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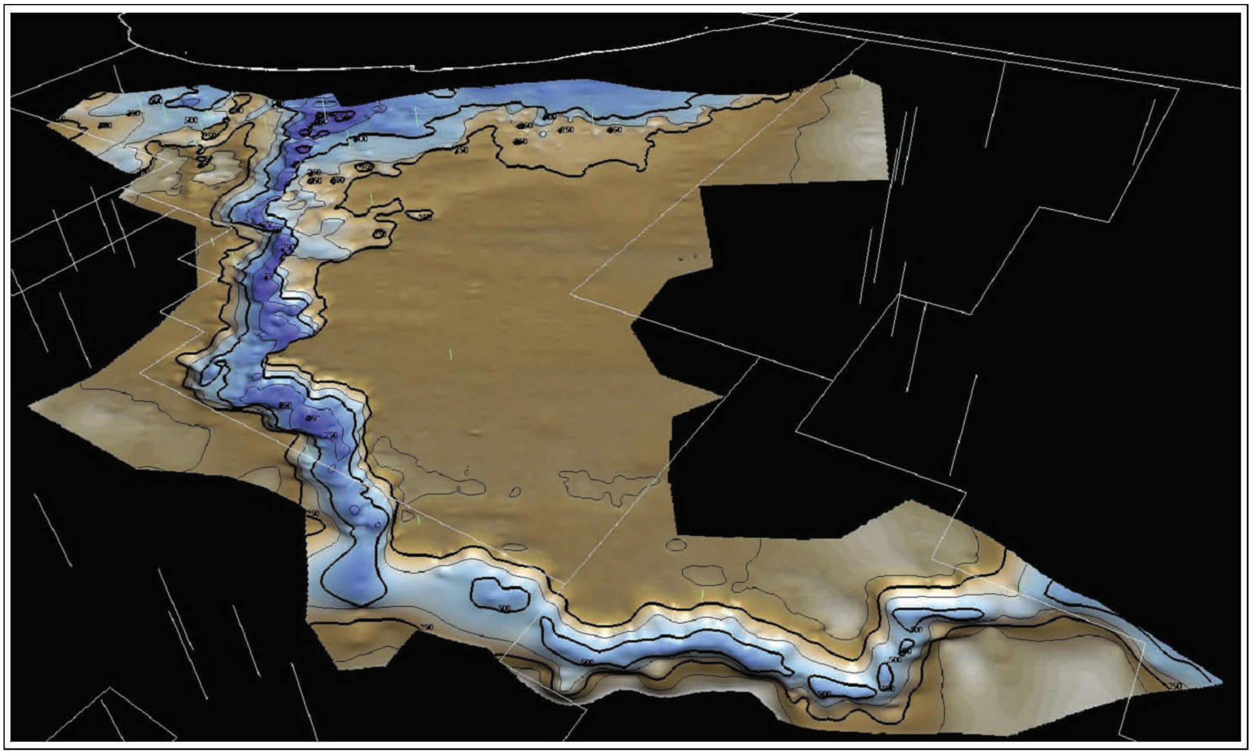

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A View to the South: Eo-Sahabi Palaeoenvironments Compared and Implications for Hominid Origins in Neogene North Africa

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ABSTRACT

A major Eo-Sahabi River connected the two important fossil sites of As Sahabi and Toros Menalla, Chad during the Neogene, although direct stratigraphic correlations have not yet been demonstrated. A detailed comparison of vertebrate faunas indicates that 1) Toros Menalla compares best with the Sahabi Formation upper Member U/V levels, predominantly sampled by Italian palaeontological collections in the 1930's. This level is younger than the Unit U-1 Sahabi Formation fauna, mainly collected since the 1970's; 2) the striking faunal similarities between As Sahabi and Toros Menalla indicate a distinct Libyco-Chadian or North-Central African palaeobiogeographic province in the Neogene, as previously hypothesised; and 3) both the Libyan and Chadian sites are largely open-country faunas dominated by bovids, equids, and giraffids, but with the significant presence of water-tied taxa such as anthracotheres and hippopotamids. As Sahabi preserves marine taxa, such as cetaceans, the sirenian *Metaxytherium serresii*, and sharks, and more abundant forest-adapted taxa, such as monkeys and an insectivore, whereas Toros Menalla preserves some more arid-adapted taxa, such as an aardvark. Faunal differences between the two sites are ascribed to 1) relatively small-scale temporal differences, 2) palaeoecological differences, 3) endemism, and 4) sampling error. The dearth of definitive hominid remains so far from As Sahabi is ascribed most likely to sampling error, although palaeoecological and temporal effects cannot be ruled out.

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INTRODUCTION

Northern Africa is a key region, both in terms of time and palaeobiogeography, for understanding the relationships of the hominoid-bearing localities of Neogene Eurasia, the hominid-bearing localities of sub-Saharan Africa, and the localities in the region itself that have now yielded remains of Hominidae. In addition to Middle Pliocene *Australopithecus bahrelghazali*, the Late Miocene *Sahelanthropus tchadensis* has now been documented from Chad (Brunet *et al*. 2002, 2005). Boaz (1987:132) pointed out that As Sahabi was important for providing the “first indications of what role northern Africa might have played in later hominoid evolution.” Now that hominids have been clearly recognised in the region, an examination of the geological and palaecological contexts is in order so that the similarities and differences between the As Sahabi and Toros Menalla faunas can be appreciated.

Correlational studies in this region have until recently been hampered by a dearth of faunas with absolute dates and a lack of clear stratigraphic control. The increasingly well-known stratigraphic and geochronological contexts of the Sahabi Formation, as documented in this volume, as well as much recently published work by the Mission Paleanthropologique Franco-Tchadienne, headed by M. Brunet, now permit new analyses and new insights regarding these important palaeontological sites.

GEOLOGICAL BACKGROUND

The structural depression in which the Sahabi Formation sediments were deposited is known as the Ajdabiya Trough. The trough’s Mesozoic origins long pre-date the sedimentary deposits of the Sahabi Formation and are likely related to early rifting in the central Sahara (El-Arnauti and El-Sogher, 2004:12). An arm of this rift system extended from the Gulf of Sirt in northern Libya southwards to the Chad Basin and was occupied during the latter Neogene by an inland sea, so-called “Mega Lake Chad” (Griffin, 2006, Drake *et al*., this volume). The Chad Basin was separated from eastern Africa by uplifted topography eventually forming the western and northern margins of the incipient Western Rift (Sepulchre *et al*., 2006). Mega Lake Chad flowed out to the north and gave rise to a large river, named by Griffin (2006) the Eo-Sahabi. This palaeo-river ran in a roughly parallel course some 1000 km to the west of the Nile Valley. Drake and colleagues in the current volume have demonstrated with remote imagery the course of the Eo-Sahabi from the Chad Basin to the Mediterranean up to the Pleistocene. Nicolai in this volume has illustrated with seismic data the deep channel that this river cut into basement sediments during the Mediterranean desiccation at the end of the Miocene.

The geology of the Sahabi Formation and related deposits has been exhaustively investigated and reported by de Heinzelin *et al*. (1980), de

Heinzelin and El-Arnauti (1982) and (1987), El-Arnauti and de Heinzelin (1985), El-Shawaihdi (1995), El-Arnauti and El-Sogher (2004), and authors in the present volume. Exposures of the fossiliferous Sahabi Formation are located to the west of the Sebkhat al Qunayyin. They are comprised of sands, fine clays, and sedimentary dolomites, interspersed with evaporates, such as gypsum. Overall thickness of the deposits is 80 to 100 m.

The geological age of Neogene sedimentary deposits in the Ajdabiya Trough, including the Sahabi Formation, has been problematical. It is now clear from calcareous nannofossil biostratigraphy (Muftah *et al.*, this volume) that the base of the Sahabi Formation rests on Late Miocene (Tortonian) deposits – Formations “M” and “P.” The latter formation, characterised by thick gypsum deposits, was previously interpreted to be of Messinian (terminal Miocene) age. Interpreted now as a localized lagoonal deposit and not a basin-wide marker of Messinian salinity crisis desiccation, the age of Formation P is revised to be somewhat older. The overlying base of the Sahabi Formation also has a putative older maximum age, i.e. Tortonian.

Now with recently reported potassium-argon analyses of sedimentary glauconite, from “Formation M” exposed at As Sahabi, and palaeomagnetic stratigraphy of the overlying sediments, Beyer in this volume dates Formation M to 7.5 to 7.7 ma and the overlying fossiliferous Sahabi Formation to between 7.3 and 7.5 ma. The Sahabi Formation thus is interpreted to be Late Miocene in age and largely earlier than the Messinian Period (ca. 6.8-5.3.ma) although the upper stratigraphic levels have not yet been intensively sampled and further work is needed to refine the upper absolute age limit of the formation.

The fossiliferous sediments exposed in the Djurab Desert of northern Chad are less well-known geologically. Vignaud *et al*. (2002) have published the only general discussion of the geology. Deposits are grouped based on biostratigraphy into one of four major sectors, the oldest being the Toros Menalla sector. Collecting areas are extensive, being several km^2 in extent and separated from one another by overlying dune sand. The low-lying topography does not afford sedimentary outcrops more than a few meters in thickness.

The Toros Menalla localities have a lower 3-4-metre-thick layer of fine sands, interpreted by Schuster *et al.* (2006) to be aeolian dunes, which they claim to be the earliest evidence of the developing Sahara Desert. Above this level is a sandstone deposit indicated to be about 2 m thick with matrix-consolidated sands interspersed with lacustrine clays. It is informally named the “anthracotheriid unit” and is interpreted to preserve a peri-lacustrine depositional environment. All the terrestrial vertebrates, including hominids, are from this layer. A level of green, fine clayey pelite of ca. 0.5 m thickness caps the sequence and indicates full lacustrine conditions.

Beryllium-10 dates on sedimentary pelites from the Chadian Toros Menalla site were recently reported by Lebatard *et al.* (2008). The authors quote an age bracket for the Toros Menalla fauna to be “between 6.8 and 7.2” ma, but their actual age analyses (6.83 ± 0.45 and 7.12 ± 0.31) have a wider range of error, i.e. as young as 6.38 ma for the upper age limit and as old as 7.43 ma for the older. Mean age from these age determinations is 6.9 ma but with an error range of one million years (6.4-7.4 ma).

BIOSTRATIGRAPHIC AGE OF THE LIBYCO-CHADIAN FAUNAS

The biostratigraphic age of the fossil assemblage from As Sahabi has been debated since the inception of recent work at the site in the 1970's. Biostratigraphic evidence initially allowed a reassessment of age to the Late Neogene, i.e. Late Miocene to Early Pliocene (Boaz *et al*., 1979; Bernor and Pavlakis, 1987), as opposed to earlier age attributions to older reaches of the Miocene (e.g. Petrocchi, 1951). There has been a general acceptance among researchers that the Sahabi Formation is peri-Messinian, but whether it is pre-Messinian, thus Late Miocene in age, post-Messinian, earliest Pliocene in age, or intra-Messinian, spanning a period of time at the Mio-Pliocene boundary during which the Mediterranean underwent desiccation, has been difficult to obtain consensus on.

Boaz *et al.* (2008) summarised primarily biostratigraphic evidence and posited a Late Miocene age for the bulk of the As Sahabi vertebrate fauna, overturning an earlier consensus driven by an interpretation of lithostratigraphic evidence (see chapters in Boaz *et al.*, 1987) that As Sahabi was basal Pliocene. Although new data and the analyses presented in this volume support this conclusion for the most part, there are also some indications that there is possible significant time represented within the Sahabi Formation itself, i.e. more time in the less well-known upper Sahabi Formation.

Gentry in his new study of the As Sahabi bovids points out differences between the assemblage collected by the Italian teams in the 1930's, primarily in Members U-2 and V of the Sahabi Formation (see Boaz *et al.*, this volume), and specimens collected by field teams from the 1970's to the present, primarily from Unit U-1 of the Sahabi Formation (Ibid.). Gentry concludes that the newly collected specimen of *Miotragoceros cyrenaicus* (10P103A), from U-1, shows more primitive characters than the type specimen in Rome, collected in the 1930's, presumably from U-2. Another indication of temporal differences in the As Sahabi bovid collection is the lack in the well-sampled U-1 localities of any remains of the distinctive bovid *"Leptobos" syrticus*, named by Petrocchi (1956) from a specimen collected at As Sahabi in the 1930's, also presumably from U-2.

Sanders in his review of the As Sahabi proboscideans (this volume) notes that newly re-discovered fossils collected in the 1930's are all referrable to *Anancus petrocchii*, a taxon not recovered in the well-sampled localities of Unit U-1. Again, these fossils derived from localities that have now been located in the areas of exposure of Members U-2 and V. They would thus appear to be later in time.

The hypothesis that there was a "mixed" or diachronous fauna from As Sahabi, specifically as regards the fossils collected by the Italian teams in the 1930's and those collected from the 1970's onward, is not new. It was put forward by Cooke (1987) who noted that the As Sahabi suid *Nyanzachoerus kanamensis*, described by Leonardi (1952), appeared anomalously young compared to the suids discovered in U-1 localities (see also Gallai *et al.*, this volume). Geraads (1989) made a similar suggestion based on his study of "*Leptobos" syrticus*. Dechant Boaz (1987) and Boaz (1996) both noted faunal differences between Units U-1 and U-2, e.g. an increase in the ratio to hippopotamids to anthracotheriids in U-2 compared to U-1, but ascribed these to possible ecological change or differences in habitat sampling. One reason for this interpretation was the lack of geological evidence for any major temporal hiatus at the interface of Units U-1 and U-2.

There is thus evidence that suggests that a significant amount of evolutionary time separates Sahabi Formation lower Member U (with the underlying primarily marine Member T) from upper levels (upper Member U and Member V). A Late Miocene age, approximately 7 ma, is consistent with faunal studies of the U-1 fauna (Boaz *et al.,* 2008) but the upper age boundary would appear to be younger. Further geochronological research must attempt to refine age assessments for the upper Sahabi Formation. This conclusion has implications for faunal dating of the Toros Menalla site in Chad (see below).

The faunal age of Toros Menalla has been estimated by comparison of fauna from localities in the Kenyan Rift Valley with absolute dating control - Lukeino at ca. 6.0 ma and the lower Nawata Formation of Lothagam at 6.5 - 7.4 ma, cited by Vignaud *et al*. (2002) who suggested that Toros Menalla was between 6 and 7 ma. Brunet *et al.* (2004) opted to place Toros Menalla at the earliest margin of this age interval, at 7 ma. However, the recently well-dated site of Lemudong'o, Kenya also shares with Toros Menalla several biostratigraphically informative taxa, such as *Anancus kenyensis* and *Nyanzachoerus syrticus*, and it is dated to 6.1 ma (Deino and Ambrose, 2007).

NEOGENE LIBYCO-CHADIAN PALAEOENVIRONMENTS

There has generally been consensus on the overall palaeoenvironmental reconstruction as represented by the preserved sediments, fauna, and flora from As Sahabi. The presence of marine vertebrates and marine microfauna, especially in Member T but in higher levels as well, has been a clear indication of the proximity of shallow marine environments. Member T preserves the fossil "sirenian fields" with semi-articulated skeletons bearing bite marks of sharks (Domning and Thomas, 1987) and provides the scenario for peri-Messinian dwarfing of *Metaxytherium* (Ibid.; Biannucci *et al*, this volume).

The fossil wood assemblage, and the fish, avian, herpetological, and mammalian faunas have all indicated the proximity of terrestrial habitats to a large river emptying into a low-lying system of estuaries and lagoons. Mammalian microfaunal remains, particularly the dominant presence of the gerbil, *Abudhabia yardangi* (Munthe, 1987; Agusti, this volume), have importantly documented the presence of arid environments inland from the water bodies. Fire-scarred fossil wood demonstrates the presence of "savanna" woodland habitats – trees with interspersed grassland (Dechamps, 1987). The mammalian fauna has a terrestrial component of bovids, equids, suids, giraffids, a rhinocerotid, proboscideans, many carnivores (dominantly hyaenids), monkeys, and an insectivore, with habitat preferences ranging from open-country to forested; a semi-aquatic component, consisting of anthracotheres, hippopotamids, and perhaps amebelodont "shovel-tuskers;" and an aquatic component with a whale, both river and salt-water dolphins, a seal, and abundant fish.

The Toros Menalla vertebrate faunal assemblage is dominated by bovids (more than half) and amphibious mammals (a quarter) and has been interpreted to represent more or less open habitats (Brunet *et al.*, 2004). The Okavango delta in Botswana has been cited as a modern habitat analogue of the peri-lacustrine mosaic of wooded habitats, wooded savanna, open savanna, and desert. One difference between Late Miocene Mega Lake Chad and the modern Okavango is, however, that the former served as the source for a major Eo-Sahabi River emptying into the Mediterranean, and the Okavango has no outlet to the sea.

COMPARISON OF AS SAHABI AND TOROS MENALLA FAUNAS

As Sahabi and Toros Menalla, although they share taxa with localities in other regions of Africa and Eurasia, are by far most closely similar to one another. A detailed comparison of faunas from the two sites was undertaken in order to assess differences and similarities.

Tables 1, 2, and 3 present comparisons of the vertebrate faunas from As Sahabi and Toros Menalla. Table 1 lists the fish taxa identified at the two sites. Simpson's Faunal Resemblance Index (FRI, see Bernor and Rook, this volume) calculated for the ichthyan fauna between the two sites is 0.72. Table 2 lists the reptilian and avian taxa from the two sites, and their FRIs are 0.9 and 0.92, respectively. Table 3 lists the relatively larger mammalian faunas, and the FRI between As Sahabi and Toros Menalla is 0.85. These are high indices of similarity and in general support the point made by numerous authors that there is a Late Neogene Libyco-Chadian palaeo-biogeographic region or zone (termed by Boaz 1997, "A2", Figure 1). More detailed taxon-by-taxon comparisons are beyond the scope of this paper but in the future will provide important data on the broader regional biogeographical and, for water-tied taxa, hydrographic connections.

Because As Sahabi and Toros Menalla are shown to be biostratigraphically and geochronologically close in age, differences in their faunal inventories may be ascribed to 1) small-scale temporal differences, 2) palaeoecological differences, 3) endemism, or 4) sampling error.

Temporal Differences

The proboscidean faunas argue for a temporal difference. The absence

Table 1. Comparison of Sahabi Formation, Member U ichthyan fauna with that reported from Toros Menalla, Anthracotheriid Unit, Locality TM 266, Chad. Reference for the Sahabi Formation is Gaudant (1987) and for Toros Menalla references are Pinton *et al*. (2006), Otero *et al.* (2006, 2007), and Vignaud, *et al*. (2002).

SAHABI FM. MB. U	ANTHRACOTHERIID UNIT, TM266
PISCES	PISCES
Polypteriformes: *Polypterus* sp.	Polypteriformes: *Polypterus faraou*
Siluriformes: Bagridae: *Clarotes* sp.	Siluriformes: Bagridae: “*Bagrus* Group”
Siluriformes: Clariidae: *Clarias* sp. or *Heterobranchus* sp.	
Perciformes: *Lates* sp.	Perciformes: Indet.
Perciformes: Sparidae indet.	
Mochokidae: *Synodontis* sp.	
Ariidae: *Arius* (?) sp.	
	Mormyriformes: *Gymnarchus* sp.
	Cypriniformes: *Labeo* sp.
	Characiformes: *Sindacharax* sp.
	Characiformes: *Hydrocynus* sp.
	Characiformes: Alestini indet.
	Tetraodontiformes: *Tetraodon* sp.
Selachia: *Carcaradon* sp.	

Table 2. Comparison of Sahabi Formation, Member U reptile and avian fauna with that reported from Toros Menalla, Anthracotheriid Unit, Locality TM 266, Chad. References for the As Sahabi fauna are Hecht, Wood, and Ballmann in Boaz *et al.* (1987), and for Toros Menalla Vignaud *et al.* (2002), Louchart, Mourer-Chauviré *et al.* (2005), and Louchart, Vignaud, *et al.* (2005).

SAHABI FM. U	ANTHRACOTHERIID UNIT, TM266
REPTILIA	REPTILIA
Crocodilia: *Euthecodon* sp.	Crocodilia: *Euthecodon* cf. *E. nitriae*
	Crocodilia: Gavialidae gen. et sp. nov.
Crocodilia: *Crocodylus checchiai*	
	Crocodilia: *Crocodylus niloticus*
Serpentes: Booidae indet.	Serpentes: *Python* cf. *P. sebae*
	Serpentes: Colubridae indet.
	Lacertilia: *Varanus* sp.
Testudines: Trionychidae: *Trionyx* cf. *triunguis*	Testudines: Trionychidae indet.
Testudines: Testudidae: cf. *Geochelone* sp.	Testudines: Testudidae: Testudinae indet.
AVES	AVES
Ciconiidae: *Leptoptilos* sp.	Ciconiidae: sp. 1
Ciconiidae: Ciconiidarum gen. sp.	Ciconiidae: sp. 2
Phalacrocoracidae: *Phalacrocórax* sp.	Phalacrocoracidae
Anhingidae: *Anhinga* sp.	Anhingidae
Pelecanidae *Pelecanus* sp.	
Accipitridae: Accipitridarum gen. sp.	Accipitridae
Anatidae: *Afrocygnus* cf. *A. chauvireae*	Anatidae: *Afrocygnus chauvireae*
Anatidae: *Anatidarum* gen. sp. B	
Anatidae: *Anatidarum* gen. sp. C	
Anatidae: *Anatidarum* gen. sp. D	
	Gruidae
	Rallidae
	Heliornithidae: *Heliopais* cf. *personata*

Table 3. Comparison of Sahabi Formation, Member U mammalian fauna with that reported from Toros Menalla, Anthracotheriid Unit, Locality TM 266, Chad. References for Sahabi Formation are in Boaz *et al*. (1987) and this volume. References for Toros Menalla mammal fauna are Vignaud *et al*. (2002), de Bonis *et al*. (2005), de Bonis *et al*. (2007), Boisserie, Likius *et al*. (2005), Boisserie, Zazzo *et al*. (2005), Lehmann *et al*. (2006), Likius *et al*. (2007), and Peigné *et al*. (2005a,b). Asterisk indicates Sahabi Fm. U/V.

SAHABI FM. T	SAHABI FM. U	ANTHRACOTHERIID UNIT, TM266
MAMMALIA	MAMMALIA	MAMMALIA
	Primates: Cercopithecidae: Colobinae: gen. sp.	Primates: Cercopithecidae: Colobinae indet.
	Primates: Cercopithecidae: Papionini: sp. nov.	
		Primates: Hominidae: *Sahelanthropus tchadensis*
	Insectivora: Soricidae: Crocidurinae	
	Rodentia: Xerini: cf. *Atlantoxerus getulus*	Rodentia: Sciuridae: Xerini: *Xerus* sp.
	Rodentia: Murinae: *Progonomys* cf. *mauretanicus*.	Rodentia: Muridae: Murinae indet.
	Rodentia: Gerbillinae: *Abudhabia yardangi*	
	Rodentia: Cricetidae: Myocricetodontinae:*Myocricetodon* sp.	
	Rodentia: Ctenodactylidae*: Irhoudia* sp.	
		Rodentia: Hystricidae: *Hystrix* sp.
		Tubulidentata: Oryteropidae: *Orycteropus abundulafus*
	Cetacea: Delphinidae: cf. *Lagenorhynchus* sp.	
	Cetacea: Platanistidae: Iniinae indet.	
Cetacea: Large, indet.	Cetacea: Large, indet.	
	Carnivora: Phocidae: Monachinae indet.	
	Carnivora: Viverridae: *Viverra howelli*	
	Carnivora: Hyaenidae: *Hyaenictiherium* sp.	Carnivora: Hyaenidae: *Hyaenictitherium* cf. *H. hyanoides*
	Carnivora: Hyaenidae: *Percrocuta eximia*	
	Carnivora: Felidae: *Machairodus* sp.	Carnivora: Felidae: *Machairodus kabir*
	Carnivora: Ursidae: *Agriotherium* sp.	
	Carnivora: Ursidae: *Indarctos* sp.	
		Carnivora: Mustelidae: Lutrinae indet.
		Carnivora: Canidae: *Vulpes riffautae*
		Carnivora: Herpestidae: *Galerella sanguinae*
	Proboscidea: Gomphotheriidae: *Anancus* sp. ? *	Proboscidea: Gomphotheriidae: *Anancus kenyensis*
	Proboscidea: Gomphotheriidae: *Amebelodon cyrenaicus*	
	Proboscidea: *Stegotetrabelodon syrticus*	
		Proboscidea: *Loxodonta* sp. aff. *L.* sp. indet. "Lukeino stage"
Sirenia: *Metaxytherium serresi*	Sirenia: *Metaxytherium serresi*	

Table 3 (cont.)

SAHABI FM. T	SAHABI FM. U	ANTHRACOTHERIID UNIT, TM266
MAMMALIA	MAMMALIA	MAMMALIA
	Equidae: Hipparioninae: *Cremohipparion* aff. *matthewi*	Equidae: Hipparioninae: *Hipparion* cf. *H. abudhabiense*
	Equidae: Hipparioninae: *C. nikosi*	
	Equidae: Hipparioninae: *Hipparion* s.s.	
	Equidae: Hipparioninae: *“Sivalhippus”* Complex	
	Rhinocerotidae: *Ceratotherium neumayeri*	
	Suidae: *Nyanzachoerus syrticus*	Suidae: *Nyanzachoerus syrticus*
	Nyanzachoerus cf. *devauxi*	
	Nyanzachoerus kanamensis *	
	Anthracotheriidae: *Libycosaurus petrocchii*	Anthracotheriidae: *Libycosaurus petrocchii*
	Hippopotamidae: *Hexaprotodon sahabiensis*	
		Hippopotamidae: *Hexaprotodon garyam*
	Giraffidae: *Samotherium* sp.	Giraffidae: *Sivatherium* cf. *S. hendeyi*
		Giraffidae: *Bohlinia adoumi*
	Bovidae: Antilopini *Gazella* sp.	Bovidae: Antilopini Indet.
	Antilopini *Dytikodorcas libycus*	
		Ovibovini Indet aff. *Palaeoryx*
	Bovini Gen. indet. *“Leptobos” syrticus* *	Bovini Indet.
	Reduncinae *Kobus* aff. *subdolus*	Reduncini *Kobus* sp.
	?*Hippotragus* sp.	cf. Hippotragini gen. et sp. indet.
	Boselaphinae *Miotragoceros cyrenaicus*	
	Neotragini *Raphicerus* sp.	
	Alcelaphini cf. *Damalacra*	

of *Stegotetrabelodon* and *Amebelodon* in apparently appropriate habitats at Toros Menalla coupled with the presence of *Anancus* and *Loxodonta* there, and the preponderance of *Anancus* only in the upper Member U/V section of the Sahabi Formation, suggests that Toros Menalla is slightly younger than the bulk of the As Sahabi fauna.

Palaeocological Differences

Palaeoecological differences between the two sites may explain a number of faunal differences between the them. As Sahabi preserves a fauna representative of a range of aquatic habitats: large riverine freshwater, brackish estuarine, and lagoonal near-marine, as well as a range of terrestrial habitats: gallery forest (probably of limited extent) fringing the Eo-Sahabi River, open-country wooded grassland extending away from the river, swampy floodplain flats near water bodies, and arid near-desertic conditions distal to water bodies. Toros Menalla indicates an overall similar range of habitats but lacks or

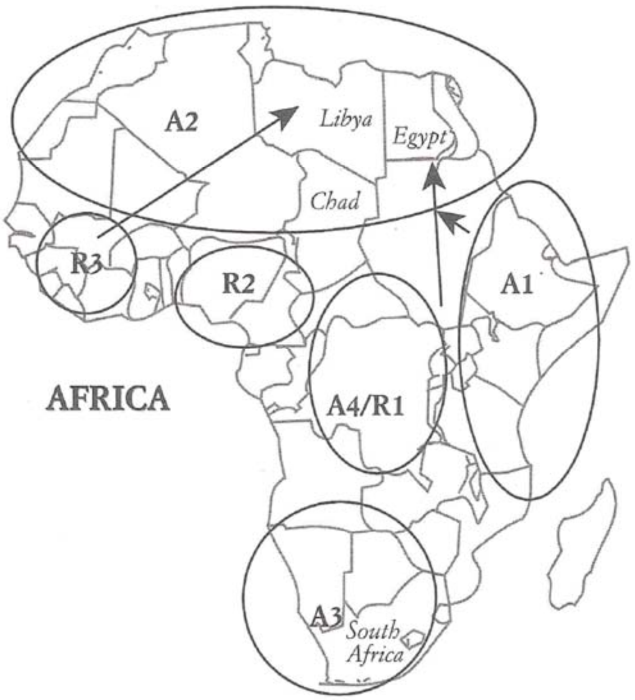

Figure 1. Late Neogene African biogeography. Forest refugia in Africa are indicated by extant mammalian biogeography (regions R1, R2, and R3). Late Neogene palaeobiogeoraphic regions are indicated by regions A1-4. From Boaz (1997).

has in very small numbers 1) all marine faunal elements, such as sharks, sparid fish, sirenians, cetaceans, and seals, and 2) forest- or woodland-adapted mammalian species, such as insectivores, monkeys, and ursids. It shares with As Sahabi 1) water-tied, swampy, floodplain-adapted species, such as abundant anthracotheres, which likely lived in a similar but peri-lacustrine floodplain habitat (versus riverine or estuarine floodplain at As Sahabi), and 2) more open-country-adapted species that lived away from water, including bovids, equids, giraffids, and carnivores. Toros Menalla perhaps sampled slightly more arid habitats than are preserved in the As Sahabi fauna, as indicated by the presence of termite mounds and fossils of aardvarks, both absent at As Sahabi.

Endemism

The presence of two related but different species of hippoptamids — *Hex. sahabiensis* at As Sahabi and a larger *Hex. garyam* at Toros Menalla might be due to differing evolutionary adaptations to riverine and lacustrine habitats, respectively.

Toros Menalla evinces the surprising discovery of a southern Asian bird species, *Heliopais* cf. *personata,* the finfoot, which probably lived in “forested margins of a freshwater body with thick overhanging vegetation” (Louchart, Mourer-Chauviré *et al*., 2005:7). This species may have been a relictual forest denizen isolated by surrounding open country and desert.

Sampling Error

Some faunal differences between the two sites are attributed to sampling error when habitats and biostratigraphic age are deemed to have been appropriate but species are not shared. Most species of micromammals that have been discovered at As Sahabi world be expected at Toros Menalla if intensive wet-sieving had been done at that site.

Brunet *et al.* (2004) reports that over 10,000 identified specimens have been recovered in the Toros Menalla sector. As of the end of the February-March, 2008 field season at As Sahabi, 5147 fossil specimens had been collected, identified, and catalogued. This number includes marine fauna as well as excavated specimens of taphonomic importance not unidentifiable to family, reducing the comparable number of terrestrial specimens at As Sahabi to less than 5000. With roughly twice the number of specimens collected at Toros Menalla, it would be expected that some “missing” taxa at Sahabi such as low-density carnivores (canids, lutrine otters, and mongooses), and hominids, would turn up as sample sizes increase. The liklihood that the Toros Menalla fauna is also not completely known is shown by such expected but “missing” taxa as viverrid and ursid carnivores and rhinocerotids.

CONCLUSIONS AND DISCUSSION

From recent discoveries and analyses from As Sahabi there is a probable temporal difference in the two fossiliferous zones of the Sahabi Formation, Members U-1 and U-2/V. It is probable that the Toros Menalla fauna shares salient features with the later, U-2/V fauna. Although absolute dating still remains elusive at As Sahabi, best estimates are 7.3-7.5 ma based on recent geochronological results and ca. 7 ma based on comparative mammalian biostratigraphy for the U-1 fauna. Bernor and Rook (this volume) suggest an age for the As Sahabi fauna of 6.7 ma (MN12-13). The U-2/V fauna is younger than U-1 but by how much is difficult to ascertain until more dating analyses are done. Similarities observed between the As Sahabi U-2/V and Toros Menalla faunas indicate that the age of the fossiliferous levels at Toros Menalla, and thus the hominid *Sahelanthropus tchadensis*, is younger than As Sahabi U-1.

Faunal differences between As Sahabi and Toros Menalla point up the proximity of marine habitats in the former. This difference is particularly pronounced in the lagoonal and estuarine Member T with its preserved mass death sites of sirenians preyed upon by great white sharks (Domning and Thomas 1987; Bianucci *et al.,* this volume). Sahabi Formation Member U, however, also records the presence of sirenians, marine fish such as sharks and sparids, a monachine seal, and cetaceans. None of these taxa are present at Toros Menalla, at a distance of some 1100 km from the sea.

The terrestrial vertebrate faunas from both Libyan and Chadian sites show significant similarlities in probable palaeo-habitat representations. The water-tied components, particularly the common anthracotheres and hippotamids, indicate widespread marshy or shallow shoreline conditions. Wear on anterior teeth of anthacotheres suggests to Pickford (2006) that they were feeding on soft vegetation near the shore. Hippopotamids, then as now, may indicate proximity of grassland near permanent water bodies (Boisserie, Zazzo *et al.*, 2005). The As Sahabi proboscidean *Stegotetrabelodon*, with its long lower tusks, and *Amebelodon*, with its lower “shovel tusks,” are both thought to have employed these adaptations in procuring food by digging in soft or marshy substrates (Sanders, this volume). The absence of both these taxa at Toros Menalla might suggest that marshy habitats were less common at that site, but this interpretation is complicated by the likely temporal difference in the faunas.

There are abundant taxa that record the presence of grasslands and wooded “savanna” at both As Sahabi and Toros Menalla. Bovids are common ungulates at both sites, and equids and giraffids also occur. McCrossin’s (1987) analysis of the As Sahabi *Nyanzachoerus syrticus* forelimb led him to postulate a “fast-running” adaptation to probable open country for this suid. A similar cursorial adaptation has been postulated for the “running hyena” *Chasmaporthetes*, also now known from As Sahabi (Rook and Sardella, this volume).

Over half of the microfaunal assemblage at As Sahabi consists of the gerbil *Abudhabia yardangi* (Munthe, 1987), an indicator of semi-arid conditions. Microfauna is not fully reported from Toros Menalla but one significant indicator of semi-arid to arid conditions is the documentation of the aardvark, *Orycteropus (*Lehman *et al.*, 2006*)*. Aardvarks are not known from the As Sahabi fauna. Another indicator of aridity at Toros Menalla not known from As Sahabi is the presence of termitaries (Vignaud *et al.*, 2002).

The abundant fossils of wood in the Sahabi Formation, identified by Dechamps (1987), including drifted tree trunks, record the presence of forest at As Sahabi. An insectivore (shrew) in the As Sahabi microfauna, as well as a squirrel, are likely indicators of forest habitats. There are some 20 specimens of monkeys known from As Sahabi, ascribed to a cercopithecine and colobine, whereas only one specimen, a putative colobine, is known from Toros Menalla. If monkeys are taken as general indicators of wooded to forested conditions, even though the As Sahabi cercopithecine postcrania are suggestive of terrestrial adaptations (see Benefit *et al.*, this volume) then this is another indicator that Toros Menalla may have sampled more open-habitat conditions than As Sahabi.

Permanent fresh water was present in abundance at both As Sahabi, in the form of the large Eo-Sahabi River emptying into an estuary of the paleo-Gulf of Sirt, and at Toros Menalla, where peri-lacustrine sediments on the borders of Mega-Lake Chad preserve the bulk of the fauna.

Toros Menalla has yielded some half-dozen craniodental remains of the hominid *Sahelanthropus* while the presence of hominids at As Sahabi is still a matter of debate. As suggested here this is most likely a function of sampling error, but another possible interpretation is that the apparent greater abundance of hominids at Toros Menalla is a reflection of a biostratigraphic difference with As Sahabi, i.e. the less well known Unit U-2/V deposits at As Sahabi when investigated more fully may yet yield hominids. Alternatively, this apparent difference in hominid fossil density could be a reflection of real preferences of early hominids for more open, less marshy, and/or less near-marine habitats, which seem on the evidence available so far to be better represented at Toros Menalla.

Data are yet insufficient to decide between a phylogeographic model of African Rift Valley vicariance ("Hypothesis 2" of Boaz, 1997) or proto-Saharan aridification ("Hypothesis 3" of Boaz, 1997) as explanatory for early hominid origins in northern Africa. Palaeobiogeographical arguments for a Eurasian source of northern African hominoids may be improbable, but not impossible, as there are a number of Eurasian faunal elements shared between As Sahabi and Toros Menalla. A better fossil record in the Middle Miocene will be an important test for such a scenario. A differential lack of knowledge of northern African late Neogene faunas is due to demonstrable collection biases against small- to medium-sized taxa by earlier collectors, taphonomic factors affecting animals of small to medium body size, and the vast reaches of still unexplored fossiliferous exposures in northern Africa. The absence of appropriate fossil candidates for Late Miocene hominid ancestors in Africa cannot be accepted as evidence of their absence. Further research in Libya at the sites of As Sahabi and Jabal Zaltan offer opportunities to address many of these important questions. The range of non-marine palaeoenvironments reconstructed for As Sahabi is similar overall not only to the *Sahelanthropus* localities of Chad but also to those discovered for the early hominids of sub-Saharan Africa (e.g. Senut, 2006; White *et al*., 2006).

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