation with planktonic foraminiferal Zone P11, which indicate an age comprises between 45.8 and 43.6 Ma (Tabuce et al. 2005). The mammalian fossil remains recovered from Aznag are very fragmentary and document chiropterans, indeterminate rodent, indeterminate soricomorph, a small primate and two condylarths while mammals from the Mahenge locality of Tanzania are only represented by the microbat *Tanzanycteris mannardi* (Gunnell et al. 2003). Unfortunately, Aznag and the Mahenge localities, which are the only settled middle Eocene continental mammalian sites in Africa, yielded scarce poorly preserved fossil remains.

The early-middle Eocene localities of Glib Zegdou Formation in Hammada du Dra have produced a much more diverse mammalian assemblage, including primates (Gevin et al. 1975; Sudre 1975, 1979; Godinot and Mahboubi 1992, 1994; Vianey-Liaud et al. 1994; Mahboubi 1995; Crochet et al. 2001; Mahboubi et al. 2002; Adaci et al. 2007; Tabuce et al. 2001, 2004, 2007, 2009). However, despite the abundance of fossils, the relative ages of these sites and that of the early to middle Eocene purely continental formation of Algeria (El Kohol) and Tunisia (Chambi) are still controversial. The charophytes, fresh water gasteropods and ostracodes (Gevin et al. 1974; Mebrouk et al. 1997; Mebrouk and Feist 1999; Faid 1999) found in association with unique assemblages of mostly primitive endemic mammals yield low resolution biostratigraphic evidence and the limited occurrence of comparable sites has made relative faunal correlation tenuous.

A dated framework of these deposits is now essential to calibrate the Eocene African biochronologic scale and the purpose of this study is to establish a high-resolution magnetostratigraphy and biochronology calibration for the Eocene continental formations of El Kohol and Gour Lazib.

The 400m thick section of Eocene deposits, exposed at El Kohol locality, on the southern border of the Saharan Atlas, is relevant for African early Eocene stratigraphy study due to its excellent exposures and its diversified mammalian fauna. The establishment of its magnetic polarity stratigraphy could be used as a magnetic polarity reference sequence for early Eocene continental African deposits. The Lower Detrital and Intermediate Marly and Calcareous Members have yielded the main fossiliferous horizons of El Kohol sequence and the magnetic polarity stratigraphy study of the serie would provide the first precise data concerning their geological age.

In the area of the Gour Lazib vertebrate locality, located in the western part of the Algerian Sahara at about 400 km southwest of Bechar, the maximum thickness of the continental series is about 50 meters at the Glib Zegdou, the highest resthill of the area. The fossil assemblages, discovered from distinct loci in this area, indicate a Ypresian to basal Lutetian age.



Nevertheless, Rasmussen et al. (1992) interpreted the fossil record of Gour Lazib (including Glib Zegdou) as being similar in age to that of uppermost Fayum localities, based on hyracoid faunas. In order to constrain the age, the lithological section exposed on the Glib Zegdou outlier, which offers the most complete continental section of the studied area, has been sampled for magnetic polarity stratigraphic study.

The precise age estimates, provided by magnetozone studies and correlations with the Geological polarity Time scale, would precise the age of these two localities which document the poorly known early-middle Eocene African mammal evolutionary history and contribute to the establishment of reliable continental references for the Eocene of Africa. Our new results may also allow more precise faunal comparisons and correlations with other sections and would lead to a better understanding of the early Tertiary emergence, diversification and paleobiogeographic history of mammals in Africa.

## **2. GEOLOGICAL SETTING**

The Saharan Atlas, extending across northern Africa from Algeria into Tunisia, is part of the Atlas Mountains. The Atlas system, bounded to the South by the Saharan Platform and to the North by the Tell rift system, has undergone episodes of subsidence and uplift since the Triassic. Structural evolution of Atlas Mountains has been mainly related to the rifting associated with the opening of the Tethyan and Central Atlantic Ocean during late Triassic to early Jurassic times. During Cenozoic and early Quaternary times, the inversion of the Atlas basins has been related to the convergence between European and African plates (Mattauer et al. 1977; Bracene and Frizon de la Motte 2002).

The Saharan Atlas constitutes a succession of NE-SW oriented reliefs spreading from the Moroccan border to Tunisia and has been a part of the African-Eurasian plate boundary zone in the western Mediterranean during the Cenozoic (Gomez et al. 2000). Northern Algeria constitutes a structural unit separated from the Saharan Platform by the Atlas fault. Exposures of continental Paleogene deposits in Algeria are scarce and Eocene deposits outcrops have been reported from the north-western Saharian Hammadas of the Saharan Platform, from the Saharian Atlas and from the Algerian 'Hauts Plateaux' of the Oran Meseta (Figure 1.1). These sites have yielded ostracods, fresh-water gasteropods and charophytes but vertebrate remains are restricted to few localities. Fossil mammals have been described from the Eocene of the Gour Lazib area (Hammada du Dra, Western part of the Algerian Sahara), from the locality of Bir El Ater in the Nementcha mountains (Eastern Saharan Atlas) and from the locality of El Kohol, located on the southern flank of the Saharan Atlas, near Brezina (Figure 1.1).

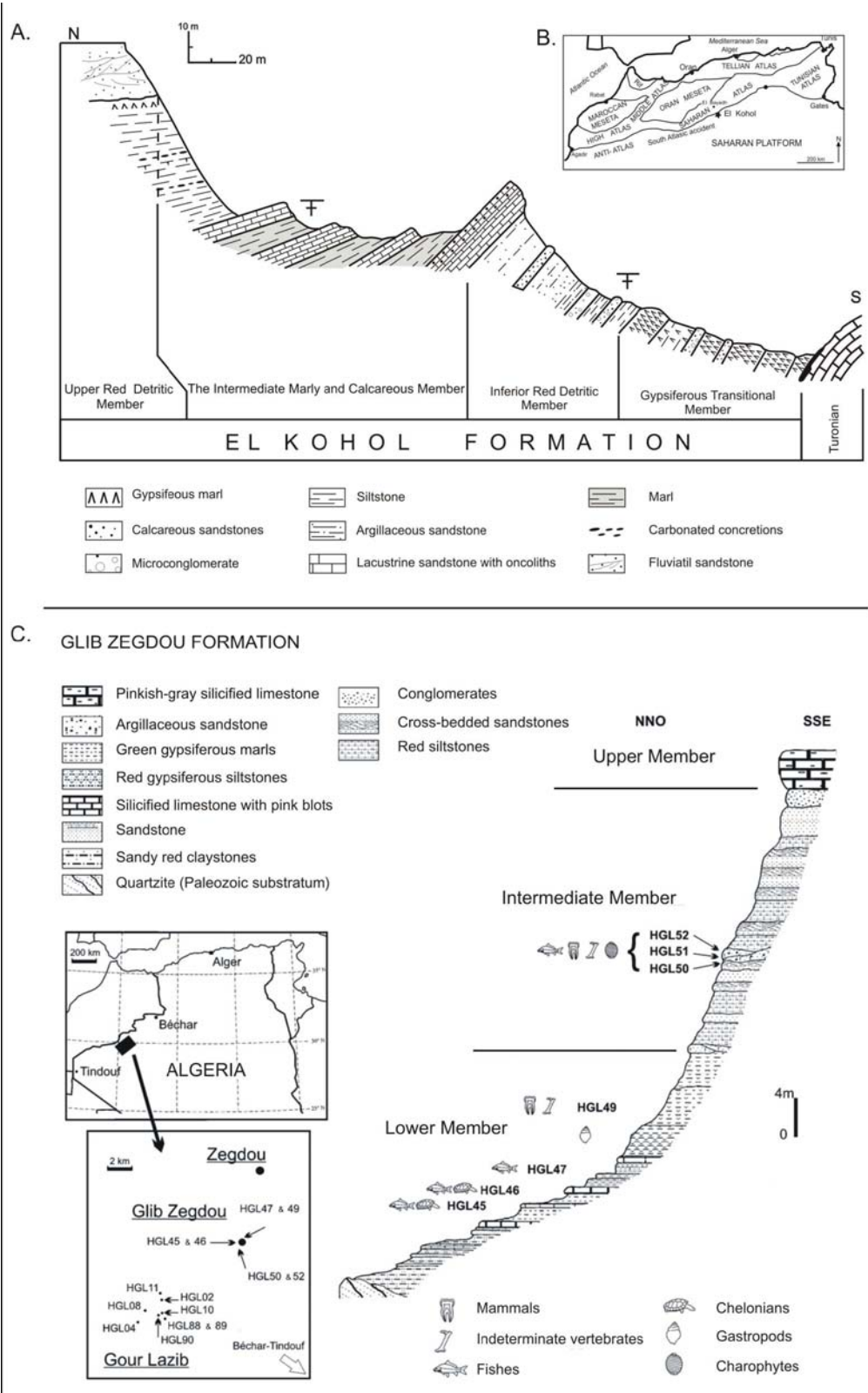
### **2.1. EL KOHOL**

The folded Continental deposits, exposed South East of the city of Brezina, have been defined as the El Kohol Formation by Mahboubi et al. (1986). This thick continental formation unconformably overlies marine late Cretaceous (Turonian) sediments. Four Members were described in this series: a Gypsiferous Transitional Member, an Inferior Red Detritic Member, an Intermediate Marly and Calcareous Member and an Upper Red Detritic Member.

The lower Gypsiferous Transitional Member overlies an erosional surface underlain by the marine Turonian. This member, described as azoic, is overlain by the Inferior Red Detritic Member. This lowermost detritic series is composed of red silts, claystones, cross-bedded sandstones, micro-conglomerates and conglomerates. It is about 50m thick and has yielded wood fragments and pulmonate gasteropods (Jodot 1952; Mahboubi et al. 1986). The Intermediate Marly and Calcareous Member consists of a series of white to pink lacustrine limestones intercalated with grey-greenish marls. The topmost part of the member corresponds to a series of red silts with gypsum and carbonates concretions. Limestones strata comprise many oncolithes and have yielded seeds of *Celtis* sp. Vertebrate remains, molluscs and oogonia of charophytes have been reported from the marly levels (Mahboubi et al. 1984, 1986). The main fossiliferous level of the formation, which has yielded abundant mammals remains, corresponds to marl horizons intercalated within lacustrine limestones with oncolithes, in the middle portion of this member (Figure 1.1).

The uppermost member of El Kohol Formation is transgressive on the Intermediate Marly and Calcareous Member and separated from it by an unconformity. No fossil remains have been reported from this member, mainly composed of fluvial cross-bedded sandstones.

The whole El Kohol Formation has been deformed and tilted in response to the Atlasic phase of the Pyrenean orogeny, dated from middle to late Eocene. El Kohol sequence underlies the Miocene Formation referred as 'Terrains des Gour'. The horizontally strata of this formation, composed of reddish claystones and sandstones, produce an angular unconformity with the underlying folded layers of El Kohol Formation. They have been assigned to indeterminate Miocene on the basis of the discovery of very scarce remains of *Helix* shells by Mahboubi et al. (1986).



**Figure 1.1.** (A.) Section of El Khol, at Brezina (After Mahboubi et al. 1984). (B.) Structural map of North Africa positioning El Khol locality. (C.) Geographic localisation of Glib Zegdou vertebrate localities and stratigraphic section of Glib Zegdou outlier (After Adaci et al. 2007).

We have carried out a paleomagnetic sampling through El Kohol Formation in the type area of the formation. Rock samples for paleomagnetic analysis were collected from 51 sites with a portable gasoline-powered drill and orientated in situ with a magnetic compass. At least three samples were collected from each site with a vertical interval of each site ranging from 0.5 to 30 meters, depending on the exposure of the outcrops.

## 2.2. GLIB ZEGDOU

The Eocene continental deposits of the Hammada du Dra (Glib Zegdou and Gour Lazib areas) are located in the occidental part of the Algerian Sahara, at approximately 400km in the South-West of Bechar. In this area, the Paleogene deposits constitute a multitude of outliers (“gara”, plural “gour” in arabic), resulting from the erosion of the desertic and rocky tabular Hammada. Mahboubi (1995) first used the name Glib Zegdou Formation for these Paleogene deposits that extend for up to 50km from the Glib Zegdou to the west of the Gour Lazib (Figure 1.1). They unconformably overlay the Paleozoic substratum or the marine Cenomano-Turonian series of the Kem Kem (Adaci et al. 2007). The study of several geological sections, notably that of the Glib Zegdou, allow to subdivide the Glib Zegdou Formation into three sedimentary members.

The lower member, about 23m thick, unconformably overlies the Paleozoic deposits of the Oussada ridge. Its lower levels are composed by a succession of red silty clay, coarse sandstone, and pinkish-gray silicified limestone in which are intercalated two levels of green gypsiferous marls, with vertebrate remains. Two sites, HGL45 and HGL46, have yielded scales of polypterid fishes, broken bones of siluriforms, and a skull plus a carapace of a podocnemidid chelonian. These deposits underlay a remarkable 0.40m massive silicified limestone. Having found no fossils, ancient authors considered this layer as Cenomanian–Turonian in age. The upper part of the lower member contains two fossiliferous levels: HGL47 yielded remains of undeterminable vertebrates, and HGL49 is the type-locality of the giant hyrax *Titanohyrax mongereaui* (Sudre 1979). These levels are characterized by a succession of red siltstones and marls with gypsum, sandwiched by a thin level of whitish limestone with undetermined gastropods and white to beige sandstone with gypsum.

The intermediate fossiliferous detrital member, approximately 24m thick, shows an alternation of yellow to red sandstone and siltstone underlying a succession of cross-bedded sandstones, clays and red silts. This member has yielded several rich fossiliferous sites. HGL50, HGL51, and HGL52 have yielded numerous remains of fishes and mammals in association with a rich flora of charophytes. The fish fauna consists of, at least, six taxa assigned to Polypteridae, Protopteridae, Characiformes, Siluriformes and Perciformes. The mammalian fauna is represented by more than 25 species, including rodents, primates, hyraxes, bats, creodonts, condylarths and macroscelidids; no proboscideans have been reported so far (contra Adaci et al. 2007).

The upper sandstone-limestone member, 10m thick, have yielded poorly preserved shells of the gastropod *Pseudoceratodes* sp. This member was initially described as a lacustrine limestone (Mahboubi 1995), but it is actually composed of calccrete and silcrete. Two major phases of epigenesis (calcitisation and silicification) of the original detrital sediments have been

identified. This epigenesis is manifested by various structures: spheroidal partings, desquamations, glaeboles, silicified concretions, with relics of the original sediment.

Samples for paleomagnetic analysis were collected from 48 sites with a rock hammer and orientated in situ with a magnetic compass.

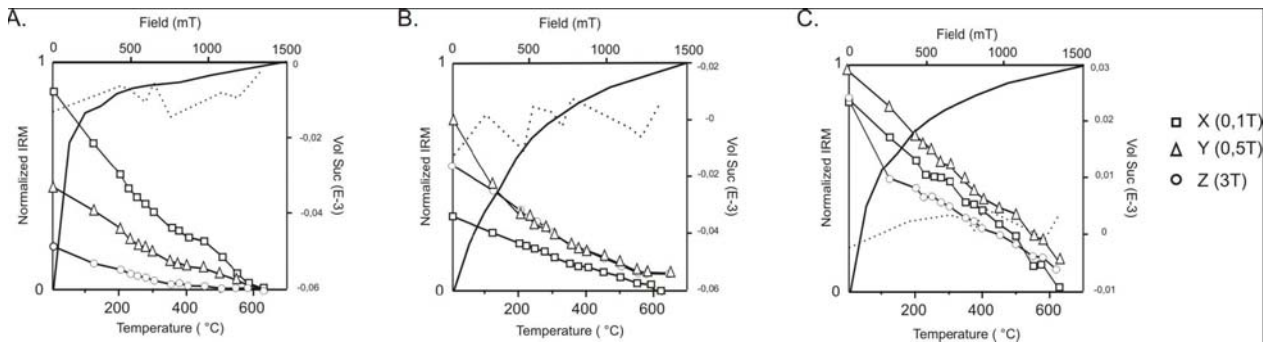
### 3. PALEOMAGNETISM

#### 3.1. EL KOHOL SECTION

##### 3.1.1. Isothermal Remanent Magnetization (IRM)

Rock magnetic mineralogy analysis was undertaken at the laboratory of environmental magnetism at the University of La Rochelle. In order to identify the minerals carrying remanent magnetization, 10 samples, which were selected on the basis of lithology and stratigraphic positions, were subjected to IRM acquisition in fields up to 1.5 T with a pulse magnetizer MMPM10. The intensity of the acquired IRM was measured after each step on a JR6 magnetometer. The determination of ferromagnetic mineralogy was improved by stepwise thermal demagnetization of three-axis differential IRM following Lowrie's method (1990). Differential IRM have been applied along the three orthogonal axes of the samples (0.1 T along the x-axis, 0.5 T along the y-axis and 3 T along the z-axis). Magnetic susceptibility was measured, on a magnetic susceptibility meter SM10, after each heating step to detect any chemical or mineralogical changes in the magnetic minerals.

Samples of the section display different patterns of IRM acquisition and demagnetization (Figure 1.2).



**Figure 1.2.** Normalized magnetization intensity curves showing IRM acquisition (ascending) and thermal demagnetization (descending) of IRM components for representative specimens of El Kohol section. Dashed line indicates evolution of susceptibility. (A.) 99EK010C, red claystone sample. (B.) 99EK056C, pink lacustrine limestone sample. (C.) 99EK174C, red sandstone sample.

IRM acquisition curves of the reddish claystones samples, collected from the Gypsiferous Transitional Member (Figure 1.2A), increase sharply in low field but do not completely saturate at high field. The specimen acquires almost complete saturation of acquired IRM (90%) at low to intermediate fields (between 100 and 500 mT) and shows a decay of a large part of the initial IRM between 100–400°C. Marked loss of IRM intensity of the soft-coercivity component within the 100–400°C range, and almost complete saturation of IRM at relatively low field are indicative of pyrrhotite, titanomaghemite or titanomagnetite. In addition, unblocking of a fraction of IRM between 400–600°C range and medium coercivity fraction of IRM suggest the presence of



magnetite as well. Pink limestone samples from the Intermediate Marly and Calcareous Member present different behavior. Samples display no saturation of acquired IRM within the applied fields. The most part of the three IRM components decays almost linearly with temperature between 100 and 600°C (Figure 1.2B). The dominantly linear nature of the IRM acquisition curves at relatively high fields resulting in lack of saturation even at 1500mT and thermal demagnetization curves showing the predominance of high unblocking temperature minerals (>600°C) are interpreted to reflect the presence of hematite. The inflexion at 200°C, of the medium coercivity component demagnetization curve, suggests the presence of iron sulfides.

Regarding the samples collected from red sandstones of the detritic Members, IRM acquisition curves increase gradually but do not reach saturation at 1500mT (Figure 1.2C). Thermal demagnetization curve of the hard coercivity fraction show an inflexion around 120°C, probably indicating the presence of goethite (Figure 1.2C). The high unblocking temperatures (>600°C) of the three IRM components point to the presence of hematite.

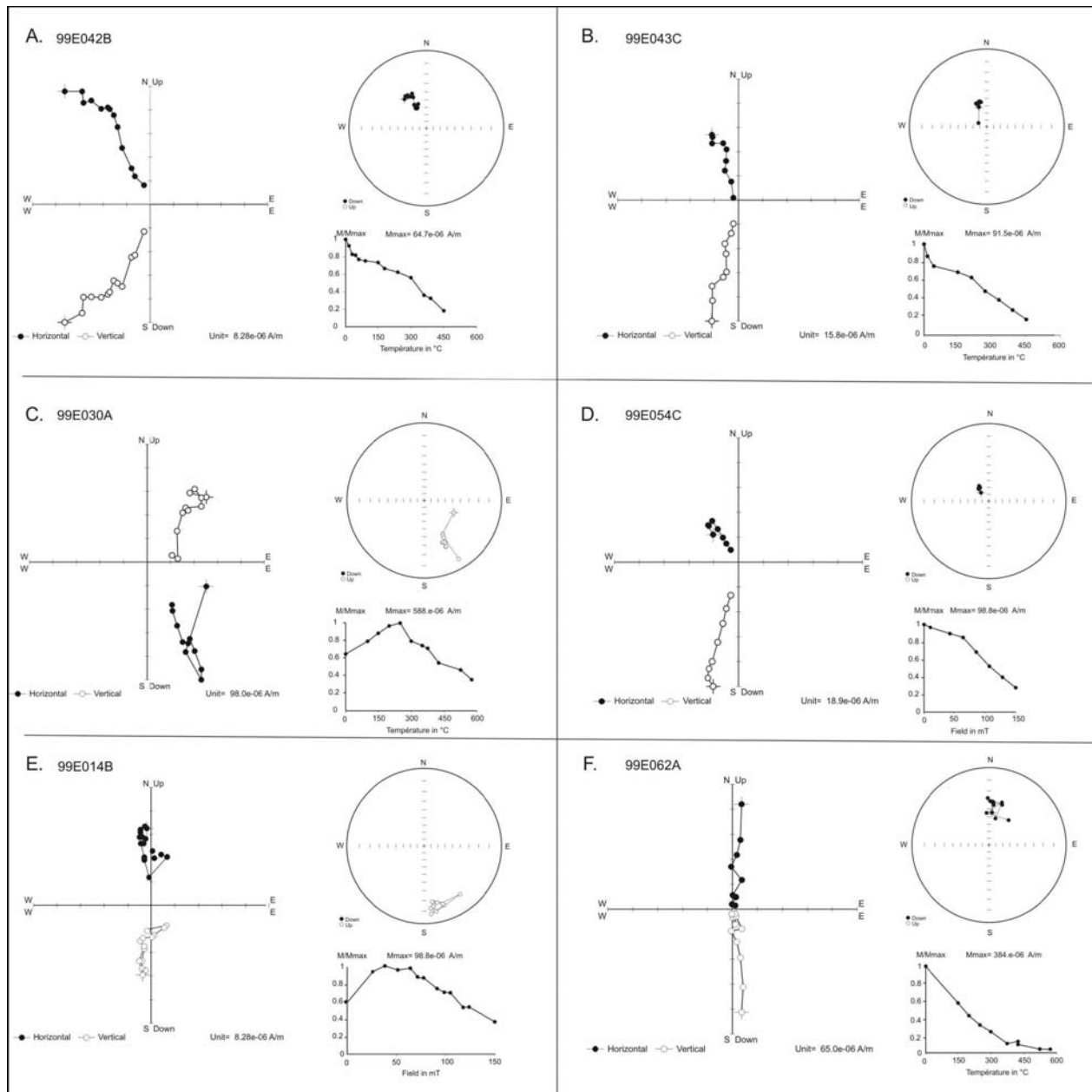
The susceptibility of analysed samples stay roughly constant during heating but show variation in intensity during heating (Figure 1.2A, B, C). As the measured susceptibilities were very weak and close to the detection limit of the material, these variations in susceptibility intensity are probably reflecting noise perturbation affecting the signal. The range of unblocking temperature and coercivity spectra observed during IRM acquisition and demagnetization suggest that goethite, (titano)-magnetite, and hematite are the main magnetic minerals in the section.

### *3.1.2. Natural Remanent Magnetization (NRM)*

The intensity and direction of the Natural Remanent Magnetization (NRM) were measured on a JR6 magnetometer at the iPHEP of University of Poitiers and on a vertical cryogenic magnetometer 2G at the laboratory of paleomagnetism of the Institut de Physique du Globe de Paris. Samples were subjected to progressive thermal demagnetization from 100°C up to 650°C with 25–50°C increments, using a Magnetic Measurement Thermal Demagnetizer (MMTD Model 80). Other samples were submitted to stepwise alternating field demagnetization with increments of 3–10mT, up to a maximum field of 150mT utilizing a High Field Shielded Demagnetizer Molspin Ltd. Alternating field demagnetization and thermal demagnetization were both adequate to isolate the characteristic remanent magnetization (ChRM) after removal of the soft component of magnetization. The principal components direction was calculated by best-fit line using the principal component analysis (Kirschvink 1980). The initial NRM intensities of the samples were often low and intensities were of the order of  $10^{-6}$  A/m. Samples collected from the lacustrine limestone levels display usually lower NRM intensity than those collected from the detritic members of the sequence.

For thermal demagnetized samples, low temperature overprint was successfully removed and ChRM directions were determined using high temperature component (>250-400°C). Component >30mT were used for alternating field demagnetized samples. Samples with maximum angular deviation larger than 15° were rejected for further analyses. Based on these criteria, 39 sites had reliable ChRM directions. Site mean from each site are presented in Table 1.1. Calculations were made using the paleomagnetic data browser and analyser Remasoft 3.0. Results of demagnetization were plotted on orthogonal vector diagrams (Zijderveld 1967) and stereograms (Figure 1.3A-F).

Both reverse and normal polarities are present. In order to evaluate our results and determine whether the normal and reversed populations share a common mean direction, we carried out a reversal test (McFadden and McElhinny 1990). The angle observed between directions of the two polarity groups is  $21.3^\circ$ . Mean directions of opposing polarity sites have a critical angle at 95% of confidence level of  $22.5^\circ$ . El Kohol paleomagnetic data pass a positive reversal test with an indeterminate classification.

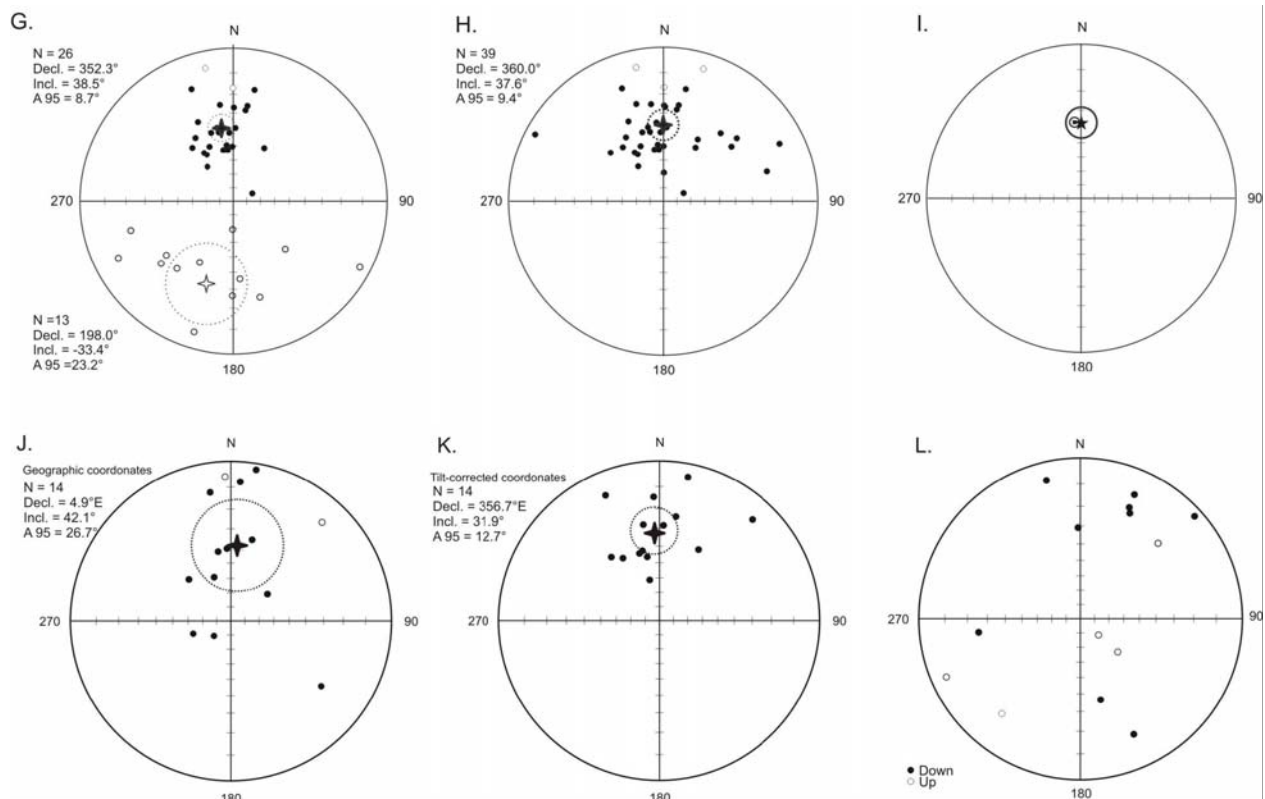


**Figure 1.3.** (A-F). Orthogonal vector diagrams (closed and/or open symbols correspond to the horizontal and/or vertical component), stereoplots (open and/or closed circles indicate directions in the upper and/or lower hemisphere), and intensity and step plots for representative samples from El Kohol section after thermal and alternating field (AF) demagnetization.

**Table 1.1.** Site mean paleomagnetic directions from El Kohol, Algeria. N: Number of specimens per site, Decl.: declination in °N; Incl.: inclination in°E;  $\alpha_{95}$ : mean direction 95% confidence ellipse, k: the best estimate of Fisher precision parameter. VGP latitude: Virtual Geomagnetic pole latitude in °. Polarity: N=Normal; R=Reverse.

| Site | N | Decl. | Incl. | $\alpha_{95}$ (°) | (°)    | k      | VGP latitude (°) | polarity |
|------|---|-------|-------|-------------------|--------|--------|------------------|----------|
| 1    | 3 | 348.2 | -6.9  | 25.3              | 14.19  | 51.81  |                  | N        |
| 2    | 3 | 352.9 | 25.1  | 24.3              | 26.88  | 69.10  |                  | N        |
| 3    | 3 | 349.2 | 40.6  | 26.8              | 22.2   | 76.31  |                  | N        |
| 4    | 4 | 336.6 | 31    | 13.6              | 46.53  | 63.33  |                  | N        |
| 5    | 3 | 164.6 | -23.5 | 22.3              | 31.75  | -64.89 |                  | R        |
| 6    | 2 | 117.7 | -3.9  | 25.6              | 97.62  | -24.08 |                  | R        |
| 7    | 3 | 180.5 | -26.2 | 35                | 13.44  | -70.76 |                  | R        |
| 8    | 2 | 0.4   | -17   | 26.7              | 89.57  | 48.25  |                  | N        |
| 9    | 1 | 9.1   | 25.4  | **                | 68.63  |        |                  | N        |
| 10   | 2 | 0.3   | 50.5  | 40.1              | 40.9   | 88.17  |                  | N        |
| 11   | 2 | 337.8 | 47.7  | 32.5              | 61.07  | 70.52  |                  | N        |
| 12   | 3 | 350.4 | 52.4  | 20.9              | 35.8   | 81.95  |                  | N        |
| 13   | 2 | 331.6 | 51.8  | 39.3              | 42.4   | 66.18  |                  | N        |
| 14   | 3 | 348.4 | 37.7  | 7.3               | 282.98 | 74.25  |                  | N        |
| 15   | 3 | 329.8 | 49.8  | 30.6              | 17.28  | 64.31  |                  | N        |
| 16   | 4 | 355.2 | 52.7  | 22.7              | 17.36  | 85.98  |                  | N        |
| 17   | 3 | 2.6   | 38.6  | 23.6              | 28.33  | 78.47  |                  | N        |
| 18   | 3 | 340   | 14.1  | 22.2              | 31.8   | 58.15  |                  | N        |
| 19   | 3 | 329.9 | 38.7  | 14.8              | 70.3   | 61.16  |                  | N        |
| 20   | 3 | 343.2 | 39.8  | 14.6              | 71.9   | 71.88  |                  | N        |
| 21   | 5 | 1.1   | 26.9  | 20.3              | 15.1   | 71.15  |                  | N        |
| 22   | 3 | 231.1 | -31   | 26.7              | 22.34  | -41.38 |                  | R        |
| 23   | 6 | 209   | -40.6 | 36.2              | 4.37   | -62.70 |                  | R        |
| 24   | 2 | 324.4 | 59    | 27.3              | 85.87  | 60.78  |                  | N        |
| 25   | 2 | 354.5 | 49.4  | 19.9              | 159.2  | 84.55  |                  | N        |
| 26   | 3 | 357.7 | 41.6  | 70.7              | 4.12   | 80.66  |                  | N        |
| 27   | 2 | 323.3 | 42.8  | 26.1              | 93.75  | 57.03  |                  | N        |
| 28   | 1 | 11.3  | 16.8  | **                | 63.40  |        |                  | N        |
| 29   | 2 | 30.9  | 45.8  | 10.7              | 549.03 | 62.75  |                  | N        |
| 30   | 3 | 68.5  | 73.9  | 23                | 29.72  | 38.75  |                  | N        |
| 31   | 2 | 254   | -20   | 50.1              | 26.99  | -18.96 |                  | R        |
| 32   | 2 | 220   | -30   | 18                | 194.6  | -50.19 |                  | R        |
| 33   | 2 | 229.2 | -25.8 | 20.4              | 152    | -41.34 |                  | R        |
| 34   | 1 | 175.1 | -35.6 | **                | -75.94 |        |                  | R        |
| 35   | 4 | 196.8 | 6.2   | 92.2              | 1.99   | -50.50 |                  | R        |
| 36   | 3 | 8.3   | 27.9  | 30.1              | 17.9   | 70.28  |                  | N        |
| 37   | 3 | 132.8 | -40.3 | 12.3              | 102.8  | -47.50 |                  | R        |
| 38   | 3 | 181.3 | -69   | 31                | 16.85  | -70.55 |                  | R        |
| 39   | 1 | 243.6 | -9.8  | **                | -24.72 |        |                  | R        |

To assess primary origin of ChRM, fold test was performed by comparing mean direction from sites on opposing limbs of a fold. Tilt-corrected directions of magnetization appear to be more tightly grouped than in geographic coordinates (Figure 1.3 J,K). Better clustering of paleomagnetic data after tectonic tilt correction indicate ChRM magnetisation prior to folding and represent a positive fold test. A conglomerate test has been performed on the ChRM directions of pebbles sampled from a conglomerate stratum of the Upper Red Detritic Member. The magnetizations characteristic of the clasts and that of the matrix are randomly distributed (Figure 1.3L), implying ChRM acquisition is antecedent to the inclusion of the clasts in the conglomerate which represents a positive conglomerate test.



**Figure 1.3 (continued).** (G.) Equal-area stereographic projection and Fisher statistics (1953) of characteristic directions for all the sites (listed in Table 1.1). Open and/or closed circles indicate directions in the upper and/or lower hemisphere. Mean directions calculated by Fisher statistics (see Table 1.1) are represented by a star, and the ellipse indicates the 95% confidence ellipse. (H.) Equalarea stereographic projection and Fisher statistics of characteristic directions for all the sites when reversed polarity sites are inverted. (I.) Equal-area stereographic projection of overall mean sites direction (black star) of the section and ellipse at the 95% confidence ellipse. Solid square shows the direction derived from the 50 Ma apparent polar wander path of Torsvik et al. (2008). (J.-K.) Equal area projection of a set of site directions collected from two opposed limbs of the fold, in geographic coordinates (J.) and tilt-corrected (K.). (L.) Equal area projection of a set of site directions collected from different pebbles within a conglomerate stratum.

Overall mean direction of the section as well as a calculation of paleopoles are presented in Table 1.2. The overall mean direction of the section is: Declination =  $360^\circ$  Inclination =  $37.6^\circ$  ( $\alpha_{95} = 9.4^\circ$ ), corresponding to the paleomagnetic pole at  $78.0^\circ\text{N}$  and  $181.5^\circ\text{E}$  (confidence ellipse about the pole has  $dp$  [semi-axis of the confidence ellipse along the great circle path from site to pole] of  $11.1^\circ$  and  $dm$  [semi-axis of confidence ellipse perpendicular to that great circle path] of  $6.5^\circ$ ). The mean direction of the section was calculated by the Fisher statistics (Fisher 1953) and plotted on stereographic diagrams (Figure 1.3G).

**TABLE 1.2. PALEOMAGNETIC POLARITY MEAN DIRECTIONS OF EL KOHOL SECTION, ALGERIA**

| Pole position | N  | Decl. | Incl. | $\alpha_{95}$ | k   | $\Phi$ | $\lambda$ | dp/dm    | ( $^\circ$ ) | ( $^\circ$ ) | ( $^\circ$ ) | ( $^\circ$ ) | ( $^\circ$ ) |
|---------------|----|-------|-------|---------------|-----|--------|-----------|----------|--------------|--------------|--------------|--------------|--------------|
| El Kohol      | 39 | 360   | 37.6  | 9.4           | 6.9 | 181.5  | 78        | 11.1/6.5 |              |              |              |              |              |

Note: Decl.; mean tilt corrected declination in  $^\circ\text{E}$ ; Incl.; mean tilt corrected inclination in degree to the horizontal;  $\alpha_{95}$ : mean direction 95% confidence ellipse; k : Fisher precision parameter;  $\Phi$ : longitude of paleopole for mean direction in  $^\circ\text{E}$ ,  $\lambda$ : latitude of paleopole for mean direction in  $^\circ\text{N}$ ; dp : semi-axis of the confidence ellipse along the

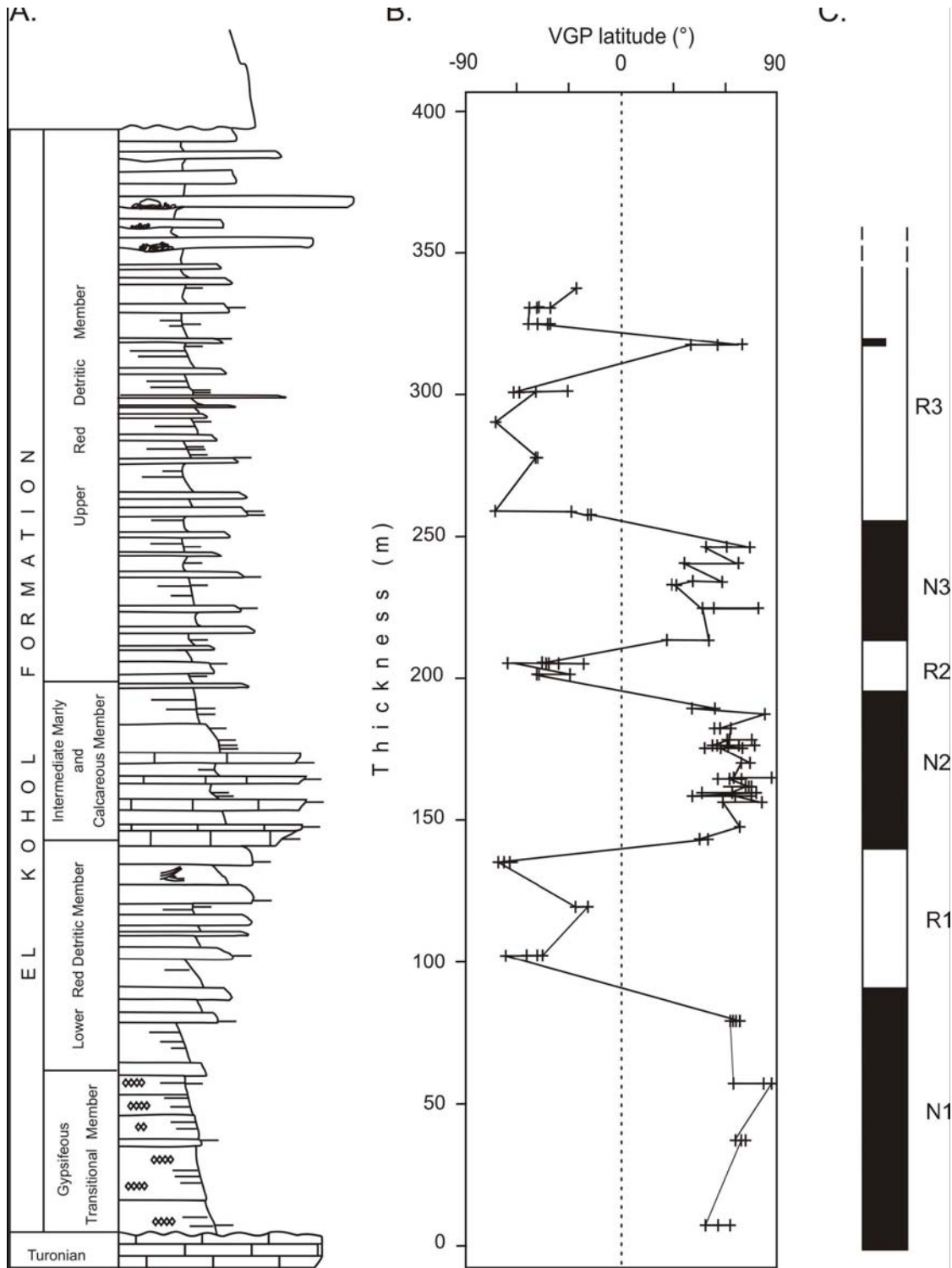
great circle path from site to pole;  $dm$  : semi-axis of the confidence ellipse perpendicular to that the great circle path.  
El Kohol location: 33°03'19.2"N, 001°27'25.8"E

We compared the overall mean direction of the section to the expected dipole paleomagnetic field direction (Declination: 355.2°, Inclination: 36.9°,  $\alpha_{95} = 2.9^\circ$ ) calculated at the site latitude for 50 Ma African plate pole position from the apparent polar wander path (APWP) of Torsvik et al. (2008) (Figure 1.3I). Using Demarest (1983) methods, comparison of the reference and observed directions yields no significant vertical axis rotation of declination. Observed paleomagnetic inclination is slightly shallower but is not significantly different from the expected inclination at the site position.

### *3.1.3. Magnetic polarity zonation*

Virtual Geomagnetic Pole (VGP) latitudes calculated from the least-squares directions of all samples are plotted in Figure 1.4 with respect to stratigraphic position within the section.





**Figure 1.4.** Paleomagnetic reversal stratigraphy of El Kohol section. (A.) stratigraphic section of El Kohol. (B.) Virtual geomagnetic pole (VGP) latitudes are plotted as a function of stratigraphic levels. (C.) polarity column (black/white bars represent normal/reverse polarity zones).

In total, three normal (N1 to N3) and three reversed (R1 to R3) polarity zones are recognized from the studied section. The reverse polarity zone R3 presents a short normal polarity interval in its upper portion. This short normal polarity interval is defined by only one

site therefore its reliability is relatively low. The normal polarity interval from the Gypsiferous Transitional Member is assigned to N1. The Lower Red Detritic Member is characterized by the uppermost part of the normal zone N1 and the reverse polarity zone R1. The normal polarity zone of N2 dominates the Intermediate Marly and Calcareous Member. The interval from the Upper Red Detritic Member is characterized by an R2–N3–R3 polarity sequence. Future re-sampling could better define the level of transition between polarity intervals, as well as the existence of the short normal polarity zone that is represented by a single site within the reversal polarity zone R3.

The number of reversals event recorded in the section can be used to estimate the temporal duration represented in the magnetic polarity sequence of El Kohol. Using statistical method of Johnson and McGee (1983), the amount of time,  $t$ , represented by a sampled section can be calculated using the formula:

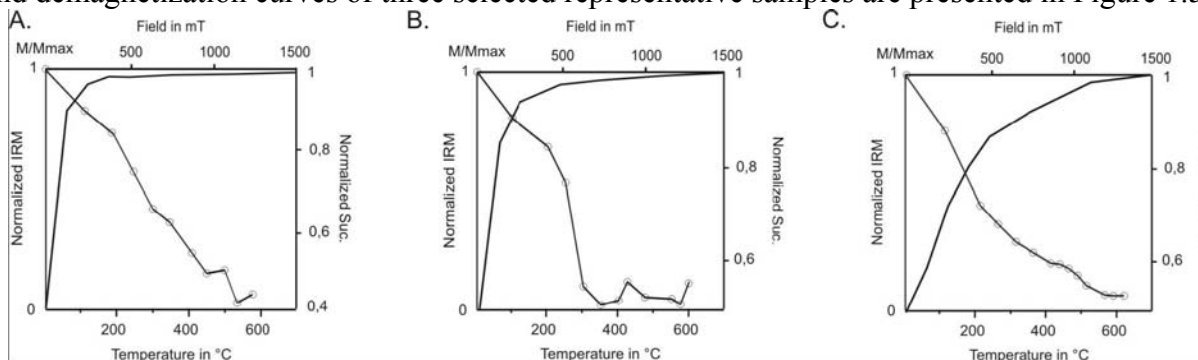
$t$  (myr) =  $S \tau N$  where  $S = -\ln(1 - 2p)/2$ ;  $\tau$  = mean time span of polarity intervals;  $N$  = the number of paleomagnetic sites; and  $p = R/(N - 1)$ , where  $R$  is the number of reversals encountered. For the El Kohol deposits sampled in this study,  $N = 39$ ,  $R = 6$  and thus  $p = 6/38 = 0.16$  and  $S = 0.215$ . Using the GPTS of Gradstein et al. (2004), 11 polarity intervals occur during the Ypresian (between 55.8 and 48.6 Ma) which correspond to the probable age range of these sediments based upon fauna. This yields a mean interval polarity length of 0.65 myr.

Thus, the estimated amount of time required to deposit El Kohol Formation is calculated at  $4.8 \pm 2$  myr.

### 3.2. GOUR LAZIB

#### 3.2.1. Isothermal Remanent Magnetization (IRM)

In order to identify the nature of the main magnetic carriers, we carried out a series of rock magnetic experiments at Paleomagnetic Laboratory of the Institut de Physique du Globe de Paris on a subset of selected specimens. The rock magnetic measurements included stepwise acquisition of an isothermal remanent magnetization (IRM) by applying increasing pulse magnetic fields up to a maximum value of 1.5T. The samples were then subjected to stepwise thermal demagnetization of IRM by using thermal method in steps up to 600°C. IRM acquisition and demagnetization curves of three selected representative samples are presented in Figure 1.5.



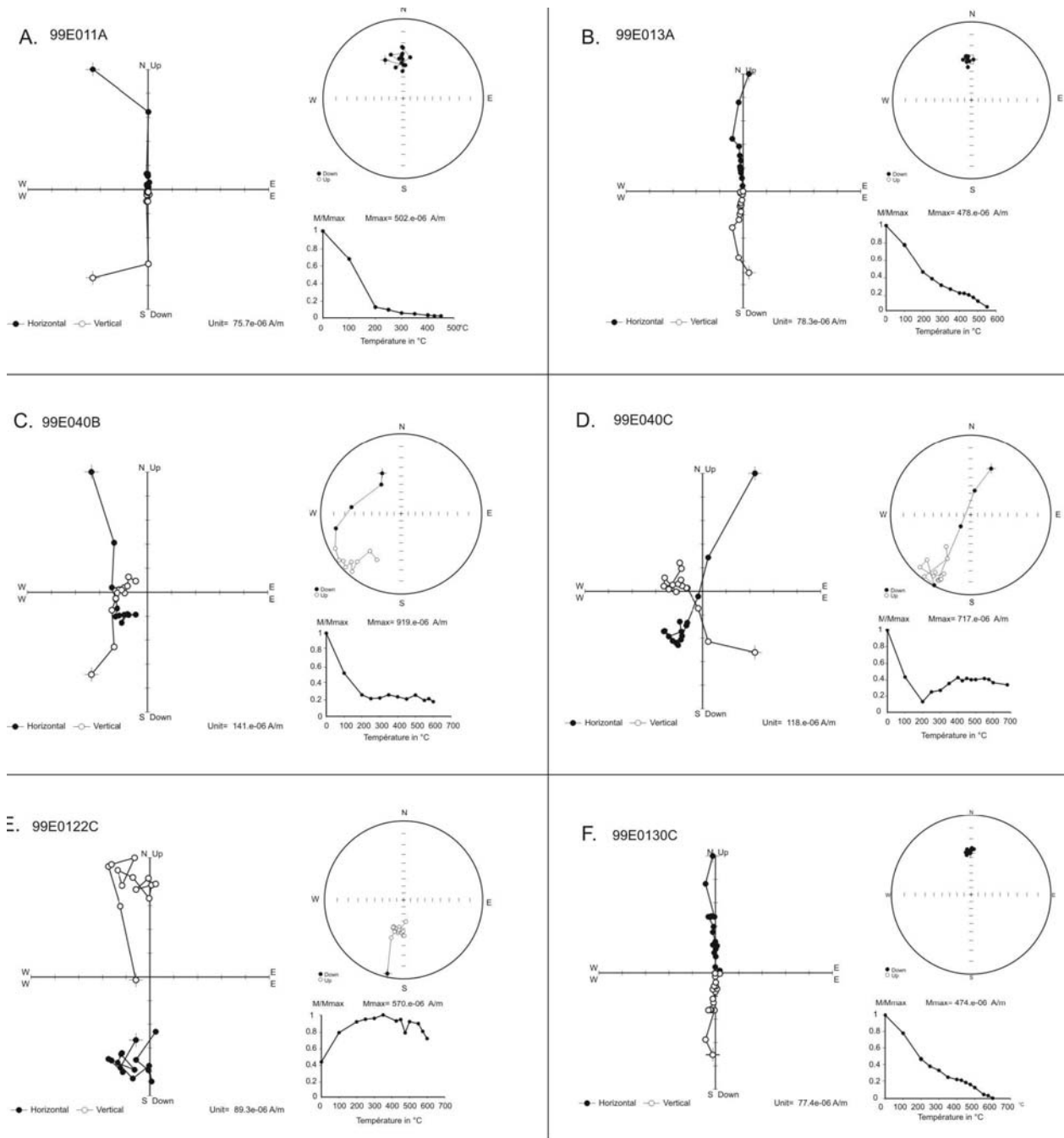
**Figure 1.5.** Normalized magnetization intensity curves showing IRM acquisition (ascending) and thermal demagnetization (descending) for representative specimens of Gour Lazib section. (A.) 99GL011A, argillaceous calcareous sample. (B.) 99GL025A, siltstone sample. (C.) 99GL039A, claystone sample.

Samples collected from calcareous (Figure 1.5A) and siltstones levels (Figure 1.5B) are characterized by a dominance of low coercivity minerals. IRM values increase rapidly in relatively low field. The samples acquired more than 80 % of saturation remanence in field as low as 300mT, indicating the presence of coarse grained pyrrhotite, titanomaghemite or titanomagnetite. Sample from calcareous level (Figure 1.5A) show a maximum unblocking temperature around 525°C reveals that this sample is dominated by titanomagnetite. The demagnetization curve of siltstone sample (Figure 1.5B) decreases strongly at temperature of 350°C, identical to unblocking temperature of maghemite, pyrrhotite or titanomagnetite.

IRM acquisition of the sample collected from argillaceous sandstones (Figure 1.5C), increase slowly at low field and do not saturate beyond 1500mT, implying that magnetization is carried by both low and high coercivity minerals. The slight inflexion of the demagnetization curve at 400°C reveals the presence of titanomagnetite. The combination of high coercivity and unblocking temperature higher than 600°C also indicate the presence of hematite.

### 3.2.2. Natural Remanent Magnetization (NRM)

Samples collected from Gour Lazib section, during field trips in 2008 and 2009, were incrementally demagnetized and measured on a cryogenic magnetometer 2G, in a magnetically shielded room, at the laboratory of paleomagnetism of the Institut de Physique du Globe de Paris. Paleomagnetic samples were subjected to the progressive thermal demagnetizations from 100 to 600 °C at 25–50 °C intervals. Thermal treatments yielded consistent characteristic remanent magnetizations (ChRM). The viscous component was generally removed at 200-400°C. Two magnetization components were isolated in most samples and the higher temperature component that decays toward the origin was recognized as ChRM. Demagnetization results are shown in Figure 1.6. ChRM directions were calculated using principal component analysis (Kirschvink 1980). Site mean from each site were calculated with Fisher statistics (1953) and are presented in Table 1.3. ChRM directions oriented either north down or south up were interpreted as normal and reversed ChRM, respectively. The mean directions of the both ChRM groups were calculated using the Fisher statistics and shown as an equal-area projection in Figure 1.6G. The mean directions of the normal and reverse sites are Declination = 353.8°, Inclination = 34.9° ( $\alpha_{95} = 16.2^\circ$ ) and Declination = 183.3°,  $I = -23.3^\circ$  ( $\alpha_{95} = 22.6^\circ$ ), respectively.

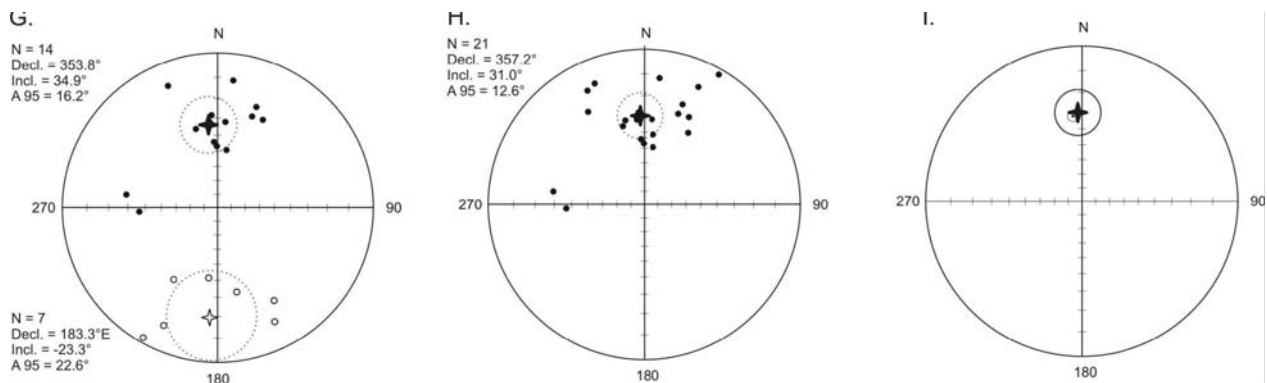


**Figure 1.6.** (A-F.). Orthogonal vector diagrams (closed and/or open symbols correspond to the horizontal and/or vertical component), stereoplots (open and/or closed circles indicate directions in the upper and/or lower hemisphere), and intensity and step plots for representative samples from Gour Lazib section after thermal demagnetization.

**Table 1.3.** Site mean paleomagnetic directions from Gour Lazib, Algeria. N: Number of specimens per site, Decl.: declination in °N; Incl.: inclination in °E;  $\alpha_{95}$ : mean direction 95% confidence ellipse, k: the best estimate of Fisher precision parameter. VGP latitude: Virtual Geomagnetic pole latitude in °N. Polarity: N=Normal; R=Reverse. Incl.

| Site | N | Decl. (°) | $\alpha_{95}$ (°) | Incl. (°) | k | VGP latitude (°) | Polarity |
|------|---|-----------|-------------------|-----------|---|------------------|----------|
| 1    | 1 | 359.3     | 46.8              | *         | * | 88.21            | N        |
| 2    | 1 | 27.1      | 25.2              | *         | * | 60.01            | N        |

3 2 5.2 32.1 9 188.55 76.81 N  
 4 3 357 44.1 19.3 41.86 85.31 N  
 5 3 354.9 32.3 3.2 1513.37 76.96 N  
 6 3 8.7 48.8 34.7 13.67 82.45 N  
 7 3 344.7 34.6 43.6 9.07 72.47 N  
 8 2 337.7 9.6 \* \* 57.40 N  
 9 2 278.3 28.7 \* \* 14.58 N  
 10 1 266.9 36.5 \* \* 7.35 N  
 11 1 20.6 25.9 \* \* 65.09 N  
 12 1 7 11.1 \* \* 64.99 N  
 13 1 356.3 28.4 43.6 35 75.02 N  
 14 3 21 20.6 \* \* -62.67 N  
 15 2 187.2 -40.9 28.6 19.62 -80.99 R  
 16 2 209.8 -1.9 30 18 -49.62 R  
 17 5 167.2 -31.7 130.1 6.28 -72.83 R  
 18 2 204.7 -10.2 78.9 3.53 -56.12 R  
 19 3 148.8 -20 17.6 204.06 -55.05 R  
 20 1 153.5 -11.2 59.2 19.98 -55.31 R  
 21 2 211.5 -32.9 \* \* -58.99 R



**Figure 1.6 (continued).** (G.) Equal-area stereographic projection and Fisher statistics (1953) of characteristic directions for all the sites (listed in Table 1.3). Open and/or closed circles indicate directions in the upper and/or lower hemisphere. Mean directions calculated by Fisher statistics are represented by a star, and the ellipse indicates the 95% confidence ellipse. (H.) Equal-area stereographic projection and Fisher statistics of characteristic directions for all the sites when reversed polarity sites are inverted. (I.) Equal-area stereographic projection of overall mean sites direction (black star) of the section and ellipse at the 95% confidence ellipse. Solid square shows the direction derived from the 50 Ma apparent polar wander path of Torsvik et al. (2008).

To determine if the normal and reverse populations are statistically antipodal at the 95% confidence level, a reversal test was carried out using McFadden and McElhinny (1990). The angle between the mean directions of the normal and reversed polarities was 14.2°, which was smaller than the critical angle (95% confidence) of 16.41°. Thus, mean paleomagnetic directions of the normal and reversed polarities passed the reversal test with a C qualification. This positive result of the reversal test indicates that the Gour Lazib deposit preserve reliable primary magnetization. The strata of Gour Lazib area are flat lying, thus it was not possible to carry out a fold test.

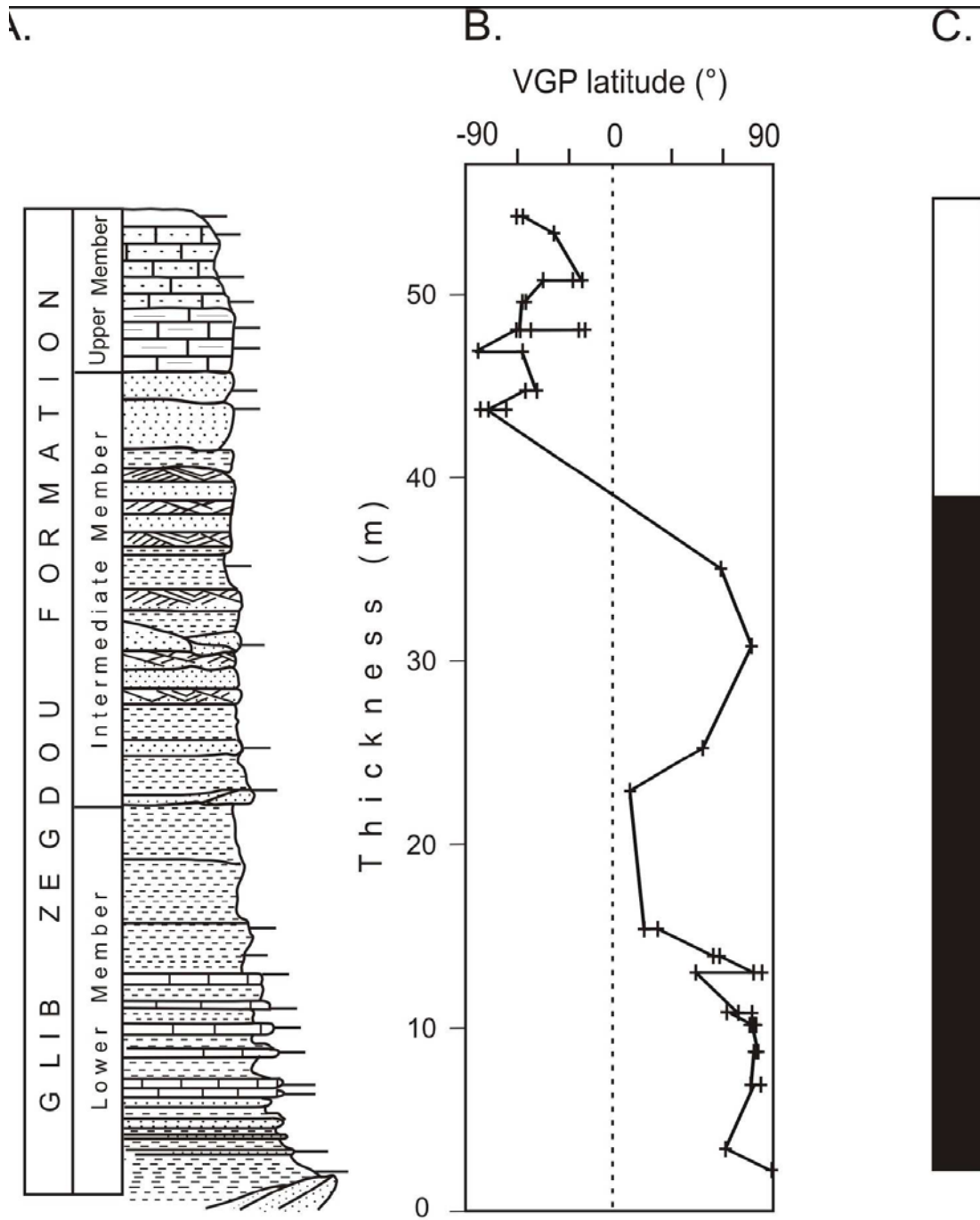
The overall mean direction of site mean ChRM directions for the 21 sites from Gour Lazib section is Declination = 357.2°, Inclination = 31.0°, ( $\alpha_{95} = 12.6^\circ$ ). Torsvik et al. (2008) provided a 50 Ma reference paleomagnetic pole for Africa located at 76.8 °N, 201.6°E with



confidence limit  $\alpha_{95} = 2.6^\circ$  (Figure 1.6I). The expected paleomagnetic field at Gour Lazib locality associated with this reference pole is Declination =  $353.9^\circ$ , Inclination =  $32.6^\circ$ , ( $\alpha_{95} = 3.1^\circ$ ). Using Demarest method (1983), the comparison of the expected and observed directions yields no significant flattening of inclination ( $F=1.63^\circ$ ) or significant vertical axis rotation of declination ( $R=3.3^\circ$ ).

### *3.2.3. Magnetic polarity zonation*

The virtual geomagnetic pole position, calculated from mean ChRM directions, are plotted in Figure 1.7 as a function of stratigraphic levels along the section. One normal and one reversed polarity zones are recognized from the studied section. A normal polarity zone of nearly 40m is recognized from the Lower Member to the lower part of the Intermediate Member of the Formation. The upper part of the Intermediate Member and the Upper Member are characterized by a reverse polarity zone. Chronology of Gour Lazib section and correlation with the GPTS of Gradstein et al. (2004) has been only constrained by biostratigraphic data.



**Figure 1.7.** Paleomagnetic reversal stratigraphy of Gour Lazib section. (A.) Stratigraphic section of Gour Lazib. (B.) Virtual geomagnetic pole (VGP) latitudes are plotted as a function of stratigraphic levels. (C.) polarity column (black/white bars represent normal/reverse polarity zones).

## 4. CORRELATION

### 4.1. EL KOHOL SECTION

#### 4.1.1 Stratigraphic and structural data

El Kohol Formation unconformably overlays marine Turonian marly and dolomitic limestones. The tectonic events recorded by the folded post-Turonian continental deposits of El Kohol Formation are correlated to major events, recognized as the Atlasic compressional phase of the Pyrenean orogeny. The middle-late Eocene event of compressional north–south Pyrenean phase is well recognized in the Algerian Atlas mountains (Dubourdieu 1956; Guiraud 1975; Naak et al. 1992; Frizon de Lamotte et al. 2000; Herkat and Delfaud 2000; Bracène and Frizon de Lamotte 2002) and was named “Atlasic phase” by Laffitte (1939). The Atlasic phase, considered as a major tectonic event largely expressed in the whole Atlasic domain of North Africa (Khomsî et al. 2006), has been dated from the Lutetian to Priabonian times. This indicates a minimum Lutetian age to the El Kohol sediments deposition which pre-dates the folding.

The horizontal formation, unconformably overlying the El Kohol Formation, is designated as ‘Terrain des Gour’ (Flamand 1911). Terrestrial pulmonate gasteropod molluscs, belonging to the genus *Helix*, have been recovered from this formation, indicating a Miocene age.

#### 4.1.2 Biostratigraphic data

Age constraints of the El Kohol Formation were provided by paleontological analysis but the high level of endemism of the mammalian fauna could not support direct paleontological correlations with faunas outside Africa. A comprehensive fauna and flora list and biostratigraphic repartition from El Kohol Formation has been published by Mahboubi et al. (1986).

The transgressive lowermost portion of El Kohol Formation, corresponding to the Gypsiferous Transitional Member, is not well dated, being devoid of fossil remains. Gasteropod fauna (*Ampullaria* cf. *assermoensis*, *Pseudoceratodes flandrini* and *Melanoides brezinaensis*), described from the Lower Red Detritic Member and the Intermediate Marly and Calcareous Member (Jodot 1952; Mahboubi et al. 1986), seems to indicate a Paleocene to early Eocene age.

Charophyte remains from the Intermediate Marly and Calcareous Member, assigned to *Nitellopsis (Tectochara) dutemplei* and *Peckichara* aff. *disermas*, display similarities with forms described from the Ypresian of Europe (Mebrouk et al. 1997).

The Marly and Calcareous Member of El Kohol Formation contains a unique assemblage including primitive representatives of African groups and non endemic taxa (Mahboubi et al. 1986).

El Kohol locality yields *Numidotherium koholense* which represents one of the oldest known representatives of Proboscidea (Mahboubi et al. 1984, Noubhani et al. 2008). It displays primitive cranial and postcranial anatomy, associated with a strictly lophodont dentition and represents an ancestral morphotype of the order (Delmer 2009). *Numidotherium koholense* appears to be a closely related species to *Phosphatherium escuilliei* (Gheerbrant et al. 1998b) and *Daouitherium rebouli* (Gheerbrant et al. 2002). *Eritherium*, *Phosphatherium*, *Daouitherium* from the Ouled Abdoun Basin in Morocco and *Numidotherium* are considered as the most primitive proboscideans known (Delmer 2009; Gheerbrant et al. 1996, 2005; Gheerbrant 2009). The proboscidean from El Kohol exhibits some less derived characters than *Arcanotherium savagei* and *Barytherium grave* from the locality of Dur At-Talah (Delmer 2009), dated from the Bartonian (Jaeger et al. 2010a). The hyracoid *Seggeurius amourensis* (Crochet in Mahboubi et al. 1986; Court and Mahboubi 1993) from El Kohol, is characterized by its small size, bunodont and

low-crowned teeth and simple premolar morphology. It appears to be more primitive than the other genera of hyracoids described from the locality of Gour Lazib (Sudre 1979; Tabuce et al. 2001, 2007; Adaci et al. 2007), Chambi (Court and Hartenberger 1992) and from the late middle Eocene locality of Bir El Ater (Tabuce et al. 2000). An isolated lower molar of hyracoid identified from the early Ypresian of Ouled Abdoun Basin has been described as belonging to a new species close to the genus *Seggeurius* (Gheerbrant et al. 2003). *Seggeurius* is considered as the most primitive hyracoid yet recovered along with an indeterminate species from the Ypresian of N'Tagourt 2 (Morocco).

El Kohol also yields a species of African creodont, *Koholia atlasense* (Crochet 1988). This latter seems to be more derived than related forms of Koholiinae from the early Ypresian deposits of Ouled Abdoun basin in Morocco (Gheerbrant et al. 2006; Solé et al. 2009). A genus of adapisoriculid, *Garatherium* (Crochet 1984; Mahboubi et al. 1986) is found at El Kohol. This genus has also been described from the latest Paleocene locality of Adrar Mgorn 1 in the Ouarzazate basin (Gheerbrant et al. 1998a). Recently, an upper molar and two fragments of lower molars of Eochiroptera have been reported from El Kohol deposits (Ravel et al. 2010). These remains constitute the oldest evidence of chiropterans in Africa. The mammalian fossil collection recovered from El Kohol, dominated by early proboscidean remains, displays a unique taxonomic association and it is difficult to constrain precisely the chronology of these deposits. However, faunal and floral data seem to indicate that El Kohol locality is probably younger than the earliest Ypresian Moroccan localities (N'Tagourt 2 and Ouled Abdoun basin) and older than the localities of Gour Lazib and Chambi, indicating an age of middle-late Ypresian age for the fossiliferous strata.

Taking into account these paleontological constraints, we consider the potential correlations of El Kohol magnetic polarity sequence to the Geomagnetic Polarity Time Scale (GPTS) (Gradstein et al. 2004) (Figure 1.8). Based upon overall pattern of the polarity sequence and biostratigraphic control, our section appears to be most likely correlated to an interval comprised between chron C24n.1n to chron C22r. The normal polarity zone N1 at the base of the section is correlated to subchron C24n. The polarity zones from R1 to N3 (R1, N2, R2 and N3) are identified as chron C23 of the GPTS and the reverse polarity zone R3 is correlated to the base of subchron C22r. According to that correlation, El Kohol Formation would extend in age from about 53 to 50 Ma and would span approximately 3 Ma which is quite consistent with the estimated duration calculated using Johnson and McGee statistical model (1983). This correlation indicates an age bracketed between 51.9 and 51 Ma for the fossiliferous level of the Marly and Calcareous Member.

Alternatively, another correlation of the section to the GPTS can also be taken in account. According to this latter hypothesis, the magnetic polarity sequence zone of the section could be interpreted to represent chrons C24n.3n to C23r. This correlation would imply an age of ~53 Ma for the fossiliferous levels of the Marly and Calcareous Member. However, this correlation would imply exceedingly high sedimentation rates (108cm/kyr) through the Intermediate Marly and Calcareous Member and much lower sedimentation rate for the Upper Red Detritic Member. This hypothesis of correlation is not consistent with the depositional environmental condition inferred from the lithology and is considered as being less likely.



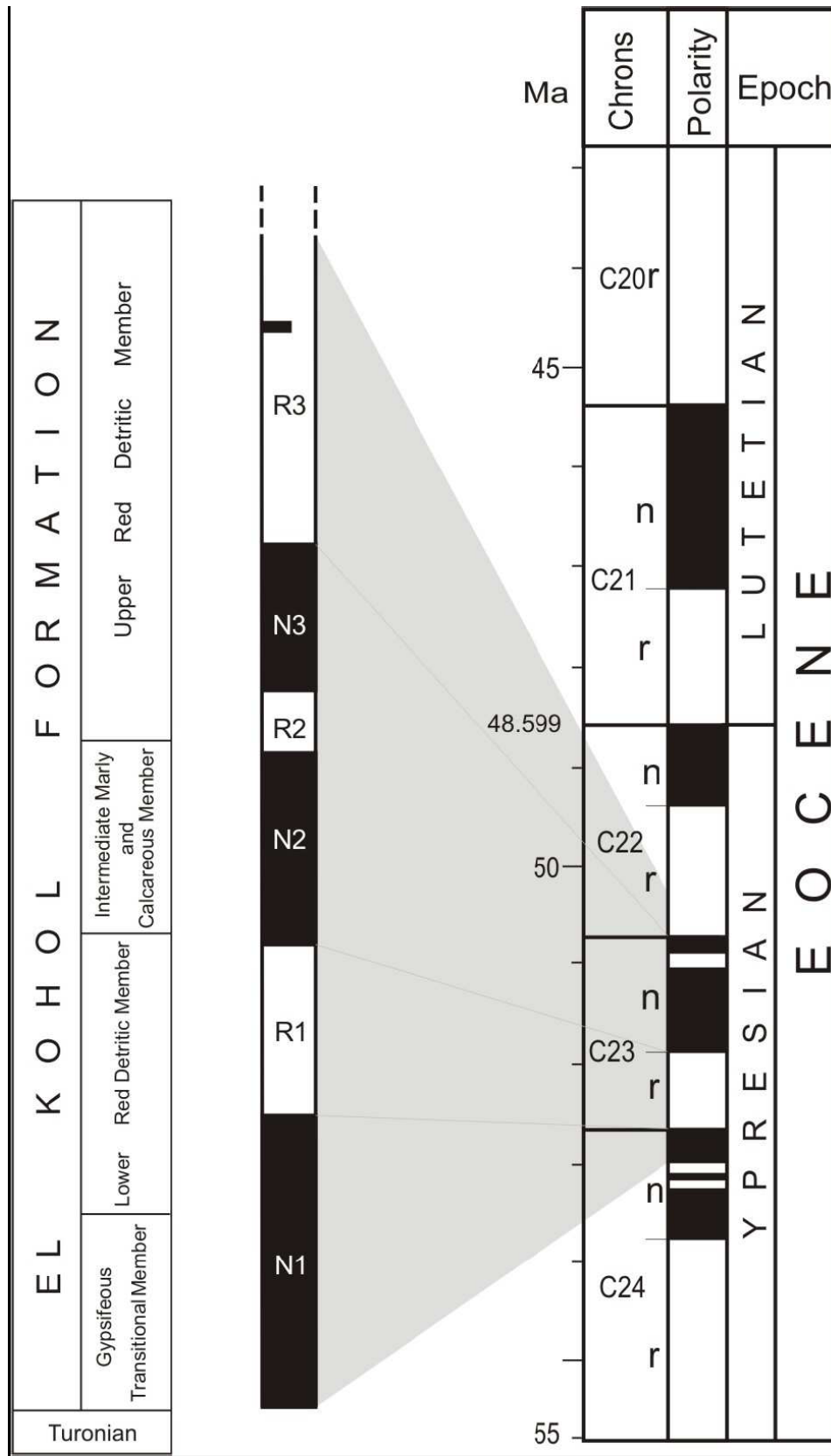
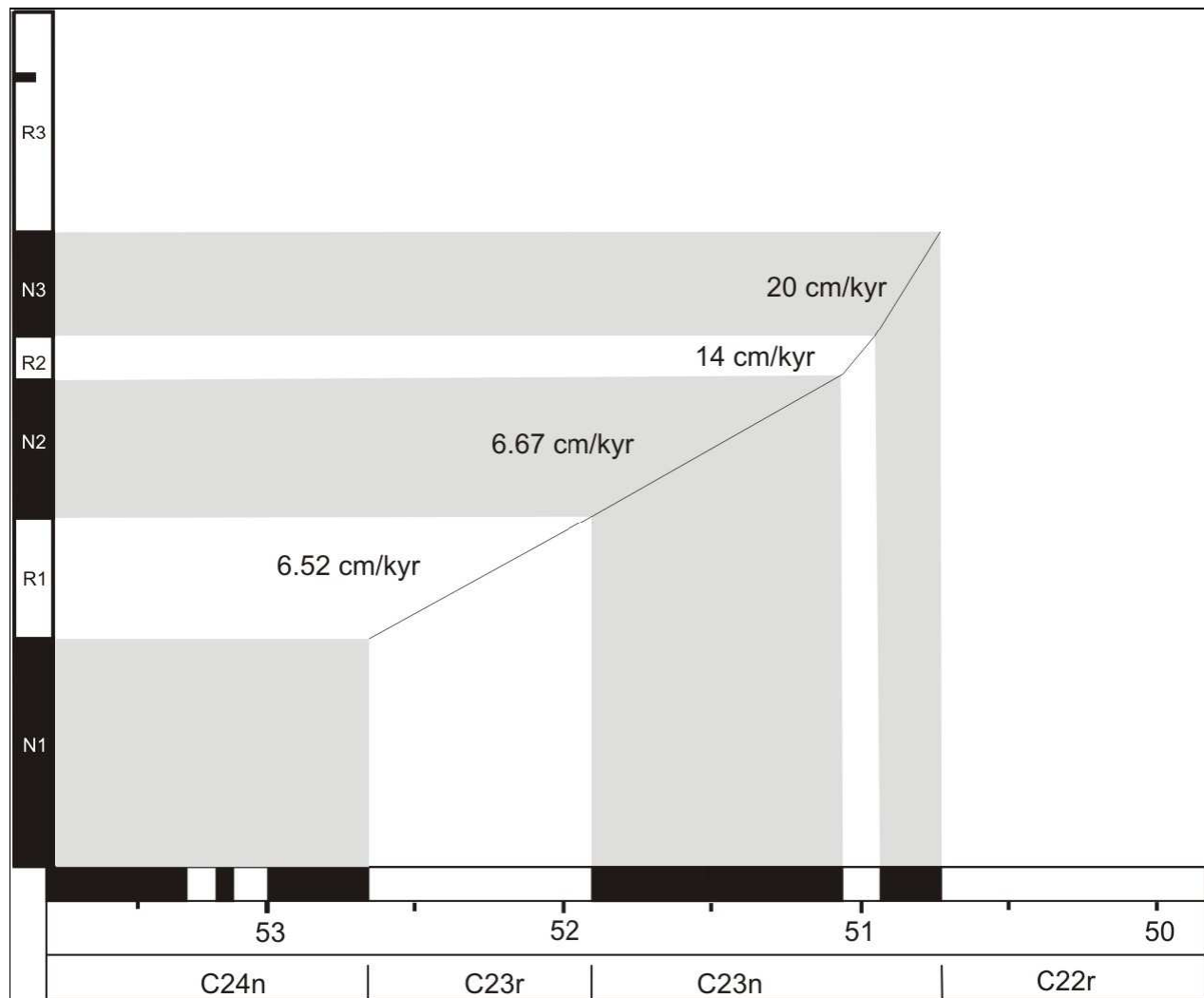


Figure 1.8. Preferred correlations of El Kohol section with geomagnetic-polarity time scale (GPTS) of Gradstein et al. (2004).

### 4.1.3 Sedimentation rates

The correlation of the section to the GPTS permits an assessment of the compacted sedimentation rates accumulation and allows comparison with the results from other continental basins. The variability in sedimentary accumulation for the El Kohol sequence is shown in Figure 1.9. Sedimentation rates have been calculated for each chron. They range from 6 to 20 cm/kyr with a mean rate of 8.6 cm/kyr. The variability in sedimentation rates of the fluvio-lacustrine deposits of El Kohol reveals different stages of the deposit process. Sedimentation rates inferred for Intermediate Marly and Calcareous Member (~6.5 cm/kyr) are lower than those obtained for the Upper Red Detritic Member (~17 cm/kyr). The lower rates observed from the marly and calcareous levels are consistent with the lithology since these deposits are associated to lacustrine depositional environment.



**Figure 1.9.** Comparison of El Kohol magnetic polarity stratigraphy with the GPTS of Gradstein et al. (2004). Slopes are proportional to sedimentation rate.

The polarity interval zones R1 and N2 observed in the Upper detritic Member show higher sedimentation rates. This interval corresponds to fluvial channel environments, which generally

have high sedimentation rates. These rates are within the observed range of sedimentation rates estimated for the continental channel and overbank deposits on fluvial sequences (Johnson et al. 1982; Sen et al. 1986; Kappelman et al. 1991; Benammi and Jaeger 2001; Suganuma et al. 2006). Thus, the variation in the sedimentation rates calculated from this correlation of our magnetostratigraphic polarity zones to the GPTS is generally consistent with the paleoenvironmental interpretation based on lithology.

## 4.2. GOUR LAZIB SECTION

### 4.2.1 Biostratigraphic data

The Glib Zegdou Formation, unconformably overlying Paleozoic strata or marine Cenomanian-Turonian series of the Kem Kem, has yielded the most diverse African early to middle Eocene mammalian fauna. The fossil collection from this formation has been remarkably enriched during the last five years when several new localities have been discovered. Actually, five main mammal-bearing localities are now recognized from this formation, three in the Gour Lazib and two on the northern and southern side of Glib Zegdou (Gevin et al. 1975; Sudre 1975, 1979; Godinot and Mahboubi 1992, 1994; Vianey-Liaud et al. 1994; Mahboubi 1995; Crochet et al. 2001; Mahboubi et al. 2002; Adaci et al. 2007; Tabuce et al. 2007, 2009).

The Glib Zegdou Formation has produced more than 500 mammalian identifiable remains, comprising mainly micromammal fossils, documenting the occurrence of rodents, primates, hyracoids, soricomorph, condylarthrans, macroscelidids and hyaenodontid creodonts associated to many remains of aquatic vertebrates. Along the sites that may be early to early middle Eocene in age, Gour Lazib fauna displays more similarities with the faunal assemblage recovered from Chambi in Tunisia.

The Lower Member of Glib Zegdou Formation has yielded actinopterygians fishes and lungfish, a podocnemidid chelonian and the hyracoid *Titanohyrax mongereai*. *T. mongereai*, exhibiting brachyodont and less selenodont cheek teeth, seems more primitive than *T. tantulus* described from the Intermediate Member of Glib Zegdou Formation and from the early to middle Eocene deposits of Chambi (Adaci et al. 2007). However, according to Barrow et al. (2010) which compare this material to the Fayum species of *Titanohyrax*, the attribution of this Algerian material to this genus is questionable.

The Intermediate Member includes the richest fossiliferous strata of the formation. Charophytes, numerous fish remains and more than 20 species of mammals have been recovered from several loci in the red to yellow siltstone and sandstone levels of this member. The mammal-bearing strata have yielded a rich collection of charophytes, homogeneous along the sequence. Charophyte assemblage comprises several genera, including *Raskyella*, *Maedleriella*, *Stephanochara*, *Nodosochara*, *Nitellopsis*, *Harrisichara*, and *Chara*, which indicate a stratigraphic range from late early to early middle Eocene (Gevin et al. 1974; Mebrouk et al. 1997).

The Intermediate Member mammal faunas are dominated by Zegdoumyidae rodents, hyracoids and stem strepsirrhine primates. The extinct rodent family Zegdoumyidae represents the oldest known African rodents but its origin and phylogenetic relationships are not firmly established. Zegdoumyids have a restricted geographical and temporal distribution. They are only

known from the deposits of Glib Zegdou and Chambi and are represented by isolated teeth assigned to three genera (*Zegdoumys*, *Glibia*, *Glibemys*) (Vianey-Liaud et al. 1994). Gour Lazib Zegdoumyid fauna comprises more than 5 taxa and appears as more diversified than that of Chambi which yielded only four isolated teeth belonging to one species (*Zegdoumys sbeitlai*). Zegdoumyids have low crowned, lophodont molars and the incisor enamel is transitional pauciserial-uniserial. According to Martin (1993), *Z. sbeitlai* displays a more primitive subtype of pauciserial to uniserial Hunter-Schreger bands in the incisor enamel compared to *Z. lavocati* from Gour Lazib which displays pauciserial enamel microstructure. The hyracoid fauna from the Intermediate Member displays a remarkable diversity and includes the small primitive Titanohyracid *Titanohyrax tantulus* along with *Microhyrax lavocati*, *Megalohyrax gevini*, *Bunohyrax* sp. and *Thyrohyrax* sp. (Sudre 1979; Tabuce et al. 2001; Adaci et al. 2007). The hyracoid *T. tantulus* has been initially described from Chambi (Court and Hartenberger 1992). However, the stratigraphic range of this species is not well known and, on the basis of hyracoids alone, it is difficult to assess the relative ages of the Tunisian and Algerian sites. Moreover, the attribution of the Algerian and Tunisian hyracoid species to the genera *Megalohyrax* and *Titanohyrax* has been recently questioned (Barrow et al. 2010). The species of *Microhyrax* is slightly smaller but somewhat higher crowned and has stronger cristids than *Seggeurius* from El Kohol and is considered as more derived than this later taxon (Court and Mahboubi 1993; Tabuce et al. 2001). Unfortunately, little is known about the early stages of Hyracoid radiation and most of our knowledge of the early evolutionary history of this order comes from the Jebel Qatrani Formation of the Fayum Depression, which is significantly younger than Gour Lazib Formation. The Azibiid primates, *Algeripithecus* and *Azibius*, also recovered from the Intermediate Member, provide the first record of offshoots of an Afro–Arabian endemic strepsirrhine clade. Within this strepsirrhine group, Azibiids seem closely related to *Djebelemur* from Chambi and to crown Strepsirrhines (Tabuce et al. 2009). Only one specimen of Macroscelidid, corresponding to an isolated M<sub>3</sub>, has been described from the Intermediate Member of Glib Zegdou Formation and assigned to the genus *Chambius* (Adaci et al. 2007). The subfamily of Herodotiinae are only documented by four species: *Chambius* sp. from Gour Lazib, *Chambius kasserinensis* from the early to middle Eocene of Chambi, *Nementchatherium senarhense* from the late middle deposits of Bir El Ater and *Herodotius pattersoni* from late Eocene of Fayum (Hartenberger 1986; Simons et al. 1991; Tabuce et al. 2001, 2007). Within the subfamily, the taxon from Gour Lazib more closely resembles to *Chambius kasserinensis* but seems more primitive. Gour Lazib taxon might thus be recognized as the oldest known and most primitive known elephant-shrew. However, little can be told regarding the scarcity of the material attributable to Macroscelidids from Gour Lazib and additional discoveries of representatives of this taxon are needed to allow further comparison.

Actually, the mammalian fauna from Glib Zegdou Formation is more similar to Chambi mammalian assemblage than to any other African early to middle Eocene fauna. These localities share common occurrences of the zegdoumyid rodents, the macroscelid *Chambius* and the hyracoid *Titanohyrax tantulus* which are absent from younger localities. Chambi, on the basis of charophytes and mammalian biostratigraphic data, is believed to be late early to early middle Eocene in age (Hartenberger et al. 2001) but the age of this locality is poorly constrained.

El Kohol Formation, dated from middle Ypresian, has yielded abundant remains of early proboscidean. The ordinal diversity of this locality is low and El Kohol fossil record seems to exhibit a taphonomic size bias in microfauna diversity, yielding to the underrepresentation of



small species, only represented so far by very few and poorly preserved remains of chiropterans (Ravel et al. 2010). On the basis of the composition of the faunas, it is thus difficult to propose a chronology for the relative ages of Gour Lazib and El Kohol localities, which do not yield common taxa at generic levels. The study of charophytes led Mebrouk et al. (1997) to suggest an age of late early to early middle Eocene age for Gour Lazib section, younger than El Kohol Formation which has yielded charophytes characteristic of early Eocene. The occurrence of a species of hyracoid in Gour Lazib Formation, which seems somewhat more derived than that of El Kohol, may also supports a slightly younger age for Gour Lazib.

Taking in account the late early to early middle Eocene age range suggested by biostratigraphical data, we considered the potential correlation of Gour Lazib magnetostratigraphic column to the GPTS of Gradstein et al. (2004). Within this time interval, two correlations seem more likely (Figure 1.10). The normal polarity zone at the base of Gour Lazib polarity sequence is likely to be correlated with the topmost part of chron C22n (48.5-49.4Ma) or chron C21n (47.2-45.3) of GPTS. Paleomagnetic data suggest therefore that Gour Lazib fossiliferous strata would probably be about 49 Ma at Ypresian-Lutetian boundary or earliest Lutetian in age (~45.5Ma). Additional paleontological data may permit to propose stronger correlations with GPTS than those proposed here.

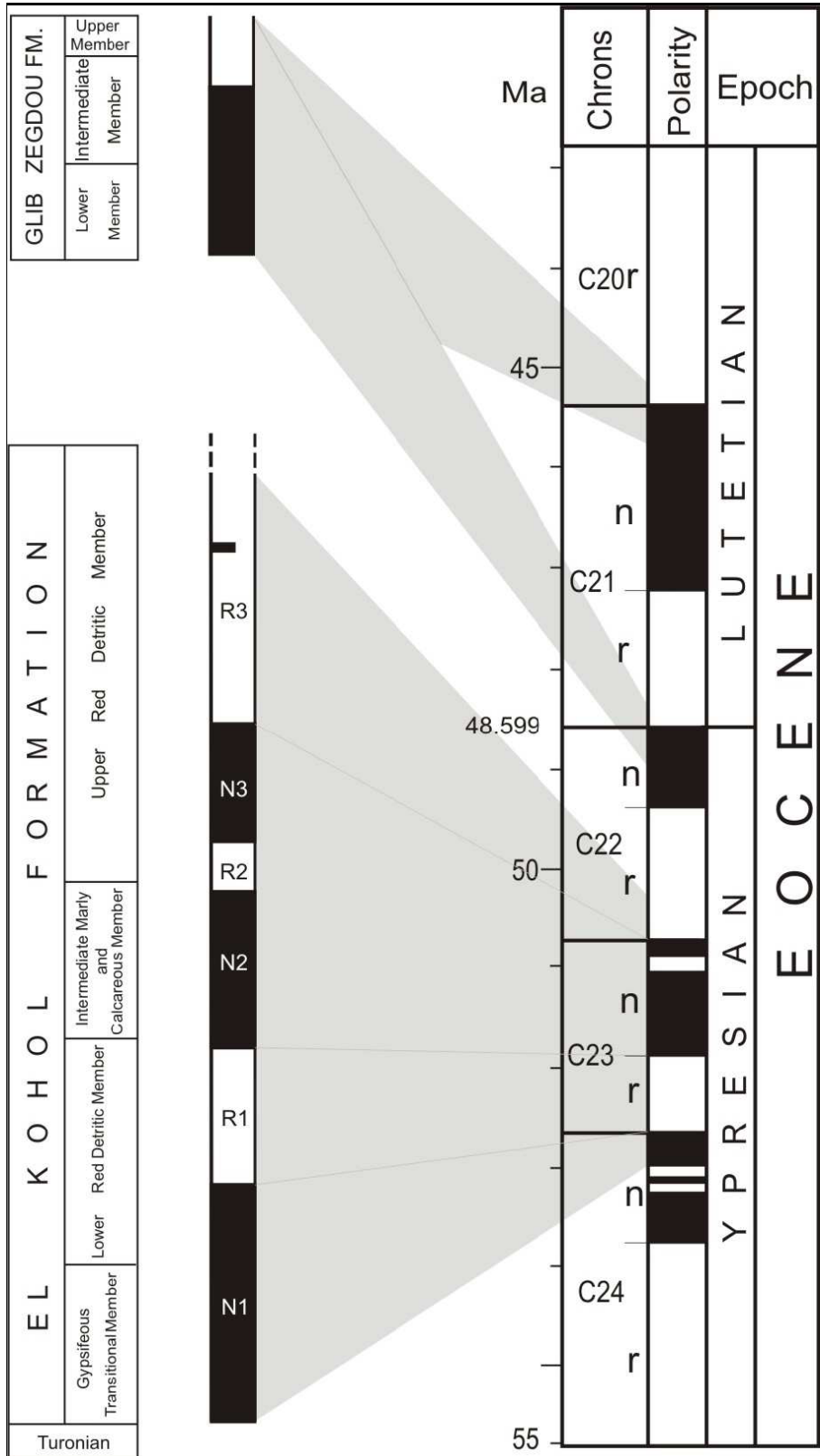


Figure 1.10. Preferred correlations of El Kohol and Gour Lazib sections with geomagnetic-polarity time scale (GPTS) of Gradstein et al. (2004).

## 5. CONCLUSION

The Afro-Arabian fossil record of Paleogene mammalian evolution is poor. Insufficient age constraints and discrepancies in paleontological interpretations on early African mammal localities have led, over the years, to different chronological relative estimations (e.g., Rasmussen et al. 1992; Seiffert et al. 2008; Seiffert 2010). During the past decades, temporal control through magnetostratigraphic studies and advancement in stratigraphical and biochronological resolutions of the African Paleogene record have helped improving the calibration of land-mammal bearing horizons and correlation among the different localities. The chronology of the Eocene continental sites of Africa is, however, still particularly difficult to assess, because of the singularity of the faunal assemblages and the limited occurrence of comparable sites. The precise temporal framework provided here by magnetic-polarity stratigraphy studies of El Kohol and Gour Lazib fossiliferous localities, which document the poorly known mammalian African history during early Eocene Epoch, represents a great improvement of the situation. The favoured correlation between the El Kohol magnetic polarity stratigraphy and the Geological Polarity Time Scale suggests that these deposits range from Chron C24n to C22r. This correlation provides the first direct age estimates for the El Kohol fossiliferous strata which are considered to range between 52 and 51 Ma. The magnetostratigraphic study of Gour Lazib Formation indicates that the two most probable correlations for this section with the Geological Polarity Time Scale are with chrons C22n-C21r (Ypresian-Lutetian boundary) or with chrons C21n-C20r (mid-Lutetian). The proposed correlations suggest that the age of Gour Lazib Formation ranges between 49 and 45Ma, but additional paleontological finds are needed in the early and middle Eocene deposits of Africa to further constrain the age of this site and allow a better understanding of early mammal evolution in Africa. Besides, fossil evidences that might bear answers on the question of Anthropoid origins remain virtually unknown from all of Africa before the latest part of Eocene Epoch. The growing Eocene fossil record in Asia suggests that this continent played a major role in Anthropoid evolution but we necessitate now more data from the key period of African middle Eocene to allow definitive determination of the geographic center of Anthropoids and to reconstruct their early migration pattern.

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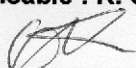
**Annexe n°8**

# RAPPORT D'ESSAI

N° : D86 /2009

## IDENTIFICATION

### ANALYSE MINERALOGIQUE D'ECHANTILLONS DE TERRAIN PAR DRX (COUPES GZ & D)

| Nom et adresse du client  | Travaux réalisés   |
|---|--|
| Université Abou Bekr BELKAÏD<br>Faculté des sciences de la Nature<br>Rocade 2 - B.P. 119<br>TLEMCEM – 13000 | Direction : Géologie   |
|   | Laboratoire : Sédimentologie   |
|   | Nom du responsable : K. GUELLIL  |
|   | Signature :  |
|   | Date ou période d'exécution: Juillet 2009  |

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En cas d'émission du présent rapport par voie électronique et/ou sur support physique électronique, seul le rapport sous forme de support papier signé par le responsable de l'essai fait foi en cas de litige.  
Les incertitudes établies par le laboratoire sont communiquées sur demande.  
Ce rapport comporte 17 pages et 0 annexe.

**Détail des travaux**

| <b>Nature des opérations<br/>(Échantillonnage, Essai, Étude...)</b> | <b>Code de<br/>l'opération</b> | <b>Intitulé de l'opération</b> | <b>Noms des responsables<br/>d'Essai</b> |
|---|--------------------------------|--------------------------------|--|
| Essai   | MO-GEO-S1                      | Analyse minéralogique par DRX  | M. Belkadi et K. Guellil                 |
|   |                                |                                |  |
|   |                                |                                |  |

**SOMMAIRE**

**DIFFRACTOMETRIE DES RAYONS X (DRX)**

- 1-Principe d'analyse :
- 2-Condition expérimentale :
- 3- Résultats d'analyse DRX

**PREAMBULE**

Treize échantillons de terrain, conformes et en quantité suffisante, remis par le client, en vue d'une caractérisation minéralogique qualitative par diffractométrie des rayons X (DRX), conformément à sa demande, émise par le Directeur du Laboratoire N° 25 de la Faculté des Sciences de la Nature, de la Vie, de la Terre et de l'Univers de l'université Abou Bekr BELKAÏD de Tlemcen, sise Rocade-2 B.P. 119 Tlemcen 13000, assortie d'un bon de commande N° 007704 du 15/07/09. Cette étude (DRX) a été réalisée par K. GUELLIL, ingénieur analyste N3, en juillet 2009.



**Rapport d'Essai N° : D86/2009 (Osil : 09-0189)**

**Identification de l'essai : MO-GEO-S1**

**Lieu où l'essai a été effectué : UEM (Rayons X) CRD Boumerdès**

❖ Laboratoire : Diffractométrie des rayons X (DRX)

❖ N° du local : 309

❖ Code Equipement : 21703

**Responsable de l'essai : Belkadi M.**

**Date ou période d'exécution de l'essai : Juillet 2009**

**DIFFRACTOMETRIE DES RAYONS X (DRX)**

**1-Principe d'analyse :**

Les échantillons solides finement broyés, sont montés sur des porte échantillons adéquats, sont soumis à un faisceau des rayons X pour être diffractés par les plans réticulaires des phases cristallines, en effet il existe une relation entre l'angle du faisceau diffracté et la distance réticulaire séparant les plans d'atomes au sein d'un réseau cristallin ; celle-ci est régie par la loi de Bragg  $n \lambda = 2d \sin \theta$  (où  $\lambda$  =longueur d'onde en angströms,  $d$ = distance réticulaire en angströms et  $\theta$  = angle de diffraction ou de réflexion en degrés).

Des diffractogrammes sont obtenus à l'aide d'un diffractomètre à rayon X. Les positions et les intensités de pics observés sont comparés aux fichiers de référence PDF-ICDD (Powder Diffraction File - International Center for Diffraction Data) pour l'identification des phases minéralogiques présentes. Et éventuellement l'utilisation de RIR (Reference Intensity Ratio) inclus dans le logiciel HighScore Plus du fichier PDF-ICDD pour l'estimation semi quantitative des phases correspondantes quand celle-ci est requise et/ou possible.

**2-Condition expérimentale :**

Diffractomètre X'Pert PRO, tube radiogène à anticathode de cuivre

Logiciel pour traitement des données: HighScore Plus

Longueur d'onde  $\text{CuK}\alpha$  [Å]: 1,5418

Angle de départ [ $^{\circ}2\theta$ .]: 2,0000

Angle final [ $^{\circ}2\theta$ .]: 70,0000

Taille du pas [ $^{\circ}2\theta$ °]: 0.0170

Temps du pas [s]: 45.8746

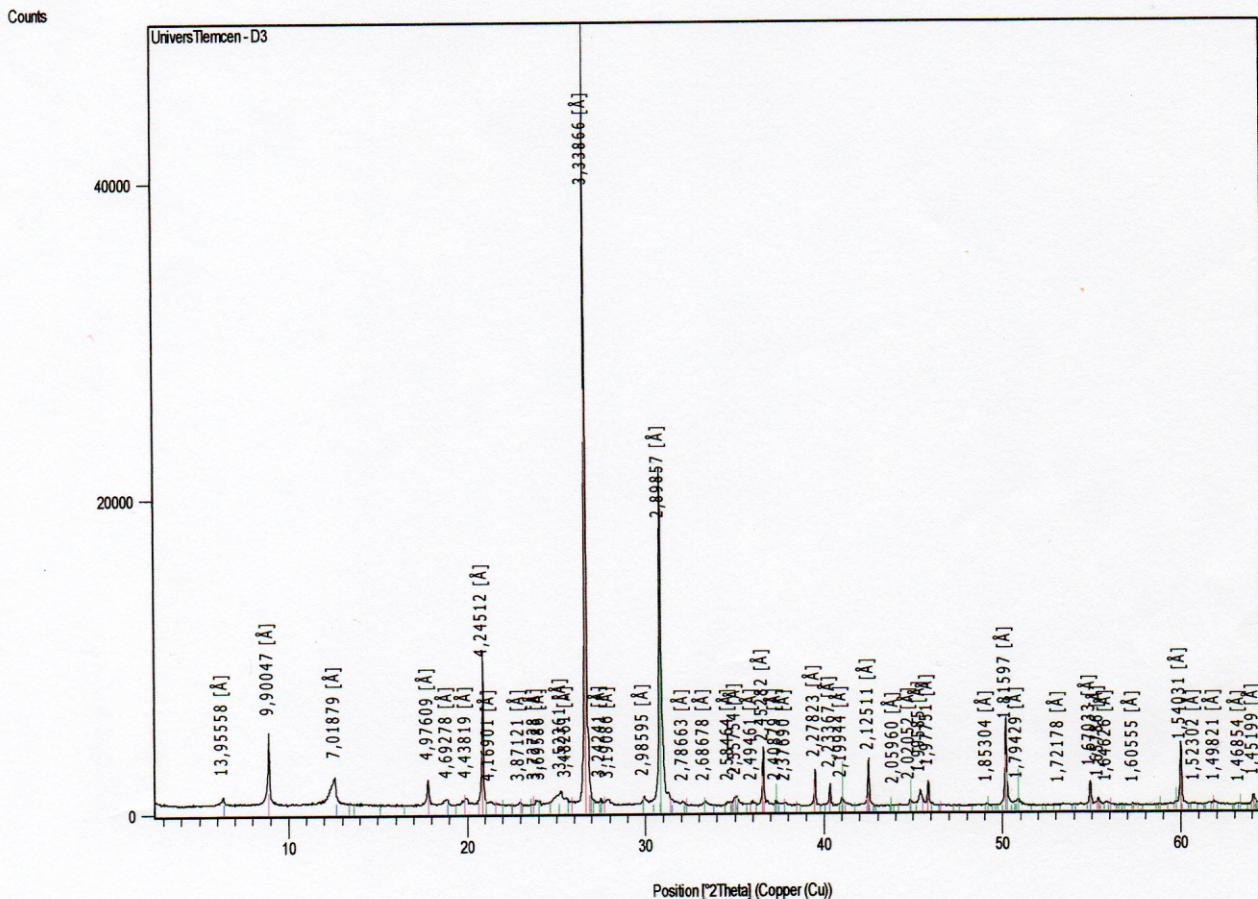
Puissance du générateur à RX: 45 mA, 40 kV

**3- RESULTATS D'ANALYSE DRX**

L'analyse par radiocristallographie des échantillons étudiés, a mis en évidence les phases minéralogiques suivantes :

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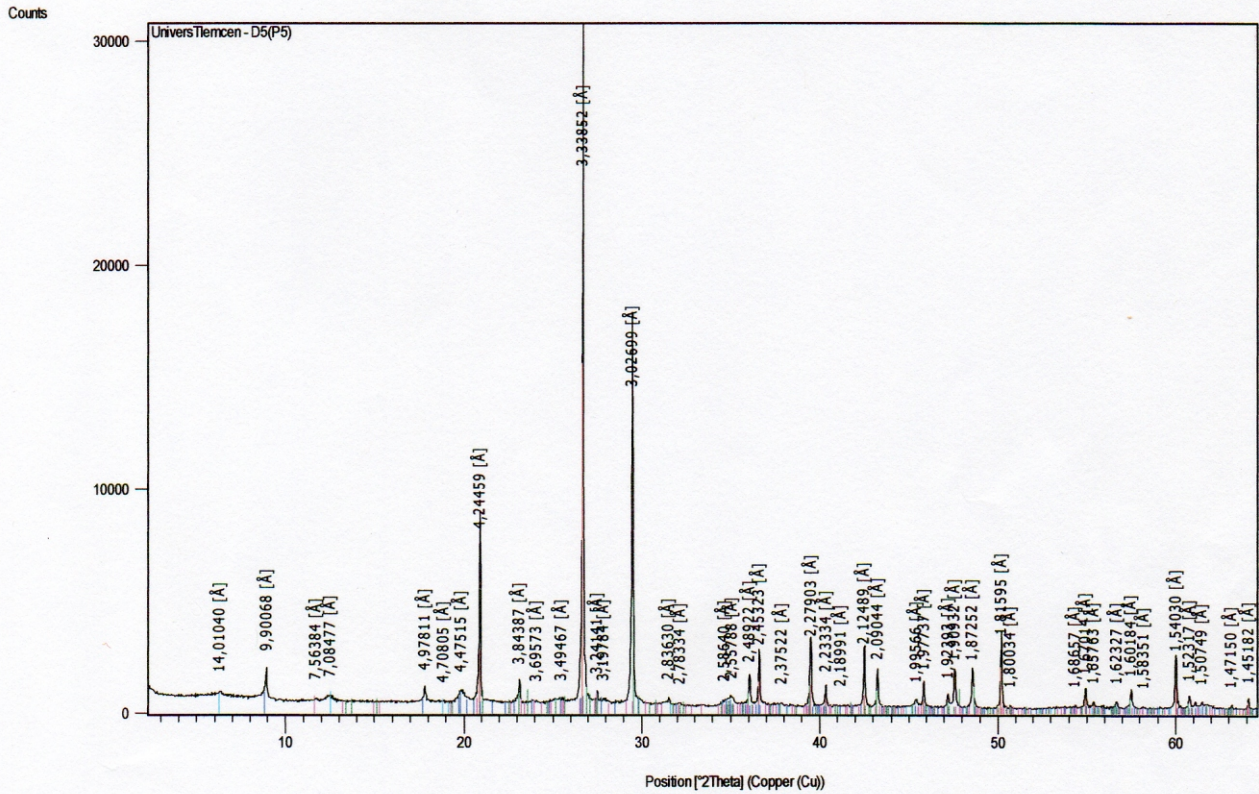
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- ✓ Dolomite  $\text{Ca Mg ( C O}_3)_2$
- ✓ Orthoclase  $\text{K Al Si}_3\text{O}_8$
- ✓ Illite  $\text{K Al}_2\text{Si}_3\text{Al O}_{10} ( \text{O H} )_2$
- ✓ Chlorite  $( \text{Mg , Fe} )_5 ( \text{Al , Si} )_5 \text{O}_{10} ( \text{O H} )_8$





**Echantillon N°2 : D5(P5)**

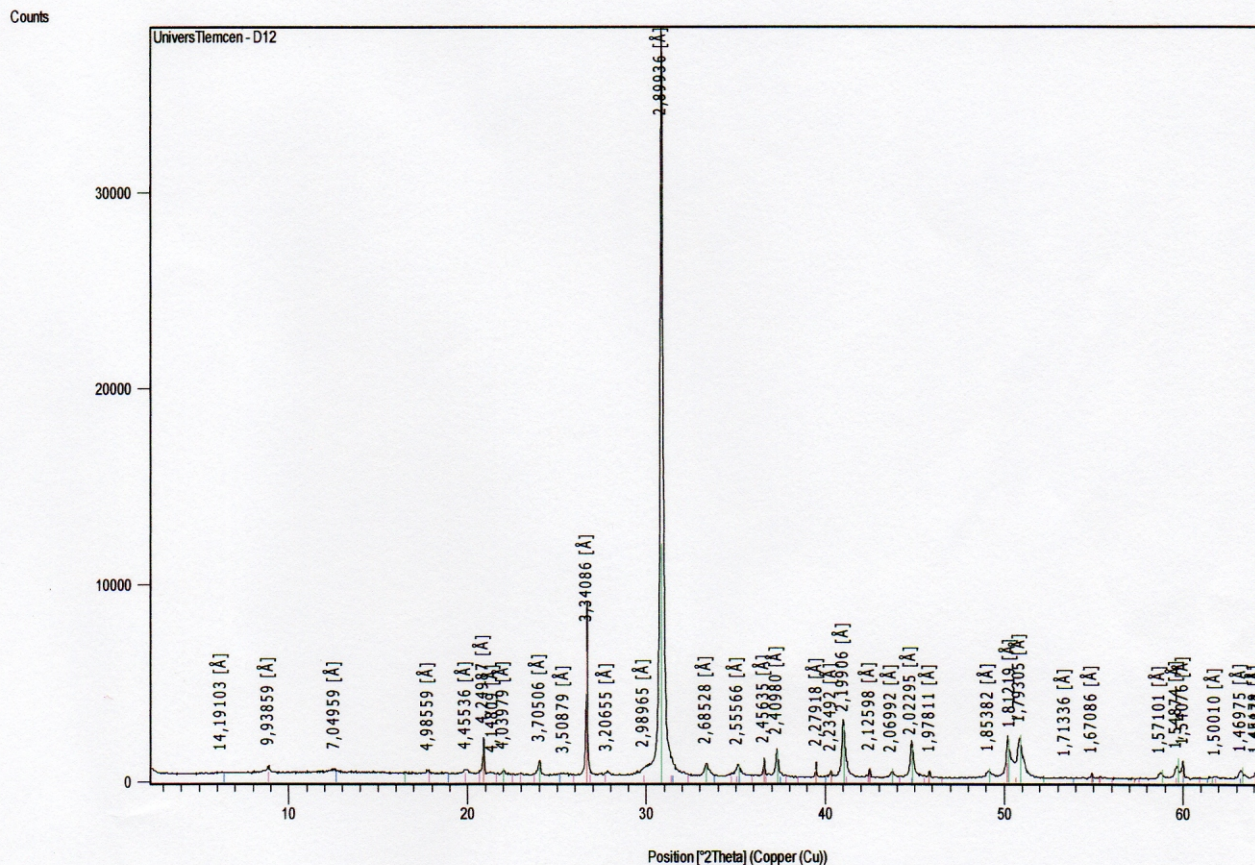
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- ✓ Calcite  $\text{Ca C O}_3$
- ✓ Illite  $\text{K ( Al}_4\text{ Si}_2\text{ O}_9\text{ ( O H )}_3\text{)}$
- ✓ Clinocllore  $\text{( Mg , Fe )}_6\text{ ( Si , Al )}_4\text{ O}_{10}\text{ ( O H )}_8$
- ✓ Orthoclase (trace)  $\text{K Al Si}_3\text{ O}_8$
- ✓ Gypse (trace)  $\text{Ca S O}_4 \cdot 2\text{ H}_2\text{ O}$





**Echantillon N°3 : D12**

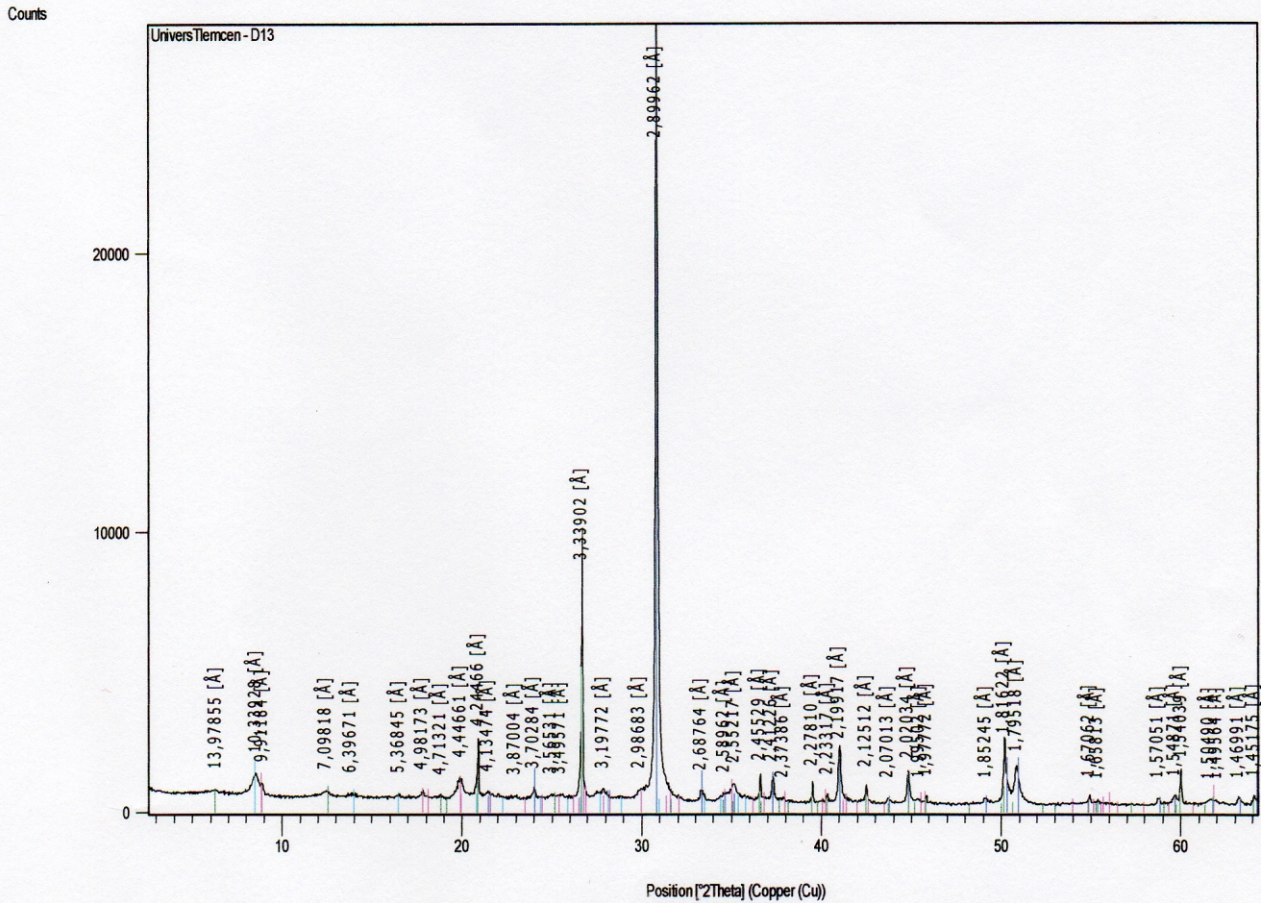
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- ✓ Dolomite  $\text{Ca Mg ( C O}_3 \text{ )}_2$
- ✓ Orthoclase  $\text{K Al Si}_3 \text{ O}_8$
- ✓ Illite  $\text{K Al}_2 \text{ Si}_3 \text{ Al O}_{10} ( \text{ O H } )_2$
- ✓ Chlorite  $( \text{ Mg , Fe } )_5 ( \text{ Al , Si } )_5 \text{ O}_{10} ( \text{ O H } )_8$





**Echantillon N°4 : D13**

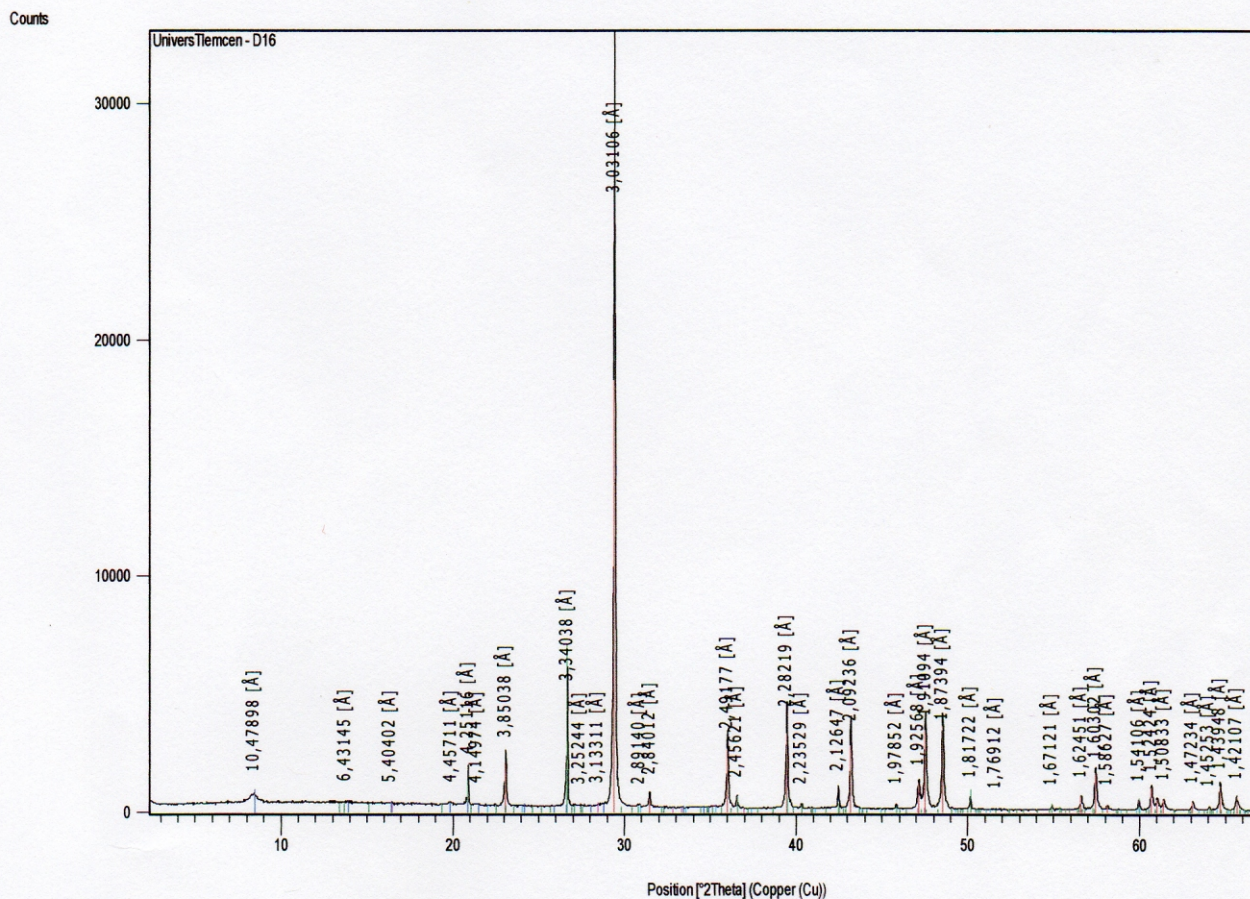
- ✓ Quartz Si O<sub>2</sub>
- ✓ Dolomite Ca ( Mg , Fe ) ( C O<sub>3</sub> )<sub>2</sub>
- ✓ Palygorskite ( Mg , Al )<sub>5</sub> ( Si , Al )<sub>8</sub> O<sub>20</sub> ( O H )<sub>2</sub> ! 8 H<sub>2</sub> O
- ✓ Clinocllore ( Mg , Fe )<sub>6</sub> ( Si , Al )<sub>4</sub> O<sub>10</sub> ( O H )<sub>8</sub>
- ✓ Illite 2 K<sub>2</sub> O ! 3 Mg O ! Al<sub>2</sub> O<sub>3</sub> ! 24 Si O<sub>2</sub> ! 12 H<sub>2</sub> O





**Echantillon N°5 : D16**

- ✓ Calcite  $\text{Ca}(\text{CO}_3)$
- ✓ Quartz  $\text{SiO}_2$
- ✓ Palygorskite  $\text{Mg}_5(\text{Si}, \text{Al})_8\text{O}_{20}(\text{OH})_2 \cdot 8\text{H}_2\text{O}$
- ✓ Dolomite en trace  $\text{CaMg}(\text{CO}_3)_2$



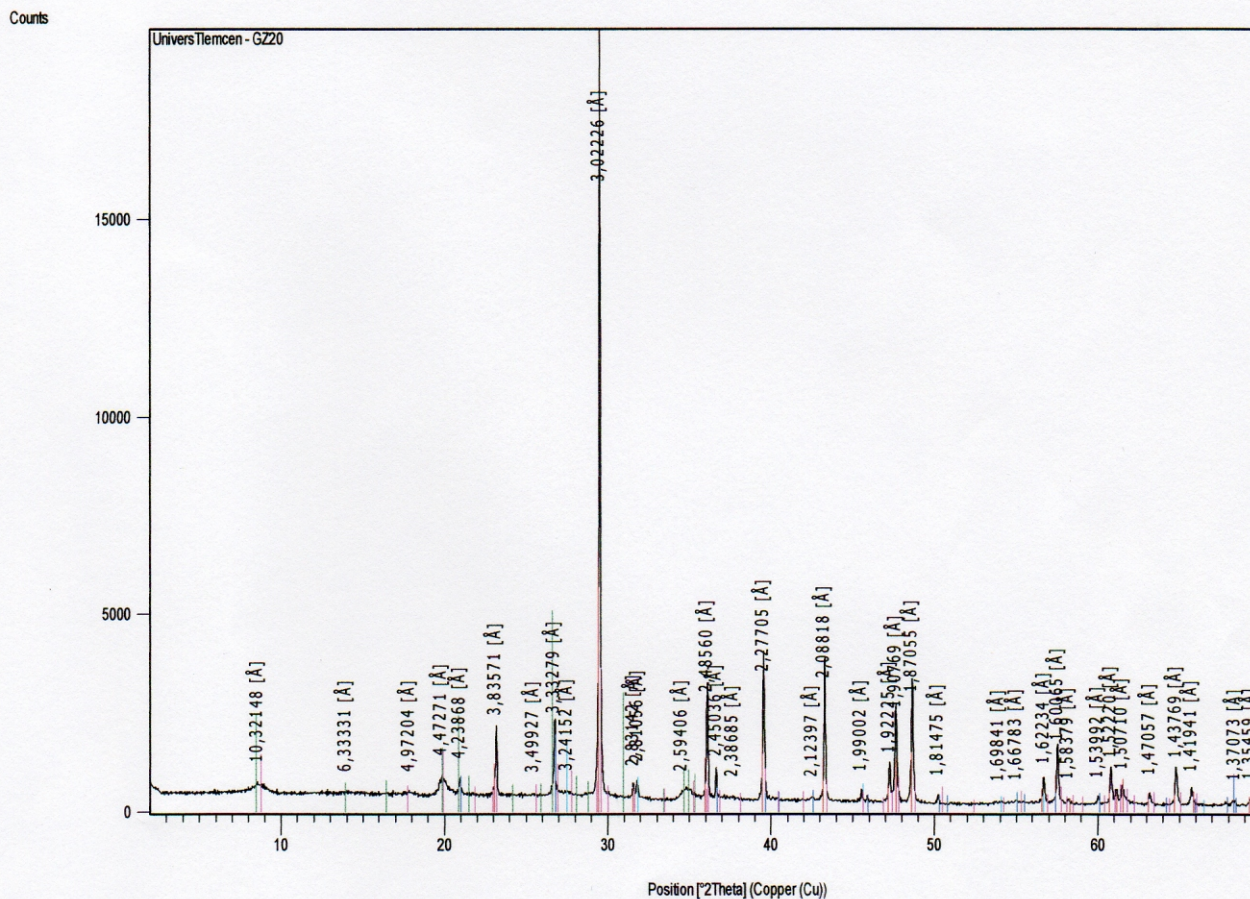






**Echantillon N°7 : GZ20**

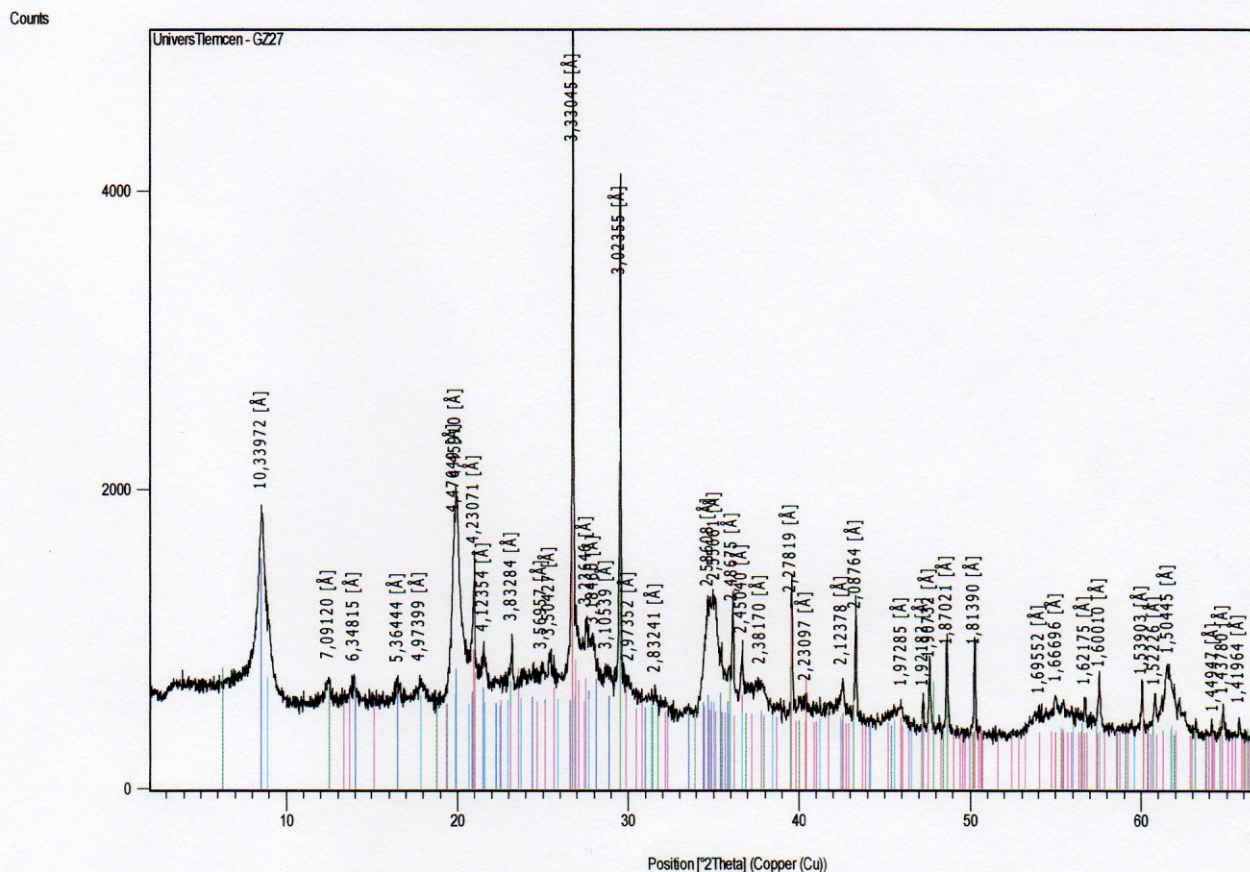
- ✓ Calcite  $\text{CaCO}_3$
- ✓ Quartz  $\text{SiO}_2$
- ✓ Halite  $\text{NaCl}$
- ✓ Palygorskite  $(\text{Mg}, \text{Al})_5(\text{Si}, \text{Al})_8\text{O}_{20}(\text{OH})_2 \cdot 8\text{H}_2\text{O}$
- ✓ Illite en trace,  $\text{K}(\text{AlFe})_2\text{AlSi}_3\text{O}_{10}(\text{OH})_2 \cdot \text{H}_2\text{O}$





**Echantillon N°8 :GZ27**

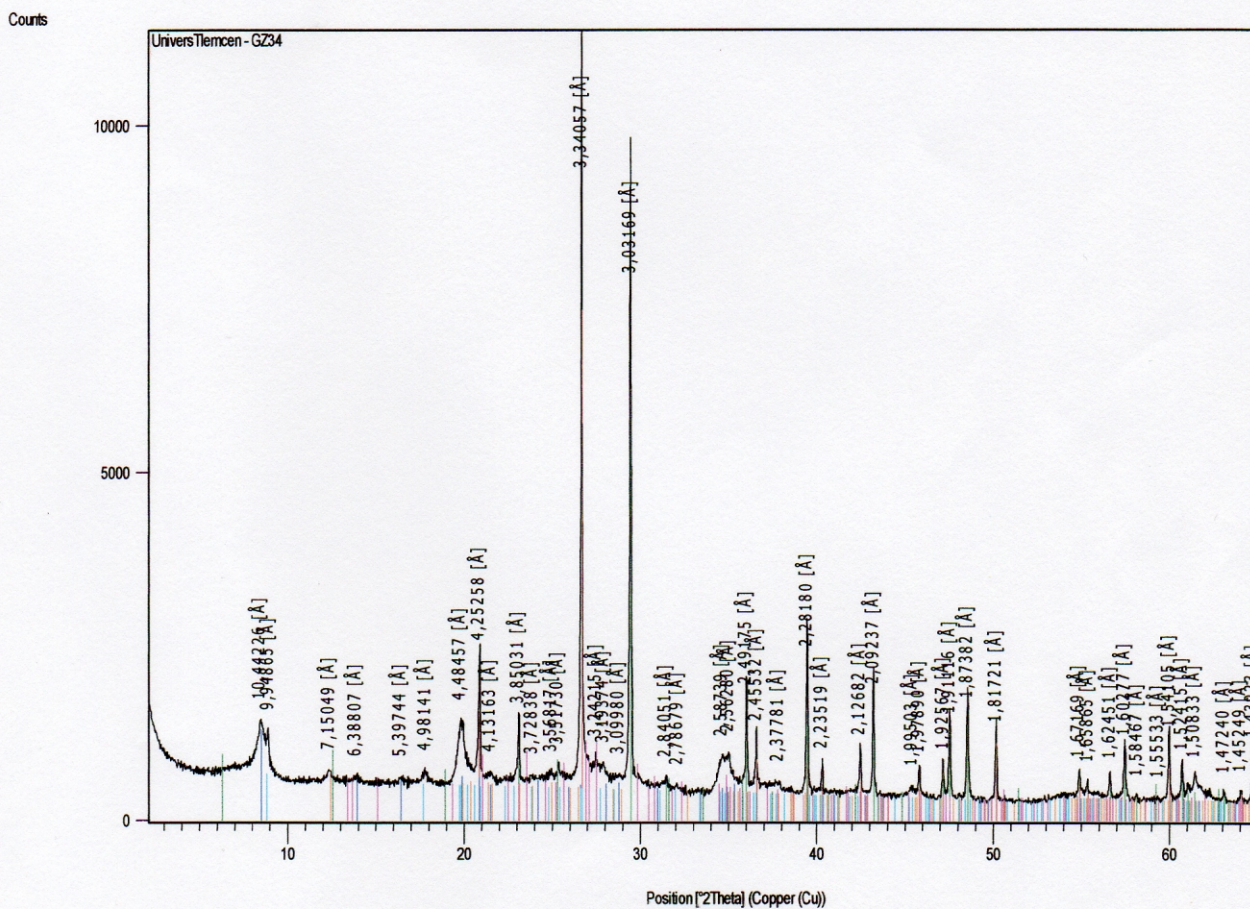
- ✓ Quartz Si O<sub>2</sub>
- ✓ Calcite Ca C O<sub>3</sub>
- ✓ Palygorskite ( Mg , Al )<sub>5</sub> ( Si , Al )<sub>8</sub> O<sub>20</sub> ( O H )<sub>2</sub> 18 H<sub>2</sub> O
- ✓ Illite K Al<sub>2</sub> Si<sub>3</sub> Al O<sub>10</sub> ( O H )<sub>2</sub>
- ✓ Clinocllore ( Mg , Fe , Al )<sub>6</sub> ( Si , Al )<sub>4</sub> O<sub>10</sub> ( O H )<sub>8</sub>
- ✓ Orthoclase K Al Si<sub>3</sub> O<sub>8</sub>





**Echantillon N°9 : GZ34**

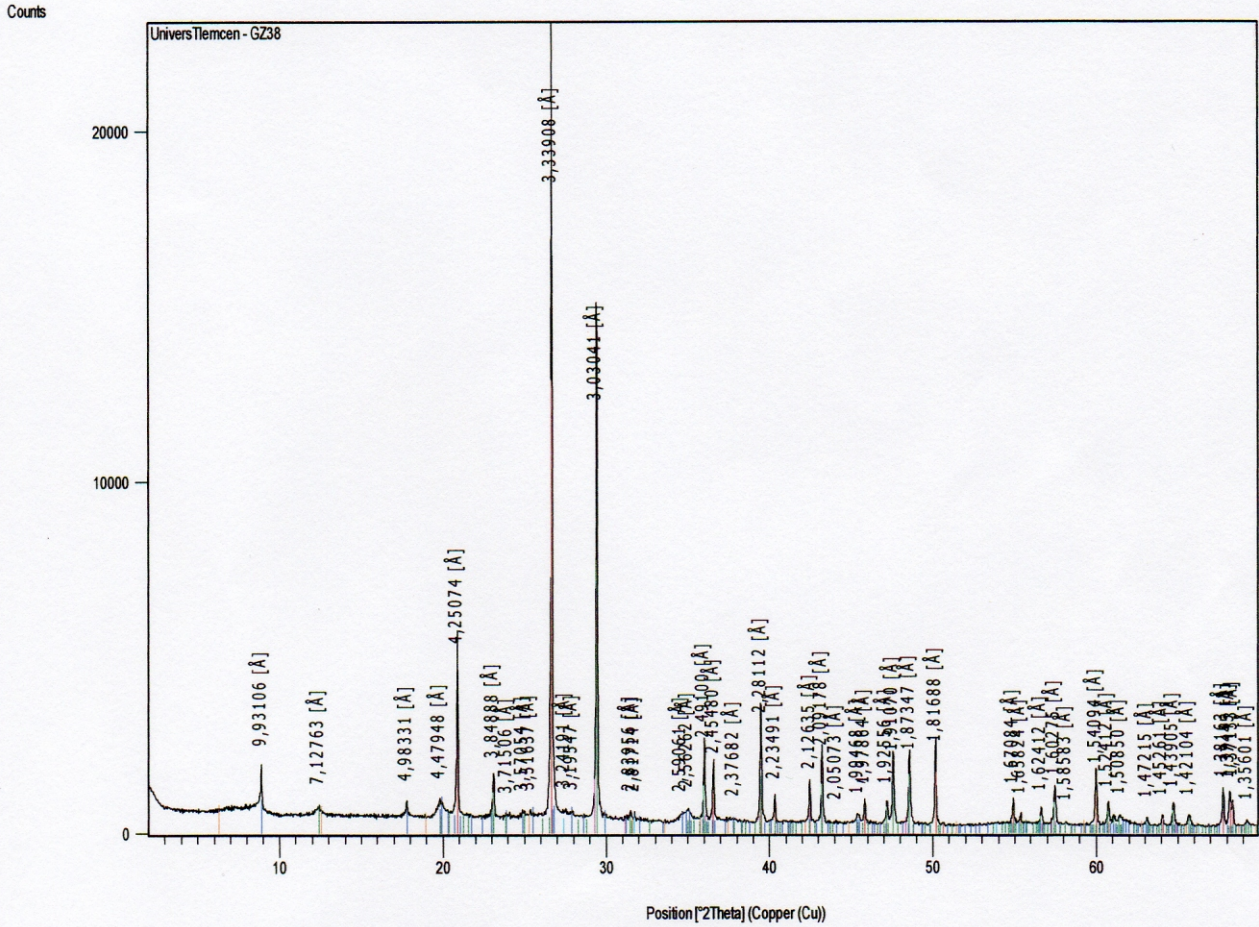
- ✓ Quartz  $\text{Si O}_2$
- ✓ Calcite  $\text{Ca ( C O}_3)$
- ✓ Palygorskite  $( \text{Mg , Al } )_5 ( \text{Si , Al } )_8 \text{O}_{20} ( \text{O H } )_2 \cdot 8 \text{H}_2 \text{O}$
- ✓ Illite  $\text{K ( Al}_4 \text{Si}_2 \text{O}_9 ( \text{O H } )_3)$
- ✓ Kaolinite  $\text{Al}_2 \text{Si}_2 \text{O}_5 ( \text{O H } )_4$
- ✓ Orthoclase  $( \text{K}_{.88} \text{Na}_{.10} \text{Ca}_{.009} \text{Ba}_{.012} ) ( \text{Al}_{1.005} \text{Si}_{2.995} \text{O}_8 )$
- ✓ Clinocllore  $\text{Mg - Fe - Fe - Al - Si - O - O H}$





**Echantillon N°10 : GZ38**

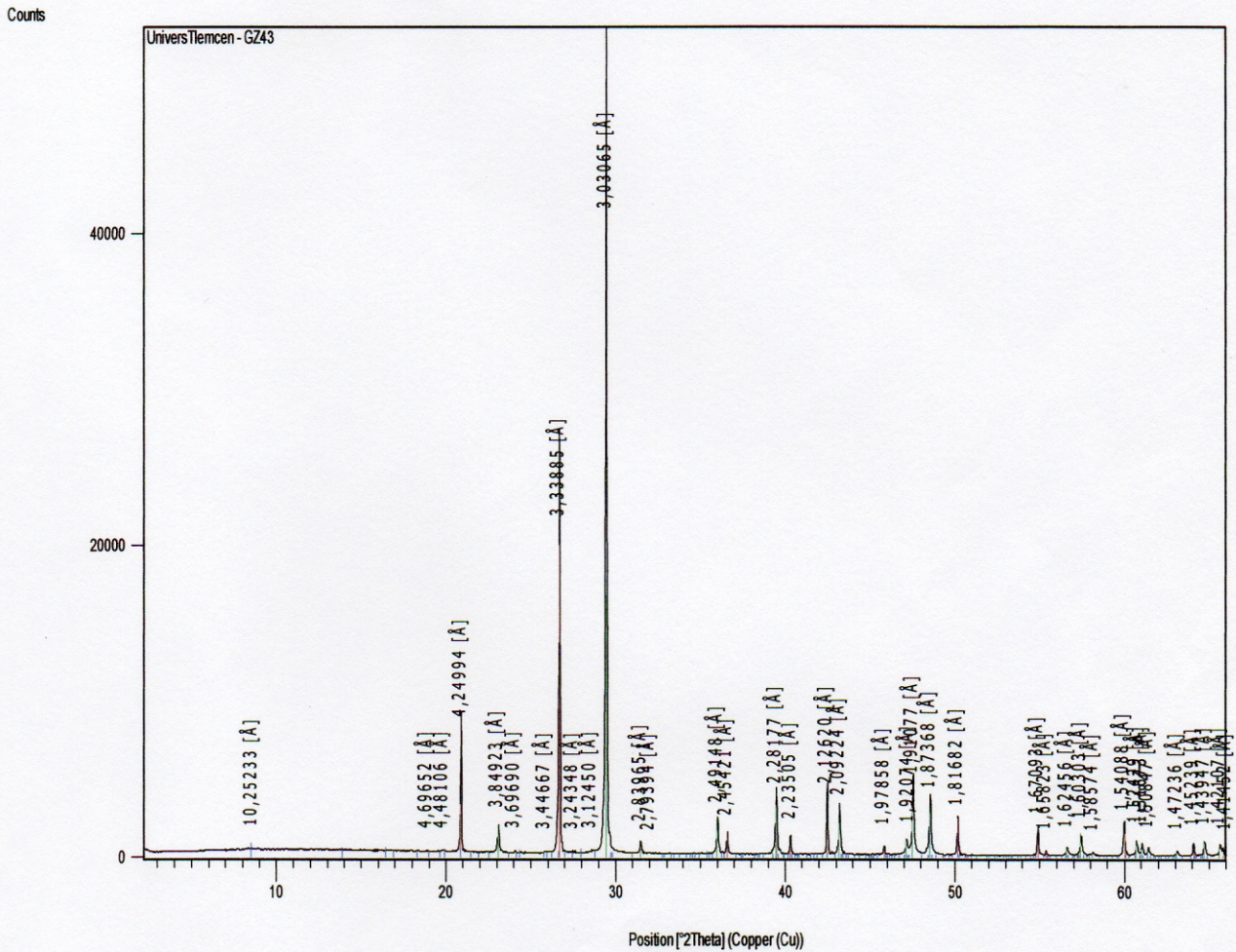
- ✓ Quartz Si O<sub>2</sub>
- ✓ Calcite Ca (CO<sub>3</sub>)
- ✓ Halite en trace Na Cl
- ✓ Illite K ( Al<sub>4</sub> Si<sub>2</sub> O<sub>9</sub> ( O H )<sub>3</sub> )
- ✓ Kaolinite Al<sub>2</sub> ( Si<sub>2</sub> O<sub>5</sub> ) ( O H )<sub>4</sub>
- ✓ Clinocllore en trace Mg - Fe - Fe - Al - Si - O - O H





**Echantillon N°11 : GZ43**

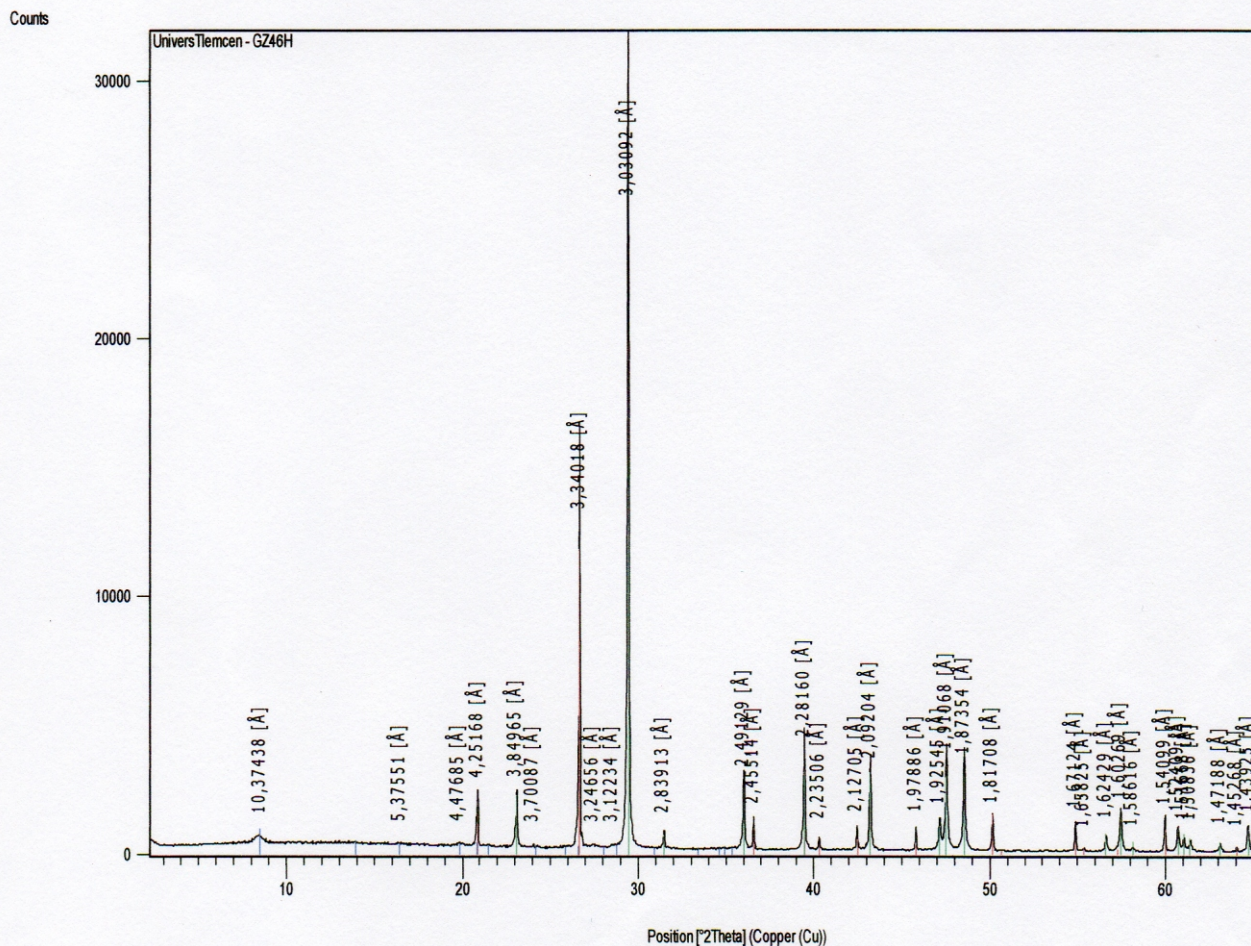
- ✓ Quartz  $\text{Si O}_2$
- ✓ Calcite  $\text{Ca C O}_3$
- ✓ Palygorskite en trace  $(\text{Mg}_{2.074} \text{Al}_{1.026}) (\text{Si}_4 \text{O}_{10.48})_2 (\text{O H})_2 (\text{H}_2 \text{O})_{10.68}$





**Echantillon N°12 : GZ46H**

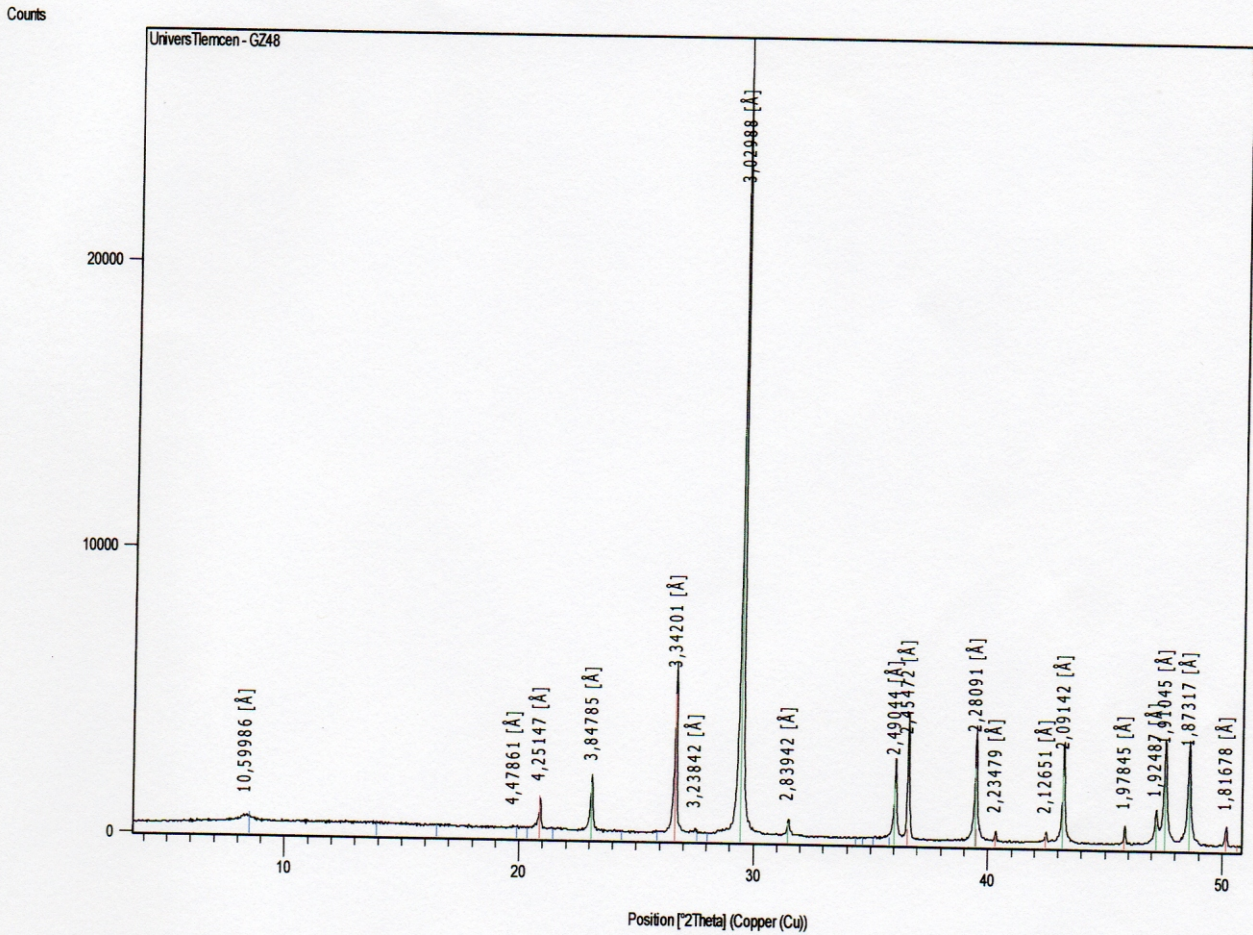
- ✓ Quartz  $\text{Si O}_2$
- ✓ Calcite  $\text{Ca C O}_3$
- ✓ Palygorskite  $(\text{Mg}_{2.074} \text{Al}_{1.026}) (\text{Si}_4 \text{O}_{10.48})_2 (\text{O H})_2 (\text{H}_2 \text{O})_{10.68}$





**Echantillon N°13 : GZ48**

- ✓ Quartz  $\text{Si O}_2$
- ✓ Calcite  $\text{Ca C O}_3$
- ✓ Palygorskite en trace  $(\text{Mg}_{2.074} \text{Al}_{1.026}) (\text{Si}_4 \text{O}_{10.48})_2 (\text{O H})_2 (\text{H}_2 \text{O})_{10.68}$



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**Annexe n°9**

## I- METHODE DE COLORATION DES LAMES MINCES A L'ALIZARINE

La méthode utilisée est celle de Dickson (1965) modifiée. Elle consiste à colorer les lames minces polies avec un mélange d'Alizarine rouge S / ferricyanure de potassium dans les proportions de 2/3 et dont la préparation est la suivante :

a- préparation de la solution de ferricyanure de Potassium. 598 ml d'eau distillée

3,18 ml d'HCl concentré (37 %)

3 gr de ferricyanure de Potassium

b- préparation de la solution d'alizarine rouge S. 998 ml d'eau distillée

5,3 ml d'HCl concentré (37 %)

1 gr d'Alizarine rouge S

c- méthode.

1- Préparer un mélange de ferricyanure de Potassium / Alizarine rouge S dans les proportions 3/2 et laisser reposer 24 heures avant usage.

2- Le temps d'attaque est de 4 minutes pour les échantillons analysés dans cette étude.

3- Après l'attaque, laver à l'eau distillée. L'eau du robinet contient du fer qui peut coller à l'échantillon.

L'alizarine a pour effet de colorer la calcite en rouge-rose, sans affecter la dolomite, ce qui permet de différencier les ciments calcitiques des ciments dolomitiques.

Le ferricyanure de potassium réagit en présence de fer en donnant une couleur bleu aux ciments qui en contiennent.

L'utilisation des deux solutions combinées permet d'obtenir pour chacun des ciments des couleurs différentes permettant de les différencier :

- la calcite non ferreuse prend une coloration rose à rouge,
- la calcite faiblement ferreuse est colorée en mauve,
- la calcite ferreuse est teintée en violet pouvant virer au bleu en fonction de la teneur en  $Fe^{2+}$ ,
- la dolomite non ferreuse ne présente aucune coloration,
- la dolomite faiblement ferreuse ( $Fe^{2+}/Mg^{2+} < 1$ ) est colorée en bleu pâle,
- la dolomite ferreuse (ankérite,  $Fe^{2+}/Mg^{2+} > 1$ ) est colorée en bleu foncé.

En plus de permettre la distinction des natures calcitique ou dolomitique des ciments et la proportion d'ions  $Fe^{2+}$  qu'ils contiennent, cette méthode permet d'évaluer l'évolution des fluides à partir desquels les ciments précipitent.

## II- CATHODOLUMINESCENCE

### Introduction

#### *Qu'est-ce que la cathodoluminescence ?*

Lorsque un atome est bombardé par un faisceau d'électron, il peut être plus ou moins excité, et émettre différents rayonnements selon sa nature et l'intensité du faisceau. Cet ainsi que des rayons X, des électrons secondaires, des électrons rétrodiffusés ou encore des photons peuvent être émis. Lorsque ces derniers sont dans le domaine du visible, il s'agit de cathodoluminescence.

#### *Quelles sont ses utilisations possibles en géologie ?*

En géologie, la cathodoluminescence permet d'avoir une image différente de celle que l'on peut obtenir en lumière transmise. Les applications suivantes sont parmi les plus courantes, bien que beaucoup d'autres ne demandent probablement qu'à être découvertes... :

#### **Roches volcaniques et métamorphiques et détritiques terrigènes :**

De par les comportements très différents des minéraux en cathodoluminescence, il est possible de distinguer parfois aisément deux minéraux d'habitude très semblable. Deux plagioclases de compositions légèrement différentes pourront ainsi donner une cathodoluminescence bien différenciable. La CL permet également de faire ressortir certaines zonations, ou encore de distinguer des fantômes de minéraux recristallisés. L'habitus de certains quartz /feldspaths dans une brèche permet également parfois d'outre les distinguer les uns des autres, de déterminer leur origine authigène ou terrigène.

#### **Roches carbonatées :**

La calcite et la dolomie sont aisément différenciables en CL.

Deux atomes semblent jouer un rôle prépondérant quant à l'intensité de la CL. Le Mn a un effet d'activateur, et le Fe d'inhibiteur important. Une faible variation du rapport de Fe/Mn pourra donc induire une différence de cathodoluminescence.

Fe et Mn se trouvant souvent à l'état d'impuretés dans les carbonates, leur faible mobilité permet de distinguer encore des fantômes de fossiles, clastes ou autres, même dans des roches entièrement recristallisées. La variation des paramètres de P°, T°, pH, Eh influençant le coefficient de distribution de ces deux éléments, la cathodoluminescence permet également parfois de préciser l'histoire de la cimentation d'une roche.

Pour plus de précisions, consulter: D.J. Marshall (1988), Cathodoluminescence of geological materials, Allen & Unwin Inc, USA, disponible à la bibliothèque.



## Préparation des échantillons

La meilleure façon d'observer une roche en cathodoluminescence est en lame mince, non couverte et polie. Il est possible de faire des premiers tests sans polissage mais le polissage est recommandé, pour les photographies notamment. L'épaisseur n'est pas importante, mais 30 microns conviennent bien.

Avant de mettre les lames dans l'appareillage, faire attention de ne pas mettre les doigts dessus et de nettoyer les lames à l'alcool.

## Appareillage :

TECHNOSYN : Cold cathode luminescence model 8200 MkII

## Mode d'emploi de l'appareillage

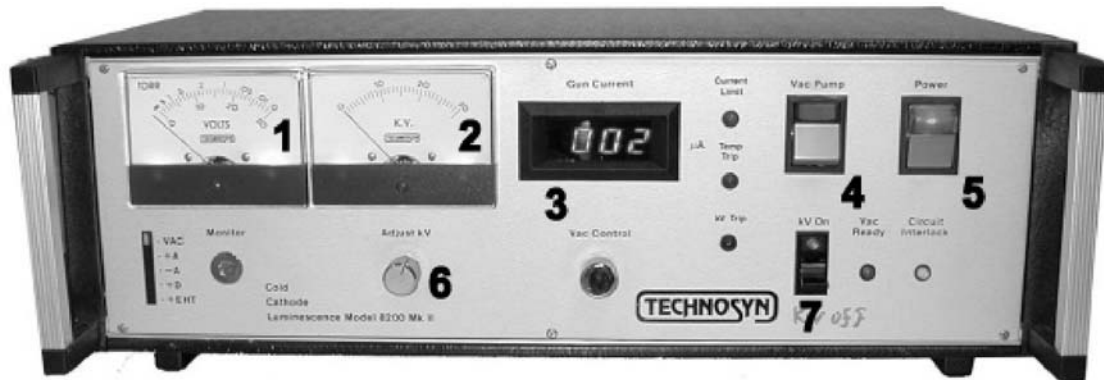


A : Bombonne d'Hélium

B : Console

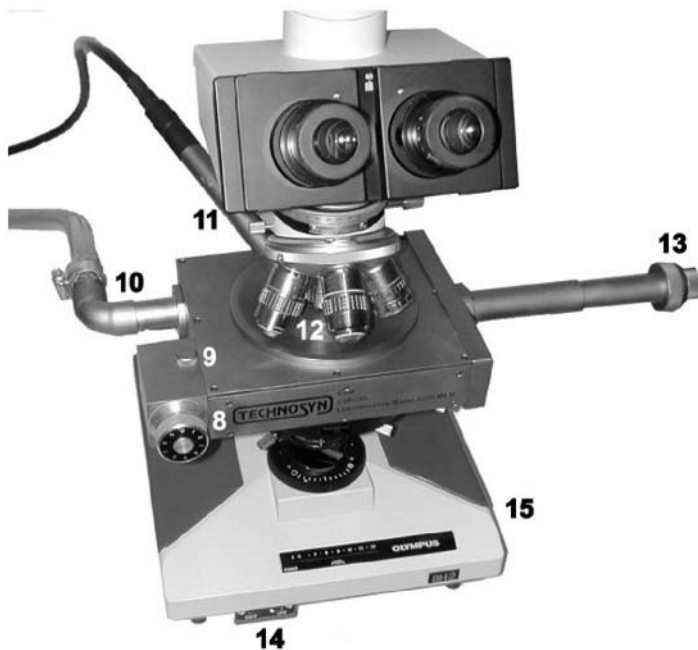
C : Microscope et chambre à échantillon.

## B Console



1. Cadran d'affichage du vide d'air [Torr]
2. Cadran d'affichage du voltage [k.V]
3. Affichage de l'ampérage appliqué au canon à électrons [ $\mu$ A]
4. Enclenchement de la pompe à vide
5. Interrupteur principal de la console
6. Réglage du voltage appliqué [k.V]
7. Mise sous tension du canon

## C Microscope et chambre à échantillon



8. Réglage du flux d'Hélium
9. Valve d'admission d'air
10. Raccord à la pompe
11. Canon à électron
12. Chambre à échantillon
13. Vis pour le déplacement de l'échantillon à l'intérieur de la chambre
14. Enclenchement de la lumière naturelle transmise
15. Réglage de l'intensité de la lumière naturelle transmise

### *Mise en route : marche à suivre*

1. Placer l'échantillon dans la chambre [12], et la refermer.
2. Fermer la valve d'admission d'air [9].
3. Mettre la console principale sous tension [5].
4. Enclencher la pompe [4]. *Lors de la première utilisation de la journée, laisser pomper pendant quelques dizaines de minutes, afin que toutes les impuretés soient aspirées.*
5. Une fois que l'indicateur de pression d'air [1] est vers les 0.05 Torr, ouvrir la bouteille d'Hélium, et régler la pression au moyen du bouton [8], afin qu'elle se trouve vers les 0.5 Torr.
6. Vérifier que le bouton de réglage du voltage [6] soit au minimum (complètement dans le sens contraire des aiguilles d'une montre), et enclencher le canon à électron [7].
7. Augmenter ensuite délicatement les volts [6] en faisant attention à ne pas dépasser 20 sur le cadran [2], jusqu'à ce que le canon se mette en marche et atteigne une valeur de 400 – 500 sur le petit écran à affichage rouge [3]. Si les ampères [3] ne montent pas assez, régler délicatement le flux d'Hélium avec le bouton de réglage [8]. Les k.V, les ampères et la pression d'air sont étroitement liés, et la modification de l'un des paramètres influe sur les deux autres. Ces paramètres changent également en fonction de l'échauffement de la machine et de l'échantillon. Il faut donc continuellement les régler au mieux.
8. Dès que les ampérages indiquent une valeur de 300 ou plus, l'observation en cathodoluminescence est possible. Il est possible de voir l'échantillon en lumière naturelle également, en utilisant le microscope comme un microscope normal [14 – 15].

### *Changement d'échantillon :*

1. Eteindre le canon [7 ] et la pompe [4]. Remettre le bouton de réglage des volts [6] à zéro.
2. Fermer la bouteille d'Hélium et ouvrir la valve d'admission d'air [9].
3. Attendre que la pression à l'intérieur de la chambre soit en équilibre avec la pression atmosphérique, puis soulever le couvercle et changer les échantillons.
4. Pour reprendre les observations, refaire comme décrit ci-dessus.

### *Fin du travail :*

1. Effectuer les mêmes opérations que celles décrites ci-dessus dans les points 1 à 3 de *changement d'échantillon*.
2. Déclencher le bouton principal [5].
3. Refermer la chambre, la valve d'admission d'air [9] et refaire un bon vide en enclenchant la pompe [4].
4. Lorsque le vide est suffisant, arrêter la pompe, et laisser comme ceci.
5. Vérifier que la bouteille d'Hélium est bien fermée.
6. Eteindre les lumières et fermer le local à clé.



**ملخص:** يدرس هذا البحث العصر الباليوجيني القاري لبعض المناطق في جنوب غرب الجزائر من ناحية الطبقات الصخرية وبقايا الكائنات المتحجرة بالإضافة إلى دراسة البيئة القديمة لتلك الكائنات. تختص هذه دراسة الطبقات الرسوبية القارية المتواجدة بقور لعزيب (حمادرا) ومريجة ودرمشان. هاته الترسبات متصفة بفقرها من حيث المستحاثات وتشكل مساحات كبيرة في كلا المنطقتين على شكل هضاب صحراوية حجرية تدعى حماد. منذ ألفين وأربعة (2004) البحوث الجيولوجية التي خصت هاته المناطق سمحت باكتشاف عدة مواقع نظم متحجرات ذات أهمية تاريخية كبيرة. الدراسة الجيولوجية لقور لعزيب سمحت بإكمال الجزء السفلي لمقطع قلب زقدو المشهور من الناحية الستراتيغرافية. هذا الجزء كان ينسب في ما قبل إلى العصر السينوماني، الاكتشافات الجديدة سمحت بتصحيح و نسب هاته الطبقات إلى العصر الباليوجيني. مقطع قلب زقدو قسم إلى ثلاث وحدات ذات أصل ترسيبي بحري وبحري: وحدة سفلى ذات أصل بحري مكونة من طبقات طينية جسيمة ترسبت فوق طبقات تعود إلى الحقبة الجيولوجية الأولى، ووحدة متوسطة وأخرى عليا ذات أصل بحري مكونة من طبقات حجر رملي كلسي.

\*التقيب والبحث المتواصل في الطبقات الوحدية المتوسطة أدى إلى اكتشاف عدة مواقع للمتحجرات قارية فقارية (أسماك، سلحفاة، طيور، وخاصة الثدييات) بالإضافة إلى بقايا نباتية على شكل مستحاثات تنسب إلى العصر الحديث السابق (إوسين) القاري. هذا التاريخ تؤكد دراسة باليومغناطيسية لقلب زقدو بعمر قدره 49 مليون سنة.

\*المقطع الجيولوجي لمريجة-درمشان قسم أيضا إلى ثلاث وحدات: وحدة سفلى طينية كلسية ذات أصل بحري، ووحدة متوسطة وأخرى عليا ذات أصل بحري مكونة من طبقات طينية، حجر رملي وكلسي. المستحاثات المتواجدة بهذه الترسبات نسبت للوحدة السفلى إلى العصر الحديث السابق السفلي (إوسين القديم). نسبت الوحدتان المتوسطة والعليا إلى العصر الحديث السابق المتوسط والعلوي (إوسين الحديث).

\*دراسة البيئة القديمة للحيوانات الثديية المتحجرة بقور لعزيب منحنتها بيئة غاية ذات مناخ مداري ساخن ورطب متضمن التواء بحري محاط بغابة مفتوحة.

إن دراسة هذه الرسوبيات اعتمدت على الدراسة الميدانية والشرائح الصخرية ودراسة المعادن بالأشعة السينية (DRX). كل هذا سمح بوصف للمرة الأولى في جنوب غرب الجزائر ظاهرة تحويل الرسوبيات عن طريق الاستبدال الكلسي. عملية كانت وراء تكوين ما يسمى بكلكريت ودولوكريت، ويتحديد بحريتي زقدو ومريجة. في العصر الحديث السابق.

أخيرا تم الكشف عن مرحلة تكتونية مسجلة في طبقات العصر الحديث السابق لمريجة-درمشان. هذه المرحلة التكتونية معروفة في المناطق المغرب العربي وفي جنوب أوروبا الغربية الكلمات المفتاحية:

الجزائر، الباليوجين القاري، قور لعزيب، مريجة، ستراتيجرافيا، الفقارية، كاروفيت، بوليم بيئة قديمة، كلكريت.

**Résumé:** Une description lithologique, paléontologique et sédimentologique ainsi qu'une interprétation paléoenvironnementale sont effectuées sur le Paléogène continental du Sud-Ouest algérien. Il s'agit notamment des séries continentales du complexe des Gour Lazib (Hammada du Dra) et de la Hammada de Méridja-Dermchane (rive droite du Guir). Ces dépôts, réputés pauvre en documents paléontologiques, couvrent dans ces deux secteurs de larges étendues sous forme d'un ensemble de buttes-témoins aux sommets tabulaires et de vastes plateaux désertiques et pierreux appelés Hammadas.

Depuis 2004, les prospections géologiques et paléontologiques y ont conduit à la découverte de plusieurs sites fossilifères remarquables. L'étude de plusieurs coupes dans le complexe des Gour Lazib a permis de compléter la lithostratigraphie de la formation continentale du Glib Zegdou vers sa base où ont été découverts des vertébrés continentaux permettant de reconsidérer l'âge paléogène de ces niveaux, autrefois attribués au Cénomano-Turonien. Cette formation est subdivisée en trois membres d'origine fluvio-lacustre: un membre inférieur argilo-marne-gypseux lacustre reposant en discontinuité sur un substratum paléozoïque, un membre intermédiaire détritique et un membre supérieur grés-carbonaté. Les fouilles systématiques, dans le membre intermédiaire de cette série sédimentaire, ont permis de découvrir plusieurs sites à vertébrés (dipneustes, actinoptérygiens, chéloniens, oiseaux et mammifères notamment), associés à des oogones de charophytes d'âge Yprésien terminal-Lutétien basal. Cet âge est confirmé par les analyses magnétostratigraphiques qui indiquent un âge d'environ 49 Ma.

La formation continentale fluviatile de Méridja-Dermchane est aussi subdivisée en trois membres: un inférieur argilo-carbonaté lacustre, un intermédiaire détritique et un supérieur grés-carbonaté. La malacofaune et la flore récoltées permettent d'y attribuer un âge yprésien au membre carbonaté, lutétien-bartonien aux autres membres.

La reconstitution du paléo-habitat de la communauté mammalienne du complexe des Gour Lazib (réalisée par la méthode des cenogrammes et complétée par celle des taxons arboricoles et la diversité écologique) suggère un milieu forestier tropical, chaud et humide, soumis à des saisons marquées. La présence d'un système fluviatile avec méandres à faible courant bordé d'une forêt galerie et de milieux plus ouverts en périphérie est plus plausible.

L'étude sédimentologique, basées sur les observations de terrain, les lames minces et l'analyse minéralogique (DRX), a permis de décrire pour la première fois les différents phénomènes d'épigénies ayant affectés ces dépôts d'origine fluvio-lacustres, décrit autrefois comme lacustre, et de mettre en évidence les lacs éocènes de Glib Zegdou et de Méridja.

Enfin, sur le plan tectonique, une phase d'orogénèse d'âge Eocène moyen-supérieur, est enregistrée dans la Hammada de Méridja. Cette phase tectonique est largement reconnue dans le Maghreb et dans le sud de l'Europe occidentale.

**Mots clés:** Algérie, Paléogène continental, Gour Lazib, Méridja, Stratigraphie, Vertébrés, Charophytes, Bulimes, Paléoenvironnements, Cenogrammes, Calcrète, Silcrète.

**Abstract:** Lithological, paleontological and sedimentological descriptions with palaeoenvironmental interpretation have been realized on the continental Palaeogene of the South-western Algeria. These include continental series of the Gour Lazib complex (Hammada du Dra) and the Hammada of Meridja (right bank of the Guir). These deposits are known poor in paleontological documents; they cover in this both regions large areas in the form of a buttes and vast desert and stony plateau called Hammada.

Since 2004, the paleontological and geological prospections have led to the discovery a several remarkable fossiliferous localities. The study of several outcrops in the Gour Lazib area has led to complement the lithostratigraphy of the continental formation of Glib Zegdou. The continental vertebrate remains discovered in his base allowed us to attribute these layers to the Palaeogene, previously attributed to the Cenomanian-turonian. This formation is subdivided in three fluvial and lacustrine sedimentary members: A lacustrine lower member, containing clay, marl and gypsum, unconformably overlies a Palaeozoic substratum, a detrital intermediate member, and a carbonate sandstone upper member. The prospecting-exploration works in the middle member of this sedimentary formation allowed us to discover several new vertebrate sites (with lungfish, actinopterygians, chelonians, birds, and notably mammals), associated with Early to Middle Eocene charophyte. This age is confirmed by magnetostratigraphic study which indicates an age of about 49 Ma.

The fluvial and lacustrine continental formation of Meridja-Dermchane is also subdivided in three members: a lacustrine clay-carbonate lower member, a detrital middle member and a clastic carbonate upper member. The malacofauna and flora collected can assign an ypresian age to the carbonate member, and Lutetian-Bartonian to the other members.

The palaeoenvironmental reconstruction of fossil mammalian community, by means of cenograms method, supplemented by tree taxa and ecological diversity analysis, suggest a tropical forest environment, hot, wet and prone to marked seasonality for this fauna. The presence of a meandering fluvial system with low current bordered by a forest gallery and more open environments in the periphery is likely.

The sedimentological study based on field observations, the thin section and mineralogical analysis (XRD), allowed to describe for the first time the various phenomena of epigenesis which have affected the fluvio-lacustrine deposits, once described as lacustrine, and highlights the Eocene lakes of Glib Zegdou and Meridja.

Finally, in terms of tectonics, an Middle-Upper Eocene orogeny phase is recorded in the Hammada of Meridja. This tectonic phase is widely recognized in the Maghreb and south of Western Europe.

**Keywords:** Algeria, Continental Paleogene, Gour Lazib, Méridja, Stratigraphy, Vertebrates, Charophytes, Bulimes, Palaeoenvironment, Cenograms, Calcrete, Silcrete.