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Discovery of an Upper Miocene Vertebrate fauna near Tizi N'Tadderht, Skoura, Ouarzazate Basin (Central High Atlas, Morocco)

Découverte d'une faune de vertébrés dans le Miocène supérieur de Tizi N'Tadderht, Skoura, Bassin d'Ouarzazate (Haut Atlas Central, Maroc)

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ABSTRACT

The discovery of Upper Miocene vertebrates at Tizi N'Tadderht in the Ouarzazate basin (Morocco) helps to fill a gap in our knowledge of Neogene faunas in North Africa. The new fauna includes an ostrich cf. *Struthio* sp, a turtle cf. *Centrochelys* sp., *Crocodylus* cf. *niloticus*, and a relatively diverse fauna of large mammals. The mammal assemblage probably includes three hipparion species, including a very small form not previously reported from Africa, aff. *Cremohipparion periafricanum*, two species of rhinoceros cf. *Ceratotherium* sp. and aff. *Chilotherium* sp., a Proboscidean cf. *Tetralophodon* sp., a large member of the Giraffidae similar to "*Palaeotragus*" *germaini* and two bovids of which one is likely related to *Prostrepsiceros*, while the other is a new medium-sized antelope with spiral horns, certainly a representative of the Caprinae, a group that is rare in Africa. A late Miocene age, corresponding to the European Turolian Mammal age, is most likely for this fauna.

Mots clés :
Vertébrés
Miocène supérieur
Bassin d'Ouarzazate
Tizi N'Tadderht
Maroc

RÉSUMÉ

La découverte de vertébrés du Miocène supérieur à Tizi N'Tadderht, dans le bassin de Ouarzazate au Maroc, contribue à combler une lacune dans la documentation faunique du Néogène d'Afrique du Nord. Cette faune comporte cf. *Struthio* sp, cf. *Centrochelys*, un crocodile de la lignée de *Crocodylus niloticus*, ainsi qu'une faune relativement diversifiée de grands mammifères. L'assemblage mammalien comprend probablement trois espèces d'Hipparions dont notamment une forme de très petite taille jamais signalée en Afrique, cf. *Cremohipparion periafricanum*, deux espèces de rhinocéros : cf. *Ceratotherium* sp. et aff. *Chilotherium* sp., un Proboscidien cf. *Tetralophodon* sp., un Giraffidé gen. et sp. indet. de grande taille comparable à celle du « *Palaeotragus* » *germaini* et deux bovidés dont l'un est probablement voisin de *Prostrepsiceros*, tandis que l'autre est une nouvelle antilope de taille moyenne et à cornes spiralées, certainement un représentant des Caprinae, groupe très rare en Afrique, où aucune forme semblable n'a été signalée. C'est avec un âge Miocène supérieur correspondant plus précisément au Turolien d'Europe, que la faune s'accorde le mieux.

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1. Introduction

As in other countries of North Africa, the Neogene macromammal faunas of Morocco are still very poorly documented. In fact, only two localities have yielded significant remains. One is the late Middle Miocene locality of Beni Mellal (Choubert and Faure-Muret, 1961; Lavocat, 1961), the first important locality of Miocene vertebrates in Morocco, and the other is the Late Pliocene/Earliest Pleistocene locality of Ahl al Oughlam, the most productive site of the late Neogene of North Africa and indeed one of the richest of the entire African continent (Geraads, 2006; Raynal et al., 1990). Most other vertebrate localities of this period have only yielded micromammals. The discovery of large vertebrate remains in the Miocene of the Ouarzazate basin is of great paleontological and geological interest. Indeed, while the new fossils help to bridge a gap in the Neogene of North Africa, and Morocco in particular, they also provide some elements of dating that will help to interpret the geodynamic evolution of the region.

2. Geographical and geological setting

On the southern slope of the Central High Atlas in Morocco, Cenozoic continental deposits are known from the Ouarzazate foreland basin and the Aït Kandoula and Aït Sedrat deposits (Fig. 1). Together, these continental deposits form the "Group of Imerhane" (Herbig, 1991) which includes four continental formations ranging in age from the Late Eocene to the Quaternary (El Harfi et al., 2001: Fig. 4). Their geological history represents a major episode of sedimentation lasting from the Eocene to the Quaternary, during which a large basin was fragmented and filled with thick continental series, largely due to the uplift of the central High Atlas (El Harfi et al., 1996, 2001; Fraissinet et al., 1988; Gauthier, 1960; Görler and Zucht, 1986; Görler et al., 1988; Tesón et al., 2010).

The Ouarzazate basin is an asymmetric syncline located in the eastern extension of the Souss basin, between the mobile uplift area of the High Atlas in the North and the stable domain of the Anti-Atlas in the South, on the Northern edge of the West African Craton. It belongs to the structural domain of the Anti-Atlas and is separated from the High Atlas by the South-Atlas fault, which is the eastern extension of the Hayes transform fault. The basin, oriented on an east-west axis, is 145 km long and about 40 km wide at its maximum in the western part (Fig. 1).

This basin is filled with continental sediments ranging from the Upper Cretaceous (Senonian) to the Quaternary. Paleogene deposits, mostly marine and lagoonal sediments, are exposed almost exclusively in the Northeast of the Ouarzazate basin (Gauthier, 1960). Herbig (1986, 1991) and Herbig and Trappe (1993) distinguished five formations in this Subatlasic Group. Their location was governed principally by tectonic but also by eustatic controls. In contrast, the Neogene deposits outcrop widely throughout the Ouarzazate basin (Fig. 1). They correspond to a megasequence of lacustrine and palustrine sediments deposited in the context of an alluvial plain, and dotted with local sabkhas. Their thickness varies considerably from the north, where they can reach 700 m (Görler et al., 1988) to the south, where the sediments are bevelled on the Anti-Atlas Precambrian basement. They were attributed to the Aït Kandoula Formation, originally defined in the small basin of the same name (Aït Kandoula, Fig. 1) by Görler and Zucht (1986) and Görler et al. (1988). This formation was initially composed of three members that have been reduced to two (Fig. 2) (El Harfi et al., 2001; see below). It is locally exposed in vertical outcrops in the immediate vicinity of the High Atlas zone, and it becomes subhorizontal southwards. This formation lies unconformably over all older strata and in many places, for example on the southern edges of the basin, where the fossils described here were found; the deposits fill topographic depressions cut into older strata. The deposits of this formation have been subdivided into two members (El Harfi et al., 2001):

- a lower palustrine and lacustrine member with a thickness of up to 500 m. It consists of limestone, travertine, marls, silty clay, gypsum and sapropelite;
- an upper member which consists of alluvial deposits: sandstone and especially conglomerates.

The vertebrate fossils studied in this work are from the southern Ouarzazate basin between the city of Skoura and Imassine village, near Tizi N'Tadderht.

3. Paleontological background

In the Ouarzazate basin, strata consisting largely of Paleogene deposits in the northeast of the basin yielded a rich assemblage of marine and continental vertebrates, including hundreds of species of sharks and rays, bony fishes, amphibians, turtles, crocodiles, lizards, snakes and mammals. The mammals represent one of the oldest records of the radiation of Eutheria in Africa. Gheerbrant et al. (1992, 1998) reviewed these faunas in their stratigraphic and palaeogeographic context. The last major paleontological discovery in the Ouarzazate basin was made in the Lutetian locality of Aznag (Tabuce et al., 2005) which yielded a fauna of mammals and elasmobranchs associated with planktonic foraminifera. Unlike the Paleogene, the Neogene deposits that outcrop widely throughout the Ouarzazate basin have only yielded ostracods, diatoms, algae, fish and micromammals, reported by Görler and Zucht (1986), Görler et al. (1988) and Helmdach (1988), which suggest a Langhian to Lower Serravalian age for the lower palustrine and lacustrine unit of the Neogene series.

North of the Ouarzazate basin, a set of fossil sites discovered in the Aït Kandoula Basin yield charophytes, fishes, reptiles and mammals, and range from the Middle Miocene to the Pliocene (Benammi, 1997, 2001; Benammi et al., 1995, 1996; Görler and Zucht, 1986), while the remains of large mammals are rare and fragmentary. Benammi et al. (1995) and Rémy and Benammi (2006) report the presence, in various localities that have mostly yielded micromammals, of Gomphotheriidae indet., "*Hipparion*" sp., *Parapliohyrax* sp., *Sivatherium maurusium*, Giraffidae indet., *Gazella* sp., and a Hippotragini, but this material has not been described.

In this work, we report the first large vertebrate assemblage from the Miocene, discovered in the region of Skoura,

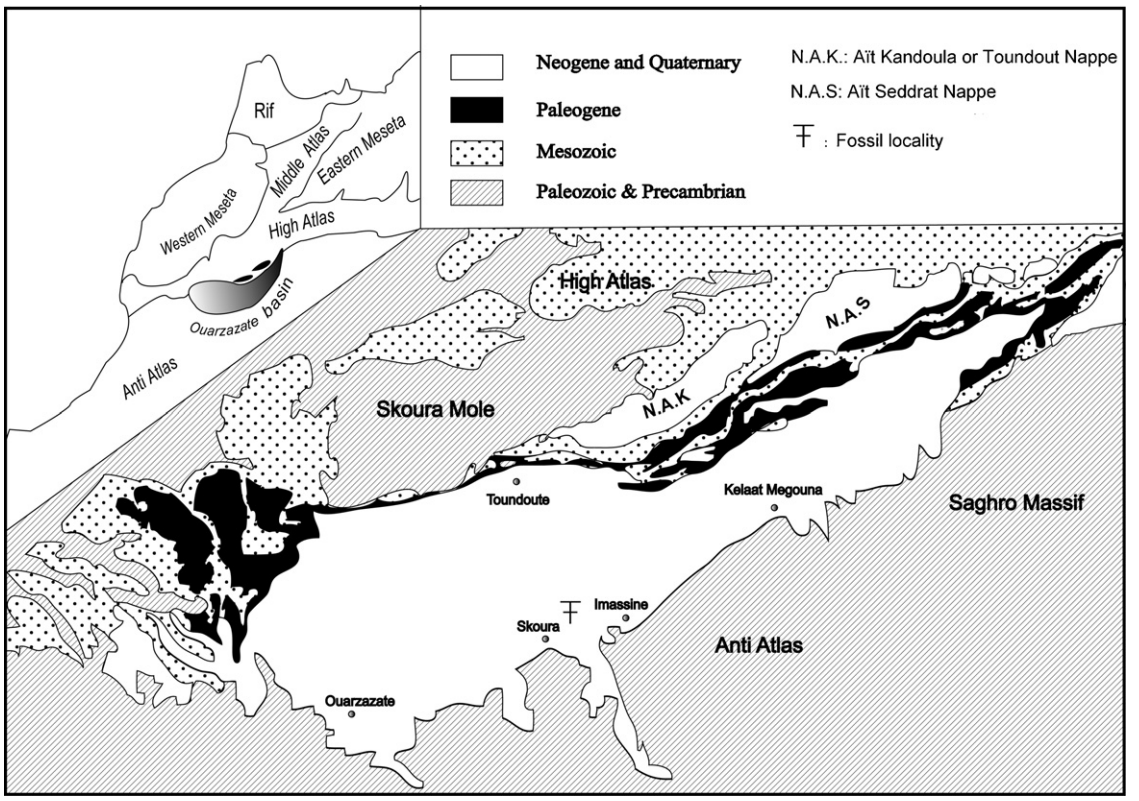

Fig. 1. Geology and structural units of the southern slopes of Central High Atlas western part (modified after El Harfi et al., 2001; Laville et al., 1977) and situation of the fossiliferous localities.
Fig. 1. Géologie et unités structurales de la partie occidentale du flanc sud du Haut Atlas central (d'après El Harfi et al., 2001 ; Laville et al., 1977 modifié) et situation des localités fossilifères.

in the southern part of the Ouarzazate basin. It provides a first insight into the composition of the various faunas, particularly that of large mammals and their evolution in the South-Atlas area, and it also contributes to the dating of sedimentary and tectonic events that affected the basin. The precise dating of continental Formations of the Ouarzazate basin is critical to interpreting the tectonic-sedimentary evolution of the area, in particular the lifting of the High Atlas.

4. Systematic palaeontology

The material was collected by amateur collectors, which naturally raises the problem of geographic and stratigraphic provenance of the fossils. Some new specimens have been collected by the authors in December 2010. These are the only ones whose origin is known with certainty (coordinates UTM zone 29, WGS84). One part of the material (about 20 specimens) is kept in a private museum in Erfoud (Morocco), while the other part (about 126 specimens) is housed at the Faculty of Sciences Ain Chock of Casablanca (FSAC). The faunal list is as follows:

Aves – cf. *Struthio* sp. shell fragments (FSAC) (739770/3450916).

Chelonia – cf. *Centrochelys* sp. A peripheral plate from the right rear edge of the bridge; at the separation of marginal scales, a groove relief is characteristic of terrestrial Testudinidae. The size of this plate is reminiscent of the genus *Centrochelys*, which is known since the Middle Miocene in northern Africa and Arabia but is now confined to the Sahel (Lapparent de Broin, 2000).

Crocodylia – *Crocodylus* cf. *niloticus* Laurenti, 1768. An almost complete skull of a young crocodile (Fig. 3I; Erfoud), only lacking the basicranium and quadrate, is indistinguishable in its morphology and cranial proportions, studied in detail by Tchernov (1986) and Pickford (1996, 2003), from the modern *C. niloticus*. Among the few noteworthy differences, we note the short length of the premaxilla relative to the width of the cranial table (index 23/15 Tchernov, 1986). The median nasal ridge ("preorbital promontorium" of Hecht, 1987; "longitudinal nasal ridge" of Storrs, 2003), listed by Storrs as a characteristic of this species among African crocodiles, is barely visible here, which may be due to the young age of the animal. It appears that the skull is part of the lineage of the Nile crocodile, and may even represent the same species. The latter appeared in Africa in the Late Miocene in the lower member of the Nawata Formation at Lothagam (Storrs, 2003), and according to Storrs (2003), the crocodile from Sahabi, *C. checchia* (Maccagno, 1948; Hecht, 1987) is also of the same species. In this case, it is possible that the older remains from Jebel Krechem in Tunisia, described under that name (Geraads, 1989), should also be referred to *C. niloticus*, pushing the

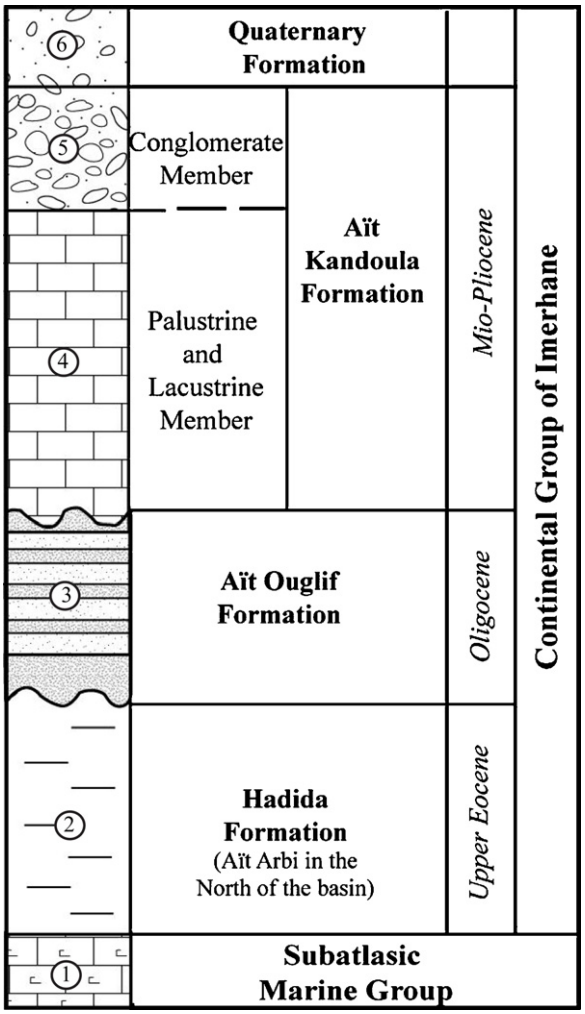

Fig. 2. Simplified lithostratigraphic section of the Imerhane continental Group in the Ouarzazate basin. 1: Mesozoic limestone and marls (marine deposits); 2: Red Beds (siltstone and claystone with gypsum at the base becoming sandstones upward); 3: Coarse sandstone Complex (couplets of sandstone and microconglomeratics facies); 4: Palustrine and lacustrine Complex (palustrine and lacustrine limestone with evaporitic playa deposits); 5: Mio-Pliocene conglomerates (fluvial and siliciclastic alluvial fan deposits); 6: Quaternary conglomerates (conglomeratic pediment and alluvial terraces deposits).

Fig. 2. Section lithostratigraphique simplifiée du Groupe continental d'Imerhane dans le bassin de Ouarzazate. 1 : calcaires et marnes mésozoïques (dépôts marins) ; 2 : couches rouges (siltites et argilites à gypse à la base devenant gréseuses au sommet) ; 3 : complexe gréseux grossier (alternance de niveaux gréseux et microconglomératiques) ; 4 : complexe palustro-lacustre (calcaires palustro-lacustres et localement dépôts évaporitiques de playa) ; 5 : conglomérats mio-pliocènes (dépôts fluviatiles et localement de cônes alluviaux) ; 6 : conglomérats quaternaires (dépôts de terrasses alluviales).

origin of the species back to the first part of the Upper Miocene.

Mammalia – Equidae – Aff. *Cremohipparion periafricanum* (Villalta and Crusafont, 1957). A fragment of mandible (Fig. 3C; FSAC) is distinguished from all other specimens of Hipparions found at Skoura by its very small size, reminiscent of the small Spanish species "*Hipparion*" *periafricanum* placed in the genus *Cremohipparion* (Zouhri and Bensalmia, 2005). The new fragment of mandible has a characteristic equine morphology and is clearly different from those of other Perissodactyla such as tapirs or small suids. It consists of the symphysis and a portion of the left anterior portion of the horizontal ramus. However, the incisor arch is destroyed. The horizontal ramus of the mandibular is broken on the left side just before the front edge of the second premolar (p2) and a little further forward on the right side. Unfortunately, although some measures (7; 12; 13 and 14 of Eisenmann et al., 1988: Fig. 4A–B) of the mandible can be estimated in this specimen, it is impossible to compare it with the Spanish dwarf forms whose jaw is unknown. It is in any case much smaller than the other known small hipparions such as *Cremohipparion matthewi* Abel, 1926; *Cremohipparion nikosi* Bernor and Tobien, 1989 or "*Hipparion*" *elegans* Gromova, 1952. In North Africa, the only small hipparions reported are "*Hipparion*" *sitifense*, now considered a *nomen dubium* (Bernor and Scott, 2003), and *C. matthewi* and *C. nikosi* from Sahabi, recently identified by Bernor et al. (2008) from postcranial material in the first case (*C. matthewi*), and a lower tooth fragment in the second. Irrespective of the taxonomic validity of "*Hipparion*" *sitifense*, material associated with this taxon (Eisenmann, 1980) indicates a much more larger species than the dwarf one of Tizi N'Tadderht. The Tizi N'Tadderht hipparion should be attributed to the smallest known hipparion sensu lato, *C. periafricanum*, considered until now endemic to Spain, where it is known from numerous Upper Turolian (MN13) localities, as is the case of Valdecebro II (Alberdi and Alcala, 1989-1990), Valdecebro 3, Las Casiones and El Arquillo (Van Dam et al., 2001).

Cf. *Hippotherium primigenium* (Von Meyer, 1829). The rest of the hipparion material from Tizi N'Tadderht is divided into two lots. The first consists largely of jugal teeth of hipparions (most of which belong to the same individual), two astragali, a fragment of Mc III and some phalanges (FSAC). These specimens belong to a large and heavily built species with a series of plesiomorphic characters including notably brachyodont teeth, a lenticular protocone, and a lack of the articular facet for the trapezoid on the proximal articular end of MC III. This form suggests affinities with *Hippotherium* Kaup, 1833, an Old World group known throughout the Upper Miocene (Vallesian and Turolian) and even Pliocene. The robustness of the postcranial bones and the degree of brachyodonty of the upper cheek teeth evoke *H. primigenium* (Von Meyer, 1829) rather than *Hippotherium africanum* Arambourg, 1959, a notably more slender-limbed and more hypsodont species.

Hippotheriini gen. and sp. indet. The other part of the material of Tizi N'Tadderht hipparions consist of three fragments of mandibles (Fig. 3B), a partial Mc III, a complete MT III, a calcaneum and a few phalanges (FSAC). They belong to a notably smaller and much more gracile species than the previous form (*H. primigenium*) with derived characters such as the presence of a well developed articular facet for the small cuneiform on the proximal articular surface of Mt III. The typically hipparionine double knots and the absence of a developed ectostylid on the lower cheek teeth exclude the assignment of this form to the African genus *Eurygnathohippus* Van Hoepen 1930, which

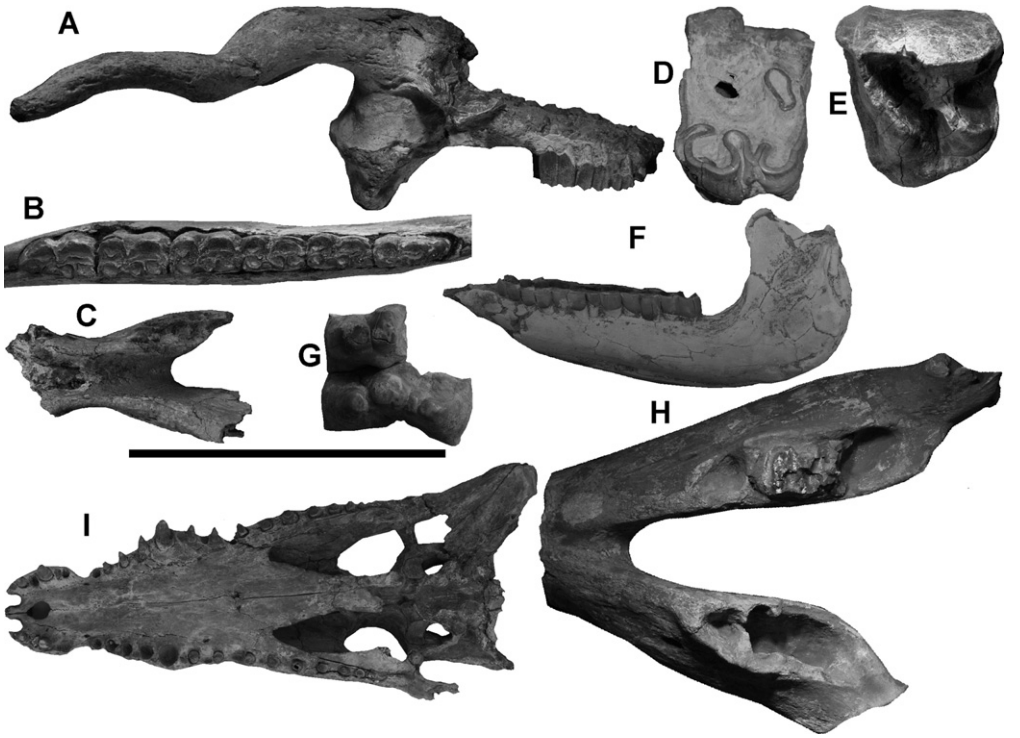

Fig. 3. Some fossils from Tizi N'Tadderht. **A**. Bovidae gen. et sp. indet., skull in right lateral view. **B**. Hippotheriini gen. and sp. indet., right lower tooth-row. **C**. Aff. *Cremohipparion periafricanum*, mandibular symphysis. **D**. Aff. *Chilotherium* sp., P4. **E**–**F**. cf. *Ceratotherium* sp. **E**. P4. **F**. Mandible in left lateral view. **G**–**H**. Cf. *Tetralophodon* sp. **G**. Molar fragment. **H**. Mandible. **I**. *Crocodylus* cf. *niloticus*, skull in ventral view. Scale = 10 cm for Figs. **B**–**E**; 20 cm for Figs. **A**, **G**, **I**; 40 cm for Figs. **F**, **H**.

Fig. 3. Quelques fossiles du Tizi N'Tadderht. **A**. Bovidae gen. et sp. indet., crâne en vue latérale droite. **B**. Hippotheriini gen. and sp. indet., rangée dentaire inférieure droite. **C**. Aff. *Cremohipparion periafricanum*, symphyse mandibulaire. **D**. Aff. *Chilotherium* sp., P4. **E**–**F**. cf. *Ceratotherium* sp. **E**. P4. **F**. Mandibule en vue latérale gauche. **G**–**H**. Cf. *Tetralophodon* sp. **G**. Fragment de molaire. **H**. Mandibule. **I**. *Crocodylus* cf. *niloticus*, crâne en vue ventrale. Échelle = 10 cm pour les Figs. **B**–**E** ; 20 cm pour les Figs. **A**, **G**, **I** ; 40 cm pour les Figs. **F**, **H**.

has a caballine double knot and always an ectostylid on the lower cheek teeth. It is difficult to determine even the supraspecific affinities of this material because we recognize at present several genera of African hipparions, mainly defined by skull characters and the association between skull and postcranial is not yet established for most of these taxa. Consequently, the Hippotheriini material of Tizi N'Tadderht is attributed to a gen. and sp. indet.

Rhinocerotidae – cf. *Ceratotherium* sp. (FSC, Erfoud). This large rhinoceros with robust legs is the most common form and is probably linked to the group Dicerotini because of the drastic reduction, if not absence, of incisors in the virtually complete mandible (Fig. 3F). This group, now exclusively African, was common in the Late Miocene in the Balkano-Iranian province, where it was represented by *Ceratotherium neumayri* (or *Diceros* for some authors). It is also documented in the Vallesian of Algeria with "*Dicerorhinus*" *primaevus* Arambourg, 1959 (Geraads, 1986), perhaps Sahabi in Libya, but its extension farther south in Africa at this time is uncertain. A well-preserved MCIII from Tizi N'Tadderht is more robust than that of the Algerian form, but lacks the strong concave side of *C. neumayri* (Giaourtsakis, 2009), so a specific determination would be too speculative.

Aff. *Chilotherium* sp. A single upper tooth (FSAC), certainly a P4, belongs to another rhinoceros species. Despite the wear, a strongly pinched protoloph almost completely isolating the protocone, and a very long antecrochet interposed between the protocone and a reduced hypocone, distinguish it clearly from that of the Dicerotini (compare Fig. 3D and E). A detailed comparison is beyond the scope of this note, but such morphology is radically different from that of Dicerotini, but also from that of the brachypotheres, another group known in the Late Miocene in Africa, and from that of the elasmotheres, another set of Neogene rhinoceroses, where the medifossette tends to close lingually. The characters of this tooth are more similar to a form that Guérin (1966) had described from the Miocene of Tunisia under the name *Diceros douariensis*, and compare even better with the Eurasian *Chilotherium*, unknown in Africa. It goes without saying, however, that such determination would be insufficiently founded, and somewhat problematic for biogeographical reasons.

Gomphotheriidae – Cf. *Tetralophodon* sp. A mandible (Fig. 3H; Erfoud) certainly had strong incisors but their exact size or orientation cannot be determined because the symphysis was largely reconstructed in plaster. No teeth remain, with the exception of a small part of the dentin of the right m3. This tooth had to have 4 or 5 thick and

transverse lophids. The little that remains, however, shows that it was certainly not a form close to the Upper Miocene *Stegotetrabelodon* from Sahabi, whose lophids were far more numerous, nor a *Choerolophodon*, whose lophids are arranged in chevrons, nor a form with lophids showing an anancoid contact. These characters are confirmed by a fragment of tooth (Fig. 3G; FSC) with one half of a relatively thin lophid without accessory conules. The most likely hypothesis is that this material belongs to a *Tetralophodon*, or to an Amebelodontidae, two taxa known in the Miocene of North Africa (Geraads, 1989; Sanders et al., 2010).

Giraffidae – Giraffid gen. et sp. indet. This species is represented only by a few limb bones (FSAC): a distorted distal end of a radius, a lunar (738283/3444137), and a cubo-navicular. It is a form of large size, comparable to "*Palaeotragus*" *germaini* from the Vallesian of Bou Hanifia in Algeria (Arambourg, 1959), and probably also present in Bled Douarah and Jebel Krechem (Geraads, 1989). All Middle Miocene Giraffidae, and particularly those from North Africa (*Palaeotragus lavocati* Heintz, 1976 from Beni Mellal) are much smaller.

Bovidae – cf. *Prostrepsiceros* sp. The base of a slightly compressed bovid horn-core (FSAC) cannot belong to a gazelle because of its subtle but significant twisting. Some other fragments correspond in size to the same form, which should probably be referred to a taxon close to *Prostrepsiceros*, a genus known mainly in the eastern Mediterranean, but also reported from Sahabi (Lehmann and Thomas, 1987) and Jebel Krechem (Geraads, 1989). It is not certain, however, that the North African forms really belong to the same genus as the ones from the Balkano-Iranian Province (Bouvrain and Bonis, 2007).

Bovidae gen. et sp. indet. A skull of a medium-sized antelope (Fig. 3A; Erfoud), complete with the exception of the anterior and dorsal parts of the face, is probably the most interesting fossil from Tizi N'Tadderht. The skull has long horns that are slender, divergent, fairly tightly spiraled with a homonymous torsion, thereby excluding any relationship with most spiral horned antelopes from the Miocene. The rear of the skull is very inclined with respect to the facial region, the tuberosities of the basioccipital are broad and flattened, and the dentition is "aegodont". This shows that it is certainly a representative of the Caprinae. This group is common in the Late Miocene Balkano-Iranian province, but the horns are never spiraled, and very rare in Africa, where no similar form has been reported.

5. Conclusions: age of fauna

The precise origin of most of the fossils identified above is unknown; their contemporaneity is naturally in question. However, there is no evidence that the fauna is heterochronous, although the extent and thickness of the upper member of the Aït Kandoula Formation make it difficult to establish the strict contemporaneity of all the elements. Still, there is no major change in depositional environments within this member, and it is unlikely that it documents a very long period of time, as such detritic deposits may accumulate quite rapidly. Paradoxically, it is a "reptile" that can hardly be distinguished from an extant form, which might provide the strongest argument in favor of a heterochrony of the assembly, but the age range of *C. niloticus* might stretch back to at least the second half of the Miocene (Turolian mammal age in Europe). This age is the most consistent with the rest of the fauna. The presence of a hipparion naturally excludes an age older than the Upper Miocene, while the large size of the giraffid, the massiveness of the main bones of the rhinoceros, and the derived features of the new bovid are consistent with faunas of this age, rather than with older faunas (Vallesian). The main argument that would suggest a post-Miocene age is the total absence of anthracotheres. Indeed, this group is present in most deposits of the upper Miocene in Central Africa (Toros-Menalla in Chad), Tunisia (Bled Douarah, Jebel Krechem) and Libya (Sahabi). However, it is absent in Bou Hanifia in Algeria and in the middle Miocene of Beni Mellal in Morocco, and we can therefore hypothesize that it was related to a water system that did not extend to the west (Lihoreau et al., 2006), and its absence in a Moroccan site would be of no chronological significance. The scarcity of "Turolian" deposits in North Africa is obviously an obstacle to the precise dating of faunas of the Aït Kandoula Formation.

Although it is represented by a small sample, the fauna of Tizi N'Tadderht is interesting in several aspects. Besides its contribution to the dating of the upper member of the Aït Kandoula Formation, it links older Miocene faunas from Africa (Beni Mellal and Vallesian faunas of Algeria and Tunisia) with more recent ones (Sahabi). The presence of an unusual antelope hints at how much remains to be learned about mammalian faunas from the late Neogene of Africa.

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