THESE

Pour l'Obtention du Grade de
DOCTEUR DE L'UNIVERSITE DE POITIERS
Faculté des Sciences Fondamentales et Appliquées
Diplôme National - Arrêté du 7 août 2006

Ecole doctorale : Sciences pour l'Environnement Gay-Lussac

Secteur de Recherche : Paléoprimatologie et Paléontologie Humaine

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CONTRIBUTION DE LA MAGNETOSTRATIGRAPHIE ET DE LA BIOCHRONOLOGIE A L'HISTOIRE EVOLUTIVE DES PRIMATES : APPLICATION AU PALEOGENE CONTINENTAL D'AFRIQUE DU NORD ET AU MIOCENE MOYEN ET SUPERIEUR D'ASIE DU SUD-EST

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Soutenue le 25 novembre 2010

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Pigmaei gigantum humeris impositi plusquam ipsi gigantes vident

Bernardus Carnotensis

REMERCIEMENTS

Mes remerciements vont en premier lieu à mon directeur de thèse Jean Jacques Jaeger, sans qui cette thèse n'aurait jamais vu le jour. Je tiens à lui exprimer toute ma gratitude pour sa confiance, son apport scientifique de premier ordre et ses précieux conseils. Cette thèse n'aurait pas été ce qu'elle est sans son soutien. Merci de m'avoir intégré à de nombreuses missions paléontologiques et de m'avoir donné l'opportunité d'acquérir de l'expérience de terrain et de faire des passionnants voyages ces dernières années. Ce fut une grande chance pour moi de l'avoir en tant que directeur de thèse.

J'aimerais remercier tout particulièrement mon co-directeur, Mouloud Benammi, sans qui cette thèse n'aurait jamais commencé ni abouti. Merci tout d'abord de m'avoir initié au paléomagnétisme, puis d'avoir proposé ce sujet et supervisé l'évolution de mes recherches. Ses conseils et son expérience de terrain ont été très enrichissants. Je tiens également à lui exprimer toute ma gratitude pour m'avoir accueilli au Mexique et facilité mon séjour là-bas.

J'exprime ma profonde gratitude à tous les membres du jury qui ont bien voulu accepter d'examiner mon travail. Merci, tout d'abord, à Larry Flynn et Sevket Sen, rapporteurs, d'avoir accepté de juger ce travail. Je tiens à remercier Michel Brunet pour m'avoir soutenu dans mon projet post-doctoral et pour l'honneur qu'il me fait en participant à mon jury de thèse. Merci à Mustafa Salem et Mohamed Mahboubi, examinateurs, qui grâce à leur expérience de terrain pour m'avoir prodigué des remarques déterminantes et pour les moments agréables que nous avons partagés sur le terrain. Merci à Yves Gallet, examinateur, pour sa disponibilité et son accueil lors de mes visites à l'Institut de Physique du Globe de Paris.

Au cours de ma thèse, j'ai eu l'occasion de visiter de nombreux laboratoires et le succès de ces visites a été rendu possible par l'accueil et la disponibilité des chercheurs et techniciens. Je tiens notamment à remercier toute l'équipe du laboratoire de paléomagnétisme de l' Universidad Nacional Autónoma de México pour leur chaleureux accueil. Merci à John Kappelman du laboratoire de Paléoanthropologie d'Austin pour m'avoir accueilli et pour avoir facilité mon séjour au Texas. Merci à toute l'équipe du laboratoire de paléomagnétisme de l'Institut de physique du Globe de Paris, avec une mention spéciale pour Maxime Legoff pour sa gentillesse et sa disponibilité, et à Hélène Bouquerel et Yves Gallet, pour leur chaleureux accueil.

Ma reconnaissance va également à de nombreux spécialistes qui m'ont communiqué de précieuses informations. Merci à Laurent Marivaux pour ses discussions sur les faunes de rongeurs africains ainsi que pour m'avoir donné accès à ses collections. Je voudrais également remercier Rodolphe Tabuce pour ses conseils et l'équipe franco-algérienne qui travaille en Algérie, pour la collecte d'échantillons paléomagnétiques au Gour Lazib. Merci à Guillaume Billet pour m'avoir initié à la cladistique et donné goût à la phylogénie. Merci à Claude Fontaine de l'Hydrasa pour son aide plus que précieuse, et le temps qu'il a pu consacrer pour m'initier à l'étude des lames minces. Merci à Jean-Louis Hartenberger, Gilles Escarguel, Jens L. Franzen, Jean A. Remy, Mary Dawson et Michael Woodburne pour l'enrichissement qu'ils ont pu apporter à mon travail à travers nos discussions via emails.

Au cours de mes trois années de thèse, les missions de terrain ont représenté un aspect essentiel de mon doctorat et je tiens à remercier tous les membres des équipes avec qui j'ai eu l'occasion de fouiller au Myanmar, en Algérie et en Libye.

Je voudrais spécialement remercier Mustafa Salem sans qui nos séjours dans le désert libyen n'auraient pas été possible mais également pour son aide lors de la collecte d'échantillon et pour ses conseils. Je souhaiterais également remercier Mohamed Mahboubi pour avoir facilité notre mission à El Kohol. Merci également à toute sa famille et, en particulier, à Salamet pour m'avoir appris à faire le thé à la menthe et pour sa précieuse amitié. J'aimerais également adresser toute ma gratitude à Xavier Valentin et Olivier Chavasseau pour leur aide sur le terrain lors de l'échantillonnage de mes blocs.

Le personnel du laboratoire de l'iPHEP a toujours été la pour me faciliter mes conditions de travail et je tiens à remercier son directeur, Patrick Vignaud, pour sa sympathie et son soutien. Mes pensées vont aussi à toute l'équipe du labo, Carine, Ghislaine, Franck, Stéphane, Renaud, Géraldine, Sabine, Aurélie, Olga, Vincent, Olivier, Xavier et Cécile, qui par leur sympathie, leur conseil et leur aide ont contribué à ce travail. Merci également au personnel de l'Université de Poitiers et plus particulièrement à Anne Brunelière de la bibliothèque universitaire des sciences, pour sa gentillesse et son efficacité.

Cette thèse n'aurait probablement jamais abouti si je n'avais pas été entouré à Poitiers par un groupe d'étudiants en doctorat ou stagiaire, dont le dynamisme, la joie de vivre et la chaleur m'ont permis de surmonter nombres de moment difficiles. La liste des contributions est trop longue et je ne peux pas exprimer en quelques lignes toute la reconnaissance qu'ils méritent. Une mention spéciale cependant pour Thibault Bienvenu avec qui j'ai pu partager un nombre d'heure incalculable ces derniers mois. Merci à lui pour sa bonne humeur constante, sa profonde gentillesse et son amitié, la fin de ma thèse sans son soutien m'aurait semblé insurmontable.

Merci également à toutes les personnes que j'ai pu rencontrer au cours de ces dernières années, qui sont devenues mes amis et qui ont su rendre excitante et palpitante ma vie à Poitiers. Aux musiciens de St Eloi, à l'équipe du boulevard des rocs, de Parthenay, celle de Limoges, aux acousticiens, à Golpar et à tous les autres, merci.

Enfin merci à ma famille pour m'avoir apporté tout le soutien dont j'avais besoin et j'espère que je saurai leur exprimer un jour combien ils ont pu m'aider. Merci à mes soeurs Maria, Jeanne, Inès et Adèle et mon petit frère Léopold, mon cousin Nicolas, et à mes tantes, Dany et Edith, pour m'avoir poussée à poursuivre mes études dans les moments difficiles.

Merci à ma mère ainsi qu'a Jean-Marc d'être toujours présents et de m'avoir toujours encouragée.

Enfin, cette thèse est dédiée à mon père, qui probablement plus que tout autre, par son courage, sa force de caractère et son soutien sans faille, a su me motiver à aller au bout des choses.

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INTRODUCTION

INTRODUCTION

Au début des années 1960, l'équipe américaine d'Elwyn Simons (Duke University) a mis au jour les premiers restes de primates en Egypte apparentés aux lointains ancêtres de l'homme (Simons 1965). Depuis, plus d'une vingtaine d'espèces de primates ont été découvertes dans les dépôts de l'Eocène terminal et de l'Oligocène basal d'Afrique du Nord (e.g. Seiffert et al. 2010). La plupart de ces formes appartiennent au groupe des anthropoïdes. Le nombre et la diversité des taxons découverts ont plaidé, pendant longtemps, en faveur d'une origine et d'une évolution africaines des anthropoïdes. De ce fait, l'Afrique a été traditionnellement considérée comme le centre d'évolution principal de ce groupe.

Cependant, la découverte d'anthropoïdes primitifs dans l'Eocène moyen et supérieur d'Asie a conduit à reconsidérer l'origine biogéographique de ce groupe de primates (e.g. Jaeger et Marivaux 2005). Dans le même temps, certaines des données qui soutenaient une origine africaine ont été ébranlées par de nouvelles découvertes paléontologiques en Algérie. En effet, la description récente de restes crâniens et dentaires de primates fossiles dans l'Eocène moyen africain a révélé que le primate algérien *Algeripithecus*, jusque là considéré comme un des plus anciens anthropoïdes africains, appartenait en fait au groupe des strepsirrhiniens (Tabuce et al. 2009). Avec de lourdes conséquences sur l'histoire évolutive des primates anthropoïdes en Afrique, ce constat a d'autant plus renforcé l'hypothèse alternative de l'origine asiatique des anthropoïdes.

Les primates anthropoïdes fossiles de Chine (Beard et al. 1994, 1996 ; Beard et Wang 2004), de Thaïlande (Chaimanee et al. 1997, Ducrocq 1999), du Myanmar (Jaeger et al. 1998, 1999 ; Takai et al. 2001 ; Takai et al. 2005 ; Beard et al. 2009) et d'Inde (Bajpai et al. 2008) ont apporté la preuve indiscutable que ce groupe a subi une évolution et une radiation importante en Asie du Sud dès l'Eocène moyen et ont révélé l'existence de relations biogéographiques et d'échanges fauniques entre l'Asie du Sud et l'Afrique du Nord durant

l'Eocène moyen.

Un tel scenario semble d'ailleurs s'être répété, plus tard, au cours de la différenciation des grands singes pendant le Miocène. En effet, l'Asie et l'Afrique tropicale n'ont pas été seulement des centres de diversification des premiers anthropoïdes, mais également des hominoïdes (Kelley et al. 2002). Alors que les plus vieux hominoïdes sont connus dans le Miocène inférieur d'Afrique (Harrison 2002), la forte diversité et la vaste répartition géographique et temporelle de ce groupe en Asie à partir du Miocène inférieur/moyen suggèrent fortement que cette région a été un centre important de diversification des hominoïdes au Miocène.

Au cours de ces dernières années, les recherches de l'équipe de Jean-Jacques Jaeger, menées dans le Paléogène africain et le Néogène asiatique, ont permis la découverte de nouveaux fossiles qui sont venus combler de nombreuses lacunes dans notre compréhension de l'histoire ancienne des primates. Cependant, les conditions paléoenvironnementales qui ont contraint ces différenciations initiales, et les modalités de dispersion ainsi que la chronologie précise des échanges fauniques entre Asie et Afrique restent encore à élucider. L'établissement d'un cadre temporel, essentiel à la compréhension de l'histoire évolutive des faunes, s'est donc avéré nécessaire et cette thèse a été en grande partie consacrée à ce travail.

La détermination de l'âge et l'étude des faunes de mammifères terrestres sont difficiles car de nombreux obstacles s'opposent à l'établissement d'échelles biochronologiques précises dans les formations continentales. Les dépôts en milieux continentaux (lacustre, fluvio-lacustre, fluvial ou loessique) ont généralement une étendue limitée dans l'espace et l'évolution de la sédimentation varie d'un bassin sédimentaire à l'autre. Les corrélations lithologiques sont donc difficiles à établir. De plus, par opposition au domaine marin profond, la nature de la sédimentation est discontinue et les séquences, particulièrement celles mises en place en domaine fluviatile, présentent souvent des lacunes de sédimentation. Par ailleurs, les fossiles étant souvent rares, absents ou endémiques, le manque de contrôle chronologique affecte souvent l'étude des formations continentales. La biochronologie, basée sur la succession des faunes établie à partir des grades évolutifs des espèces, est une des méthodes

les plus communément utilisées pour la datation des dépôts sédimentaires continentaux, mais c'est une chronologie relative isolée des échelles stratigraphiques élaborées en domaine marin. Les points d'ancrage pour caler cette chronologie relative sont rares en domaine continental. En outre, l'absence fréquente d'intercalations marines à microfossiles, de repères lithostratigraphiques corrélables, et le manque de données radiométriques dans certains sites continentaux limitent la résolution de la méthode biochronologique et rendent délicate toute interprétation de l'âge exact des sites à mammifères. Dans ce contexte, la magnétostratigraphie, qui permet de caler des séries biostratigraphiques indépendantes les unes des autres, est apparue comme l'outil de datation adéquat pour un calage chronologique de ces séries fossilifères continentales.

L'objectif de ce travail a consisté, dans un premier temps, à parfaire la connaissance des formes primitives d'anthropoïdes africains, encore insuffisamment documentées, et à rechercher les premiers témoins de ce groupe, au moment de leur migration en Afrique. Plusieurs missions de terrain ont été organisées dans les dépôts Eocène d'Afrique du Nord, notamment en Libye et en Algérie.

La présence d'une communauté d'anthropoïdes déjà diversifiée à la fin de l'Eocène moyen/début de l'Eocène supérieur indique que les sites fossilifères de l'Eocène inférieur et moyen d'Afrique comportent des informations essentielles pour comprendre les prémices de leur histoire en Afrique. Cependant les localités documentant cette époque sont rares, pauvres en fossiles et leur chronologie relative est mal établie. Dans le but d'obtenir de nouvelles données paléontologiques et chronologiques, l'étude magnétostratigraphique associée à l'étude des faunes de mammifères des sites algériens de l'Eocène inférieur (El Kohol) et moyen (Gour Lazib) a été réalisée.

Par ailleurs, les récentes missions de terrain de l'équipe franco-libyenne au Dur At-Talah ont conduit à la découverte d'une des plus anciennes communautés d'anthropoïdes africains connus. Ainsi, afin d'apporter des précisions quant à l'âge de ce site et le corréler avec d'autres sites à primates anthropoïdes africains anciens (i.e. BQ-2 du Fayum, Egypte et

Bir El Ater des montagnes des Nementcha en Algérie), l'étude magnétostratigraphique et biochronologique de la série sédimentaire du Dur At-Talah a été entreprise.

D'autre part, les rongeurs hystricognathes, souvent associés à ces primates, partagent également une origine asiatique et semblent avoir une histoire paléobiogéographique analogue à celle des anthropoïdes. Il était donc nécessaire d'entreprendre l'étude taxonomique et phylogénétique des premiers représentants de la radiation des rongeurs hystricognathes en Afrique, en Asie et en Amérique du Sud à l'Eocène et l'Oligocène pour connaitre l'histoire évolutive de ce groupe et apporter des éléments de réponse aux problèmes posés par leur répartition géographique.

Un deuxième objectif majeur de mes recherches a porté sur les séries sédimentaires néogènes du Sud-Est asiatique, région qui a joué un rôle majeur dans l'émergence et la diversification des grands singes actuels. Des études magnétostratigraphiques, combinées aux résultats de l'étude biostratigraphique des faunes associées, ont été réalisées dans les dépôts du Miocène moyen de Thaïlande et du Myanmar afin de préciser l'âge des faunes sud-asiatiques, la chronologie des différentes phases de divergences et la diversification initiale des hominoïdes, et apporter ainsi des réponses sur leur histoire évolutive et paléobiogéographique.

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PARTIE I.

ETUDE MAGNETOSTRATIGRAPHIQUE ET PALEONTOLOGIQUE DES SITES CONTINENTAUX PALEOGENES D'AFRIQUE DU NORD ET IMPLICATIONS POUR L'HISTOIRE EVOLUTIVE DES PRIMATES ANTHROPOÏDES

INTRODUCTION

Malgré les nombreuses découvertes qui ont considérablement enrichi le registre fossile durant les dernières décennies, les sites du Paléogène à vertébrés terrestres à vertébrés terrestres du Paléogène sont encore très peu nombreux sur le continent arabo-africain. L'histoire évolutive de nombreux groupes de mammifères, différenciés et/ou diversifiés en Afrique au cours de cette période, est par conséquent encore obscure. Le Paléogène d'Afrique du Nord recèle pourtant des gisements à mammifères d'une importance capitale ; plus d'un tiers des ordres actuels de mammifères sont d'origine africaine.

Par ailleurs, l'Afrique a été traditionnellement considérée comme le berceau des anthropoïdes en raison de l'importante diversité du groupe dans l'Éocène/Oligocène du Fayum (Egypte) (e.g. Seiffert et al. 2005) et l'Oligocène de la péninsule arabique (Thomas et al. 1989). Ce scénario était soutenu par la découverte probable d'anthropoïdes dans l'Éocène d'Algérie (sites de Bir El Ater et Glib Zegdou) (de Bonis et al. 1988 ; Godinot et Mahboubi 1992) et par la mise en évidence d'un primate dans le Paléocène supérieur au Maroc (Bassin de Ouarzazate) (Sigé et al. 1990). Ainsi, toute l'histoire de la lignée humaine, des origines les plus profondes à l'homme, était censée se dérouler en Afrique. Cependant, la mise au jour de nouveaux fossiles de primates dans l'Éocène d'Algérie (Tabuce et al. 2009) a montré que ces fossiles appartenaient non pas au groupe des primates anthropoïdes mais qu'ils étaient très probablement parmi les plus anciens représentants en Afrique des lémuriformes. D'autre part, le scénario d'une origine africaine des anthropoïdes semble avoir été battu en brèche par les découvertes faites en Asie, notamment dans l'Éocène de Chine, du Myanmar, et de Thaïlande (e.g. Jaeger et al. 1999 ; Beard et Wang 2004). Ainsi, l'origine paléobiogéographique des anthropoïdes est devenue un sujet très controversé depuis plusieurs années.

Au-delà des problèmes phylogénétiques, un obstacle majeur à notre connaissance est inhérent au manque de données liées à l'âge des sites fossilifères africains. Les mammifères

découverts sont généralement des groupes endémiques qui rendent difficile toute précision biochronologique intercontinentale ; il est en effet impossible de comparer et corréler ces faunes avec les échelles mammaliennes européennes, nord-américaines ou asiatiques. De plus, l'absence d'intercalations marines à microfossiles, de repères lithostratigraphiques corrélables, ainsi que le manque de données radiométriques et d'analyses magnétostratigraphiques ont rendu délicate toute interprétation sur l'âge exact des sites à mammifères au Maghreb. Malgré tout, les résultats biochronologiques issus de l'étude des foraminifères, des sélaciens et des mammifères, ont permis de préciser l'âge de certains sites.

Les gisements à influence marine marquée sont généralement assez bien datés. Au Maroc, c'est le cas des gisements du bassin de Ouarzazate et des Ouled Abdoun, où la présence de faunes marines associées, notamment de sélaciens, assure une datation relative assez précise (Cappetta et al. 1987 ; Gheerbrant et al. 1998, 2001, 2003 ; Tabuce et al. 2005). Des données magnétostratigraphiques pour le bassin de Ouarzazate soutiennent les résultats biochronologiques (Gheerbrant et al. 1998). Concernant les localités de l'Éocène à influence continentale plus marquée, des incertitudes subsistent. Malgré la présence de nombreux éléments marins (sélaciens) à Bir El Ater (Est Algérien), l'âge de la localité n'est pas clairement défini (Jaeger et al. 1985 ; de Bonis et al. 1988). En domaine purement continental (sites d'El Kohol, Gour Lazib, Glib Zegdou en Algérie et Chambi en Tunisie), seuls le contexte géologique local (Mahboubi 1995), les charophytes (Mebrouk et al. 1997), les gastéropodes terrestres (Abdeljaoued et al. 1984), et le grade évolutif des mammifères ont pu apporter quelques informations chronologiques, mais les résultats restent insuffisants. Pour l'Éocène/Oligocène de Libye (sites de Dur At-Talah et Zallah), les comparaisons des faunes de grands mammifères ont donné des âges relatifs approximatifs.

Ainsi, pour le Paléocène et l'Eocène africains, les analyses magnétostratigraphiques, associées à des études biostratigraphiques, menées dans le Bassin de Ouarzazate, au Fayum, et en Oman, ont apporté des données chronologiques essentielles à la compréhension de l'histoire évolutive des faunes (e.g. Seiffert 2010). Conséquemment, il est apparu comme primordial de mener une étude magnétostratigraphique pour l'ensemble des sites éocènes

marocains, algériens, tunisiens et libyens afin, entre autres, de discuter les échanges mammaliens Afrique/Asie au cours de l'Éocène, notamment ceux ayant concerné les primates anthropoïdes. Les études paléomagnétiques et biostratigraphiques de nombreuses séquences paléogènes en Afrique du Nord, présentées dans les chapitres suivants, ont permis de corréler et de dater avec précision les sites à primates et donner des indications fiables quant aux différentes phases de migrations mammaliennes trans-téthysiennes au cours du Paléogène. Ces nouvelles données ont apporté de nouveaux éléments de réponse pour comprendre à quelle occasion les premiers anthropoïdes sont arrivés en Afrique, par quelle voie de dispersion et quelles conditions environnementales ont contraint les différenciations initiales et l'apparition des caractères morpho-anatomiques qui définissent notre groupe.

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1.1. MAGNETIC POLARITY STRATIGRAPHY AND AGE OF THE EARLY-MIDDLE CONTINENTAL EOCENE DEPOSITS OF EL KOHOL AND GOUR LAZIB (ALGERIA)

MAGNETIC POLARITY STRATIGRAPHY AND AGE OF THE EARLY-MIDDLE 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 19th 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 ($^{40}Ar/^{39}Ar$ method) of the Widan el Faras Basalt, which uncomformably 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 parapithecid 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 azzouzorum* (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 (Gheebrant et al. 1998a). Based on the foraminifera and selacian 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 Zegdoumyidae (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 macroscelidid *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 though 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 (Harrisson 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 though 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 magnetozonation 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-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 uncomformably 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, mollusks 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 fluviatile 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).

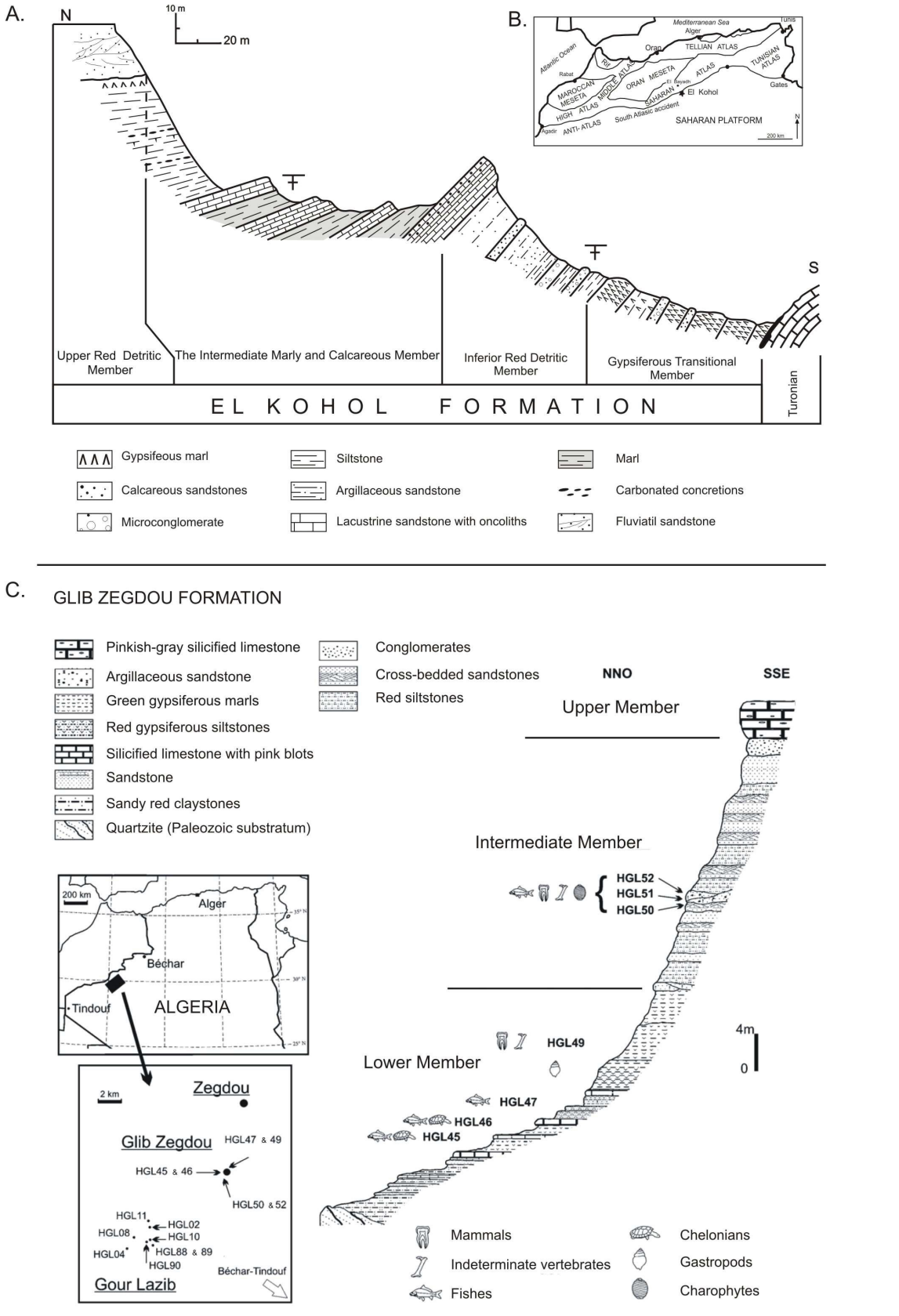


Figure 1.1. (A.) Section of El Kohol, at Brezina (After Mahboubi et al. 1984). (B.) Structural map of North Africa positioning El Kohol locality. (C.) Geographic localisation of Glib Zegdou vertebrate localities and stratigraphic section of Glib Zegou outlier (After Adaci et al. 2007).

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 calcrete 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, glaebules, 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).

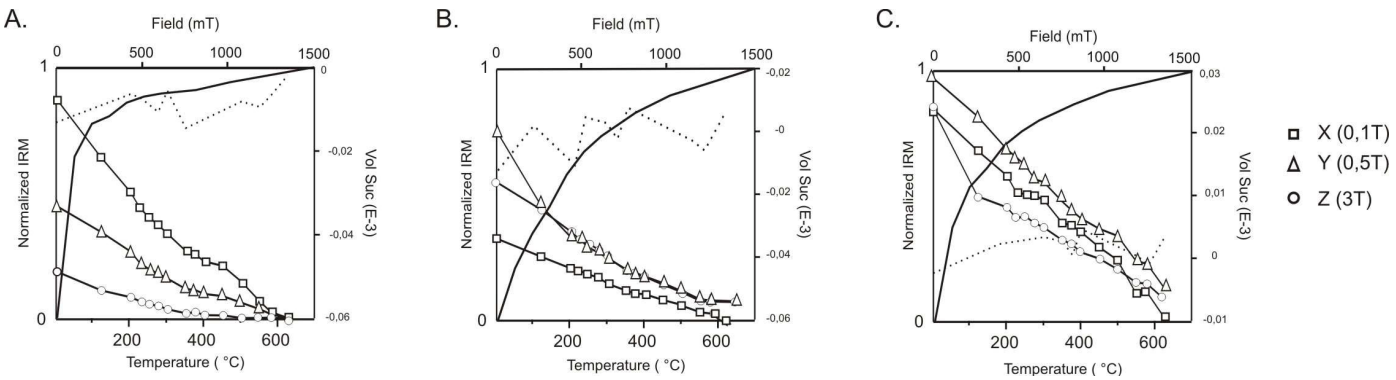


Figure 1.2. Normalized magnetization intensity curves showing IRM acquisition (ascending) and thermal demagnetization (descending) of IRM components for representative specimens of El Kohol section. Dashed line indicates evolution of susceptibility. (A.) 99EK010C, red claystone sample. (B.) 99EK056C, 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 saturated 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 IRM intensity of the soft-coercitivity component within the 100–400°C, and almost complete saturation of IRM at relatively low field are indicative of pyrrhotite, titano-maghemite or titano-magnetite. In

addition, unblocking of a fraction of IRM between 400–600°C range and medium coercitivity 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 coercitivity 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 coercitivity 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°. Mean directions of opposing polarity sites have a critical angle at 95% of confidence level of 22.5°. El Kohol paleomagnetic data pass a positive reversal test with an indeterminate classification.

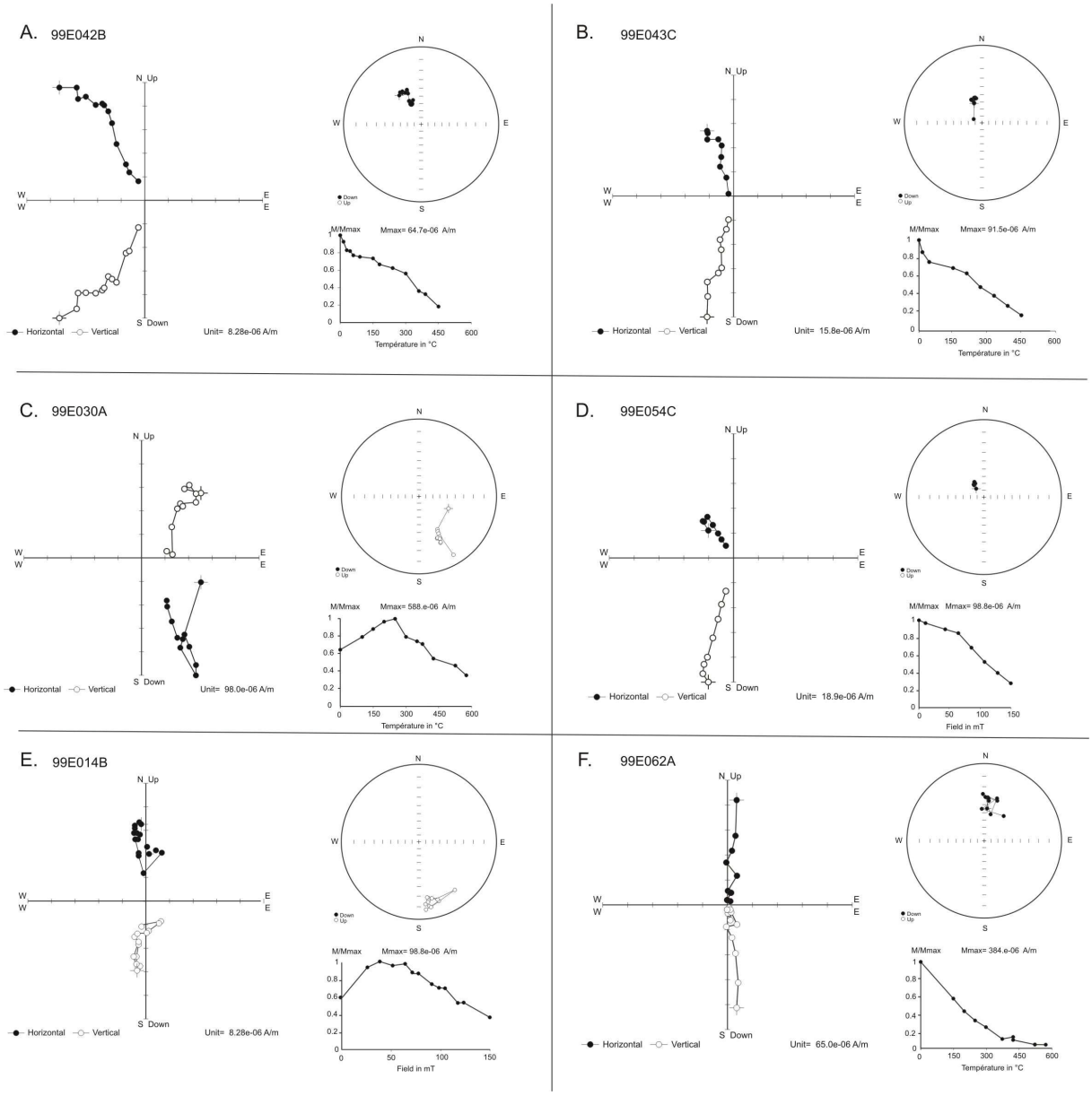


Figure 1.3. (A.-F.). Orthogonal vector diagrams (closed and/or open symbols correspond to the horizontal and/or vertical component), stereoplots (open and/or closed circles indicate directions in the upper and/or lower hemisphere), and intensity and step plots for representative samples from El Kohol 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; α_{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. (°)	α_{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.

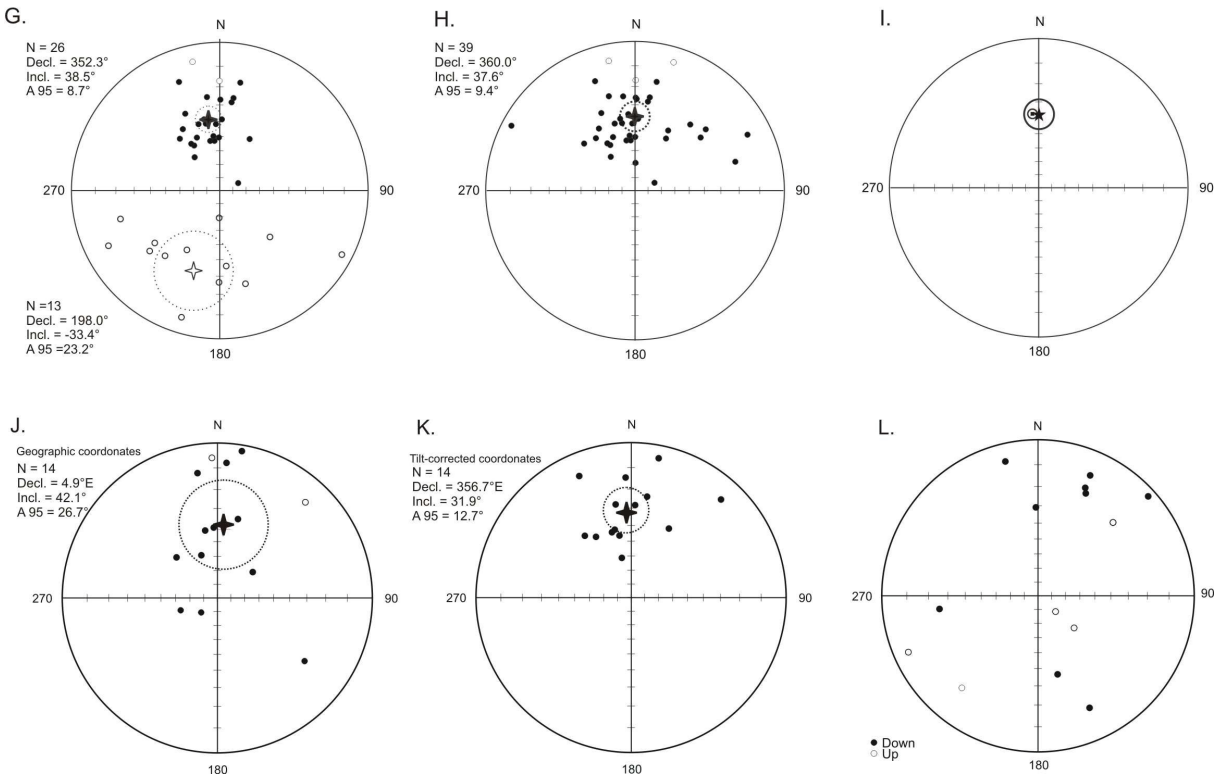


Figure 1.3 (continued). (G.) Equal-area stereographic projection and Fisher statistics (1953) of characteristic directions for all the sites (listed in Table 1.1). Open and/or closed circles indicate directions in the upper and/or lower hemisphere. Mean directions calculated by Fisher statistics (see Table 1.1) are represented by a star, and the ellipse indicates the 95% confidence ellipse. (H.) 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). (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° Inclination = 37.6° (α_{95} = 9.4°), corresponding to the paleomagnetic pole at 78.0°N and 181.5°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° and dm [semi-axis of confidence ellipse perpendicular to that great circle path] of 6.5°). 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

	N	Decl, (°)	Incl, (°)	α_{95} (°)	k	Pole postiton Φ (°E)	Pole postiton λ (°N)	dp/dm (°)
El Kohol	39	360	37.6	9.4	6.9	181.5	78	11.1/6.5

Note: Decl,: mean tilt corrected declination in °E; Incl,: mean tilt corrected inclination in degree to the horizontal; α_{95}: mean direction 95% confidence ellipse; k : Fisher precision parameter; Φ: longitude of paleopole for mean direction in °E, λ: latitude of paleopole for mean direction in °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°, α_{95} = 2.9°) 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.

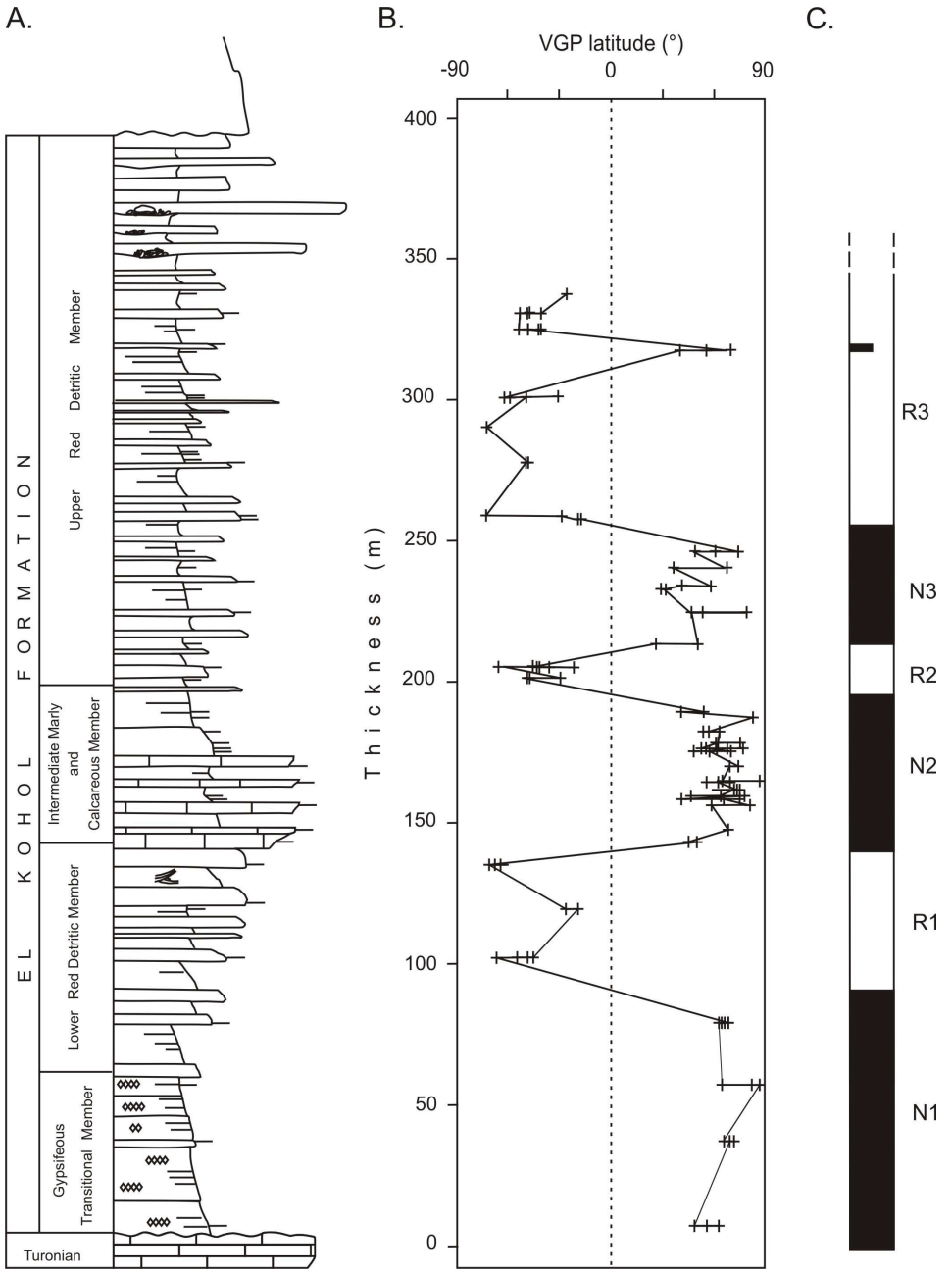


Figure 1.4. Paleomagnetic reversal stratigraphy of El Kohol section. (A.) stratigraphic section of El Kohol. (B.) Virtual geomagnetic pole (VGP) latitudes are plotted as a function of stratigraphic levels. (C.) polarity column (black/white bars represent normal/reverse polarity zones).

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, Δt, represented by a sampled section can be calculated using the formula:

Δt (myr) = $S\tau N$ where $S = - \ln (1 - 2p)/2$; τ = 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±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.

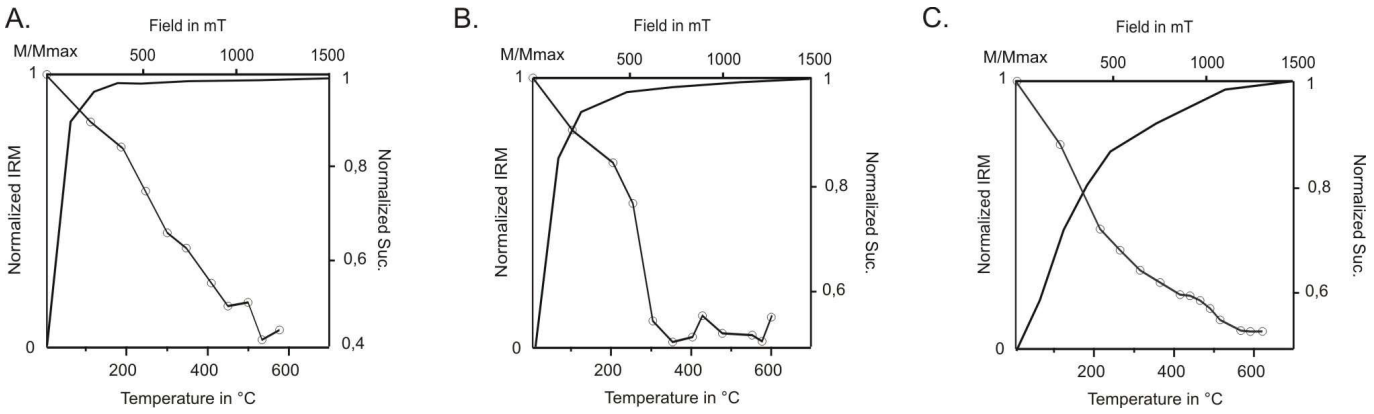


Figure 1.5. Normalized magnetization intensity curves showing IRM acquisition (ascending) and thermal demagnetization (descending) for representative specimens of Gour Lazib section. (A.) 99GL011A, argillaceous calcareous sample. (B.) 99GL025A, siltstone sample. (C.) 99GL039A, claystone sample.

Samples collected from calcareous (Figure 1.5A) and siltstones levels (Figure 1.5B) are characterized by a dominance of low coercitivity 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, titano-maghemite 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° (α_{95} = 16.2°) and Declination = 183.3°, I = −23.3° (α_{95} = 22.6°), respectively.

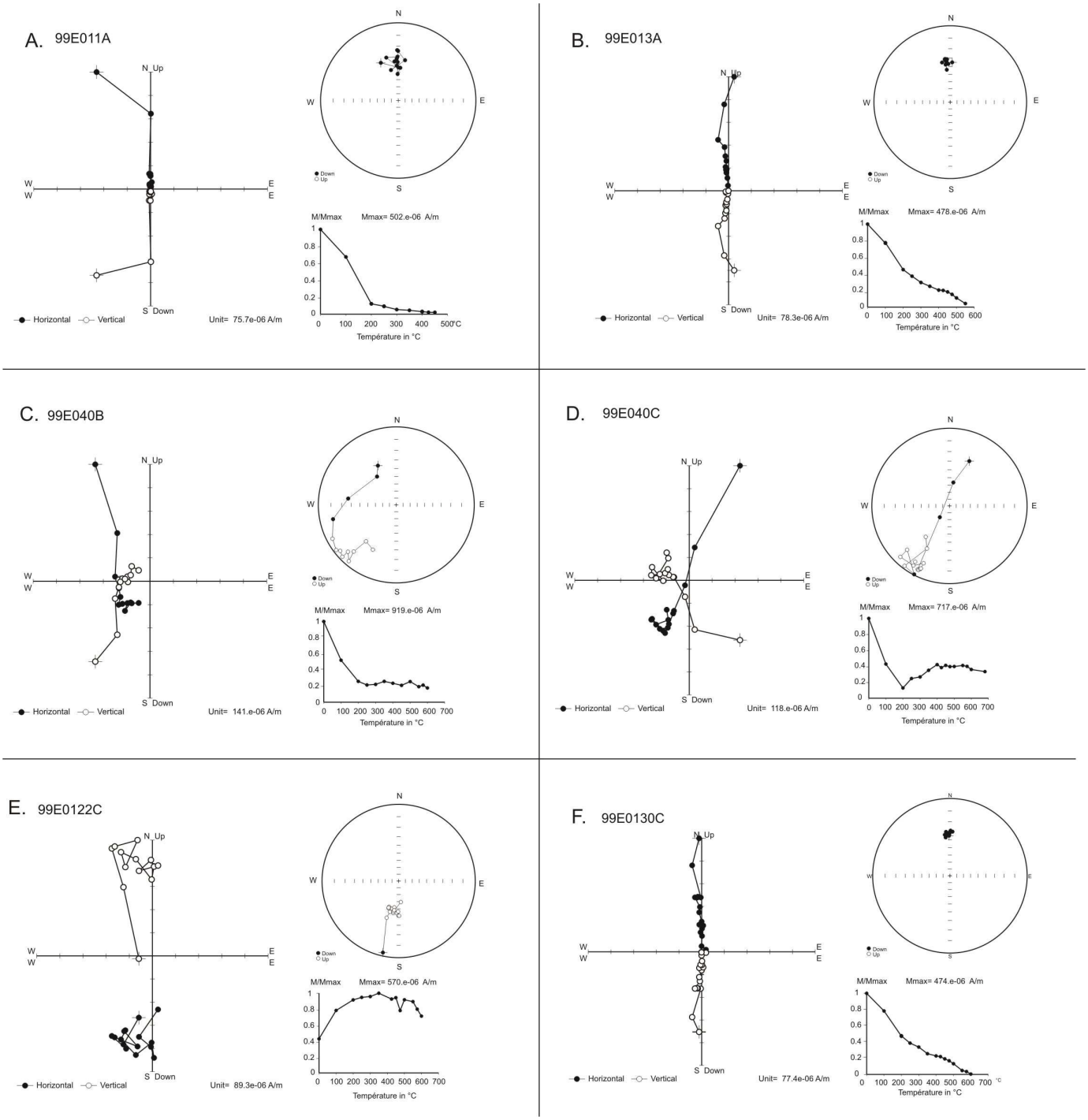


Figure 1.6. (A.-F.). Orthogonal vector diagrams (closed and/or open symbols correspond to the horizontal and/or vertical component), stereoplots (open and/or closed circles indicate directions in the upper and/or lower hemisphere), and intensity and step plots for representative samples from Gour Lazib 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; α95: 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.

Site	N	Incl. (°)	Decl. (°)	α_{95} (°)	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

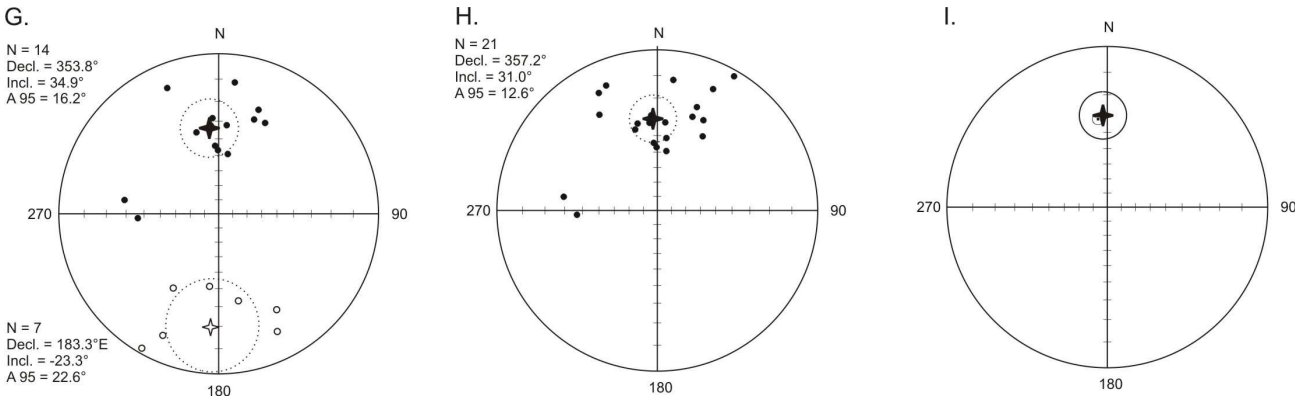


Figure 1.6 (continued). (G.) Equal-area stereographic projection and Fisher statistics (1953) of characteristic directions for all the sites (listed in Table 1.3). Open and/or closed circles indicate directions in the upper and/or lower hemisphere. Mean directions calculated by Fisher statistics are 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°, (α_{95} = 12.6°). Torsvik et al. (2008) provided a 50 Ma reference paleomagnetic pole for Africa located at 76.8 °N, 201.6°E with confidence limit α_{95} = 2.6° (Figure 1.6I). The expected paleomagnetic field at Gour Lazib locality associated with this reference pole is Declination = 353.9°, Inclination = 32.6°, (α_{95} = 3.1°). Using Demarest method (1983), the comparison of the expected and observed directions yields no significant flattening of inclination (F=1.63°) or significant vertical axis rotation of declination (R=3.3°).

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.

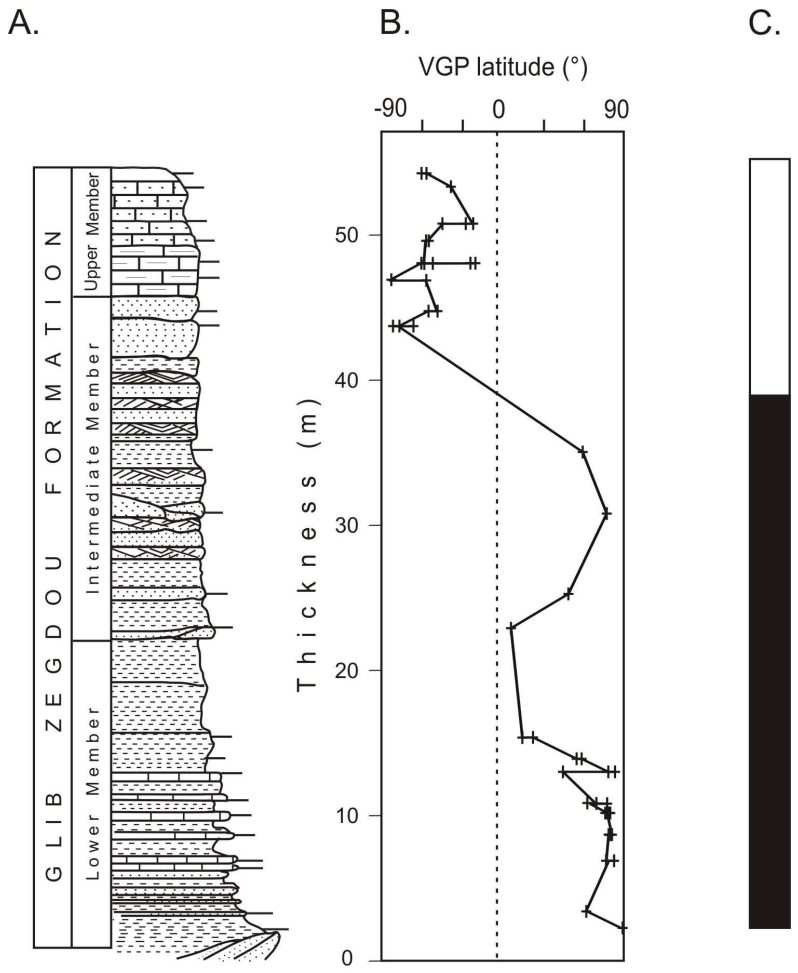


Figure 1.7. Paleomagnetic reversal stratigraphy of Gour Lazib section. (A.) Stratigraphic section of Gour Lazib. (B.) Virtual geomagnetic pole (VGP) latitudes are plotted as a function of stratigraphic levels. (C.) polarity column (black/white bars represent normal/reverse polarity zones).

4. CORRELATION

4.1. EL KOHOL SECTION

4.1.1 Stratigraphic and structural data

El Kohol Formation uncomformably 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 (Khomsi 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, uncomformably 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 Marocco 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.

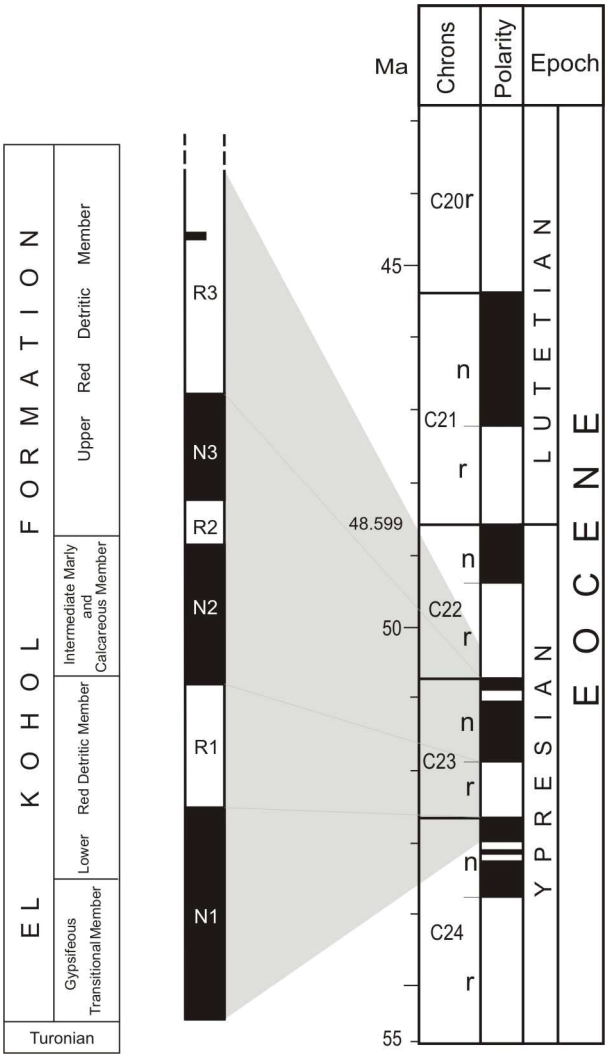


Figure 1.8. Preferred correlations of El Kohol section with geomagnetic-polarity time scale (GPTS) of Gradstein et al. (2004).

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.

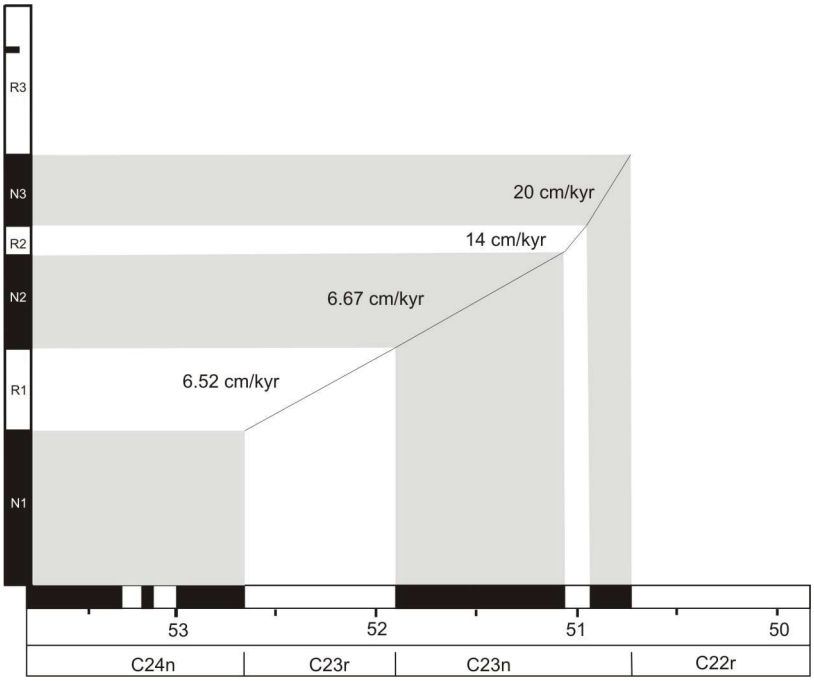


Figure 1.9. Comparison of El Kohol magnetic polarity stratigraphy with the GPTS of Gradstein et al. (2004). Slopes are proportional to sedimentation rate.

The polarity interval zones R1 and N2 observed in the Upper detritic Member show higher sedimentation rates. This interval corresponds to fluviatil 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, uncomformably overlying Paleozoic stratas 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 mongereaui*. *T. mongereaui,* 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 questionnable.

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 know 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 questionned

(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_3, has been described from the Intermediate Member of Glib Zegdou Formation and assigned to the genus *Chambius* (Adaci et al. 2007). The subfamily of Herotodotiinae 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.

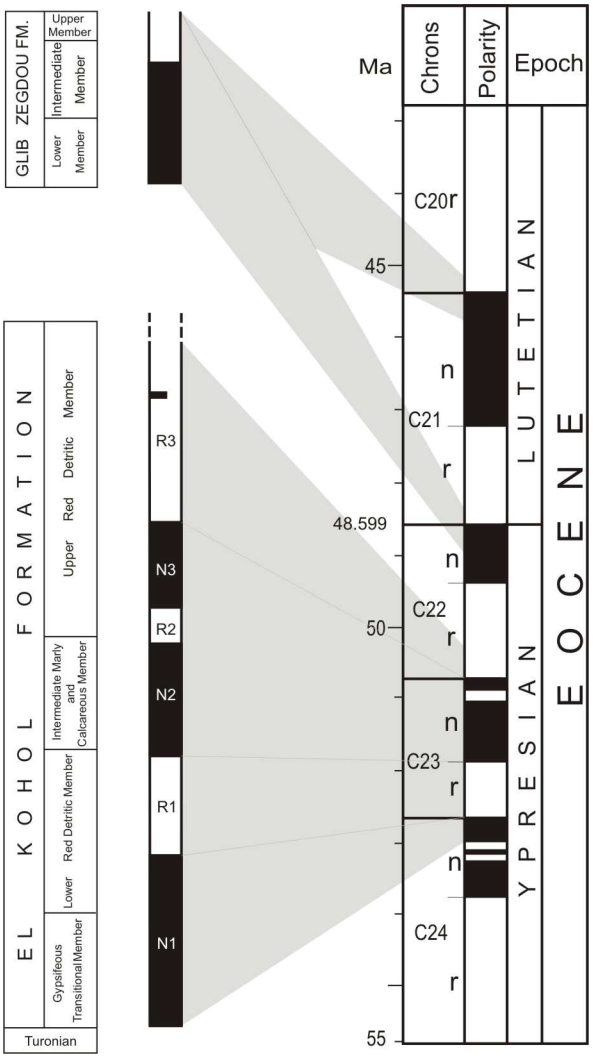


Figure 1.10. Preferred correlations of El Kohol and Gour Lazib sections with geomagnetic-polarity time scale (GPTS) of Gradstein et al. (2004).

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 lead, 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 particulary 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-Lutetien 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 Eocence Epoch. The growing Eocene fossil record in Asia suggests that this continent played a major role in Anthropoid evolution but we necessisate 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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1.2. MAGNETIC POLARITY STRATIGRAPHY OF THE MIDDLE-LATE EOCENE DEPOSITS OF CENTRAL LIBYA (DUR AT-TALAH ESCARPMENT, SAHARIAN DESERT) AND AGE OF THE EARLIEST KNOWN RADIATION OF AFRICAN ANTHROPOIDS

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1. INTRODUCTION

During the second half of the last century, the early Tertiary deposits of Central Libya were surveyed by French geologists who reported the occurrence of few fossiliferous vertebrate sites from south western Sirt basin, including Zallah and Dur At-Talah localities (Bellair et al. 1954; Arambourg and Magnier 1961; Arambourg 1963). Vertebrate paleontological researches at Dur At-Talah escarpment were then carried out in the late sixties, when Savage and his student Wight, initiated field projects in Libya, characterized the geology of the site and collected fossils (Savage 1969, 1971; Wight 1980). During the next 40 years, the paleontological exploration effort was interrupted but geological surveys, mainly focused on oil prospection, greatly improved the knowledge of tertiary sedimentologic framework of Libya. In 2005, a short visit to the Dur At-Talah deposits (Rasmussen et al. 2008), yielded a new collection of large to medium-sized vertebrate fossils but did not extend

the taxonomical list drawn up by Savage and Wight. Since 2006, field prospection in the early Tertiary of Libya by the "Mission paléontologique Franco-libyenne" and intensive fossil research and screening of Dur At-Talah sediments, led to the discovery of new fossil taxa, including micro-vertebrate fossil assemblages, so far poorly sampled from this site (Jaeger et al. 2008, 2010a,b). Mammal remains have been recovered from the lower lithological units of the Dur At-Talah Formation, identified as the Oyster Shell Bed, Clinoform and Bioturbated Units.

Our recent paleontological work resulted in the discovery of two new localities along the scarp (DT-loc1 and DT-loc2, Bioturbated Unit) yielding a rich primate fauna, actually considered as the oldest known diverse assemblage of African anthropoids (Jaeger et al. 2010b). Early evolutionary history of this group in Africa is poorly known, only documented by a few fossils before late Eocene times. The oldest African anthropoid primates, (except the controversial *Altiatlasius koulchii* from the late Paleocene of Morocco), had been described from the late middle Eocene Bir El Ater locality of Algeria (de Bonis et al. 1988) and from the earliest Priabonian Birket Qarun Locality 2 in the Fayum Depression of northern Egypt (Seiffert et al. 2005, 2008) but these localities have only yielded three species of the Parapithecid *Biretia*. The Dur At-Talah primate fauna, which comprises the anthropoids *Talahpithecus parvus, Afrotarsius libycus* and *Biretia piveteaui,* and the early strepsirhine primate *Karanisia savagei* (Jaeger et al. 2010b), greatly extends the taxonomic diversity of early known Eocene African anthropoids. Besides, fossil rodents, previously only documented at Dur At-Talah by fragments of isolated incisors (Savage 1971; Wight 1980), have also been recovered from the two new localities and assigned to five phiomyid taxa, including three new species (Jaeger et al. 2010a). This remarkable rodent assemblage, comprising one of the most primitive members of the clade Phiomorpha, is of great interest to constrain the early stages of hystricognathous rodent evolution in Afro-Arabia. Representatives of the endemic mammalian orders Macroscelididea, Hyracoidea, Proboscidea, Sirenia along with creodonts, chiropterans and marsupials have also been recovered along the escarpment. Actually, Dur At-Talah sedimentary series has produced one

of the richest Paleogene fauna of Africa (Savage and White 1965; Savage 1969, 1971; Wight 1980; Tassy 1981; Court 1995; Jaeger et al. 2010a,b) and documents a poorly known period of African mammal evolutionary history.

The knowledge of the latest part of Eocene Epoch in Africa is restricted to the Dur At-Talah escarpment, the Fayum Depression (BQ-2 and L-41) and the Nementcha Mountains (Bir El Ater). Dur At-Talah, BQ-2 and Bir El Ater sites have produced a similar faunal assemblage, comprising earliest African anthropoids (de Bonis et al. 1988; Seiffert et al. 2005; Jaeger et al. 2010b), early representatives of phiomorph radiation (Jaeger et al. 1985, 2010a; Sallam et al. 2009) and the primitive proboscidean *Moeritherium* (Andrews 1901; Tassy 1981; Delmer et al. 2006), which likely supports a roughly similar age for these faunas.

However, the age of Dur At-Talah sedimentary sequence had never been clearly established and has been matter of controversy over the years. Wight (1980) and Van Couvering and Harris (1991), first suggested that the Dur At-Talah sequence may be analogous to the Qasr el-Sagha and Jebel Qatrani Formations of Fayum, of which revised age estimates indicate a latest Eocene age (Seiffert 2006). Rasmussen et al. (1992), by faunal comparisons, conjectured then that the Libyan sequence may be as young as the Upper Sequence of Jebel Qatrani Formation. Recently, Seiffert (2010), based on mammalian biochronological studies, correlates the Clinoform Unit with the mid-Priabonian Dir Abu Lifa Member of the Qasr el-Sagha Formation and the Bioturbated Unit with part of the Lower Sequence of the Jebel Qatrani Formation. He proposed an early Oligocene age for the uppermost fossiliferous horizons of Dur At-Talah. Jaeger et al. (2010a,b), on the basis of new fossil micro-mammal and proboscidean discoveries and in the light of the magnetic-polarity stratigraphic study of the sequence, suggested that Dur At-Talah Formation may be better late Bartonian in age.

New fieldwork, in 2009, allowed us to expand the paleomagnetic sampling of Jaeger et al. (2010a) and the additional paleomagnetic data have permitted the extension of the magnetozonation downward and upward into the Dur At-Talah Formation. To better constrain

the age of the sequence, two further sections were sampled in the underlying marine Wadi Thamat Formation which preserves middle Eocene planktonic microfauna (Goudarzi 1970).
The purpose of this study is to establish a high-resolution magnetostratigraphy and biochronology calibration for these deposits. A dated framework of Dur At-Talah deposits, which recorded the poorly known Eocene interval in Africa and which displays one of the most diverse late Paleogene African fauna with the three anthropoid clades Afrotarsiidae, Parapithecidae, and Oligopithecidae, is now crucial for understanding the early radiation of African Anthropoids and the African mammalian evolutionary history.

2. GEOLOGICAL SETTING

Libya comprises four main sedimentary basins, including Al Kufrah, Ghadamis, Murzuq and Sirt basins (Figure 2.1). The studied area lies in the south western Sirt basin, Central Libya. The Sirt basin is a Tethyan rift basin, which consists of a NW-SE trending system of horsts and grabens, initiated during Early Cretaceous (Bar and Weegar 1972; Banerjee 1980; Gumati and Kanes 1985; Butt 1986; Gumati and Nairn 1991; Van der Meer and Cloetingh 1993; Baird et al. 1996; Schroter 1996). The basement consists of metamorphic and igneous rocks of Precambrian age (Conant and Goudarzi 1967; Hallett 2002). The pre-rift sequence comprises Paleozoic and Late Mesozoic clastic sediments (Pomeyrol 1968; Klitzsch and Squyres 1990; Hallett 2002). The syn-rift sequence, composed of Upper Cretaceous and early Tertiary open marine calcareous shales and shelf carbonates, is overlain by Eocene-early Miocene sediments post rift-sequence, characterized by continental and shallow marine facies (Harding 1984; Bezan and Malak 1996; Schroter 1996; Van der Meer and Cloetingh 1993; Hallett 2002).

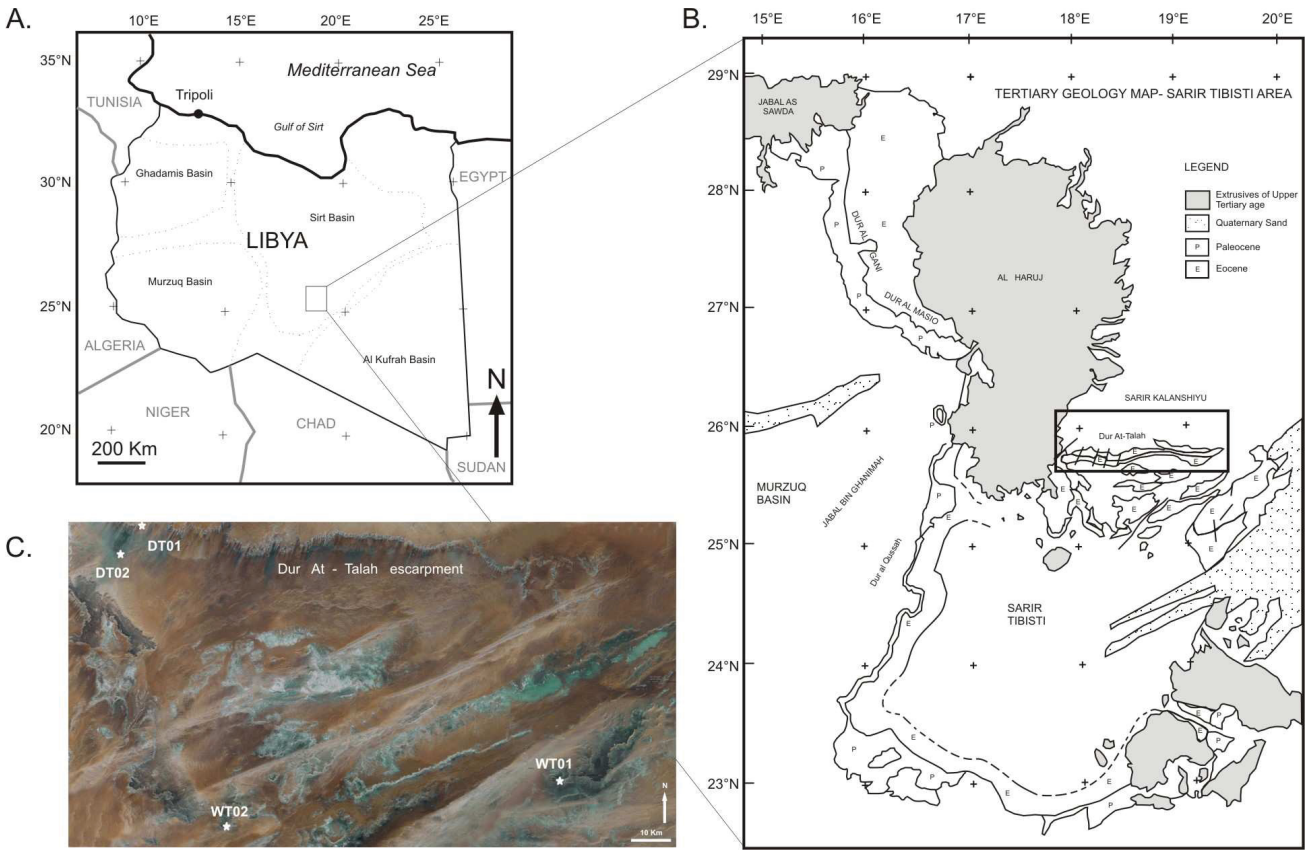


Figure 2.1. (A.) Location map of the Dur At-Talah escarpment in Central Libya. (B.) Tertiary geologic map of Sarir Tibisti area (After Klitsch 1966). (C.) Satellite view of the Dur At-Talah escarpment showing the location of the sampled sections for paleomagnetic analyses.

The exposed tertiary sequence in west Sirt Basin comprises late Paleocene through middle Eocene limestones, dolomitic limestones, marls and gypsiferous marls of Al Jir Formation (Burollet 1960; Bar and Weegar 1972) which are overlain by middle Eocene limestones, dolomitic marls and minor beds of gypsum of Wadi Thamat Formation (Desio 1943). The middle Eocene strata of Wadi Thamat Formation are overlain by the shallow marine to continental clastic sediments of the Dur At-Talah Formation. The Oligocene to middle Miocene strata of the Maradah Formation uncomformably overlies these Eocene strata (Abadi and Van Djik 1993; Rundić et al. 2008; Swezey 2009).

2.1. WADI THAMAT FORMATION

The Eocene stratigraphic sequence, exposed in the south western part of Sirt basin, includes the marine deposits of Al Jir Formation (Burollet 1960; Barr and Weegar 1972; Mijalkovic 1977; Shakoor and Shagroni 1984) and Wadi Thamat Formation (Desio 1943, 1971; Burollet 1960; Goudarzi 1970; Megerisi and Mamgain 1980; Jurak 1985; Vesely 1985). Al Jir Formation consists mainly of thick white dolomite, anhydrite and halite with chert nodules and gypsum and has been dated as late early or middle Eocene (Barr and Weegar 1972; Shakoor and Shaqroni 1984; Megerisi and Mamgain 1980). The upper most part of this formation is composed of chalky limestones interbedded with dolomite, containing calcareous algae with a rich fauna of pelecypods, bryozoa, echinoids and foraminifera (Vesely 1985). The foraminifera indicate a Lutetian age for this formation (Hallett 2002).

The middle Eocene sequence, overlying the Al Jir Formation, has been recognized as the Wadi Thamat Formation (Desio 1943; Burollet 1960). The Wadi Thamat Formation is generally represented by greenish/grey claystones, bioclastic marly limestones, oyster lumachelles and (chalky) limestones abounding in marine fossils (Desio 1943; Burollet 1960; Goudarzi 1970; Jurak 1985; Vesely 1985). This formation has been subdivided into three members by sedimentary bodies as Al Gata Member, Thmed al Qusur Member and Qrarat al Jifah Member (Magnier and Duval 1958; Burollet 1960; Goudarzi 1970; Megerisi and Mamgain 1980) (Figure 2.2D).

The lowermost Al Gata Member, about 75m thick at the type locality in the Zallah Trough, consists mainly of claystones, marls, dolomitic limestones and micritic limestones containing oyster shells, reflecting neritic and shallow marine environments (Vesely 1985; Hallett 2002) (Figure 2.2C). Al Gata Member has yielded a fauna of pelecypods, gastropods, echinoids and foraminifera, suggesting a late middle Eocene age (Vesely 1985; Goudarzi 1970, Megerisi and Mamgain 1980; Abadi and Van Dijk 1993). The Thmed al Qusur Member, about 15m thick, corresponds to the middle member of the Wadi Thamat Formation (Figure 2.2B) and comprises mainly chalky limestones with chert nodules and thin interbeds of claystones and gypsum. This member, deposited in a littoral to lagoonal environment, contains the large gastropod *Rostellaria* (Jurak 1985; Vesely 1985; Hallett 2002).

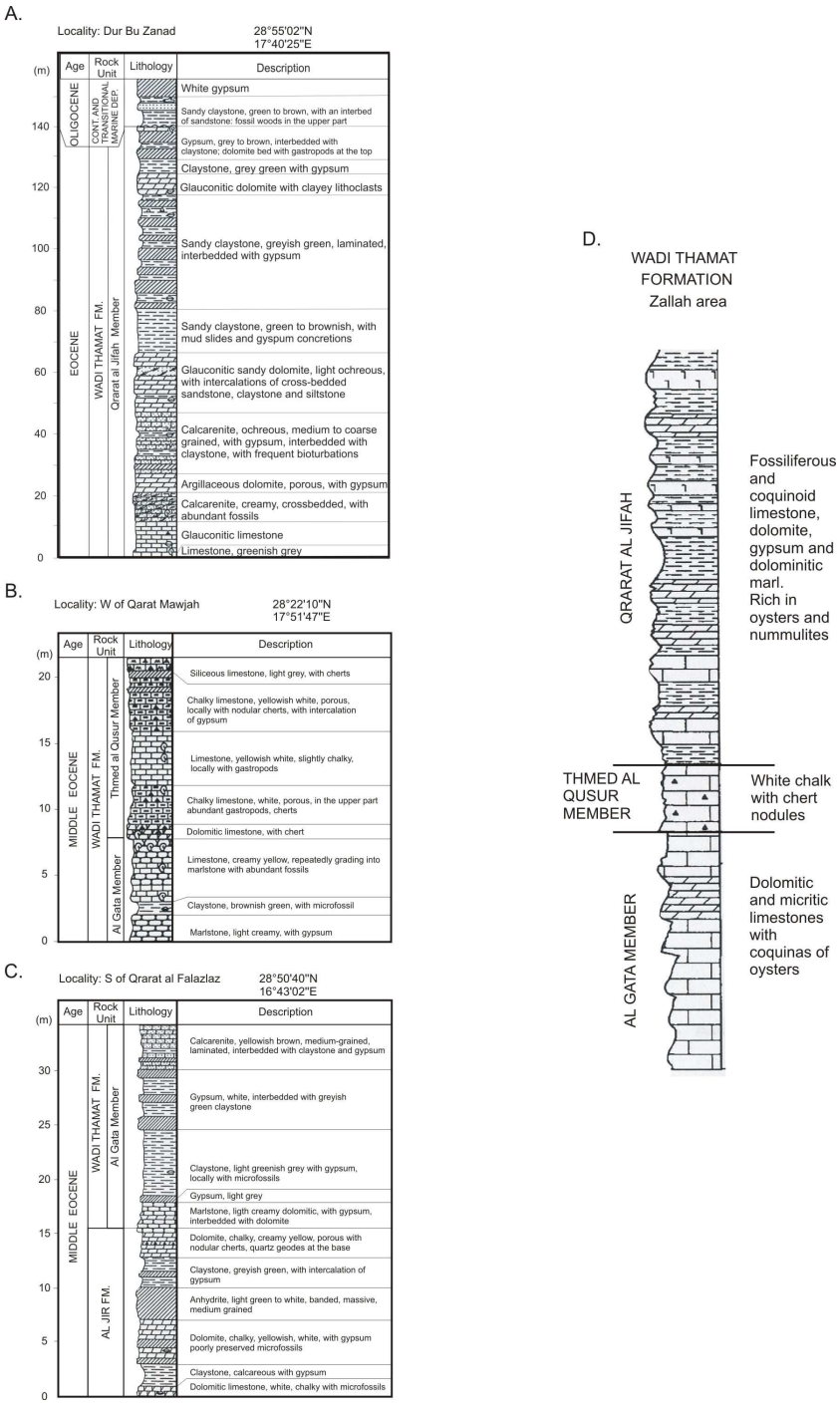


Figure 2.2. (A.-D.) Columnar sections of Al Jir Formation and Al Gata, Thmed al Qusur and Qrarat al Jifah Members of Wadi Thamat Formation (After Vesely 1985).

The Qrarat al Jifah uppermost member of Wadi Thamat Formation, 130 m thick at the type locality in Zallah Trough, is composed of chalky and marly massive limestones, dolomitic limestones with gypsum (Goudarzi 1970) (Figure 2.2A). The upper part of this member is characterized by marly claystones with minor sandy claystone beds alternating with calcareous claystones with large oyster shells and gypsum. The limestone contains a fauna of oysters, molluscs, gastropods, nummulites, and also some vertebrate remains (Megerisi and Mamgain 1980; Goudarzi 1970, Hallett 2002).

The Wadi Thamat Formation is overlain by the Dur At-Talah Formation which is widely exposed throughout a long escarpment extending est-west over about 150km, south east of Al Haruj volcano (Figure 2.1).

2.2. DUR AT-TALAH FORMATION

Savage and Wight, in 1969, carried out the first detailed study of Dur At-Talah area. Wight, (1980) subdivided the sedimentary Dur At-Talah Formation into three major lithological units, evolving from marine to terrestrial depositional environments: the Evaporite Unit, the Idam Unit and the Sarir Unit. New geological investigations leaded Duringer et al. (2008) to rename these three facies units and to establish a nomenclature matching better the lithology. The new nomenclature, which will be adopted in this paper, is as follow: the Clinoform Unit (Evaporite Unit after Wight 1980), the Bioturbated Unit (Idam Unit after Wight), and the Channelized Sandstone Unit (Sarir Unit after Wight).

Very recently, geological investigations have permitted to define a new unit at the base of the sequence, which underlains the Clinoform Unit (Figure 2.3). This basal unit, designed as the Oyster Shell Bed Unit, consists of greenish calcareous claystones with occasional secondary gypsiferous veins and iron concretion levels, and brownish bioclastic marly mudstones yielding many gastropod shells (Jaeger et al. 2010b). These deposits are intercalated between several oyster beds, 0.2 to 1m thick, comprising well preserved shells of *Ostrea clotbeyi* and *Ostrea cubitus* (Wight 1980). This unit, about 30m thick, outcrops south

of the escarpment. It has been interpreted to be deposited in a shallow marine paleoenvironment. The following unit, defined by Wight (1980) as the Evaporite Unit, ~30m thick, consists mainly of tidal marl and sandstone alternations and claystones, with secondary gypsum within oblique and vertical joints and fractures. Duringer et al. (2008) identified this unit as the Clinoform Unit on the basis of the presence of clinoforms in its middle part. The designation as "Evaporite Unit" is regarded as unconsistent with the lithology, considering that the occurrence of gypsum clearly not reflected evaporitic depositional conditions but secondary mineralization. The molluscan fauna is characterized by the presence of oysters (*Ostrea clotbeyi*, *Ostrea cubitus)*, pelecypods (Lucinidae, Glycymeridae) and gastropods (Calyptraeoidae, Turritellidae) (Wight 1980). The limited vertebrate fauna recovered from the base of this unit includes cetaceans, early proboscideans, sirenians, turtles, crocodiles, selacians and bony fishes (Savage and White 1965; Savage 1969, 1971; Wight 1980; Court 1995; Llinas Agrasar 2004).

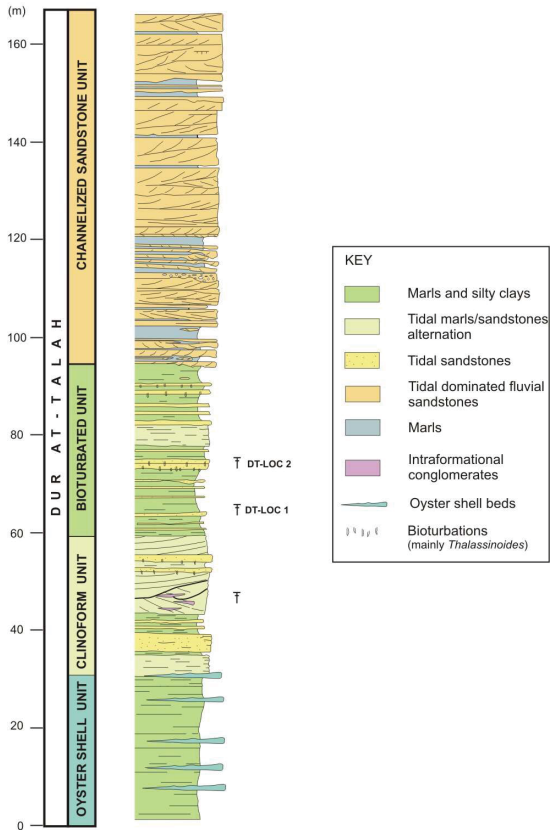


Figure 2.3. Dur At-Talah cliff section. Stratigraphic units, lithology and sedimentology of the section with stratigraphic location of vertebrate fossil occurrences.

The next stratigraphic unit, the Bioturbated Unit (Idam Unit after Wight 1980), up to 30m thick, is composed of nearshore facies in mixed tidal/storm dominated deposits (Duringer et al. 2008) (Figure 2.3). The tidal sandstone beds of this unit contain abundant bioturbation traces, including rhizolithes and a great diversity of ichnofossils (*Thalassionoides, Gastrochaenolites, Balanoglossites, Skolithos, Teichichnus, Diplocraterion*) (Duringer et al. 2008). The main terrestrial vertebrate-bearing localities of the sequence have been reported from the tidal marls and sandstone horizons, which preserved a remarkable vertebrate fauna including primates, rodents, hyracoids, macroscelidids, proboscideans, creodonts, bats, crocodiles, chelonians, snakes and freshwater fishes and (Savage and White 1965; Savage 1969, 1971; Wight 1980; Tassy 1981; Court 1995; Rasmussen et al. 2008; Jaeger et al. 2010a,b).

The uppermost unit of Dur At-Talah Formation, namely the Channelized Sandstone Unit (Sarir Unit after Wight 1980), is dominated by medium to coarse-grained channelized sandstone bodies interbedded with occasional claystone beds (Figure 2.3). The depositional setting of this unit range from mixed fluvial/coastal for the lowermost part to braided fluvial environment for the topmost part. This unit yielded abundant fossil silicified wood remains and water-lilies fruits (Wight 1980) but no identifiable vertebrate remains.

The Dur At-Talah Formation, up to ~150m thick, exhibits a considerable diversity of sedimentary facies. The sequence starts with sandy marl facies containing numerous shell beds with abundant molluscan fauna. Oyster beds are abundant and composed almost entirely of oyster shells with blue-grey calcareous matrix. These deposits are attributed to fully marine shallow depositional environments. These marine lithofacies are then succeeded by marly/sandy tidalites which yielded predominantly aquatic and semi-aquatic terrestrial vertebrates. The middle sequence comprises silts and fine marly sandstones rich in tidalites. The presence of abundant bioturbations, combined with the occurrence of terrestrial vertebrates, plants as well as aquatic vertebrates, indicate transition to nearshore facies in mixed tidal/storm dominated environments. The braided fluvial to mixed fluvial/coastal sandstone deposits characterize the upper part of the section. The sedimentary succession of

littoral marine, fluvio-deltaic and fluvial dominated facies, distributed along Dur At-Talah Formation, characterized by a transition from nearshore marine to continental conditions, seems to provide a good recorder of a northward Eocene regressive episode (Wight 1980; Duringer et al. 2008; Jaeger et al. 2010a).

Jaeger et al. (2010a) performed the first magnetic-polarity stratigraphic study of the Dur At-Talah Formation. Their sampling started at the basalmost oyster bed of the Clinoform Unit and ended in the middle part of the Channelized Sandstone Unit. Due to a recent field expedition, we extended the section of the previous study to the bottom and to the top.

3. PALEOMAGNETISM

3.1. SAMPLING

3.1.1. Field procedures

Samples were collected from unweathered sediments and oriented on the outcrop using a Brunton compass. A minimum of three drilled samples have been collected from the indurated stratigraphic levels with a portable gasoline-powered drill. Most of the sampled levels were not suitable for drilling and oriented block samples were collected and drilled in the laboratory. The average spacing between sampled levels varies between 0.2 to 3.2 m, depending on the lithology and availability of suitable sediments.

3.1.2. Sampled sections

Rock samples for paleomagnetic analyses were collected from two sections along the Dur At-Talah Formation and from two sections throughout the underlying marine Wadi Thamat Formation (Figure 2.4).

The first section, Section DT01, completes the section of Jaeger et al. (2010a) by collecting samples from 23 higher stratigraphic levels within the Channelized Sandstone Unit. This section, 40m thick, displays fine to coarse-grained sandstones with minor argillaceous

sandstone and claystone horizons, reflecting a fluviatile depositional environment. Samples were taken preferentially from claystone or fine-grained sandstone horizons; sandstones showing signs of weathering were avoided.

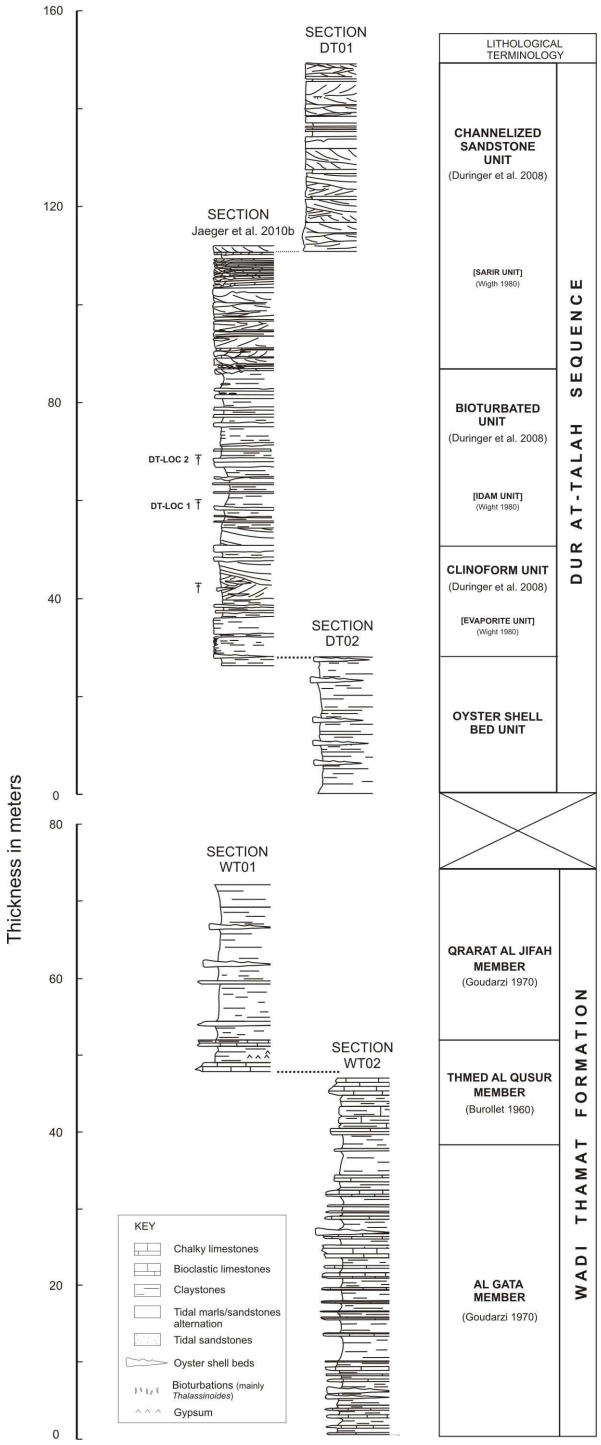


Figure 2.4. Lithology, sedimentology and range of the studied sections sampled within the Dur At-Talah and Wadi Thamat Formations.

The second section, named Section DT02, was sampled along the Oyster Shell Bed Unit, corresponding to the lowermost part of the Dur At-Talah Formation (Figure 2.4). It is approximatively 30m thick and 22 stratigraphic levels were sampled. This section consists principally of green-grey calcareous claystones, occasionally gypsiferous, intercalated with oyster shell beds. Section DT02 completes that of Jaeger et al. (2010a) by sampling lowermost levels.

Two additional sections, sections WT01 and WT02, have been sampled within the marine Wadi Thamat Formation, underlying Dur At-Talah deposits (Figure 2.4). Section WT01 has been sampled ~120km south east from Section DT02 (Figure 2.1) and consists principally of greenish claystones intercalated with few oyster beds. It is about 25m thick and was sampled by collecting samples from 16 stratigraphic levels. Section WT02, approximately 60m thick, was sampled ~80km west from Section WT01 (Figure 2.1) and consists of an alternation of green claystones, oyster beds and bioclastic limestones. 23 stratigraphic levels have been sampled along this section. These two sections were correlated by means of the limestone units, traced by Rundić et al. (2008).

Unfortunately, 23 of the oriented blocks collected from these four sections broke down during the travel or were lost during sample preparation.

Beddings of the strata are subhorizontal, slightly tilted northeast. The observed difference in elevation between the top of Section WT01 and the base of Section DT02 is approximatively 30m. A depression filled with fine-grained aeolian accumulation, known as *feshfesh,* extends south of Dur At-Talah escarpment. Between Wadi Thamat Formation outcrops and Dur At-Talah escarpment, the Eocene sediments are covered by these very fine aeolian deposits and tracing of marker beds, necessary to allow unambiguous stratigraphic correlation of our magnetic sections, was not possible.

Lithological facies of the basal Oyster Shell Bed Unit of Dur At-Talah Formation and Qrarat al Jifah Member of Wadi Thamat Formation, displaying alternation of marly claystones and calcareous claystones with large oyster shells, are quite similar. According to compacted

accumulation sediments rates corresponding to such deposits and the observed difference in elevation between the two sections, the time gap separating these sequences seems to not be greater than some hundreds of thousands of years.

3.2. LABORATORY PROCEDURES

Samples were incrementally demagnetized and measured on Spinner JR6-magnetometer at the laboratory of paleomagnetism of the Institut International de Paléoprimatologie, Paléontologie Humaine of Poitiers University. Paleomagnetic samples were either subjected to the progressive thermal demagnetizations from 100 to 600°C at 25–50°C intervals or submitted to stepwise alternating field demagnetization with increments of 3–10mT, up to a maximum field of 150mT. Both treatments yielded usually consistent Characteristic Remanent Magnetizations (ChRM). Results of demagnetization were plotted on orthogonal vector diagrams (Zijderveld 1967) and equal-area stereographic projections. ChRM directions were calculated using principal component analysis (Kirschvink 1980). Site mean from each site and the mean directions of ChRM polarity groups were calculated using the Fisher statistics (Fisher 1953).

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, samples were subjected to Isothermal Remanent Magnetization (IRM) acquisition in fields up to 1T 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 (0.1T along the x-axis, 0.5T along the y-axis and 3T along the z-axis). Magnetic susceptibility was measured after each heating step to detect any chemical or mineralogical changes in the magnetic minerals on a magnetic susceptibility meter SM10 (ZH instruments).

3.3. PALEOMAGNETIC RESULTS

3.3.1. Wadi Thamat Formation

Isothermal Remanent Magnetization (IRM)

The magnetic mineralogy of the Wadi Thamat Formation deposits was studied using Isothermal Remanent Magnetization (IRM) acquisition curves and subsequent thermal demagnetization of orthogonal component.

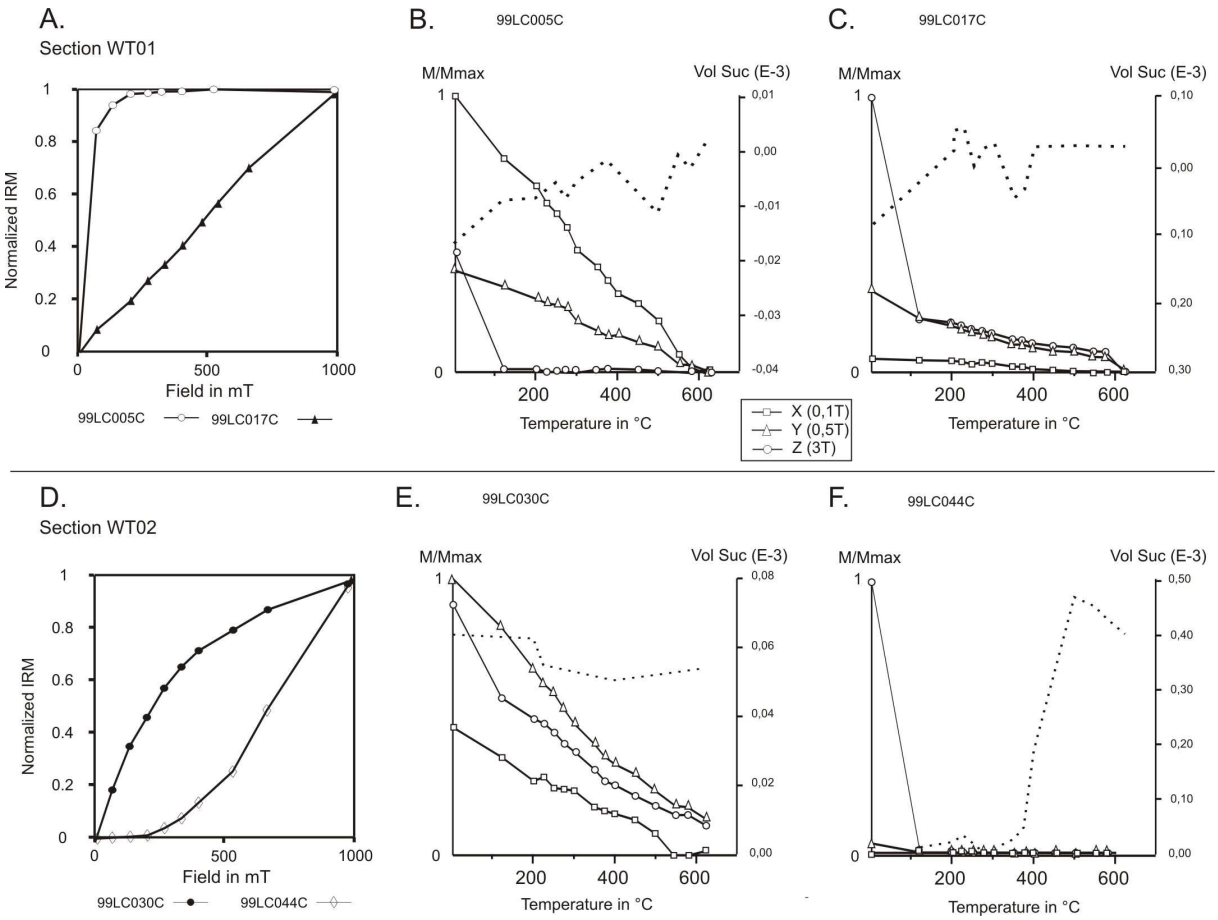


Figure 2.5. (A., D.) Isothermal Remanent Magnetization (IRM) acquisition (normalized values) curves of selected samples from Section WT01 (A.) and Section WT02 (D.). (B., C., E., F.) Examples of stepwise thermal demagnetization of the IRM components for representative samples from Section WT01 and WT02. (B.) 99LC005C, chalky limestone sample. (C.) 99LC017C, green claystone sample. (E.) 99LC030C, bioclastic limestone sample (F.) 99LC044C, brownish claystone sample.

The two representative samples of Section WT01 display a different pattern of IRM acquisition (Figure 2.5A). IRM acquisition curve of Sample 99LC005C, collected from chalky limestones, is characterized by a predominant low coercitivity mineral fraction, which saturate in field less than 200mT. Thermal demagnetization of this sample (Figure 2.5B) shows that the low coercitivity fraction component has an unblocking temperature comprised between 550 and 600°C, which suggest the presence of magnetite. The inflexion of the thermal demagnetization curve of the hard coercitivity component around 125°C indicates the presence of goethite. The green claystone sample 99LC017C exhibits saturation magnetization behavior indicative of high coercitivity minerals. IRM acquisition curve increases gradually but do not reach saturation at 1T (Figure 2.5A). Thermal demagnetization of the hard fraction (0.5-3T) shows an unblocking temperature of ~125°C, which suggests the presence of goethite (Figure 2.5C). The susceptibility of analysed samples of this section are very weak and stay roughly constant during heating but the measured susceptibilities, approaching the detection limit of the material, show variation in intensity during heating.

The representative samples of Section WT02, samples 99LC030C and 99LC044C, were collected from bioclastic limestones and brownish claystones, respectively.

Sample 99LC030C acquires more than 70% of the final saturation IRM value in field as low as 500mT but does not saturate beyond 1T (Figure 2.5D), implying that magnetization is carried by both low and high coercivity minerals. The IRM thermal demagnetization curve of the soft coercitivity fraction (<0.1T) shows a maximum unblocking temperature around 550°C (Figure 2.5E), indicating the presence of (titano)-magnetite. Thermal demagnetization of the medium (0.1-0.5T) and hard components (0.5-3T) of IRM exhibit unblocking temperature >600°C, probably indicative of hematite.

IRM acquisition curve of Sample 99LC044C is indicative of a predominant high coercitivity fraction (Figure 2.5D). The demagnetization curve shows that hard fraction (0.5-3T) of IRM is totally demagnetized at low temperature (~125°C) (Figure 2.5F). The predominance of high coercitivity fraction and the complete demagnetization of Z component (0.5-3T) at 125°C, clearly reflect the prevalence of goethite. The susceptibility curve remains

constant until the temperature of 400°C from which it starts to increase. This increase is probably due to the transformation of paramagnetic minerals into magnetic minerals.

Natural Remanent Magnetization (NRM)

The initial NRM intensities of samples from Section WT01 and WT02 are often low and are found to range between 10^{-3} and 10^{-6} A/m. The NRM of most samples is characterized by one or two components. The demagnetization results show that often the viscous overprint was removed below 200°C (20mT). Higher field or temperature demagnetization, in most of the case, yielded a stable, characteristic component, which decayed toward the origin. Thermal demagnetization shows that the characteristic remanent magnetization resides mainly in (titano-)magnetite since most of the total NRM was removed at temperature comprise between 400 and 600°C (Figure 2.6A,I). Some hematite is also present as the remanent magnetization of some sample is not completely removed at temperature >600°C (Figure 2.6F). Sample 99LC049 (Figure 2.6G-H) demonstrates a preponderance of a hard coercitivity fraction. Alternating field demagnetization was inefficient and thermal demagnetization treatment show an extremely large decrease in NRM intensity at 120°C. This result support the presence of goethite as based on IRM studies.

Following Kirschvink's (1980) method, the ChRM directions were calculated by principal component analysis. For 34 samples from 22 sites of Section WT01 and WT02, thermal and alternating field demagnetization resulted in erratic behavior from which no ChRM direction could be determined. These samples and other samples, for which principal component analysis yielded a maximum angular deviation >15°, were rejected from further analyses.

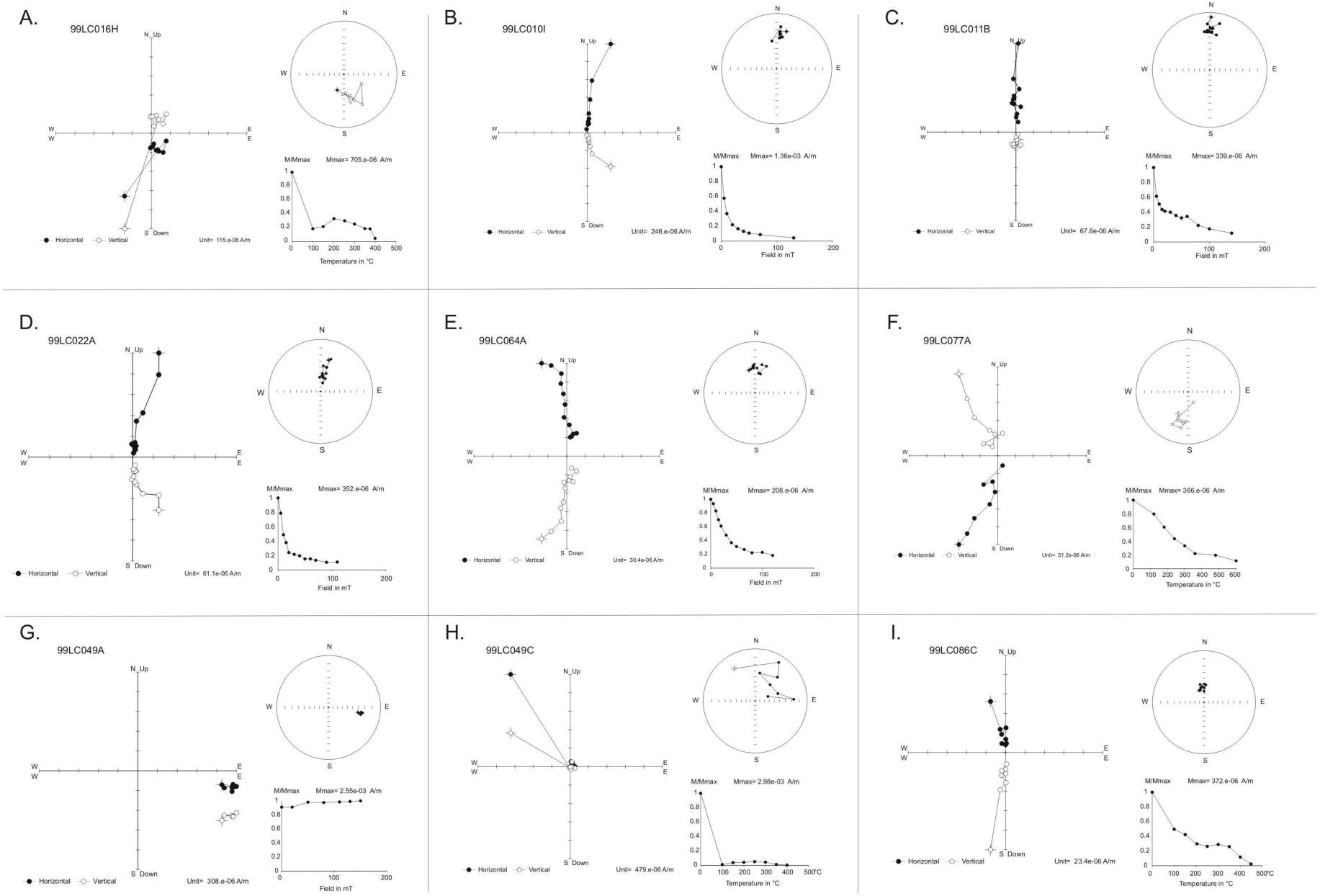


Figure 2.6. (A-I) Orthogonal vector diagrams (closed/open symbols correspond to the horizontal/vertical component), stereoplots (open/closed circles indicate directions in the upper/lower hemisphere), and intensity and step plots for representative samples from section WT01 and WT02 after thermal and alternating field demagnetization.

Site means were calculated by Fisher statistic (Fisher 1953) and are presented in Table 2.1. Statistical significance of site means, determined from three or more samples, was tested with the Watson criteria (Watson 1956). All the sites, with three or more samples, satisfied the Watson criterion. Sites which have only two samples, but which agreed closely on the mean polarity group, were also included for further analysis. Of the 39 sites sampled along Section WT01 and WT02, 23 sites yield ChRM directions that seem nonrandom.

TABLE 2.1. PALEOMAGNETIC SITE MEAN DIRECTIONS OF WADI THAMAT SECTIONS

Site	N	Decl. (°)	Incl. (°)	α95 (°)	k	R
SECTION WT01						
1	2	349.4	21.8	8.2	930.72	2
2	2	318	64.3	34.1	55.88	1.98
3	1	340.4	-6.2	*	*	*
4	2	340	12.6	21.3	139.87	1.99
5	3	2.7	27.4	18.9	43.39	2.95
6	2	18.5	28.5	10.3	454	2
7	2	332.2	29.5	47.4	29.87	1.97
8	3	21.6	49.8	29.7	18.23	2.89
9	3	165.6	-54.6	19.4	41.52	2.95
SECTION WT02						
10	2	352.4	56.6	12.1	426.88	2
11	3	342.1	39.4	10	153.44	2.99
12	2	346.7	24	18.8	178.39	1.99
13	2	252.8	-65.2	15.5	260.09	2
14	2	183.3	-45.8	13.8	329.44	2
15	2	355.5	2.6	29.4	74.07	1.99
16	4	176.1	-33.5	14.1	43.63	3.93
17	2	24.9	9.9	56.2	21.92	1.95
18	2	2.9	39.3	36.1	49.98	1.98
19	2	65.1	17.4	29	76.15	1.99
20	1	27.1	20.3	*	*	*
21	2	58.2	53	35.7	51.03	1.98
22	5	347.8	28.2	23.8	11.3	4.65
23	3	12.3	25.5	26.9	22.03	2.91

Note: Decl,: mean tilt corrected declination in °E; Incl,: mean tilt corrected inclination in degree to the horizontal; α95 : mean direction 95% confidence ellipse; k : Fisher precision parameter; R : length of the resultant vector.

The mean directions for both sections were calculated by the Fisher statistics (Fisher 1953) and plotted on stereographic diagrams (Figure 2.7).

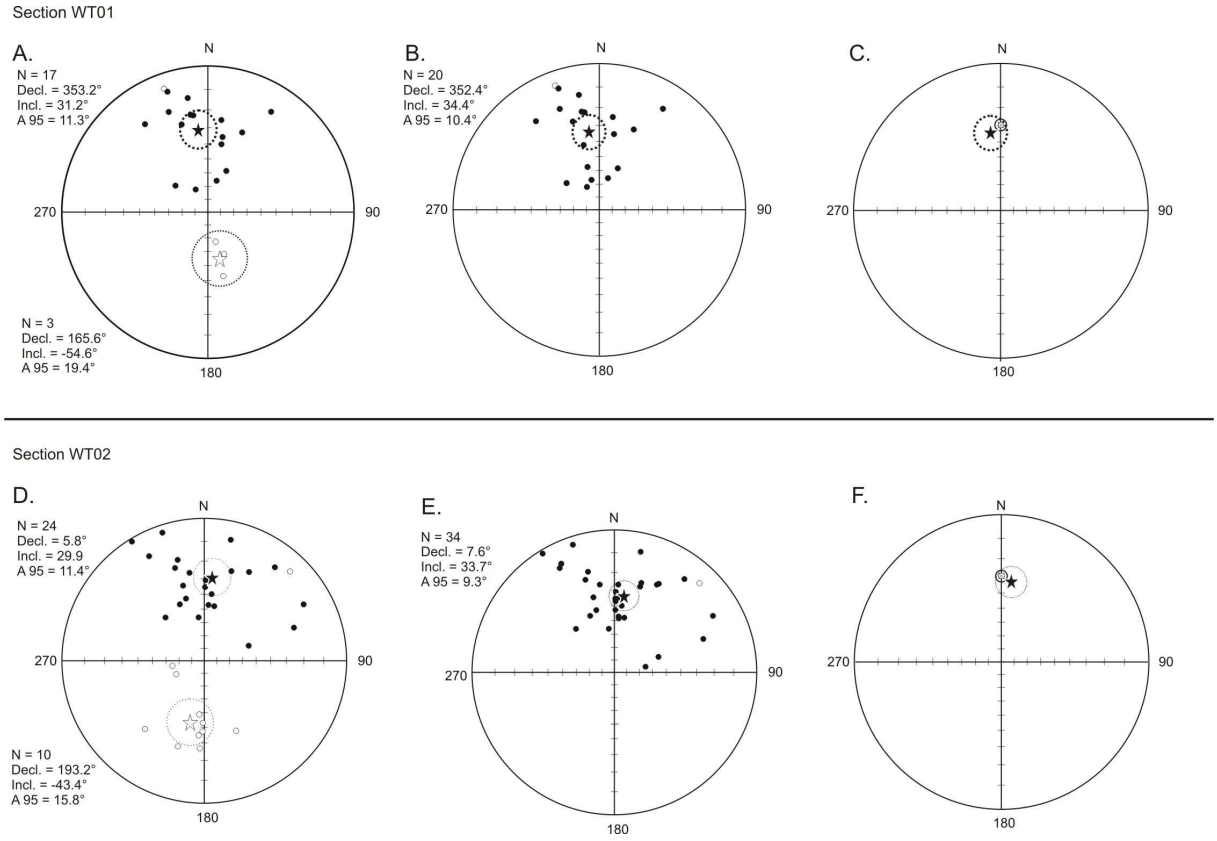


Figure 2.7. (A., D.) Equal-area stereographic projections and Fisher statistics of characteristic directions for all specimens of Section WT01 (A.) and Section WT02 (D.). Open/closed circles indicate directions in the upper/lower hemisphere. Mean directions calculated by Fisher statistics are represented by a star, and the ellipse indicates the 95% confidence ellipse. (B., E.) Equal-area stereographic projections and Fisher statistics of characteristic directions for all specimens of Section WT01 (B.) and Section WT02 (E.), when the reversed polarity samples are inverted. Mean directions calculated by Fisher statistics are represented by a star, and the ellipse indicates the 95% confidence ellipse. (C., F.) Equal-area stereographic projections and Fisher statistics of overall mean directions of Section WT01 (C.) and Section WT02 (F.). Hollow square shows the direction derived from the 40Ma apparent polar wander path of Torsvik et al. (2008).

In order to evaluate our results, a reversal test of McFadden and McElhinny (1990) was carried out using. The angle between the mean directions of the normal and reversed polarities of Section WT01 is 24° and 14.7° for Section WT02. Mean directions of opposing polarity sites have a critical angle at 95% of confidence level of 29° for Section WT01 and 16.5° for Section WT02. Section WT01 paleomagnetic data pass a positive reversal test with

an indeterminate classification and the reversal test is passed with a C classification for Section WT02 according to McFadden and McElhinny's criteria.

The overall mean direction of Section WT01 is: declination = 352.4°, inclination = 34.4° (α_{95} = 10.4°). The overall mean direction of ChRM directions for Section WT02 is: declination = 7.6°, inclination = 33.7° (α_{95} = 9.3°). Mean directions of the sections as well as a calculation of corresponding paleopoles are presented in Table 2.2.

TABLE 2.2. PALEOMAGNETIC POLARITY MEAN DIRECTIONS OF WADI THAMAT SECTIONS

	N	Decl. (°)	Incl. (°)	α 95 (°)	k	Pole postiton Φ (°E)	λ (°N)	dp/dm (°)
SECTION WT01	23	352.4	34.4	10.4	9.4	248.4	80.6	11.9/6.8
SECTION WT02	38	7.6	33.7	9.3	7.2	151.7	80.2	10.6/6

Note: Decl,: mean tilt corrected declination in °E; Incl,: mean tilt corrected inclination in degree to the horizontal; α95: mean direction 95% confidence ellipse; k : Fisher precision parameter; Φ: longitude of paleopole for mean direction in °E, λ: latitude of paleopole for mean direction in °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.

Torsvik et al. (2008) provided a 40 Ma reference paleomagnetic pole for Africa located at -80.8°N, 17.5°E with a confidence limit α_{95} = 2.8°. This reference pole predicts an expected magnetic field direction at Section WT01 locality of: declination = 0.1°, inclination = 29. 7° (α_{95} = 3.4°) and of declination = 0.3°, inclination = 29. 9° (α_{95} = 3.4°) at Section WT02 locality (Figure 2.7). Using Demarest method (1983), a comparison of the expected and observed directions yields a vertical rotation of declination of D = -7.7±10.3° and D= 7.3±9.2° for Section WT01 and WT02 respectively. The sense of rotation of the two section are not in agreement considering that Section WT01 display a counterclockwise vertical axis rotation from the expected directions while Section WT02 recorded a clockwise vertical-axis rotation of declination. These observed differential rotations of declination may be interpreted here as a response to local tectonic effects rather than a response to regional tectonics. The inclination values observed for Section WT01 and WT02 are slightly higher than the expected

inclination of the paleomagnetic field at this latitude, although inclination of depositional remanent magnetism is usually shallower than the expected geomagnetic field direction (Tauxe and Kent 2004).

Magnetic polarity zonation

The declination and inclination obtained for the ChRM of each sample were used to calculate the virtual geomagnetic pole (VGP) latitude, yielding a magnetic polarity sequence in the studied sections. The virtual geomagnetic pole (VGP) latitudes and position of stratigraphic levels of each site were reported in Figure 2.8.

The magnetic stratigraphy of Section WT01 reveals two polarities with about 20m thick normal polarity zone in the lower portion of the section and a reverse polarity zone at the top represented by the uppermost sampled stratigraphic levels of the section (Figure 2.8A). Section WT02 is characterized by a normal-reverse-normal polarity zone succession (Figure 2.8B). The reverse polarity zone, about 15m thick, presents a short normal polarity interval in its middle portion. This normal polarity interval is defined by only two specimens sampled from the same block therefore its reliability is quite low. It could either represent a short duration normal polarity event or these results could also arise from incomplete demagnetization. Actually, the sampling spacing through the base of Section WT02 is not as dense as it could be likely that a short duration normal polarity event was missed; however, the resolution of this question will have to wait future high density sampling.

Section WT01 has been correlated to Section WT02 by limestone marker bed. Actually, the topmost strata of Section WT02, corresponding to medium layered silicified limestones badly cracked and joined, top with chert, capping all the hammada of the area, are stratigraphically equivalent to the chalky limestones at the base of Section WT01.

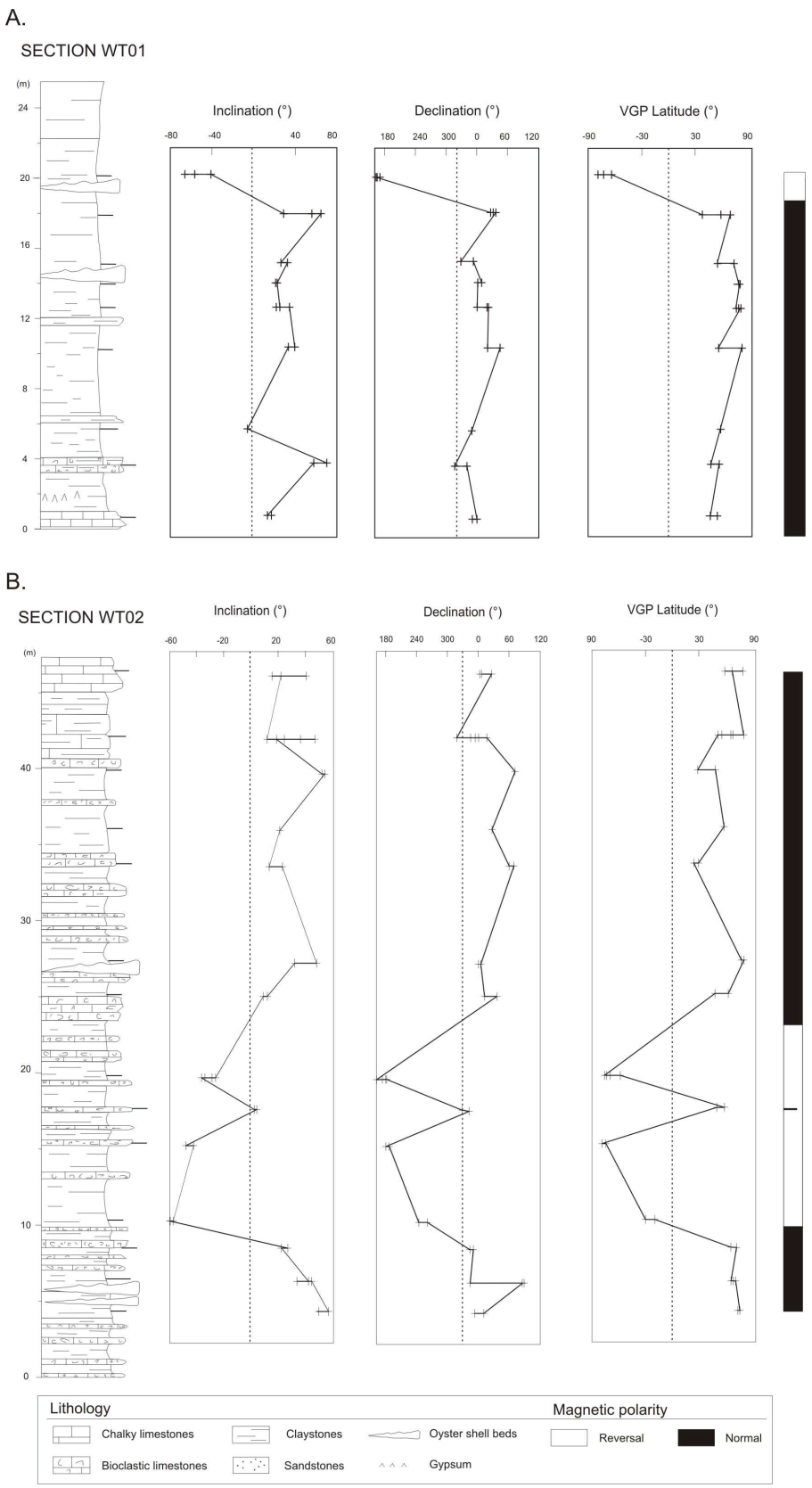


Figure 2.8. (A.-B.) Paleomagnetic reversal stratigraphy of Sections WT01 (A.) and WT02 (B.). Inclination (in degrees to the horizontal), declination (°E), and the virtual geomagnetic pole (VGP) paleolatitudes (°N) of Characteristic Remanent Magnetization (ChRM) are plotted as a function of stratigraphic levels. The lines at the right of the stratigraphic column indicate the position of the sites.

3.3.2. Dur At-Talah Formation

Isothermal Remanent Magnetization (IRM)

Rock magnetic analyses, including IRM acquisition and subsequent thermal demagnetization, were carried out on samples of various lithologies present in Section DT01 and DT02 to investigate on the minerals carrying the magnetization.

The IRM acquisition curves (Figure 2.9A) are quite similar for the three samples (99LT117C, 129C and 156C), collected from fine-grained sandstones along Section DT01 and indicate that almost complete saturation of acquired IRM (80%) at low to intermediate fields (<300 mT). Sample 99LT117C (Figure 2.9B) is characterized by a dominance of low coercitivity minerals and the IRM demagnetization curve show a maximum unblocking temperature around 500°C, indicating the presence of titanomagnetite but iron sulfides are also present as suggested by the inflexion point at 200°C of the low-corcitivity IRM component. The IRM of the high-coercitivity axis is almost completely erased at temperature higher than 120°C, revealing the presence of goethite.

IRM demagnetization curves indicate the main magnetic minerals of sample 99LT129C (Figure 2.9C) consist of low coercitivity phase with maximum unblocking temperature of 500°C, suggesting that the main magnetic mineral may be titanomagnetite. IRM demagnetization curves of the soft and intermediate coercitivity component of Sample 99LT156C (Figure 2.9D), show an inflexion at about 400°C, probably indicating the presence of titanomagnetite. The susceptibility remains constant up to 350°C and then starts to increase, which is probably due to transformation of the original paramagnetic or magnetic minerals into new magnetic phase.

The argillaceous sandstone sample 99LT144C, IRM acquisition curve increase gradually but do not reach saturation at 1000mT (Figure 2.9E). This sample is characterized by the predominance of high-coercitivity minerals like goethite, which is confirmed by unblocking temperature at 120°C. Goethite seems to be the only ferromagnetic mineral carrier of this sample.

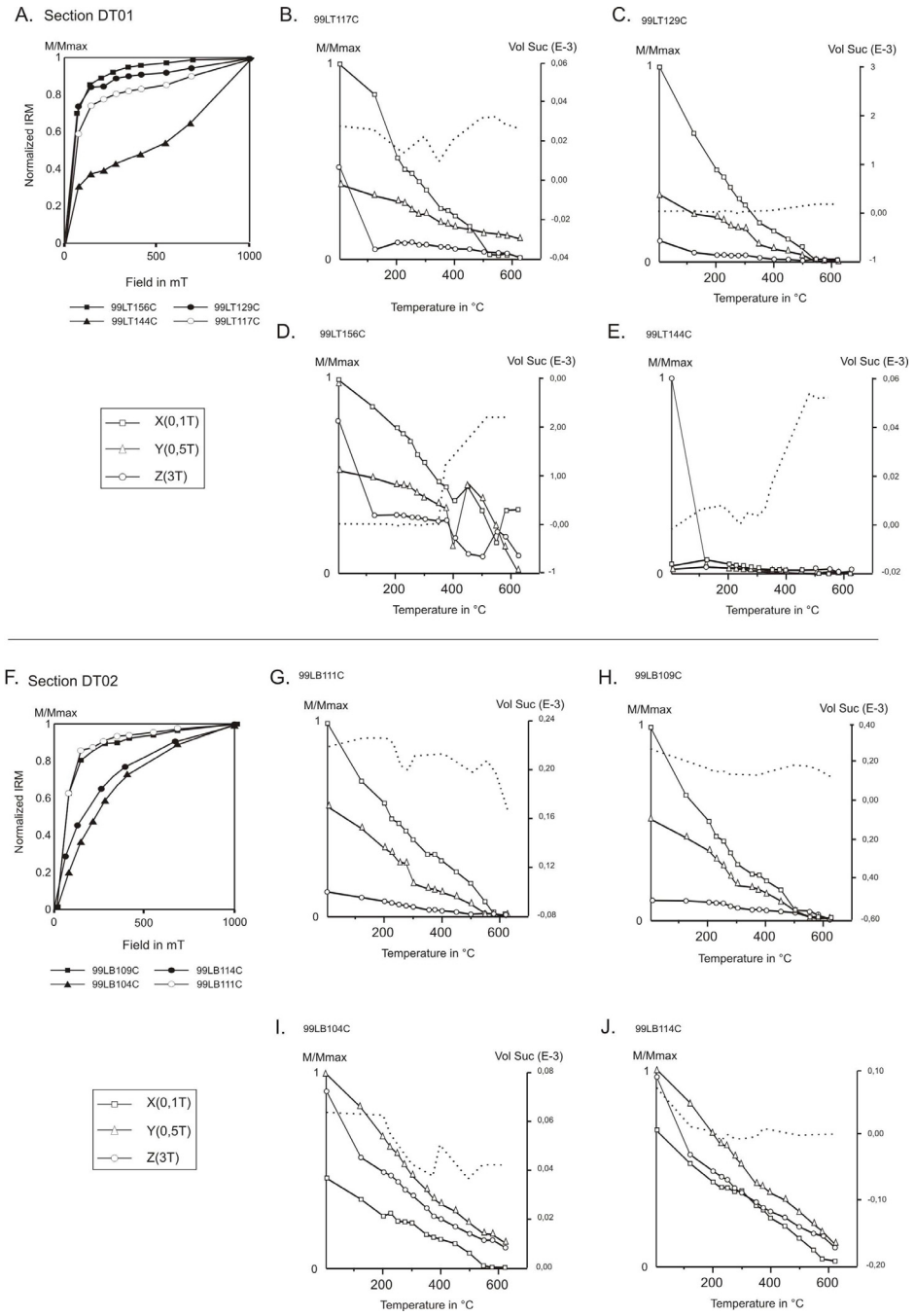


Figure 2.9. (A., F.) Isothermal Remanent Magnetization (IRM) acquisition (normalized values) curves of selected samples of Section DT01 (A.) and Section DT02 (F.). (B., C., D., E., G., H., I., J.) Examples of stepwise thermal demagnetization of the IRM components for representative samples from Section DT01 and DT02. (B.) 99LT117C, fine-grained sandstone sample. (C.) 99LT129C, fine-grained sandstone sample. (D.) 99LT156C, fine-grained sandstone sample. (E.) 99LT144C, argillaceous sandstone sample. (G.) 99LB111C, green claystone sample. (H.) 99LB109C, green claystone sample. (I.) 99LB104C, brownish marly mudstone sample (J.) 99LT114C, grey calcareous claystone sample.

Samples of Section DT02 (Figure 2.9F) display different patterns of IRM acquisition. Green claystones samples (99LB111C and 109C) acquired more than 90 % of the final saturation IRM value at 300mT. The thermal demagnetization of the composite IRM shows that most of the remanence of these samples (Figure 2.9G, H) is carried by low and intermediate coercitivity minerals. The IRM demagnetizations show a maximum blocking temperature between 500 and 600°C indicating the presence of magnetite. The decrease around 300°C of the intermediate-IRM components may be due to the presence of iron sulphides (like greigite and/or pyrrothite), maghemite or titanomagnetite. Sample 99LB104C, collected from a brownish marly mudstones and sample 99LB114C, collected from grey calcareous claystones, show the same IRM acquisition pattern (Figure 2.9F) and similar demagnetization curves (Figure 2.9I, J). The values of IRM increase rapidly at low field (<500mT), but do not saturate beyond 1000mT, implying that magnetization is carried by both low- and high-coercivity minerals (Figure 2.9F). The unblocking temperature of the low-coercitivity component of IRM is in the range of 550-600°C (Figure 2.9I), suggesting the presence of magnetite. The intermediate and high coercitivity fraction of IRM are not completely demagnetized at temperature >600°C, indicating the presence of high-unblocking temperature such as hematite.

Natural Remanent Magnetization

The NRM intensities of Dur At-Talah sections are generally low and average 100 x 10^{-6} A/m.

Figure 2.10 shows demagnetization results of sample demagnetized from Section DT01 and DT02. Alternating field and thermal demagnetization were both efficient to isolate the Characteristic Remanent Magnetization (ChRM) but most of the samples were demagnetized by alternating field. The majority of the samples were characterized by one or two magnetization components.

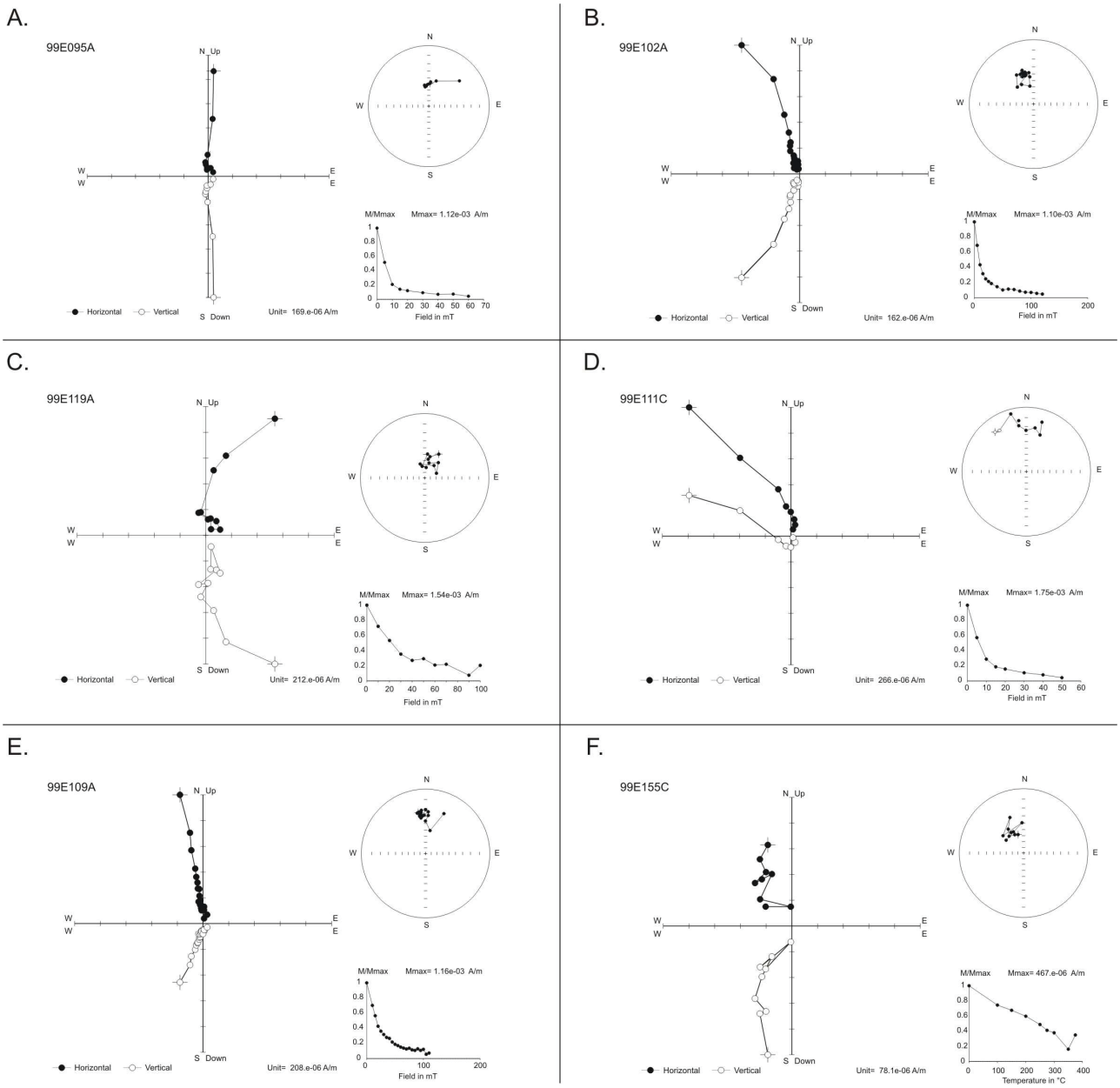


Figure 2.10. (A.-F.) Orthogonal vector diagrams (closed/open symbols correspond to the horizontal/vertical components), stereoplots (open/closed circles indicate directions in the upper/lower hemisphere), and intensity and step plots for representative samples of section DT01 and DT02 after thermal and alternating field demagnetization.

The secondary component could be removed by low intensity alternating field (<20mT) and by thermal demagnetization below 250°C. Through thermal and alternating field treatments, 30% of analyzed samples displayed incoherent demagnetization trajectories. Demagnetization of almost half of the sample collected along section DT01 from the channelized sandstones resulted in erratic behavior from which no reliable ChRM directions

could be determined. Samples characterised by a low temperature component which present an extremely large decrease in intensity at 100°C, indicating the predominance of goethite, and followed by incoherent demagnetization behaviors, were rejected for further analyses. The paleomagnetic directions of the secondary component are clustered near the present Earth's magnetic field direction at the study area and it probably represents a recent viscous overprint (Figure 2.11C). The higher temperature component, considered as characteristic remanent component was generally removed at temperature between 400 and 450°C, suggesting the presence of titanomagnetite as the main carrier of NRM.

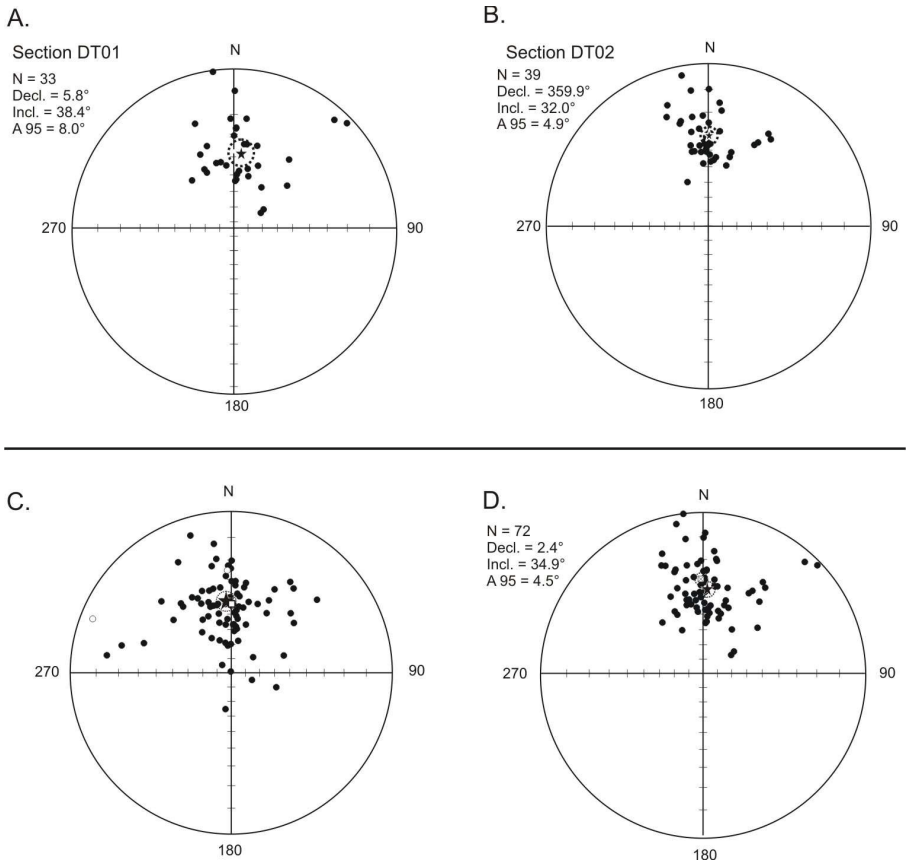


Figure 2.11. (A.-B.) Equal-area stereographic projection and Fisher statistics of characteristic directions for all specimens of Section DT01 (A.) and Section DT02 (B.). Open /closed circles indicate directions in the upper/lower hemisphere. Mean directions calculated by Fisher statistics are represented by a star, and the ellipse indicates the 95% confidence ellipse. (C.) Equal-area stereographic projection and Fisher statistics of NRM (0°C) direction directions for all specimens of Section DT01 and DT02. Mean directions calculated by Fisher statistics are represented by a star, and the ellipse indicates the 95% confidence ellipse. Hollow square shows present Earth's magnetic field direction at the study area. (D). Equal-area stereographic projection and Fisher statistics of overall mean directions of Section DT01 and DT02. Hollow square shows the direction derived from the 40Ma apparent polar wander path of Torsvik et al. (2008).

To determine characteristic magnetic directions, principal component analysis was carried out (Kirschvink 1980). ChRM paleomagnetic directions were then analysed using Fisher statistics (1953), to determine site mean declination, inclination and associated precision parameters (Table 2.3). To test the significance of our paleomagnetic directional data, we performed the Watson test of randomness (Watson 1956) and all the sites, with at least three samples, appear to satisfy the Watson criterion.

The polarity of characteristic component was found to be normal in all the samples.

TABLE 2.3. PALEOMAGNETIC POLARITY SITE MEAN DIRECTIONS OF DUR AT-TALAH SECTIONS

Site	N	Decl. (°)	Incl. (°)	α95 (°)	k	R
SECTION DT01						
1	3	346.8	47.3	16.2	58.98	2.97
2	2	359.4	28.3	11.7	461.27	2
3	3	342.4	16.3	14.3	75.05	2.97
4	3	26.2	39.6	18.1	47.29	2.96
5	3	23.4	50.2	6.5	361.92	2.99
6	3	0.2	46.4	16.7	55.79	2.96
7	3	358.7	27.5	16.8	54.61	2.96
8	3	327.9	40.6	20.8	36.05	2.94
9	1	335.2	36.3	*	*	*
10	1	359.2	34.8	*	*	*
11	1	15.4	40.8	*	*	*
12	3	10.3	45.9	17.7	49.8	2.96
13	3	347.5	49.6	20.3	38.08	2.95
14	1	328.1	46.2	*	*	*
SECTION DT02						
15	2	0.2	42.1	21.4	138.6	1.99
16	3	4	37.4	14.5	7349	2.97
17	2	359	14	6.7	1403.9	2
18	3	349.7	37.8	4.9	646.5	3
19	2	10.4	13.7	12.7	386.36	2
20	3	0.3	33.7	12.6	97.33	2.98
21	3	31.9	27.6	7.1	301.22	2.99
22	3	1.8	40.6	38.9	11.09	2.82
23	2	357	26.6	12.7	358.86	2
24	2	344.8	20.3	26.7	89.3	1.99
25	3	351.1	11.2	14.8	70.29	2.97
26	3	358.5	25.3	17.1	52.79	2.96
27	3	358.5	45.8	17.7	49.74	2.96
28	2	350.8	28.8	24.4	107.8	1.99
29	3	3.4	44.3	3.8	1052.79	3

Note: Decl,: mean tilt corrected declination in °E; Incl,: mean tilt corrected inclination in degree to the horizontal; α95 : mean direction 95% confidence ellipse; k : Fisher precision parameter; R: length of the resultant vector.

The sampled sections exhibit nearly monoclinal beds thus the fold test could not be carried out to investigate the paleomagnetic stability of the data. Dur At-Talah strata reveal a uniformly normal polarity characteristic remanence and the lack of reverse polarity magnetizations Mean directions of normal sites of Section DT01, Section DT02, and the previous results of the magnetic stratigraphic study of Dur At-Talah section (Jaeger et al. 2010a) as well as a calculation of paleopoles are presented in Table 2.4.

TABLE 2.4. PALEOMAGNETIC POLARITY MEAN DIRECTIONS OF DUR AT-TALAH SECTIONS

	N	Decl. (°)	Incl. (°)	α 95 (°)	k	Pole postiton Φ (°E)	λ (°N)	dp/dm (°)
SECTION DT01	33	5.8	38.4	8	10.7	145	83.3	9.5/5.6
SECTION DT02	40	359.9	32	4.9	22.3	198.8	81.6	5.1/2.9
SECTION (Jaeger et al. 2010a)	129	3.5	36.9	8	*	165.6	83.9	9.4/5.5

Note: Decl,: mean tilt corrected declination in °E; Incl,: mean tilt corrected inclination in degree to the horizontal; α95: mean direction 95% confidence ellipse; k : Fisher precision parameter; Φ: longitude of paleopole for mean direction in °E, λ: latitude of paleopole for mean direction in °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.

The overall mean direction of Sections DT01 and DT02 is: declination = 2.4°, inclination = 34.9° (α95 = 4.5°), corresponding to a paleomagnetic pole at 83.1°N and 179.0°E (dp/dm = 5.2°/3.0°). The apparent polar wander path of Torsvik et al. (2008) at 40 Ma predicts an expected paleomagnetic direction at the studied area of: declinaison = 0.1°, inclination = 30.8°, α_{95} = 3.4° (Figure 2.11D). Using the Demarest method (1953), the comparison of the expected and observed direction yields no significant vertical axis rotation of declination. The observed inclination is 4.1±5.1° higher than the expected inclination of the

paleomagnetic field at this latitude while paleomagnetic data usually show a biais toward shallower inclinations. Directions of the data from Wadi Thamat Formation and from Dur-At Talah section do not display any flattening of inclination. The observed inclination correspond to a paleolatitude of 19.2°N. The anomalously higher inclination at Dur At-Talah, inconsistent with the expected paleomagnetic field direction at this latitude, may indicate that either in Eocene, Libya occupied a more northward position than its predicted location, which is not realistic considering Cenozoic North African tectonics or error in bedding measurements and underestimated dipping. Indeed, more sections need to be sampled to evaluate the reliability of this observed pattern.

Magnetic polarity zonation

Virtual geomagnetic pole (VGP) latitude, calculated from the ChRM direction of each sample, yield a magnetic polarity sequence of the studied sections (Figure 2.12). The stratigraphic correlation, between Sections DT01 and DT02 and the section of Jaeger et al. (2010a), lead to a 160 m thick composite section. Section DT02 completes that of Jaeger et al. (2010a), by sampling lowermost levels, and Section DT01 completes this latter section to the top levels. The composite section is characterized by one single long normal polarity event.

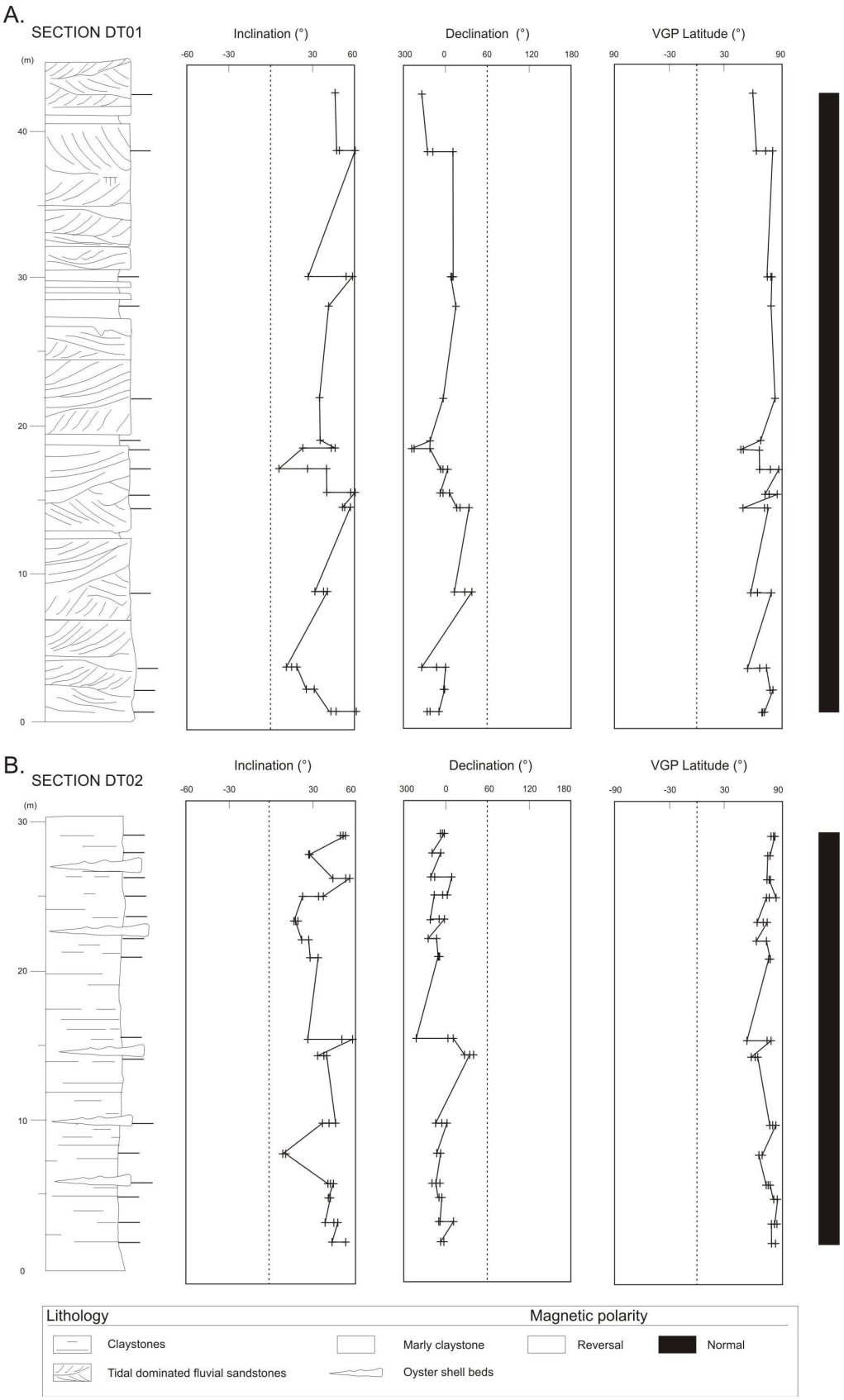


Figure 2.12. (A.-B.). Paleomagnetic reversal stratigraphy of Sections DT01 (A.) and DT02 (B.). Inclination (in degrees to the horizontal), declination (°E), and the virtual geomagnetic pole (VGP) paleolatitudes (°N) of characteristic remanent magnetization (ChRM) are plotted as a function of stratigraphic levels. The lines at the right of the stratigraphic column indicate the position of the sites.

4. AGE OF THE WADI THAMAT AND DUR AT-TALAH FORMATIONS

4.1. BIOSTRATIGRAPHIC DATA

Wadi Thamat Formation

The Eocene strata of the Wadi Thamat Formation were deposited in shallow marine littoral to neritic environment and are rich in Tethys marine invertebrate fossils. A microfauna list, from the Wadi Thamat Formation outcrops, exposed in south western Sirt basin, has been provided by Rundić et al. (2008).

In addition to benthic foraminifera (large nummulites), several groups of invertebrates are recorded in this formation, as molluscs and echinoids (Magnier and Duval 1958; Burollet 1960; Goudarzi 1970; Megerisi and Mamgain 1980; Vesely 1985; Jurak 1985; Abadi and Van Dijk 1993). Fossil remains of molluscs are the most common with dominant occurrence of gastropods and bivalves. Most of the recovered bivalves belong to the Ostreidea (*Ostrea roncana*, *O. multicostata*, *Exogyra* sp.) and other pelecypods. Numerous gastropods (*Conus colossus, Voluta, Cerithium plicatum*), cephalopoda (*Nautilus* sp.), scaphopoda and echinoidea (*Echinolampas* sp.) are also present.

Regarding planktonic foraminifera assemblages, the association of the *Truncorotaloides rohri* together with the Globigerinids (*Globigerina gr. yeguaensis*, *G. eoceana*, *G. pseudoeoceana* and *G. gr. cerrozulensis),* recognized from Wadi Thamat deposits, is reminiscent to the microfauna assemblage described in the middle-late Eocene deposits of Al Jabal at Akhdar of north east Libya (Khoudary 1980). This assemblage ranges into the late middle Eocene P14 *Truncorotaloides rohri* biostratigraphic zone of the standard planktonic foraminiferal zonation (Gradstein et al. 2004). According to Rundić et al. (2008), common occurrence of *Pseudohastigerina micra* may also support a middle Eocene age, time of the species optimum. The presence of *Nummulites fabiani* in the Qrarat al Jifah Member, may indicate a late middle Eocene age (Goudarzi 1970). The other few identified and poorly preserved foraminifera (*Nummulites* cf. *gizehensis*, *Alabamia perlata Nonion micrum, Quinqueloculina simplex*) and ostracoda (*Quadracythere angusticostata*, *Uroleberis parnensis, Pontocyprella eocenica*), which have also been reported from these deposits (Megerisi and Mamgain 1980; Rundić et al. 2008), do not provide further evidences for more precise relative age.

The analysis of the microfossil assemblage recovered from the Wadi Thamat Formation leads to the conclusion that the age of these deposits correspond best to late middle Eocene.

Dur At-Talah Formation

Age constraints of the Dur At-Talah Formation were provided by paleontological analysis. The mammalian fossils, recovered from the vertebrate-bearing localities of the Clinoform and Bioturbated Units, include primates, rodents, macroscelidids, hyracoids, proboscideans, creodonts, chiroptera, crocodilians, chelonians, snakes and fishes. The large sized mammalian fauna recovered from the base of the Clinoform Unit is similar to that from the top of the Bioturbated Unit which may indicate that the sedimentary series of Dur At-Talah may have been deposited in a short interval of time with high sedimentation rates.

Recent field expeditions to the Dur At-Talah escarpment yielded to the discovery of an assemblage of primates, including the primitive anthropoids *Afrotarsius libycus, Biretia piveteaui* and *Talahpithecus parvus,* and the early strepsirhine primate *Karanisia savagei* (Jaeger et al. 2010b). This assemblage, comprising representatives of the three early anthropoid clades of Afrotarsiidae, Parapithecidae, and Oligopithecidae, displays a more important diversity than that described from the earliest Priabonian Birket Qarun 2 (BQ-2) locality of Fayum (Seiffert et al. 2005). According to Jaeger et al. (2010b), the small size of the strepsirhine primate *Karanisia arenula* compared to *K. clarki* from BQ-2 and the primitive anatomy of *Talahpithecus parvus,* may support a older age for Dur At-Talah deposits. In addition, Dur At-Talah site shares the common occurrence of the parapithecid *Biretia piveteaui* with the late middle Eocene Bir El Ater locality of the Nementcha Mountains (de Bonis et al. 1988), which may indicate a similar age for these faunas. Both localities share also the occurrence of the same species of *Moeritherium*, *M. chehbeurameuri*, which has not been recorded from BQ-2.

Jaeger et al. (2010a) reported a rich assemblage of hystricognathous rodents from the Bioturbated Unit. Five phiomyid taxa, assigned to three genera (*Phiomys, Protophiomys*, and *Talahphiomys*) (Jaeger et al. 2010a), including three new species (*Phiomys hammudai*, *Protophiomys durattalahensis* and *Talahphiomys libycus)* have been identified.

Compared to the rodent fauna described from the Fayum Jebel Qatrani Formation, Dur At-Talah assemblage seems to display a more primitive and less diversified set of phiomyids. *Phiomys hammudai*

displays a quite similar dental pattern as *Phiomys andrewsi* which appears at quarry A and B in the Jebel Qatrani Lower Sequence. The Libyan taxon, however, is characterized by a larger size, the constant presence of the mesolophid, a better developed mesolophule and a lower anteroloph. The metaloph, disto-lingually directed, develops, in some case, a double connexion. It displays a mesial connection to the mesoloph and connects distally to the middle of the posteroloph as in the Oligocene phiomyids *Ph. andrewsi, Neophiomys*, *Metaphiomys* and *Paraphiomys*. A backwardly directed metaloph, connected to the posteroloph, appears as a derived condition among hystricognathous rodents (Marivaux et al. 2004). Most of the specimens, referred to *Ph. hammudai*, lack this distal connexion or display an incipient connexion to the posteroloph. This species may therefore represent a more primitive morphological grade compare to the phiomyids *Ph. andrewsi, Neophiomys* and *Metaphiomys,* described from Jebel Qatrani Formation (Wood 1968).

The genus *Talahphiomys* is represented in Dur At-Talah assemblage by *T. lavocati* and a new species, *T. libycus,* identified from six isolated teeth from DT-loc1. This latter species differs from *T. lavocati* in being less bunodont, in having more elevated transverse crests and in showing a better development of the mesolophule. However, these two species are morphologically very close but the paucity of material ascribed to *T. libycus* does not allow further comparison.

Compared to the rodent faunas described from the early Oligocene deposits of Dhofar Province in Oman and Zallah locality in Libya, the fauna of Dur At-Talah displays different generic taxonomic composition which lacks derived phiomyid taxa such as *Metaphiomys* and *Gaudeamus*, supporting an earlier age for Dur At-Talah. Dur At-Talah rodent fauna display more similarities with those from the late middle Eocene Bir El Ater locality and the earliest late Eocene BQ-2 Fayum locality. These sites share common occurrence of *Protophiomys* (Jaeger et al. 1985; Sallam et al. 2009; Jaeger et al. 2010a), a primitive representative of the phiomyid radiation (Marivaux et al. 2002). From Umm Rigl Member of Birket Qarun Formation, Sallam et al. (2009) described a new species belonging to a new genus of hystricognathous rodents, *Waslamys attiai*. This taxon is very close in morphology to *P. durattalahensis* but differs from this latter in having a slightly stronger endoloph and in exhibiting a lesser development of the mure which varies from being absent, incipient or complete in a small number of cases. *Protophiomys aegyptensis*, also described from BQ-2 locality (Sallam et al. 2009), exhibits a less developed labial wall and show a lesser development of the mesolophule compared to *P. durattalahensis*. The Libyan species displays, in comparison to *P. algeriensis* from Bir El Ater, a more lophate dental pattern

and exhibits an achieved pentalophodont pattern characterized by a low but complete mesoloph. The mesolophule and mure are either very weak or absent in *P. aegyptensis* and *P. algeriensis* whereas in *P. durattalahenis,* these crests show a better development. According to Jaeger et al. (2010a), these characters confer to the Dur At-Talah species a slightly more derived dental morphology than *P. algeriensis* of Bir el Ater which could indicate a slightly younger age for the Dur At-Talah deposits.

The larger size mammalian fauna comprises the proboscideans *Barytherium grave*, *Arcanotherium savagei* and *Moeritherium chehbeurameuri* (Wight 1980; Court 1995; Delmer 2005; Delmer et al. 2009). Fragmentary fossil remains of *Barytherium,* a large size primitive bunolophodont proboscidean, were first recovered from the Dir Abu Lifa Member of the Qasr el-Sagha Formation in the Fayum region at the beginning of the 20th century (Andrews 1901, 1906). Further specimens of *Barytherium* were identified from Birket Qarun locality of Fayum (Seiffert et al. 2008). One of the major differences between the Libyan and Egyptian localities lies in the abundance of the early proboscidean genus *Barytherium* in the Clinoform Unit of Dur At-Talah. *Moeritherium*, which displays bunodont teeth and chisel-like tusks, has also been recovered from the locality of Bir El Ater (Delmer et al. 2006) and from BQ-2 (Seiffert et al. 2005). *Arcanotherium savagei,* identified from the Clinoform and Bioturbated Units, is less lophodont than *Barytherium* and *Numidotherium,* and displays a combination of primitive and derived dental and post cranial features of early proboscideans. It has not been recorded, so far, from BQ-2 locality nor from Bir El Ater. Remains of the proboscideans *Palaeomastodon* and *Phiomia* and the embrithopod *Arsinoitherium* were reported from Dur At-Talah (Savage 1969, 1971; Wight 1980), but none of these taxa has been recovered during our last years extensive paleontological search of the Dur At-Talah outcrops.

Isolated teeth and fragmentary jaws of Macroscelididae have been recovered from the Bioturbated Unit. These specimens, currently under study by R. Tabuce, seem to belong to three different species. One of them has been ascribed to the genus *Nementchatherium* (Tabuce com. pers.). This later genus, assigned to the subfamily Herodotiinae, has been described from the late middle Eocene deposits of Bir El Ater (Tabuce et al. 2001). The few specimens of creodonts recently recovered from Dur At-Talah deposits include cranial and post-cranial remains which are now under study by C. Grohé.

On the basis of the occurrence of the proboscideans *Palaeomastodon* and *Phiomia*, the embrithopod *Arsinoitherium* identified by Savage (1969), Rasmussen et al. (1992) and Seiffert (2010) correlate the Dur At-

Talah Bioturbated Unit with the Jebel Qatrani Lower Sequence and argue that the Libyan sedimentary sequence may be as young as early Oligocene in age. However, this statement is clearly not in agreement with the mammalian biostratigraphic data mentioned above. Actually, the mammalian fauna recovered from Dur At-Talah Bioturbated Unit is very similar to that from BQ-2 and Bir El Ater localities. These three sites share the anthropoid *Biretia* (de Bonis et al. 1988; Seiffert et al. 2005; Jaeger et al. 2010b), the hystricognathous rodent *Protophiomys* (Jaeger et al. 1985, 2010a; Sallam et al. 2009) and the early proboscidean *Moeritherium* (Andrews 1901; Tassy 1981; Delmer et al. 2006). Some of the specimens of macroscelidids known from Dur At-Talah are morphologically close to *Nementchaterium senarhense* from Bir El Ater (Tabuce et al. 2001) and the common occurrence of *Biretia piveteaui* at these two localities (De bonis et al. 1988; Jaeger et al. 2010b) also supports a similar age for both of these faunas. Seiffert et al. (2008, 2010) argues that the appearance of Anthracotheriidae, an immigrant artiodactyl group from Asia, at Bir El Ater locality, indicates a younger ager for this site compared to BQ-2. However, the presence at the Algerian locality of Anthracotheriid, of which dispersal scenario between Asia and Africa may have been similar to that of hystricognathous rodents and early anthropoid primates (Ducrocq 1994; Jaeger et al. 1999, Beard et al. 2004; Marivaux et al. 2002, 2004; Bajpai et al. 2008), is not considered here as supporting this hypothesis. Moreover, Sallam et al. (2010) described, from BQ-2, a highly derived anomaluroid rodent species, *Shazurus minutus.* This species, which is most similar in dental morphology to early Miocene *Paranomalurus* and extant *Anomalurus* than to *Nementchamys* from Bir El Ater and *Pondaungimys* from the late middle Eocene of Myanmar, may indicate a younger age for BQ-2 locality. Anomaluroid rodents are so far absent at Dur At-Talah, although this absence may be due to insufficient sampling of the micromammal fauna. The fauna of hyracoids, from the Algerian and Egyptian sites, *Bunohyrax matsumotoi* from Bir El Ater and *Dimaitherium patnaiki* from BQ-2, are very generalized and small-bodied species and display a similar dental morphology (Barrow et al. 2010). The hyracoid specimens recovered from Dur At-Talah are bunodont, small-sized and seems to display a primitive molar pattern. The currently undergoing study of the specimens may bring further informations bearing on their age.

The age of BQ-2, Umm Rigl Member of the Birket Qarun Formation, has been well constrained by sequence stratigraphic studies (Gingerich 1992), foraminiferal and mammalian biostratigraphic data, and magnetostratigraphy (Seiffert et al. 2005, 2008). The biochronostratigraphic data of the Fayum sedimentary sequence indicate that BQ-2 is likely correlated to the lower part of Chron C17n.1n. An age of about 37 Ma is

therefore proposed for the fossiliferous levels, corresponding to an earliest Priabonian age. The age of the fluvio-delatic deposits of Bir El Ater locality, which overlies uncomformably early Lutetian marine deposits, is not as well constrained. This locality has yielded a rich mammalian fauna, including macroscelidids, creodonts, insectivores, hystricognathous and anomaluroid rodents, primates, hyracoids, anthracotheriids, proboscideans and the age of this site, only based on mammalian biostratigraphic data, is believed to range from late middle to late Eocene (Coiffait et al. 1984; Tabuce et al. 2000, 2001).

In sum, the age of Dur At-Talah sequence seems to range from late middle to early late Eocene but, regarding only vertebrate biostratigraphical evidences, the relative age of the three mammalian localities of Dur At-Talah, Bir El Ater and BQ-2 is difficult to assess conclusively.

Stratigraphical data

The lithological succession recorded in the Dur At-Talah Formation provides evidence of a wide range of different facies which show rapid vertical variations. The evolution of paleoenvironmental conditions in this sequence, evolving from marine to fluvial depositional environments, is interpreted as recording a tethyan regressive episode (Wight 1980; Duringer et al. 2008; Jaeger et al. 2010a). According to Wight (1980), Van Couvering and Harris (1991), Dur At-Talah sequence can be correlated to the late Eocene-early Oligocene Qasr el-Sagha and Jebel Qatrani Formations of Fayum which show similar transition from shallow marine to more continental sedimentary facies. However, Dur At-Talah Formation is much thinner and biostratigraphical data are not in agreement with such a correlation.

In the Fayum sequence, the marine Gehannam Formation, which underlies the Birket Qarun Formation, is a sequence of marly limestone and sandstone intercalations, corresponding to shallow shelf marine deposits (Gingerich 1992). Based on planktonic biostratigraphic study, Gehannam Formation has been correlated with the calcareous nannofossils zones NP16/NP17 and planktonic foraminiferal zone P14, which indicate that these deposits are Bartonian in age (Toumarkine and Luterbacher 1985; Van Couvering and Harris 1991; Morsi et al. 2003). This formation represents the uppermost fully marine Eocene Formation of the Fayum sequence. The marine Wadi Thamat Formation, underlying Dur At-Talah Formation, also correlated with the Bartonian zone P14 and may be considered to be coeval with the Gehannam Formation of Fayum.

4.2. CORRELATION

Taking in account the late middle-early late Eocene age range suggested by biostratigraphical data, we considered the potential correlations of Wadi Thamat and Dur At-Talah magnetostratigraphic composite sequences to the GPTS of Gradstein et al. (2004). Several potential correlations are possible and the three most likely ones are detailed below.

A first possible correlation interprets the long normal polarity event of Wadi Thamat Formation and the normal polarity interval of Dur At-Talah Formation as belonging to chron C18n.1n (Figure 2.13). According to this correlation, the Thmed al Qusur and Qrarat al Jifah Members of Wadi Thamat Formation, and Dur At-Talah Formation would have been deposited in a relatively short time, chron C18n.1n having a duration of ~1Ma. This correlation would imply the presence of the single site reversed zone, at the top of Qrarat al Jifah Member, within the normal zone of Chron C18n.1n. No studies of which we are aware suggest an interval of reverse polarity within the normal chron C18n.1n. However, this reverse polarity interval is defined by three samples from the same block therefore its reliability is relatively low. Future fieldwork and detailed sampling are needed to test the presence of this reversal event. According to this correlation, the age of Dur At-Talah fossiliferous strata would range from ~39-38 Ma. This correlation involves quite high minimum sedimentation rate (~24cm.kyr^{-1}) throughout the sedimentary sequence. Dur At-Talah Formation displays a succession of sedimentary succession varying from littoral marine, fluvio-deltaic to fluvial dominated and it is quite difficult to evaluate of the amount of time preserved in the sequence and to assess the duration of its deposition. Further detailed sedimentological studies of the escarpment are needed to enlight this issue.

Under a second hypothesis of correlation, the long normal interval characterizing Dur At-Talah Formation would correlate with Chron C17n (37.7-36.5Ma). Wadi Thamat Formation magnetic sequence would then correlate with Chron C18n or with Chrons C17n.3n-C17n.2n.

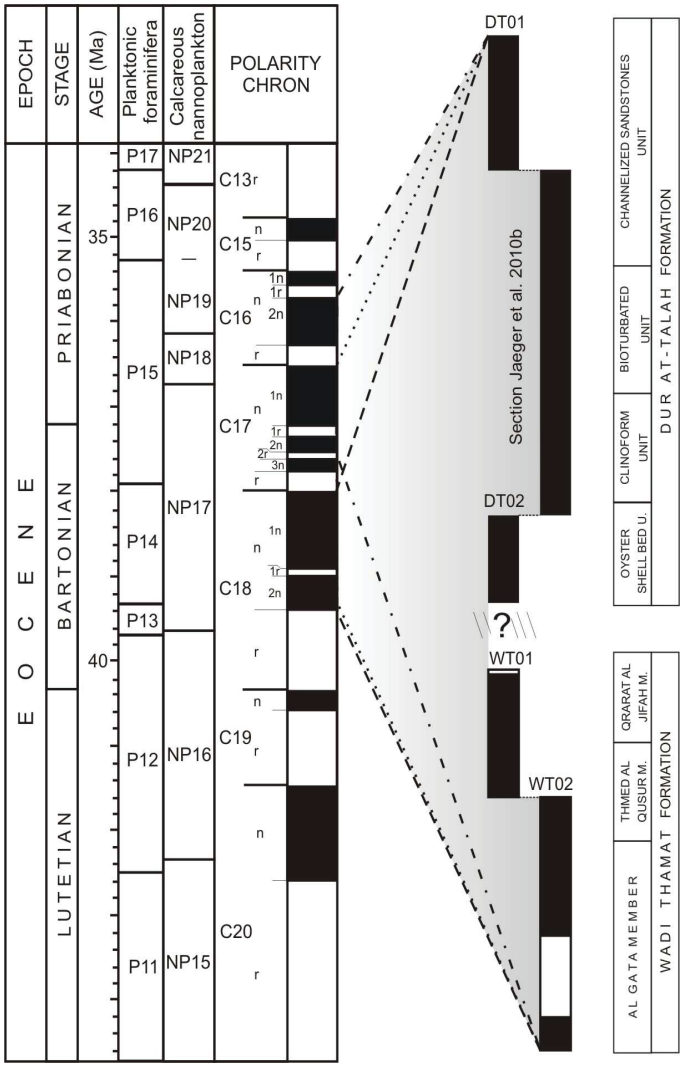


Figure 2.13. Potential correlations of the Dur At-Talah and Wadi Thamat composite sections with geomagnetic-polarity time scale (GPTS) of Gradstein et al. (2004).

Correlation of Wadi Thamat section to C18n suggests that the minimum sedimentation rate for the composite section was 5.6cm/kyr, which is coherent for such nearshore depositional setting (2-10cm/kyr; Meier and Willems, 2003; Gammon and James**,** 2003) while correlation with C17n.3n-C17n.2n provides minimum compacted sedimentation rates accumulation of 20 cm/kyr that seems too high for such sedimentary regime. Moreover, this last hypothesis imply that Wadi Thamat sequence correlates with planktonic foraminiferal biozone P15, which is not supported by the biostratigraphic analysis provided by Rundić et al. (2008).

Assuming correlation of Dur At-Talah sequence to Chron C17n and correlation of Wadi Thamat series to Chron C18n would require that the too short reversal events C17n.1r and C17n.2r were lost in the

stratigraphical gap separating the top of Wadi Thamat sections and the base of Dur At-Talah Formation or that paleomagnetic sampling of Dur At-Talah Formation would have missed these reverse events. The sample spacing through the base of Dur At-Talah Formation is quite dense but small uncomformities could be discerned in the Clinoform Unit and it could be possible that the short duration reversal events within Chron C17n were lost. According to this correlation, an age of about 37.5 to 36.5 Ma is suggested for the fossiliferous levels, corresponding to a latest Bartonian to earliest Priabonian age. This correlation implies that Dur At-Talah fauna is similar in age to that of BQ-2 locality of Fayum, which is believed to correlate with the base of C17n.1n (Seiffert et al. 2008). Although biostratigraphic data from anthropoids seem to indicate that Dur At-Talah fauna is roughly equivalent in age to Bir El Ater and older than BQ-2 (Jaeger et al. 2010a,b), we cannot presently reject this possible alternative of correlation, pending recovery of more meaningful faunal element of comparison from these sites.

Under a third hypothesis of correlation, the Dur At-Talah long normal polarity interval is interpreted as C16n.2n, and Wadi Thamat Formation long normal event matches Chron C17n.1n. The correlation of the Wadi Thamat deposits with Chron C17.1n, corresponding to the standard planktonic foraminiferal zone P15, is again, not in accordance with Wadi Thamat foraminiferal assemblage which seems to range into P14 *Truncorotaloides rohri* biostratigraphic zone (Rundić et al. 2008). Moreover, this second correlation, implying that marine Wadi Thamat Formation encompassed the Bartonian-Priabonian boundary and was deposited during a relatively low sea level (Haq et al. 1987), is not consistent with stratigraphical sequence data and is regarded as less likely. Foraminiferal and stratigraphical data offer limited support to this latter correlation.

Of the three correlations presented here, we prefer the first two as the last one makes some assumptions that are not well supported. Correlation 1 and 2 indicate a late Bartonian or earliest Priabonian age for the fossiliferous levels of Dur At-Talah Formation, respectively.

5. CONCLUSION

Dur At-Talah escarpment of Central Libya has produced a great collection of Paleogene vertebrate remains including anthropoid and strepsirhine primates, proboscideans, hyracoids, macroscelidids,

hystricognathous rodents, chiropterans and creodonts (Savage and White 1965; Savage 1969, 1971; Wight 1980; Tassy 1981; Court 1995; Jaeger et al. 2010a,b). The main fossiliferous strata at Dur At-Talah are found in the Bioturbated Unit, characterized by a mosaic of coastal facies in mixed tidal/storm dominated environment. Paleomagnetic rock analyses of the Dur At-Talah series and underlying marine Wadi Thamat Formation reveals several likely potential correlations with the geomagnetic polarity time scale. Mammalian biostratigraphic evidences and comparison with biochronological data from the late Eocene quarries of Fayum and Bir El Ater locality of Nementcha Mountains, along with magnetostratigraphic constraints, indicate that Dur At-Talah fossiliferous horizons are likely to be late Bartonian (~39-38Ma) or earliest Priabonian (~37.2-36.5Ma) in age.

The recently recovered collection of anthropoid primates at Dur At-Talah (Jaeger et al. 2010b) appears as the oldest known diverse assemblage of African anthropoids, revealing evidence of high taxonomic diversity among early African anthropoids. The presence of basal anthropoid in India, China, Thailand and Myanmar indicates that Asia has been a major centre of origin and subsequent evolution of anthropoid primates (Beard et al. 1994, 1996, 2004; Kay et al. 1997; Jaeger et al. 1999; Jaeger and Marivaux 2005; Bajpai et al. 2008). The recent discovery of early Eocene Eosimiids in India, considered as one of the earliest branch of anthropoids (Bajpai et al. 2008), might reinforce Asia as an ancestral homeland of anthropoid clade. An Asian anthropoid origin implies a dispersal event from Asia toward Africa during middle Eocene times and the possibility of such a dispersal event is also documented by hystricognathous rodents (Flynn and Cheema 1994; Marivaux et al. 2000; Marivaux and Welcome 2003). The rodent assemblage at Dur At-Talah, recovered from the same fossiliferous levels as the anthropoids, documents a remarkable morphological and taxonomic diversity among early African hystricognathous rodents (Jaeger et al. 2010a).

Actually, the high taxonomic diversity of anthropoids and hystricognathous rodents recorded in the late middle/early late Eocene deposits of North Africa may be the result of one dispersal event from Asia followed by subsequent adaptative radiation in Africa or may either reflect a more recent dispersion of different lineages from Asia, that may have occurred shortly before the end of middle Eocene. In fact, key events of evolutionary history of these African groups must have occurred during middle Eocene, which correspond to a very poorly documented interval of the African fossil record. Future paleontological research in the middle Eocene of Africa should help to illuminate the antiquity and the pattern of African anthropoid and hystricognathous rodent radiation.

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1.3. *GAUDEAMUS LAVOCATI* SP. NOV. (RODENTIA, HYSTRICOGNATHI) FROM THE EARLY OLIGOCENE OF ZALLAH, LIBYA: FIRST AFRICAN CAVIOMORPH?

Naturwissenschaften
DOI 10.1007/s00114-010-0683-x

ORIGINAL PAPER

Gaudeamus lavocati sp. nov. (Rodentia, Hystricognathi) from the early Oligocene of Zallah, Libya: first African caviomorph?

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Received: 21 March 2010 / Revised: 21 May 2010 / Accepted: 22 May 2010
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Abstract A new African species of hystricognathous rodent, *Gaudeamus lavocati* sp. nov., is described herein from the early Oligocene deposits of Zallah locality (Sirt basin, Central Libya). The dental morphology of this species is very close to that of some earliest South American caviomorphs. It allows a reinterpretation of molar crest homologies among earliest caviomorphs, pentalophodonty being confirmed as the plesiomorphic molar condition in Caviomorpha. This morphological resemblance argues for close affinities between *Gaudeamus* and earliest South American hystricognaths. Cladistic analysis supports *Gaudeamus lavocati* sp. nov. as the first known African representative of Caviomorpha, implying that its ancestors were part of the African phiomyid group that crossed the South Atlantic by a direct immigration route. Alternatively, the series of derived dental features of *Gaudeamus* could also be interpreted as evolutionary synchronous convergences of an African hystricognath lineage towards the specialized pattern of some caviomorphs. However, the high level of similarities concerning teeth morphology and enamel microstructure and the similar age of fossiliferous strata on both continents make this interpretation less probable. The phylogenetic position of this taxon is of considerable importance because it represents an enigmatic component of the phiomorph–caviomorph radiation in Africa and appears as a new clue toward the understanding of caviomorph origins.

Keywords Hystricognathi · Phiomorpha · Caviomorpha · Eocene · Africa · South America

Communicated by Robert Reisz.

Electronic supplementary material The online version of this article (doi:10.1007/s00114-010-0683-x) contains supplementary material, which is available to authorized users.

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Published online: 12 June 2010

Introduction

Caviomorpha represents an extremely diversified endemic South American group of Hystricognathi. The oldest known South American caviomorphs have been described from the late Eocene deposits of Peru (Frailey and Campbell 2004). Older South American localities, albeit numerous and fossiliferous, never documented any fossil rodents. The early phase of the rodent immigration and radiation in South America is therefore not well-understood. This absence of fossil rodents in sites older than the Peruvian locality and the isolation of South America during most of the Cenozoic have raised critical issues regarding the timing of arrival of rodents and their routes of colonization.

The current preferred hypothesis favors an African origin for caviomorphs from phiomorph Hystricognathi and suggests that their ancestors rafted or migrated from Africa to South America during Eocene times. Molecular and fossil analyses clearly indicate that the caviomorph South American lineages are closely related to African forms (e.g., Lavocat 1969; Parent 1980; Wyss et al. 1993; Martin 1994; Huchon and Douzery 2001; Poux et al. 2006). They both seem to share a common Asian hystricognathous ancestor (Marivaux et al. 2002).

The phiomorphs represent an adaptive radiation of hystricognathous rodents that occurred during the Paleogene in Africa (Wood 1968; Jaeger et al. 1985; Hartenberger 1985; Tabuce et al. 2001), of which the extant Thryonomyidae (cane rat), Petromuridae (dassie rat), and Bathyergidae (mole rat) are the descendants.

The Jebel El Qatrani Formation in the Fayum depression, Egypt, has yielded the richest collection of late Paleogene phiomorphs (Osborn 1908; Schlosser 1911; Wood 1968; Holroyd 1994; Sallam et al. 2009). Late Eocene and early Oligocene hystricognathous fossils have also been reported from Libya (Fejfar 1987; Jaeger et al. 2010), from Oman (Thomas et al. 1989) and from Kenya (Ducrocq et al. 2010). However, the fossil record has not allowed clear identification of an African representative of Hystricognathi as the ancestor of the Caviomorpha.

Here we describe a new species of the hystricognathous rodent genus *Gaudeamus* from a newly discovered locality from the lower Oligocene of Zallah (Libya). This species displays a tetralophodont and taeniodont dental pattern which is nearly identical in its morphology to some of the earliest known South American caviomorphs recently described from the ?Eocene of Santa Rosa, Peru (Frailey and Campbell 2004). This discovery bears implications on molar crest homologies and allows discussing the nature of the primitive molar pattern of the caviomorph ancestors. It also brings new insights to the phylogenetic and paleobiogeographic debates on the early history of caviomorphs.

Systematic paleontology

Order Rodentia Bowdich 1821

Suborder Ctenohystrica Huchon, Catzelfis, and Douzery 2000

Infraorder Hystricognathi Tullberg 1899

Genus *Gaudeamus* Wood 1968

Type species *Gaudeamus aegyptius* Wood 1968

Gaudeamus lavocati sp. nov.

Material

Holotype: ZR5-69, right lower jaw fragment with M_1–M_3 (Fig. 1a)

Referred material: 159 isolated teeth (see Online Resource 1 for a complete list of specimens referred to *G. lavocati*).

The material is temporarily deposited in the collections of iPHEP, University of Poitiers, and it will be deposited after publication in the Collections of El Fateh University in Tripoli (Libya).

Measurements: see Table S1 in the Online Resource 1.

Type locality

G. lavocati derives from Zallah 5 locality, a newly discovered micro-mammal locality in the Oligocene deltaic-continental deposits of Sirt basin, located near the oasis of Zallah (Central Libya). Several large and small mammal localities have been mentioned previously (Arnoult-Saget and Magnier 1961; Arambourg 1963; Fejfar 1987) from this area. Biostratigraphic evidences suggest an early Oligocene age for Zallah deposits.

Derivatio nominis

In honor of the late R. Lavocat who suggested and supported the idea of an African origin of South American caviomorph rodents.

Diagnosis

Species of *Gaudeamus* (M_2 of the holotype=2.19× 2.14 mm) of larger size than *G. aegyptius* Wood 1968. It differs from the latter by its tetralophodont molar pattern (Fig. 1). Lower molars with a mesolophid which delimits an extra basin on the posterior side of the metaconid. Lack of connection between the hypolophid and the hypoconid. Mesoloph backwardly directed and connected to the posteroloph on upper molars. Development of a labial (lingual) wall in upper (lower) worn molars. Marked unilateral hypsodonty on upper cheek teeth. Three-rooted molars, except for a two-rooted M^3. dP_4 elongated,

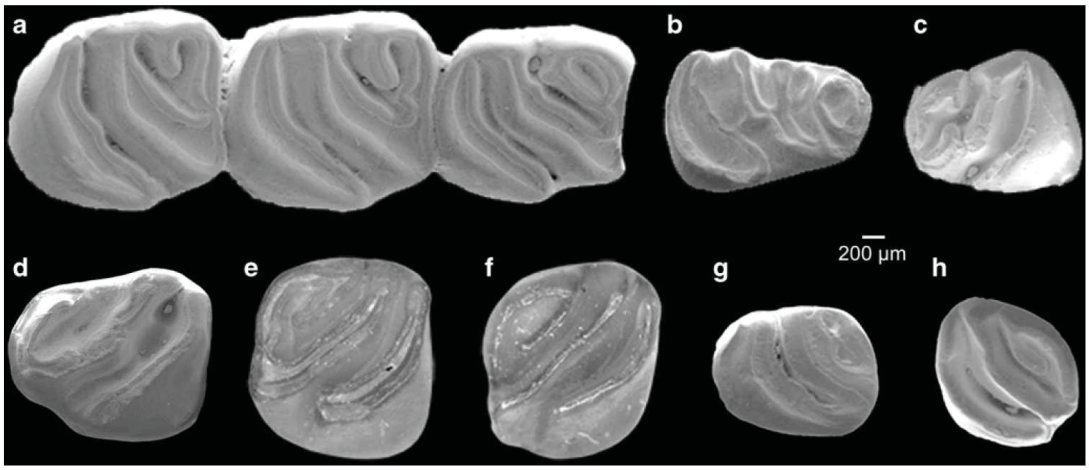


Fig. 1 Cheek teeth of *Gaudeamus lavocati* sp. nov. **a** ZR5-69, holotype, *right lower* jaw with M_1–M_3. **b** Z5R-133, *right* dP_4. **c** Z5R-136, *left* P_4. **d** Z5R-121, *right* M^3. **e** Z5R-90, *right* M^2. **f** Z5R-70, *right* M^1. **g** Z5R-139, *left* dP^4. **h** Z5R-144, *left* P^4

pentalophodont, molariform, differing from that of *G. aegyptius* by more oblique lophids.

G. lavocati is slightly larger in size than species of *Eoincamys* and differs from them in some respects: less oblique molar crests, absence of connection between the mesoloph and the anterior arm of the hypocone on upper molars, connection of the mesolophid with the metalophulid I rather than with the ectolophid and lack of hypoconid/hypolophid connection on lower molars, and dP_4 with more oblique lophids.

(For detailed description of *G. lavocati* cheek teeth, see Online Resource 1)

Comparison

Occlusal dental pattern

The genus *Gaudeamus* was initially erected by A.E. Wood (1968) from the lower Oligocene of Fayum (Egypt). By its semi-hypsodonty, its great differentiation of transverse crests and its simplified occlusal molar pattern, *Gaudeamus* was considered as an evolutionarily advanced species compared to other Oligocene phiomyids (Wood 1968; Holroyd 1994).

G. aegyptius and *G. lavocati* exhibit a common pattern comprising three principal lophs in the molars: an anteroloph, a transverse loph connecting the paracone to the hypocone, and a posteroloph on upper molars (a metalophulid I, a continuous loph connecting the protoconid to the entoconid, and a posterolophid on lowers). In both species, the posteroloph runs from the hypocone to the metacone and the metaloph is fused with the posteroloph. However, *G. lavocati* displays, in comparison to *G. aegyptius*, a more lophodont pattern with a greater differentiation of transverse crests. The obliquity of the crests in its dP_4 is more pronounced than in *G. aegyptius* (Fig. 2d, i). But the main difference between the two taxa lies in the presence of a supplementary fourth crest in *G. lavocati* molars. From the medial part of the labial margin of upper molars, a short crest extends distolingually toward the middle of the posteroloph. This crest has been previously described as a neoloph by Holroyd (1994) who mentioned a yet undescribed new tetralophodont species of *Gaudeamus* from the Fayum L-41 quarry (Holroyd 1994; Sallam et al. 2009). This crest is interpreted here as a reduced mesoloph because of its homology in crest position and on the basis of the presence in *G. aegyptius* of a minute mesostyle from which the mesoloph is likely to develop. It corresponds to a modification of the ancestral pentalophodont structure otherwise present in phiomyid rodents rather than to a new structure.

When considering the earliest known South American members of caviomorphs, it appears that the dental morphology of *G. lavocati* sp. nov. is very close to that of *Eoincamys* from the ?Eocene Santa Rosa fauna of Peru (Fig. 3c–h). Both display moderately high-crowned and unilaterally hypsodont cheek teeth and a taeniodont tetralophodont molar pattern. Frailey and Campbell (2004) nevertheless interpreted the third crest of *Eoincamys* molar as a metaloph/metalophid. Their identification implies a forward displacement of the metacone and raises questions concerning the nature of the cusp (if it is not a metacone)

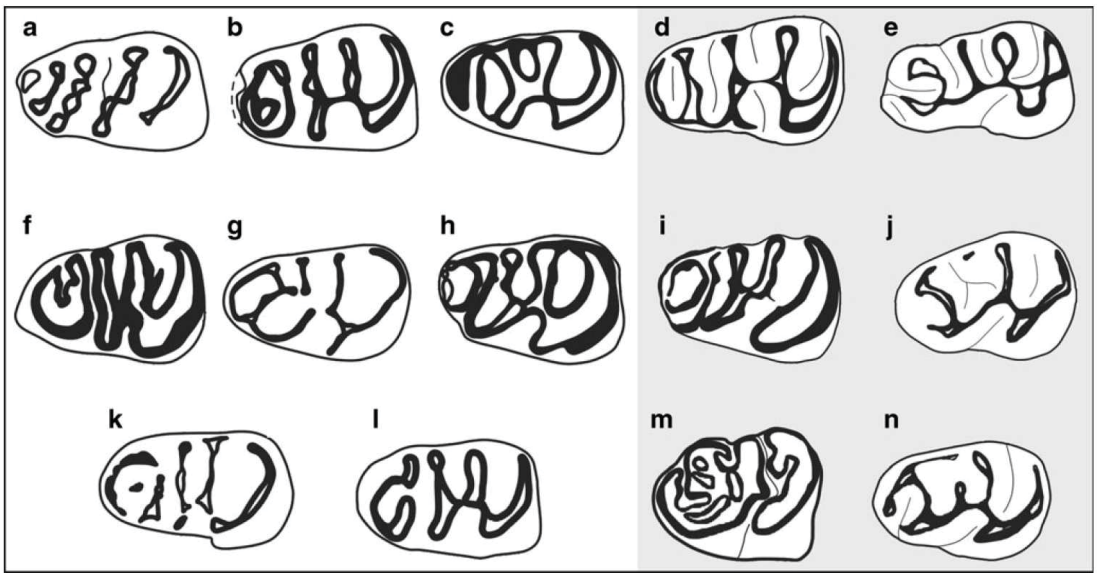


Fig. 2 Sketches of *lower* deciduous premolars patterns of Santa Rosa rodents (*white area*) and Old World hystricognathous rodents (*light gray area*). Not to scale. **a** *Eobranisamys romeropittmanae*, LACM 143352. **b** *Eobranisamys riverai*, LACM 143371 (reversed drawing). **c** *Eoespina woodi*, LACM 143405 (*reversed drawing*). **d** *Gaudeamus aegyptius*, YPM 18024 (*reversed drawing*; Wood 1968). **e** *Phiomys andrewsi*, AMNH 13271 (Wood 1968). **f** *Eobranisamys riverai*, LACM 143369. **g** *Eosallamys paulacoutoi*, LACM 143420 (*reversed drawing*). **h** *Eosallamys palacoutoi*, LACM 143451. **i** *Gaudeamus lavocati*, Z5R-139 (*reversed drawing*). **j** *Protophiomys durattalhahensis*, DT-2-007 (Jaeger et al. 2010). **k** *Eosallamys simpsoni*, LACM 143452. **l** *Eoespina woodi*, LACM 143391 (*reversed drawing*). **m** *Hystrix depereti*, PR-147 (Sen 2001). **n** *Phiomys hammudai*, DT-1-011 (Jaeger et al. 2010). After Frailey and Campbell 2004, completed

lying at the labial extremity of the posteroloph. We instead interpret this third loph as homologous to the mesoloph. From this point of view, *Eoincamys* dental pattern appears to be very close to that of *G. lavocati* but less derived. The mesoloph is less oblique, its lingual tip tends to join the anterior arm of a more distinct hypocone instead of being confluent with the posteroloph (Fig. 3e–h). Remnants of the former ectolophid are still distinguishable in *Eoincamys*. A raised portion in the posterior sinusid tends to connect the hypoconid to the hypolophid in advanced stage of wear. Deciduous lower premolars of Santa Rosa rodent taxa display slight variation of a pentalophodont theme very similar to that of *Gaudeamus* (Fig. 2). These taxa share in common an occlusal pattern composed of an anterolophid, a metalophulid II, a mesolophid, a hypolophid, and a posterolophid. Differences between some Santa Rosan genera and *Gaudeamus* in the lower deciduous premolar are small and consist mainly of different degrees in inclination of the crests.

The comparison of the newly discovered primitive forms of caviomorph teeth from South America which include pentalophodont and tetralophodont forms, to those of the African phiomorphs, provides valuable information on cheek teeth crest homology (Fig. 3). Phiomorphs and caviomorphs are widely recognized as related taxa (e.g., Luckett and Hartenberger 1993; Catzeflis et al. 1995; Nedbal et al. 1996; Huchon and Douzery 2001; Marivaux et al. 2002) but terminology used to describe their cheek teeth has always differed among authors in important aspects. These problems of dental structure recognition in earliest hystricognathous rodents have brought on confusion regarding their phylogenetic affinities (e.g., Wood and Patterson 1959; Hoffstetter and Lavocat 1970; Patterson and Wood 1982). The central point of the differing interpretations in caviomorph dental morphology has been the nature of the third and fourth lophs of the tetralophodont and pentalophodont forms (variously metaloph, mesoloph, or neoloph depending on the authors). Hoffstetter and Lavocat (1970) interpreted the fourth loph of pentalophodont caviomorphs (*Branisamys*) as a rudimentary metaloph on the anterior face of the posteroloph. By contrast, Patterson and Wood (1982) considered *Branisamys* molar pattern as a basic tetralophodont form with an additional small loph (a neoloph) that projects from the posteroloph. The loph described as a mesoloph by Hoffstetter and Lavocat (1970) is considered by them as a metaloph. The key to identify the

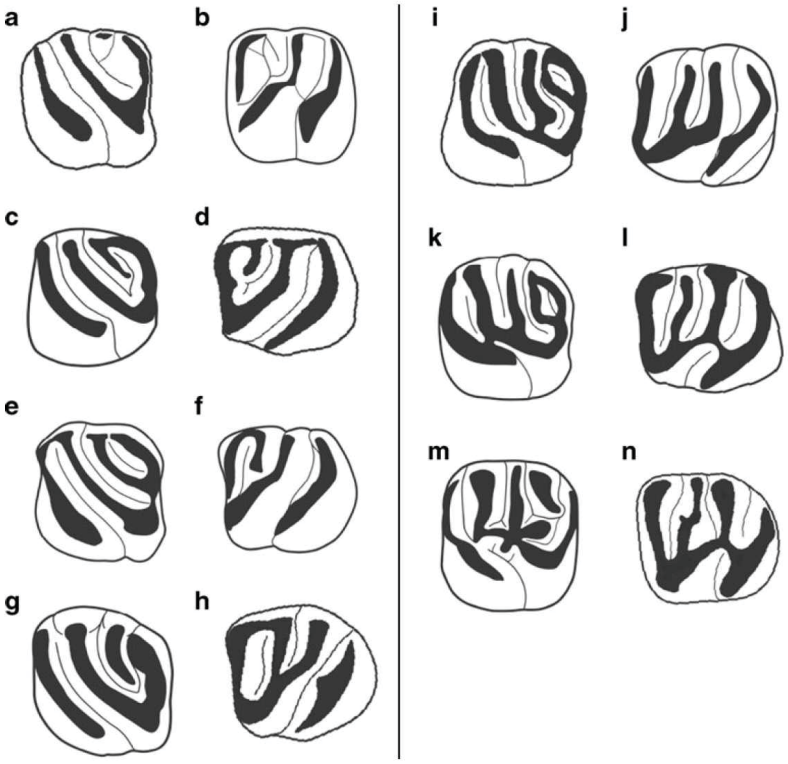


Fig. 3 Comparative *upper* (*left*) and *lower* (*right*) molar dental pattern of some Santa Rosan genera and some Eocene/ Oligocene African Hystricognathi. **a** *Gaudeamus aegyptius*, YPM 18044, *right* M^2 (*reversed drawing*). **b** CM 26920, *left* M_2 (Wood 1968). **c** *Gaudeamus lavocati*, Z5R-98, *right* M^2. **d** ZR5-69, *right* M_2 (*reversed drawings*). **e** *Eoincamys pascuali*, 143319, *left* M^x. **f** 143306, *left* M_x (Frailey and Campbell 2004). **g** *Eoincamys ameghinoi*, 143339, *left* M^x. **h** 149435, left M_x (Frailey and Campbell 2004). **i** *Eobranisamys romeropittmanae*, 143362, *right* M^x (*reversed drawing*). **j** 143346, *left* M_x (Frailey and Campbell 2004). **k** *Eosallamys simpsoni*, 143374, *left* M^x. **l** 143276, *left* M_x (Frailey and Campbell 2004). **m** *Phiomys hammudai*, DT-1-003, *right* M^1. **n** DT-1-006, *right* M_2 (*reversed drawing*; Jaeger et al. 2010)

homology of these dental structures seems to lie in the set of morphological stages displayed by earliest caviomorphs. The pentalophodont pattern, representing the plesiomorphic molar condition among Eocene Hystricognathi (Hoffstetter and Lavocat 1970; Bryant and McKenna 1995; Marivaux et al. 2002, 2004), shows an anteroloph, a protoloph, a mesoloph, a metaloph, and a posteroloph (Fig. 4). It is clearly expressed in *Phiomys andrewsi* or *Phiomys hammudai* (Fig. 3m). In caviomorph pentalophodont forms (*Eobranisamys*, *Branisamys*), the metaloph displays a derived state (Marivaux et al. 2004) being short and directed back to join the posteroloph (Fig. 3k, i). The metaloph, as in their close African relatives, show tendencies to fuse with the posteroloph. The simplification of the basic pentalophodont molar condition leads to a tetralophodont pattern by the loss of the metaloph by fusion with the posteroloph (Fig. 3e, g). The metaloph and the mesoloph are progressively confined to the postero-labial corner of the tooth and removed as the degree of unilateral hypsodonty increases. As demonstrated by Jaeger (1989), unilateral hypsodonty developed in caviomorph taxa results in decreasing the size of the postero-labial corner of the tooth as wear proceeds. The

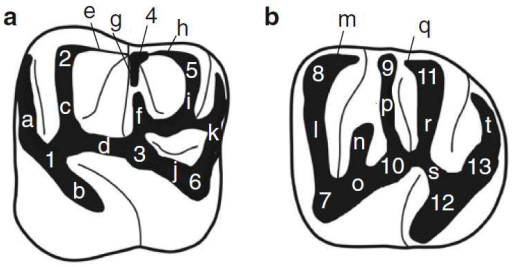


Fig. 4 Occlusal dental nomenclature (after Marivaux et al. 2004). **a** *Upper* molar: *1* protocone, *2* paracone, *3* metaconule, *4* mesostyle, *5* metacone, *6* hypocone, *a* anteroloph, *b* neo-endoloph, *c* protoloph, *d* mure, *e* posterior arm of paracone, *f* mesolophule, *g* mesoloph, *h* anterior arm of metacone, *i* metaloph, *j* anterior arm of hypocone, *k* posteroloph. **b** *Lower* molar: *7* protoconid, *8* metaconid, *9* mesostylid, *10* mesoconid, *11* entoconid, *12* hypoconid, *13* hypoconulid, *l* metalophulid I, *m* posterior arm of metaconid, *n* posterior arm of protoconid, *o* ectolophid, *p* mesolophid, *q* anterior arm of entoconid, *r* hypolophid, *s* anterior arm of hypoconid, *t* postelorophid

lingual features appear to shift toward the labial side of the tooth and are gradually wiped out. In *G. aegyptius* (Fig. 3a), and also in other African taxa like *Paraulacodus* or *Neosciuromys*, the loss of both metaloph and mesoloph finally leads to a trilophodont state.

These morphological stages, related to different degree of semi-hypsodonty, allows identification of the homology of dental crest in earliest caviomorphs, shedding new lights on crest homologies among hystricognath rodents.

Incisor enamel microstructure

Both lower and upper incisors of *G. lavocati* display double layered enamel with multiserial Hunter–Schreger bands (HSB) and a clearly distinct portio externa. This multiserial enamel is characterized by a slightly angular and anastomosing interprismatic matrix (IPM; see Online Resource 2).

The incisor enamel microstructure of *G. lavocati* is typical for hystricognath rodents (Martin 1993). In addition, *G. lavocati* displays a primitive subtype of multiserial HSB (defined by Martin 2004), with an IPM running at a slight angle to the prism long axes and slightly anastomosing between the prisms in the cross sections in both upper and lower incisors. Such a condition is congruent with the oldest enamel microstructures described for the Paleogene South American Caviomorpha. The caviomorph incisors discovered in the Late Eocene (or earliest Oligocene ?) locality of Santa Rosa indeed display an important diversity, with three subtypes of multiserial HSB (Martin 2004) including the primitive condition observed in *G. lavocati*. The locality of Santa Rosa delivered the two known species of the genus *Eoincamys*, but up to now the incisor material from there has not been attributed to taxa, therefore no direct comparison between the enamel microstructures of *G. lavocati* and *Eoincamys* is possible.

Phylogenetic analysis

The new information presented here enables a fuller test of the hypothesis of close relationship between caviomorphs and phiomorphs and an exploration of the affinities of *Gaudeamus*. A cladistic analysis including 65 dental characters and 37 taxa has been performed to assess these hypotheses (see Online Resource 1 for a complete character list and data matrix for all included taxa). Outgroups selected to study relationships within Hystricognathi are extinct members of the family Ctenodactylidae, represented by *Birbalomys woodi*, and of the Yuomyidae, represented by *Yuomys cavioides*. Ingroup taxa include 35 species which represent the majority of extinct Eocene–Oligocene hystricognathous rodents and the extant taxon *Thryonomys*. We mostly focused on the African Eocene–Oligocene phiomorphs (16 species, see Online Resource 1 for a complete list of the sampled species) and the Eocene–Oligocene South American caviomorphs (ten species). Earliest Asiatic members of Hystricognathi, the Baluchimyines, have also been included. In order to investigate the phylogenetic relationship recently assumed between *Gaudeamus* and Hystricidae (Sallam et al. 2009), three Old World porcupines (*Hystrix primigenia*, *Hystrix depereti*, and *Hystrix cristata*) were added to our analysis. The analysis was performed with PAUP (v.4.0b10, Swofford 1998) using heuristic search methods (1,000 replications with random stepwise addition and a randomized input order of taxa). Parsimony analyses result in one most parsimonious tree of 249 steps (Fig. 5; CI=0.36; RI=0.68).

The most significant aspect of the analysis is the nesting of *Gaudeamus* within the clade that groups all the oldest known South American caviomorphs. Caviomorpha clade including *Gaudeamus* is supported by the following unambiguous synapomorphies: crested pattern, cusps indistinct or absent (ch. 1), high-crowned cheek teeth (ch. 3), the absence of the mesolophule on upper molars (ch. 33), the absence or indistinctness of the anteroconid on lower deciduous premolars (ch. 37), the indistinctness of the hypoconulid on lower deciduous premolars (ch. 44), the absence of the hypoconulid on lower premolars (ch. 53), and the metaloph fused with the posteroloph on upper premolars (ch. 65; see Fig. S1 in the Online Resource 1).

The Caviomorpha present two basal divergent clades. The first clade is characterized by a lack or incomplete taeniodont pattern (ch. 2) and includes most of the Paleogene South American taxa described as primitive Octodontoidea. The second clade is characterized by fully taeniodont molars and includes the Paleogene South American taxa described as primitive Cavioidea plus the genera *Sallamys* and *Platypittamys*.

The Hystricidae constitute the sister taxon to the clade that clusters *Gaudeamus* and the caviomorphs. The immediately more inclusive clade shows the African species *P. andrewsi* and *P. hammudai* as the sister taxa to the clade Hystricidae + Caviomorpha The immediate sister taxon is a clade consisting of a Phiomorpha subset (*Paraulacodus*, *Paraphiomys*, *Metaphiomys*, *Phiomys paraphiomyoides*) including the extant *Thryonomys*. The clade Phiomorpha defined by Sallam et al. (2009) appears to be therefore paraphyletic in our analysis. The remaining taxa traditionally attributed to Phiomorpha are variously nested along with baluchimyines at the base of the Hystricognathi.

The Hystricidae are supported as the sister taxon of the Caviomorpha by our analysis. This result is not in agreement with the chronobiogeographically and backbone constrained phylogenetic analyses which support *Gaudeamus* as a sister taxon of Hystricidae, outside the Caviomorpha (Sallam et al.

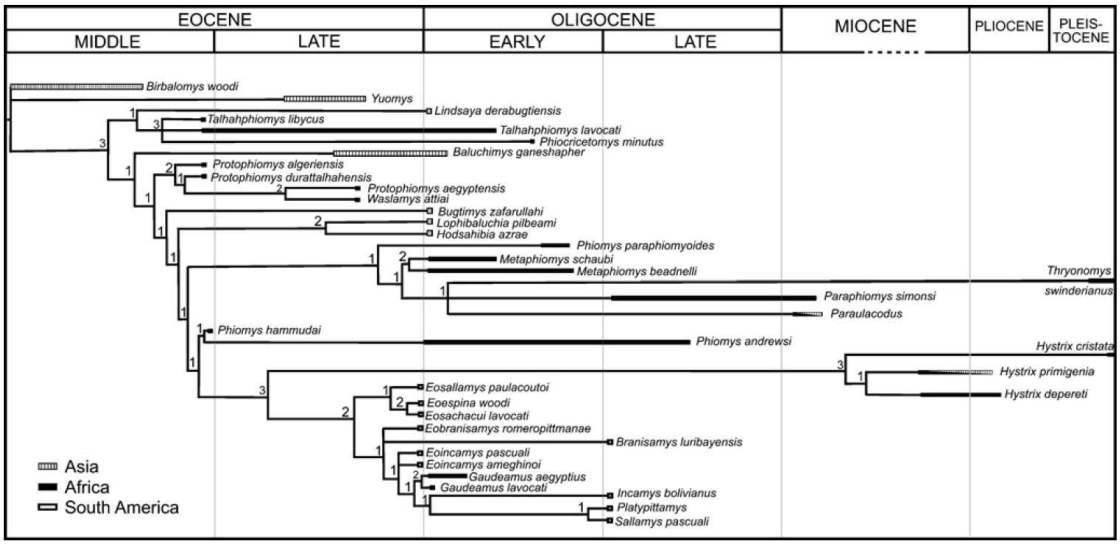


Fig. 5 Most parsimonious tree showing the temporal range and geographical extent of the 37 hystricognath taxa included in this study. Bremer support values (Bremer 1988), calculated using TNT (Goloboff et al. 2003), are labeled at each node

2009; it is noteworthy however that these authors found both *Gaudeamus* and Hystricidae nested among Caviomorpha in various locations in their unconstrained morphological analysis). The Hystricidae are generally classified as a divergent and basal hystricognath lineage (Adkins et al. 2001, 2003; Huchon et al. 1999; Blanga-Kanfi et al. 2009); however, parasitology (Hugot 2002) and a subset of a molecular-based study (Huchon and Douzery 2001) support them as the sister taxa of Caviomorpha. Up to now, hystricid fossils are actually only recognized since middle Miocene (Flynn et al. 1998) and molecular studies project a ghost lineage originating in late Eocene (Huchon and Douzery 2001). Actually, the lack of Paleogene hystricids likely clouds their phylogenetic relationships among Hystricognathi. Concerning the geographic origin of *Hystrix*, their earliest occurrences are recorded from Central Europe and Spain (Van Weers and Montoya 1996). However, paleontologists hypothesized that hystricids have an Asian or Indian origin due to their extant diversity in these regions (Hussain et al. 1978; Winkler 1994).

Discussion

Tetralophodont and trilophodont molars in hystricognathous rodents correspond to derived structures evolved from an ancestral basic pentalophodont pattern, preserved in some Eocene and Oligocene African Phiomorpha (Hoffstetter and Lavocat 1970; Bryant and McKenna 1995; Marivaux et al. 2002), following two distinct pathways. On the first hand, the tetralophodont pattern is achieved in some Phiomorpha (e.g., *Metaphiomys*, *Paraphiomys*) by the reduction of the mesolophule (ch. 33 state 1) combined with the absence of the mesoloph (ch. 31 state 0). On the other hand, the tetralophodont pattern in South American caviomorphs is obtained with the merging of the metaloph and the posteroloph (ch. 34, state 3).

G. lavocati sp. nov. is the only African taxon displaying the latter tetralophodont condition currently known. *Gaudeamus* sp. nov. from Quarry L-41 (Fayum depression, Egypt) may also present such a pattern (Sallam et al. 2009) but is not described yet, while *G. aegyptius* displays a trilophodont pattern associated with the loss of mesoloph/id.

Gaudeamus was classically referred as a phiomorph and its type species, *G. aegyptius*, was grouped into the Phiomyidae family (Wood 1968) or into the Thryonomyidae family (Lavocat 1978). Phylogenetic analyses of dental and enamel microstructure characters found *Gaudeamus* to be nested among Caviomorpha (this study and unconstrained analysis in Sallam et al. 2009). This genus exhibits features present in the South American taxa and appears to be more closely related to these latter than to the African Phiomyidae. The nesting of this African taxon within the caviomorphs raises problems concerning its taxonomic assignment. At present, we prefer not to allocate it to a precise family, pending the revision of Phiomyidae which constitute a paraphyletic group.

According to molecular data, the arrival of caviomorphs in South America is believed to have taken place during the middle-late Eocene (Poux et al. 2006). The migration

scheme to explain the current distributional pattern of hystricognathous rodents has been extensively discussed and various paleobiogeographic scenarii have been proposed for the caviomorph origin. A trans-Atlantic route is, until now, the prevailing hypothesis despite the fact that South America and Africa were already separated by the Atlantic Ocean barrier. Colonization by rafting would have been aided by marine paleocurrents, paleowinds, or "stepping stone" islands (e.g., Wyss et al. 1993; Houle 1999). Secondly, a migration route via Antarctica, which was connected to South America until late Eocene (Barker et al. 1991), has been pointed out (e.g., Houle 1999). This southern migration route seems however unlikely because of major water barriers separating Antarctica and Australia since the Early Eocene (Woodburne and Zinsmeister 1984) and because no relevant rodent remains have ever been reported from these continents. The alternative possible migration route, via the Bering Strait and North America (e.g., Hussain et al. 1978), is disregarded because of the obvious lack of hystricognath fossils in North America.

The fact that Paleogene South American and African hystricognathous rodents share a common Asian hystricognathous ancestor (Flynn et al. 1986; Bryant and McKenna 1995; Marivaux et al. 2002) has raised the question of whether caviomorphs are descended from an Asian group of hystricognaths and has opened the possibility of a dispersal of hystricognathous rodents to South America from Asia (Hussain et al. 1978; Marivaux et al. 2002). However, data of multiple sources support the hypothesis of a Paleogene African origin of caviomorphs (Lavocat 1969; Parent 1980; Wyss et al. 1993; Martin 1994; Houle 1999; Huchon and Douzery 2001; Poux et al. 2006).

Considering this hypothesis, it is noteworthy that in our analysis, some African Phiomorphs constitute the immediate outgroup to the Hystricidae + Caviomorpha clade. The dental morphology exhibited by some *Phiomys* species (*P. hammudai* and *P. andrewsi*) would identify them as good African candidates to be stem representatives of the *Gaudeamus* lineage and all other primitive caviomorphs. The earliest caviomorph might have arose on the African continent before Oligocene times and *Gaudeamus* ancestors may belong to the African group that migrated to South America during middle-late Eocene. Although an African origin for caviomorphs has been advocated in the past, ancestor group is lacking from the fossil record of that continent. Additional new fossil findings in middle and late Eocene deposits of African caviomorphs are required to test our hypothesis concerning the early paleobiogeographical history of that group. The high morphological similarities in dental characters and incisor enamel microstructure of *Gaudeamus* and some contemporaneous caviomorph taxa may indicate that the beginning of caviomorphs radiation occurred in Africa within the time period of Phiomyid radiation. This reinforces the hypothesis of a direct migration route between Africa and South America during Eocene.

However, there are still no evidences of migration corridors between Africa toward South America and the dental pattern of *Gaudeamus* could also illustrate the result of a parallel evolution of an African phiomorph lineage towards the specialized pattern of some caviomorphs. Evolution of *Gaudeamus* parallel to tetralophodont Caviomorpha would constitute an exceptional case of synchronized convergence, given the very close similarity between *Eoincamys pascuali* and *G. lavocati*. Such a convergent case of dental morphology has already been documented among Murid rodents, with the great similarity observed between extant *Deomyinae* and *Murinae* (e.g., Chevret et al. 1993; Jansa and Weskler 2004), but in this last case there is no evidence of synchronized convergence.

The latter hypothesis, also based on the implications of our cladistic analysis, of a South American caviomorph migration into Africa is hardly likely considering that the possibility of migration were rather limited.

At present, dental and enamel microstructure morphologies invariably indicate phylogenetic affinities between *Gaudeamus* and the earliest caviomorphs (this study and unconstrained analysis of Sallam et al. 2009) and *Gaudeamus* can be considered, tentatively, as an African caviomorph. New fossils from slightly older localities, both in Africa and South America, may shed more light on the exact affinities of *Gaudeamus* within Paleogene Hystricognathi.

Acknowledgments The authors would like to thank L. Marivaux and B. Marandat who participated to the field work in Zallah and IBrahim Lameen of Umm Al Ghozlan Logistic Company who facilitated the screening operation, giving us access to his farm and to unrestricted amount of water. We are extremely grateful to L. Marivaux for his constructive comments and fruitful discussions. We finally would like to thank Sabine Riffaut for the drawings of *G. lavocati* cheek teeth. This work has been completed in the frame of the cooperative program between University of Poitiers and University El Fateh, Tripoli, Libya. It was supported by the University of Poitiers, the C.N.R.S. "Eclipse II" program and the ANR-05-BLAN-0235.

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ELECTRONIC SUPPLEMENTARY MATERIAL 1

FOR “*GAUDEAMUS LAVOCATI* SP. NOV. (RODENTIA, HYSTRICOGNATHI) FROM THE LOWER OLIGOCENE OF ZALLAH, LIBYA: FIRST AFRICAN CAVIOMORPH?”

1. LIST OF SPECIMENS REFERRED TO GAUDEAMUS LAVOCATI

Z5R-1, left M_1; Z5R-2, left M_1; Z5R-3, left M_1; Z5R-4, left M_1; Z5R-5, left M_1; Z5R-6, left M_1; Z5R-7, left M_1; Z5R-8, left M_1; Z5R-9, left M_1; Z5R-10, left M_1; Z5R-11, left M_1; Z5R-12, left M_1; Z5R-13, left M_1; Z5R-14, left M_1; Z5R-15, left M_1; Z5R-16, right M_1; Z5R-17, right M_1; Z5R-18, right M_1; Z5R-19, right M_1; Z5R-20, right M_1; Z5R-21, right M_1; Z5R-22, right M_1; Z5R-23, right M_1; Z5R-24, right M_1; Z5R-25, right M_1; Z5R-26, right M_1; Z5R-27, right M_1; Z5R-28, right M_1; Z5R-29, right M_1; Z5R-30; left M_2; Z5R-31, left M_2; Z5R-32, left M_2; Z5R-33, left M_2; Z5R-34, left M_2; Z5R-35, left M_2; Z5R-36, left M_2; Z5R-37, left M_2; Z5R-38, right M_2; Z5R-39, right M_2; Z5R-40, right M_2; Z5R-41, right M_2; Z5R-42, right M_2; Z5R-43, right M_2; Z5R-44, right M_2; Z5R-45, right M_2; Z5R-46, right M_2; Z5R-47, left M_3; Z5R-48, left M_3; Z5R-49, left M_3; Z5R-50, left M_3; Z5R-51, left M_3; Z5R-52, left M_3; Z5R-53, left M_3; Z5R-54, left M_3; Z5R-55, left M_3; Z5R-56, left M_3; Z5R-57, left M_3; Z5R-58, right M_3; Z5R-59, right M_3; Z5R-60, right M_3; Z5R-61, right M_3; Z5R-62, right M_3; Z5R-63, right M_3; Z5R-64, right M_3; Z5R-65, right M_3; Z5R-66, right M_3; Z5R-67, right M_3; Z5R-68, right M_3; Z5R-69, right lower jaw with M_1-M_3; Z5R-70, right M^1; Z5R-71, right M^1; Z5R-72, right M^1; Z5R-73, right M^1; Z5R-74, right M^1; Z5R-75, right M^1; Z5R-76, right M^1; Z5R-77, left M^1; Z5R-78, left M^1; Z5R-79, left M^1; Z5R-80, left M^1; Z5R-81, left M^1; Z5R-82, left M1; Z5R-83, left M1; Z5R-84, left M1; Z5R-85, left M1; Z5R-86, left M1; Z5R-87, left M^1; Z5R-88, left M^1; Z5R-89, left M^1; Z5R-90, left M^1;,Z5R-90, right M^2; Z5R-91, right M^2; Z5R-92, right M^2; Z5R-93, right M^2; Z5R-94, right M^2; Z5R-95, right M^2; Z5R-96, right M^2; Z5R-97, right M^2; Z5R-98, right M^2; Z5R-99, right M^2; Z5R-100, right M^2; Z5R-101, right M^2; Z5R-102, right M^2; Z5R-103, right M^2; Z5R-104, left M^2; Z5R-105, left M^2; Z5R-106, left M^2; Z5R-107, left M^2; Z5R-108, left M^2; Z5R-109, left M^2; Z5R-110, left M^2; Z5R-111, left M^2; Z5R-112, left M^2; Z5R-113, left M^2; Z5R-114, left M^2; Z5R-115, left M^2; Z5R-116, left M^2; Z5R-117, left M^2; Z5R-118, left M^2; Z5R-119, left M^2; Z5R-120, left M^2; Z5R-121, right M^3; Z5R-122, right M^3; Z5R-123, right M^3; Z5R-124, right M^3; Z5R-125, right M^3; Z5R-126, right M^3; Z5R-127, right M^3; Z5R-128, left M^3; Z5R-129, left M^3; Z5R-130, left M^3; Z5R-131, left M^3; Z5R-132, left dP_4; Z5R-133, right dP_4; Z5R-134, right dP_4; Z5R-135, right dP_4; Z5R-136, left P_4; Z5R-137, right P_4; Z5R-138, left P_4; Z5R-139, left dP^4; Z5R-140, left dP^4; Z5R-141, left P^4; Z5R-142, left P^4; Z5R-143, right P^4; Z5R-144, left P^4; Z5R-145, left P^4; Z5R-146, left P^4; Z5R-147, right P^4; Z5R-148, left P^4; Z5R-149, left P^4; Z5R-150, left P^4; Z5R-151, right P^4; Z5R-152, left P^4; Z5R-153, left P^4; Z5R-154, right P^4; Z5R-155, right P^4; Z5R-156, right P^4; MA 310, left I_1; MA 311, left I_1; MA 312, left I^1.

2. TABLE S1

MEASUREMENT OF CHEEK TEETH OF *GAUDEAMUS LAVOCATI*

	N	O.R. (mm)	X (mm)	S.D.	c.v.
Length					
M_1	29	1.74-2.18	2.05	0.1	4.88
M_2	15	2.06-2.50	2.23	0.11	4.93
M_3	15	1.36-2.08	1.8	0.18	10
P_4	4	2.24-2.43	2.31	0.09	3.90
dP_4	3	1.91-2.02	1.98	0.06	3.03
M^1	15	1.76-2.02	1.91	0.08	4.19
M^2	18	1.96-2.38	2.13	0.11	5.16
M^3	7	1.51-1.87	1.74	0.15	8.62
P^4	8	1.44-1.62	1.53	0.06	3.92
dP^4	2	1.41-1.48	1.44	0.05	3.47
Width					
M_1	29	1.70-2.32	2.04	0.13	6.37
M_2	15	2.10-2.54	2.29	0.14	6.11
M_3	15	1.50-2.07	1.79	0.17	9.50
P_4	4	1.46-1.57	1.49	0.05	3.36
dP_4	3	1.48-1.81	1.69	0.18	10.65
M^1	15	2.09-2.48	2.26	0.13	5.75
M^2	18	2.08-2.89	2.49	0.2	8.03
M^3	7	1.76-2.13	1.95	0.14	7.18
P^4	8	1.70-2.15	1.91	0.14	7.33
dP^4	2	1.81-2.09	1.95	0.19	9.74

3. DESCRIPTION

The holotype (figure 1*a*), an incomplete right lower jaw, displays an incomplete tooth row with M_1-M_3. This mandible is broken mesially just ahead the M_1. The bad condition of preservation of the jaw does not allow exhaustive comparison.

Lower molars display a tetralophodont pattern. Cusps are indistinct, submerged into strong transverse lophs. M_1 is square-shaped. There is no anterior cingulid. The protoconid and metaconid are bucco-lingually opposed and united at the front of the tooth by way of a metalophulid I. A short mesolophid extends mesially from a small to indistinct mesostylid. The mesolophid is short and surrounds a closed basin on the disto-labial side of the metaconid. It shows different pattern of development. It is sometimes complete and reaches the mesial edge of the tooth. It could either be interrupted in its medial part or its buccal part can be lacking. The metaconid develops a mesio-distal enlargement which forms a small lingual wall connecting metaconid and mesostylid as wear proceeds. In most worn teeth, this lingual wall is continuous, connecting the rear of the metaconid to the entoconid. A straight, strong transverse crest joins the protoconid to the entoconid. The ectolophid is transverse and connects the protoconid to the labial tip of a mesio-labially oriented hypolophid. There is no mesoconid. On M_1 of the holotype, a longitudinal and small enamel spur arises from the disto-lingual edge of the mesolophid, and tends to connect the hypolophid. The posterolophid runs from the hypoconid to the lingual margin of the tooth. There is no anterior arm of hypoconid. The hypolophid is not connected to the hypoconid as it does in others phiomyids and in baluchimyines. A large transverse sinusid isolates the hypoconid and the posterolophid on the disto-labial side of the tooth. On worn teeth, the entoconid displays a distal enlargement which connects the lingual tip of the posterolophid, closing the sinusid lingually.

M_2 displays the same morphological pattern but is rectangular in outline and larger in size than M_1. M_3 is smaller than the other molars, and more variable in size. It displays a narrower posterior portion. It differs from the other molars in having no mesolophid or one reduced to its lingual part.

dP_4 is lower crowned than permanent teeth (figure 1*b*). The tooth is oval-shaped; the talonid is wider than the trigonid. It is pentalophodont, and displays the following transverse crests: an anterolophid, a metalophulid II, a mesolophid, a hypolophid, and a posterolophid. The anterolophid connects the protoconid and the metaconid. The protoconid links to the rear of the metaconid through a metalophulid II. These two anterior ridges are variously developed. The mesolophid, stemming from a small mesostylid, joins labially the posterior arm of the protoconid. The protoconid connects distally with the hypolophid by the way of a transverse ectolophid. As in

the molars, there is no connection between hypolophid and hypoconid. The posterolophid, running from the hypoconid to buccal margin of the tooth, is isolated from others crests by a mesio-labially to disto-lingually directed deep sinus.

The three-crested P_4 are oval shaped and the cusps are more expressed than on other cheek teeth (figure 1*c*). They are higher-crowned than dP_4 and develop a stronger lingual wall than the molars. The protoconid is mesially located with respect to the metaconid. The metalophulid II is interrupted. There is no mesolophid.

As the lowers, upper cheek teeth are tetralophodont and the cusps are barely distinguable, merged into strong lophs (figure 1*d-h*). They display a notable unilateral hypsodonty, the lingual height of the crown being almost twice of the buccal in unworn or slightly worn teeth.

The anteroloph is well developed and extends posteriorly toward the hypocone. The protocone is crestiform, submerged in the anteroloph and doesn't display connexion with the other cusps of the tooth. The internal lingual sinus is wide and reaches the labial side of the tooth. In late stage of wear, the labial tip of the anteroloph connects the paracone. The paracone joins the anterior arm of the hypocone through a transverse protoloph, disto-lingually directed. This crest is long and slender and doesn't bear any conule. A mesoloph extends disto-lingually, from a small to indistinct mesostyle, back to the middle of the posteroloph. *G. lavocati* lacks a metaloph, the metacone has merged with the posteroloph. The posteroloph runs from the hypocone toward the buccal edge of the tooth. In worn teeth, the metacone, merged in the buccal tip of the posteroloph, is connected to the mesostyle through a slender wall on the labial margin of the tooth. Worn tooth exhibits a complete buccal union of the four crests.

M^2 is similar in morphology, larger in size and rectangular-shaped; being wider than long (figure 1*e*). M^3 is shorter and narrower distally, with a triangular outline. The hypocone and the metacone get closer; the posteroloph runs buccally and connects these two cusps (figure 1*d*).

dP^4 is known for this species from 2 badly worn teeth (figure 1*g*). They are oval in shape, longer than wide and basically three crested, the mesoloph is not developed. The anteroloph is strong and separated from the other crests by a deep sinus as in the molars.

P^4 is high-crowned and exhibits a simple pattern (figure 1*h*). The organisation of the lophs is similar as in the molars. The mesoloph is variably developed. On some individuals, it is absent, usually only its buccal part is developed. The anteroloph is extended distally and tends to join the hypocone.

4. TABLE S2 - SAMPLED TAXA USED FOR PHYLOGENETIC ANALYSIS

Genera sampling

Taxa		Location	Age	references
Baluchimyinae	*Baluchimys*	Thailand (Ban Pu Dam Pit, Krabi basin) ; Pakistan (Balochistan, Bugti Hills, Bugti Member, Chitarwata Formation)	late Eocene, early Oligocene	Flynn *et al.* 1986
	Lophibaluchia	Pakistan (Balochistan, Bugti Hills, Bugti Member, Chitarwata Formation)	early Oligocene	Flynn *et al.* 1986
	Lindsaya	Pakistan (Balochistan, Bugti Hills, Bugti Member, Chitarwata Formation)	early Oligocene	Flynn *et al.* 1986
	Hodsahibia	Pakistan (Balochistan, Bugti Hills, Bugti Member, Chitarwata Formation)	early Oligocene	Flynn *et al*. 1986
	Bugtimys	Pakistan (Balochistan, Bugti Hills, Bugti Member, Chitarwata Formation)	early Oligocene	Marivaux *et al*, 2002
Yuomyidae	*Yuomys*	China (Jentsen, Mienchi district, Honan)	late Eocene	Li 1975
Chapattimyidae	*Birbalomys*	Pakistan (Mami Khel Clay, Subthu Group, Kuldana Formation); India	early-middle Eocene	Sahni & Khare 1973
Phiomyidae	*Protophiomys*	Algeria (Bir el Ater); Libya (Dur at Talhah); Egypt (Fayum depression, Jebel el Qatrani Formation)	late Middle/late Eocene	Jaeger *et al.* 1985
	Waslamys	Egypt (Fayum depression, Jebel el Qatrani Formation)	late Eocene-early Oligocene	Sallam *et al.* 2009
	Talhahphiomys	Egypt (Fayum depression, Jebel el Qatrani Formation); Libya (Dur at Talhah)	late middle/late Eocene, early Oligocene	Wood 1968
	Phiomys	Egypt (Fayum depression, Jebel el Qatrani Formation); Libya (Dur at Talhah)	late Middle/late Eocene, early Oligocene	Osborn 1908
	Metaphiomys	Egypt (Fayum depression, Jebel el Qatrani Formation); Oman (Thaytiniti and Taqah, Dhofar Province, Oman); Tanzania	early Oligocene	Osborn 1908
	Phiocricetomys	Egypt (Fayum depression, Jebel el Qatrani Formation)	early Oligocene	Wood 1968
Thryonomyidae	*Paraphiomys*	Egypt (Fayum depression, Jebel el Qatrani Formation); Kenya; Saudi Arabia	late Oligocene, Miocene	Andrews 1914
	Paraulacodus	Pakistan (Lower Siwalik)	middle Miocene	Hinton 1933
	Gaudeamus	Egypt (Fayum depression, Jebel el Qatrani Formation); Libya (Zallah)	early Oligocene	Wood 1968
	Thryonomys	Sub-saharan Africa	Pleistocene to recent	Fitzinger, 1867
Octodontidae	*Platypittamys*	Patagonia (Deseado)	late Oligocene	Wood 1949
Echimyidae	*Sallamys*	Bolivia (Salla Luribay)	late Oligocene	Hoffstetter &Lavocat 1970
	Eosallamys	Peru (Santa Rosa)	?-Eocene	Frailey & Campbell 2004
	Eoespina	Peru (Santa Rosa)	?-Eocene	Frailey & Campbell 2004
	Eosachacui	Peru (Santa Rosa)	?-Eocene	Frailey & Campbell 2004
Agoutidea	*Eoincamys*	Peru (Santa Rosa)	?-Eocene	Frailey & Campbell 2004
	Eobranisamys	Peru (Santa Rosa)	?-Eocene	Frailey &Campbell 2004
Dinomyidae	*Branisamys*	Bolivia (Salla Luribay)	late Oligocene	Hoffstetter & Lavocat 1970
Dasyproctidae	*Incamys*	Bolivia (Salla Luribay)	late Oligocene	Hoffstetter & Lavocat 1970
Hystricidae	*Hystrix*	China, Southeast Asia, Indonesia, Indo-Pakistan, Mediterranean region, eastern and sub-Saharan Africa	Miocene, Pliocene, Pleistocene	Linnaeus 1758
Erethizontidae	*Erethizon*	North America	Pliocene to recent	Cuvier 1822

5. LIST OF CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

Characters have been taken or modified from previous analysis (Marivaux *et al*. 2004).
*Characters treated as ordered.

General characters
1. Degree of crest development: (0). Bunodont; (1). crests present but low; (2). crested but cusps still well distinguable; (3). crested, cusps indistinct or absent*
2. Taenidonty: (0). Absent; (1). Incipient; (2) present.*
3. Crown height: (0). low crowned, brachydont; (1). moderately high crowned; (2). high crowned *

Incisor enamel microstructure
4. Prisms per HSB: (0). 1; (1). 1-3; (2) 2-4; (3) 3-5; (4) 4-6
5. IPM crystallite arrangement in PI: (0) parallel to and surrounding prism sheath; (1) slightly angular, anastomosing; (2) acute angular (45°), anastomosing; (3) acute angle, anastomosing; (3) perpendicular, forming interrow sheets.
6. IPM thickness: (0) thick; (1) thin
7. Percentage of PE thickness: (0) PE>25%; (1) PE reduced (<25%); (2) PE lacking
8. Band inclination relative to EDJ: (0) 0°; (1) <10°; (2) 10-20°; (3) 20-30°; (4) 30-40°; (5) 40-50°

Lower Molars
9. Anterior cingulid: (0). Absent; (1).present
10. Metalophulid I: (0). Complete; (1). incomplete; (2) absent
11. Metaconid position relative to protoconid: (0). Opposite; (1). anterior
12. Posterior arm of protoconid: (0). Absent; (1). present
13. Posterior arm of protoconid development: (0). Small to absent; (1).weak; (2). well developed
14. Connexion of the posterior arm of the protoconid: (0). To the metaconid, (1). to the mesostylid
15. Posterior arm of metaconid: (0). Absent; (1). present
16. Posterior arm of metaconid-mesostylid connexion: (0). Absent; (1). present;
17. Ectolophid: (0). Absent; (1). incomplete; (2). complete;
18. Mesoconid: (0). Absent; (1). present;
19. Mesostylid: (0). Absent; (1). present;
20. Mesolophid: (0). Absent; (1). present;
21. Entoconid position relative to the hypoconid: (0). Opposite; (1). anterior;
22. Hypoconulid: (0). Absent; (1). present;
23. Hypoconulid size: (0). Subsumed in the posterolophid; (1). small; (2). large;

Upper molars
24. Anteroloph: (0). Absent; (1). present;
25. Anterostyle: (0). Absent; (1). present
26. Parastyle: (0). Absent; (1). small; (2). well developped
27. Protocone: (0). Rounded; (1). oval; (2). crestiform
28. Posterior outgrowth of protocone: (0). Absent; (1). weak; (2). connected to the hypocone (endoloph)

29. Mure: (0).Absent; (1). present
30. Mesostyle: (0). Absent; (1). present
31. Mesoloph: (0). Absent; (1). present
32. Mesoloph connexion: (0). Connected to the mure; (1). connected to the posteroloph; (2). fused to the posteroloph
33. Mesolophule: (0). Absent; (1). extends from the metaconule toward the labial edge of the tooth (doesn't connect the mesoloph); (2). reaches the labial side
34. Metaloph connection: (0). Connected to the metaconule (or anterior arm of hypocone); (1). double connexion to the metaconule and the posteroloph; (2). connected to the posteroloph; (3). fused in the posteroloph
35. Metaconule: (0). Strong; (1). small; (2). indistinct, subsumed in the mure or absent

Lower deciduous premolars
36. Anterior cingulid: (0). Present; (1). absent
37. Anteroconid: (0). Absent or indistinct; (1). weak; (2). strong
38. Metaconid postion relative to the protoconid: (0). Opposite; (1). anterior
39. Metalophulid I: (0). Absent; (1).present
40. Metalophulid II: (0). Absent; (1). incomplete; (2). complete
41. Mesoconid: (0). Absent; (1). present
42. Mesolophid: (0). Absent; (1). weak; (2). well developed
43. Ectolophid: (0). Absent; (1). incomplete; (2). complete
44. Hypoconulid: (0). Indistinct; (1). weak; (2). strong
45. P3: (0). Present; (1). absent

Lower premolars
46. Talonid: (0). Wider than trigonid; (1). subequal to trigonid; (2). narrower than trigonid
47. Length: (0). Smaller or subequal in size to M_1; (1). longer than M_1
48. Anterior cingulid: (0). Absent; (1). present
49. Metalophulid I: (0). Absent; (1). present
50. Metalophulid II: (0). Absent; (1). present
51. Mesoconid: (0). Absent; (1). present
52. Mesolophid: (0). Absent; (1). present
53. Hypoconulid: (0). Absent; (1). weak; (2). strong

Upper deciduous premolars
54. Endoloph: (0). Absent; (1). present
55. Mesoloph: (0). Absent; (1). present
56. Mesolophule: (0). Absent; (1). present
57. Metaconule: (0). Strong; (1). weak; (2). indistinct
58. Metaloph-posteroloph connection: (0). Absent; (1). present

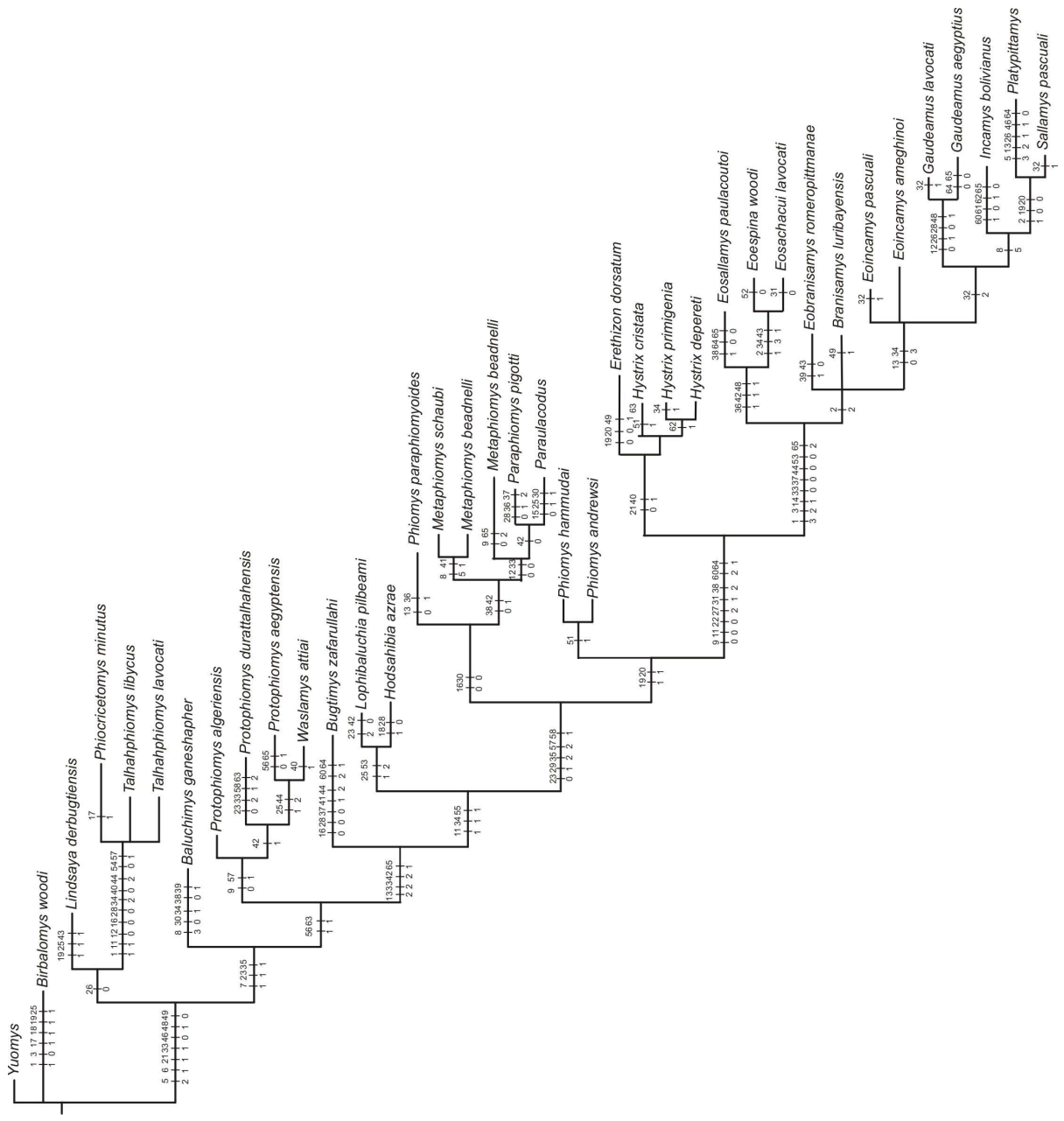
Upper premolars
59. Length: (0). Subequal or smaller than M^1; (1). longer than M^1
60. Anteroloph: (0). Low and unconnected to the protocone; (1). low and connected to the protocone; (2). well developed and connected to the protocone
61. Endoloph: (0). Absent; (1). present

62. Mure: (0). Absent; (1). present
63. Metaconule: (0). Large; (1). weak; (2). indistinct
64. Mesoloph: (0). Absent; (1). present
65. Metaloph connexion: (0). Connected to the metaconule (or to the anterior arm of hypocone); (1). connected to the posteroloph; (2). fused with the posteroloph.

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Yuomys	2	0	1	1/2	0	0	0/1	2	0	0	0	1	0	-	0	0	2	0	0	0	0	1	1/2	0	0	1	?	1	0
Birbalomys woodi	1	0	0	2	0	0	0	0	1	0	0	1	0/1	-	1	1	1	1	1	0	0	1	2	1	1	1	1	1	0
Baluchimys ganeshapher	2	0	1	?	2	1	1	3	1	0	0	1	1	-	1	1	2	0	0	0	1	1	1	1	0	1	1	1	0
Lophibaluchia pilbeami	2	0	1	?	?	?	?	?	1	0	1	1	2	0	1	-	2	0	0	0	1	1	2	1	1	1	1	1	0
Lindsaya derabugtiensis	2	0	1	?	?	?	?	?	1	0	0	1	1	-	1	1	2	0	1	0	1	1	2	1	1	0	1	1	0
Hodsahibia azrae	2	0	1	3	2	1	0	3	?	0	1	1	2	0	1	1	2	1	0	0/1	1	1	1	1	1	1	1	0	0/1
Bugtimys zafarullahi	2	0	1	3	2/3	1	1	4	1	0	0	1	2	0	1	0	2	0	0	0	1	1	1	1	0	1	1	0	0
Protophiomys algeriensis	2	0	1	3	2	1	1	5	0	0	0	1	1	-	1	1	2	0	0/1	0	1	1	0/1	1	0	1	1	1	0
Protophiomys aegyptensis	2	0	1	?	?	?	?	?	0/1	0	0	1	1	-	1	1	2	0	1	0	1	1	1	1	1	1	1	1/2	0
Protophiomys durattalhahensis	2	0	1	?	?	?	?	?	0	0	0	1	1	-	1	1	2	0	0/1	0	1	1	0	1	0	1	1	1	0
Waslamys attiai	2	0	1	?	?	?	?	?	0	0	0	1	1/2	-	1	1	2	0	1	0	1	1	1	1	1	1	1	1/2	0/1
Phiomys hammudai	2	0	1	?	?	?	?	?	1	0	1	1	2	0/1	1	1	2	0	1	1	1	1	0	1	0	1	1	1	1
Phiomys andrewsi	2	0	1	2	2	1	0	4	1	0	1	1	2	0/1	1	1	2	0	1	0/1	1	1	0	1	0	1	1	1	1
Phiomys paraphiomyoides	2	0	1	?	?	?	?	?	1	0	1	1	0	-	1	0	2	0	0	0	1	1	0	1	0	1	1	1	1
Metaphiomys schaubi	2	0	1	3	3	1	1	5	1	0	1	1	2	0	1	0	2	0	0	0	1	1	0	1	0	1	1	1	1
Metaphiomys beadnelli	2	0	1	3	3	1	1	5	1	0	1	1	2	0	1	0	2	0	0	0	1	1	0	?	?	?	?	?	?
Paraphiomys pigotti	2	0	1	4	3	1	1	4	1	0	1	0	-	-	1	0	2	0	0	0	1	1	0	1	0	1	1	0	1
Paraulacodus	2	0	1	?	?	?	?	?	1	0	1	0	-	-	0	-	2	0	0	0	1	1	0	1	1	1	1	1	1
Thryonomys swinderianus	2	0	1	2	3	?	?	4	0	0	1	0	-	-	1	0	2	0	0	0	1	1	0	1	0	1	1	1	1
Talhahphiomys libycus	1	0	1	?	?	?	?	?	1	0/1	1	0	-	-	1	0	2	0	0	0	1	1	2	0/1	0	0	1	0	0
Talhahphiomys lavocati	1	0	1	2	2	1	0	4	1	0	1	0	-	-	1	0	2	0	0	0	1	1	2	0	0	0	1	0	0
Phiocricetomys minutus	1	0	1	?	?	?	?	?	1	1	1	0	-	-	1	0	1	0	0	0	1	1	2	?	?	?	?	?	?
Gaudeamus lavocati	3	2	2	3	1	1	1	4	0	0	0	0	-	-	1	1	2	0	1	1	1	0	0	1	0	1	2	0	1
Gaudeamus aegyptius	3	2	2	?	?	?	?	?	0	0	0	0	-	-	1	1	2	0	0/1	0/1	1	0	0	1	0	1	2	0	1
Eobranisamys romeropittmanae	3	2	2	?	?	?	?	?	0	0	0	1	2	1	1	1	2	0	1	1	1	0	0	1	0	2	2	1	1
Eoincamys pascuali	3	2	2	?	?	?	?	?	0	0/1	0	1	0	-	1	1	2	0	1	1	1	0	0	1	0	2	2	1	1
Eoincamys ameghinoi	3	2	2	?	?	?	?	?	0	1	0	1	0	-	1	1	2	0	1	1	1	0	0	1	0	2	2	1	1
Branisamys luribayensis	3	2	2	4	2	1	1	4	0	0	0	1	2	1	1	1	2	0	1	1	1	0	0	1	0	2	2	1	1
Incamys bolivianus	3	2	2	2	2	1	1	5	0	0	0	1	0	-	1	1	2	0	1	1	1	0	0	1	0	2	2	1	1
Platypittamys	3	1	2	2	3	1	1	5	0	0	0	1	2	1	1	1	2	0	0	0	1	1	0	1	0	1	2	1	1
Sallamys pascuali	3	1	2	2	2	1	1	5	0	0	0	1	0	-	1	-	2	0	0	0	1	0/1	0	1	0	2	2	1	1
Eosallamys paulacoutoi	3	0	2	?	?	?	?	?	0	0	0	1	2	1	1	1	2	0	1	1	1	0	-	1	0	2	2	1	1
Eoespina woodi	3	1	2	?	?	?	?	?	0	0	0	1	2	1	1	1	2	0	1	1	1	0	-	1	0	2	2	1	1
Eosachacui lavocati	3	1	2	?	?	?	?	?	0	0	0	1	2	1	1	1	2	0	1	1	1	0	-	1	0	2	2	1	1
Hystrix primigenia	2	0	1	?	?	?	?	?	0	0	0	0	-	-	1	0/1	2	0	1	1	0	0	-	1	0	0	2	1/2	1
Hystrix depereti	2	0	1	?	?	?	?	?	0	0	0	0	-	-	1	0/1	2	0	1	1	0	0	-	1	0	0	2	1/2	1
Hystrix cristata	2	0	1	4	1	1	0	2	0	0	0	0	-	-	1	1	2	0	1	1	0	0	-	1	0	0	2	1/2	1
Erethizon dorsatum	2	0	1	4	2	1	?	5	0	0	0	1	2	0	?	?	2	0	0	0	0	0	-	1	0	0	2	1	1

Taxa	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Yuomys	1	0	-	0	0	0	?	?	?	?	?	?	?	?	?	0	1	1	0	1	1	0	0	1	?	?	?	?	?	0	-
Birbalomys woodi	1	0	-	0	0	0	1	1	1	0	1	1	0	1/2	1	?	1	0	0	1	1	1	0	1	1	0	0	0	0	0	0
Baluchimys ganeshapher	0	0	-	1	1	1	0	2	0	1	2	0	0	2	1	?	0	0	1	0	1	0	0	2	1	0	0	0	-	0	1
Lophibaluchia pilbeami	1	0	-	2	1	1	?	?	?	?	?	?	0	?	?	?	0	0	1	0	1	0	0	2	?	?	?	?	?	0	1
Lindsaya derabugtiensis	1	0	-	1	0	0	0	2	1	0	2	0	0	1	1	?	0	0	1	0	1	1	0	2	1	0	0	0	0	0	1
Hodsahibia azrae	1	0	-	2	1	1	1	?	?	?	?	?	2	?	?	?	0	?	1	0	1	0/1	1	2	0	1	1	0	0	0	?
Bugtimys zafarullahi	1	0	-	2	0	1	0	0	1	0	2	1	2	2	2	0	0	0	1	0	1	0	1	1	1	0	1	0	0	0	2
Protophiomys algeriensis	0/1	0	-	1	0	1	0	1	1	0	2	0	0	2	1	?	0	0	0/1	0/1	1	0	0	1	0	0	0/1	1	0	?	?
Protophiomys aegyptensis	1	0	0	1	0	1	0	1	1	0	2	1	1	2	2	?	?	?	?	?	?	?	?	?	0	0	0	1	0	0	0
Protophiomys durattalhahensis	1	0	-	2	0	1	0	1	1	0	2	0	1	2	1	?	0	0	0	1	1	0	0	1	0	0	1	1	1	0	0
Waslamys attiai	1	0	0	1/2	0	1	0	1	1	0	1	0/1	1	2	2	?	0	0	0	1	0/1	0	0	1	0	0	1	1	0	0	0
Phiomys hammudai	1	0	-	2	1	2	0	1	0	0	2	0	2	2	1	?	0	0	0	0	1	1	0	1	?	?	?	?	?	0	0/1
Phiomys andrewsi	1	0	-	1/2	1	2	0	1	1	0	2	0	2	2	1	?	0	0	0	0	1	1	0	1	0	1	1	2	1	?	?
Phiomys paraphiomyoides	0	0	-	1	1	2	1	1	1	0	2	0	2	2	1	?	?	?	?	?	?	?	?	?	?	0	1	1	2	1	?	?
Metaphiomys schaubi	0	0	-	1/2	2	2	0	1	0	0	1/2	1	1	2	1	?	?	?	?	?	?	?	?	?	?	0	?	1	2	1	?	?
Metaphiomys beadnelli	?	?	?	?	?	?	0	1	0	?	?	1	1	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Paraphiomys pigotti	0	0	-	0	2/3	2	1	2	0	0	?	0	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Paraulacodus	1	0	-	0	3	2	0	1	0	0	2	0	0	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
Thryonomys swinderianus	0	0	-	0	3	2	0	1	0	0	2	0	1	2	1	?	0	0	?	?	?	0	?	0	0	0	0	2	1	?	?
Talhahphiomys libycus	1	0	-	1	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0/1	?	?
Talhahphiomys lavocati	1	0	-	1	2	0	0	2	1	0	0	0	0	2	2	?	?	?	?	?	?	?	?	?	0	0	0	1	0/1	?	?
Phiocricetomys minutus	?	?	?	?	?	?	1	2	1	0	0	0	0	0	2	1	-	-	-	-	-	-	-	-	?	?	?	?	?	?	?
Gaudeamus lavocati	1	1	1	0	3	2	0	0	0	0	2	0	2	2	0	?	0	0	1	0	0/1	0	0/1	0	1	0	1	2	1	0	2
Gaudeamus aegyptius	0/1	1	2	0	3	2	0	0	0	0	2	0	2	2	0	?	0	0	1	0	0	0	0	0	?	?	?	?	?	0	2
Eobranisamys romeropittmanae	1	1	0	0	2	2	0	0	0	1	2	0	2	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eoincamys pascuali	1	1	1	0	3	2	0	?	?	?	1	0	?	?	0	?	0	0	0	0	1	0	1	0	1	1	1	2	1	0	2
Eoincamys ameghinoi	1	1	0	0	3	2	?	?	?	?	?	?	?	?	?	?	0	0	0	0	1	0	1	0	?	?	?	?	?	?	?
Branisamys luribayensis	1	1	0	0	2	2	?	?	?	?	?	?	?	?	?	0	0	1	0	1	0	0	1	0	1	1	1	2	1	0	2
Incamys bolivianus	1	1	2	0	3	2	0	?	0	?	2	0	?	2	?	1	0	0	0	1	0	0	1	0	1	1	1	2	-	0	1
Platypittamys	1	1	2	0	3	2	?	?	?	?	?	?	?	?	?	1	1	0	0	1	0	0	?	?	?	?	?	?	?	0	2
Sallamys pascuali	1	1	1	0	3	2	0	1	0	0	2	0	1	2	0	?	0	0	0	0	0	0	1	0	?	?	?	?	?	0	2
Eosallamys paulacoutoi	1	1	0	0	2	2	1	0	1	0	2	0	1	2	0	?	0	1	1	0	1	0	1	0	?	?	?	?	?	0	2
Eoespina woodi	1	1	0	0	3	2	1	0	0	0	2	0	1	1	0	?	0	0	1	0	1	0	0	?	?	?	?	?	?	0	2
Eosachacui lavocati	1	0	0	0	3	2	1	0	0	0	2	0	1	1	0	?	0	0	?	?	1	0	1	0	?	?	?	?	?	?	?
Hystrix primigenia	1	1	0	2	1	2	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0	1	1	?	?	?	?	?	1	2
Hystrix depereti	1	1	0	2	2	2	0	1	0	0	1	0	2	2	1	?	0	1	0	0	0	0	1	1	?	?	?	?	?	1	2
Hystrix cristata	1	1	0	2	2	2	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	1	1	1	?	?	?	?	?	1	2
Erethizon dorsatum	1	1	0	2	2	2	0	1	0	0	1	0	2	2	1	?	0	1	0	1	1	0	1	1	?	?	?	?	?	?	2

Taxa	61	62	63	64	65
Yuomys	1	0	0	0	-
Birbalomys woodi	1	0	0	0	0
Baluchimys ganeshapher	1	0	0	0	-
Lophibaluchia pilbeami	1	0	1	0	1
Lindsaya derabugtiensis	0	0	0	0	-
Hodsahibia azrae	?	?	?	?	?
Bugtimys zafarullahi	1	0	1	1	1
Protophiomys algeriensis	?	?	?	?	?
Protophiomys aegyptensis	1	0	1	0	1
Protophiomys durattalhahensis	1	0	2	0	0
Waslamys attiai	1	0	1	0	0
Phiomys hammudai	1	0	2	0	0
Phiomys andrewsi	?	?	?	?	?
Phiomys paraphiomyoides	?	?	?	?	?
Metaphiomys schaubi	?	?	?	?	?
Metaphiomys beadnelli	?	?	?	?	?
Paraphiomys pigotti	?	?	?	?	?
Paraulacodus	0	1	2	0	1
Thryonomys swinderianus	?	1	1	?	2
Talhahphiomys libycus	?	?	?	?	?
Talhahphiomys lavocati	?	?	?	?	?
Phiocricetomys minutus	?	?	?	?	?
Gaudeamus lavocati	1	0	2	1	2
Gaudeamus aegyptius	1	0	2	0	0
Eobranisamys romeropittmanae	?	?	?	?	?
Eoincamys pascuali	?	0	2	0/1	2
Eoincamys ameghinoi	?	?	?	?	?
Branisamys luribayensis	1	0	1	1	-
Incamys bolivianus	0	1	2	0/1	0
Platypittamys	?	0	2	0	2
Sallamys pascuali	1	0	2	1	2
Eosallamys paulacoutoi	1	0/1	2	0	0
Eoespina woodi	1	1	2	1	2
Eosachacui lavocati	?	?	?	?	?
Hystrix primigenia	0	1	2	1	1
Hystrix depereti	0	1	2	1	1
Hystrix cristata	0	0	1	1	?
Erethizon dorsatum	?	?	1	1	1



7. FIGURE S1 - Strict consensus cladogram with positionned unambigous synampomorphies.
The data-matrix includes 2340 character states of which 651correspond to missing data. Among these, 577 correspond to unknown condition ('?') and 74 correspond to non applicable data ('-').
The analysis of the data matrix was performed in PAUP (v.4.0b10 Swofford, 1998) using heuristic search methods (1000 replications with random stepwise addition and a randomized input order of taxa). The analysis results in 108 most parsimonious trees of 244 steps. The consistency index of these trees is weak (CI: 0.38) showing that the amount of homoplasy in the data is significant. However the higher retention index (RI:0.69) indicates that, even largely homoplastic, the data are well structured.

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ELECTRONIC SUPPLEMENTARY MATERIAL 2

FOR “*GAUDEAMUS LAVOCATI* SP. NOV. (RODENTIA, HYSTRICOGNATHI) FROM THE LOWER OLIGOCENE OF ZALLAH, LIBYA: FIRST AFRICAN CAVIOMORPH?”

ELECTRONIC SUPPLEMENTARY MATERIAL 2

1. GAUDEAMUS LAVOCATI INCISOR ENAMEL MICROSTRUCTURE

Specimens examined:

One left upper (MA 312) and two left lower (MA 310, MA 311) isolated incisor fragments attributed to *Gaudemus lavocati* sp. nov. were studied. Attribution of the incisor fragments was made based on size and morphology. The incisors of *Gaudeamus lavocati* sp. nov. are clearly distinct from those of the other rodents from the locality by their superior size, this species displaying the largest size in this rodent fauna.

Enamel Preparation:

Incisor fragments were embedded in polyester resin for easier handling. After hardening of resin, specimens were cut transversely with a low speed saw. Longitudinal sections were ground on a grinding wheel with wet abrasive paper (gradation 240 and 600). Subsequently, specimens were ground smooth (1200 corundum slurry on glass plate), dried, and etched for 2-4 seconds with 7% (2N) HCl to make morphological details visible. After ultrasonic cleansing and rinsing with distilled water, the specimens were dried, mounted on SEM stubs and sputtercoated with gold (3 min). The specimens were studied by SEM at magnifications from 300 to 1,500x. Following general convention, schmelzmuster descriptions refer to the zone which is close to the sagittal plane of the incisor (Flynn & Wahlert 1978: fig. 2).

The enamel of the upper incisor of *Gaudeamus* (MA 312) is double-layered with multiserial Hunter-Schreger bands (HSB) in the portio interna (PI) and radial enamel in the portio externa (PE). In the PI, HSB comprise 3-5 prisms and the thin interprismatic matrix (IPM) runs at a slight angle to the prism long axes. In the cross sections, the IPM anastomozes between the prisms. Between HSB, frequent prism transitions occur that form transition zones. In the PI,

HSB are inclined 35° apically. PE comprises 25% of the total enamel thickness of 100 µm, and prisms are 50° inclined apically. Prism cross sections are oval in the PI and lancet shaped in the PE. A very thin prismless external layer (PLEX) is present.

The enamel of the studied lower incisors of *Gaudeamus* (MA 310 and 311) is very similar and varies only in minor details. The enamel is double-layered with multiserial HSB in the PI and radial enamel in the PE. HSB in the PI comprise 2-6 prisms and the thin IPM runs at a slight angle to the prisms long axes. In the cross sections, IPM anastomozes between the prisms. Between HSB, frequent prism transitions occur that form transition zones. In the PI, prisms are inclined 35° apically. PE comprises 25% of the total enamel thickness of 130 µm (MA 311) resp.145 µm (MA 310). In the PE, prisms are inclined 50° apically. Prisms cross sections are oval in the PI and lancet-shaped in the PE. A very thin PLEX is present.

2. FIGURES



Figure S2. Cross sections of *Gaudeamus lavocati* incisors.

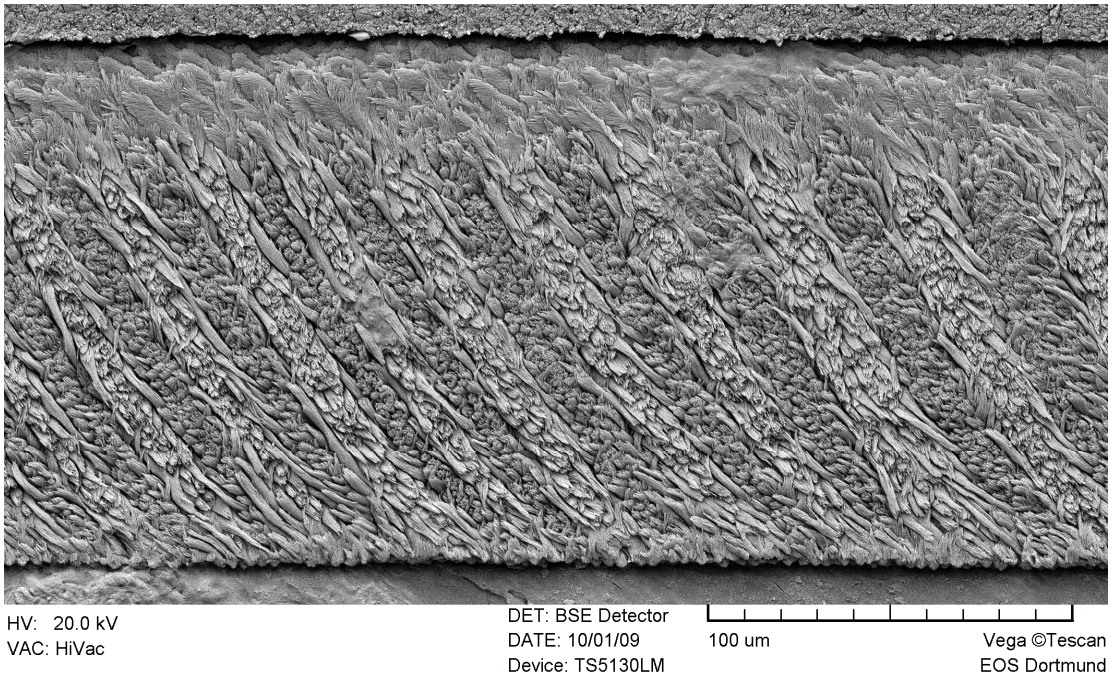


Figure S3. SEM micrograph of enamel longitudinal sections of lower incisor MA 310 from Zallah 5 locality, Sirt basin, Central Libya.

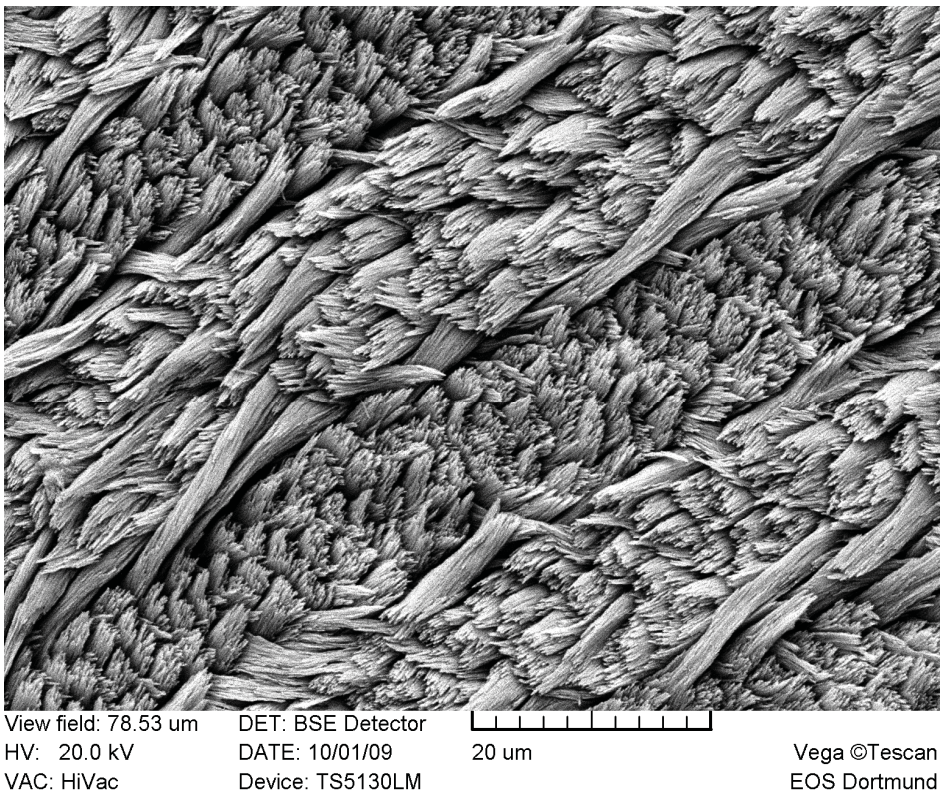


Figure S4. Detail of PI with HSB, lower incisor MA 310 from Zallah 5 locality, Sirt basin, Central Libya.

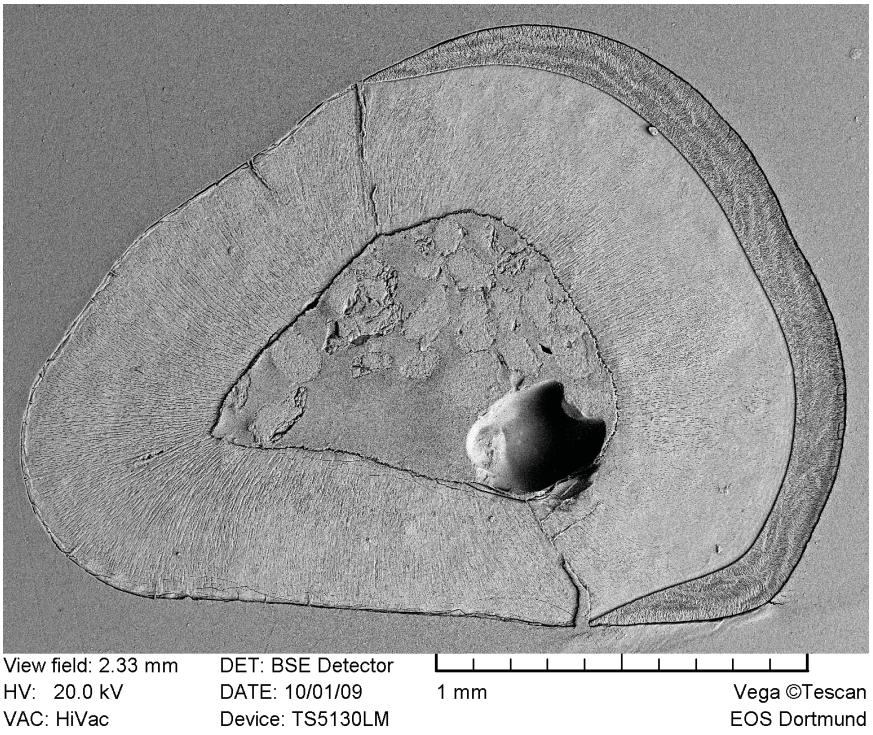


Figure S5. Cross section of lower incisor MA 311 of *Gaudeamus lavocati* from Zallah 5 locality, Sirt basin, Central Libya.

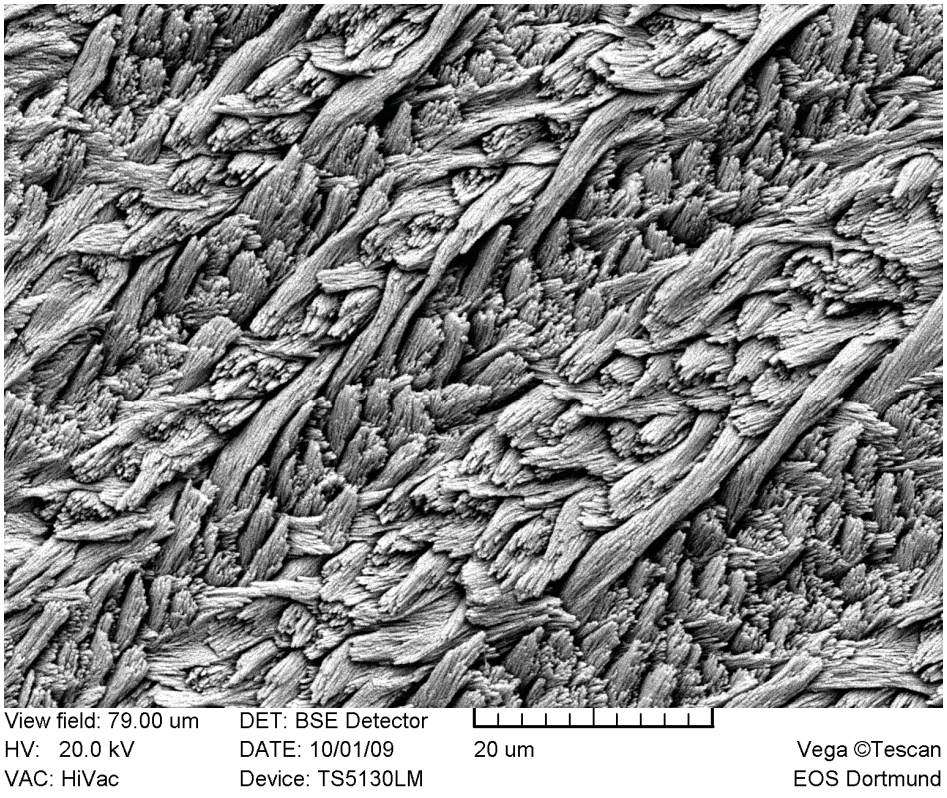


Figure S6. Detail of PI with HSB, lower incisor MA 311 from Zallah 5 locality, Sirt basin, Central Libya.

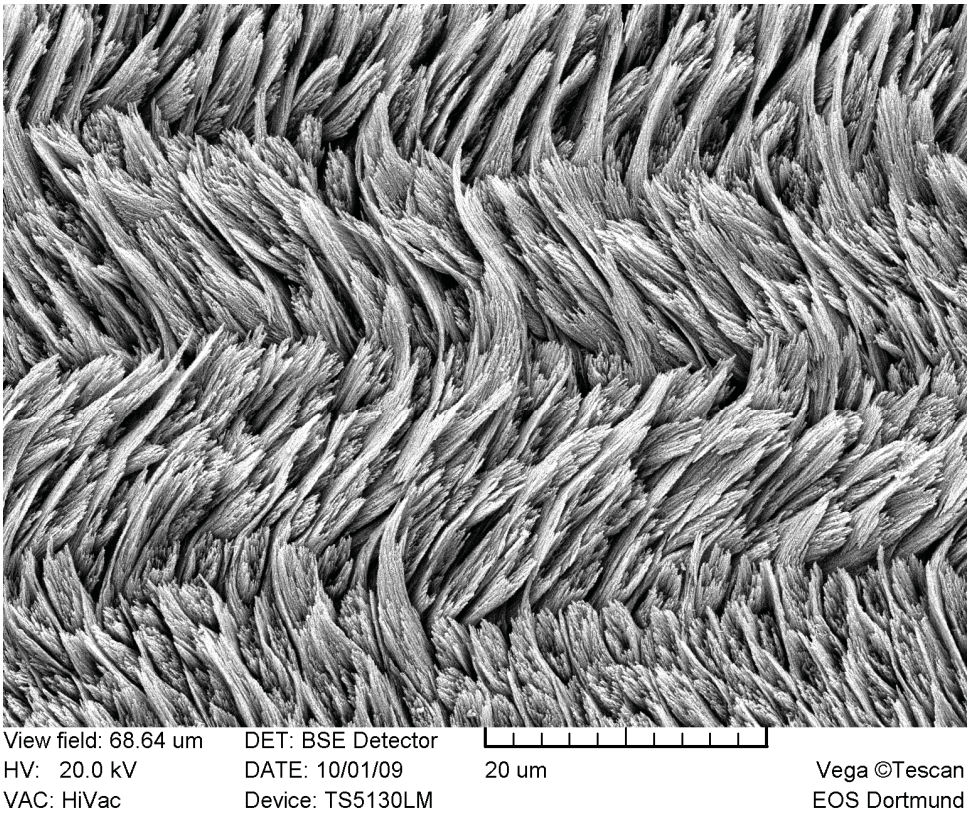


Figure S7. Detail of PI with HSB, upper incisor MA 312 from Zallah 5 locality, Sirt basin, Central Libya.

REFERENCE

Flynn, L.J. and Wahlert, J.H. (1978). SEM study of rodent incisors: preparation and viewing. Curator, 21**,** 303-310.

1.4. NEW HYSTRICOGNATHOUS RODENTS FROM THE LOWER OLIGOCENE OF CENTRAL LIBYA (ZALLAH OASIS, SAHARIAN DESERT): SYSTEMATIC, PHYLOGENY AND BIOCHRONOLOGIC IMPLICATIONS

NEW HYSTRICOGNATHOUS RODENTS FROM THE LOWER OLIGOCENE OF CENTRAL LIBYA (ZALLAH OASIS, SAHARIAN DESERT): SYSTEMATIC, PHYLOGENY AND BIOCHRONOLOGIC IMPLICATIONS

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1. INTRODUCTION

Hystricognathous rodents include the extant Old World porcupines (Hystricidae), mole rats (Bathyergidae), rock rats (Petromuridae), cane rats (Thryonomyidae), New World porcupines (Erethizontidae) and caviomorphs. Their fossil record extends in Afro-Arabia, South America and Eurasia back to the late Eocene-early Oligocene times (e.g. Wood 1968;

Jaeger et al. 1985; Flynn et al. 1986; Wyss et al. 1993; Marivaux et al. 2002; Frailey and Campbell 2004; Sallam et al. 2009; Jaeger et al. 2010).

The earliest offshoots of Hystricognathi, the baluchimyinae, have been reported from the early Oligocene deposits of Pakistan (Flynn and Cheema 1994; Marivaux et al. 2000; Marivaux and Welcome 2003) and from the late Eocene of Thailand (Marivaux et al. 2000). The phiomorphs, closely related to the baluchimyines, represent an adaptive radiation of hystricognathous rodents that occurred during the late Paleogene in Africa (e.g. Wood 1968; Jaeger et al. 1985; Sallam et al. 2009; Jaeger et al. 2010). *Protophiomys*, the oldest African member of Hystricognathi, is considered as a representative of this South Asian group (Marivaux et al. 2002; 2004). As for South American members of Hystricognathi, first representatives of the early diversification of caviomorphs appeared in the late Eocene deposits of Peru (Frailey and Campbell 2004). Paleontological and molecular data point out close phylogenetic relationship between South American caviomorphs and African phiomorphs (Lavocat 1969; Parent 1980; Wyss et al. 1993; Martin 1994; Huchon and Douzery 2001; Poux et al. 2006; Coster et al. 2010) and indicate that they may share a common hystricognathous ancestor (Flynn et al. 1986; Bryant and McKenna 1995; Marivaux et al. 2002, 2004).

In Africa, the oldest known hystricognathous rodents have been described from the middle-late Eocene deposits of Bir el Ater locality in the Nementcha Mountains, Algeria (*Protophiomys algeriensis* Jaeger et al. 1985) and from the Dur At-Talah escarpment in Central Libya (*P. durattalahensis, Phiomys hammudai, Talahphiomys lavocati* and *Talahphiomys libycus* Jaeger et al. 2010). Primitive representatives of Phiomyidae (*Protophiomys aegyptensis* and *Waslamys attiai* Sallam et al. 2009) have been recently reported from the late Eocene locality of Birket Qarun 2 in the Fayum Depression, Egypt. Knowledge of African Hystricognathi evolutionary history has been long-based almost exclusively on the few fossiliferous localities of Jebel Qatrani Formation of Fayum, which has yielded a rich assemblage of late Eocene-early Oligocene phiomorphs, including seven genera of phiomyids (Osborn 1908; Schlosser 1911; Wood 1968). In Arabia, primary record of early

Oligocene phiomyids was reported from the sites of Thaytiniti and Taqah in the Ashawq Formation of Dohfar province in Oman (Thomas et al. 1989). Further Oligocene phiomyid remains were recovered from the Rukwa rift basin in Tanzania (Stevens et al. 2004) and from Lokichar basin in Kenya (Ducrocq et al. 2010).

We report here the discovery of a rich assemblage of hystricognathous rodents from a newly discovered fossiliferous site in the early Oligocene deposits of Zallah Trough, south western Sirt basin, Central Libya. Paleogene fossil mammal occurrences in the fluvial deposits exposed in Zallah area were first reported by Arnould–Saget and Magnier (1961) and Arambourg (1963). Later works by Fejfar (1987) expanded this earlier fossil collection and led to the identification of three taxa of phiomyids. Recent field expeditions have led to the discovery of a new micro-mammal site, Zallah 5 Rodent (Z-5R) locality. Five additional phiomyid taxa, including a new species of the intriguing genus *Phiocricetomys,* whose upper molars are first documented here, associated to one new species of *Metaphiomys,* a new genus *Neophiomys,* are described herein with a special emphasis on chronological implications for the Paleogene of Libya. A new species of the hystricognathous rodent genus *Gaudeamus* has already been described from Z-5R locality (Coster et al. 2010) and recognized as a possible representative of the South American caviomorphs.

To provide an accurate chronology of the Zallah deposits, a biostratigraphic study has been combined to a magnetostratigraphic study. For a better understanding of the early evolutionary and biogeographic history of Hystricognathi, a morphological cladistic analysis of dental characters, including the new Libyan taxa, has also been performed. One main result concerns the paraphyly of the “Phiomyids” and the definition of three new monophyletic groups among this former taxonomic unit. The discovery of this new collection of Oligocene hystricognathous rodents is of considerable importance because it improves our knowledge of the evolutionary history of African rodents and offers additional evidence to achieve biostratigraphic correlation with other Paleogene Afro-Arabian mammal localities.

2. GEOLOGICAL SETTING

The Sirt basin is located in the northern part of the Sahara desert, in Central Libya (Figure 4.1). It is bordered to the east by the Dakhla basin of Egypt, to the south by Al Kufrah basin and in its northern side by the Cyrenaica platform and the Mediterranean basin.

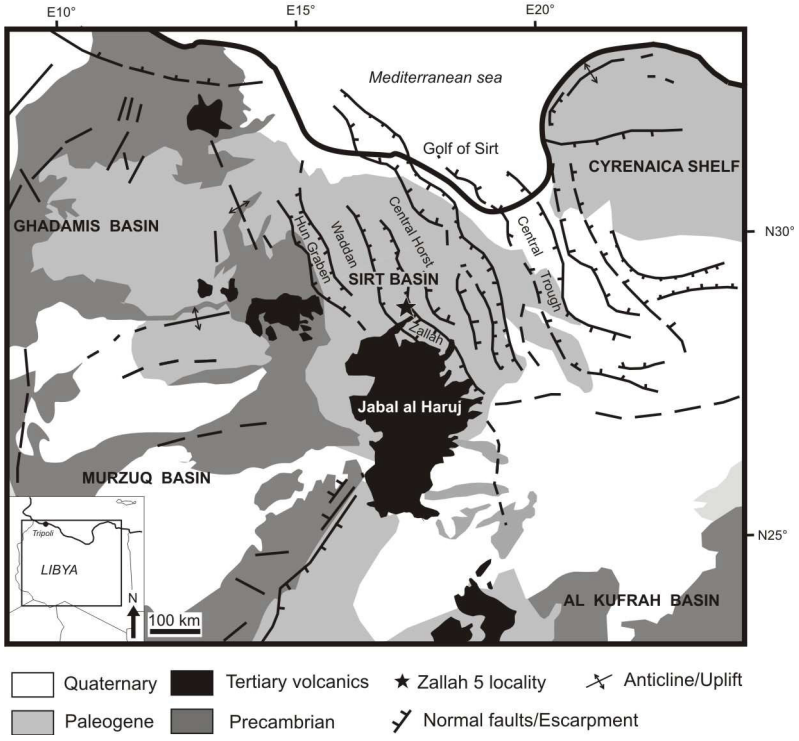


Figure 4.1. Geological and structural map of Libya showing the main sedimentary basins, major faults, tectonics and localisation of the studied area (modified after Abadi and van Dijk 1993).

The Sirt basin is delimited to the west by the Hun Graben. This basin follows a NW-SE general trend and lies on a basement of Precambrian igneous and metamorphic rocks (Abadi and Van Dijk 1993). The horst and graben structures of Sirt basin were formed by rifting initiated during Early Cretaceous in the context of African-Eurasian plates interaction (Schröter 1996). The early Paleogene period corresponds to the infilling of the cretaceous rift and was characterized by a transgressive sedimentary phase associated with high

sedimentation rates. The syn-rift sequence is overlain by middle Eocene-early Miocene sediments, characterized by continental and shallow marine facies (Van Der Meer and Cloetingh 1993). A major tectonic event attributed to the uplift of the African plate during the Oligocene time led to a marine regression within the Sirt embayment as a result of northward tilting of the Sirt Basin (Bezan and Malak 1996).

The Sirt basin comprises five main grabens, including the Zallah Trough in its south western part. The Tertiary sequence, exposed in Zallah area, corresponds to nearshore to continental Oligocene sediments, overlying the marine Eocene Wadi Thamat Formation (Schroter 1996) (Figure 4.2A).

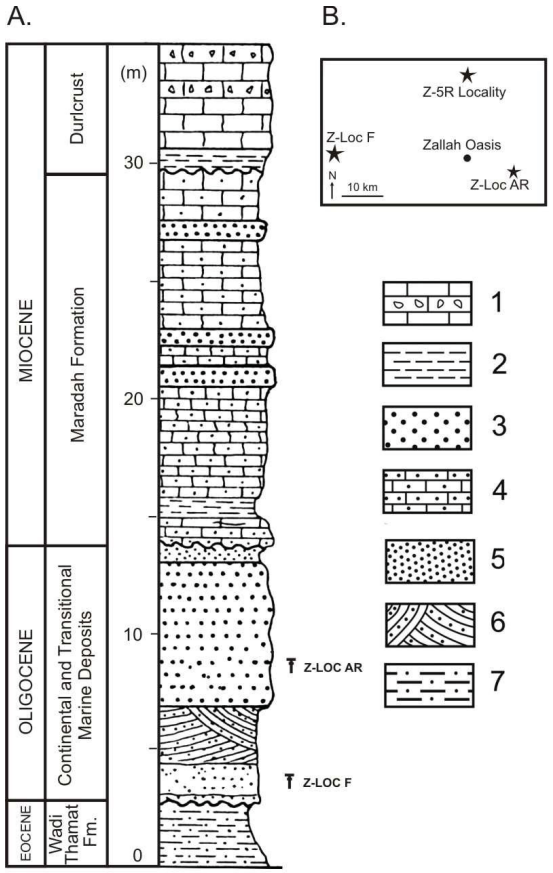


Figure 4.2. (A.) Stratigraphy of Zallah section (7 km SE of Zallah Oasis). 1: light gray sandy limestones; 2: claystone layers; 3: conglomerates, partly cross-bedded; 4: calcareous claystones of Maraddah Miocene Formation; 5: medium grained, yellowish-brown sandstones; 6: sandstones/sands-claystones/clays, partly fine laminated or cross-bedded, reddish, rosty brown, greenish with vertebrate remains on the sandy base; 7: upper Eocene yellowish-brown siltstones (After Fejfar 1987). (B.) Localisation of the discovered vertebrate sites in Zallah area (Sirt basin, Libya).

The Oligocene mixed marine and continental deposits, identified as the Continental and Transitional Marine Deposits, correspond to cross-bedded channelized sandstones, coarse conglomerates and claystones rich in silicified wood and vertebrate fossils. South east of Zallah Oasis, a well defined angular unconformity is described between river channel Oligocene deposits and the marine Eocene Qrarat al Jifah Member of Wadi Thamat Formation (Vesely 1985). In the western part of Zallah area, the uppermost members of the Wadi Thamat Formation (Qrarat al Jifah and Thmed al Qusur Members) are missing (El Hawat and Pawellek 2004) and the Eocene deposits are represented by Al Gata Member, the lowermost unit of Wadi Thamat Formation. Al Gata Member, dated from middle Eocene (Goudarzi 1970), is reported to be directly unconformably overlain by Oligocene deposits which are poor in fossils (Vesely 1985). The Oligocene sequence of Zallah area underlies the Miocene Maradah Formation composed of marine calcareous sandstones (Vesely 1985).

The Oligocene Continental and Transitional Marine Deposits, exposed in our studied area, are dominated by claystones and cross-bedded channel sandstones with silt intercalations. They correspond to estuarine, lagoon and deltaic depositional environments (Bezan 1996) and have yielded abundant fossil wood and vertebrate remains. At Z-locAR locality, ~10 km south east of Zallah Oasis (Figure 4.2B), proboscidean, sirenian, hyracoid, anthracotherid, carnivore, turtle, shark and crocodile remains were recovered from cross-bedded conglomerate levels in the upper part of the Continental and Transitional Marine Deposits (Arnould-Saget and Magnier 1961; Arambourg 1963). In addition, Fejfar (1987) reported three phiomorph taxa and an early Oligocene foraminiferal assemblage, composed of *Bolivina melettica* and *Nummulites fichteli,* from locality Z-locF, ~35km west of Zallah Oasis (Figure 4.2B). Our new fossilferous locality, namely Zallah 5 Rodent locality (Z-5R), is located approximatively 15km north of Zallah Oasis (Figure 4.2B). The part of Zallah area, where the new locality is situated, is locally covered by basaltic lava flow of the Jabal Al Haruj volcanics complex, dated of late Miocene-Pleistocene age (Vesely 1985). Z-5R micro-mammal locality has yielded five genera of phiomorphs including three new species. The

occurrence of *Gaudeamus lavocati,* recovered from this locality, is mentioned here but detailed description has already been reported previously (Coster et al. 2010).

The terminology used for the description of cheek teeth is illustrated in the following figure.

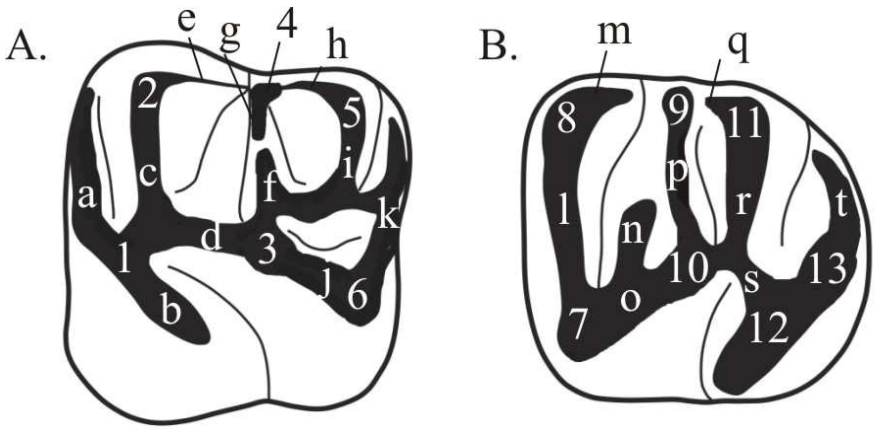


Figure 4.3. Occlusal dental nomenclature (A.) Upper molar: 1-protocone; 2-paracone; 3-metaconule; 4-mesostyle; 5-metacone; 6-hypocone; a-anteroloph; b-neo-endoloph; c-protoloph; d-mure; e-posterior arm of paracone; f-mesolophule; g-mesoloph; h-anterior arm of metacone; i-metaloph; j-anterior arm of hypocone; k-posteroloph; (B.) Lower molar: 7-protoconid; 8-metaconid; 9-mesostylid; 10-mesoconid; 11-entoconid; 12-hypoconid; 13-hypoconulid; l-metalophulid I; m-posterior arm of metaconid; n-posterior arm of protoconid; o-ectolophid; p-mesolophid; q-anterior arm of entoconid; r-hypolophid; s-anterior arm of hypoconid; t-postelorophid.

3. SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich 1821

Suborder Ctenohystrica Huchon, Catzeflis and Douzery 2000

Infraorder Hystricognathi Tullberg 1899

Super-Family Phiocaviomorpha (this study)

Genus *Metaphiomys* Osborn 1908

Metaphiomys zallahensis sp. nov. (Figure 4.4a-h)

Holotype: Z5R-165, left M_2 (Figure 4.4c)

Referred material: Z5R-162, left P_4; Z5R-163, left dP_4; Z5R-164, right dP_4; Z5R-165, left M_2; Z5R-166, right M_2; Z5R-167, left M_3; Z5R-168; right dP^4; Z5R-169, left $M^{1/2}$; Z5R-170, left $M^{1/2}$; Z5R-171, left M^3

Etymology: The species name refers to Zallah, the geographic provenance of this species

Type locality: Zallah 5 Rodent locality, Sirt basin, Libya

Age: Lower Oligocene

Measurement: see Table 4.1

The material is temporarily deposited in the collections of iPHEP, University of Poitiers and it will be deposited after publication in the Collections of El Fateh University in Tripoli (Libya).

TABLE 4.1. measurements of *Metaphiomys zallahensis* cheek teeth

		Width (mm)	Length (mm)
Z5R-162	P_4	1.28	1.78
Z5R-163	dP_4	1.35	1.88
Z5R-164	dP_4	1.52	1.78
Z5R-165	M_2	2.02	2.23
Z5R-166	M_2	1.65	2.02
Z5R-167	M_3	1.79	2.04
Z5R-168	dP^4	1.51	1.86
Z5R-169	$M^{1/2}$	1.87	1.93
Z5R-170	$M^{1/2}$	1.98	1.77
Z5R-171	M^3	2.13	1.88

Diagnosis:

Species slightly smaller than *Metaphiomys schaubi* and *M. beadnelli* but larger than any known species of *Phiomys.* Lophodont cheek teeth, moderately high crowned. Pentalophodont upper molars characterized by an anteroloph, a protoloph, a mesoloph, a backwardly directed metaloph and a posteroloph. The mesoloph is variously developed and the paracone is the highest cusp of the tooth. Pentalophodont upper premolars with a low mesoloph, variously developed and connected to the anterior arm of the hypocone. Four-crested lower molars

displaying a metalophulid I, a strong posterior arm of protoconid bearing a protospur joining the posterior arm of the metaconid, a hypolophid and a posterolophid. Lower molars with no trace of mesoconid. Differs from *M. schaubi* and *M. beadnelli* in exhibiting a connection between the mesoloph and the metaloph as in *Ph. andrewsi.* Differs from *M. beadnelli* in having a less developed protospur and in having a posterior arm of protoconid which does not extend as close to the metaconid.

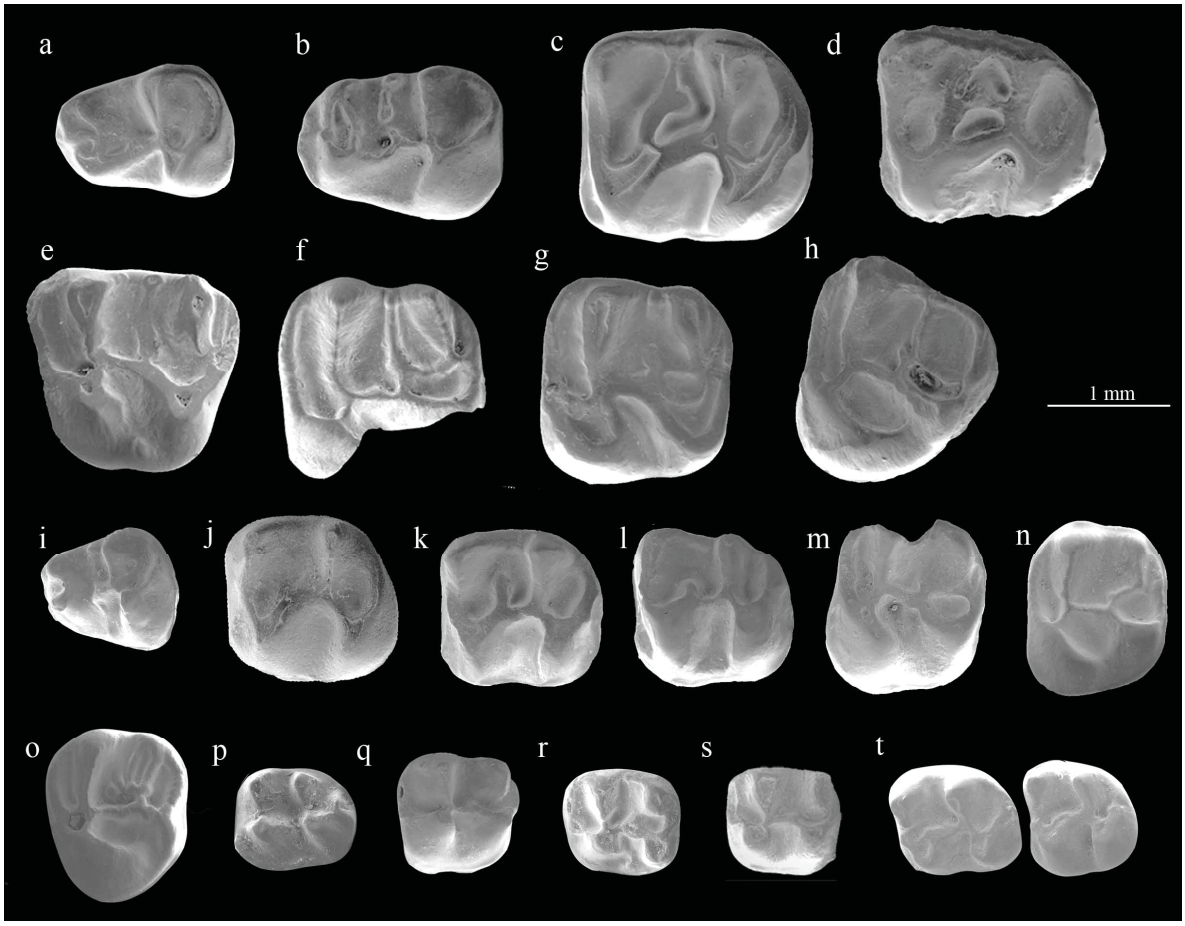


Figure 4.4. Cheek teeth of the Phiomyidae from Zallah 5 Rodent locality, Sirt basin, Libya. a-h, *Metaphiomys zallahensis*: a. Z5R-162, left P_4; b. Z5R-163, left dP_4; c. Z5R-165, left M_2; d. Z5R-167, left M_3. e. Z5R-168, right dP^4 (reversed); f. Z5R-169, left $M^{1/2}$; g. Z5R-170, left $M^{1/2}$; h. Z5R-171, M^3; i-o, *Neophiomys paraphiomyoides*: i. Z5R-173, left dP_4; j. Z5R-177, right M_1 (reversed); k. Z5R-178, left M_2; l. Z5R-185, left M_3; m. Z5R-188, left M^1; n. Z5R-191, right M^2 (reversed); o. Z5R-187, right M^3 (reversed). p-s, *Phiocricetomys atavus*: p. Z5R-193, right M_2 (reversed); q. Z5R-201, left $M^{1/2}$ r. Z5R-203, left $M^{1/2}$; s. Z5R-202, left $M^{1/2}$; t., *Talahphiomys lavocati*: Z5R-192, left lower jaw with M_{2-3}.

Description

Lower cheek teeth are moderately high-crowned with distinct main cusps connected by crests. They are similar in overall pattern to specimens referred to *M. schaubi* but are slighty smaller in size (Table 4.1) and differ by some characters.

The M_2 (Figure 4.4c) is rectangular-shaped and displays a well developed tetralophodont pattern with cusps still distinguishable. The low anterocingulid is enlarged buccally. The metalophulid I is complete. The metaconid is more anteriorly positioned than the protoconid. The posterior arm of the protoconid is strong, but weaker than what observed in *M. beadnelli*. *M. beadnelli* displays, in comparison to *M. schaubi* and *M. zallahensis,* a closer connexion between the posterior arm of protoconid to the metaconid and a closer connexion between the posterolophid and the entoconid. In *M. zallahensis,* the posterior arm of protoconid extends distally toward a small mesostylid submerged within a low continuous lingual wall. The mesostylid tends to connect to the posterior arm of metaconid after wear. The tip of the posterior arm of the protoconid does not come as close to the metaconid as it does in the other species of *Metaphiomys* and reaches the lingual side of the tooth at a more distal level. This configuration of the posterior arm of the protoconid is reminiscent to what can be observed on some specimens of *Phiomys andrewsi.* A posterior small crest, called a protospur, is extending backwardly from the middle of the posterior arm of the protoconid. Such a minute spur has been observed in some specimens of *Ph. andrewsi* but this character is diagnostic of *Metaphiomys*. In *Metaphiomys beadnelli*, this protospur is not straight but splits in multiple tiny crests. The protoconid and the hypoconid are the largest cusps. There is no mesoconid. The ectolophid connects the disto-labial side of the protoconid to the anterior arm of hypoconid. The entoconid is slightly more mesial to the hypoconid. The hypolophid is parallel to the metalophulid I and connects buccaly the anterior arm of the hypoconid. The ectolophid delimits lingually a wide retroverse buccal sinusid, as it does in other Phiomyidae (except *Gaudeamus*). A continuous posterolophid, exhibiting a small distinct hypoconulid, runs from the hypoconid to the base of the entoconid.

M_3 (Figure 4.4d) is smaller than the other molars and has a trigonid wider than the talonid. The hypoconid is more lingual. The anterior cingulid is weak. The longitunal spur extending posteriorly from the posterior arm of the protoconid reaches and connects the hypolophid. This spur, together with the buccal part of the hypolophid, the buccal part of the posterior arm of the protoconid and the ectolophid, isolates a small oval fovea at the center of the tooth as in some specimens of *Metaphiomys schaubi.*

The dP_4 (Figure 4.4b) are oval in outline, with a trigonid narrower than the talonid. Protoconid and hypoconid are subequal in size. The protoconid is labio-lingually opposed to the metaconid and develops an anterior arm that reaches the metaconid to form a complete metalophulid I. The anterocingulid is more prominent than that described in *M. schaubi* and remains unconnected to the metaconid and protoconid. The posterior arm of the protoconid constitutes a complete metalophulid II. The ectolophid is complete and displays a small mesoconid in its central part. The lingual mesolophid stems from the mesostylid on the lingual margin of the tooth and does not reach the reduced mesoconid. The entoconid is mesially located with respect to the hypoconid. The short anterior arm of the hypoconid attaches to the ectolophid, bounding lingually the wide and retroverse buccal sinusid. A strong hypolophid, originating from the entoconid, connects buccally the anterior arm of the hypoconid. The posterolophid runs from the hypoconid toward the disto-lingual side of the entoconid and bears a moderately developed hypoconulid.

On P_4 (Figure 4.4a), the talonid is larger than the trigonid. The metaconid and the protoconid are united by a metalophulid II. There is no anterocingulid. A tiny anteroconid, mesially located to the metaconid, lies at the front of the tooth. The tooth exhibits a small distinct mesoconid on the ectolophid but there is no trace of mesolophid. The entoconid is slightly more mesial than the hypoconid. The postelorophid is well developed and bears a reduced hypoconulid.

The upper $M^{1/2}$ (Figure 4.4f-g) are characterized by their pentalophodont pattern. The anteroloph runs buccally from a large and oblique protocone but does not connect mesio-buccally the paracone. The paracone is the highest cusps on the tooth. The protoloph is

straight buccally and parallel to the anteroloph. Lingually, it curves slightly backwardly to joins the buccal extremity of the short posterior arm of the protocone. The mesolophule is variously developed. In one specimen (Figure 4.4g), the mesolophule is incipient and never reaches the low mesostyle isolated on the buccal margin of the tooth. At another extreme, the mesolophule is long and reaches the labial margin of the tooth. The metaconule is indistinct. The metaloph, disto-lingually directed, runs lingually from the metacone. As in *Phiomys andrewsi, Ph. hammudai* and *Ph. paraphiomyoide*s, the metaloph develops a double connexion. It displays a mesial connection to the mesolophule, as it does in *Baluchimys, Hodsahibia, Bugtimys, Asterattus* and *Protophiomys*. The crestule connecting the lingual part of the metaloph to the mesoloph is orthogonal to these latter crests. This mesial connection between the metaloph and the mesoloph has been lost in the other species ascribed to *Metaphiomys*. Further, the metaloph connects distally to the middle of the posteroloph. The anterior arm of the hypocone, the lingual part of the posteroloph, together with the crestules connecting the mesoloph to the metaloph to the posteroloph, surround a small oval fovea. By contrast with *Protophiomys*, *Talahphiomys,* and the South Asian "baluchimyines" *Hodsahibia*, *Lophibaluchia* and *Lindsaya*, a complete longitudinal mure, linking the anterior arm of the hypocone to the postero-buccal side of the protocone, at its junction with the protoloph, closes the lingual sinus buccally.

The M^3 (Figure 4.4h) has a similar lophate pattern as the other molars. The hypocone is more buccally positioned and comes closer to the metacone. The paracone is the largest cusp of the tooth and is mesio-distally enlarged. It connects mesially the buccal tip of the anteroloph and extends backwardly to the mesostyle. The metacone is greatly reduced and crestiform, the metaloph being fused within the posteroloph. The mesoloph connects the anterior arm of the hypocone. The protocone develops a long posterior arm which extends backwardly and tends to connect the lingual side of the hypocone. The lingual sinus has a disto-mesial orientation and a narrow disto-lingual opening.

The upper dP^4 (Figure 4.4e) is characterized by well-distinct and mesio-distally compressed cusps. The paracone and the protocone are labio-lingually opposed. A low

anteroloph tends to connect mesio-buccally the paracone and joins mesio-lingually the anterior arm of the protocone. The cone-shaped paracone is the largest cusp of the teeth. The anterior arm of the hypocone is strong and elongated. The metaconule is not distinct. A low lingual mesolophule reaches a minute buccal mesostyle and constitutes a complete but low mesoloph. The hypocone, as high as the protocone but larger, is prolongated posteriorly into a low posteroloph. The metacone, bucco-lingually elongated, is slighty more distally positioned with regard to the hypocone. The metaloph is short and connects disto-lingually the posteroloph.

Remark:

Wood (1968) described, from the Jebel Qatrani Formation, a number of isolated teeth which are somewhat close in morphology and in size to some of the teeth recovered from Zallah. Wood ascribed these Fayum teeth to an unknown species, belonging to *Phiomys* or *Metaphiomys*, suggesting that they may represent intergrades between these two genera. The size of the molars of our specimens and those described by Wood, do not significantly differ (test U, Mann-Whitney) from those of *Phiomys andrewsi* and *Metaphiomys schaubi.* Therefore they cannot be distinguished from these latter two species by their size. However the dental morphology of the species from Zallah (displaying lophodont cheek teeth, moderately high crowned, with a prominent posterior arm of protoconid bearing a backwardly directed protospur, lacking a mesolophid on lower molars, exhibiting pentalophodont upper molars with a variously developed mesoloph and a metaloph connected to the middle of the posteroloph) is consistent with the diagnosis of *Metaphiomys* suggested by Wood (1968). For these reasons, we assign this new species to the genus *Metaphiomys*.

Genus *Neophiomys* gen. nov. (Figure 4.4 i-o)

Type species: *Phiomys paraphiomyoides* (Wood 1968)

Etymology: From *Neo,* in Latin for "new"

Distribution: Jebel Qatrani Formation, (Quarry G, I), Fayum Depression; Zallah 5 Rodent locality, Sirt basin, Libya.

Age: early Oligocene

Original diagnosis from Wood 1968: "Jaw slender; cheek teeth significantly smaller than in genotype but incisors nearly as large; mesolophid or posterior arm of protoconid present but small; mesoconid not distinguishable; hypoconulid rather distinct; anterior cingula strong; metaloph connects with both posteroloph and mesoloph; diametric ratio of lower incisor about .64"

Emended diagnosis:

Small bunolophodont phiomyid characterized by moderately developed transverse lophs with cusps still individualized. The weak development of the posterior arm of protoconid, the absence of mesolophid on lower molars, the presence of a reduced mesolophule, the absence of mesoloph and the rarely developed connexion between metaloph and posteroloph discriminate this taxon from *Phiomys*. Upper molars differ from those of *Metaphiomys* in being much smaller and in having tetralophodont pattern characterized by the absence of a developed mesoloph. *Neophiomys* differs from *Paraphiomys* in being lower crowned, smaller in size, in showing a lesser development of transverses crests and more bunodont cusps. It differs from *Protophiomys* and *Talahphiomys* in exhibiting a well developed and continuous lingual mure closing labially the deep sinus and in the lack of metaconule.

Lower molars differ from those of *Metaphiomys* in having a less lophate pattern with cusps well discernible and in having a very short posterior arm of protoconid.

Differs from the Palaeogene South Asian "baluchimyines" in the absence of metaconule (*Baluchimys, Lindsaya*), in the loss of the endoloph (*Baluchimys, Lindsaya*), in the better development of the anterior arm of hypoconid and in the elaboration of a complete mure. Lower molars differ from those of the latter taxa in displaying a reduced posterior arm of protoconid and less developed lingual wall.

Neophiomys paraphiomyoides Wood 1968 (Figure 4.4i-o)

Holotype: CM26904, Lower jaw fragment with dP_4-M_3 and the incisor.

Referred material: Z5R-172, right P_4; Z5R-173, right P_4; Z5R-174, right M_1; Z5R-175, right M_1; Z5R-176, right M_1; Z5R-177, right M_1; Z5R-178, left M_2; Z5R-179, left M_2 ; Z5R-180, right M_2; Z5R-181, right M_2; Z5R-182, right M_2; Z5R-183, right M_2; Z5R-184, right M_2; Z5R-185, left M_3; Z5R-186, right M^3; Z5R-187, right M^3; Z5R-188, left M^1; Z5R-189, left M^2; Z5R-190, left M^2; Z5R-191, left M^2

Type-Locality: Quarry G of Jebel Qatrani Formation, Fayum, Egypt.

Distribution: Jebel Qatrani Formation, (Quarry G, I), Fayum Depression, Egypt; Zallah 5 Rodent locality, Sirt basin, Libya

Age: early Oligocene

Measurements: see Table 4.2

The material is temporarily deposited in the collections of iPHEP, University of Poitiers and it will be deposited after publication in the Collections of El Fateh University in Tripoli (Libya).

TABLE 4.2. measurements of *Neophiomys paraphiomyoides* cheek teeth

		Width (mm)	Length (mm)
Z5R-172	P_4	1.01	1.39
Z5R-173	P_4	1.07	1.44
Z5R-174	M_1	1.48	1.48
Z5R-175	M_1	1.44	1.4
Z5R-176	M_1	1.33	1.44
Z5R-177	M_1	1.29	1.39
Z5R-178	M_2	1.43	1.61
Z5R-179	M_2	1.4	1.49
Z5R-180	M_2	1.42	1.44
Z5R-181	M_2	1.44	1.39
Z5R-182	M_2	1.48	1.58
Z5R-183	M_2	1.36	1.6
Z5R-184	M_2	1.38	1.64
Z5R-185	M_3	1.31	1.43
Z5R-186	M^3	1.28	1.19
Z5R-187	M^3	1.26	1.09
Z5R-188	M^1	1.24	1.13
Z5R-189	M^2	1.39	1.31
Z5R-190	M^2	1.5	1.28
Z5R-191	M^2	1.65	1.36

Diagnosis: As for genus

Description

Lower molars of *Neophiomys paraphiomyoides* are rectangular in outline, lophodont with cups still well expressed. The anterocingulid is low, weak and slightly enlarged mesio-buccally as in *Ph. andrewsi.* A minute isolated anterostylid is developed on its buccal part.

$M_{1/2}$ (Figure 4.4j-k) are characterized by a trilophodont pattern with a metalophulid I, a hypolophid and a posterolophid. The metaconid is more mesial than the protoconid. The posterior arm of the protoconid is short, it decreases in strength lingually and ends long before it can reach the lingual border of the tooth. It is reduced to its most buccal part. In some cases, there is no more than a slight swelling where the posterior arm of the protoconid should be developed. This structure is strongly reduced with respect to what observed in *Phiomys*, *Metaphiomys* and *Protophiomys*. There is neither indication of mesolophid, mesostylid nor of

mesoconid. The hypolophid, stemming from a large entoconid, is straight and connects the anterior arm of the hypoconid buccally. The hypoconid, slightly more distal to the entoconid, is separated from the protoconid by a wide buccal sinusid. This sinusid is bounded lingually by a complete mure which connects the ectolophid to the extended anterior arm of hypoconid at its junction with the hypolophid. A short posterolophid expands from the hypoconid and decreases in height as it comes nearer to the entoconid. Metaconid and entoconid are cuspidate but the hypoconulid is barely distinguable.

M_3 (Figure 4.4l) differs in its smaller size and in a reduced and more lingual hypoconid, which involves a more linguo-buccally pinched talonid. The anterior cingulid is reduced and only remains on the mesio-buccal corner of the tooth as a tiny stylid.

Two dP_4 have been ascribed to this species. The dP_4 (Figure 4.4i) are longer than wide and exhibit a trilophodont pattern. Metaconid and protoconid are labio-buccally opposed and are closely positioned, the trigonid being pinched labio-buccally and narrower than the talonid. The metalophulid I is absent. The protoconid connects to the metaconid through an arching metalophulid II, convex distally. The anterocingulid is low. There is no anteroconid. The ectolophid, running distally from the protoconid to join the short anterior arm of the hypoconid, is long and slender. One of the teeth exhibits an incipient mesolophulid that extend lingually from a small mesoconid centrally positioned on the ectolophid. The hypoconulid is well marked on the posterolophid.

Upper molars are rectangular, being wider than long. $M^{1/2}$ exhibits a tetralophodont pattern characterized by an anteroloph, a protoloph, a metaloph and a posteroloph (Figure 4.4m-n). The anteroloph is well developed, lower than the other lophs and does not connect to the paracone. This latter cusp is the highest one of the tooth. It is slightly enlarged disto-buccally and its posterior arm tends to connect distally to the metacone in some specimens to constitute a mure on the buccal side of the tooth. The protocone is disto-lingually directed and more oblique than the hypocone. Protocone and hypocone are separated by a wide lingual sinus. As in *Phiomys*, *Metaphiomys* and *Paraphiomys*, this sinus is closed by a complete mure which extends from the anterior arm of the hypocone and is connected to the lingual part of

the protoloph at its bending point. The metaloph is short, extending only approximately one third of the distance across the tooth. It connects mesially to a very short mesolophule. The metaloph also joins the posteroloph via a mesio-distally oriented thin crest, as it does in *Phiomys*, *Metaphiomys* and *Paraphiomys*. However this latter connection is incipient and present only in worn teeth. Two fifth only of the recovered molars clearly display this distal connection. The mesolophule is poorly developed and in some case submerged in the lingual part of the metaloph. As in some "baluchimyines" (*Lophibaluchia pilbeami, Baluchimys chaudryi, Hodsahibia beamshaiensis, Zindapiria*), *Phiomys*, *Metaphiomys* and *Paraphiomys*, the metaconule is indistinct. Neither mesostyle nor mesoloph have been observed in any specimen, excluding them from the material referred to *Phiomys*.

M^3 (Figure 4.4o) is characterized by the occurrence of a strong and long lingual posterior arm of the protocone directed toward the hypocone, which lingual arm tends to close lingually the internal sinus. As on the molars, the paracone is the largest and highest cusp of the tooth. The mesolophule is developed but is very low. It stems from an indistinct metaconule and reaches the metacone buccally. Mesio-buccally, the anteroloph tends to connect to the protoloph.

Order Rodentia Bowdich 1821

Suborder Ctenohystrica Huchon, Catzeflis and Douzery 2000

Infraorder Hystricognathi Tullberg 1899

Super-Family Talahphiomyidae (this study)

Genus *Phiocricetomys* Wood 1968

Remark:

By its great bunodonty, its small size and the reduction of the dental row to three teeth, *Phiocricetomys* has always been considered as a very specialized member of the family (Wood 1968; Lavocat 1973). Wood (1968) has described *Phiocricetomys minutus,* on the basis of a partial mandible, as a species which had lost its permanent and deciduous premolars and reduced its M_3. He interpreted the first tooth of the row as representing a modified M_1, elongated to maintain a constant tooth row length. Considering the newly recovered material referable to this genus, and similarities in shape and in morphology between *Phiocricetomys* M_1 and deciduous premolars of other members of the family, the anterior tooth of the tooth row is rather considered as being homologous to a dP_4. Therefore, *Phiocricetomys* is recognized as a highly derived Talahphiomyidae which has retained permanently its deciduous premolars, lost its M_3, and reduced the size of its M_2. This general pattern of the retention of the dP_4 is in accordance with the evolutionary trends observed among the other members of the family.

Phiocricetomys atavus sp. nov. (Figure 4.4p-s)

Holotype: Z5R-193, left M_2 (Figure 4.4p)

Referred material: Z5R-193, right M_2; Z5R-201, left $M^{1/2}$, Z5R-202, left $M^{1/2}$; Z5R-203, left $M^{1/2}$

Type-Locality: Zallah 5 Rodent locality, Sirt basin, Libya

Etymology: atavus, latin name for “ancestor”

Age: early Oligocene

Measurements: see Table 4.3

The material is temporarily deposited in the collections of iPHEP, University of Poitiers and will be deposited after publication in the Collections of El Fateh University in Tripoli (Libya).

TABLE 4.3. Measurements of *Phiocricetomys atavus* cheek teeth

		Width (mm)	Length (mm)
Z5R-193	M_2	0.88	0.98
Z5R-201	$M^{1/2}$	0.97	1.05
Z5R-202	$M^{1/2}$	0.85	1.01
Z5R-203	$M^{1/2}$	0.96	1.05

Diagnosis:

Smallest known species of *Phiocricetomys* characterized by bunodont cheek teeth displaying salient cusps. Upper molars longer than wide characterized by the absence of mesoloph, a reduced metaloph, a metacone almost fused within the posteroloph. Upper molars exhibit a low and poorly developed anteroloph which is slightly connected to the protocone. Rounded protocone smaller than the hypocone; weak or absent development of the metaloph-metaconule connexion; complete mure closing the internal sinus. Metaconule varies from being well developed to small. Bunodont lower molars characterized by the lack of mesoconid and mesolophid and by the absence of posterior arm of the protoconid. Anterior and labial cingulid well developed on lower molars as in *P. minutus* but differs from this latter in bearing no trace of any cusps on the labial cingulid. Differs also from *P. minutus* in having more sharpened cuspids and by the lesser development of the crests.

Description

Only 4 isolated teeth have been referred to this species, including one lower and three uppers, which represent the first upper teeth known from that taxon.

A small isolated bunodont tooth characterized by very bulbous and prominent cusps is interpreted as an M_2 (Figure 4.4p) and defined as the holotype. Cresting is very poorly developed on this tooth and much lesser than that observed in *P. minutus*. Protoconid and

hypoconid are cuspidate, subequal in size and larger than metaconid and entoconid. A small hypoconulid is developed on the disto-lingual side of the postelorophid. There is neither mesoconid nor mesostylid. As in *P. minutus*, the metalophulid I, II and the ectolophid are absent, the postelorophid is much reduced and there is no hypolophid. The tooth displays a low mesio-labial cingulid, running mesially from the hypoconid toward the front of the protoconid. This cingulid is less prominent than that of *P. minutus*. *P. atavus* displays a small anteroconid in front of the protoconid but contrary to *P. minutus*, the labial cingulid does not bear any cuspules.

Two upper molars (Figure 4.4r-s) and one tooth germ (Figure 4.4q) have been identified. They exhibit a tetralophodont pattern with an anteroloph, a protoloph, a poorly developed metaloph and a posteroloph. The anteroloph is low but higher than that of *Talahphiomys.* Cusps are more sharpened than in this latter genus. The connection between the anteroloph and the protocone is slight. The protocone is rounded and not submerged in the anteroloph as in *Phiomys*, *Protophiomys*, *Metaphiomys* and some Asian "baluchimyines". Protocone and hypocone are sharpened and rounded while the labial cuspids are mesio-distally compressed. The hypocone is larger than the protocone. The paracone is cone-shaped and extends lingually to connect the disto-labial side of the protocone. It is sligthly more distal than the protocone. A longitudinal mure links the anterior arm of the hypocone to the distal side of the protocone, closing labially the internal sinus as it does in *Phiomys*, *Metaphiomys* and *Paraphiomys*. The lingual sinus is shallow and proverse. The hypocone displays a short anterior arm which connects mesially to a well distinct metaconule as in Asian "baluchimyines" (*Baluchimys, Lindsaya* and *Bugtimys*). The metaconule is greatly developed as that of *Baluchimys*, *Lindsaya, Asterattus*, *Bugtimys*, *Protophiomys* and *Talahphiomys*. There is no endoloph, neither mesostyle nor mesoloph. The metaloph is faintly developed, reminiscent to what is observed in *Talahphiomys* and in some "baluchimyines". A short and low crest running from the hypocone along the distal edge of the tooth appears to be homologous to the posteroloph.

Unfortunately no upper molars of *Phiocricetomys minutus* have been described from the Fayum so comparison between the two species is strenuous. However *P. atavus* lower molars by their very bunodont pattern, the lesser development of the marginal cingulid and the poor degree of crest development could be however regarded as less specialized than *P. minutus* and more primitive.

Genus *Talahphiomys* Jaeger et al. 2010

Talahphiomys lavocati (Wood) 1968 (Figure 4.4t)

Holotype: CM 26903, right lower jaw with M_1-M_3

Referred material: Z5R-192, left lower jaw with $M_{2\text{-}3;}$ Z5R-194, right $M_{1;}$ Z5R-196, left M_2; Z5R-197, left M_3, Z5R-198, right M_3; Z5R-200, left M_3

Type-Locality: Quarry E of Jebel Qatrani Formation, Fayum Depression, Egypt

Distribution: Jebel Qatrani Formation, (Quarry E, L-41), Fayum Depression, Egypt; Dur At-Talah escarpment, Central Libya; Zallah 5 Rodent locality, Sirt basin, Libya

Age: late middle Eocene - early Oligocene

Measurements: see Table 4.4

The material is temporarily deposited in the collections of iPHEP, University of Poitiers and it will be deposited after publication in the Collections of El Fateh University in Tripoli (Libya).

Diagnosis: see Jaeger et al. 2010

TABLE 4.4. Measurements of *Talahphiomys lavocati* cheek teeth

		Width (mm)	Length (mm)
Z5R-192	M_2	0.95	1.10
Z5R-192	M_3	0.97	0.93
Z5R-194	M_1	0.93	1.13
Z5R-196	M_2	1.03	1.27
Z5R-197	M_3	1.01	1.17
Z5R-198	M_3	0.89	-
Z5R-200	M_3	1.07	1.11

Description

Only 5 isolated incomplete lower teeth and a left lower jaw, badly broken and abraded, displaying an incomplete tooth row, have been recovered. The jaw is damaged distally, as no part of the ascending ramus is present. Because it is broken mesially through the diastema at the mental foramen position, only a short posteromost fragment part of the diastema is preserved. The jaw is slender, the masseteric fossa is pronounced and the mental foramen is not preserved. The anterior tip of the masseteric crest lies under the mesial margin of M_2.

M_2 and M_3 are preserved on the jaw (Figure 4.4t). The presence of a third lacking tooth is inferred from the shallow alveolus located just ahead the M_2 and by the interdental contact facet exposed on its anterior margin. The second tooth present on the jaw has a rounded and reduced posterior half, identifying it as an M_3.

Lower molars display a trilophodont pattern with well marked cuspids connected by slender crests. Protoconid, metaconid, entoconid and hypoconid are subequal in size, sharpened and slightly inclined forward. Metaconid and entoconid are slightly compressed mesio-distally. Protoconid and hypoconid are more rounded and lower than the lingual cuspids. M_2 exhibits a low mesial anterocingulid enlarged buccally as it does in *Phiomys andrewsi* and *Neophiomys*. The metaconid is a bit more mesially located with respect to the protoconid, and connects it through a slender metalophulid I. The metaconid displays a short posterior arm. The lack of posterior arm of the protoconid is reminiscent to what observed in *Neophiomys*, *Paraphiomys, Phiocricetomys* and *Paraulacodus*. There is no indication of mesoconid or mesolophid. The ectolophid is well developed. The hypoconid displays a short anterior arm which connects the labial extremity of the hypolophid. The posterolophid runs from the hypoconid toward the entoconid but doesn't reach it. A well developed hypoconulid lays on the medial part of posterolophid. There is no trace of lingual wall as the trigonid and the talonid remain open lingually.

M_3 is smaller than M_2 but very similar in morphology. The talonid is more rounded and labio-lingually and mesio-distally pinched with a smaller hypoconulid, barely distinguishable on a very short posterolophid.

This species is very close in morphology and in size to *T. lavocati*, described by Wood (1968) from the Fayum, and it is therefore ascribed to the same species.

4. PHYLOGENETIC ANALYSIS

A cladistic study, based on morphological dental characters, has been undertaken to investigate the phylogenetic relationships of the new taxa described herein among hystricognathous rodents.

The data matrix was constructed by adding the new taxa to the data matrix previously established (Coster et al. 2010). The analysis was based on 2 outgroup taxa, namely *Yuomys cavioides* (Yuomyidae) and *Birbalomys woodi* (Ctenodactylidae) and 36 ingroup taxa, including the African Eocene - Oligocene phiomorphs (18 species) and Eocene - Oligocene South American caviomorphs (ten species), earliest Asiatic members of Hystricognathi, the "baluchimyines" (*Lindsaya derbugtiensis, Baluchimys ganeshaper, Bugtimys zafarullahi, Hodsahibia azrae, Lophibaluchia pilbeami)* and three species of Hystricidae (*Hystrix cristata, Hystrix depereti, Hystrix primigenia*). The data matrix comprised 65 morphological dental characters. Cladistic analysis of the data was conducted using TNT (Goloboff et al. 2003). Heuristic searches for most parsimonious trees used 1000 replications with random stepwise addition, a randomized input order of taxa and tree bisection-reconnection. Characters were unweighted and three characters were ordered (character 1-3). The polarisation of character state transformations of multistate characters was based on the outgroup comparison criterion (Watrous and Wheeler 1981). The following description and discussion of the results only deal with unambiguous changes of characters on the cladograms. Parsimony analysis results in 8 most parsimonious trees. The strict consensus (251 steps, CI=0.35, RI=0.67) is represented in Figure 4.5.

The relationships obtained from this cladistic analysis are quite similar to those obtained previously (Coster et al. 2010), despite small differences in taxa sampling. As these relationships have already been discussed previously, we will mainly focus on the relative position of taxa described herein.

Several characters show marked homoplasy on the most parsimonious trees and this study demonstrates the paraphyly of both "Phiomorpha" and that of the "baluchimyines", as previously recognized (Marivaux et al. 2002, 2004). Considering the paraphyly of these later groups, the proposal of new taxonomic units within hystricognathous rodents is required. Nevertheless, the results of our analysis are not particularly robust, as illustrated by the Bremer support values, which are no more than one at the majority of nodes (Figure 4.5). However, if we combine the informations from different phylogenetic trees obtained recently by various authors (Marivaux et al. 2002, 2004; Sallam et al. 2009), one can recognize at least three distinct monophyletic groups which correspond respectively to the Talahphiomyidae, the Protophiomyidae and to a last huge group associating part of the former African "phiomyids", the hystricids and the caviomorphs that we propose to unit under a new super-family Phiocaviomorpha.

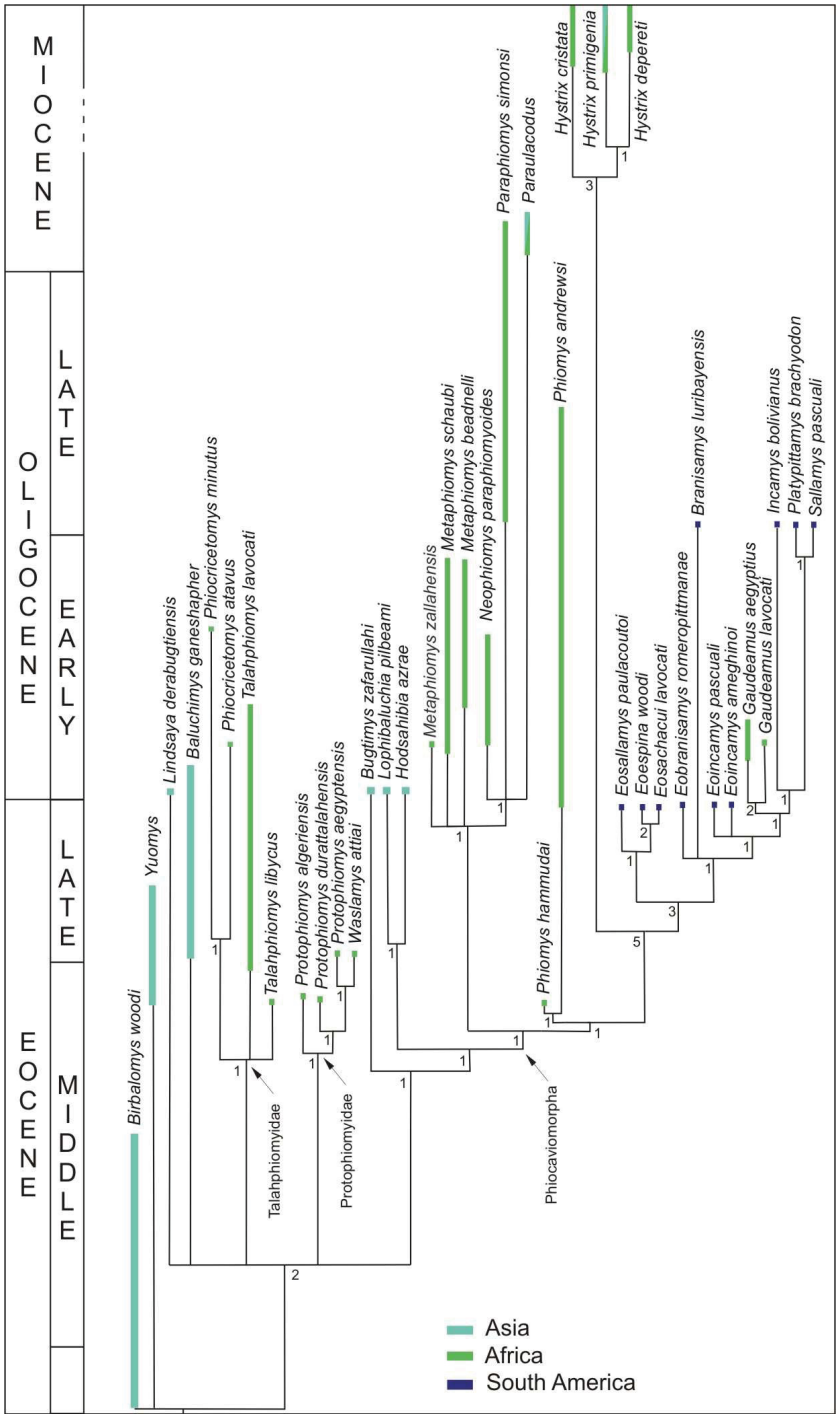


Figure 4.5. Strict consensus trees of 8 equally most parsimonious tree showing the temporal range and geographical extent of the 36 hystricognath taxa included in this study. Bremer support values (Bremer 1988), calculated using TNT (Goloboff et al. 2003) are labelled at each node.

Four genera of Phiomyidae, *Talahphiomys*, *Phiocricetomys*, *Protophiomys* and *Waslamys,* are scattered in various position at the base of the tree with members of Asian

"baluchimyines". However, the genera *Talahphiomys* and *Phiocricetomys* together constitute a basal clade, the Talahphiomyidae. The basal position of these two genera within hystricognathi is supported by 7 unambiguous character state changes synapomorphies, which are homoplastic (character 1, state 1: bunodont pattern, ch. 11, state 1: metaconid position relative to protoconid, ch. 12, state 0: posterior arm of protoconid, ch.26, state 0: parastyle; ch. 28, state 0: posterior outgrowth of the protocone, ch. 34, state 2: metaloph connexion; ch. 57, state 1: metaconule on upper deciduous premolars). The analysis supports the statement that, within the former "Phiomyidae" family, *Talahphiomys* exhibits the highest degree of similarities with *Phiocricetomys.* Wood (1968) interpreted *Talahphiomys lavocati* as "a basal taxon in the lineage leading to *Paraphiomys".* The results from our analysis are far from supporting such a statement, *Talahphiomy*s is not closer to *Paraphiomys* (nor to many other phiomyids) than to some Asian "baluchimyines".

In the present study, the three species belonging to the genus *Protophiomys*, (*P. algeriensis*, *P. durattalahensis*, *P. aegyptensis)* are associated with *Waslamys* in a clade*,* the Protophiomyidae*,* which is supported by three convergent characters, including two on the upper deciduous premolars (ch. 9, state 0: Anterior cingulid; ch. 54, state 0: endoloph on upper deciduous premolars, ch.57, state 1: metaconule on upper deciduous premolars). According to Sallam et al. (2009), the principal characteristics that distinguish the genus *Waslamys* from the genus *Protophiomys* are a well-developed labial wall on upper molars, a relatively well-developed mesolophule, a relatively well-developed endoloph on $M^{2–3}$ and a metaloph that varies from being posteriorly oriented or in contact with the anterior arm of the hypocone. These three latter characters are respectively character 33, 28 and 34 of our analysis and constitute in fact symplesiomorphies within the ingroup. Therefore, these characters do not offer support to the distinction of the genus *Waslamys*. Jaeger et al. (2010) described a new species of *Protophiomys* from Dur At-Talah and expanded the original diagnosis of the genus to include additional morphological occlusal dental features (incipient or achieved pentalophodont pattern depending on the degree of development of the mesolophule, an internal sinus often lingually closed by an endoloph and a tendency to

develop a buccal wall connecting the posterior arm of the paracone to the anterior arm of the metacone). The occlusal dental morphology of *Waslamys* fits in the new definition of the genus *Protophiomys.* The comparison of the morphological characteristics of *Waslamys,* as determined by Sallam et al. (2009), with those defined in the emended genera diagnosis of *Protophiomys* (Jaeger et al. 2010) and the nesting of *Waslamys* in the clade regrouping *P. aegyptensis, P. algeriensis* and *P. durattalahensis*, demonstrate that the species *Waslamys attitai* should be reassigned to the genus *Protophiomys.*

A clade composed of a former "Phiomorpha" subset (*Paraulacodus*, *Paraphiomys*, *Metaphiomys* and *Neophiomys*) display a basal quadritomy with the three species assigned to *Metaphiomys* and a subclade comprising three "phiomyid" genera (*Paraphiomys, Paraulacodus, Neophiomys*). This "phiomorpha" subset (*Paraulacodus*, *Paraphiomys*, *Metaphiomys* and *Neophiomys*) constitutes the sister taxa of the clade clustering *Phiomys, Hystrix* and caviomorphs, forming a huge clade, the Phiocaviomorpha, supported by five synapomorphies (ch. 23, state 0: hypoconulid size, ch. 29, state 1: presence of the mure; ch. 35, state 2: absence of metaconule; ch. 57, state 2: indistinct metacoule on uppers deciduous premolars; ch. 58, state 1: metaloph-posteroloph connexion on upper deciduous premolars). The Phiocaviomorpha are also supported by the result of previous phylogenetic analysis (Coster et al. 2010). The clade that groups *Neophiomys* with *Paraphiomys* and *Paraulacodus* is supported by four synapomorphies (ch.12, state 0: posterior arm of protoconid, ch. 33, state 0: mesolophule; ch. 41, state 0: mesoconid on lower deciduous premolars; ch. 42, state 0: mesolophid on lower deciduous premolars). However, these four character state changes are homoplasic within hystricognathous rodents in our analysis. *Neophiomys* was first identified from the Oligocene of Egypt (Wood, 1968), as a *Phiomys* and interpreted as "structurally intermediate between *Phiomys andrewsi* and *Ph. lavocati*". According to our analysis and regarding its occlusal dental morphology (characterized by the great reduction of the posterior arm of the protoconid (ch. 13), the absence of mesolophid (ch.20), the connexion of the metaloph to the posteroloph (ch. 34) and a short lingual mesolophule which does not reach the buccal margin of the tooth but connect the lingual tip of the metaloph (ch. 33)), it seems to

represent a close ally to *Paraphiomys* and *Paraulacodus,* possibly the earliest diverging member of this clade.

In this analysis, primitive African members of Hystricognathi (*Protophiomys*, *Waslamys, Talahphiomys* and *Phiocricetomys*) appear phylogenetically closer to South Asian 'baluchimyines' than to other African phiomyids. On the other hand, some 'baluchimyines' (*Lophibaluchia, Bugtimys* and *Hodsahibia)* exhibit a higher degree of similarities with derived Phiomyids than with other Asian hystricognathous rodents. It is assumed that the phiomyids are closely related to the "baluchimyines", which are considered as the earliest Asiatic offshoots of Hystricognathi (Flynn and Cheema 1994; Marivaux et al. 2000; Marivaux 2003; Marivaux and Welcome 2003). The oldest known African hystricognathous rodents have been recovered from late middle to early late Eocene deposits of Algeria (Jaeger et al. 1985), Libya (Jaeger et al. 2010) and Egypt (Sallam et al. 2009) while earlier fossiliferous localities in Africa display peculiar rodents fauna composed of Zegdoumyidae (Vianey-Liaud et al. 1994). Hystricognathous rodents might have entered in Africa sometimes during middle Eocene but the fossil record of Africa displays a large gap through the upper Lutetian and almost the entire Bartonian. The Asia to Africa migration pattern of hystricognathous rodents is thus difficult to infer. Regarding phylogenetic analyses, our results may reflect a multiple dispersal history during the middle Eocene or may be the result of one dispersal event from Asia followed by diversification and subsequent convergent evolution. Unfortunately, the middle Eocene Epoch in Africa is very poorly documented and additional finds from this time gap in the African fossil record are needed to further constrain the timing and pattern of hystricognathous rodent migration in Africa.

5. PALEOMAGNETIC ANALYSES

Rock samples for paleomagnetic analyses were collected from 11 stratigraphic levels along a 50 m thick section sampled at Z-5R locality. The section displays an alternation of laminated red claystones, green claystones interbedded with siltstone and gypsum reflecting

an estuarine-lagoonal to deltaic depositional environment. The section is capped by basaltic lava flows which uncomformably overlies a 2m thick clast-supported conglomerate bed on the topmost part of the section.

Oriented blocks samples have been collected from each stratigraphic level and prepared at the laboratory. The paleomagnetic analyses of the samples were carried out at the Laboratory of Paleomagnetism of the University of Austin, Texas. The intensity and direction of the remanent magnetization were measured on a vertical-oriented cryogenic magnetometer (model 2G) equipped with an automatic sample changer.

In order to investigate the minerals carrying remanent magnetization, Isothermal Remanent Magnetization (IRM) acquisition was performed (Figure 4.6).

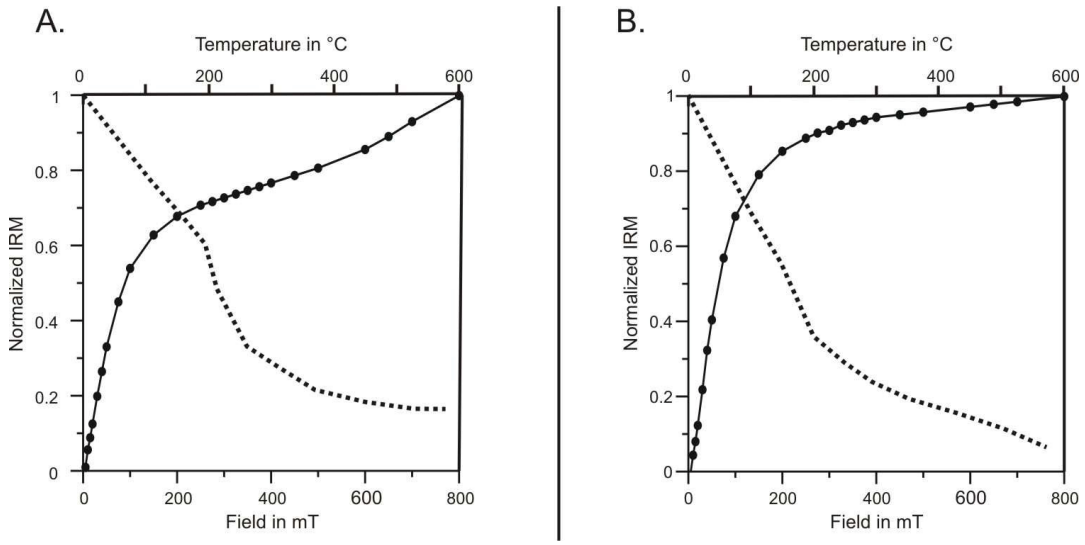


Figure 4.6. (A.) Isothermal Remanent Magnetization (IRM) acquisition (normalized values) and stepwise thermal demagnetization (dashed line) curves of a red claystone sample. (B.) IRM acquisition (normalized values) and stepwise thermal demagnetization (dashed line) curves of a grey claystone sample.

An increasing field up to 0.8 T was applied on samples of various lithologies. Stepwise IRM acquisition shows that red claystone samples have two magnetic components, one saturated at field of 200-400 mT and another unsaturated at 800 mT (Figure 4.6A).

Change in slope of thermal demagnetization curve between 200 and 300°C is likely to indicate the presence of iron-sulfides or titanomagnetite. The remanent magnetization is still not completely removed at 580°C, indicative of high unblocking temperature minerals, probably hematite. Green claystone samples show in general an initial rapid acquisition of about the total IRM at 200mT but do not saturate beyond 800 mT (Figure 4.6B). Marked loss IRM intensity within the 0–300°C are indicative of iron-sulfides, titano-maghemite or titano-magnetite. The thermal decay of the intensity at 580°C reveals the presence of magnetite. This result agrees in demonstrating the presence of two mineralogical phases: a low coercivity phase ascribed to magnetite, titanomagnetite and/or iron-sulfides with a minor contribution of high coercivity grains in the grey claystones. Red claystones exhibits a larger proportion of high coercitivity minerals.

To isolate the Characteristic Remanent Magnetization (ChRM), samples were subjected to progressive thermal demagnetization from 100°C with 25-50°C increments up to 600°C. Results of demagnetization were plotted on orthogonal vector diagrams (Zijderveld 1967) and stereograms (Figure 4.7). The ChRM directions were calculated by principal component analysis following Kirschvink's method (1980). Mean directions were calculated by the Fisher statistics (Fisher 1953). Demagnetization analysis indicates that there are two components of magnetization in most treated samples. Some samples, however, display only one component of remanent magnetization. Statistical significance of site mean directions calculated by Fisher statistics (Table 4.5) was tested by Watson randomness criteria (Watson 1956). All the sites yielding three samples pass the test of randomness of direction. The sampled section exhibits monoclinal beds so the fold test could not be carried out. The normal and reverse polarity populations appear to be antipodal. A test of the Fisher precision parameter shows that means of normal and reverse sites overlap at the 95% level. The observed angle between the mean of normal and reverse polarity site is 2.5° and mean directions of opposing polarity sites have a critical angle of 15.4°. Mean directions pass the reversal test of McFadden and McElhinny (1990) with a C classification.

TABLE 4.5. PALEOMAGNETIC SITES MEAN DIRECTIONS OF ZALLAH SECTION, CENTRAL LIBYA

Site	N	Incl. (°)	Decl. (°)	α_{95} (°)	k	R	VGP latitude (°N)	polarity
1	3	-28.1	171.7	25.1	35.5	2.92	-73.8	R
2	2	-31.2	182.7	33.8	17.2	1.94	-77.9	R
3	3	-24.9	189.2	39	12.9	2.84	-72.2	R
4	3	-55.2	189.7	16.7	70.3	2.97	-79.2	R
5	3	-12.8	214.8	59.9	5.5	2.63	-50.3	R
6	3	-43	242.5	12.7	121.5	2.98	-34.8	R
7	2	-27.9	187.1	40.7	11.8	1.92	-74.7	R
8	2	-14.9	166.3	61.8	5.1	1.81	-65.2	R
9	2	18	18.2	6.4	478.5	2	64.5	N
10	3	29.6	20.5	44.6	9.85	2.8	67.2	N
11	3	33.7	6.4	55.3	6.41	2.69	78.2	N

Note: Incl.: mean tilt corrected inclination in degree to the horizontal; Decl.: mean tilt corrected declination in °E; α_{95}: mean direction 95% confidence ellipse; k : Fisher precision parameter; R : length of the resultant vector; VGP latitude: latitude of the virtual geomagnetic pole in °N; polarity: R: reverse, N: normal. Section location : 28°41'45"N, 17°30'48"E.

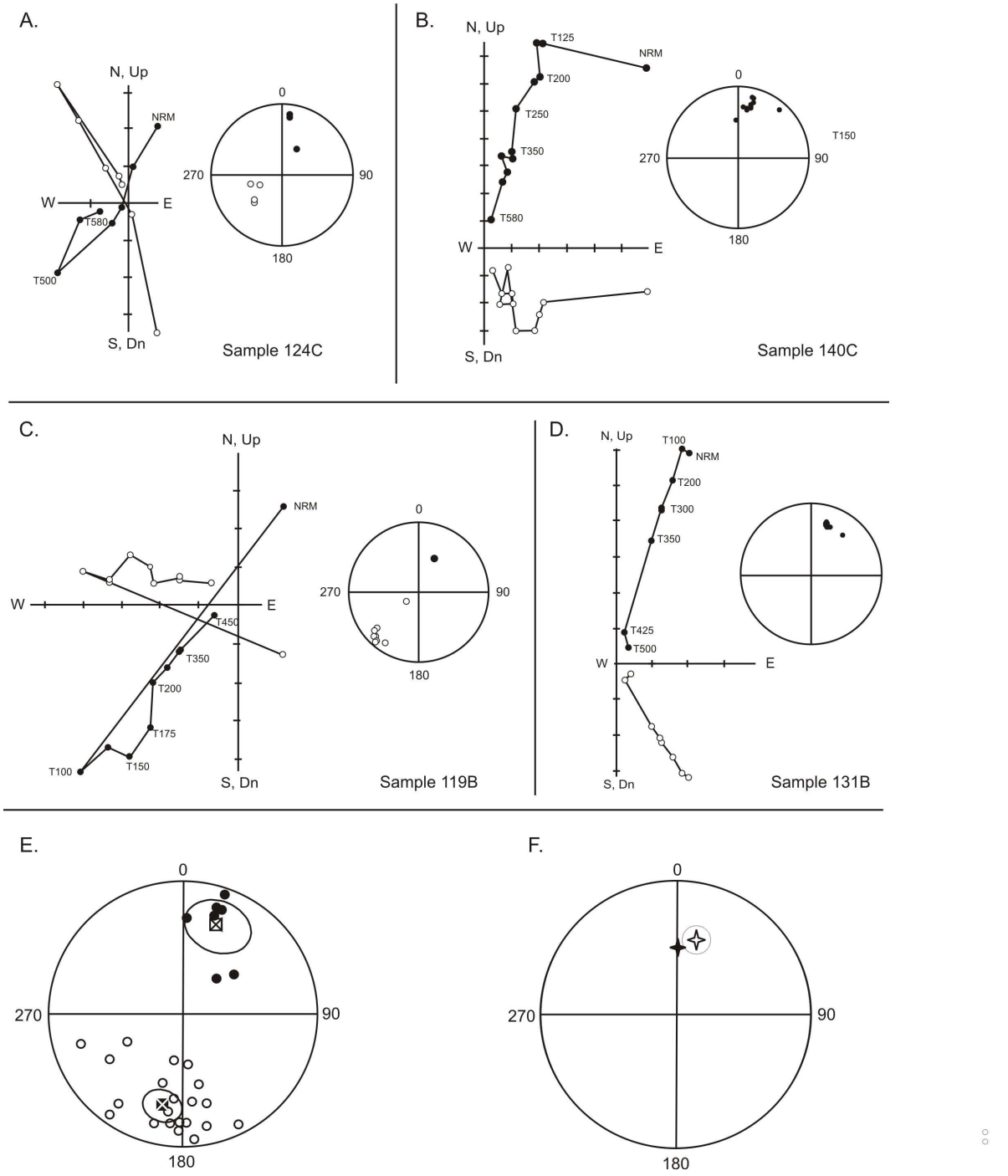


Figure 4.7. (A.-D.) Examples of orthogonal vector diagrams (closed (open) symbols correspond to the horizontal (vertical) component), equal-area stereographic projections (solid (open) symbols indicate positive (negative) inclinations) during thermal demagnetization. Demagnetization temperatures are given in °C. (E.) Equal-area stereographic projection and Fisher statistics of characteristic directions. Open (closed) circles indicate directions in the upper (lower) hemisphere. Mean directions calculated by fisherian statistic are represented by a square and the ellipse indicates the 95% confidence ellipse. (F.) Equal-area stereographic projection of mean site direction (hollow star) and solid star shows the direction derived from the 30 Ma Apparent Polar Wander Path of Torsvik et al. (2008).

The overall mean direction of ChRM directions is Decl.:15.5°, Incl.: 30.5°, α_{95}: 9.1°, and indicate a paleopole of 71.2°N and 144.9°E (dp/dm: 10.1/5.6) (Table 4.6). The APWP of Torsvik et al. (2008) at 30 Ma predicts an expected paleomagnetic direction at the studied area of: Decl.: 1.7°, Incl.: 37.4°, α_{95}:3.1° (Figure 4.7F).

TABLE 4.6. PALEOMAGNETIC POLARITY MEAN DIRECTIONS OF ZALLAH SECTION, CENTRAL LIBYA

	N	Decl. (°)	Incl. (°)	α 95 (°)	k	Pole postiton		dp/dm (°)
						Φ (°E)	λ (°N)	
Reverse specimens	21	193.8	-30.6	10.9	9.5	148.5	72.4	12.1/6.8
Normal specimens	8	21.0	30.2	18	10.4	135.8	67.0	20.0/11
Overall mean direction	29	15.5	30.5	9.1	9.9	144.9	71.2	10.1/5.6

Note: Decl.: mean tilt corrected declination in °E; Incl.: mean tilt corrected inclination in degree to the horizontal; α_{95} : mean direction 95% confidence ellipse; k : Fisher precision parameter; Φ: longitude of paleopole for mean direction in °E, λ: latitude of paleopole for mean direction in °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. Section location : 28°41'45"N, 17°30'48"E.

Using Demarest method (1953), the comparison of the expected and observed direction yields a vertical axis rotation of declinaison of 13.8°. This result indicates that the locality underwent a clockwise rotation which may present tectonic implications. Main bounding fault zones of Zallah Trough are predominantly normal. Sinistrial strike-slip fault systems are also observed. An anticlinal affecting the Paleogene sequence denotes a compressive phase leading to a slight inversion of Zallah Trough during Miocene (Abadi and van Dijk 1993). The clockwise vertical rotation observed in the studied area may be related to the numerous faults which deformed Zallah Trough or alternatively could have a broader tectonic significance. Large-scale compressional structures, related to the stress induced by the differential movement of African subplates, the Miocene Eurasian/Afro-Arabian collision, and the Red Sea rift opening, have been observed in Sirt basin (Van Der Meer and Cloetingh 1993; Schröter 1996). More sections need to be sampled to evaluate if the observed pattern is a response to local or regional tectonic.

The inclination values calculated for the section are lower than the expected values; this is interpreted as the sedimentary inclination error (King 1955). The inclination record in the sediments is generally influenced by depositional and post-depositional processes that produce flattened directions (Verosub 1977; Tauxe and Kent 1984; Anson and Kodama 1987).

The Virtual Geomagnetic Pole (VGP) latitudes and longitudes were calculated from the ChRM declination and inclination of each sample and were reported according to their stratigraphic level. The paleomagnetic reversal stratigraphy of Zallah section is shown on Figure 4.8. The magnetic stratigraphy reveals two polarities with about 30m thick reverse zone in the lower portion of the section where the rodent locality is located and a normal polarity zone at the top represented by the three uppermost stratigraphic levels of the section (Figure 4.8).

6. CORRELATION AND DISCUSSION

The age of Zallah deposits were poorly constrained, being only based on biostratigraphical data. Fossil occurrences are rare in this area and restricted to few localities. At about 10km south east of Zallah Oasis and more than 20km south of Z-5R locality, Arnould-Saguet and Magnier (1961) first described vertebrate remains at Z-locAR (Figure 4. 1B) from Oligocene deltaic and fluvial facies. Shark teeth (*Oxyrhina sp., Aetobatis sp.* and *Carcharhinus ergertoni*), crocodiles, turtles, bird remains and three teeth attributed to *Palaeomastodon intermedius* were originally described. Arambourg (1963) afterward identified from this locality the proboscidean *Phiomia wintoni,* the anthracothere *Bothriogenys* cf. *gorringei* and the hyracoid *Titanohyrax angustidens.* This hyracoid species is also known from the Fayum Jebel Qatrani Upper Sequence and first appears at the Oligocene Quarry V and I (Rasmussen and Simons 1988). Remains of *Bothriogenys* have been recognized from the Jebel Qatrani Formation but there is no precise indication concerning their stratigraphical occurrences. Based on this fossil assemblage, this site has been generally

believed to be early Oligocene in age, roughly contemporaneous with the Jebel Qatrani Formation (Arambourg 1963; Savage 1969, 1971; Wight 1980; Rasmussen et al. 1992).

Fossil rodents have later been described by Fejfar (1987) from Z-locF locality. He assigned 28 isolated teeth to three different species. 90% of the recovered specimens were referred to *Metaphiomys schaubi,* two isolated teeth were ascribed to *Phiomys andrewsi* and *Neophiomys paraphiomyoides.* On the basis of his newly micro-fauna recovery together with the previously described large mammals, Fejfar assumed a strong faunal correlation between Zallah locality and Quarry G of Jebel Qatrani Formation and enhance the presumed early Oligocene age of the Libyan deposits. The rodent assemblage described herein comprises four additional genera which include three new species (*Metaphiomys zallahensis, Phiocricetomys atavus* and *Gaudeamus lavocati*) but lacks *Metaphiomys schaubi* which is strikingly the most abundant taxon identified by Fejfar (1987).

Fejfar locality (Z-locF) is described as a small outcrop on a resthill 35km west of Zallah Oasis but it is difficult to locate its exact position. Several visits of the area have failed to recover this locality. Therefore it is arduous to correlate Fejfar site to our new Z-5R locality and to infer if the differences in taxonomic composition of the two localities rodent assemblages are related to taphonomic processes or to the respective stratigraphic position of these two localities.

The Oligocene Continental and Transitional Marine Deposits, in Zallah area, are represented by a transitional zone which is distinguished by continental deposits that are mixed with marginal sea sediments of estuarine, lagoonal and deltaic deposits. At Z-5R locality, the Oligocene estuarine-lagoonal to deltaic deposits uncomformably overlies marine Eocene Qrarat al Jifah Member of the Wadi Thamat Formation. The uncomformity between the fully marine Eocene deposits and the continental Oligocene sediments is located above Qrarat al Jifah Member which is quite thick. In the western part of Zallah area, the uncomformity is more prominent; Qrarat al Jifah and Thmed al Qusur Members of Wadi Thamat Formation are both missing and the lower part of Wadi Thamat Formation (Al Gata Member) is directly overlain unconformably by the Oligocene deposits of Ma'zul Ninah

Formation, which is supposed to be equivalent to the Continental and Transitional Marine Deposits. It seems thus that more section is missing in the western part of Zallah area which may have implications on the age of deposits located above the unconformity. It is possible, therefore, that the section at Fejfar rodent locality is not exactly equivalent to our section due to the uncomformity in the area.

Regarding biostratigraphic data, Z-5R locality, in comparison to the nearby Dur At-Talah locality, yields an evolutionary advanced set of phiomyids. It lacks the primitive representatives of phiomyid radiation, described from the late middle-early late Eocene deposits of Dur At-Talah (Jaeger et al. 2010), Bir el Ater locality in Algeria (Jaeger et al. 1985) and Birket Qarun locality 2 of Fayum (Sallam et al. 2009), which substantiates a more recent age. Zallah rodent assemblage displays further similarities to Fayum rodents from Jebel Qatrani Formation, of which revised magnetic polarity correlation assumes a latest Eocene to early Oligocene age (Seiffert 2006).

The locality of Zallah yielded isolated teeth of *Metaphiomys* which appears at quarry A and B of the Jebel Qatrani Lower Sequence. However, the Fayum localities display different species belonging to this genus but do not share common species of *Metaphiomys* with the locality of Zallah. *Gaudeamus,* restricted to the Lower Sequence of the Jebel Qatrani Formation*,* represents almost 80% of the recovered specimens at Z-5R locality. The dental pattern of *Gaudeamus aegyptius* from the quarries E, A and B appears to be very close to that of *G. lavocati* but seems more derived. Specimens of *Neophiomys paraphiomyoides,* similar in size and morphological dental pattern to the Libyan ones, were described by Wood (1968) in the Jebel Qatrani Upper Sequence. *Phiocricetomys atavus*, which exhibits more sharpened cuspids and a lesser development of the crests, seems to display more primitive characters than *P. minutus* described from the Jebel Qatrani Upper Sequence.

Holroyd (1994) described an assemblage of hystricognathous rodents from quarry L-41 of Jebel Qatrani Lower Sequence, comprising *Acritophiomys bowni*, *A. woodi, Gaudeamus hylaeus* and *Elwynomys lavocati.* The new species of *Metaphiomys* from Z-5R locality appears to be very close in occlusal dental morphology to *Acritophiomys*. Both taxa, which

are similar in size, share bunolophodont cheek teeth, lower molars with a posterior arm of protoconid extending distally toward the mesostylid, upper molars with a metaloph joining the posteroloph and a variously developed mesoloph displaying a distal connection to the metaloph. L-41 and Z-5R localities further share the occurrence of rodent taxa belonging to the genus *Gaudeamus* Unfortunately, the species from L-41 is only documented in Holroyd unpublished Ph.D (1994), and, in the light of the new specimens recovered from Zallah, it seems to us that upper and lower molars belonging to two different taxa have been attributed to the L-41 *Gaudeamus* species. Therefore, further comparisons between the *Gaudeamus* from Zallah and that from L-41 are awaiting a more complete description of the L-41 taxon. In addition, Holroyd reported, at L-41, the presence of *Elwynomys lavocati,* which is synonymous to *Talahphiomys lavocati*, also present at Z-5R locality. Regarding the similitude between the rodent assemblages, Z-5R locality is regarded as close in age to L-41. L-41 locality has been dated as latest Eocene in age but an earliest Oligocene age for this locality cannot be rejected (Seiffert 2006).

Besides, our rodent assemblage also bears resemblance to Thaytiniti fauna, Dhofar province of Oman. Based on magnetostratigraphic and biostratigraphic constraints, Thaytiniti mammal locality has been dated from the earliest Oligocene (Thomas et al. 1988, 1989, 2004; Pickford et al. 1994; Gheerbrant et al. 1995; Seiffert 2006). Two rodent taxa, *Metaphiomys* and *Talahphiomys,* are shared by the Zallah and the Omani fauna. The "phiomyid" described by Thomas et al. (1989) as cf. *Metaphiomys* exhibits a similar dental pattern as *Metaphiomys zallahensis*. Lower molars from Oman, initially described as *Phiomys lavocati* and now referred to *Talahphiomys lavocati,* are a bit smaller and display a slightly longer posterior arm of protoconid, a stronger anterocingulid, a more mesial entoconid, compared to those from Egypt and Libya (Wood 1968; Jaeger et al. 2010). The Omani upper teeth ascribed to *Talahphiomys* differ from those of the other species belonging to this genus in being more crested, in lacking a marked metaconule, in having a well developed metaloph, in having an incipient mesolophule and a well developed lingual mure. Although Thaytiniti lower molars are quite similar to those of *T. lavocati,* associated upper molars are morphologically very

different from those of Dur At-Talah. Unfortunately, no upper molars belonging to this species have been excavated from the Fayum and from Zallah deposits which prevents any exhaustive comparison. An isolated lophodont left upper molar has been described from Thaytiniti as "rodentia indet." (Thomas et al. 1989). This tooth exhibits a trilophodont pattern characterized by a crestiform protocone submerged in strong anteroloph, a transverse crest linking the paracone to the hypocone and a posteroloph and is referred here to the genus *Gaudeamus*. Although geographically far away, the Thaytiniti microfauna is reminiscent to the taxonomic association described at Z-5R locality and may indicate a roughly similar age for the two localities.

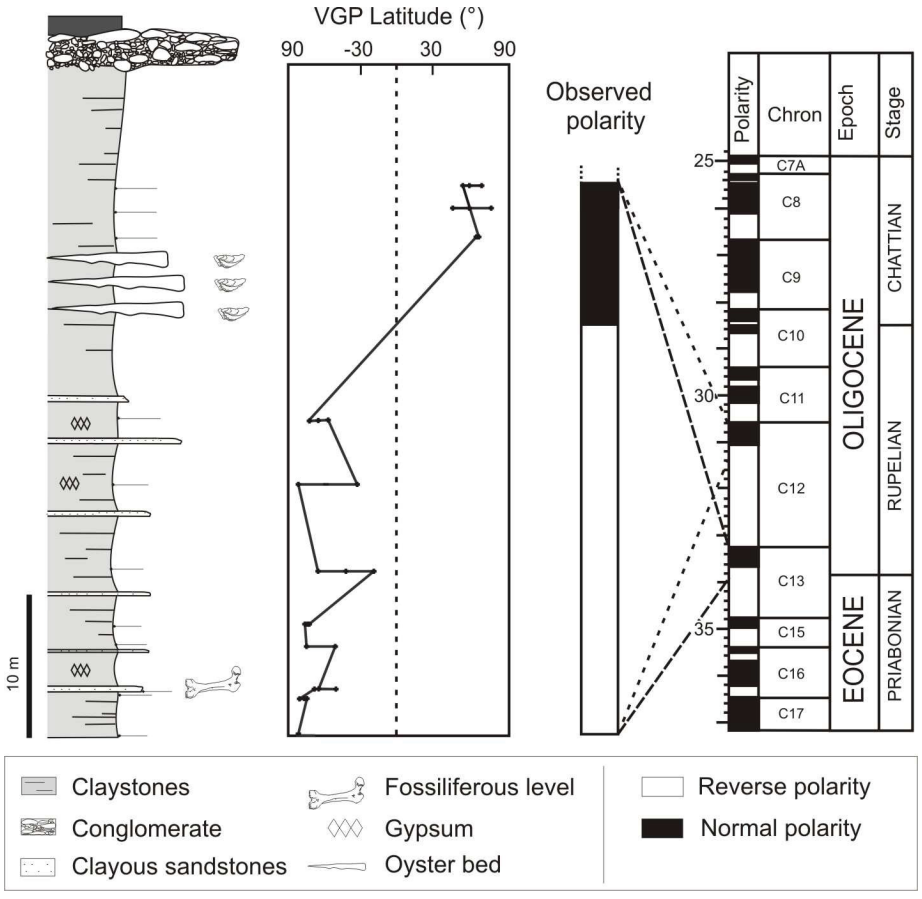


Figure 4.8. Paleomagnetic reversal stratigraphy of Zallah Section and preferred correlations with GPTS of Gradstein et al. 2004. Reversed (normal) magnetic polarity zones are represented in white (black). Virtual Geomagnetic Pole paleolatitudes of ChRM are plotted as function of stratigraphic levels. The lines at the right of the stratigraphic column indicate the position of the sites.

The biostratigraphic evidences summarized above suggest that Z-5R locality is certainly earliest Oligocene in age. The age of this locality is likely to range between the age of the quarries of the Jebel Qatrani Lower Sequence (Chron 13) and the oldest quarry of the Upper Sequence (Chron 12). Within this interval, comprised between approximately 35 and 30 Ma, two correlations are likely. The first correlation interprets the reverse polarity zone recorded in the lower part of Zallah section as chron C13r (34.8-33.7 Ma) and the topmost normal polarity zone of the section as belonging to chron C13n (33.7-33.3 Ma) (Figure 4.8). The second one correlates the polarity sequence of the section to chrons C12r-C12n (33.3-30.6 Ma).

Zallah 5 rodent fauna shares common occurrences of *Gaudeamus*, *Metaphiomys* and *Talahphiomys* with the Lower Sequence quarries (L41, A, B and E) of Jebel Qatrani Formation which substantiate an equivalent age. The relative abundance of *Gaudeamus* at Zallah 5 locality, which represents 80% of the recovered rodent specimens and the similarities in taxonomic composition with the Omani Thaytiniti fauna, may indicate that Zallah fossiliferous strata are more probably similar in age to the earliest Oligocene Lower Sequence of the Jebel Qatrani Formation. The first correlation with Chron C13, implying an earliest Oligocene age close to the Eocene-Oligocene boundary, may thus seem more likely.

7. CONCLUSION

Zallah 5 Rodent locality, a new fossiliferous site, located in the south western part of the Sirt basin, Central Libya, has yielded five phiomyid genera including one new genus and three new species. These discoveries significantly increase our knowledge of the early African hystricognathous rodents whose first record is documented from the latest part of Eocene Epoch (Jaeger et al. 1985; Sallam et al. 2009; Jaeger et al. 2010). The rich Paleogene Afro-Arabian fossiliferous localities of the Fayum Depression, Egypt and the Dhofar province, Oman, have produced rodent assemblages that are somewhat close to that of Zallah site. Biostratigraphic data restrict the age of Zallah rodent-bearing layers to the age of the Lower

Sequence of the Jebel Qatrani Formation, and indicate an age close to that of quarry L-41, i.e. close to the Eocene Oligocene Boundary. Magnetic polarity data suggest an earliest Oligocene age for Zallah 5 Rodent locality, or even a latest Eocene age. The new collection of Oligocene African rodents described herein does not extend the geographic and chronologic range of African hystricognathous rodents but improves our knowledge of their evolutionary history. The age of the Afro-Arabian Paleogene mammalian bearing sites are still poorly constrained and the precise dating of Zallah deposits represents major improvement to this situation. The placement of the Libyan locality into a consistent chronological framework constitutes considerable advancement to achieve biostratigraphic correlation of the Paleogene Afro-Arabian mammal localities.

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1.5. EOCENE CONTINENTAL MAMMALIAN INTERCHANGES AND EARLY DISPERSAL OF ANTHROPOID PRIMATES

1.5. EOCENE CONTINENTAL MAMMALIAN INTERCHANGES AND EARLY DISPERSAL OF ANTHROPOID PRIMATES

1. INTRODUCTION

The early Tertiary appears as a critical period in mammalian evolution and is understood as a time of significant ordinal-level diversification (Rose 1981; Stucky 1990; Alroy 1999; Foote et al. 1999; Archibald and Deutschman 2001; Springer et al. 2003). The worldwide Paleogene fossil record provides a clear outline of an early Tertiary adaptative radiation of mammals and the rise of many vertebrate groups that persist today (e.g. McKenna and Bell 1997; Alroy 1999; Novacek 1999; Archibald and Deutschman 2001; Rose 2006). The composition of the Paleocene and Eocene land mammal faunas may be considered in light of early Tertiary terrestrial paleogeography, resulting from the fragmentation and drifting of continental blocks, so-called the break up of Pangea, under way since the Jurassic (e.g. Dietz and Holden 1970; Smith et al. 1994; Scotese 1997; Veevers 2004). Marked similarities among Holoarctic Paleogene land vertebrates (McKenna 1971, 1975, 1983; Navacek 1999) and plants (Collinson 2000) indicate that the Laurasian northern landmasses were connected, at least intermittently, through land bridges between Asia and North America by the way of the Bering Strait and North America and Europe via Norwegian-Greenland Sea (e.g. Savage and Russell 1983). In contrast to the fairly cosmopolitan nature of fauna and flora in the holoarctic continents, the break-up of Gondwana, initiated during Jurassic, led to the isolation of southern landmasses during Paleogene, with the drifting of India and Australia-Antarctica from southern South America and Africa (e.g. Hames et al. 2000; Bartolini and Larson 2001; Veevers 2004). The Eocene fossil record from the southern

hemisphere is less complete than that from Laurasian continents and the mammalian faunas from South America and Africa display a high degree of endemism.

The paleobiogeographical history of Africa, isolated from mid-Cretaceous to early Miocene (Smith et al. 1994), is complex and despite a clear endemic character of Paleogene mammalian fauna, the distribution of several mammalian groups indicates terrestrial faunal interchanges between Africa and other Gondwanian continents and Laurasia during Paleogene (e.g. Tabuce and Marivaux 2005; Gheerbrant and Rage 2006). Unfortunately, the early tertiary record of Africa, though improved during the last past decades, is still poor and our knowledge of the appearance and diversification of many groups of continental vertebrates in Africa during the Eocene epoch is far from being as advanced as that concerning Europe or America.

2. EOCENE AFRICAN MAMMALIAN FAUNAS

The first Eocene mammals in Africa were collected from the Fayum Depression of Egypt and first described during the late 19th – early 20th century (Owen 1875; Dames 1894; Beadnell 1901; Andrews 1906; Stromer von Reich 1903; Schlosser 1911). Since these early discoveries, numerous field expeditions throughout the continental tertiary deposits in Africa have allowed to complete substantially the Afro-Arabian fossil record of Eocene mammals.

The oldest known Eocene mammal-bearing localities in Afro-Arabia, the Grand Daoui quarries of Ouled Abdoun phosphate basin and N'Tagourt 2 from Ouarzazate basin in Morocco (Figure 5.1), have been dated as early Ypresian (Gheerbrant et al. 2003) and middle Ypresian (Gheerbrant et al. 1998), respectively (Figure 5.2).

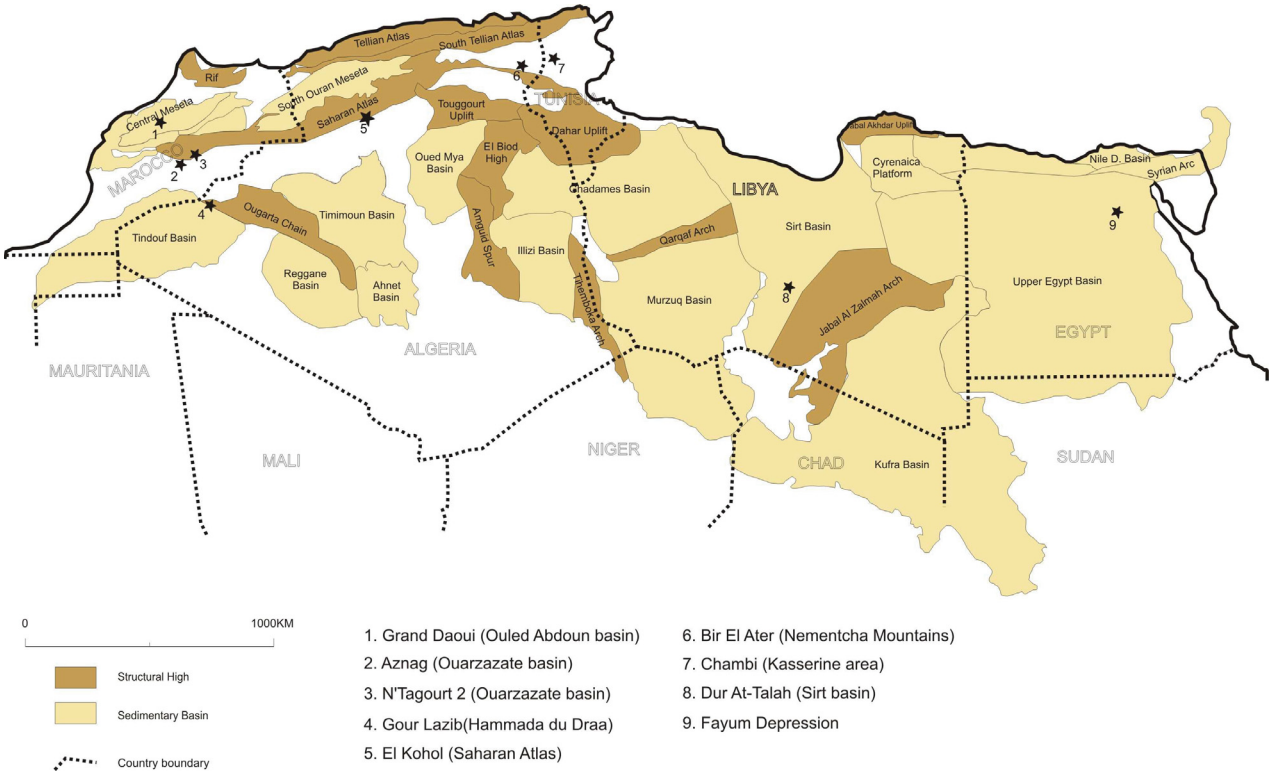


Figure 5.1. Major sedimentary basins and tectonic elements of North Africa and localisation of the North African Eocene terrestrial mammalian localities (modified after Badalini et al. 2002).

Other Eocene African mammalian faunas have been described from the mid-Ypresian El Kohol locality in Algeria (Mahboubi et al. 1986; Mehbrouk et al. 1997) and the late early-early middle Eocene localities of Chambi in Tunisia (Hartenberger 1986; Hartenberger et al. 2001) and Gour Lazib in Algeria (Sudre 1979; Tabuce et al. 2001; Adaci et al. 2007). South of the Saharan desert, collection of early Eocene mammalian fauna has been described from Tamaguélelt phosphate conglomerate in Mali (O'Leary et al. 2006). The five mammals-bearing localities, M'Bodione Dadere in Senegal (Lutetian (Gorodiski and Lavocat 1953; Gheerbrant et al. 1998)), In Tafidet in Mali (middle Eocene (Gheerbrant et al. 1998) or late Eocene (Arambourg et al. 1951)), Mahenge in Tanzania (Lutetian (Harrisson et al. 2001; Gunnell et al. 2003; Kaiser et al. 2006)), Sperrgebiet in Mali (Pickford et al. 2008) and Aznag in Morocco (Lutetian (Tabuce et al. 2005)) are documented the poorly known middle Eocene time interval in Africa (Figure 5.2). Unfortunately, these localities have only produced sparse

and badly preserved mammalian fossil remains. Faunas from the latest part of Eocene Epoch in Africa are known from the Dur At-Talah escarpment in Libya, the Fayum Depression (quarries BQ-2 and L-41) of Egypt and Bir El Ater locality in the Nementcha Mountains of Algeria (Figure 5.1).

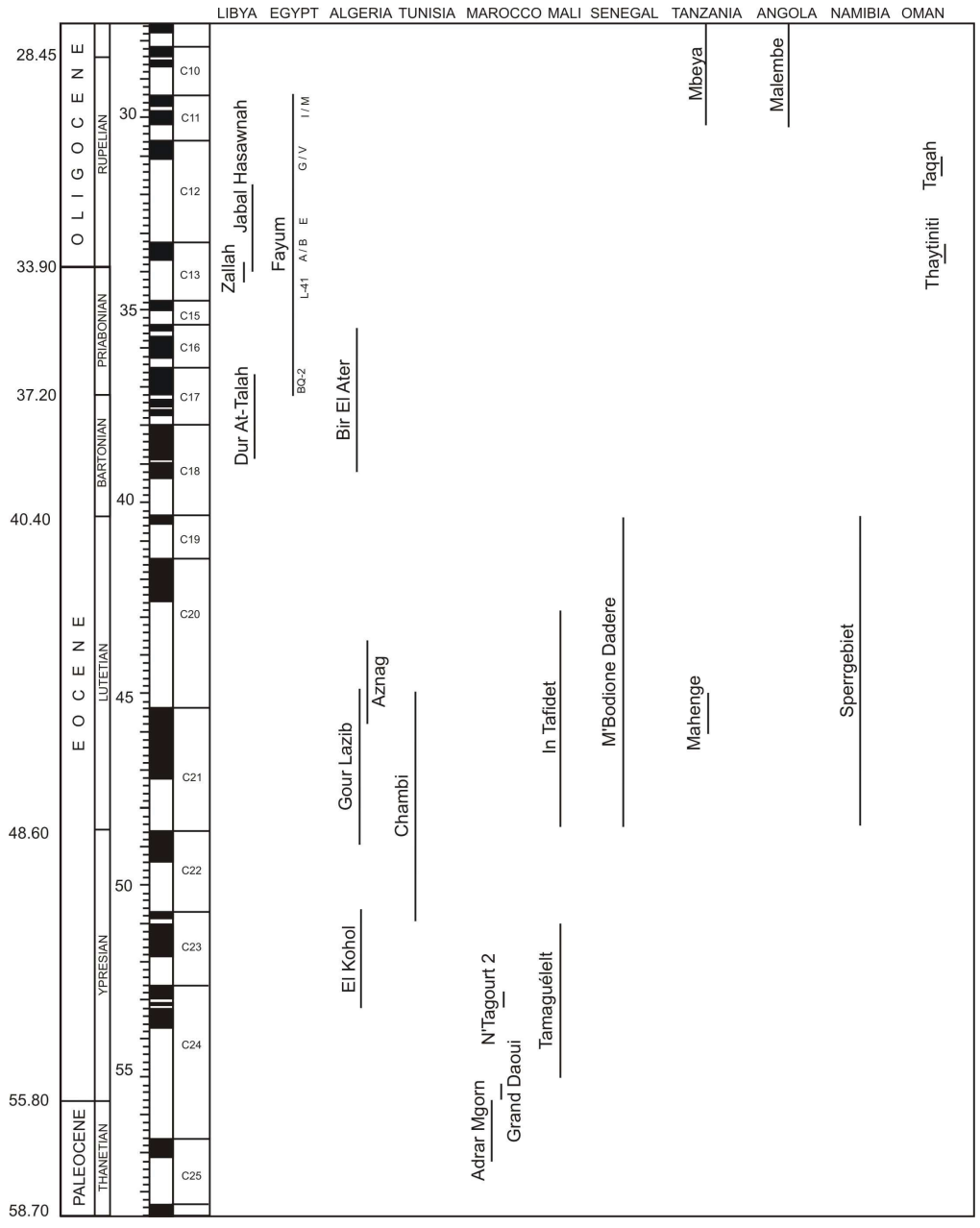


Figure 5.2. Correlation of African Paleogene terrestrial mammalian localities to the global timescale of Gradstein et al. (2004).

During the first part of Eocene, the African mammalian fossil record is characterized by endemic taxa such as hyracoids, macroscelidids, proboscideans, ptolemaiids and sirenians as well as several cosmopolitan groups as for example marsupials, "condylarths", chiropterans, creodonts and anthracotheriids which attest the occurrence of several trans-Tethyan dispersal and faunal exchanges ante-Eocene or during early Eocene between Europe and/or Asia into Afro-Arabia (Tabuce and Marivaux 2005; Gheerbrant and Rage 2006). The Eocene record of terrestrial mammalian African evolution displays a large gap through the late Lutetian and the Bartonian, spanning about ~8Ma. Between the mid-Lutetian locality of Aznag and the late middle-early late Eocene African localities, no substantial mammalian-bearing localities have been recognized in Africa. This time interval represents for the African mammalian faunas important faunal changes and is marked by first appearance of several mammalian groups such as anthracotheriid artiodactyls, anomaluroid and hystricognathous rodents and possibly anthropoid primates (Tabuce and Marivaux 2005; Gheerbrant and Rage 2006).

ANOMALUROID AND HYSTRICOGNATHOUS RODENTS

The early Eocene rodent fauna of Africa is characterized by the occurrence of Zegdoumyidae which represent the oldest known African rodent family. Three genera (*Zegdoumys, Glibia* and *Glibemys*), belonging to this extinct peculiar family, have been described from Algeria (Gour Lazib) and Tunisia (Chambi) (Vianey-Liaud et al. 1994; Marivaux et al. 2010). Zegdoumyids are believed to share a common ancestor with North American Eocene Sciuravidae and stem Myodonta (Marivaux et al. 2010) but their phylogenetic affinities and dispersal history, poorly documented, remain however controversial and are not well resolved (Vianey-Liaud et al. 1994; Vianey-Liaud and Jaeger 1996; Mahboubi et al. 2002; Marivaux et al. 2004; Tabuce and Marivaux 2005; Marivaux et al. 2010). By the latest part of Eocene epoch, the rodent records diverge with occurrence of primitive hystricognathous and anomaluroid rodents. Anomaluroid rodents are first

documented from *Nementchamys lavocati* at Bir El Ater locality of Nementcha Mountains (Coiffait et al. 1984; Jaeger et al. 1985; Mahboubi et al. 2003) and from two species (*Shazurus minutus* and anomalurid sp.) at BQ-2 locality of Fayum (Sallam et al. 2009; 2010). These taxa seem to share common Afro-Arabian ancestor, possibly derived from the more primitive zegdoumyids (Vianey-Liaud and Jaeger 1996; Marivaux et al. 2005; Marivaux et al. 2010). The anomaluroid *Nementchamys* from Bir El Ater shares derived dental features with the anomaluroid *Pondaungimys anomaluropsis* from the late middle Eocene of Myanmar (Dawson et al. 2003; Marivaux et al. 2004, 2005). The widespread South Asian-North African distribution of the late middle Eocene anomaluroid forms may suggest that faunal exchanges between Africa and Asia took place during middle Eocene. However, considering the lack of postcranial diagnosic material for *Nementchamys* and *Pondaungimys,* phylogenetic affinities between these two taxa may also reflect convergent evolution of similar dental features.

The African rodent record of the latest part of Eocene is, besides, marked by the arrival of the invading immigrant *Protophiomys*, first representative of the African hystricognathous radiation. The earliest African phiomyid assemblages have been described from the Bir El Ater (Jaeger et al. 1985), BQ-2 (Sallam et al. 2009) and Dur At-Talah (Jaeger et al. 2010b). Phylogenetic analyses point out an Asian origin and initial diversification of hystricognathous rodents (Marivaux et al. 2002, 2004; Sallam et al. 2009) and support the hypothesis of a direct migration route between South Asia and North Africa during middle Eocene. Hystricognathous rodents have been well diversified in Africa since late Eocene (Wood 1968; Jaeger et al. 1985; Hartenberger 1985; Tabuce et al. 2001) and their subsequent adaptative African radiation gave rise to three extant families: Petromuridae, the rock rats of South Africa, the Bathyergidae, mole rats of sub-Saharan Africa and the West African rodents Thryonomyidae or cane rats.

ANTHROPOID PRIMATES

The poorly known early Eocene primate radiation in Africa is documented by the azibiid primates, *Azibius* and *Algeripithecus* (Sudre 1975; Godinot and Mahboubi 1992; 1994; Godinot 1994; Tabuce et al. 2004, 2009), which first appeared at Gour Lazib and *Djebelemur martinezi* described from Chambi in Tunisia (Hartenberger and Marandat 1992; Hartenberger et al. 1997). These taxa represent the earliest offshoot of the Afro-Arabian strepsirrhine clade (Tabuce et al. 2009). Azibiid primates are absent from the late middle-late Eocene African deposits where strepshirhines are represented by the stem galagids *Wadilemur elegans* (Seiffert et al. 2005) and *Saharagalago* (Seiffert et al. 2003), and the loris-like strepsirrhine *Karanisia* (Seiffert et al. 2003, 2005; Jaeger et al. 2010b). The major event among Eocene primate African fossil record is the important increase of diversity of early anthropoids during late Eocene times which record an important radiation of African anthropoids. The earliest unambiguous anthropoid occurrence in Africa is attested by the appearance of first parapithecids during the latest part of Eocene Epoch. One of the oldest African anthropoid, *Biretia piveteaui,* has been recovered from the late middle Eocene deposits of Bir El Ater locality (de Bonis et al. 1988) (Figure 5.3). Two species of the primitive parapithecoid anthropoid *Biretia (B. fayumensis* and *B. megalopsis)* have also been more recently recovered from early late Eocene deposits of ~37 Ma at BQ-2 (Seiffert et al. 2005). Recently, Jaeger et al. (2010b) described, from the late Bartonian-earliest Priabonian deposits of Dur At-Talah, a micromammal assemblage which yielded an unexpected diversity of basal anthropoids, including primitive representatives of Afrotarsiidae, Parapithecidae, and Oligopithecidae.

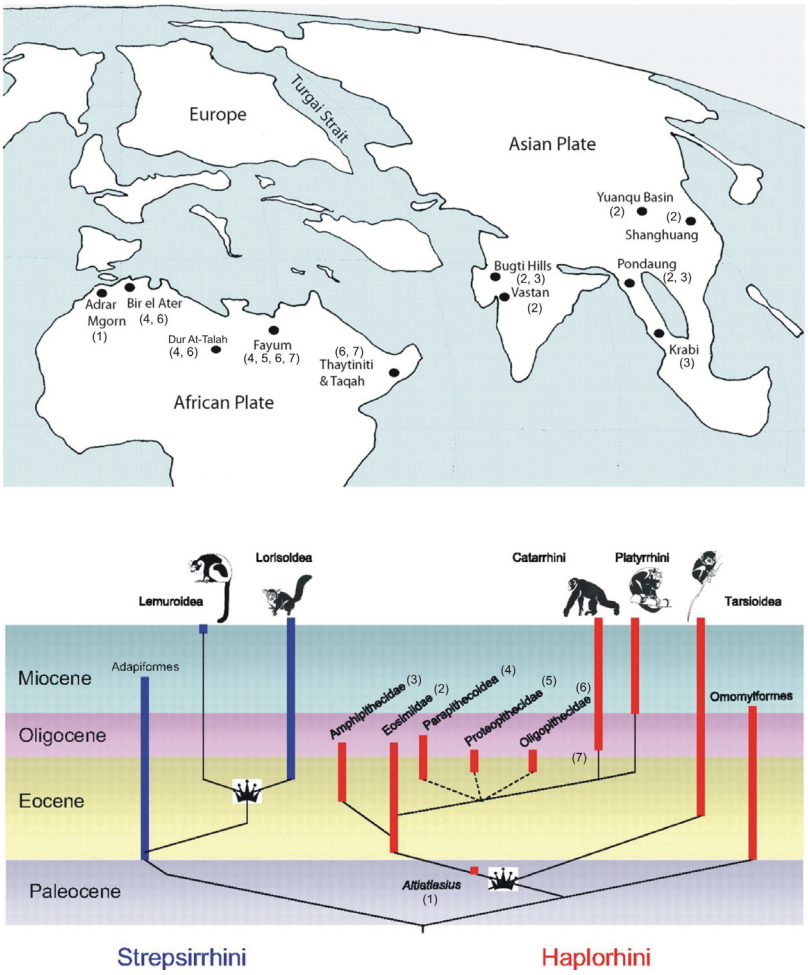


Figure 5.3. Map showing Paleogene Old World anthropoids localities and dendrogram of primate phylogeny. Coastlines and continental positions represent early Eocene to early Oligocene paleogeography (After Williams et al. 2009).

The occurrence of Eosimiids in the early Eocene of India (Bajpai et al. 2008), the middle Eocene of China (Beard et al. 1994; 1996; Gebo et al. 2000; Beard and Wang 2004) and Myanmar (Jaeger et al. 1999; Takai et al. 2005) and the diversity of amphipithecids in the middle Eocene of Myanmar (Jaeger et al. 1998; Chaimanee et al. 2000; Takai et al. 2001; Beard et al. 2009) and Thailand (Chaimanee et al. 1997) seem to establish South-East Asia as ancestral homeland of the anthropoid clade (Beard et al. 1994, 1996; Chaimanee et al. 1997; Kay et al. 1997; Jaeger et al. 1998, 1999; Ross et al. 1998; Ducroq et al. 1999; Ross 2000; Beard 2002; Beard and Wang 2004; Bajpai et al. 2008), a subsequent dispersal into Africa during the middle Eocene and marked diversification through late Eocene and Oligocene. The

Fayum primate-bearing deposits, dated from late Eocene to early Oligocene, display 15 known anthropoid genera from the four clades parapithecoids, proteopithecids, oligopithecids, and propliopithecids (Figure 5.3).

Their high level of diversity and rapid diversification of early anthropoid during late Eocene has marked the evolutionary history of primate in Africa. The hypothesis of dispersal into Africa from Asia of early anthropoid during the middle Eocene is however challenged by the presence of *Altiatlasius* in the late Paleocene deposits of Morocco (Sigé et al. 1990). Two fragmentary lower molars recovered from the mid-Lutetian locality of Aznag, have also been described as being very similar to *Altiatlasius* (Tabuce et al. 2005). This taxon has been considered either as a stem primate (Tabuce et al. 2004; Marivaux 2006; Silcox 2008), as a omomyid (Sigé et al. 1990), as a toliapinid adapiform (Hooker et al. 1999) or as a possible anthropoid (Godinot 1994; Beard 2004, 2006; Seiffert et al. 2005; Marivaux 2006; Bajpai et al. 2008; Tabuce et al. 2009). This latter migth be recognize as the potential earliest African anthropoid but Seiffert et al. (2010) considered that the dental similarities shared with anthropoids may be subject to homoplasy and its taxonomical attribution stands speculative considering the scanty fossil remains attributable to this taxon.

ANTHRACOTHERIID ARTIODACTYLS

The African late middle Eocene fossil record is finally marked by the first appearance of Anthracotheriid artiodactyls. The first appearance datum for this taxon in Africa is at Bir El Ater where fragmentary remains of indeterminate anthracothere have been recovered (Mahboubi et al. 2003). In the Fayum, earliest evidence comes from the Dir Abu Lifa Member of the Qasr el Sagha Formation (Holroyd et al. 1996; Holroyd 2010) and Quarry L-41 where the earliest well preserved craniodental and skeletal remains belonging to a species of anthracothere were found (Black 1978). The discovery of an anthracotheriid at Bir El Ater (Mahboubi et al. 2003), showing affinities with Eocene Asian forms, constrains the immigration event of anthracotheriids into Africa at least back to the middle Eocene (Ducrocq

1997, 1999). When the anthracotheres first arrived, the endemic hyracoids dominated most African grazing and browsing niches (Rasmussen 1989) and had already radiated into many genera and species. Anthracotheres become then more common, as documented by the later deposits of the Jebel Qatrani Formation of Fayum (e.g. Simons 2005).

3. MIDDLE EOCENE TERRESTRIAL DISPERSAL EVENTS

The Eocene of Africa is globally characterized by an endemic evolution with diversification of endemic lineage, such as proboscideans, hyracoids and macroscelidids but the early diversification during late middle-late Eocene of the above-mentioned invading immigrant mammalian groups, including anthropoids, anthracotheriid artiodactyls and hystricognathous and anomaluroid rdents showing affinities with Eocene Asian forms, demonstrates the occurrence of faunal dispersal from Asia to Africa (e.g. Jaeger et al. 1998; Ducrocq 1997; Tabuce and Marivaux 2005; Gheerbrant and Rage 2006). Considering that Ypresian and early Lutetian localities lack any evidence for the presence of the immigrant taxa, these mammalian groups must have invaded Africa sometime during middle Eocene. Unfortunately, a long time gap, through the upper Lutetian to the Bartonian, affects the African fossil record of terrestrial mammals, and prevents a clear understanding and unambiguous reconstruction of the nature, the timing and the impact on African faunas of the middle Eocene immigrations of Asian terrestrial mammals in Africa.

During middle Eocene times, Africa was isolated as an island-continent, separated from Laurasia by the Tethys Sea which was, however, a permeable barrier as demonstrated diverse mammalian dispersal events during Paleogene (e.g. Tabuce and Marivaux 2005; Gheerbrant and Rage 2006). Geological data indicate the lack of any land corridors between Africa, Asia and/or Europe. The middle Eocene dispersal phase was apparently unidirectional, only going from Asia to Africa and the Asian immigrant mammalian groups may have followed a possible route of faunal interchange which was unlikely to be used by other mammals, a dispersal hypothesis that favours sweepstakes mode of dispersal (Simpson 1940,

1965; McKenna 1973). Gheerbrant and Rage (2006) assume that the middle Eocene Asian immigrants were able to reach North Africa through an eastern trans-tethyan dispersal route via the Iranian block and Arabian Peninsula. Migration through Europe is considered as unlikely because of the evident lack of hystricognathous rodents, anthropoid primates and anthracotheres in the well known Eocene European fauna

The Eocene of Europe is actually better known than that of Africa (e.g. Savage and Russell 1983; Remy et al. 1987; Legendre et al. 1997) and the late Lutetian- early Bartonian times is also recognized as a period of important change in faunal composition of European fossil record. During middle Eocene, Europe was an archipelago inhabitated by a fauna with a high endemic component. The Tethys separated Europe from Africa to the south and the Eocene dispersal routes between Europe and Asia were interrupted by the presence of the epicontinental Obik and West Siberian Seaways (McKenna 1975; Iakovleva et al. 2000). Early Eocene faunal exchanges between Europe and North America were numerous (e.g. Simpson 1947; McKenna 1975, 1983; Savage 1971; Rose et al. 2004; Gheerbrant et al. 2005) but subsequent faunal disparities between the European and North American middle Eocene faunas indicate interruption of the Euramerican land bridges (Mc Kenna 1983; Krause and Maas 1990; Janis 1993; Novacek 1999). The middle Eocene European record documents an important faunal turnover at Geiseltalian-Robiacian boundary (Figure 5.4) (e.g. Franzen 2003).

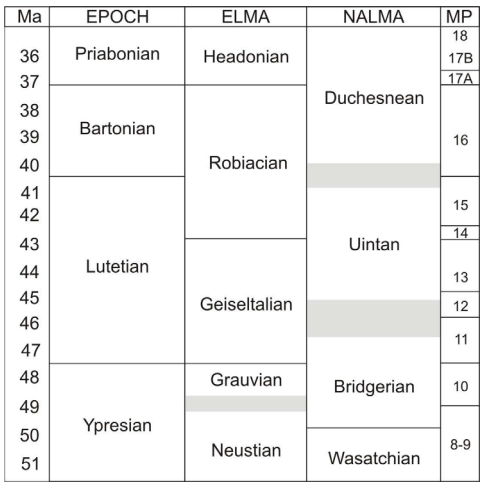


Figure 5.4. Time table showing correlations of the European and North American land mammal age (ELMA versus NALMAs). Boundaries of uncertain age are indicated by grey bars. (After Franzen 2003).

A first immigration event brought in Europe the first adapines that replaced cercamoniine adapids. The adapiforms cercamoniines flourished in Europe by late early and middle Eocene and became extinct in the early Bartonian, replaced by adapines which entered western Europe during Lutetian MP13 (Franzen 1968, 1987, 1994; Franzen and Haubold 1986; Godinot 1998; Fleagle 1999; Gebo 2002). These invaders seem to have no suitable ancestors in the known European record and the discovery of primitive adapines in the middle Eocene of China (Beard et al. 1994) seems likely to indicate that this group spread into Europe after an origin in Asia (Godinot 1998; Gebo et al. 2008). Regarding rodent community, the oldest representative of Theridomyidae, a family of hystricomorphous and sciurognathous rodents restricted to the Paleogene of western Europe (Hartenberger 1973, 1990; Luckett and Hartenberger 1985), appeared during late middle Eocene at MP13/14 (Hartenberger 1973, 1990). Theridomyidae seem to be phylogenetically close to some early Eocene European ischyromyoids (Escarguel 1999, Marivaux et al. 2004). More than a two dozen of Theridomyidae genera are known from the middle Eocene through Oligocene (Hartenberger 1990; McKenna and Bell 1997) and almost all of the Ischyromyidea, a primitive rodent family present in North America, Asia and Europe since late Paleocene (Wood 1962; Ivy 1990; Meng et al. 1994; Dawson and Beard 1996), became extinct as the first Theridomyidae appeared (Hartenberger 1990). The Lutetian European fossil record also documents changes in ungulates fossil assemblages at the base of Robiacian (MP14) when the first paleotheriids replaced step by step the equid brachiodont hyracotheres and when bunoselenodont and selenodont artiodactyls appeared, replacing the brachyodont and bunodont forms of the early Eocene and the early middle Eocene (Sudre 1978; Franzen 2003). The whole turnover in middle Eocene European fauna, affecting the ungulates, primates and rodents communities, is estimated to span 3-6 millons years through reference levels MP 13-14 of Lutetian (Mertz et al. 2000; Franzen 2003). This period corresponds with the early to middle Uintan of North America stratigraphy (Figure 5.4) which also recorded important faunal changes (Wall 1980; Woodburne and Swisher 1995).

The deposits of Uinta Formation have yielded a rich collection of middle Eocene terrestrial mammal fossils characterized by the first appearance of lagomorpha Leporidae, Amynodontidae perissodactyls and many primates as well as a radiation of selenodont artidactyls, an increase in rodent species diversity, radiations of carnivorans and perissodactyls (Prothero and Emry 1996, 1998; Rasmussen et al. 1999; Woodburne et al. 2009). The appearance of *Mytonolagus* during the middle Eocene Uintan age is the first evidence of lagomorphs in North America (Burke 1934; Black and Dawson 1966; Dawson 1970). The rich Paleogene lagomorph fossil collections from Asia (e.g. Tong and Lei 1987; Qi 1988; Shevyreva 1995; Tong 1997; Averianov and Godinot 1998; Erbajeva 1999; Meng and Hu 2004) testify the earliest Asian radiation of the lagomorphs (McKenna 1982) and bring strong evidence that lagomorphs initially evolved in Asia and subsequently migrated to North America during Uintan (Black and Dawson 1966; Walsh 1996). The oldest North American representative of the rhinocerotoid Amynodontidae, *Amynodon,* has also been described from the middle Eocene North American Uintan deposits (Marsh 1875). The early/middle Eocene Irdin Manha deposits of Mongolia have yielded the oldest known representative of this group (Yu-Xuan 1966) and Asia, which displays during Eocene a high amynodontid taxonomic diversity, appears as the center of origin for the family (Wall and Manning 1986; Tong 1989; Lucas and Emry 1996). Migration between Asia and North America through Bering Strait during middle Eocene seems to have played a significant role in their evolution (Wall 1998). Regarding primate communities, the middle Eocene fossil record also document faunal exchange between Asia and North America involving several clades of omomyid primates. The Asian primate, *Tarkops mckennai* (Ni et al. 2010), recently discovered from the early middle Eocene Irdinmanha Formation of Inner Mongolia, appears to be very close in morphology to the omomyid primates *Tarka* and *Tarkadectes*, identified from the North American middle Eocene Uintan deposits (McKenna 1990). Ni et al. (2010) suggest that *Tarkops, Tarka* and *Tarkadectes* belong to the monophyletic group of Tarkadectinae and *Tarkops* appears then as the first Asian member of this North American clade. Other middle Eocene Asian primate taxa seem to have close relatives in North America

Uintan deposits. *Asiomomys,* from the Lutetian deposits of the Jilin Province of China, is very similar to the Uintan California primate *Stockia* (Beard and Wang 1991), while the late Lutetian *Macrotarsius* from Shanghuang fissure fillings of Jiangsu Province of China (Beard et al. 1994) displays close relatives in the Uintan-Duchesnean faunas of North America. The phylogenetic relationship and geographic distribution of *Tarkadectinae, Macrotarsius* and the *Stockia-Asiomomys* clade demonstrate the existence of primate dispersal between North America and Asia during middle Eocene time and provide further evidence to the existence of direct dispersal routes between Asia and North America as suggested by the geographic repartition of other groups of mammals during middle Eocene (Granger and Gregory 1943; Wall 1980; Woodburne and Swisher 1995). Ni et al. (2010) conjectured that the trans-pacific distribution of these groups was the result of the development of suitable paleoenvironmental conditions which would have allowed the use of the Beringian Strait as a dispersal corridor. The middle Eocene warming event that occurred at 42-44Ma (Zachos et al. 2001; Sexton et al. 2006; Renaudie et al. 2010) may have permitted latidudinal displacement of climatic zones and the development of forested and warm habitats at high latitude allowed terrestrial mammals to cross high-latitude land bridges such as Beringian Strait (Woodburne and Swisher 1995; Ni et al. 2010).

The concomitant faunal turnover among ungulates, primates and rodents in European fossil record may be understood in the context of the middle Eocene warming event between 42 and 44Ma. The appearance of land bridges, which permitted terrestrial mammal dispersal and the emergence of certain adaptations, such as hypsodonty and selenodonty among ungulates, may indicate a shift of climatic conditions and a northward displacement of vegetational zones conditions (Franzen 2003). The pattern of intercontinental mammalian faunal dynamics and dispersal from Asia to Africa during Lutetian may have also been abetted by a period of climatic change but the precise timing and character of this dispersal remained unfortunately unknown. The major ecological shifts in Europe and North America faunas, likely associated with a climatic variation at a global scale possibly coincident with the middle Eocene warming event between 42 and 44Ma may be hypothesised as possible

time interval for faunal exchanges between Asia and Africa. However, several warming and cooling events have been identified within middle Eocene and major problems are the temporal pattern of immigrant distribution and the question of whether or not this overland dispersal in Africa was causally related to climatic events or driven by factors such as sea level changes, plate tectonic or an association of both.

Besides, the diversity of early primates and hystricognathous rodents in the late Bartonian-Priabonian African sites, where several distinct clades of anthropoid and numerous genera of phiomyids have been recognized, may be the result of one dispersal event from Asia followed by subsequent adaptative radiation or may reflect a multiple dispersal history with several waves of migrations involving each time distinct clades (Jaeger et al. 2010b). Actually, it is not clear whether anthropoid primates and hystricognathous rodents groups diverged already in Asia or after the migration of their ancestor in Africa which leaves different dispersion scenarii open to speculation.

In the hypothesis of a single dispersal event, one can suggest that the immigrant taxa have invaded Africa several million years before the end of Bartonian. Their subsequent divergence and differentiation would have occurred shortly after colonization and may have given rise to the different lineages of anthropoids and hystricognathous rodents recorded in the late middle/early late Eocene deposits of North Africa. According to this scenario, the African origins of these groups may extend back into the Lutetian but there is, so far, no conclusive evidence of their early presence on this continent to support this scenario.

Considering the case of one dispersal event, one can also infer that the known Paleogene clades of anthropoids and hystricognathous rodents evolved in Asia with a subsequent dispersal from Asia to the Afro-Arabian landmass. According to the close morphological resemblances between the ‘baluchimyines’ and the earliest Afro-Arabian phiomyids, the late Eocene phiomyids may be prone to record the earliest stage of hystricognathous rodents in Afro-Arabia (e.g. Sallam et al. 2009), which may indicate that these several Asian lineages reached Africa shortly before the end of Bartonian.

Alternatively, another hypothesis would assume a more complex paleobiogeographic history with several separate dispersal events and diverse migration phases from Asia to Africa during Lutetian-Bartonian time. In our cladistic analysis (this study, p. 188), some primitive African members of Hystricognathi appear phylogenetically closer to South Asian 'baluchimyines' than to other African phiomyids and some 'baluchimyines' exhibit a higher degree of similarities with derived Phiomyids than with other Asian hystricognathous rodents. These results may support the hypothesis of a multiple dispersal history during the middle Eocene but more material is needed to determine the exact phylogenetic affinities of the earliest african hystricognathous rodents.

Each of these scenario implying one or several phases of dispersion are likely but the gap in the middle Eocene fossil record of Africa and Asia do not allow to favour one of these hypothesis. More complete fossil collections from the middle Eocene of Asia and Africa are crucial to allow a better understanding of the faunal dispersal between Asia and Africa and to elaborate potential Eocene paleobiogeographical scenarii by assessing the timing, the pattern and the dispersal route of Asian primates, rodents and artiodactyls in Africa.

Actually, key event determining the distribution of late Paleogene to recent hystricognathous rodents and anthropoid primates occurred during middle Eocene. Similarly, the late Paleogene mammalian record of South America documents the arrival of anthropoid and hystricognathous rodent immigrants. Platyrrhine primates and caviomorphs rodents are clades of mammals that colonized South America during Eocene, suggesting middle to late Eocene intercontinental faunal exchanges (e.g. Hoffstetter 1972; Rosenberger et al. 1991; Wyss et al. 1993; Flynn and Wyss 1998; Poux et al. 2006). The high morphological similarities in dental characters of *Gaudeamu*s, a latest Eocene/earliest Oligocene African species of hystricognathous rodent and some contemporaneous caviomorph taxa may indicate that the beginning of caviomorphs radiation occurred in Africa within the time period of Phiomyid radiation (Coster et al. 2010).

However, the times and ways of South American colonization remains also conjectural because of the poor fossil record available to reconstruct the evolutionary history of New and

Old World anthropoids and hystricognathous rodents from their area of origin to South America. Further paleontological findings of anthropoid primates and hystricognathous rodents from the poorly documented middle Eocene times in the Old World are crucial to allow a better understanding of these open biogeographical questions.

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PARTIE II.

ETUDE MAGNETOSTRATIGRAPHIQUE ET PALEONTOLOGIQUE DES SITES CONTINENTAUX DU MIOCENE MOYEN ET SUPERIEUR D'ASIE DU SUD-EST ET IMPLICATIONS POUR L'HISTOIRE EVOLUTIVE DES PRIMATES HOMINOÏDES

INTRODUCTION

La super-famille des hominoïdes, représentée actuellement seulement par les gibbons, les orangs-outangs, les gorilles, les chimpanzés et les humains, a été beaucoup plus diversifiée pendant le Miocène, comme le démontrent les nombreux fossiles de grands singes découverts dans les dépôts du Miocène en Afrique, en Europe et en Asie. Le plus ancien hominoïde connu, *Proconsul*, exhumé dans le Miocène inférieur d'Afrique orientale, soutient l'hypothèse traditionnelle d'une origine est-africaine pour ce groupe (Rose et al. 1992 ; Begun et al. 1997 ; Fleagle 1999 ; Harrison 2002) bien qu'une origine paléogène sud-est asiatique a parfois été avancée (Jaeger et al. 1998). Après la radiation des hominoïdes proconsulidés en Afrique orientale, de nombreuses formes d'hominoïdes plus dérivées sont apparues de façon presque simultanée en Europe et en Asie au Miocène moyen (Hartwig 2002). Le Miocène moyen et supérieur semble avoir été témoin d'une radiation adaptative majeure des hominoïdes et d'une extension géographique considérable de leur aire de répartition. Cette expansion, rendue possible par les connections terrestres établies à la suite de la collision Afrique-Asie dès le Miocène inférieur (Şengör et al. 1985 ; Dewey et al. 1986 ; Yılmaz 1997; Robertson et al. 2007 ; Okay et al. 2010), est traditionnellement mise en rapport avec l'optimum climatique du Miocène moyen dont l'âge est estimé entre 17 et 13,9 Ma (Zachos et al. 2001 ; Billups et Schrag 2003). A la fin du Miocène et au début du Pliocène, la tendance générale va vers un refroidissement du climat (Billups et Schrag 2002), et le passage d'un climat subtropical à un climat tempéré à saisonnalité plus marquée semble avoir engendré la disparition de nombreux grands singes dans pratiquement toute l'Eurasie (Hartwig 2002) où ces derniers resteront confinés au Sud-Est asiatique.

Au cours de la dernière décennie, la découverte du nouveau genre d'hominoïde *Khoratpithecus* (Chaimanee et al. 2003, 2004, 2006; Jaeger et al. en révision), dans les dépôts du Miocène moyen et supérieur de Thaïlande et du Myanmar, a apporté de précieux éléments

essentiels à la compréhension de l'histoire évolutive des hominoïdes, et en particulier à celle des Pongidae. Au sein du genre *Khoratpithecus*, trois espèces ont été identifiées, *K. chiangmuanensis* (Chaimanee et al. 2003), *K. piryai* (Chaimanee et al. 2004, 2006) et *Khoratpithecus* sp. nov. (Jaeger et al. en révision), dévoilant une importante diversité morphologique et taxonomique en Asie du Sud-Est. Ce genre, considéré comme le plus proche parent connu des orangs-outangs actuels (Chaimanee et al. 2003, 2004 ; Emonet 2009), a permis de préciser les relations phylogénétiques au sein du clade *Pongo*. *Khoratpithecus* a été trouvé dans les dépôts continentaux de trois bassins différents : le bassin de Chiang Muan, au Nord-Ouest de la Thaïlande, celui du Khorat, au Nord-Est de la Thaïlande, et le Bassin Central du Myanmar.

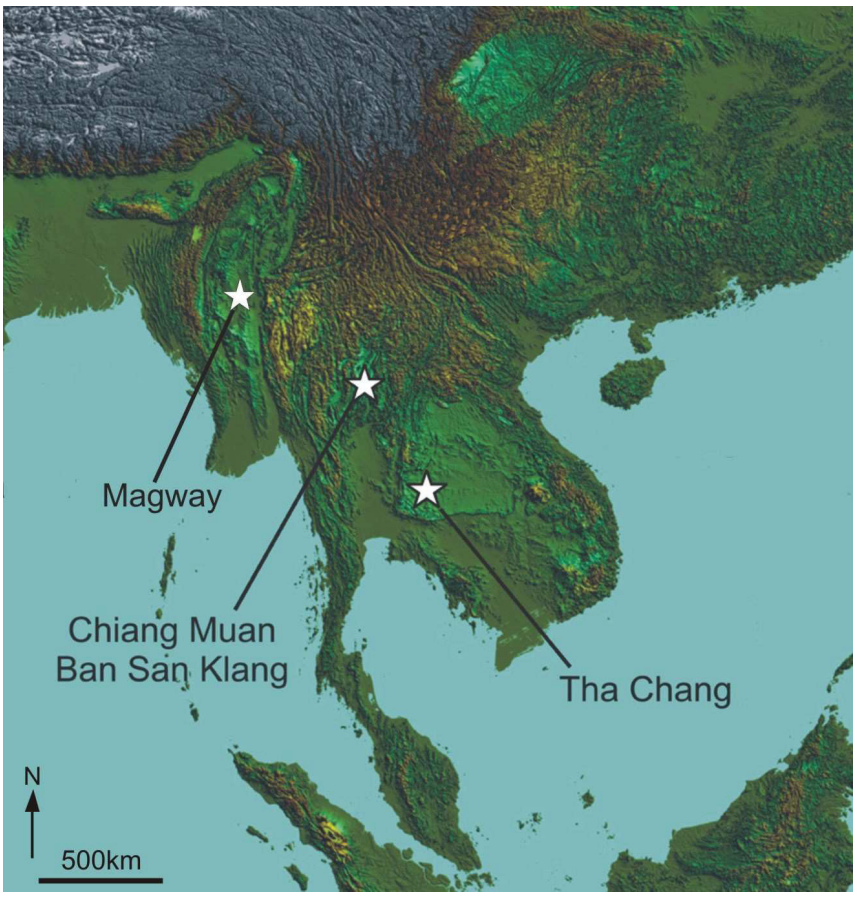


Figure 1. Carte de répartition des *Khoratpithecus* en Asie du Sud-Est (d'après Chavasseau 2008). En Thaïlande : Chiang Muan, localité-type de *K. chiangmuanensis* ; Tha Chang, localité-type de *K. piryai* ; Au Myanmar : Magway, *Khoratpithecus* sp. nov.

Le registre fossile de ces bassins documente la radiation et la diversification de nombreux autres groupes de mammifères, incluant les proboscidiens, les suidés, les cervidés, les rhinocérotidés, les giraffidés et les muridés (e.g. Ginsburg et Tassy 1985 ; Ducrocq et al. 1994 ; Chaimanee et al. 2003, 2004, 2006, 2007, 2008 ; Chavasseau et al. 2006, 2010 ; Chavasseau 2008). Ces trois bassins ont été datés du Miocène moyen et supérieur (Suganuma et al. 2002, 2006 ; Benammi et al. 2004 ; Chavasseau et al. 2006, 2009 ; Chavasseau 2008 ; Coster et al. 2010) mais les âges relatifs et les corrélations biostratigraphiques entre ces différentes localités fossilifères ont été sujets à controverse (e.g. Ducrocq et al. 1994 ; Chavasseau 2008). Le manque de données concernant l'âge des sites fossilifères asiatiques du Miocène, en plus des problèmes phylogénétiques, a constitué un obstacle majeur à la compréhension de l'histoire évolutive et paléobiogéographique des faunes en Asie du Sud, et en particulier de celle des hominoïdes.

Des études magnétostratigraphiques, combinées aux résultats de l'étude biostratigraphique des faunes associées, ont été réalisées dans les dépôts du Miocène moyen du bassin de Mae Moh en Thaïlande et dans les séries miocènes de la Formation de l'Irrawaddy afin de préciser l'âge des sites à *Khoratpithecus* birmans et thaïlandais.

Le registre fossile du Miocène moyen et récent de l'Asie du Sud-Est semble jouer un rôle crucial pour documenter l'histoire évolutive de plusieurs groupes de mammifères et l'étude magnétostratigraphique apparait comme un outil de datation puissant apportant des indications fiables quant à la chronologie des différentes phases de divergences et la diversification initiale des hominoïdes, ainsi que des réponses sur leur histoire paléobiogéographique et les relations entre climat et évolution qui ont contraint l'évolution vers les formes actuelles.

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2.1. A COMPLETE MAGNETIC-POLARITY STRATIGRAPHY OF THE MIOCENE CONTINENTAL DEPOSITS OF MAE MOH BASIN, NORTHERN THAILAND, AND A REASSESSMENT OF THE AGE OF HOMINOID-BEARING LOCALITIES IN NORTHERN THAILAND

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A complete magnetic-polarity stratigraphy of the Miocene continental deposits of Mae Moh Basin, northern Thailand, and a reassessment of the age of hominoid-bearing localities in northern Thailand

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ABSTRACT

Northern Thailand comprises more than 40 Tertiary intermontane basins. These basins, tectonically interpreted as grabens or half grabens, have yielded hominoid fossils and rich Neogene mammal faunas. Relative ages provided by biochronological studies are controversial and neither absolute ages nor correlations with marine deposits are available. A precise temporal framework provided by magnetic-polarity stratigraphy is therefore crucial to understand the evolution of these Southeast Asian mammalian faunas, to estimate the timing and duration of basin formation, and finally to allow correlations with other Neogene hominoid localities of the Old World.

A complete magnetostratigraphic study, which significantly extends previous paleomagnetic investigations, has been conducted in the Miocene sequence of Mae Moh Basin, Lampang Province, northern Thailand. Based on the biostratigraphic constraints, the 15 polarity zones recognized from the composite section have been correlated with Chrons C5ACr–C5r.3r, between 14.1 and 12.0 Ma. The present study provides a high-resolution magnetostratigraphic reference for the continental middle Miocene of all Southeast Asia. By correlation with the Miocene sequence of the nearby basin of Chiang Muan, the large-bodied hominoid (*Khoratpithecus chiangmuanensis*)–bearing levels can be precisely dated between 12.4 and 12.2 Ma.

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INTRODUCTION

Structural evolution of northern Thailand during the Cenozoic was mainly related to the activity of major strike-slip faults: the Sagaing fault to the west, the Red River fault to the northeast, and the Mae Ping and Three Pagodas faults to the south. The strike-slip movement along these fault systems, accompanying regional E-W–directed extensional stresses and N-S compression during the late Oligocene to early Miocene, led to the formation of an 800-km rift system, running from the southern part of the Gulf of Thailand to the north of the country, which contains more than 60 Tertiary sedimentary basins (Tapponnier et al., 1982; Hall, 1996; Packham, 1996; Morley et al., 2001) (Fig. 1). These continental basins are mainly N-S–trending, fault-bounded half grabens and grabens. Tertiary northern basins of Thailand, rich in lignite and oil shale deposits, are often covered by Quaternary sediments and are poorly exposed in natural outcrops due to dense vegetation. Drilling and seismic studies performed during lignite prospecting and exploitation (Chaodumrong, 1985; Strogen, 1994; Sompong et al., 1996) uncovered their structure and stratigraphy. In parallel, active paleontological surveys allowed the discovery of fossil mammals.

The main mammal-bearing localities of northern Thailand are situated in the basins of Li, Mae Teep, Mae Moh, Pong, and Chiang Muan, that latter basin having yielded the large hominoid *Khoratpithecus chiangmuanensis* Chaimanee et al. (2003) (Kunimatsu et al., 2000, 2004) (Fig. 1). Biochronological studies, based on the mammal fossils, indicate a middle Miocene age for the fossiliferous levels of these basins (Ginsburg and Tassy, 1985; Jaeger et al., 1985; Buffetaut et al., 1988; Ducrocq et al., 1994, 1995). Ducrocq et al. (1994, 1995) considered all the localities to be aged between 16 and 14 Ma. However, the age of the fossiliferous localities of the basins has been subject to controversies. This is well exemplified by the case of the Li Basin, the localities of which have been dated from the late early Miocene to the early middle Miocene by Mein and Ginsburg (1985) and Tassy et al. (1992). By contrast, Chaimanee et al. (2007) proposed a middle Miocene age for these localities on the basis of micromammal similarities with the fauna of Mae Moh.

More than discrepancies in paleontological interpretations, the scarce fossil mammal collections and the absence of geochronological dating are the main causes of the poorly constrained ages of the intermontane basin localities.

Therefore, new chronological data are absolutely required to refine the biochronological scale of the continental Neogene of northern Thailand. The middle Miocene sequence of Mae Moh Basin, well exposed in a huge open-air mine where several hundred meters thick sections are easily accessible, is likely to offer a reliable calibration for the Neogene of Thailand.

In 2002, Benammi et al. performed a partial magnetic-polarity stratigraphy of the sequence of the Mae Moh Basin (Q, K, and J coal layers) (Fig. 2). Their study resulted in a precise dating of the central portion of the sequence between 13.5 and 12.1 Ma. However, a large portion of the section remained unstudied. The aim of the present work is to establish a more complete chronology of the Miocene deposits of the Mae Moh Basin. Our new results were used to improve the correlations with other basins of the region, notably with the geographically close hominoid-bearing Chiang Muan Basin,

GSA Bulletin;

doi: 10.1130/B26568.1; 9 figures; 1 table; Data Repository item 2010071.

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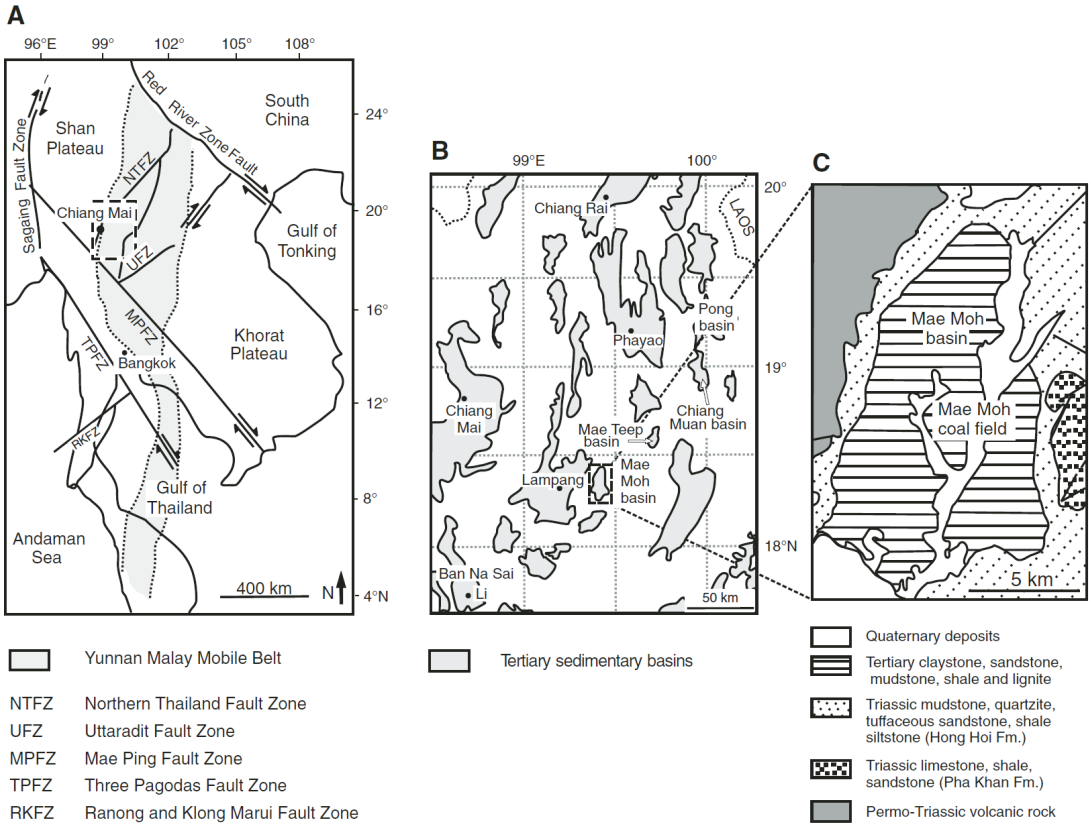


Figure 1. (A) Geologic structural map of Thailand showing major strike-slip faults (after Uttamo, 2000). (B) Location map of the Tertiary intermontane basins of northern Thailand (after Uttamo, 2000). (C) Geologic map of the Mae Moh Basin and surrounding areas (after the Department of Mineral Resources, Thailand, 1995). Abbreviation: Fm.—Formation.

of which the magnetostratigraphy has already been investigated (Suganuma et al., 2002, 2006; Benammi et al., 2004). The implication for the evolution of the hominoids in Southeast Asia will be discussed.

GEOLOGICAL SETTING

The Mae Moh Basin, which contains the largest coal deposits of Thailand, is located in the Mae Moh District, Lampang Province (Fig. 1). This basin follows a NE-SW general trend, with a maximum width of 9 km and a length of 16 km. It lies on a basement of folded and faulted Triassic rocks belonging to the Lampang Group. Seismic data demonstrated that the Cenozoic filling is up to 900 m thick (Chaodumrong, 1985). This half graben is deformed principally by N-S–striking normal faults and is bounded to the west by a graben master fault (Morley and Wonganan, 2000). The purely continental Tertiary deposits of Mae Moh Basin have been defined as the Mae Moh Group by Piyasin (1972). Three formations were described in this group by Cosiri and Crouch (1985): the Huai King, Na Khaem, and Huai Luang formations (Fig. 2). The lower unit, the Huai King Formation, unconformably overlies the Lampang Group basement rocks. It is up to 320 m thick and comprises fluvial channel sandstones, alluvial strata, and lake deposits (Sompong et al., 1996). This formation comprises a thin lignite layer named S lignite zone in its uppermost part. The Huai King Formation is overlain by the Na Khaem Formation, which is composed of lacustrine and fluviatile claystones, mudstones, and siltstones. It is ~420 m thick and comprises three main coal-bearing seams named Q, K, and J. This formation has been subdivided into three members by sedimentary deposit as Member III, Member II, and Member I (Cosiri and Crouch, 1985) (Fig. 2). The lowermost Member III consists mainly of claystones, with a thin seam of coal, identified as R coal zone. This member represents deposition in a lacustrine environment (Chaodumrong, 1985). Member II comprises two main coal zones, which are Q coal zone in its lower part and K coal zone in the upper part, with intercalated claystones. The depositional environment of this member has been interpreted as a swamp and poorly drained floodplain (Uttamo, 2000).

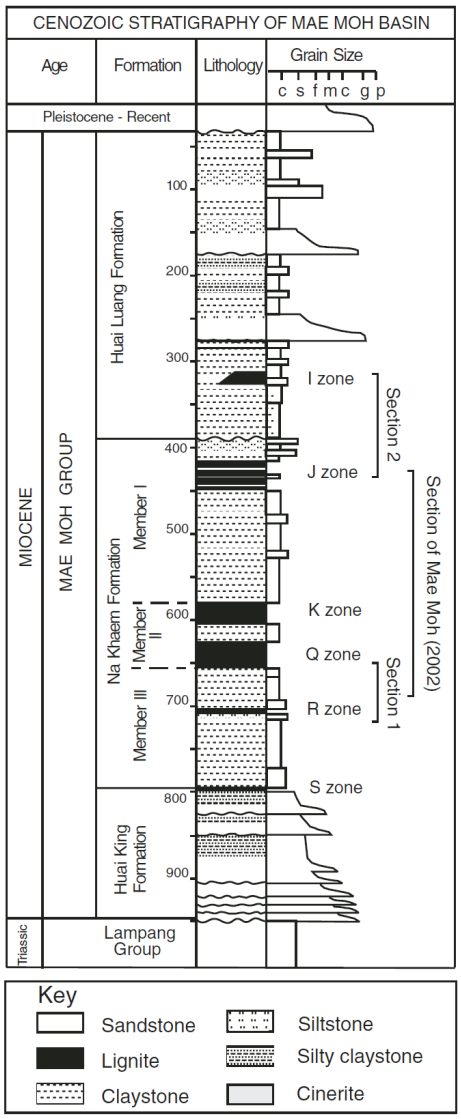


Figure 2. Cenozoic stratigraphy of the Mae Moh Basin (after Sompong et al., 1996; Chaodumrong, 1985; Corsiri and Crouch, 1985). The letters at the right of the column indicate the nomenclature applied to the lignite zones. The range of Sections 1 and 2 and the section of Benammi et al. (2002) are marked along the right side of the stratigraphic column.

Member I comprises claystones, mudstones, and rare siltstones, with a series of coal layers named J. A cinerite layer, intercalated within the J coal zone, has been recognized from the topmost part of Member I. The uppermost formation of Mae Moh Group, the Huai Luang Formation, which is up to 400 m thick, unconformably overlies the Na Khaem Formation. The Huai Luang Formation is composed of claystones, mudstones, and siltsones with some sandstones and conglomerate lenses. The lowest part of the formation has been interpreted as flood-plain, swamp, and pond deposits, while the topmost part corresponds to large braided-river, lacustrine, and well-drained, flood-plain facies (Uttamo, 2000). The middle portion of that uppermost formation, I coal zone, which is intercalated between claystones, yielded abundant fossil wood remains.

The sampling of Benammi et al. (2002), 66 different stratigraphic levels along a 245-m-thick section, started below the Q lignite zone and ended at the J lignite zone (Fig. 2). Thanks to new mining excavations, we could extend the section to the bottom and to the top. Therefore, the results obtained from a more complete section are presented.

PALEOMAGNETISM

Sampling

Two additional sections have been sampled. The first section, named Section 1, was sampled along the lowermost part of the Na Khaem Formation (Fig. 2). It is 70 m thick and corresponds to 92 samples collected from 32 stratigraphic levels (GSA Data Repository Fig. DR1[1]). This section consists principally of gray claystones deposited in a lacustrine environment. It contains two main lignite zones—the R coal zone in its lower part and the Q coal zone in the uppermost portion.

The second section, referred to as Section 2, completes the section of Benammi et al. (2002) by collecting 89 samples from 33 higher stratigraphic levels (Fig. DR1 [see footnote 1]). This section, 210 m thick, was sampled ~5 km northeast from Section 1 and comprises J and I coal zones. Section 2 displays an alternation of red claystones and sandstones, reflecting a flood-plain depositional environment (Uttamo, 2000).

For both sections, three drilled samples have been collected from each stratigraphic level with a portable gasoline-powered drill oriented with a magnetic compass. Samples were taken from fresh outcrops laid bare by mining activities. Oriented block samples were collected from levels not favorable for drilling and were drilled in the laboratory. Sampling density varies between 2 and 10 m, depending on the lithology and the outcrop exposure.

Laboratory Procedures

The paleomagnetic analysis of the 181 samples was undertaken at the Laboratorio de Paleomagnetismo, Universidad Nacional Autonoma de Mexico. In order to identify the

[1]GSA Data Repository item 2010071, additional tables and figures regarding paleomagnetic analyses: Table DR1: Paleomagnetic sites mean direction of the sections from Mae Moe Basin, northern Thailand; Figure DR1: Lithology and stratigraphic position of sampling sites of sections 1 and 2; Figure DR2: plot illustrating the correction of the inclination error using the method of Tauxe and Kent, 2004, is available at http://www.geosociety.org/pubs/ft2009.htm or by request to editing@geosociety.org.

minerals carrying remanent magnetization, isothermal remanent magnetization (IRM) acquisition was performed on 12 samples of various lithologies using a pulse magnetizer. Samples were subjected to increasing field steps up to 1 T. The intensity of the 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 (1990) method. These IRMs 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).

The intensity and direction of the natural remanent magnetization (NRM) were measured on a JR6 magnetometer. To isolate the characteristic remanent magnetization (ChRM), 75 samples were subjected to progressive thermal demagnetization from 100 °C with 25–50 °C increments. Magnetic susceptibility was measured after each heating step to detect any chemical or mineralogical changes in the magnetic minerals. One hundred sixteen samples were submitted to stepwise alternating field demagnetization with increments of 3–10 mT, up to a maximum field of 90 mT. For some red claystone samples, alternating field demagnetization was inefficient. Thus, thermal demagnetization was subsequently successfully performed. Results of demagnetization were plotted on orthogonal vector diagrams (Zijderveld, 1967) and stereograms.

PALEOMAGNETIC RESULTS

Isothermal Remanent Magnetization (IRM)

All the specimens from Section 1, collected from gray claystones, display the same IRM acquisition pattern (Fig. 3A) and similar demagnetization curves (Fig. 3C), indicating a uniform magnetic mineralogy along the section. The IRM acquisition curves increase sharply in low field and reach saturation at 200 mT. A change in slope is observable on the thermal demagnetization curve ~400 °C indicating the presence of titanomagnetite (Fig. 3C). The inflexion around 300 °C suggests the presence of iron sulfides; these ferrimagnetic minerals are common in reducing environments such as oxygen-poor depositional environment associated with the lignite deposits. The presence of magnetite is revealed by the demagnetization at 580 °C of the IRM components.

Samples of Section 2 display a different pattern of IRM acquisition (Fig. 3B). The gray claystones samples, for instance sample 34A, exhibit a similar IRM acquisition pattern to that of Section 1 samples. Red claystones samples present different behaviors. For sample 65A,

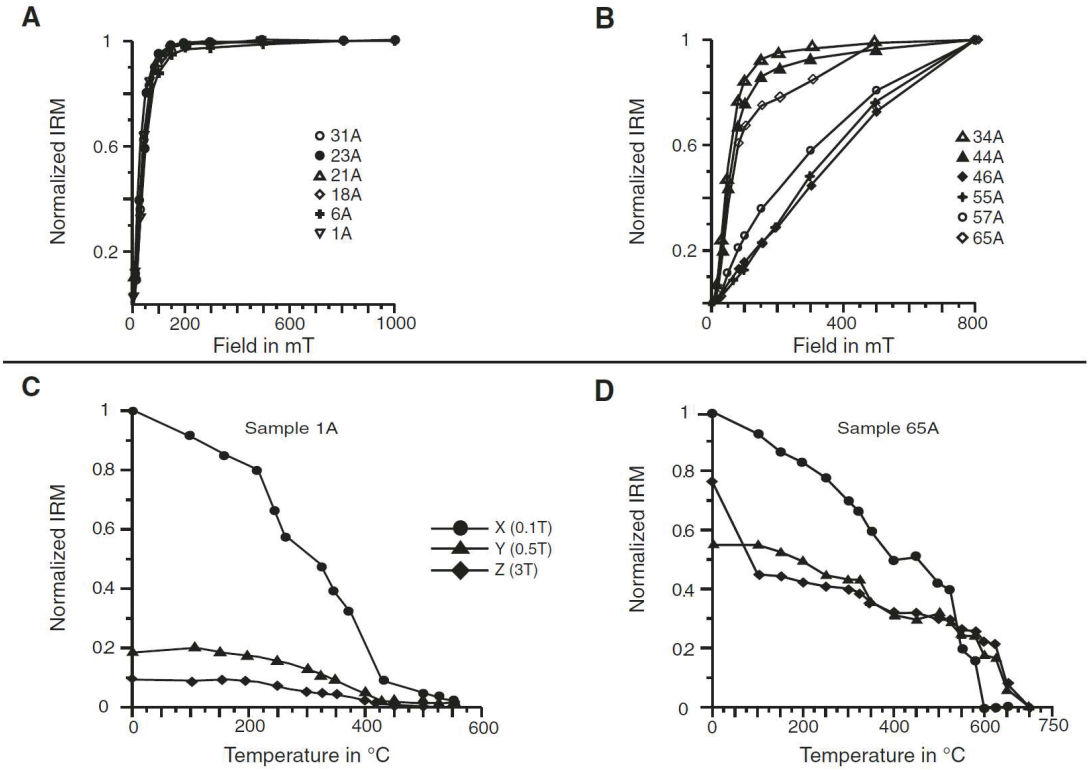


Figure 3. (A, B) Isothermal remanent magnetization (IRM) acquisition (normalized values) curves of selected samples of Section 1 (A) and Section 2 (B). (C, D) Example of stepwise thermal demagnetization of the IRM components. (C) Sample 1A, a gray claystone sample from Section 1. (D) Sample 65A, a red claystone samples from Section 2.

the values increase rapidly at low field, but do not saturate beyond 500 mT, implying that magnetization is carried by both low- and high-coercivity minerals (Fig. 3B). The analysis of the demagnetization curves (Fig. 3D) suggests the presence of magnetite, but also hematite and goethite. For the other red claystone samples (57A, 55A, and 46A), IRM acquisition curves increase gradually but do not reach saturation at 800 mT (Fig. 3B). The magnetic properties of these samples are probably due to the presence of minerals with high coercivity, such as hematite or goethite. Other red claystone samples have both magnetite and hematite.

The combined results for IRM acquisition and subsequent thermal demagnetization indicate that the main carriers of magnetization of the sediments are magnetite, titanomagnetite, and in the red-colored sediments, magnetite, hematite, and a fraction of goethite.

Natural Remanent Magnetization (NRM)

The NRM intensity measured on the samples ranges between 3.00×10^{-1} A/m^{-1} and 1.08×10^{-3} A/m. Most of the samples are characterized by two magnetization components: a low-stability component, removed between 3 and 15 mT or between 100 and 300 °C, and a high-stability component (Fig. 4). The direction of the low-stability component is close to that of the present magnetic field, and this component is interpreted as a viscous overprinted magnetization. For a few samples, NRM was not totally removed at temperatures >600 °C. This behavior is probably due to the presence of a high unblocking temperature mineral. The IRM analyses suggest that it may be hematite. During heating, the magnetic susceptibility remained constant until 600 °C, and increased abruptly over this temperature, indicating mineralogical changes (Fig. 4C).

Following Kirschvink's (1980) method, the ChRM directions were calculated by principal component analysis (Table DR1 [see footnote 1]). The mean directions for both sections were calculated by the Fisher statistics (Fisher, 1953) and plotted on stereographic diagrams (Fig. 5). Mean directions of normal and reverse sites of Section 1, Section 2, and the previous results of the magnetic stratigraphic study of Mae Moh Basin (Benammi et al., 2002) as well as a calculation of paleopoles are presented in Table 1.

The overall mean direction of Sections 1 and 2 is: declination = 5.4°, inclination = 26.5° (α_{95} = 7.1°), corresponding to the paleomagnetic pole at 83.3°N and 228.6°E (confidence ellipse about the pole has dp [semi-axis of the confidence ellipse along the great circle path from site to pole] of 7.7° and dm [semi-axis of the confidence ellipse perpendicular to that great circle path] of 4.2°).

Our results were submitted to the reversal test of McFadden and McElhinny (1990). Mean directions are not exactly antipodal, the angle calculated between mean directions of the normal and reverse polarity being 6.3° for Section 1 and 6.2° for Section 2. Mean directions of opposing polarity sites have a critical angle at 95% of confidence level of 11.3° for Section 1 and 11.5° for Section 2. The reversal test is thus passed with a C classification for both sections according to McFadden and McElhinny's criteria.

We compared the overall mean directions of Sections 1 and 2 with the expected dipole paleomagnetic field directions (declination: 4.4°, inclination: 37.6°, α_{95}: 3.4°) at the site location (18.3°N, 99.7°E) derived from the 10 Ma apparent polar wander path of Besse and Courtillot (2002). Using Demarest (1983) methods, comparison of the reference and observed directions yields no significant vertical axis rotation of declination ($R \pm \Delta R = 1 \pm 7°$). The counterclockwise vertical axis rotation of $-13 \pm 1.32°$ observed by Benammi et al. (2002) is not detectable in our results. Thus, this rotation is interpreted here as a response to local tectonics, controlled by the numerous faults present in the basin, rather than a response to regional tectonics.

The inclination values observed for Section 1 are lower than those of Section 2 and shallower than the expected inclination of the paleomagnetic field at this latitude. We applied the elongation and inclination (E/I) method (Tauxe and Kent, 2004) to investigate the bias in inclination record in both sections. It appears that corrected inclination values of Section 1 (mean corrected inclination of 31.8° with a 95% confidence interval on this mean of 24.1°–44.4°) are not significantly different from the expected values at this latitude (Fig. DR2 [see footnote 1]). E/I–corrected inclination values of Section 2 are in agreement with the observed directions and correspond to the expected inclination at the site position. The difference of inclination flattening between Section 1, mostly composed of gray claystones, and Section 2, which comprises mainly red claystones, can be reasonably related to the difference of lithology between the two sampled sections.

MAGNETOSTRATIGRAPHY

Correlation of Mae Moh Sequence

The virtual geomagnetic pole (VGP) latitudes, calculated from the ChRM directions of each site, were reported in Figure 6. Magnetic-polarity sequences were then established for both sections. The stratigraphic correlation, between Sections 1 and 2 and the section of Benammi et al. (2002), leading to our composite section, was based on lignite seams, which constitute reliable stratigraphic marker beds. Section 1 completes that of Benammi et al. (2002), by sampling lowermost levels, and Section 2 completes this latter section to the top levels. The composite section measures up to 500 m, and consists of 15 magnetozones, comprising seven normal and eight reverse-polarity zones (Fig. 7).

Chronology of our composite section was only constrained by biostratigraphic data. Numerous mammal fossils have been collected from Mae Moh lignite zones. Q and K are by far the main fossil-bearing strata in Mae Moh mine and yield the same taxa assemblages. The few fossils reported from the other lignite beds (I, J, and R) correspond to crocodile, fishes, gastropods, and some scarce proboscidean remains. The fauna comprises the proboscidean *Stegolophodon praelatidens* (Von Koenigswald, 1959; Chavasseau et al., 2009). This taxon is more primitive than *Stegolophodon stegodontoides* from the early late and late Miocene of Pakistan and more derived than *Stegolophodon nasaiensis* from the locality of Ban Na Sai, Li Basin (Ginsburg and Tassy, 1985; Tassy et al., 1992; Chavasseau et al., 2009). This statement implies a younger age for Mae Moh than Li Basin. However, deer and micromammals (Erinaceid insectivores and rodents) identified from Q and K lignite seams display similarities with Mae Long fauna from Li Basin, and suggest, contrary to what is mentioned above, that the two basins are contemporaneous (Chaimanee et al., 2007).

The Mae Moh coal mine yielded also the rhinocerotid *Gaindatherium* (Ginsburg and Tassy, 1985; Ducroq et al., 1994). This genus appears in Pakistan in the latest middle Miocene–early late Miocene (Flynn et al., 1995; Barry et al., 2002). Ginsburg and Tassy (1985) argued that the association *Gaindatherium*–primitive *Stegolophodon* at Mae Moh was relevant of a late middle Miocene or, less probably, early late Miocene age. The suid *Conohyus thailandicus* occurs in Mae Moh (Chaimanee et al., 2007). This taxon, also present in several other middle Miocene localities of northern Thailand (Ducrocq et al., 1997), is close to *Conohyus sindiensis* from Pakistan, the range of which is estimated at 14 to 10.3 Ma by Barry et al. (2002). The mustelid carnivore, *Siamogale thailandica*, described by Ginsburg et al. (1983) in Mae Moh Basin deposits exhibits less primitive characters than the *Lartetictis artenensis* (Ginsburg and Morales, 1992). Mae Moh Basin yielded also a new Southeast Asian Miocene form of amphicyonid,

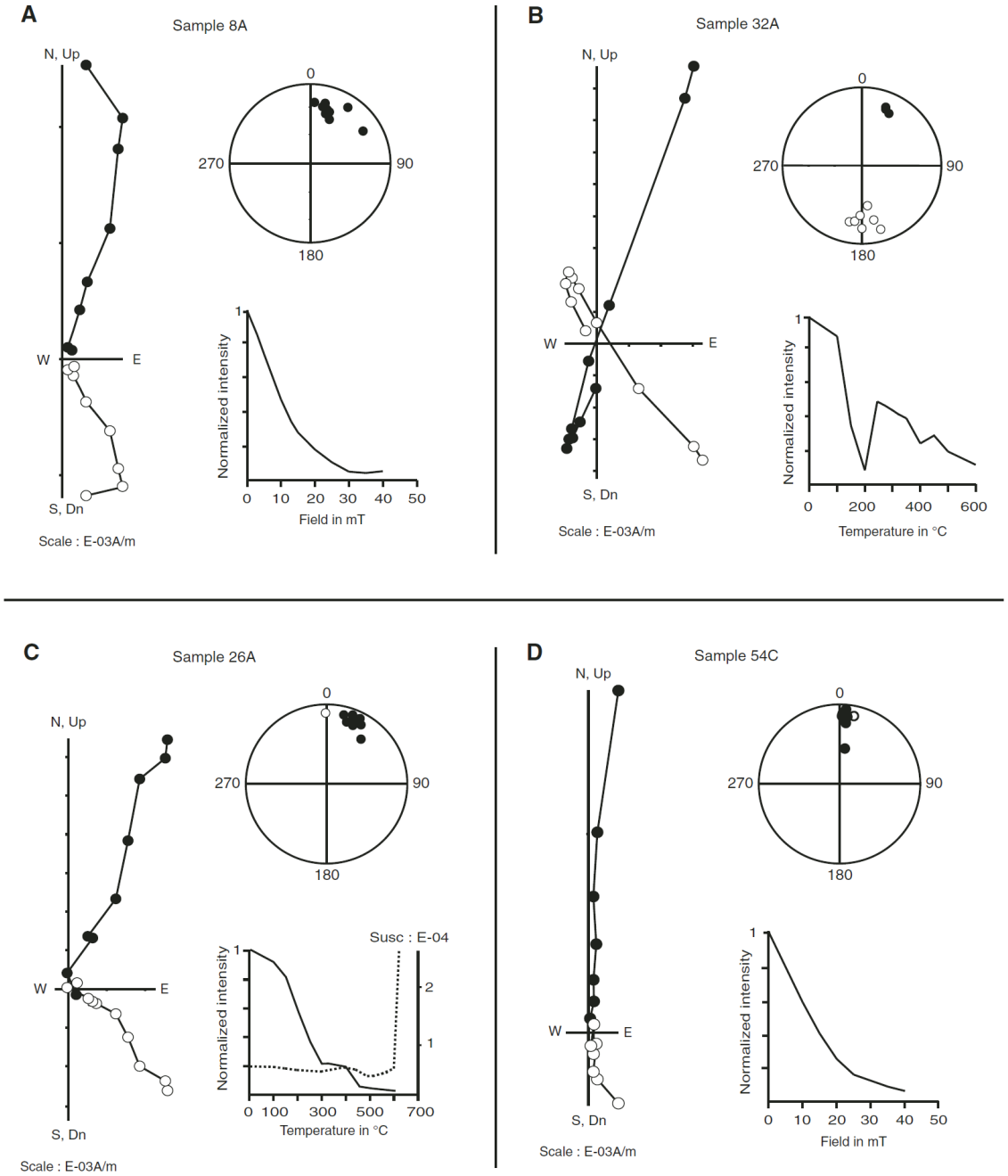


Figure 4. (A, B, C, D) Orthogonal vector diagrams (closed and/or open symbols correspond to the horizontal and/or vertical component), stereoplots (open and/or closed circles indicate directions in the upper and/or lower hemisphere), and intensity and step plots for representative samples after thermal and alternating field (AF) demagnetization (dashed line indicates evolution of susceptibility).

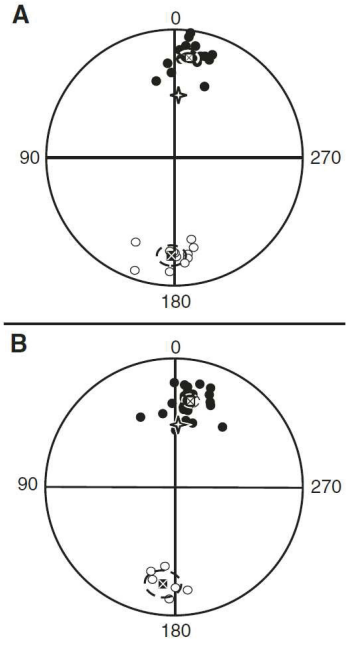


Figure 5. Equal-area stereographic projection and Fisher statistics of characteristic directions for all the sites (listed in Table DR1 [footnote 1]) of Section 1 (A) and Section 2 (B). Open and/or closed circles indicate directions in the upper and/or lower hemisphere. Mean directions calculated by Fisher statistics (see Table 1) are represented by a square, and the ellipse indicates the 95% confidence ellipse. Solid star shows the direction derived from the 10-Ma apparent polar wander path of Besse and Courtillot (2002).

TABLE 1. PALEOMAGNETIC POLARITY MEAN DIRECTIONS OF THE STUDIED SECTIONS FROM MAE MOH BASIN, NORTHERN THAILAND

						Pole position		
	N	Declination (°)	Inclination (°)	α_{95} (°)	k	Φ (°E)	λ (°N)	dp/dm (°)
Section 1								
Normal sites	20	8.4	22.2	6.3	27.6	228.4	79.4	6.7/3.5
Reverse sites	12	181.5	–23.2	7	36	266.4	83.6	7.4/4
Section 2								
Normal sites	27	8.7	34.1	4.5	39.4	185.5	81.7	5.1/2.9
Reverse sites	6	185.3	–27.2	9.7	48.7	226.3	83.6	10.6/5.8
Section Benammi et al. (2002)								
Normal sites	5	1.7	19.1	10.5	43	268	81.5	10.9/5.7
Reverse sites	4	186.6	–29.2	22.9	12.7	211.8	83.1	25.3/13.9

Note: Declination—mean tilt-corrected declination in °E; Inclination—mean tilt-corrected inclination in degrees to the horizontal; α_{95}—mean direction 95% confidence ellipse; k—Fisher precision parameter; Φ—longitude of paleopole for mean direction in °E; λ—latitude of paleopole for mean direction in °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. Section 1 location—18°18′45″N, 99°42′10″E. Section 2 location—18°19′47″N, 99°43′52″E.

Maemohcyon potisati (Peigné et al., 2006). Chaimanee et al. (2007) reported, from Mae Moh Basin, the first Southeast Asian Miocene sivaladapid primate, *Siamoadapis maemohensis* (Chaimanee et al., 2008). A closely related species has also been identified from the middle Miocene deposits of Siwaliks (Barry et al., 2002). The absence of *Hipparion* very likely indicates a minimum age of 10.7 Ma (*Hipparion* datum in the Siwaliks; Barry et al., 2002). The mammal assemblage of Mae Moh indicates thus that the fossiliferous strata are most probably late middle Miocene in age.

Taking into account the former magnetic-polarity stratigraphy performed in the Mae Moh Basin and the above-mentioned biochronological constraints, our polarity sequence is likely to be correlated from Chron C5ACr to C5r.3r of the geomagnetic-polarity time scale (GPTS) (Gradstein et al., 2004) and extends in age between 14.1 and 12.0 Ma (Fig. 7A) with a mean sedimentation rate of ~22 cm/ka^{-1}. Alternatively, another correlation of the composite section to the GPTS can also be taken in account (Fig. 7B). According to this latter hypothesis, the longest normal polarity zone of the composite section is identified as Subchron C5n.2n, the base of the section being correlated to Chron C5Ar.1r (12.4 Ma) and the top to Chron C4Ar.3r (9.7 Ma). Sedimentation rates have been calculated for each chron. They range from 5 to 93 cm/ka^{-1} with a mean rate of 17 cm/ka^{-1}. These variations of the sedimentation rate are relatively important but could be consistent with the supposed depositional environment. An age bracketed between 11.04 and 9.98 Ma has been calculated from this correlation for the fossiliferous J coal zone and 9.9 to 9.8 for the I coal zone. However, the absence of *Hipparion* seems to indicate that the whole fauna is older than 10.7 Ma, the date of the first appearance of this taxon in the Potwar Plateau of the Siwaliks of Pakistan (Barry et al., 2002). We consider that its absence is unlikely attributable to paleoecological or paleobiogeographical factors, this taxon being well represented in the late Miocene of Thailand (Nakorn Ratchasima Province, Khorat Plateau) (Chaimanee et al., 2004) and in the Irrawaddy Formation of Myanmar (Bender, 1983). This second correlation, implying an early late Miocene age for the youngest fossiliferous lignite levels, seems thus less plausible.

According to our first correlation, every polarity zone was recorded, and net sedimentation rates can be calculated for each chron. It appears that the compacted sediment accumulation rates are highly variable and reveal different stages during the infilling process of the basin. The lowest sedimentation rates are obtained for Chron C5Ar, which is correlated to polarity zones located under coal zone J. These rates are consistent with the lithology since lignites are associated to shallow depositional environment and are thought to indicate a period of low subsidence of the basin, corresponding to low sedimentation rates, nondeposition, or even erosion events. Sedimentation rates inferred for Section 1 (~6.5 cm/ka^{-1}) are lower than those obtained by Benammi et al. (2002) for the central portion of Mae Moh sequence (17.5 cm/ka^{-1}). Again, the low sedimentation rate of Section 1 matches well with the lithology—this portion of the basin being interpreted as a shallow lake or a swamp (Uttamo, 2000). Section 2, interpreted as flood-plain deposits (Uttamo, 2000), displays a higher mean sedimentation rate (~40 cm/ka^{-1}), probably related to an increasingly rapid tectonic subsidence that has affected Mae Moh Basin (Sompong et al., 1996).

Comparison and Correlation with the Chiang Muan Sequence

Correlations between the newly established Mae Moh Basin sequence and other localities in northern Thailand would contribute to improve the chronology of the numerous Neogene Thai basins. The magnetic-polarity stratigraphy of the Chiang Muan Basin, situated at ~100 km northeast of the Mae Moh Basin (Fig. 1), has been investigated by several authors (Suganuma et al., 2002, 2006; Benammi et al., 2004). There is no consensus about its interpretation; different potential correlations to the GPTS have been proposed.

Dental remains of the large-bodied hominoid *Khoratpithecus chiangmuanensis* (Chaimanee

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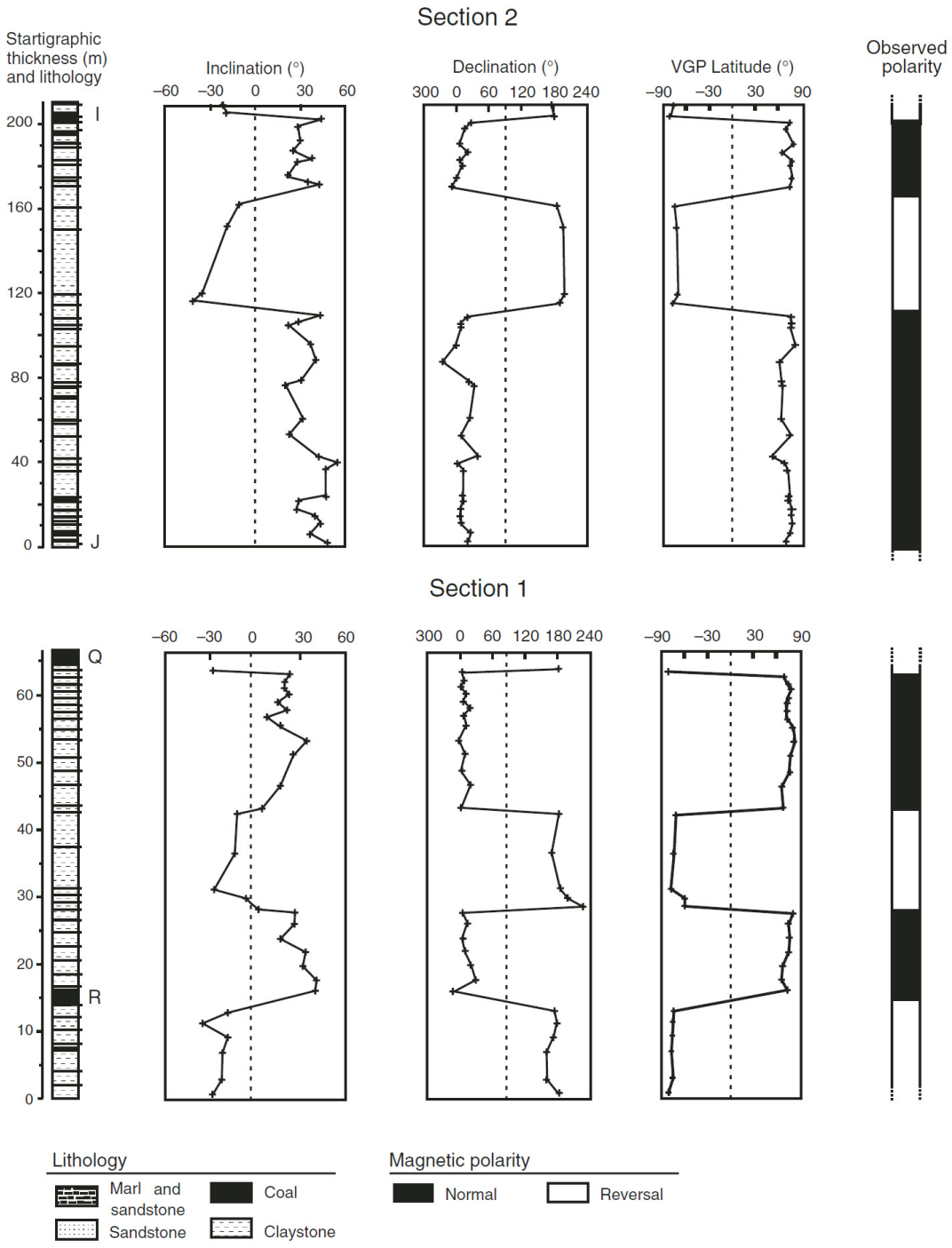


Figure 6. Paleomagnetic reversal stratigraphy of Sections 1 and 2. Inclination (in degrees to the horizontal), declination (°E), and the virtual geomagnetic pole (VGP) paleolatitudes (°N) of characteristic remanent magnetization (ChRM) are plotted as a function of stratigraphic levels. The letters at the right of the stratigraphic column indicate the nomenclature applied to the lignite zones, and lines at the right of the stratigraphic column indicate the position of the sites.

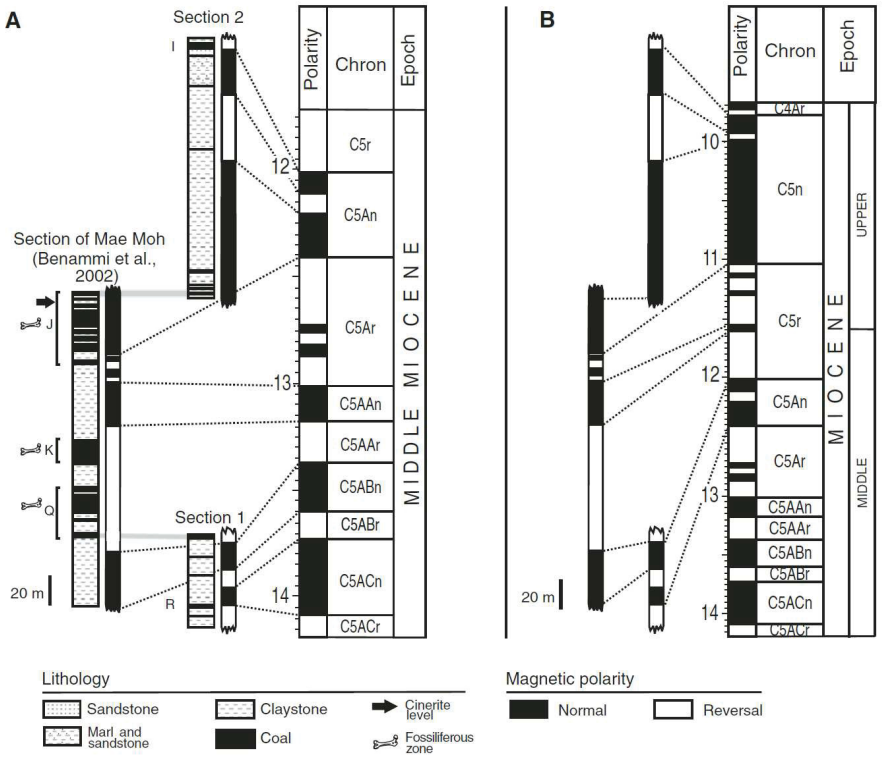


Figure 7. (A) Preferred correlation of the composite Mae Moh sequence with geomagnetic-polarity time scale (GPTS) of Gradstein et al. (2004). The letters at the left of the stratigraphic column indicate the nomenclature applied to the lignite zones. (B) Alternative correlation of the Mae Moh sequence with GPTS of Gradstein et al. (2004).

et al., 2003) have been collected from the Chiang Muan coal mine (Chaimanee et al., 2003; Kunimatsu et al., 2000, 2004); the genus *Khoratpithecus* is considered to represent the closest sister group of the orangutans (Chaimanee et al., 2004). The associated mammal fauna comprises the gomphotheriid proboscidean *Tetralophodon* cf. *xiaolongtanensis*, the suoids, *Hippopotamodon* cf. *hyotherioides*, *Conohyus sindiensis*, *Parachleuastochoerus sinensis*, and *Pecarichoerus sminthos* (Pickford et al., 2004), the rhinocerotid *Chilotherium (Subchilotherium) intermedium* (Suganuma et al., 2006), and the tragulids, *Dorcatherium*, *Eotragus*, and *Siamotragulus* (Chaimanee et al., 2003). Pickford et al. (2004) proposed an age of 12–10 Ma for the Chiang Muan sequence on the basis of the occurrence of the suids, *Parachleuastochoerus sinensis* and *Hippopotamodon* cf. *hyotherioides* and the gomphotheriid, *Tetralophodon* cf. *xiaolongtanensis*, which are known from the locality of Xiaolongtan (Yunnan Province, China) dated biochronologically from the early late Miocene (Pickford and Liu, 2001). This locality might however be slightly older (Pickford et al., 2004).

According to Benammi et al. (2004), there are four possible correlations to the GPTS for the Chiang Muan sequence within Chrons C5ACn–C5n.2n, which indicate an age between 13.5 and 10 Ma for the hominoid specimens from the Upper Lignite Member (Fig. 8). Suganuma et al. (2006) correlated the base of the Chiang Muan Formation with Chron C5AAn (ca. 13 Ma) and the top of the sequence with Chron C5n (ca. 9.8 Ma). This latter study suggests an age of ~12.1–10.5 Ma for the fossiliferous Upper Lignite Member.

Suganuma et al. (2006) attributed the inconsistency in interpretation of the Chiang Muan magnetic-polarity sequence to low sampling resolution and short stratigraphic section for the previous paleomagnetic studies (Suganuma et al., 2002; Benammi et al., 2004); however, there are some points concerning their sampling section that are debatable.

The continental Tertiary deposits are exposed in Chiang Muan coal field in sections that were a maximum of 100 m thick. They unconformably overlie the Jurassic sandstones and are overlain by Pliocene–Pleistocene deposits with pronounced unconformity. Geological investigations of the Chiang Muan sequence in the open-cast mine demonstrate that the Upper Lignite Member is overlain by a dozen meters of Miocene silts and mudstones (Uttamo, 2000). They are separated from the uppermost reddish layers by a major erosional unconformity, pointing out an important sedimentological discontinuity. Suganuma et al. (2006), by reporting

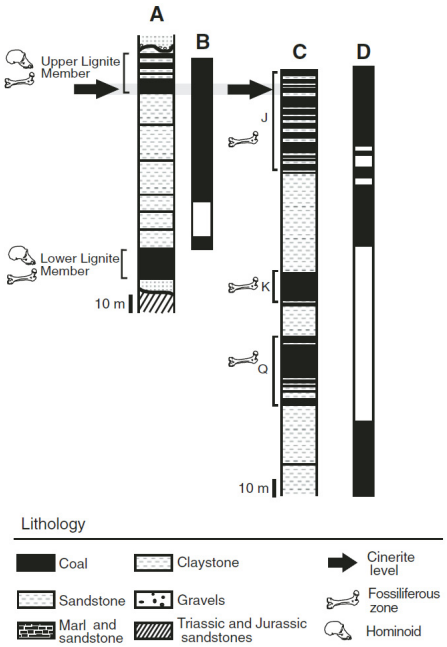


Figure 8. Stratigraphic correlation between sections of Mae Moh and Chiang Muan basins. (A) Stratigraphic section of Ban Sa coal mine, Chiang Muan Basin (after Benammi et al., 2004). (B) Magnetic-polarity stratigraphy of the Chiang Muan section (after Benammi et al., 2004). Black denotes normal polarity, and white denotes reverse-polarity zones. (C) Stratigraphic section of Mae Moh Basin (after Benammi et al., 2002). Letters at the left of the stratigraphic column indicate the nomenclature applied to the lignite zones. (D) Magnetic-polarity stratigraphy of the Mae Moh section (after Benammi et al., 2002).

a 150-m-thick section with more than 40 m of Tertiary deposits overlying the Upper Lignite Member, are not in agreement with the field data and have generated a major misinterpretation of their Chiang Muan magnetic-polarity stratigraphy.

Moreover, Chavasseau (2005) compared the Chiang Muan suids fauna with that of the Siwaliks of Pakistan. He concluded that the Chiang Muan deposits are possibly older than the age given by Pickford et al. (2004). This hypothesis is based on the presence in the Chiang Muan Basin of *Conohyus* typical suid of the Chinji Formation, which is also present in the Q and K coal levels of Mae Moh, together with the common occurrence in Chiang Muan and the Chinji Formation of *Parachleuastochoerus sinensis* (partly described under the name *Hyotherium pilgrimi* by Pickford, 1988). Moreover, Chavasseau (2005) also pointed out the striking similarity between the small suoid of Chiang Muan ('*Pecarichoerus sminthos*' of Pickford et al., 2004) and a small suid collected from levels Q and K of Mae Moh.

Recently, a cinerite has been discovered within the upper coal seams of Chiang Muan mine; these seams have yielded the holotype and the type-series of *Khoratpithecus chiangmuanensis* (Chaimanee et al., 2003) (Fig. 8). This cinerite can be compared to that of Mae Moh Basin, which is intercalated within the J coal seams. A comparative analysis of the trace elements spectra of the two ash levels from Mae Moh and Chiang Muan basins has been performed by the Institut für Isotopengeologie of Göttingen University, Germany (Fig. 9). The spectra analyses revealed strong composition identity between these two cinerites, which both correspond to an arc volcanism eruption. Considering the scarcity of ash levels in these basins and their chemical composition similarities, we may confidently conclude that the two layers correspond to the same volcanic event and are contemporaneous. The ash layer from Mae Moh is situated within the J coal zone (Fig. 8) and is correlated to the normal Subchron C5An.2n. The Chiang Muan cinerite, also of normal polarity (Suganuma et al., 2002, 2006; Benammi et al., 2004), can therefore be correlated with the same Subchron C5An.2n. This correlation indicates an age bracketed between 12.4 and 12.2 Ma for the holotype and type-series of *Khoratpithecus chiangmuanensis* from the Upper Lignite Member, an age which is older than the age of 10.5–12.1 Ma reported by Suganuma et al. (2006). The Lower Lignite Member of Chiang Muan has also yielded one half upper molar of an indeterminate hominoid (Kunimatsu et al., 2000, 2004), the age of which still appears imprecise, pending the reinterpretation of the paleomagnetic anomalies of the lower part of the Chiang Muan sequence.

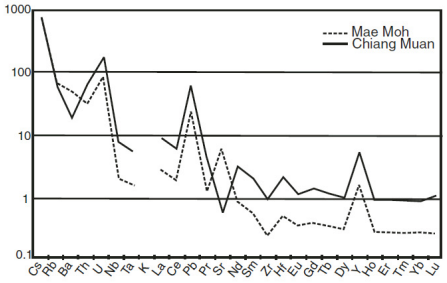


Figure 9. Analysis of the trace-element spectrum normalized to the mid-ocean ridge basalt (MORB) of two ash levels coming from the basins of Mae Moh and Chiang Muan (analysis performed by the Institut für Isotopengeologie of Göttingen University, Germany).

DISCUSSION

Khoratpithecus Age and Asian Hominoids Radiation

The genus *Khoratpithecus*, recovered in Chiang Muan Basin, is also known from the Nakorn Ratchasima Province, in northeastern Thailand (Chaimanee et al., 2004, 2006) with another species, *K. piriyai*. This latter species is dated from the late Miocene (9–6 Ma, Chaimanee et al., 2006), considerably younger than *K. chiangmuanensis*. During its long time range, *Khoratpithecus* was contemporaneous with three other large-bodied hominoids from Southeast Asia: (1) *Sivapithecus* (12.5–8.5 Ma, Barry et al., 2002), (2) *Lufengpithecus* (late middle Miocene to late Miocene, Kelley, 2002), and (3) *Indopithecus* (ca. 9 Ma, Pillans et al., 2005). However, *Khoratpithecus* is geographically restricted to northern and northeastern Thailand, while *Lufengpithecus* is only

known from Yunnan Province in China and *Sivapithecus* and *Indopithecus* are restricted to the Siwaliks and Nepal (Munthe et al., 1983; Kelley, 2002).

The four genera are considered as members of the extant *Pongo* clade by most paleoprimatologists. However, these taxa clearly differ by their facial and dental morphology, especially their anterior dentitions. This diversity among Southeast Asian Miocene hominoids is a testament to a large-scale radiation among great apes, especially pongids. However, this large-scale event is currently not precisely dated.

Begun (2005) considered "griphopiths" (*Griphopithecus*, *Equatorius*, *Kenyapithecus*, and *Nacholapithecus*) as a stem group of later great apes. Griphopiths are restricted to the early middle Miocene (from 15.5 Ma probably up to 13–12 Ma) of Africa and Europe (Kelley, 2002). The hominoid large-scale dispersal across Eurasia, and the subsequent radiation leading to the observed diversity of Southeast Asian hominoids, would therefore probably have happened after 15.5 Ma. The substitution of *Griphopithecus* with more derived Eurasian hominoids, which occurred at ca. 13–12 Ma, even suggests this radiation would have occurred after 13 Ma. An age of 12.4–12.2 Ma for the minimum first appearance of *Khoratpithecus*, which roughly corresponds to the first appearance of *Sivapithecus*, indicates that these events took place previously. Therefore, this large-scale radiation could have occurred between 15.5 and 12.4 Ma, probably between 13 and 12.4 Ma. It was contemporaneous with a huge expansion of hominoids geographical range in Southern and Eastern Asia, probably in correlation with environmental and faunal changes. Alternatively, one can also consider an older dispersal event followed by a northern range expansion of these Southeast Asian hominoids during warming climatic events (Billups and Schrag, 2003).

Paleoenvironments in Northern Thailand and Hominoid Repartition

Floral elements associated with tropical forest and warm temperate vegetation were recovered in the Q and K lignite zones of Mae Moh Basin (Sepulchre et al., 2009). The association of temperate element and tropical pollens at this latitude may indicate that Mae Moh Basin has been located in a frontier region between a tropical flora and a warm temperate flora. Such a region is likely to be highly influenced by small climate variations (Walther et al., 2002; Kelly and Goulden, 2008).

Palynological analyses carried out on some Tertiary basins from northern Thailand (Songtham et al., 2003) observed a change from an Oligocene to early Miocene warm temperate floral assemblage to middle Miocene tropical vegetation. This result suggests a change from warm temperate to tropical climate through early Miocene to middle Miocene in Thailand. During this period, brief time-scaled temperature variations occurred in the southern oceans according to geochemical data (Billups and Schrag, 2003). A deep, ocean-water cooling is observed between 15 and 13 Ma, and, between 12 and 11 Ma, temperature increased to reach a level similar to the Miocene optimum. In northern Thailand, those climatic variations should have provoked the displacement of the tropical and warm temperate vegetation boundary.

Members III and II of Na Khaem Formation (R, Q, and K lignite zones) are dated at 14.1–13.1 Ma, while hominoid-bearing Chiang Muan coal layers are dated at 12.4–12.2 Ma. Therefore, Chiang Muan deposits are likely to represent more tropical vegetation conditions than the Na Khaem Formation. The difference in fauna composition between those two basins may support this hypothesis (see taxa listed in Ginsburg and Tassy, 1985; Jaeger et al., 1985; Buffetaut et al., 1988; Ducrocq et al., 1994, 1995; Chaimanee et al., 2003, 2004; Pickford et al., 2004; Suganuma et al., 2006). *Khoratpithecus* is geographically restricted to northern and northeastern Thailand (Chaimanee et al., 2003, 2004, 2006), but hominoid remains, present in Chiang Muan Basin, are so far absent in the record of Mae Moh Basin. The supposed difference in vegetation between the Mae Moh Basin at 14.1–13.1 Ma and Chiang Muan Basin at 12.4–12.2 Ma might therefore explain the absence of hominoid remains in Mae Moh Basin.

CONCLUSION

The 525-m-thick Mae Moh sequence combines the section of Benammi et al., (2002) with the two new sections presented here. This composite sequence has recorded 15 polarity zones (seven normal and eight reverse) and has been correlated to the GPTS of Gradstein et al. (2004), from Chron C5ACr to Chron C5r.3r, between 14.1 and 12.0 Ma. The main mammal-bearing coal layers Q and K have been dated between 13.4 and 13.2 Ma; an age bracketed between 12.8 and 12.2 Ma has been assigned to the J coal zone. R and I lignite seams have been correlated to Chron C5ACr (14.2–14.1 Ma) and C5r.3r (12.0–11.6 Ma), respectively.

The lacustrine to fluviatile deposits of Chiang Muan sequence have been correlated with those of Mae Moh on the basis of the occurrence in both basins of two ash layers yielding the same trace element composition. An age of 12.4–12.2 Ma is therefore assumed for the hominoid *Khoratpithecus chiangmuanensis*, which is found in the Upper Lignite Member.

Mae Moh and Chiang Muan sequences now provide reliable continental references for the middle Miocene of Southeast Asia. Additional work on other sections in the surrounding areas, and magnetostratigraphic correlations with other fossiliferous localities, are now required to fully understand the timing of the opening and development of Tertiary basins in northern Thailand and the evolution of Tertiary Asian mammal lineages.

ACKNOWLEDGMENTS

The authors would like to thank Electricity Generating Authority of Thailand (EGAT) for providing scientific assistance and access to the mine, the Department of Mineral Resources (DMR), the Thai-French Thailand Research Fund–Centre National de la Recherche Scientifique (TRF-CNRS) Biodiversity Project, and the CNRS–*Eclipse* II Program, and B. Hansen (University of Göttingen) for cinerite spectra analyses, and M. Rugbumrung for helping in the field. We thank the Instituto de Geofisica, Departamento de Paleomagnetismo y Geofisica Nuclear, Universidad Nacional Autónoma de México, for assisting the paleomagnetic analyses.

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Manuscript Received 24 October 2008
Revised Manuscript Received 28 March 2009
Manuscript Accepted 31 March 2009

Printed in the USA

2.2. MAGNETIC POLARITY STRATIGRAPHY OF THE MIDDLE-LATE MIOCENE DEPOSITS OF THE IRRAWADDY FORMATION NEAR MAGWAY (CENTRAL MYANMAR) AND AGE OF THE EARLIEST KNOWN HOMINOID REMAINS FROM MYANMAR

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1. INTRODUCTION

The terrestrial Irrawaddian deposits, which are widely exposed in the Central Basin of Myanmar, form a remarkable terrestrial sedimentary sequence which is believed to span much of the Neogene and contains a diverse assemblage of vertebrate fossil remains. As soon as the nineteenth century, these deposits have attracted the attention of the geologists of the Geological Survey of India (e.g. Buckland 1829; Falconer 1868; Theobald 1873; Noetling

1895) but efforts at describing and collecting mammalian fossils from the Irrawaddian sedimentary sequence really started during the early part of the twentieth century (Pilgrim 1904, 1927; Stamp 1922; Chhibber 1934; Colbert 1938, 1943; Cotter 1938). The recovered fossil assemblages were soon recognized as Neogene mammalian faunas but the stratigraphical occurrences of these early fossil collections were not sufficiently documented to yield any precise chronological interpretation. The faunal assemblages recovered from these deposits were first mixed and recognized as belonging to a single faunal set (e.g. Noetling 1895; Pilgrim 1910; Chhibber 1934). The existence of two faunal sets and the distinction of Lower Irrawaddy and Upper Irrawaddy fauna Units were later established (e.g. Stamp 1922; Colbert 1938, 1943). However, the faunal content and stratigraphic limits of these two units are not clearly settled and their respective age ranges are still controversial nowadays (Colbert 1938, 1943; Bender 1983, Takai et al. 2006; Chavasseau et al. 2006, 2010, in press; Zin-Maung-Maung-Thein et al. 2010).

The highly fossiliferous Siwaliks Formation of Pakistan, which also consists of thick continental sedimentary sequence, accumulated throughout the early Miocene through the late Pliocene. The biostratigraphic terminology of the Siwaliks, has been, over the years, established on the characterization of successive faunal zones, related directly to stratigraphic sections and correlated to magnetic polarity zones (e.g. Barry et al. 2002). Thanks to this biostratigraphic framework, the Siwaliks fauna is now one of the best known Cenozoic fauna in such terrestrial setting and the Siwalik sedimentary series provide reliable continental references for the Neogene of South Asia. The Irrawaddy Formation is also renowned for yielding a rich Neogene mammalian fauna but after more than a century of research, the biostratigraphy of these Neogene series, based on inaccurate location of fossils in stratigraphy and space, and insufficiently documented fauna, is still inadequate as a precise correlation tool and yielded poorly constrained ages.

The Myanmar-French paleontological team, who prospected the terrestrial Neogene of Myanmar in the Central basin since 2002, has yielded new sedimentological and paleontological data from several fossiliferous localities throughout the Irrawaddian fluvial

deposits. Chavasseau et al. (in press), on the basis of the new fossil remains collected, refined the biochronology of the continental Neogene Irrawaddy Formation and pointed out three faunal assemblages. The oldest faunal set from Irrawaddian deposits, collected near Chaungtha, has been correlated to the middle-early late Miocene Chinji Formation of Pakistan. The fauna, collected from Magway region and Yenangyaung (the later corresponding to the type-area of the series), displays similarities to those of the Nagri and lower part of the Dhok Pathan Formations of the Potwar Plateau, suggesting an early late Miocene age. In these areas, a much younger faunal assemblage, of Plio-Pleistocene age, has also been identified (Stamp 1922; Colbert 1938).

These diverse Neogene terrestrial Irrawaddian faunas display similarities with those of India and Thailand. The Neogene fossil record of South East Asia documents the radiation and diversification of numerous extant mammalian groups, including proboscideans, suids, cervids, rhinocerotids, giraffids, bovids, murids and hominoids (e.g. Tassy 1985; Pilbeam 1979; Barry et al. 2002; Chaimanee et al. 2003). The Miocene Epoch in Southern Asia is of particular interest since it had witnessed the radiation of hominoids and the appearance of several genera belonging to the *Pongo* clade (*Sivapithecus*, *Indopithecus*, *Khoratpithecus, Lufengpithecus*) (e.g. Pilbeam 1982; Kelley et al. 2002; Chaimanee et al. 2003; Patnaik et al. 2005; Xu Qinghua and Lu Qingwu 2008). The most complete record of fossil hominoids is known from the Siwaliks sequence of Pakistan and India (Dutta et al. 1976; Pilbeam et al. 1977; Dehm 1983; Kelley 1988). Hominoid remains belonging to two new species of *Khoratpithecus*, a genus also known from two localities in Thailand (Chaimanee et al. 2003, 2004, 2006), have been recently recovered from the Irrawaddian outcrops, situated south of Magway city (Jaeger et al. *in review*). These fossils represent the first hominoid remains found in Myanmar. The long temporal range and the extensive outcrops of the Burmese Neogene series along with the central geographic position of Myanmar, neighbouring the main hominoid-bearing regions of Southeast Asia, suggest that later paleontological expeditions will yield further evidences to complete the Asian hominoid evolutionary history. However, meaningful inferences about evolutionary patterns in the hominoid and mammal

fossil record and the reconstitution of possible paleobiogeographic scenarii cannot be made until the fossils of interest can be confidently situated in an unambiguous chronostratigraphic framework.

In order to establish a more precise chronology of the Miocene Irrawaddian fluviatile deposits, we have investigated the polarity sequences of several sections with the goal of correlating them to the Geological Polarity Time Scale, in the light of the available paleontological data. Initial sampling, during fieldwork seasons 2006 and 2007, focused on the early late Miocene Irrawaddian deposits in the area of Magway Division, Central Myanmar. A short version of magnetostratigraphic results of the composite Magway section have already been reported along with the detailed description of the two species of *Khoratpithecus* (Jaeger et al., in review) but the complete detailed rock magnetic analyses are presented herein.

In 2009, an additional section was sampled in the area of Chaungtha, Sagaing Division, Northern Myanmar, where older faunal assemblages, probably of middle Miocene age, have been reported (Chavasseau et al. 2006; and *in press*).

The studies relative to the magnetic polarity stratigraphy of the Irrawaddian deposits are of great importance since they are the first one carried throughout the Neogene deposits of Myanmar. This work, based on paleomagnetic and mammalian biochronological data, presents refined chronostratigraphic analyses of the Miocene Irrawaddian deposits. Providing a temporal framework for these deposits would allow more precise correlations with other Neogene Asian hominoid localities, and may permit a better comprehension of the evolution and paleobiogeographical patterns of Miocene South Asian mammalian faunas.

2. GEOLOGICAL SETTING

The Central Basin of Myanmar lies between the Indo-Burmese ranges and the Shan Plateau and forms a large syncline extending NS on a wide area in the middle of the country. The opening of this basin was probably initiated during early Eocene in relation to the oceanic

plate subduction along the west edge of Myanmar plate and the opening of Adaman Sea (Pivnik et al. 1998; Wandrey 2006). The Tertiary filling of the basin comprises Eocene to middle Miocene marine sediments and continental detritic deposits ranging from middle Miocene to Quaternary (Bender 1983).

The Tertiary to Quaternary fluvial deposits, widely exposed throughout the Central Basin, were first described by Theobald (1873) as the "Fossil Wood Group" and by Noetling (1895) as the "Irrawaddy series" in the type area of Yenangyaung (Figure 2.1). This sedimentary series was then characterized as the "Irrawaddy Formation" (Aung Khin and Kyaw Win 1969; Kyi Khin and Myitta 1999) or as "Irrawaddy Group" (Bender 1983). The Irrawaddian deposits unconformably overlies shallow marine to freshwater clastic sediments of the Pegu Group, ranging from Oligocene to middle Miocene (Pascoe 1962; Bender 1983). Transition from the marine and alluvial sediments of Pegu Group to the continental sediments of the Irrawaddy Group appears as gradual and, according to Cotter (1938), may be heterochronous.

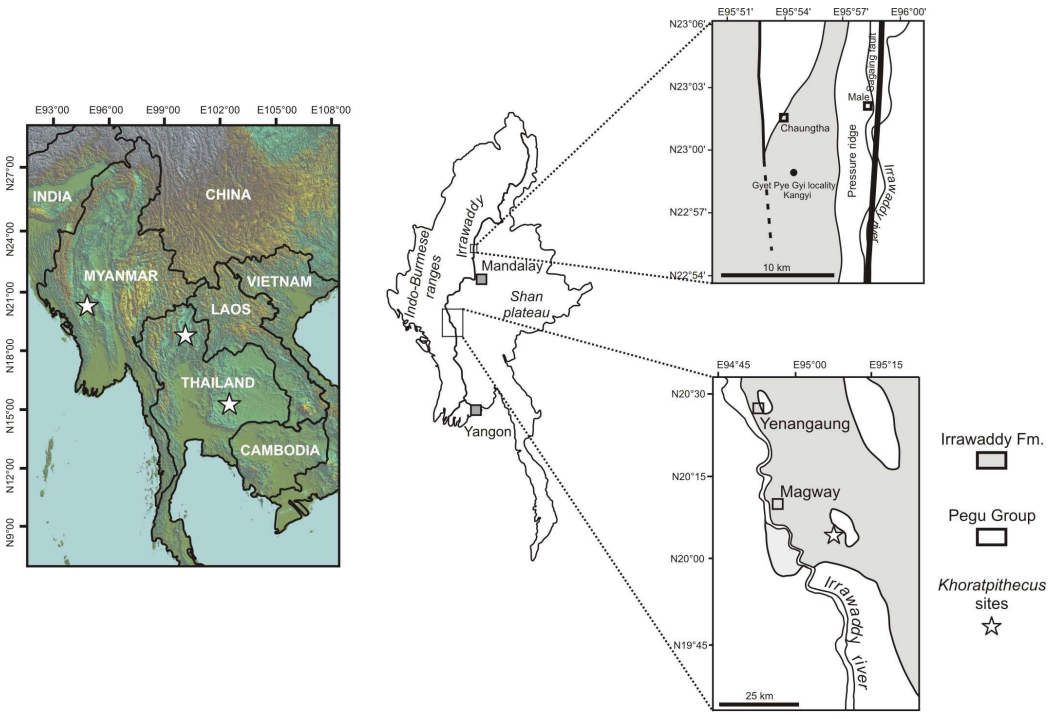


Figure 2.1. Maps of Southeast Asia and Myanmar positioning the *Khoratpithecus*-bearing localities of Thailand and Myanmar and detailed maps of Magway and Chaungtha fossiliferous areas (After Jaeger et al. in review)

The continental deposits of the Irrawaddy Formation can reach thickness of ~400 m (Kyi Khin and Myitta 1999) and have been subdivided into two lithostratigraphic units as the Lower Irrawaddy and Upper Irrawaddy Units (e.g. Colbert 1938, 1943). The stratigraphy and the age of these units are, however, not clearly defined. The Lower Irrawaddy Unit is believed to span a great time interval ranging from late Miocene to Pliocene and the Upper unit is thought to be Pliocene to Pleistocene in age (Takai et al. 2006). However, Chavasseau et al. (in press) suggested that the biostratigraphical divisions of Lower and Upper Irrawaddy are not appropriate considering that three distinct faunal assemblages of respectively late middle Miocene, late Miocene and Plio-Pleistocene age can be identified in the Irrawaddy Formation. The Irrawaddian deposits, well exposed 20 km ESE of Magway, 40km South of the Yenangyaung 'type-region' of the group (Figure 2.1), have yielded a late Miocene fauna assemblage equivalent in age to the Nagri Formation and lower part of the Dhok Pathan Formation of the Siwaliks Group of Pakistan (Chavasseau 2008; Chavasseau et al. 2010). In this area, the Irrawaddian deposits comprise claystones, soft medium to coarse grained cross-bedded sandstones with interstratified ferruginous conglomerate and pebbles beds and have yielded numerous fossil wood and vertebrate mammal remains. The main fossil-bearing localities have been reported from the conglomerate beds and sandstone horizons, which preserved diverse vertebrate fauna including primates, equids, suids, anthracotheriids, bovids, giraffids, tragulids, rhinocerotids, chalicotheriines, fresh water sharks, crocodiles and turtles (Noetling 1895; Pilgrim 1910, 1927; Stamp 1922; Colbert 1938; Chavasseau et al. 2010; Jaeger et al. *in review*). A fossiliferous channel deposit rich in iron-hydroxides nodular layers, was recovered by the Myanmar-French paleontological expedition in December 2007 and has yielded an isolated upper molar of the hominoid, assigned to a new species of *Khoratpithecus* (Jaeger et al. in review) and several other mammal remains.

350 km up North, in the area of Chaungtha, at about 130 km north of Mandalay (Figure 2.1), Tertiary deposit outcrops, ~100m thick, are composed of shales, siltstones and sandstones alternation reflecting fluviatile depositional environment and have yielded wood and vertebrate fossil remains (Chavasseau et al. 2006). The sediments of Chaungtha area were

first mapped as being middle Eocene in age (Myint Thein et al. 1982). Chavasseau et al. (2006), on the basis of new vertebrate fossil recoveries, reassessed the biostratigraphy of the site, and correlated these deposits to the Chinji Formation of Siwalik Group, suggesting a late middle Miocene or perhaps early late Miocene age for these deposits. The fluviatile deposits outcropping at Chaungtha locality are not exposed at Yenangyaung area, considered as the 'type-region' of the Irrawaddy Formation. According to Chavasseau et al. (2006), these deposits are recognized as belonging to the Irrawaddy Formation rather than to the Pegu Group. These sediments have yielded, so far, the oldest known mammalian Irrawaddian fauna.

3. PALEOMAGNETISM

3.1. SAMPLING

Section MI01, Magway area

The section at the locality yielding the hominoid isolated upper molar referred to *Khoratpithecus* sp., was sampled for paleomagnetic analyses. The magnetic polarity stratigraphy of this ~100m thick section (Figure 2.2) was established on 20 distinct levels. Three samples were collected from each stratigraphic level. Five sites (0; 1; 5; 43-44; 48), had only two samples available for laboratory analyses because the third samples were damaged during transit or sample preparation. Levels presenting sign of weathering were avoided and fine-grained sediments were preferred. Different sampling procedures have been used depending on the lithology and the outcrop exposures. During a preliminary field study in December 2006, the five uppermost levels of the section (stratigraphic levels 45 to 49) were sampled using a portable gasoline-powered driller. In December 2007, the 15 lowermost levels of the section were sampled. When the sites were not suitable for drilling, oriented samples were taken using plastic cubes of edge length 2 cm. A rock cutter was used to shape the samples, which were then placed in the cubes respecting their in situ orientation. Few

oriented blocks (levels 0, 1, 37-39) were also collected when lithology was not proper to other sampling processes and drilled at laboratory. The sampling density ranges from 1 to 15 m with a mean value of 5m. Owing to the lack of continuous exposure, approximately 10 m thick of the central part of the section have not been sampled.

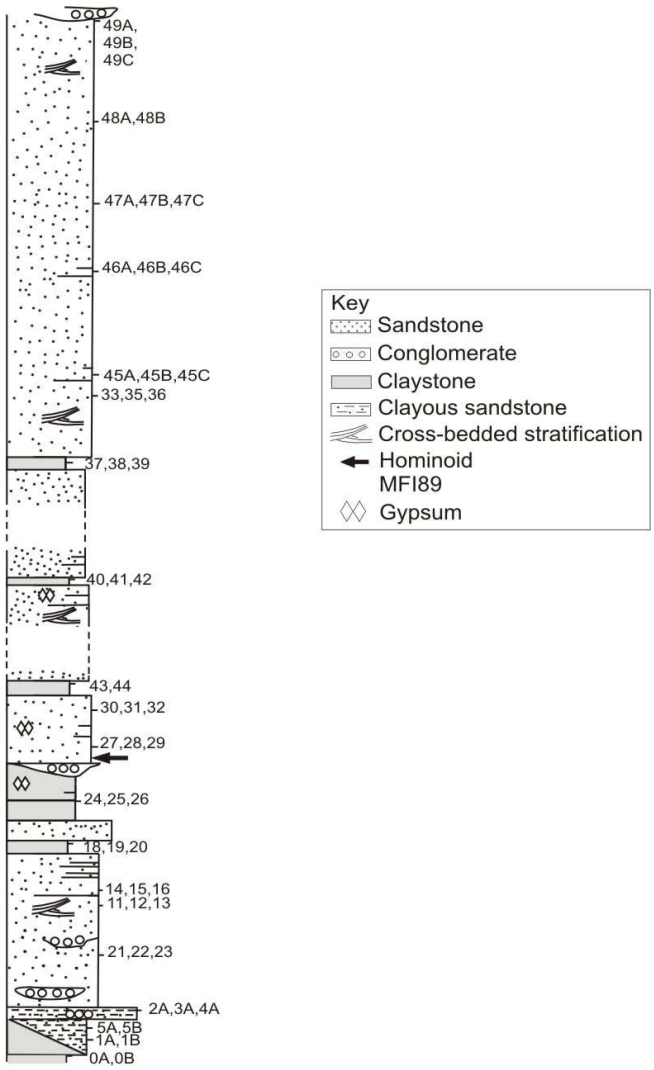


Figure 2.2. Lithology and stratigraphic position of the samples along the Magway MI01 section.

Section CI01, Chaungtha area

Rock samples for paleomagnetic analysis were further collected from the Irrawaddian outcrops, exposed at Gyet Pyi Gye locality, southeast of Chaungtha village, Northern Myanmar (Figure 2.1). Ten sites were sampled through a ~40m section, composed of claystone, siltstone and fine to medium-grained sandstone intercalations. Site sampling was constrained by the availability of suitable sediments. Samples were taken preferentially from claystone or fine-grained sandstone horizons. We could not manage to have a dense sample distribution through the section because most of the claystone horizon exposures show signs of weathering and some of the sandstone levels were too coarse to be sampled. Oriented block samples were collected and oriented on the outcrop using a Brunton compass and then drilled in the laboratory.

3.2. PALEOMAGNETIC RESULTS

3.2.1. Section MI01, Magway area

Isothermal Remanent Magnetization (IRM)

Paleomagnetic analyses were carried out at the laboratory of paleomagnetism of the Universidad Nacional Autonoma de Mexico. Isothermal Remanent Magnetization (IRM) acquisition was processed, using a pulse magnetizer, on 10 specimens of various lithologies randomly selected along the section. These samples were exposed to incremental field steps up to 1 T. The remanent magnetization was measured after each step using a JR6 spinner magnetometer. Then, differential IRM were applied along three axes of the samples (0.1 T along the x axis, 0.5 T along the y axis and 2 T along the z axis) following the Lowrie method (1990). The samples were subsequently subjected to thermal demagnetization by successive temperature increments (25 to 100°C). Magnetic susceptibility, measured after each heating step, remained constant until 600°C, suggesting the absence of neoformation of ferromagnetic minerals. All the samples displayed similar coercivity patterns and demagnetization curves

indicating the presence of the same magnetic phases along the section. Figure 2.3 shows the IRM acquisition and thermal demagnetization of two representative samples, 22A and 38A.

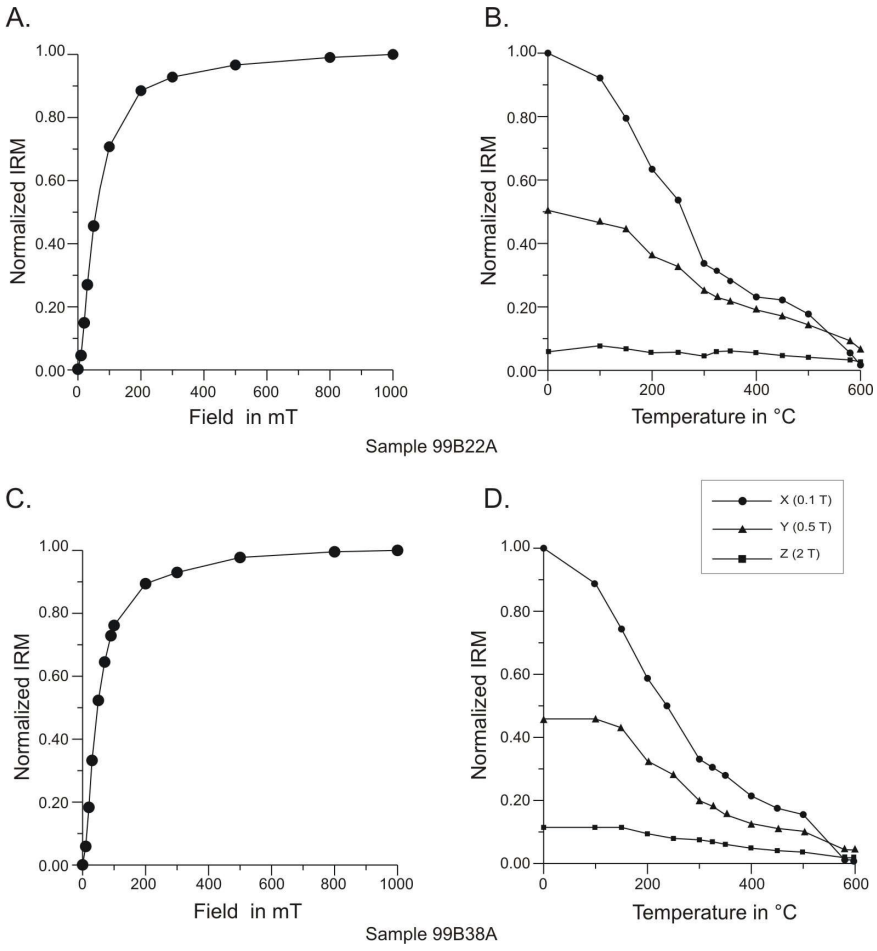


Figure 2.3. (A., C.) Isothermal Remanent Magnetization (IRM) acquisition (normalized values) curves of selected samples of Magway section MI01. (B., D.) Normalized magnetization intensity curves showing thermal demagnetization of IRM components for representative specimens of Magway section MI01.

The IRM profiles display high slope at low fields (between 0 and 200 mT) but no complete saturation beyond 1T. This reveals a dominance of low coercivity minerals such as (titano)magnetite, maghemite or iron sulfides and a lesser contribution of higher coercivity minerals such as hematite or goethite (Figure 2.3). A low blocking temperature phase is demonstrated by an inflexion of the soft coercivity component around 300 °C, revealing the

presence of titano-magnetite and/or iron sulfides. This latter component is nearly demagnetized at 580°C, denoting the presence of magnetite. The medium and high coercitivity components of IRM were not completely removed at 600°C, which indicates the presence of hematite.

These analyses indicate that the ferromagnetic carriers of remanent magnetization are mainly titanomagnetite, magnetite and, to a lesser extend, hematite and some iron sulfides.

Natural Remanent Magnetization (NRM)

Most of the samples were subjected to stepwise alternating field demagnetization up to 100 mT. Few samples were processed by thermal demagnetization up to 600°C. Results were figured in orthogonal vector plots (Figure 2.4A-C).

The NRM intensity ranged between 6 x 10^{-4} and 3.5 x 10^{-2}A.m^{-1}. Demagnetization revealed that most samples were characterized by two components, a low stability component, removed between 5 and 15 mT or below 100 °C, and a high stability component. The high stability component, displaying stable remanence directions decaying towards the origin, is interpreted as the characteristic component of NRM (ChRM).

Principal component analysis, following Kirschvink's (1980) method, was carried out to determine the ChRM directions. Mean directions and associated precisions parameters were calculated for each stratigraphic level using Fisher statistics (1953) and are presented in Table 2.1. ChRM mean directions, after stratigraphic corrections, are: Decl. = 7.30° and Incl. = 23.95° (k = 23 and α_{95} = 7.0°). The tilt correction did not significantly improve the ChRM direction clustering because the sampled strata are low-dipped (<10 °). The area of study being unfolded, no fold test was carried out. We compared the overall mean direction of the section to the expected dipole paleomagnetic field direction (Decl. = 1.5°, Incl. = 39.7°, α_{95} = 2.7°) calculated at the site latitude for 10 Ma Eurasian plate pole position from the apparent polar wander path (APWP) of Torsvik et al. (2008). The observed mean inclination value is shallower than the value expected at the site latitude (F = 15.7±6.2°). This inclination flattening could have been induced by depositional or post-depositional process in the

sediments (e.g. Tauxe and Kent 2004). Virtual geomagnetic pole paleolatitude, calculated from ChRM directions, yielded a normal magnetic polarity sequence for our whole section (Figure 2.5).

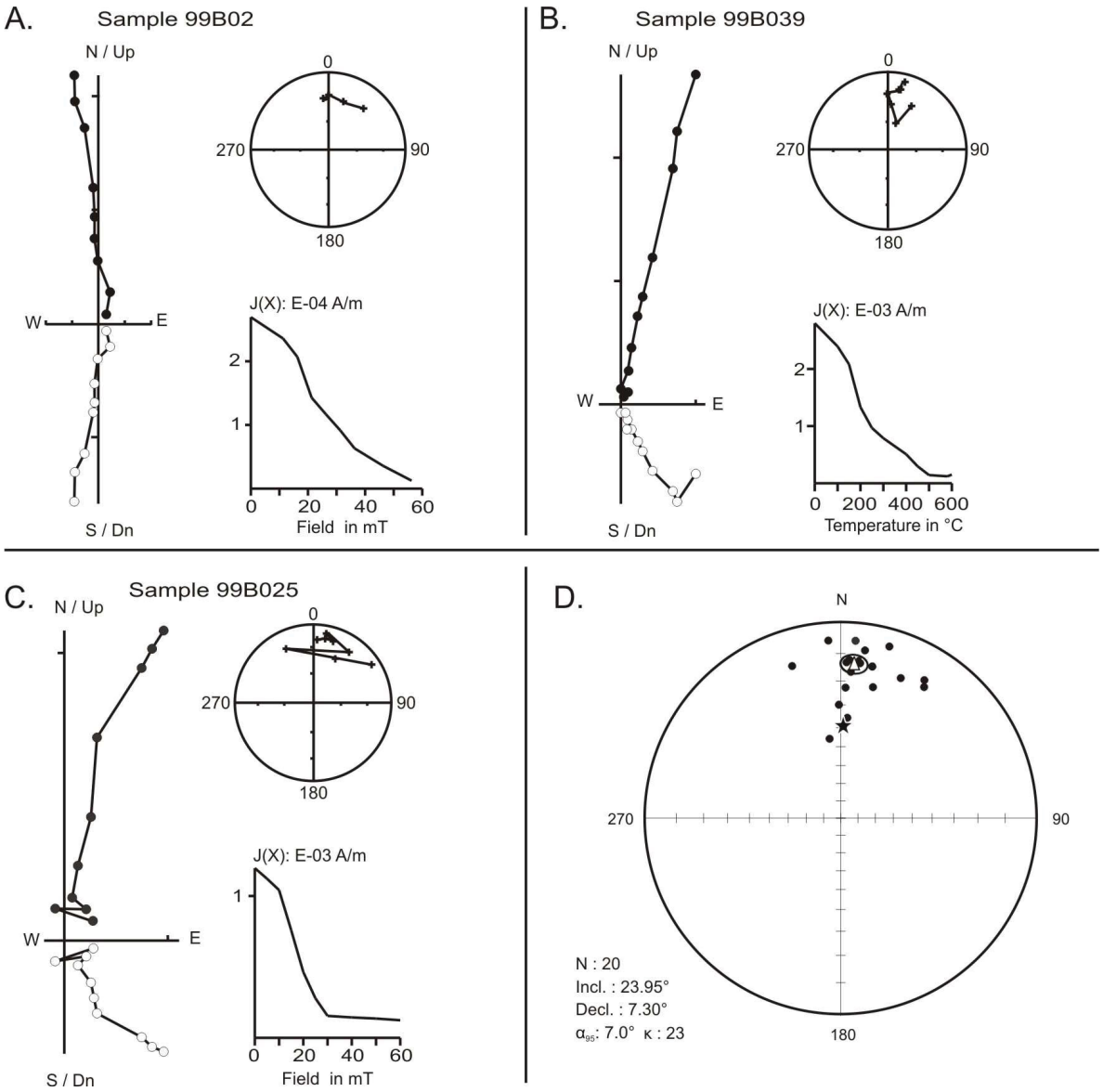


Figure 2.4. (A.-C.) Orthogonal vector diagrams (closed/open symbols correspond to the horizontal/vertical components), stereoplots (open/closed circles indicate directions in the upper/lower hemisphere), intensity and step plots for representative samples after thermal and alternating field demagnetizations. (D.) Equal-area stereographic projection of site-mean characteristic directions. Mean direction calculated by Fisher statistics is represented by a triangle and the ellipse indicates the 95% confidence. Star shows the direction derived from the 10 Ma apparent polar wander path of Torsvik et al. (2008).

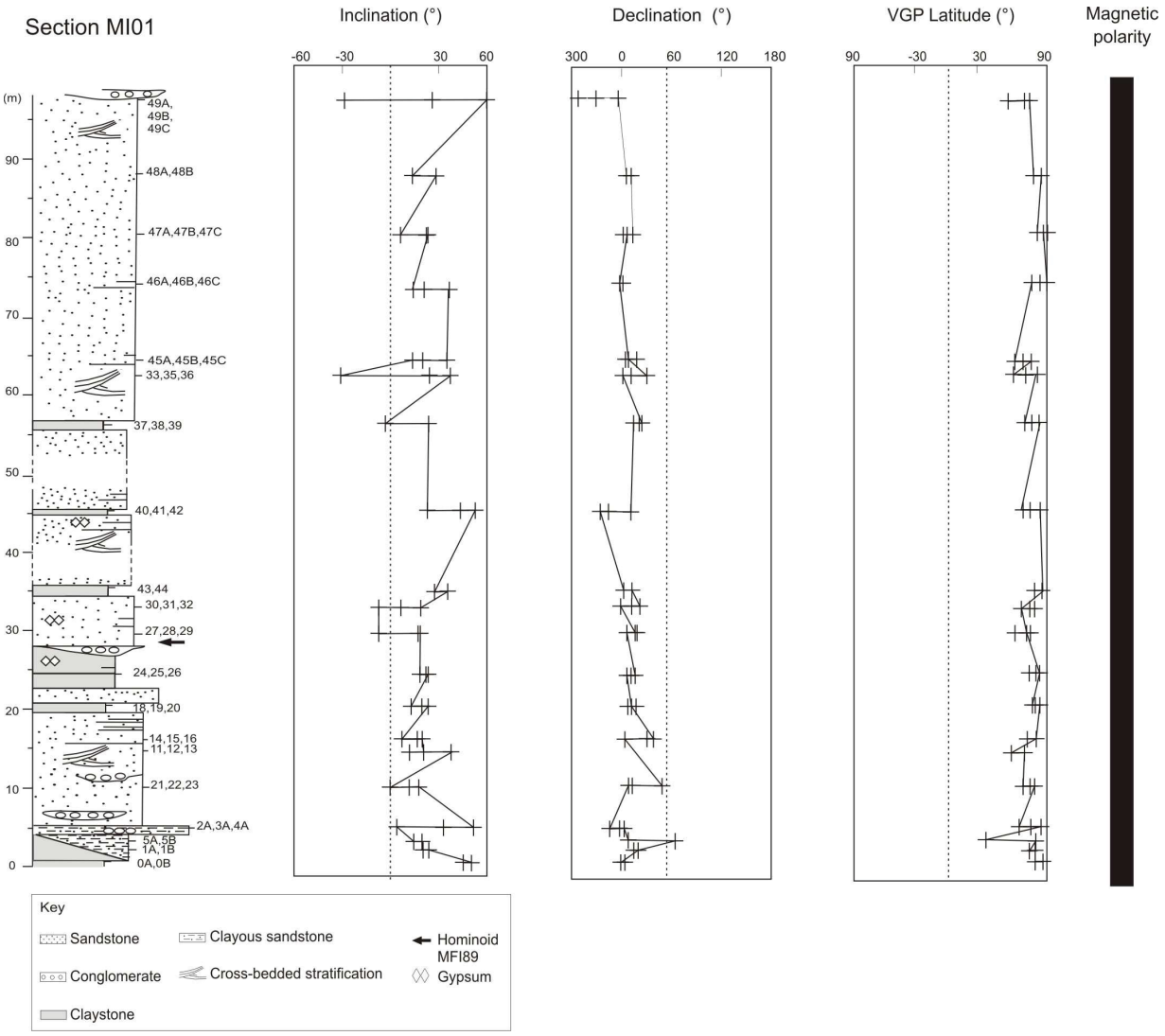


Figure 2.5. Paleomagnetic reversal stratigraphy of Section MI01. Inclination (in degrees to the horizontal), declination (°E), and the virtual geomagnetic pole (VGP) paleolatitudes (°N) of characteristic remanent magnetization (ChRM) are plotted as a function of stratigraphic levels. The lines and numbers at the right of the stratigraphic column indicate the position of the sites.

TABLE 2.1. PALEOMAGNETIC POLARITY SITE MEAN DIRECTIONS OF MAGWAY SECTION

Site	height (m)	Incl. (°)	Decl. (°)	α95 (°)	k	λ_{VGP}
MI01						
0A-0B	0	56.32	351.64	-	-	79.14
1A-1B	2	22.41	11.65	-	-	75.78
5A-5B	3	19.31	31.26	-	-	55.25
2-3-4	4.5	41.62	358.83	17.7	49	86.43
21-22-23	9.5	10.06	4.68	14	79	74.28
11-12-13	14.2	21.81	32.32	17.3	52	57.73
14-15-16	15.5	14.47	8.07	13.5	84	75.03
18-19-20	20	20.49	3.25	13.2	88	79.97
24-25-26	24	20.45	6.63	14.2	76	78.53
27-28-29	28.5	9.89	355.82	23.3	29	74.33
30-31-32	32.5	2.17	5.07	13.4	85	70.34
43-44	35	31.7	13.65	-	-	76.5
40-41-42	45	47.39	3.51	9	190	80.99
37-38-39	60	3.74	15.69	9.8	460	66.18
33-35-36	62	33.67	2.28	9.7	164	87.26
45A-45B-45C	64	23.24	23.05	19.1	43	66.49
46A-46B-46C	73.5	23.37	4.24	18.9	44	81.09
47A-47B-47C	82	22.56	2.98	15.4	35	81.15
48A-48B	87.5	21.8	1.75	-	-	81.17
49A-49B-49C	97	19.43	342.07	41.7	10	70

Note: Decl.: mean tilt corrected declination in °E; Incl.: mean tilt corrected inclination in degree to the horizontal; α95 : mean direction 95% confidence ellipse; k : Fisher precision parameter; λVGP: paleolatitude of virtual geomagnetic pole in °N

3.2.2. Section CI01, Chaungtha area

Natural Remanent Magnetization (NRM)

Paleomagnetic analyses were performed at the laboratory of Paleomagnetism of the Institut de Physique du Globe de Paris. All the samples were subjected to step-wise thermal demagnetization from 120°C up to 650°C, with 25–50°C increments, and measured on a 2G vertical cryogenic magnetometer. Data resulting from demagnetization were plotted on orthogonal vector diagrams and stereoplots (Figure 2.6). The NRM of most the specimens is characterized by two components. Demagnetization temperatures higher than 200°C usually yielded a stable characteristic paleomagnetic component.

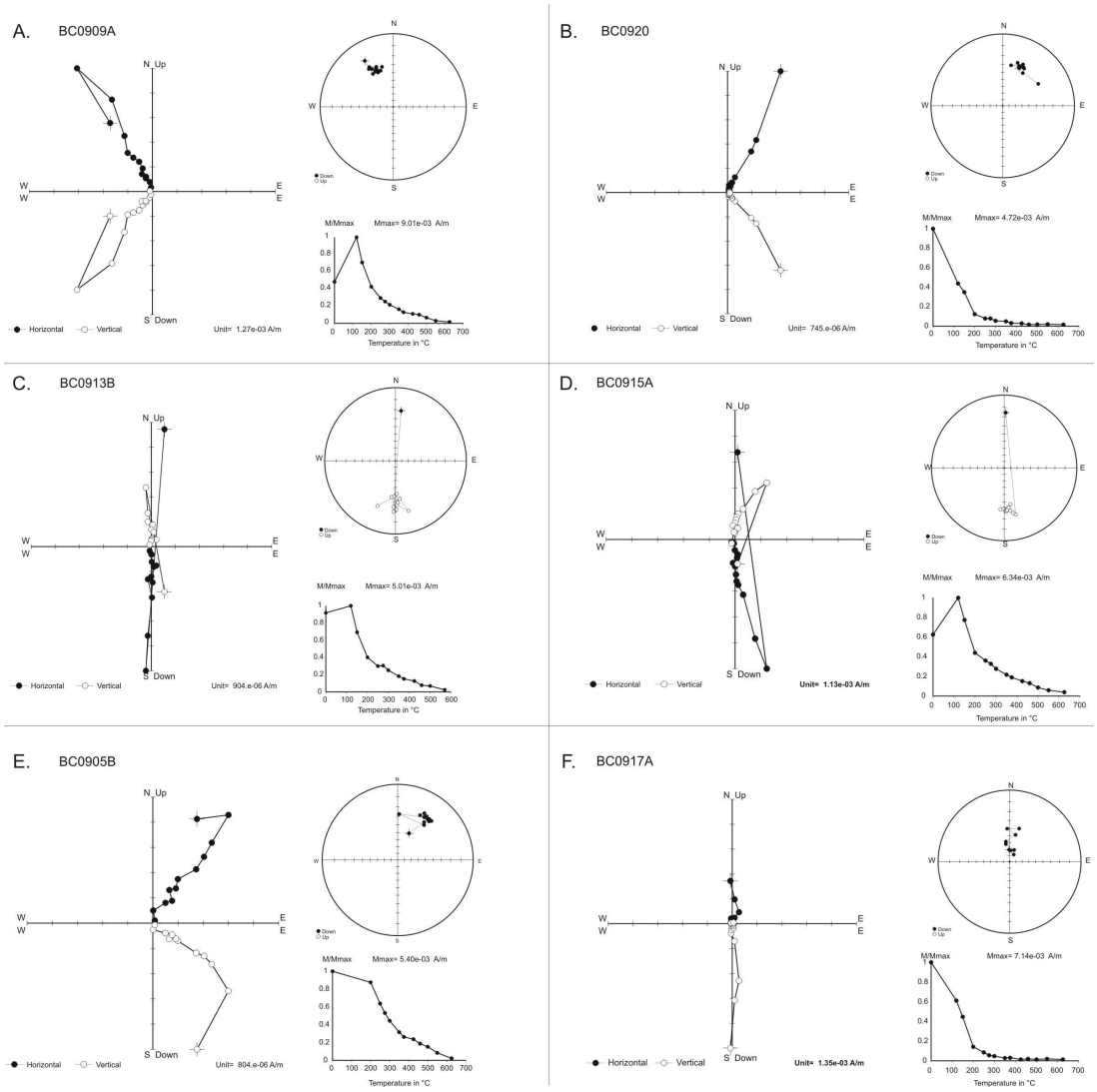


Figure 2.6. (A.-F.) Orthogonal vector diagrams (closed/open symbols correspond to the horizontal/vertical components), stereoplots (open/closed circles indicate directions in the upper/lower hemisphere), and intensity and step plots for representative samples after thermal and alternating field demagnetizations.

On the 21 analysed specimens, six were characterized by erratic behaviour and failed to yield coherent paleomagnetic data. These samples were not considered for further analyses. Some samples, during demagnetization show unblocking temperature at about 580°C (Figure 2.6C), indicating the presence of magnetite. Thermal demagnetization curves of other samples show the presence of high unblocking temperature minerals (>600°C) (Figure 2.6D, E) and are interpreted to reflect the presence of hematite. The demagnetization curve of some

claystone samples (Figure 2.6 B,F) decreases strongly at 200°C, which corresponds to the unblocking temperature of iron sulphide or titanomagnetite.

To determine characteristic paleomagnetic directions, principal component analysis (Kirschvink 1980) was performed for each sample. The resulting paleomagnetic directions were then analysed using Fisher statistics (1953) to determine site mean declination, inclination and associated precision parameters. Results are presented in Table 2.2.

TABLE 2.2. PALEOMAGNETIC POLARITY SITE MEAN DIRECTIONS OF CHAUNGTHA SECTION

Site	height (m)	Incl. (°)	Decl. (°)	α95 (°)	k	R	λ_{VGP}
CI01							
20A	1.8	27.7	29	-	-	-	61.40
19A-19B-19C	8.4	26.9	337.3	10.9	138.85	2.99	66.82
18A	10.7	55.6	339.9	-	-	-	68.19
17A	15.92	-14.8	2.3	-	-	-	59.42
16A-16B-16C	21.16	50.9	355.9	26.3	23.08	2.91	80.63
14A-14B-14C	24.6	20.6	21.9	15.6	63.54	2.97	65.73
13A-13B-13C	30.7	-35.5	177.9	14.9	69.74	2.97	-86.13

Note: Decl.: mean tilt corrected declination in °E; Incl.: mean tilt corrected inclination in degree to the horizontal; α95 : mean direction 95% confidence ellipse; k : Fisher precision parameter; R : length of the resultant vector; λVGP: paleolatitude of virtual geomagnetic pole in °N

The mean direction of normal sites is Decl. = 357.8°, Incl. = 33.4° (α_{95} = 21.4°) while mean polarity of the reverse site is Decl. = 177.9°, Incl. = -35.5° (α_{95} = 14.9°) (Figure 2.7). The overall mean sites polarity is Decl. = 357.8°, Incl. = 33.9° (α_{95} = 16.5°). The sampled section exhibit subhorizontal beds thus the fold test could not be carried out to investigate the paleomagnetic stability of the data. In order to evaluate our results, a reversal test was performed. The angle between the mean directions of the normal and reversed polarities is 2.1°, which was smaller than the critical angle of 36.34°. Thus, mean paleomagnetic directions of the normal and reversed polarities passed the reversal test with an indeterminate classification. The overall mean direction of the section is close to the expected direction at the site location (Decl. = 1.3°; Incl. = 43.2°; α_{95} = 2.6°) derived from the global apparent polar wander path of Eurasia at 10 Ma (Torsvik et al. 2008) (Figure 2.7C).

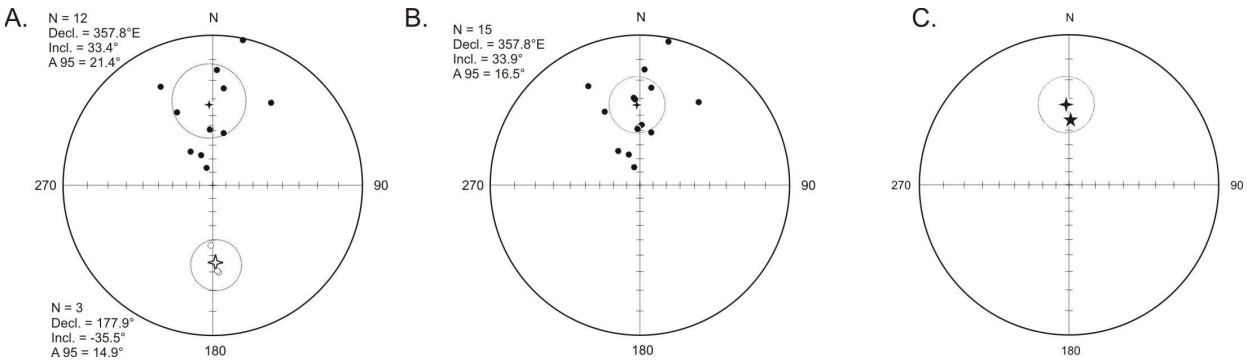


Figure 2.7. (A.) Equal-area stereographic projection and Fisher statistics of characteristic directions for all the specimens. (Open/closed circles indicate directions in the upper/lower hemisphere). Mean directions calculated by Fisher statistics are represented by a star, and the ellipse indicates the 95% confidence ellipse. (B.) Equal-area stereographic projection and Fisher statistics of characteristic directions for all the specimens when reversed polarity sites are inverted. (C.) Equal-area stereographic projection of overall mean sites direction (black star) of the section and ellipse at the 95% confidence ellipse. Solid star shows the direction derived from the 10 Ma apparent polar wander path of Torsvik et al. (2008).

The comparison of the expected and observed directions, using Demarest method (1983), yields vertical axis rotation of declination R= -3.5±16.1° and flattening of inclination of F=9.6±13.4°. The lower observed inclination value is consistent with the sedimentary inclination error for the depositional remanent magnetization (e.g. Tauxe and Kent 2004).

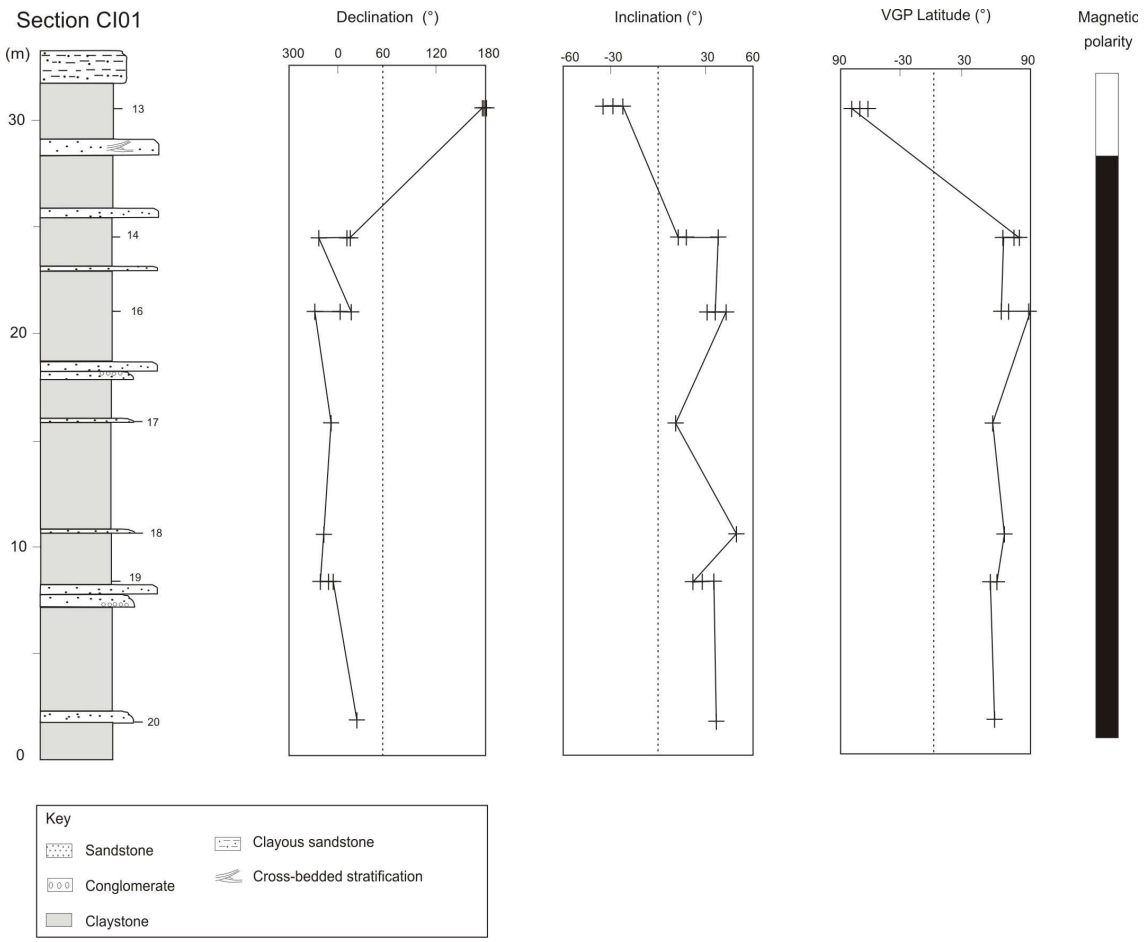


Figure 2.8. Paleomagnetic reversal stratigraphy of Section CI01. Inclination (in degrees to the horizontal), declination (°E), and the virtual geomagnetic pole (VGP) paleolatitudes (°N) of characteristic remanent magnetization (ChRM) are plotted as a function of stratigraphic levels. The lines at the right of the stratigraphic column indicate the position of the sites.

The directions of the characteristic component of each sample were used to calculate the virtual geomagnetic pole latitude, and reported in Figure 2.8. The lower part of the resulting magnetic polarity sequence display a ~25m thick normal polarity zone, represented by six sampled level. A reverse polarity zone is represented by only one site at the top of the section.

4. CORRELATION

4.1. SECTION MI01, MAGWAY AREA

Biostratigraphic study by O. Chavasseau in Jaeger et al., in review

The mammal fauna collected during our fieldwork, associated to the *Khoratpithecus,* is homogeneous along the Magway section and among the investigated area. It includes a proboscidean belonging either to *Stegolophodon* or *Tetralophodon*, the equid '*Hipparion'* (s.l.), a species of Chalicotheriinae and an indeterminate species of rhinocerotid. Artiodactyls are represented by the anthracothere *Merycopotamus medioximus*, the suids *Tetraconodon minor*, *Propotamochoerus* cf. *hysudricus* and cf. *Hippopotamodon sivalense*, the palaeochoerid *Schizochoerus* sp., a medium-sized tragulid, several bovids including an antilope, and a giraffid. A fresh water neoselacian, numerous trionychid plate fragments, crocodile dental and skeletal remains and siluriform fishes were also discovered in the section. The complete faunal list is given in Table 2.3.

This fauna, among which hipparionin fossils are most common, is obviously younger than 10.7 Ma, observed first appearance datum (FAD) of these equids in the Siwaliks of Pakistan (Barry et al. 2002). This FAD is consistent with that observed in the Turkish Sinap Formation (10.7 Ma; Kappelman et al. 2003). The anthracothere *Merycopotamus medioximus* has evolved in the Indian subcontinent from the species *Merycopotamus nanus* during the early late Miocene (Lihoreau et al. 2004). *M. medioximus* ranges from 10.4 to 8.6 Ma in the Siwaliks of Pakistan. Although a short temporal gap exists between the ranges of *M. nanus* and *M. medioximus* (Lihoreau et al. 2007), the observed FAD of the latter species in Pakistan confirms the indication of hipparionines. The tetraconodont *Tetraconodon minor* is a close relative of *Tetraconodon magnus* present between 10.0 and 9.3 Ma in Pakistan (Barry et al. 2002). Moreover, the section yielded two primitive Suinae (*Propotamochoerus* cf. *hysudricus* and cf. *Hippopotamodon sivalense*) which match best with the two dominating suids of the

late Miocene fauna of the Indian subcontinent, *Propotamochoerus hysudricus* and *Hippopotamodon sivalense*. These species are associated ~~together~~ from 10.2 to 7.2 Ma in the Potwar Plateau of Pakistan (Barry et al. 2002).

Because the Burmese fauna includes shared or closely-related species with the Siwaliks of Pakistan, the first and last appearance datum (LAD) of the Pakistani taxa are used to provide the biochronological bracket. This choice is also motivated by fossil richness and chronological precision of the sites of this region (Barry et al. 2002). As mentioned above, the FADs of the Siwalik species bring a convincing lower limit for the age bracket of the section. Uncertainty is greater for the upper bracket, the LADs of the Siwalik large mammals being not well-constrained in Southeast Asia (Chaimanee et al. 2006). Considering the biochronological constraints, an optimized bracket of 10.4-8.6 Ma is assigned to the section.

Table 2.3. Faunal lists of Magway and Chaungtha fossiliferous areas.

Faunal list of Magway area	Faunal list of Chaungtha area
MAMMALIA	MAMMALIA
Primates	Proboscidea
Hominidae	**Gomphotheriidae**
Khoratpithecus nov. sp.	Gen. sp. indet.
Khoratpithecus sp.	Perissodactyla
Proboscidea	**Rhinocerotidae**
Tetralophodon sp.	*Brachypotherium fatehjangense*
Artiodactyla	Gen. sp. indet.
Suidae	**Chalicotheriidae**
Tetraconodon minor	Chalicotheriinae indet.
cf. *Hippopotamodon sivalense*	Artiodactyla
Propotamocheorus cf. *hysudricus*	**Suidae**
Palaeochoeridae	*Conohyus thailandicus*
Schizochoerus sp.	**Anthracotheriidae**
Tragulidae	*Merycopotamus nanus*
Gen. sp. indet. (middle-sized)	**Bovidae**
Bovidae	low crowned form
Antilopini indet.	**Tragulidae**
Gen. sp. indet.	cf. *Siamotragulus sanyathanai*
Gen. sp. indet. 2	cf. *Siamotragulus* sp.
Anthracotheriidae	Carnivora
Merycopotamus medioximus	**Viverridae**
Perissodactyla	Gen. sp. indet.
Equidae	
Hipparion (s.l.) sp.	
Rhinocerotidae	
Gen. sp. indet.	
Chalicotheriidae	
Chalicotheriinae	
Gen. sp. indet.	
Carnivora	
Fam. gen. sp. indet.	
REPTILIA	
Testudines	
Trionychidae	
Trionyx sp.	
CHONDRYCHTHYES	
Carcharhiniformes	
Carcharhinidae	
Glyphis pagoda	
ICHTHYES	
Siluriformes	
Fam. gen. sp. indet.	

Correlation of our section to the Geological Polarity Time Scale of Gradstein et al. (2004) has been constrained on the basis of these biochronological data.

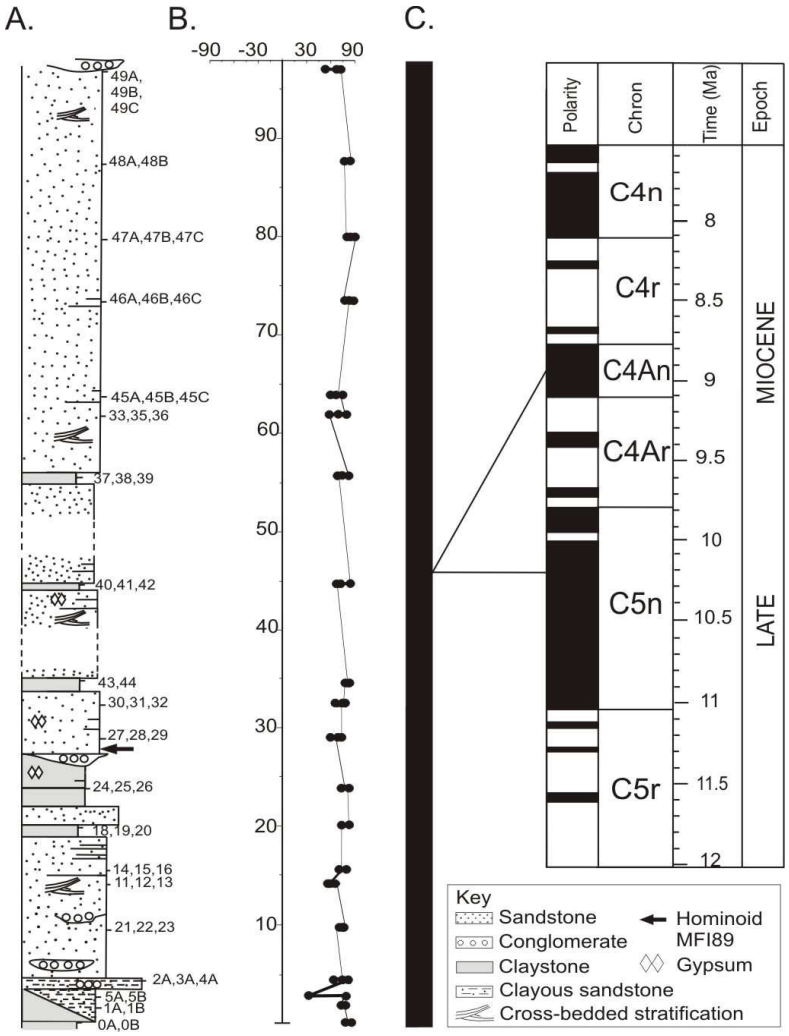


Figure 2.9. Magnetic polarity stratigraphy of the hominoid section. (A.) Lithology and stratigraphic position of the sampled levels. (B.) Latitude of the virtual geomagnetic pole. (C.) Polarity column (black bar: normal polarity zone) and potential correlations with the GPTS of Gradstein et al. (2004).

Correlation of the 97m thick section with short duration chrons (<100 kyr) are excluded because they imply net minimum sedimentation rate (>100 cm.kyr^{-1}) which are inconsistent with a fluviatile sedimentary regime (Johnson et al. 1982; Sen et al. 1986). Among the 8 normal polarity chrons included in the early late Miocene part of the GPTS, only three (C5n, C4An and C4n.2n) are likely to be correlated with our section (Figure 2.9). These correlations imply minimum sedimentation rates comprised between 10 and 30 cm.kyr^{-1}.The

normal polarity sequence of the hominoid section can be plausibly correlated to the latest part of long normal polarity chron C5n, between 10.4 and 9.8 Ma. The section would likely correlate to C5n.2n alone or both C5n.2n and C5n.1n. In this latter hypothesis, the short reversal polarity event (C5n.1r) located within this chron C5n would have not been sampled. The second potential correlation would place the section within chron C4An, between 9.1 and 8.8 Ma, which involves a maximum duration of 0.329 my and a minimum sedimentation rate of 29 cm.kyr^{-1}. The correlation with subchron C4n.2n (8.1-7.7 Ma) is less probable taking into account the biochronological data bracket of 10.4-8.6 Ma, which rather support allocating the section either within chron C4An (9.1 to 8.8 Ma) or within the latest part of chron C5n (10.4-9.8 Ma).

4.1. SECTION CI01, CHAUNGTHA AREA

Age constraints for magnetic correlation were provided by mammalian biostratigraphical study. The fossils come from two localities, the Gyet Pyi Gye and Kangyi sites, located at about 5 km SSE of Chaungtha village. The Irrawaddian deposits exposed in that area are mainly composed of siltsones, claystones and few sandstone horizons and have yielded numerous vertebrate and fossil wood remains.

Chavasseau et al. (2006) provided the first comprehensive faunal list from Chaungtha deposits (Table 2.3). New field expedition this area, in 2009, allow us to expand the earlier mammalian fossil collection (Chavasseau et al. in press).

The mammalian fauna comprises the suid *Conohyus thailandicus*, two species of tragulid assigned to *Siamotragulus* genus (cf. *Siamotragulus sanyathanai*, cf. *Siamotragulus* sp.), a low-crowned ?Bovidae, an indeterminate species of Gomphotheriidae, the rhinocerotid *Brachypotherium fatehjangense* and an indeterminate rhinocerotid, a chalicotheriid, a viverrid, and the anthracothere *Merycopotamus nanus* (Chavasseau et al. 2006; in press).

The suid *Conohyus thailandicus* has been recognized from mammal-bearing coal layers (Q, K) of Mae Moh basin (Chaimanee et al. 2007), well-dated between 13.4 and 13.2 Ma (Coster

et al. 2010). This species is also present in several other middle Miocene localities of Northern Thailand (Ducrocq et al. 1997) and display similarities with *Conohyus sindiensis* from Chinji Formation, Siwalik Group, Pakistan, ranging from 14 to 10.3 Ma (Barry et al. 2002). The fauna from Chaungtha also shares with the middle Miocene Thai localities the common occurrence of tragulid species close to the genus *Siamotragulus* (Ducrocq et al. 1997; Thomas et al. 1990; Chaimanee et al. 2003). The rhinocerotid *Brachypotherium fatehjangense*, recovered from Chaungtha deposits (Chavasseau et al. 2006), has also been described from the middle Miocene Nagri, Upper and Lower Chinji Formations of the Siwalik (Heissig 2003). Chaungtha deposits yielded the species of anthracothere *Merycopotamus nanus* (Chavasseau et al. in press), which has also been described from the late middle Miocene (13.9–11.3 Ma) Chinji Formation of Siwaliks (Lihoreau et al. 2007). Hipparions, which are well represented in the early late middle Miocene fauna assemblage from Magway and Yenangyaung, are absent from Chaungtha deposits. The absence of this taxon seems to indicate a minimum age of 10.7 Ma (*Hipparion* datum in the Siwaliks; Barry et al. 2002). The other previously mentioned mammalian taxa seem to indicate a middle Miocene age but do not provide further evidences for more precise relative age.

In sum, the mammal assemblage of Chaunghta indicates that the fossiliferous strata are most probably late middle Miocene in age, ranging from ~ 14 and 11 Ma.

The sampled section is thin (~35m) and yield only two polarity events. The lowermost normal polarity event record in Chaungtha section is about 25m thick (Figure 2.10). Considering the frequent polarity reversals of the earth magnetic field in this time interval, potential correlations of the normal-reverse magnetic sequence of Chaungtha are exceedingly numerous and a clear match of the section to the GPTS is not possible.

Paleomagnetic data here do not bring further information than biostratigraphical studies to bracket the age of the Chaungtha deposits. The only way to better constrain the age of the section by paleomagnetic analysis would be to extend the polarity record down or up the section, providing that future field work lead to the discovery of potential outcrops to sample.

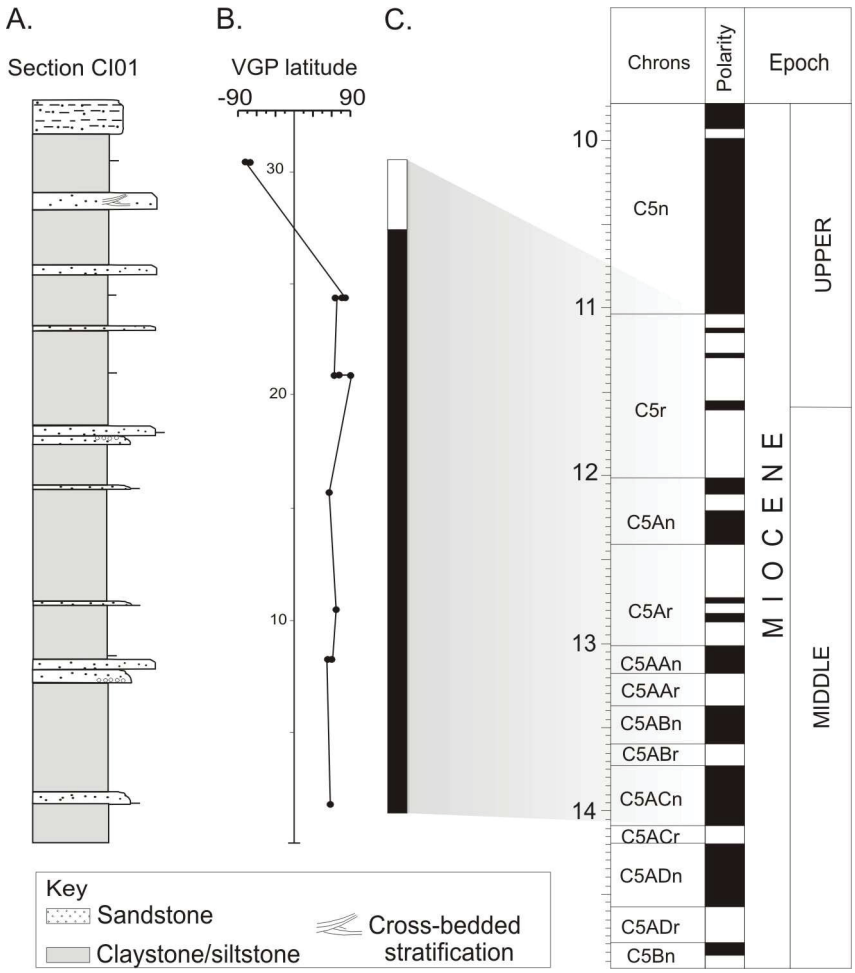


Figure 2.10. Magnetic polarity stratigraphy of Chaungtha section. (A.): lithology and stratigraphic position of the sampled levels. (B.) latitude of the virtual geomagnetic pole. (C.) polarity column (black bar: normal polarity zone) and potential correlations with the GPTS of Gradstein et al. (2004).

5. CONCLUSIONS

This work provides the first paleomagnetic investigations for the Neogene continental Irrawaddian series. Based upon faunal constraints, the composite magnetic polarity sequence of Magway deposits, which have yielded two species of the hominoid *Khoratpithecus,* have been correlated to chron C4An or to chron C5n. These two potential correlations yield an age of ~9 or ~10Ma for the *Khoratpithecus*-bearing deposits of Magway area.

The magnetic polarity chronology of the section sampled within the middle Miocene deposits of Gyet Pyi Gye locality in Chaungtha area was not long enough to allow a robust correlation to the geological polarity Time scale. Biochronological data bracket the age of this section between ~ 14 and 11 Ma but paleomagnetic data have failed to tighten the chronostratigraphic constraints for the age of these fossiliferous strata. The Myanmar-French paleontological team, which continues to prospect the area, will maintain their effort in identifying additional more complete sections.

Until now, the chronology of the Neogene faunas of Myanmar was only based on biostratigraphic studies of these series and although the biochronology of the Irrawaddian series have progressed, further work in the extensive Burmese Neogene exposures is needed to make the magnetic polarity stratigraphy study of the Irrawaddian series a useful addition to the chronologic data provided by paleontological analyses.

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2.3. ÂGE DU GENRE KHORATPITHECUS ET LA RADIATION DES HOMINOÏDES ASIATIQUES

ÂGE DU GENRE KHORATPITHECUS ET LA RADIATION DES HOMINOÏDES ASIATIQUES

L'histoire évolutive des primates hominoïdes a été marquée par une importante radiation et une dispersion à grande échelle au Miocène moyen, avec l'apparition en Asie du Sud de plusieurs genres, aujourd'hui éteints, rattachés à la lignée des orangs-outangs: *Sivapithecus, Lufengpithecus, Indopithecus* et *Khoratpithecus* (e.g. Pilbeam et al. 1977 ; Pilbeam 1982 ; Kelley 2002 ; Chaimanee et al. 2003, 2004).

Les premiers restes d'hominoïdes asiatiques du Miocène (Figure 1) ont d'abord été découverts dans les dépôts fossilifères des Siwaliks en Inde (e.g. Pilgrim 1910 ; Brown et al. 1924 ; Pandey et Sastri 1968 ; Chopra et Kaul 1975 ; Dutta et al. 1976 ; Chopra 1983), au Pakistan (Lydekker 1879 ; Pilbeam et al. 1977, 1980, 1990; Pilbeam 1982 ; Dehm 1983 ; Koenigswald 1983 ; Raza et al. 1983 ; Rose 1984, 1986, 1989 ; Kelley 1988), puis au Népal (Munthe 1983), et identifiés comme appartenant à trois espèces de *Sivapithecus*, datant de 12,7 à 8,5 Ma : *Sivapithecus indicus, Sivapithecus parvada* et *Sivapithecus sivalensis* (e.g. Barry et al. 2002 ; Kelley 2002). *Indopithecus* a, par la suite, été découvert dans les dépôts du Miocène moyen de la localité de Haritalyangar en Inde (Pilgrim 1915), datés entre 9,23 et 8,1 Ma (Pillans et al. 2005). Le genre *Lufengpithecus*, connu uniquement en Chine australe (Figure 1), a été décrit dans les dépôts du Miocène supérieur de la province du Yunnan. Trois espèces, *Lufengpithecus lufengensis* de la localité du Miocène terminal de Shihuiba dans le district du Lufeng (Xu et al. 1978 ; Flynn et Qi 1982 ; Wu 1987), *L. keiyuanensis* découverte sur le site de Xiaolungtan daté entre 12 et 10 Ma (Woo 1957, 1958), et *L. hudienensis* décrite dans les dépôts du Miocène supérieur de la formation de Xiaohe dans les régions de Zhupeng-

Xiaohe et Leilao du bassin de Yuanmou (Zhang et al. 1987 ; Zheng et Zhang 1997 ; Qi et al. 2006), ont été assignées à ce genre.

Durant la dernière décennie, des fouilles paléontologiques en Asie du Sud-Est, région jusque-là très peu prospectée, ont permis la découverte d'un nouveau genre, augmentant encore la diversité taxonomique d'hominoïdes connus au Miocène. En 2003, des fouilles dans les niveaux de lignite dans la mine de Chiang Muan en Thaïlande (Figure 1), datés entre 12,4 et 12,2 Ma (Benammi et al. 2004 ; Suganuma et al. 2006 ; Coster et al. 2010), ont mis à jour une nouvelle forme d'hominoïde, *Khoratpithecus chiangmuanensis* (Chaimanee et al. 2003 ; Pickford et al. 2004 ; Kunimatsu et al. 2004). En 2004, de nouveaux fossiles, attribués à une nouvelle espèce de *Khoratpithecus, K. piriyai* (Chaimanee et al. 2004, 2006), datés par biochronologie entre 9 et 7 Ma, ont été découverts dans un mine de lignite de la Province de Nakorn Ratchasima (Khorat) dans le Nord-Est de la Thaïlande (Figure 1). Récemment, de nouveaux restes fossiles d'hominoïdes ont été exhumés dans la région de Magway au Myanmar (Figure 1). Ces fossiles, datés autour de 9 ou 10 Ma, ont été attribués à une nouvelle espèce, *Khoratpithecus ayeyarwadyensis* (Jaeger et al. en révision) Ainsi, les faunes de primates hominoïdes en Asie du Sud apparaissent très diversifiées au Miocène moyen et supérieur, avec quatre genres et une dizaine d'espèces connus dans le sous-continent indien (*Sivapithecus, Indopithecus*), en Asie du Sud-Est (*Khoratpithecus*) et en Chine australe (*Lufengpithecus*). Une telle diversité taxonomique tranche avec la faiblesse du registre fossile à la même époque en Afrique. Une autre différence majeure des hominoïdes du Miocène asiatique par rapport aux hominoïdes européens ou africains de la même époque est leur extrême régionalisme: à l'exception du duo *Sivapithecus-Indopithecus,* les aires de répartition des genres observés ne se superposent pas.

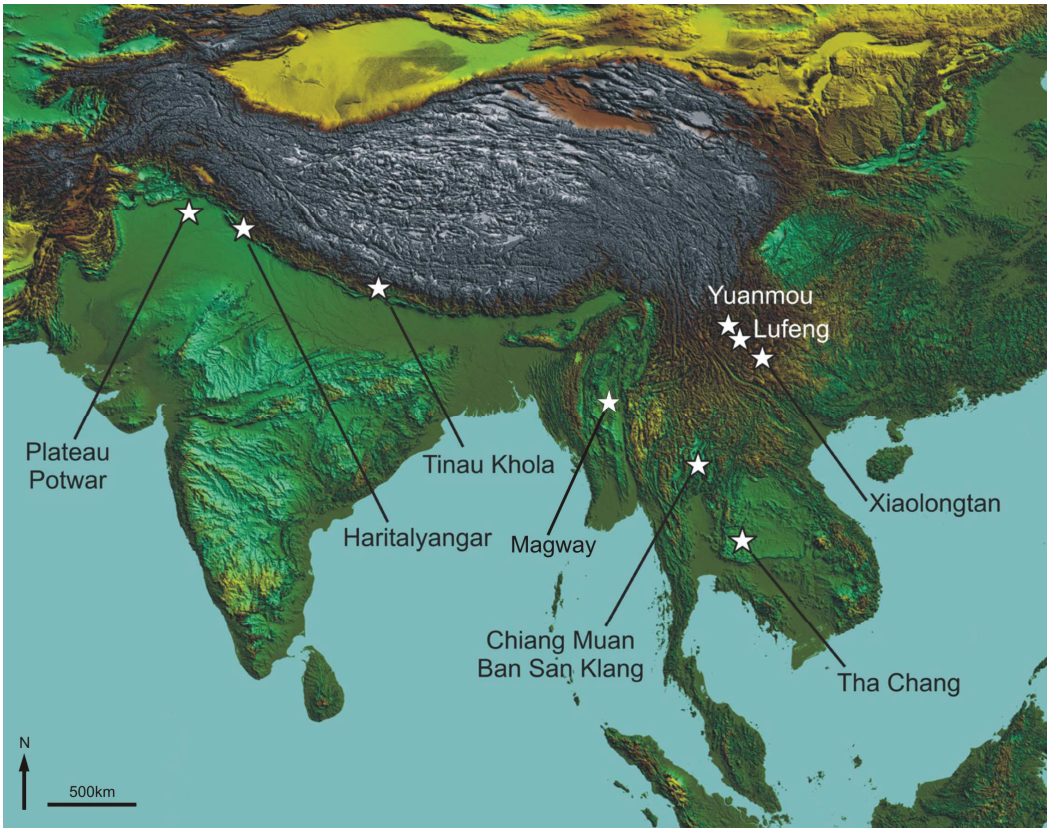


Figure 3.1. Carte de répartition des hominoïdes fossiles du Miocène en Asie du Sud-Est. Pakistan : Potwar plateau, localité à *Sivapithecus*. Inde : Haritalyangar, localité-type à *Indopithecus*. Népal : Tinau Khola, localité à *Sivapithecus*. Myanmar : Magway, localité-type à *Khoratpithecus ayeyarwadyensis*. Thaïlande : Chiang Muan, localité à *K. chiangmuanensis* ; Tha Chang, localité à *K. piryai*, Chine : Xiaolongtan, localité à *Lufengpithecus kayuanensis* ; bassin de Yuanmou, localités à *L. hudienensis* ; Lufeng, localité-type de *L. lufengensis*. (D'après Chavasseau 2008).

Le régionalisme des hominoïdes asiatiques semble révéler l'existence de différentes provinces paléobiogéographiques: une province sud-chinoise, une province indo-pakistanaise et une région birmano-thaïlandaise (Chaimanee et al. 2003, 2004, 2006 ; Chavasseau 2008 ; Sepulchre et al. 2009). Des différences paléo-environnementales dans la composition de la flore et des faunes associées aux fossiles de grands singes ont été mises en évidence et confirment ce découpage paléobiogéographique. Les résultats des analyses polliniques effectuées sur les sites de Thaïlande sont typiques de forêt tropicale humide avec des portions de zones ouvertes dans les plaines fluviales des bassins (Songtham et al. 2003). En Chine australe, les dépôts à *Lufengpithecus* ont livré une flore et une faune qui dénotent d'une végétation plus tempérée (Badgley et al. 1988 ; Xu et Lu 2008) alors que les restes fossiles de

Sivapithecus du sous-continent indien sont associés à une faune et une flore qui indiquent l'existence d'environnement plus ouvert et d'une saisonnalité plus marquée (Morgan et al. 1994 ; Barry et al. 2002). Les faunes de grands mammifères manifestent, cependant, un provincialisme moins marqué. Les sites à *Khoratpithecus* thaïlandais et birmans présentent des similarités avec la faune des sites à *Sivapithecus* et partagent la présence de nombreux taxons comme l'anthracothère *Merycopotamus medioximus* et les suidés *Propotamochoerus* et *Hippopotamodon* (Chavasseau 2008). Les faunes des régions indo-pakistanaise et d'Asie du Sud-Est sont plus proches entre elles qu'avec celle de Chine indiquant que la présence de la chaîne himalayenne et du système de la Faille de la Rivière Rouge, déjà en place au Miocène (e.g. Molnar 2005), ont pu, à l'époque, constituer des barrières majeures aux dispersions Nord-Sud des mammifères terrestres asiatiques, isolant la Chine du reste de l'Asie du Sud (Chavasseau 2008 ; Emonet 2009). L'existence de barrières géographiques filtrant les dispersions et les différences de paléoenvironnements des provinces biogéographiques subtropicales du Miocène de l'Asie du Sud ont donc dû concourir à l'endémisme des faunes d'hominoïdes asiatiques.

En plus des dimensions paléoenvironnementales et paléogéographiques, la composition des paléobiodiversités régionales présente une dimension phylogénétique. Les quatre genres miocènes d'hominoïdes présents en Asie du Sud sont tous rattachés à la lignée de l'orang-outang (e.g. Kelley 2002) mais les relations au sein du clade asiatique *Pongo* restent encore discutées. Une parenté a d'abord été suggérée entre les genres *Sivapithecus* et *Lufengpithecus* et la lignée des orangs-outangs (Pilbeam 1979, 1982 ; Kelley et Pilbeam 1986 ; Brown et Ward 1988 ; Pilbeam et al. 1990 ; Ward 1997 ; Harrison et al. 2002). Cependant, la découverte de *Khoratpithecus*, qui partage plusieurs caractères dentaires dérivés avec les orangs-outangs actuels, dans les dépôts du Miocène moyen et supérieur de Thaïlande et du Myanmar, a remis en cause de nombreuses assertions concernant l'histoire

évolutive des hominoïdes, et particulièrement la lignée des orangs-outangs. (Chaimanee et al. 2003, 2004, 2006 ; Emonet 2009). La morphologie dentaire et mandibulaire de *Khoratpithecus*, notamment la morphologie des prémolaires inférieures et l'absence de marques d'insertion des muscles digastriques sur la symphyse mandibulaire, marquent une grande proximité à la fois morphologique et phylogénétique entre *Khoratpithecus* et *Pongo*, de telle sorte que ces genres sont plus proches parents entre eux qu'avec n'importe quel autre genre (Chaimanee et al. 2003, 2004, 2006; Emonet 2009 ; Jaeger et al. en révision). Les analyses phylogénétiques incluant *Khoratpithecus* (e. g. Begun 2007 ; Emonet 2009) renforcent la robustesse du clade *Pongo*, en y incluant les genres *Pongo*, *Khoratpithecus*, *Sivapithecus*, *Indopithecus*, *Gigantopithecus* et *Ankarapithecus*.

Khoratpithecus a une large répartition stratigraphique qui s'étend de la partie supérieure du Miocène moyen à la partie terminale du Miocène supérieur. Les plus vielles formes attribuées à ce genre, découvertes dans des niveaux de lignite de la mine de Chiang Muan, ont été datées entre 12,2 et 12,4 Ma (Benammi et al. 2004 ; Coster et al. 2010). Le groupe frère du groupe *Khoratpithecus-Pongo* est le genre *Sivapithecus* (e.g. Begun 1994, 2005 ; Begun et al. 1997 ; Ward 1997 ; Kelley 2002 ; Pilbeam 2002), dont la forme la plus vielle, *S. indicus* (10.5-12.5Ma) (e.g. Kelley 2002), collectée dans les Siwaliks d'Inde et du Pakistan, est contemporaine de *K. chiangmuanensis*. Les premières apparitions d'hominoïdes en Asie du Sud datent donc de la fin du Miocène moyen alors que les plus anciennes formes d'hominoïdes connues proviennent des dépôts du Miocène ancien d'Afrique (Figure 2), (Bishop et al. 1969 ; Pickford et Andrews 1981 ; Harrison 1988 ; Walker 1993 ; Harrison 2002). A partir de la fin du Miocène inférieur, les premiers grands singes non-africains apparaissent en Europe (e.g. Begun 2002) avant que, au Miocène moyen et supérieur, de très nombreuses formes se diversifient en Europe et en Asie (e.g. Begun 2002 ; Kelley 2002), témoins d'une large radiation évolutive du groupe. Les griphopithécidés (au sens de Begun et

al. 2003 : *Griphopithecus*, *Equatorius*, *Kenyapithecus* et *Nacholapithecus*), connus dès le Miocène moyen (~16,5-16 Ma) (Begun et al. 2003) en Afrique et en Europe (e.g. Kelley 2002), sont considérés comme un groupe à la base de la radiation des crown-hominoïdes (e.g. Begun 2005). Certains genres d'hominoïdes, comme par exemple *Ankarapithecus* en Asie mineure et *Dryopithecus* en Europe (Figure 2), datant du Miocène moyen, semblent partager des caractères dentaires dérivés avec certains membres du clade (*Pongo*, *Sivapithecus*) (Schwartz 1990, 1997 ; Moyà-Solà et Kholer 1993, 1995, 1996 ; Begun et Güleç 1998; Alpagut et al. 1996).



Figure 3.2. Carte de répartition des hominoïdes fossiles au Miocène (d'après Begun 2007 et Emonet 2009).

Le registre fossile eurasiatique démontre l'existence d'une importante radiation adaptative des hominoïdes, qui a vraisemblablement du se dérouler à la fin du Miocène ancien-début du Miocène moyen, entre 17 et 12,5 Ma, contemporaine d'une grande expansion

géographique sur tout le continent eurasiatique. La migration des formes primitives d'hominoïdes, depuis l'Afrique vers l'Eurasie, pendant cette période, indique la présence d'un couloir de dispersion reliant l'Afrique à l'Asie et l'Europe. Cette observation est corroborée par les faunes de gros mammifères eurasiatiques du Miocène moyen, qui présentent également des taxons en commun avec celle de l'Afrique de l'Est (e.g. Tassy 1983, 1985 ; Pickford 1986, 1988 ; Ducrocq et al. 1994 ; Flynn et al. 1995 ; Mein et Ginsburg 1997 ; Barry et al. 2002 ; Lihoreau et al. 2004, 2007). Une partie de la faune du Miocène moyen des Siwaliks semble s'être mise en place à la fin du Miocène ancien ou au début du Miocène moyen avec notablement l'apparition de plusieurs taxons de proboscidiens d'affinité africaine dont *Protanancus* (Tassy 1986) et *Choerolophodon* (Tassy 1983), aussi connus au Miocène moyen en Turquie (Tassy 1985 ; Gaziry 1976). En Chine, des suidés de la famille des Kubanochoerinae, groupe ayant évolué en Afrique au Miocène ancien avant de se disperser en Eurasie (Pickford 2001 ; Pickford et Morales 2003), apparaissent également à cette période (Pickford 1986, 1993). Au Miocène inférieur, les ceintures tropicales étaient centrées sur l'Afrique (Bromage et Schrenk 1999) mais, sous l'influence de changements climatiques au début du Miocène moyen (Zachos et al. 2001), ces dernières se seraient vraisemblablement déplacées vers le Nord. Il semble s'établir à cette époque en Eurasie des milieux tropicaux (Jiménez-Morenoa et Suc 2007 ; Böhme 2007) vers lesquels les hominoïdes africains auraient pu migrer (Li 1991 ; Liu et al. 1997 ; Jablonski et Whitfort 1999 ; Heizmann et Begun 2001). Biogéographiquement, la présence du clade *Pongo* uniquement en Asie du Sud, sur une zone s'étendant de la Turquie (*Ankarapithecus*) à la Thaïlande (*Khoratpithecus*) et l'Indonésie (*Pongo*) indique un axe de dispersion au Sud de l'Himalaya pour les hominoïdes au Miocène moyen (Emonet 2009).

L'histoire paléobiogéographique et phylogénétique des hominoïdes est complexe et demeure encore aujourd'hui mal contrainte, malgré un nombre de fossiles croissant (e.g.

Pilbeam et Young 2004). La richesse taxonomique des hominoïdes d'Asie du Sud-Est et leur diversité morphologique, plus importantes que celle des hominoïdes africains, désignent l'Asie du Sud comme un centre important de diversification. Le registre fossile des grands singes asiatiques reste cependant relativement pauvre et de nombreuses zones, en particulier les régions de forêts tropicales humides les plus méridionales, proches de la répartition actuelle du genre *Pongo*, demeurent inexplorées. Le genre *Pongo*, connu dans les dépôts pléistocènes à Sumatra, en Thaïlande et au Vietnam (Bacon et al. 2001), vit à l'heure actuelle dans les forêts tropicales humides de Bornéo et Sumatra en Indonésie et Malaisie. Le registre fossile de ces zones est quasi-inexistant et celui de la Thaïlande et de la Birmanie est encore très incomplet, présentant des lacunes importantes au Miocène moyen, au début du Miocène récent et au Pliocène. La découverte du genre *Khoratpithecus*, considéré comme le plus proche parent connu des orangs-outangs, semble indiquer que de futures recherches dans les dépôts plus récents en Asie du Sud-Est promettent d'apporter de nouveaux éléments de réponse aux questions concernant l'histoire évolutive des orangs-outangs et probablement de permettre de mieux appréhender l'origine de la diversité passée des grands singes asiatiques.

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CONCLUSIONS ET PERSPECTIVES

CONCLUSIONS ET PERSPECTIVES

Les recherches menées ces trois dernières années dans les dépôts continentaux paléogènes d'Afrique du Nord et néogènes d'Asie du Sud-Est ont permis de découvrir de nouveaux éléments essentiels à la compréhension de l'histoire des communautés de mammifères terrestres, et en particulier les primates. Le registre fossile documentant l'émergence des anthropoïdes au Paléogène et la radiation évolutive des hominoïdes au Miocène est pauvre, ce qui, associé au manque de données concernant à l'âge des sites fossilifères, constitue une limite majeure à la compréhension de l'histoire évolutive de nombreux groupes de primates.

Dans ce travail, la confrontation de données biochronologiques et magnétostratigraphiques nous a permis de mieux calibrer la chronologie et d'étalonner l'histoire des mammifères terrestres, notamment celle des primates et des rongeurs. L'établissement d'un cadre chronologique précis a permis d'appréhender, sous un jour nouveau, les modalités de renouvellement des communautés de mammifères, les événements de dispersion et les conditions environnementales qui ont présidé aux changements évolutifs au sein de ces groupes.

1. APPORT DE LA MAGNETOSTRATIGRAPHIE ET DE LA BIOCHRONOLOGIE A L'HISTOIRE EVOLUTIVE DES ANTHROPOÏDES DANS LE PALEOGENE CONTINENTAL D'AFRIQUE DU NORD

Il était traditionnellement admis que l'origine des primates anthropoïdes se situait en Afrique au Paléogène (e.g. Simons et Rasmussen 1994). Cette hypothèse s'est trouvée modifiée du fait de la découverte d'anthropoïdes primitifs dans des niveaux de l'Eocène

moyen et supérieur d'Asie (Beard et al. 1994, 1996 ; Kay et al. 1997; Beard et Wang 2004 ; Jaeger et Marivaux 2005; Bajpai et al. 2008). L'Afrique et l'Asie tropicales semblent avoir été deux centres d'évolution et de diversification majeurs des anthropoïdes. Une connaissance plus détaillée des dispersions entre ces deux continents, potentiellement multiples, et des voies paléogéographiques suivies au Paléogène est indispensable pour suivre en détail l'histoire ancienne de ce groupe. La connaissance de l'Éocène en Afrique est particulièrement peu documentée, et limitée à quelques sites mal datés. La première partie de ce travail s'est donc principalement concentrée sur la recherche de données paléontologiques et l'établissement d'un cadre chronologique précis des sites fossilifères du Paléogène africain.

- L'étude magnétostratigraphique du site algérien d'El Kohol a permis de préciser l'âge et l'histoire des faunes mammaliennes du début de l'Eocène en Afrique. Cette localité, aux frontières sud de l'Atlas saharien, présente une épaisse série sédimentaire continentale qui a livré un assemblage unique de mammifères du début de l'Eocène (Yprésien). La corrélation de la série d'El Kohol avec l'échelle géologique des polarités magnétiques, indique un âge compris entre 52 et 51 Ma pour les niveaux fossilifères. L'établissement de la séquence magnétostratigraphique de cette épaisse série représente les premiers jalons bien datés des faunes algériennes et offre une première base solide pour établir des corrélations stratigraphiques avec d'autres séquences de l'Eocène africain.

- Les localités des Glib Zegdou et Gour Lazib, dans la partie occidentale du Sahara algérien, ont livrés plus de 500 restes fossiles identifiables, ce qui constitue l'une des plus riches collections de mammifères connue du début de l'Eocène en Afrique. Les groupes les plus abondamment représentés sont les rongeurs zegdoumyidés, les hyracoïdes et les primates (Adaci et al. 2007; Tabuce et al. 2007). La formation du Glib Zegdou a livré un petit primate, *Algeripithecus*, qui était jusqu'à récemment considéré comme un des plus anciens anthropoïdes africains mais de nouveaux restes crâniens et dentaires ont révélé son appartenance au groupe des lémuriformes (Tabuce

et al. 2009). L'ensemble des données paléomagnétiques et les études biochronologiques de la faune et la flore indiquent un âge fini-Yprésien ou Lutétien récent pour la formation du Glib Zegdou et un âge compris entre 49 et 45 Ma pour la faune de mammifères.

- La présence de formations fossilifères au Dur At-Talah (Bellair et al. 1954; Arambourg et Magnier 1961; Arambourg 1963 ; Savage 1969, 1971 ; Wight 1980), un site situé dans le Sud-Ouest du bassin de Sirt en Libye Centrale, a donné lieu à de récentes investigations, au cours desquelles ont pu être identifiés de nombreux nouveaux taxons (Jaeger et al. 2010a, b). Un abondant matériel est venu compléter les trouvailles antérieures et a permis, notamment, d'enrichir la liste faunique des micro-mammifères de ce site. La découverte au Dur At-Talah d'un des plus vieux assemblages de primates anthropoïdes en Afrique (Jaeger et al. 2010b), qui comprend des membres des clades des Afrotarsiidae (*Afrotarsius libycus),* Parapithecidae (*Biretia piveteaui*) et Oligopithecidae (*Talahpithecus parvus*), a permis d'élargir significativement notre connaissance de la diversité taxonomique des premiers anthropoïdes africains et indique une importante diversification des anthropoïdes à la fin de l'Eocène moyen qui semble marquer l'histoire des primates en Afrique.

L'étude biostratigraphique du site, combinée à l'étude paléomagnétique de la série sédimentaire et des séries marines éocènes sous-jacentes, a permis de préciser l'âge de ce site, indiquant un âge Bartonien terminal (~39-38Ma) ou Priabonien basal (~37,2-36,5Ma) pour les niveaux fossilifères.

- Les recherches paléontologiques récentes menées dans la région de Zallah, dans le bassin de Sirt en Libye centrale, ont permis la découverte d'une nouvelle localité fossilifère qui a livré cinq taxons de rongeurs hystricognathes dont un nouveau genre et trois nouvelles espèces. Ces découvertes ont apporté de nouveaux éléments essentiels à notre connaissance des débuts de la radiation évolutive des rongeurs hystricognathes africains (phiomorphes), dont les premiers représentants sont connus

dès la fin de l'Eocène en Algérie, Egypte et Libye (Jaeger et al. 1985; Sallam et al. 2009; Jaeger et al. 2010). Les données biostratigraphiques ont permis de corréler la séquence de Zallah avec la Formation de Jebel Qatrani du Fayum, et l'analyse des polarités magnétiques de la séquence indique un âge Oligocène basal, proche de la limite Eocène/Oligocène, pour les niveaux fossilifères de Zallah.

Une étude portant sur les relations phylogénétiques et paléobiogéographiques des premiers rongeurs hystricognathes a été réalisée afin d'étudier les tendances évolutives observées sur la morphologie dentaire et d'analyser les scénarios paléobiogéographiques du groupe durant sa radiation initiale. Les phiomyidés, replacés dans la phylogénie des rongeurs hystricognathes paléogènes établie à partir de l'analyse parcimonieuse de l'évolution des caractères dentaires, illustrent une phase de diversification importante de ce groupe en Afrique à la fin du Paléogène.

L'étude des caractères dentaires (morphologiques et microstructuraux) entre les rongeurs africains (phiomorphes) et sud-américains (caviomorphes) semble traduire des affinités phylogénétiques entre *Gaudeamus*, un genre de phiomorphe présent dans l'Eocene terminal/Oligocène basal de Libye et d'Egypte, et les plus vieux caviomorphes (Coster et al. 2010). Cependant, la discussion portant sur les affinités phylogénétiques des premiers hystricognathes donne lieu à des interprétations controversées et la découverte de nouveaux fossiles de rongeurs dans des localités fossilifères plus anciennes dans l'Eocène moyen en Afrique et en Amérique du Sud devrait permettre de répondre aux questions quant à la signification phylogénétique et à la nature exacte des affinités de *Gaudeamus* au sein des rongeurs hystricognathes du Paléogène.

En fin de compte, les perspectives qu'offrent ces découvertes, pour répondre aux interrogations sur l'histoire évolutive des anthropoïdes et des rongeurs hystricognathes et appréhender de façon plus cohérente la question de leurs origines, amènent de nombreuses questions et tous les handicaps ne sont pas encore levés.

La chronologie des sites continentaux paléogènes en Afrique est encore difficile à établir en raison de la singularité et du caractère endémique des assemblages fauniques, et du nombre restreint de sites fossilifères comparables. L'étude magnétostratigraphique, associée à l'étude biochronologique, est apparue comme un outil efficace et a permis de préciser l'âge de nombreux sites continentaux africains, notamment en Algérie (El Kohol et Glib Zegdou) et en Libye (Dur At-Talah et Zallah), et a permis d'établir des corrélations avec d'autre sites paléogènes. Ces résultats très encourageants démontrent l'intérêt de la contribution de la magnétostratigraphie pour calibrer l'âge des gisements continentaux à mammifères. La multiplication des données magnétostratigraphique et l'échantillonnage de nouvelles sections en Afrique, sur des sites dont la chronologie est encore mal établie, comme par exemple à Bir El Ater en Algérie ou encore à Chambi en Tunisie, apparaissent donc comme primordiaux.

Par ailleurs, plusieurs scénarios paléobiogéographiques ont été avancés concernant les voies de dispersion, la chronologie et les modalités de l'arrivée et la diversification des primates anthropoïdes, ainsi que des rongeurs hystricognathes qui apparaissent de façon contemporaine en Afrique. Les plus anciennes communautés de primates anthropoïdes et de rongeurs hystricognathes africaines connues sont déjà diversifiées à la fin de l'Eocène moyen/début de l'Eocène supérieur. De ce constat, deux scénarios ont pu être élaborés : (i) une vague unique et ancienne de dispersion, depuis l'Asie vers l'Afrique, de représentants primitifs de ces groupes suivie d'une diversification pendant l'Eocène moyen ; (ii) l'hypothèse de dispersions multiples de groupes d'anthropoïdes et de rongeurs hystricognathes primitifs asiatiques vers l'Afrique peu de temps avant la fin de l'Eocène moyen. Cependant, ces scénarios reposent sur une documentation paléontologique incomplète. Le registre fossile africain de l'Eocène moyen est particulièrement pauvre et une importante lacune (8-10Ma) pendant le Lutétien et presque tout le Bartonien ne permet pas de suivre en détail l'émergence ancienne de ces groupes et s'oppose à l'établissement de scénarios biogéographiques fiables entre l'Asie du Sud et l'Afrique à l'Eocène moyen. Malgré des progrès significatifs, la connaissance des faunes paléogènes reste limitée et l'Afrique n'a

livré pour le moment qu'une faune très incomplète pendant l'Eocène moyen. Il existe un important hiatus dans le registre fossile entre le site lutétien d'Aznag au Maroc, daté entre 45,8 and 43,6 Ma, et les sites libyen (Dur At-Talah), égyptien (Birket Qarun 2) et algérien (Bir El Ater), daté de la fin du Bartonien/début du Priabonien. Cet intervalle de temps a pourtant potentiellement enregistré l'arrivée des anthropoïdes et des rongeurs hystricognathes en Afrique. Des événements déterminant la distribution spatiale de ces groupes, dans l'Ancien Monde mais également dans le Nouveau Monde, semblent s'être déroulés à cette époque. Afin de mieux comprendre l'évolution des faunes paléogènes, des gros efforts doivent être fait pour étendre la gamme d'âge des sites africains et combler le hiatus du registre fossile de l'Eocène moyen. Dans ce contexte, mettre au jour de nouveaux sites fossilifères, susceptibles de compléter nos connaissances en Afrique de cette période clef, est indispensable à la compréhension de l'histoire évolutive de plusieurs ordres modernes de mammifères.

D'autre part, les récentes missions de terrain sur le gisement de Zallah ont contribué à la découverte d'un nouvel assemblage de rongeurs hystricognathes qui a relancé le débat, toujours ouvert, sur l'origine des rongeurs hystricognathes en Amérique du Sud, et donnent à ce site une importance fondamentale. L'histoire des rongeurs hystricognathes semble rejoindre, encore une fois, l'histoire des primates anthropoïdes, qui pose avec ce groupe les mêmes problèmes de relations intercontinentales entre l'Afrique et l'Amérique du Sud au Paléogène. Les dépôts de l'Oligocène basal de la région de Zallah affleurent sur de très grandes surfaces, qui ont été jusque-là très peu prospectées. Il apparait donc comme nécessaire d'appuyer tous les efforts pour exploiter au maximum les richesses paléontologiques que recèle encore ce gisement.

2. APPORT DE LA MAGNETOSTRATIGRAPHIE ET DE LA BIOCHRONOLOGIE A L'HISTOIRE EVOLUTIVE DES HOMINOÏDES DANS LE PALEOGENE CONTINENTAL D'ASIE DU SUD

Le Miocène de l'Ancien monde a été marqué par une radiation et une diversification importante des hominoïdes (e.g. Hartwig 2002) et le registre fossile de ce groupe présente une grande diversité taxonomique, morphologique et paléogéographique. Le Miocène moyen et supérieur, en particulier, semble avoir été témoin d'une radiation adaptative majeure des hominoïdes et une extension géographique considérable de leur aire de répartition. Ce groupe a notamment connu une radiation importante en Asie du Sud avec l'apparition des genres *Sivapithecus, Lufengpithecus, Khoratpithecus et Indopithecus* (Pilbeam et al. 1977 ; Pilbeam 1982 ; Chaimanee et al. 2003, 2004 ; Kelley 2002).

La découverte récente du genre *Khoratpithecus,* dans le Miocène moyen (*K. chiangmuanensi*s) et récent (*K. piryai ; K. ayeyarwadyensis*) en Asie du Sud-Est (Chaimanee et al. 2003, 2004 ; Jaeger et al. en révision), reconnu comme le plus proche parent fossile des orangs-outangs actuels, a élargi notre compréhension de l'histoire évolutive du groupe *Pongo*. Cependant, malgré les nombreux travaux portant sur le sujet, l'histoire évolutive des hominoïdes asiatiques reste mal comprise, principalement en raison des lacunes dans le registre fossile qui entravent l'établissement d'un cadre phylogénétique clair et limitent les interprétations paléobiogéographiques.

Ce travail, basé sur des analyses magnétostratigraphiques et sur la biochronologie des faunes mammaliennes, a permis de mieux contraindre l'âge des *Khoratpithecus* et de l'ensemble des faunes du Miocène d'Asie du Sud-Est.

-Les bassins néogènes sont bien représentés dans la partie nord de la Thaïlande et la plupart d'entre eux ont livré une faune variée. Cependant, l'estimation des âges des

localités miocènes thaïlandaises est souvent fondée sur des données peu fiables, faute de fossiles utilisables à des fins biostratigraphiques. Une étude magnétostratigraphique de la séquence du bassin de Mae Moh a été réalisée et sa corrélation avec l'échelle géologique des polarités indique un âge compris entre 14,2 et 12 ,1 Ma. L'obtention de la séquence complète des polarités magnétiques de la série du bassin de Mae Moh en Thaïlande, présentée dans ce travail, représente maintenant un enregistrement de référence et un repère chronologique fiable pour le Miocène moyen asiatique. L'établissement de la magnétostratigraphie de la séquence du bassin de Mae Moh et sa corrélation à l'échelle géomagnétique des polarités ouvrent de nombreuses perspectives quant à la datation et la corrélation des nombreux autres sites du Miocène moyen des bassins intramontagneux du nord de la Thaïlande mais également pour discuter l'âge relatif de sites fossilifères d'Asie du Sud en général.

-La corrélation de la séquence du bassin de Mae Moh avec la série sédimentaire du bassin de Chiang Muan, connue pour avoir livré les restes de l'un des plus vieux hominoïdes asiatiques, *Khoratpithecus chiangmuanensis* (Chaimanee et al 2003), a été réalisée. Cette corrélation suggère un âge compris entre 13,1 et 12 Ma pour la séquence de Chiang Muan et un âge compris entre 12,4 et 12,2 Ma pour les niveaux de lignites qui ont livré *Khoratpithecus chiangmuanensis.*

-Les données de terrains collectées par les équipes paléontologiques franco-birmanes, au cours des dernières années, ont également permis de préciser la chronologie des faunes miocènes de la formation de l'Irrawaddy dans le Bassin Central du Myanmar.
La faune de la région de Magway a été datée entre 10,5 et 8,5 Ma et les différentes potentielles corrélations de la section avec l'échelle des polarités magnétiques indiquent un âge de ~9 ou ~10 Ma pour les niveaux fossilifères qui ont livré les restes du premier hominoïde fossile connu au Myanmar, *Khoratpithecus ayeyarwadyensis.*

-Les résultats de l'analyse paléomagnétique de la localité de Chaungtha, dans les dépôts du Miocène moyen de la formation de l'Irrawaddy, n'ont pas permis d'apporter plus de précisions que l'étude biochronologique sur l'âge des niveaux fossilifères. L'échec relatif à cette étude démontre clairement la nécessité de plus amples recherches paléontologiques et l'importance d'échantillonner d'autres sections dans cette région du Myanmar afin de réduire la fourchette chronologique de l'âge des faunes collectées.

Jusqu'à présent, la chronologie des faunes néogènes du Myanmar était exclusivement basée sur l'étude biochronologique des faunes. La formation de l'Irrawaddy au Myanmar, qui a déjà livré de nombreux fossiles de mammifères, a été déposée sur une très longue période de temps allant du Miocène au Pléistocène et affleure sur de très larges surfaces. Par analogie à l'impressionnant travail qui a été réalisé dans les Siwaliks du Pakistan, qui a permis de calibrer de nombreux évènements biologiques relatifs aux mammifères néogènes à l'aide de la magnétostratigraphie, l'apport de nouvelles données magnétostratigraphiques apparaît comme essentiel pour faire progresser la connaissance de la chronologie des faunes miocènes de la Formation de l'Irrawaddy, établir des corrélations avec d'autres sites fossilifère en Asie du Sud-Est et améliorer notre compréhension de l'histoire évolutive des faunes asiatiques pendant le Miocène, une période marquée par de profondes modifications avec la radiation et la diversification de nombreux groupes de mammifères, et notamment des hominoïdes.

Ainsi, le concours de plusieurs disciplines et la constante confrontation des résultats obtenus par magnétostratigraphie et biostratigraphie ainsi que par la phylogénie et la biogéographie, ont permis d'apporter des arguments complémentaires à l'établissement d'hypothèses relatives à l'histoire évolutive des mammifères et notamment des primates et des rongeurs. Toutefois, chaque nouvelle découverte paléontologique contribue à remettre en question les modèles préexistants de l'histoire de nombreux groupes de mammifères et seule

la poursuite intensive des recherches sur le terrain permettra d'affiner notre connaissance de l'histoire évolutive des mammifères.

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ANNEXE

MATERIELS ET METHODES PALEOMAGNETIQUES

La faculté qu'ont les minéraux magnétiques dans les roches sédimentaires et volcaniques de fossiliser la direction du champ magnétique terrestre, au moment de leur formation, permet une grande variété d'applications géologiques. Les inversions du champ magnétique constituent un phénomène synchrone à l'échelle de la planète et instantané à l'échelle géologique. Une analyse magnétostratigraphique consiste à retrouver les différentes magnétozones présentes dans une coupe donnée et à établir la séquence d'inversions magnétiques enregistrées dans la série sédimentaire (e.g. Butler 1992 ; Opdyke and Channell 1996 ; Tauxe 2005). Il est important que la coupe donnée corresponde à un intervalle de temps suffisamment long, qu'elle présente un minimum de lacune et qu'elle soit calibrée précisément par des repères chronologiques afin de pouvoir la corréler le mieux possible à l'échelle de référence des inversions magnétiques. L'étude magnétostratigraphique n'est pas une méthode de corrélation totalement indépendante; un calage chronologique (isotopique ou biochronologique) est nécessaire pour l'interprétation du signal magnétique et la plupart des études magnétostratigraphiques sont accompagnées d'une étude de la zonation biostratigraphique. La précision de cette zonation dépend évidemment des espèces fossiles identifiées et de l'environnement sédimentaire. Quand la séquence des inversions magnétiques est déterminée et corrélée à l'échelle de référence, on peut alors estimer la vitesse des processus sédimentaires, structuraux ou biologiques. En outre, l'échelle géomagnétique de référence des inversions magnétiques, basée sur la compilation des polarités identifiées dans des roches bien datées et sur les anomalies magnétiques de la croûte océanique, est devenue, au cours des dernières décennies, de plus en plus précise.

La problématique de cette étude repose sur la datation magnétostratigraphique de formations sédimentaires continentales. L'étude paléomagnétique des séries sédimentaires est plus délicate que celle des séries volcaniques car elles sont rarement calibrées par datation

radiométrique. Dans les séries continentales, les contraintes chronologiques peuvent être parfois fournies par la datation absolue de produits volcaniques ou, plus souvent, par la datation relative de la faune et/ou la flore. Une étude magnétostratigraphique a besoin d'un contrôle chronologique, sans quoi il est pratiquement impossible de corréler une séquence d'inversion avec l'échelle de référence. Les faunes mammaliennes paléogènes Africaines sont, à comparaison d'autres groupes, moins favorables aux corrélations biostratigraphiques à cause de leur caractère endémique et du nombre restreint d'assemblages fossilifères d'âge comparable.

Par ailleurs, la nature de la sédimentation en domaine continental est discontinue et les formations, mise en place en domaine fluviatile particulièrement, présentent souvent des lacunes de sédimentation. La continuité de sédimentation de ce type de régime, c'est-à-dire la continuité de l'enregistrement paléomagnétique, est moins constante que celle des fonds marins et les dépôts continentaux sont donc moins appropriés à ce genre d'étude. De plus, les taux de sédimentation sont variables et difficiles à estimer. Une même épaisseur de sédiments prélevée dans deux bassins continentaux différents ne représente que très rarement le même intervalle de temps et les taux de sédimentation dépendent de plusieurs facteurs difficilement évaluables (importance de l'apport détritique, taux de subsidence, période d'arrêt de sédimentation…). Enfin, les roches sédimentaires sont souvent caractérisées par une aimantation faible et la qualité du signal paléomagnétique est moins bonne que celle des roches volcaniques.

Cependant, il est bien établi que la magnétostratigraphie est une méthode stratigraphique confirmée et apparait comme l'une des méthodes les mieux adaptées pour aborder les problèmes de chronologie des formations sédimentaires continentales. La magnétostratigraphie peut en effet apporter une plus grande précision dans la résolution stratigraphique que la biostratigraphie des faunes mammalienne. Elle est, en effet, un outil puissant de datation pour les gisements à mammifères uniquement calibrés par des méthodes biostratigraphiques et qui éprouvent le manque de chronologie absolue. De plus, l'étude magnétostratigraphique permet de corréler efficacement les chronologies de milieux marins et

continentaux ou des sections espacés dans l'espace qui contiennent des faunes différentes. Elle est maintenant un outil indispensable à la plupart des études stratigraphiques.

Ce chapitre s'attachera à présenter, de manière assez succincte, les différentes étapes successives amenant à réaliser une analyse magnétostratigraphique: l'échantillonnage et la préparation des échantillons, l'étude des propriétés magnétiques liées à la minéralogie, la mesure et l'analyse de l'aimantation rémanente des échantillons et le traitement statistique, et enfin l'interprétation des données paléomagnétiques.

1. PRELEVEMENTS ET PREPARATION DES ECHANTILLONS

L'échantillonnage des carottes pour des études paléomagnétiques se fait à l'aide d'une foreuse manuelle fonctionnant à l'essence et équipée d'un système de refroidissement à eau. En laboratoire, ces carottes sont découpées en cylindre de 25mm de diamètre et une hauteur de 22mm. Les formations sédimentaires continentales présentent parfois des faciès peu favorables à l'échantillonnage en vue d'une étude paléomagnétique. Tous les niveaux n'ont pas été échantillonnés, ceux présentant un faciès plus fin et plus homogène ont été préférés et ceux montrant des traces d'altération ou des sédiments trop grossiers ont été évités. La fréquence d'échantillonnage et l'espacement vertical entre les différents niveaux prélevés sont déterminés par la qualité des affleurements.

Suivant la lithologie des niveaux à échantillonner, deux techniques de prélèvement sont classiquement utilisées:

-Dans les niveaux indurés, on utilise directement un carottier de terrain. Malheureusement, la nécessité de refroidir le foret à l'aide de l'eau d'eau élimine la possibilité de prélever un certain nombre de facies qui perdent leur cohérence en présence d'eau (les argiles par exemple). Sur le terrain, l'orientation géographique d'une carotte est determiné par son azimut et son inclinaison, et se mesure à l'aide d'une boussole magnétique (Figure 1). L'azimut est l'angle entre le nord géographique et la ligne d'intersection entre le plan vertical du cylindre et le plan horizontal.

Cette méthode permet de gagner beaucoup de temps pour la préparation des échantillons par rapport à la méthode de prélèvement de blocs discutée ci dessous.

-Pour les niveaux moins consolidés ou plastiques qui ne peuvent pas être forés à l'eau, une autre méthode d'échantillonnage consiste à prélever des blocs en place. On reporte sur une surface l'orientation d'un axe par rapport au Nord magnétique. Au laboratoire, les blocs sont ensuite inclus dans un support de plâtre. Les blocs sont, par la suite, forés sous une circulation d'air comprimée, perpendiculairement au plan orienté. Cette méthode de prélèvement est plus contraignante à cause du poids des échantillons.

Au cours des procédures de prélèvement et de préparation des échantillons paléomagnétiques, plusieurs erreurs sont introduites et doivent être prises en compte. La mesure de l'orientation de chaque cylindre de roche sur le terrain induit une première marge d'erreur liée à la manipulation de l'utilisateur et à la précision de la boussole. Une orientation minutieuse peut induire une erreur de 1 à 3° au maximum (Tauxe 2002). Une seconde erreur s'insère lors du marquage, qui est liée à la précision de l'utilisateur et à l'épaisseur du marqueur. Finalement, une erreur de quelques degrés est possible lors de l'orientation de l'échantillon dans le magnétomètre.

Après sciage des carottes au laboratoire, le marquage des échantillons consiste à inscrire l'orientation des carottes avec une encre capable de résister à de fortes températures. Un trièdre direct (X, Y, Z) de référence est dessiné sur chaque spécimen. Ces coordonnées sont définies à partir de la génératrice, axe X et Y dans le plan perpendiculaire à l'axe de la carotte et axe Z selon cet axe (Figure 1).

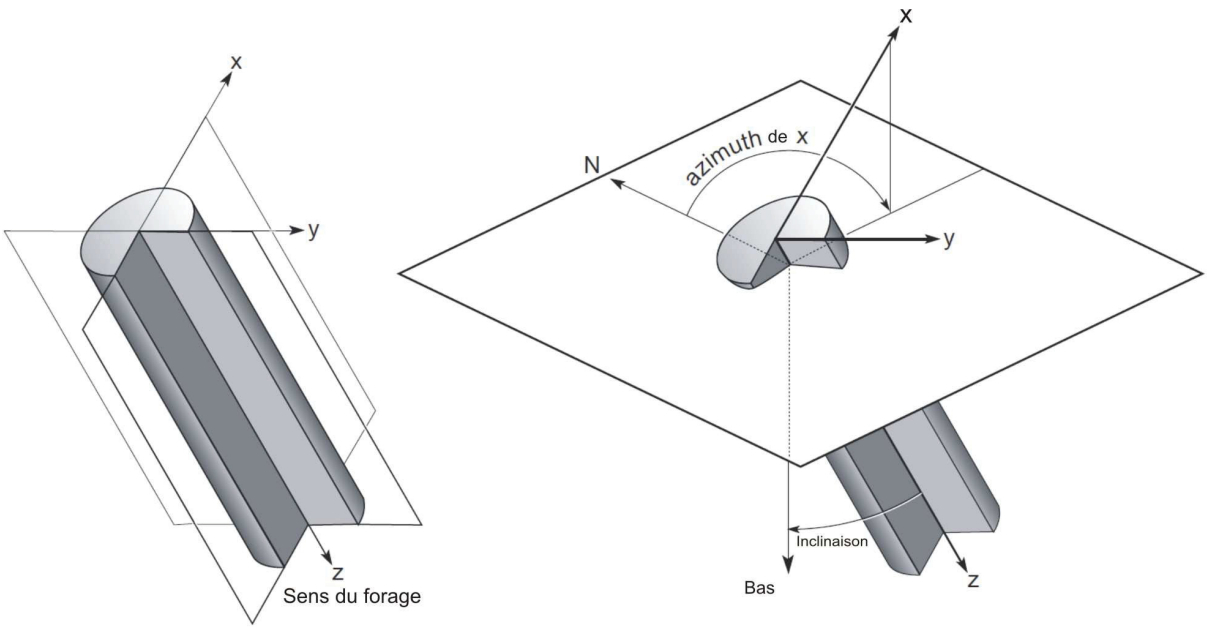


Figure 1. Système d'orientation des carottes échantillonnées. Les coordonnées de la carotte sont définies à partir de la génératrice. L'axe X est vers le haut, Y est perpendiculaire à X dans le même plan horizontal et Z est selon l'axe de la carotte dans le sens du forage (d'après Butler 1992).

2. MESURE ET ANALYSE DES PROPRIETES MAGNETIQUES LIEES A LA MINERALOGIE

Une roche est constituée d'un assemblage de minéraux diamagnétiques, paramagnétiques et ferromagnétiques. L'aimantation de la composante ferromagnétique est plus forte que celle des minéraux para et diamagnétiques, qui ne contribuent pas à l'aimantation rémanente de la roche. Seule l'identification des minéraux ferromagnétiques (oxydes de fer et de titane, hydroxydes et sulfures) nous intéresse ici. La connaissance de la nature et de la taille des minéraux porteurs de l'aimantation est importante, tant pour l'interprétation des résultats que pour le choix des méthodes d'analyse de l'Aimantation Rémanente Naturelle (ARN). La reconnaissance des minéraux ferromagnétiques est basée à la fois sur la détermination de leur température de déblocage et leur coercitivité. Les propriétés

caractéristiques des principaux minéraux ferromagnétiques sont présentées dans le tableau 1 et les deux méthodes, utilisées dans ce travail, pour l'identification des minéraux porteurs de l'aimantation sont détaillées ci-dessous.

Acquisition de l'Aimantation Rémanente Isotherme (ARI)

L'une des techniques les plus utilisées en minéralogie magnétique est la détermination des spectres de coercivité à partir de l'acquisition d'IRM (Dunlop 1983; Dunlop and Özdemir 1997; Peters et Thompson 1998; Symons and Cioppa, 2000; Kruiver et al. 2001). L'aimantation IRM est produite par l'application d'un champ continu à température constante et suivant une durée de quelques secondes. La méthode que nous avons utilisée, afin d'identifier les minéraux porteurs de l'aimantation, passe par des mesures d'Aimantation Rémanente Isotherme (ARI) en fonction de la température et du champ. Une ARI est acquise par exposition à un champ magnétique fort pendant un temps court. Des champs magnétiques d'intensité connue ont été appliqués à l'échantillon, pas à pas, avec un électroaimant jusqu'à un champ d'intensité maximum de 1,5 Tesla. L'intensité de l'ARI a été mesurée à chaque pallier. Le but est d'amener, si possible, l'échantillon à saturation; la saturation est atteinte lorsque l'intensité n'augmente plus lorsqu'on applique des champs de plus en plus forts. Les courbes d'acquisition d'ARI est utilisée pour déterminer la coercivité des minéraux porteurs de l'Aimantation Rémanente Naturelle (ARN).

Tableau 1. Propriétés caractéristiques des principaux minéraux ferromagnétiques (d'après Tauxe 2005).

Magnetite	Fe_3O_4
Density = 5197 kg m^{-3}	Dunlop and Özdemir [1997]
Curie temperature = 580°C	Dunlop and Özdemir [1997]
Saturation Magnetization = 92 Am^2kg^{-1}	O'Reilly [1984]
Anisotropy Constant = -2.6 Jkg^{-1}	Dunlop and Özdemir [1997]
Volume susceptibility = ~ 1 SI	O'Reilly [1984]
Typical coercivities are 10's of mT	O'Reilly [1984]
Verwey transition: 110-120 K	Özdemir and Dunlop [1993]
Cell edge = 0.8396 nm	Dunlop and Özdemir [1997]
Maghemite	Fe_2O_3
Density = 5074 kg m^{-3}	Dunlop and Özdemir [1997]
Curie temperature = 590-675°C	Dunlop and Özdemir [1997]
Saturation Magnetization = 74 Am^2kg^{-1}	Dunlop and Özdemir [1997]
Anisotropy Constant = 0.92 Jkg^{-1}	Dunlop and Özdemir [1997]
Verwey transition: suppressed	Dunlop and Özdemir [1997]
Breaks down to Fe_2O_3: between 250 750°C	Dunlop and Özdemir [1997]
TM60	$Fe_{2.4}Ti_{0.6}O_4$
Density = 4939 kg m^{-3}	Dunlop and Özdemir [1997]
Curie temperature = 150°C	Dunlop and Özdemir [1997]
Saturation Magnetization = 24 Am^2kg^{-1}	Dunlop and Özdemir [1997]
Anisotropy Constant = 0.41 Jkg^{-1}	Dunlop and Özdemir [1997]
Coercivity ~ 8 mT	Dunlop and Özdemir [1997]
Verwey transition: suppressed	Dunlop and Özdemir [1997]
Cell edge = 0.8482 nm	Dunlop and Özdemir [1997]
Hematite	Fe_2O_3
Density = 5271 kg m^{-3}	Dunlop and Özdemir [1997]
Néel temperature = 675°C	O'Reilly [1984]
Saturation Magnetization = 0.4 Am^2kg^{-1}	O'Reilly [1984]
Anisotropy Constant = 228 Jkg^{-1}	Dunlop and Özdemir [1997]
Volume susceptibility = ~ 1.3 x 10^{-3} SI	O'Reilly [1984]
Coercivities vary widely and can be 10's of teslas	Banerjee [1971]
Morin Transition: ~ 250-260 K (for > 0.2 m)	O'Reilly [1984]

Tableau 1 (suite)

Goethite	FeOOH
Density = 4264 kg m^{-3}	Dunlop and Özdemir [1997]
Néel temperature: 70 125°C	O'Reilly [1984]
Saturation Magnetization = 10^{-3} 1 Am^2kg^{-1}	O'Reilly [1984]
Anisotropy Constant = 0.25 2 Jkg^{-1}	Dekkers [1989]
Volume susceptibility = ~ 1 x 10^{-3} SI	Dekkers [1989]
Coercivities can be 10's of teslas	
Breaks down to hematite: 250 400°C	
Pyrrhotite	Fe_7S_8
Density = 4662 kg m^{-3}	Dunlop and Özdemir [1997]
Monoclinic:	
Curie temperature = ~ 325°C	Dekkers [1989a]
Hexagonal:	
Curie temperature = ~270°C	Dekkers [1988]
Saturation Magnetization = 0.4 -~ 20 Am^2kg^{-1}	Worm et al. [1993]
Volume susceptibility = ~ 1 x 10^{-3} 1 SI	Collinson [1983];O'Reilly [1984]
Anisotropy Constant = 20 Jkg^{-1}	O'Reilly [1984]
Coercivities vary widely and can be 100's of mT	O'Reilly [1984]
Has a transition at ~ 34 K	Dekkers et al. [1989] Rochette et al. [1990]
Hexagonal pyrrotite: transition near 200°	
Breaks down to magnetite: ~ 500°C	Dunlop and Özdemir [1997]
Greigite	Fe_3S_4
Density = 4079 kg m^{-3}	Dunlop and Özdemir [1997]
Maximum unblocking temperature = ~ 330°C	Roberts [1995]
Saturation Magnetization = ~ 25 Am^2kg^{-1}	Spender et al. [1972]
Anisotropy Constant = -0.25 Jkg^{-1}	Dunlop and Özdemir [1997]
Coercivity 60> 100 mT	Roberts [1995]
Has high M_r/ ratios ~ 70 x 10^3 Am^{-1}	Snowball and Thompson [1990]
Breaks down to magnetite: ~ 270-350°C	Roberts [1995]

Le test de Lowrie

Le Test de Lowrie est basé sur la désaimantation thermique d'une IRM tri-axiale et permet d'identifier les porteurs magnétiques à partir de leurs températures de déblocage et de leur coercivité. Le protocole expérimental repose sur de trois champs d'intensités différentes (0,1, 0,5 et 3T par exemple), affectant les minéraux de basse, moyenne et forte coercivité, dans trois directions orthogonales (x, y et z). L'aimantation induite est alors progressivement désaimantée par chauffage. L'exemple de la figure ci-dessous illustre un exemple de ce test. La fraction de faible coercivité (<0,1 T) est progressivement désaimantée à plus de 500-550°C indiquant la présence de magnétite. La fraction de moyenne et de forte coercivité montre une chute brutale de l'aimantation à environ 300-340°C, indiquant la présence de pyrrhotite; à noter que la fraction moyenne n'est totalement désaimantée qu'à 500°C.

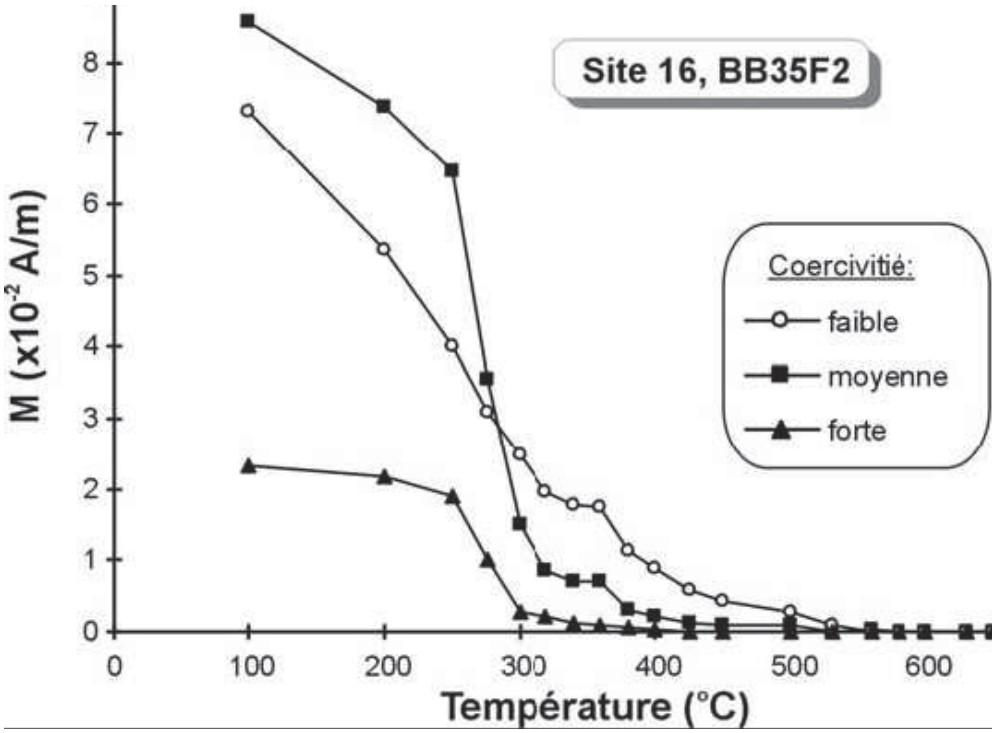


Figure 2. Courbes de désaimantation IRM tri-axiale.

Susceptibilité magnétique

Lorsque l'on applique un champ magnétique sur un matériau, celui-ci acquiert une aimantation proportionnelle au champ appliqué. Le facteur de proportionnalité est appelé susceptibilité magnétique. La susceptibilité magnétique est une mesure sans dimension qui représente la capacité de la roche à s'aimanter. La susceptibilité magnétique d'un échantillon prend en compte l'ensemble des grains ferromagnétiques, diamagnétiques et paramagnétiques. Après chaque palier de chauffe, la susceptibilité est mesurée. Lorsque celle-ci varie brusquement, cela signifie qu'un minéral présent en début de chauffe a subit une transformation. Les transformations minéralogiques ont des effets sur l'enregistrement de l'Aimantation Rémanente Naturelle. L'évolution de la susceptibilité magnétique en fonction de la température a donc été vérifiée au cours des chauffes dans le but de suivre l'évolution des minéraux magnétiques afin de vérifier s'il y a eu des transformations minéralogiques au cours du processus.

3. MESURE DE L'AIMANTATION REMANENTE NATURELLE

L'Aimantation Rémanente Naturelle d'une roche sédimentaire peut donner accès aux champs magnétiques enregistrés par les grains ferromagnétiques au cours de l'histoire de la roche. Les sédiments présentent une aimantation rémanente dite détritique. Au moment de leur dépôt, des particules présentant un moment magnétique s'orientent statistiquement dans le champ magnétique ambiant. Lorsque l'aimantation persiste en l'absence de champ, on dit qu'elle est rémanente. Les études au laboratoire consistent essentiellement à déterminer l'aimantation rémanente primaire des sédiments, acquise lors du dépôt. Pour cela l'Aimantation Rémanente Naturelle des échantillons est désaimantée par étapes successives, soit par chauffe soit en appliquant un champ alternatif.

Les aimantations rémanentes ont été mesurées après chaque étape de désaimantation au moyen de magnétomètres cryogéniques à capteurs supraconducteurs (SQUIDS) ou à l'aide de

magnétomètres de type "Spinner" JR6-AGICO. Ces instruments sont installés dans une chambre amagnétique qui protège les échantillons étudiés de l'influence du champ magnétique ambiant lors des désaimantations.

Les mesures d'aimantation ont été réalisées aux laboratoires de paléomagnétisme de l'iPHEP, Université de Poitiers ; de l'Instituto de Geofísica de l'Universidad Nacional Autónoma de México, Mexico ; du Department of Anthropology de l'University of Texas, Austin ; de l'Institut de Physique du Globe de Paris et au laboratoire de magnétisme environnementale de l'Institut du Littoral environnement et sociétés de La Rochelle.

L'Aimantation Rémanente Naturelle est souvent la résultante de plusieurs aimantations composantes. Deux méthodes différentes ont été classiquement appliquées dans le but de séparer les éventuelles composantes de l'aimantation: la désaimantation thermique et le traitement par champs alternatifs.

Désaimantation thermique

La désaimantation thermique nécessite l'utilisation d'un four à haute température dont le champ interne reste nul.

Des fours à chauffage et à refroidissement rapides ont permis la désaimantation des échantillons. Les spécimens sont introduits à l'intérieur du four qui est en champ nul grâce à un blindage amagnétique. Le traitement thermique a été commencé en général à 100°C, puis la température a été augmentée par pas de 25 à 50°C au cours d'étapes de chauffe successives. La désaimantation est poursuivie jusqu'à ce que l'évolution des vecteurs restants devienne erratique ou jusqu'à destruction totale de toutes les composantes de l'aimantation.

Désaimantation par champ alternatif

Cette méthode consiste à appliquer, en champ nul, un champ alternatif AF dont on fait décroitre l'intensité jusqu'à zéro à partir de la valeur maximale choisie. Cette opération est répétée plusieurs fois en augmentant par paliers l'intensité du champ appliqué jusqu'à un maximum de 150mT. L'inefficacité de la désaimantation par champ alternatif sur certains

échantillons est due à la présence de minéraux de forte coercivité résistant à ce traitement tels que l'hématite ou la goethite. La désaimantation de ces échantillons est poursuivie par des paliers de chauffes.

4. TRAITEMENT DES DONNEES

Acquisition et visualisation des données

L'analyse des données commence dés l'acquisition des données brutes par le magnétomètre. Les valeurs pour chacune des composantes sont affichées sur l'écran et la dispersion liée à la qualité des mesures peut être déterminée. Une fois une précision satisfaisante atteinte, les données brutes sont enregistrées et stockées dans un fichier informatique. La représentation de l'évolution de la direction et de l'intensité de l'aimantation est visualisée à l'aide des diagrammes classiques de Zijderveld (1967) et de projection à égale surface (diagramme de Schmidt). L'évolution de l'aimantation, au cours du traitement, est analysée par les méthodes classiques: analyse des différences vectorielles (aimantation éliminée entre deux étapes successives du traitement) et des vecteurs restants (aimantation restante après chaque étape du traitement) afin de séparer les différentes composantes de l'aimantation et de déterminer la direction (inclinaison et déclinaison) de l'aimantation rémanente primaire. Le problème central de la séparation et de l'identification des différentes composantes de l'ARN est traité grâce aux techniques de désaimantation progressives qui permettent de suivre l'évolution du vecteur ARN au fur et à mesure de sa destruction par des températures ou champs alternatifs croissants. On peut ainsi déterminer les différentes directions de l'aimantation rémanente portée par des populations de grains ayant des spectres de température de blocage ou de champs coercitifs différents. Lorsque la direction n'évolue plus au cours de la désaimantation, on parle d'aimantation caractéristique. On s'attend en général que les aimantations secondaires (aimantation rémanente visqueuse ou chimique par exemple) disparaissent en premier et l'aimantation caractéristique est généralement interprétée comme une aimantation primaire.

Traitement des données

Le but de l'analyse de l'ARN et de la désaimantation est la séparation des aimantations composantes. Dans les cas les plus simples, le traitement provoque l'élimination complète d'une composante avant d'affecter ensuite la seconde. Sur les diagrammes de Zijderveld, ces deux aimantations se traduisent par deux segments linéaires à partir desquels il est possible de déterminer l'orientation de chacune des aimantations composantes. L'isolation des deux composantes peut être difficile si les spectres de température ou de champ de blocage de l'aimantation sont largement superposés, c'est-à-dire si l'une des composante est éliminée en même temps qu'une partie de l'autre.

La composante la plus résistante au traitement est dite l'aimantation caractéristique quand, sur un diagramme de Zijderveld, les segments linéaires la caractérisant passent par l'origine des axes. L'application de la méthode des moindres carrés des composantes principales de Kirschvink (1980) permet de calculer les directions de l'aimantation rémanente caractéristique.

Traitements statistiques

Statistique de Fisher

La méthode statistique la plus utilisée jusqu'à maintenant pour toutes les données paléomagnétiques est une méthode d'analyse statistique de vecteurs sur une sphère développée par Fisher (1953). Elle suppose que la direction est unimodale avec une loi de distribution (dispersion fisherienne) autour de la direction moyenne. Cette méthode statistique permet d'estimer la direction moyenne pour un groupe de directions (déclinaison, inclinaison), la dispersion des directions (α_{95}) et la précision de la direction moyenne calculée (k). En général, on utilise cette méthode pour calculer la direction moyenne et les paramètres de précision associés pour chaque site échantillonné et la direction moyenne de tous les sites d'une section.

Tests paléomagnétiques

Afin d'évaluer si les directions d'aimantation peuvent être considérées comme primaires, secondaires ou aléatoires, il existe plusieurs tests.

Test du pli

Plusieurs échantillons sont prélevés sur les deux flancs opposés d'un pli. On mesure et calcule ensuite les directions de l'aimantation primaire in-situ (sans correction) puis les directions avec correction stratigraphique. Si les directions d'aimantation des échantillons provenant de deux flancs d'un pli sont mieux groupées après correction du pendage (Figure 3), on considère que l'aimantation a été acquise avant la déformation. Par contre, si les directions sont mieux groupées avant la correction, l'aimantation est postérieure au plissement, ce qui constitue un test de pli négatif.

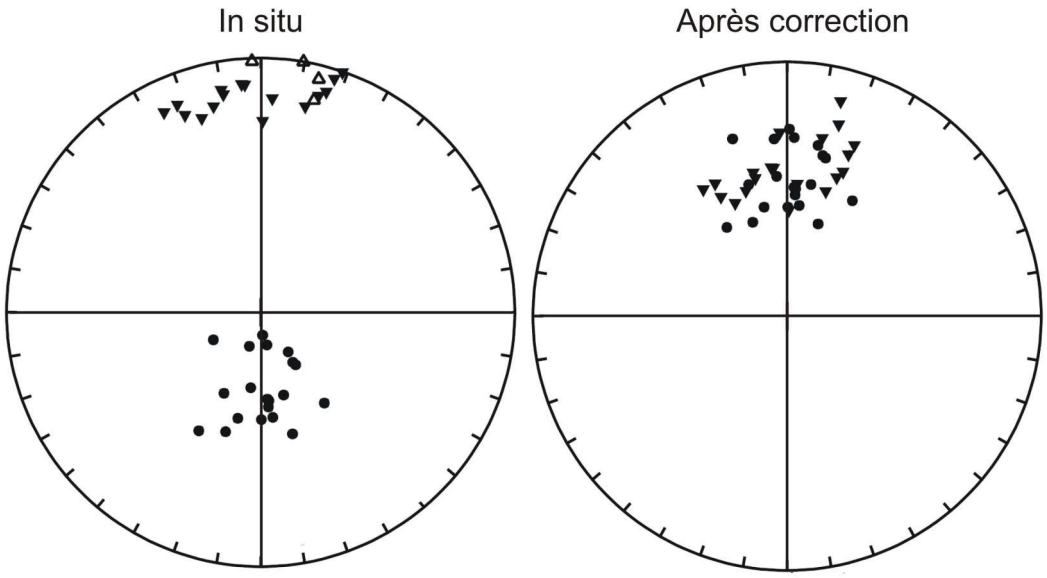


Figure 3. Exemple de test de pli. Le graphique de gauche montre les directions in situ de deux groupes de directions échantillonnées sur les deux flancs d'un pli. Sur le graphique de droite, les mêmes directions, représentées après correction de pendage, montre une amélioration du groupement ce qui constitue un test de pli positif (d'après Tauxe 2005).

Test d'inversion

Les inversions de polarité étant rapides à l'échelle des temps géologiques, les directions d'aimantation peuvent être considérée comme pratiquement constantes avant et après une inversion. De fait, les vecteurs d'aimantation de polarité opposée acquis dans des niveaux voisins doivent être antiparallèles. Un non-antiparallélisme des deux directions montre que s'est ajoutée une composante secondaire à la composante principale. C'est le test de l'inversion. Un test positif est un indice en faveur d'une origine primaire de l'aimantation.

Test du conglomérat

Un conglomérat est, par définition, une roche détritique issue de la dégradation mécanique d'autres roches et donc d'une agglomération de fragment d'autres roches. Les aimantations primaires de chacun de ces éléments ont des directions aléatoires. Une direction de l'aimantation uniforme dans tous les éléments au sien d'un conglomérat implique que cette direction d'aimantation n'a été acquise qu'après le dépôt du conglomérat. Une distribution aléatoire des directions de l'aimantation des clastes d'un conglomérat constitue un test positif alors qu'une distribution uniforme est considérée comme indiquant une origine secondaire de l'aimantation.

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CONTRIBUTION DE LA MAGNETOSTRATIGRAPHIE ET DE LA BIOCHRONOLOGIE A L'HISTOIRE EVOLUTIVE DES PRIMATES : APPLICATION AU PALEOGENE CONTINENTAL D'AFRIQUE DU NORD ET AU MIOCENE MOYEN ET SUPERIEUR D'ASIE DU SUD-EST

Au cours de ces dernières années, de nouvelles découvertes dans le Paléogène africain et le Néogène asiatique sont venues combler de nombreuses lacunes dans notre compréhension de l'histoire ancienne des primates. Ces découvertes ont amené de nouvelles problématiques concernant la chronologie et la paléobiogéographie de ce groupe. L'Asie et l'Afrique sont considérées comme des centres importants d'évolution et de diversification des primates au cours du Tertiaire mais les conditions paléoenvironnementales qui ont contraint les différenciations initiales au sein de ce groupe, les événements et les modalités de migration ainsi que la chronologie des échanges fauniques entre ces deux continents restent encore à élucider. L'établissement d'un cadre temporel, essentiel à la compréhension de l'histoire évolutive des faunes, s'est donc avéré nécessaire.

Les études paléomagnétiques et biostratigraphiques effectuées sur de nombreuses séquences paléogènes en Afrique du Nord ont permis de corréler et de dater avec précision certains gisements de mammifères et d'apporter des éléments de réponse pour comprendre à quelle occasion les premiers anthropoïdes sont arrivés en Afrique, par quelle voie de dispersion et quelles étaient les modalités des différenciations initiales au sein de ce groupe.

Le Miocène d'Asie du Sud a connu l'émergence de primates hominoïdes affiliés aux orangs-outangs. En Asie du Sud-Est, ce groupe est représenté par le genre *Khoratpithecus*, récemment décrit en Thaïlande et au Myanmar dans le Miocène moyen et le Miocène récent. Les études magnétostratigraphiques et biostratigraphiques des sites à *Khoratpithecus* ont apporté des indications fiables quant à la chronologie des différentes phases de divergences et la diversification initiale des hominoïdes, ainsi que des réponses sur leur histoire paléobiogéographique et les relations entre climat et l'évolution vers les formes actuelles.

A TIME FRAMEWORK BASED ON MAGNETOSTRATIGRAPHY FOR THE EVOLUTIONNARY HISTORY OF PRIMATES

During the past decade, new fossil discoveries from the African Paleogene and the Asian Neogene have provided new data that help reconstructing the early evolutionary history of several groups of mammals, including primates. The Asian and African continents have been both considered as major centres of evolution and diversification of primate groups during the Tertiary. However, understanding the early evolutionary history of these groups and the modes and routes of dispersal between these two landmasses have been hindered by a lack of consensus on both the timing and biogeography of their origins. New chronological data are absolutely required to provide a precise temporal framework, crucial for a better understanding of the early Tertiary emergence, diversification and paleobiogeographical history of the Asian and African groups of primates.

The age estimates, provided by magnetostratigraphic and biochronologhical studies, have precised the age of several localities which document the poorly known Paleogene African mammal evolutionary history and contribute to illuminate the antiquity and the pattern of anthropoid radiation in Africa.

This work, based on paleomagnetic and mammalian biochronological data, also presents refined chronostratigraphic analyses of the *Khoratpithecus*-bearing localities of Thailand and Myanmar. Providing a temporal framework for these deposits allows more precise correlations with other Neogene Asian hominoid localities, and permits a better comprehension of the evolution and paleobiogeographical patterns of Miocene South Asian mammalian faunas.