Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad

Patrick Vignaud*, Philippe Duringer†, Hassane Taïsso Mackaye‡, Andossa Likius*‡, Cécile Blondel*, Jean-Renaud Boisserie*, Louis de Bonis*, Véra Eisenmann§, Marie-Esther Etienne*, Denis Geraads||, Franck Guy*¶, Thomas Lehmann*, Fabrice Lihoreau*, Nieves Lopez-Martinez#, Cécile Mourer-Chauviré☆, Olga Otero*, Jean-Claude Rage§, Mathieu Schuster†, Laurent Viriot*, Antoine Zazzo & Michel Brunet***

** Faculté des Sciences et Centre National de Recherche Scientifique UMR 6046, Université de Poitiers, 40 Avenue du Recteur Pineau, 86022 Poitiers Cedex, France*
† Centre de Géochimie de la Surface, CNRS UMR 7517, Université Louis Pasteur, 1 rue Blessig, 67084 Strasbourg, France
‡ Université de N'Djaména, BP 1117 N'Djaména, Tchad
§ Muséum National d'Histoire Naturelle et CNRS UMR 8569, rue Cuvier, 75005 Paris, France
|| Centre National de Recherche Scientifique UPR 2147, 44 rue de l'Amiral Mouchez, 75014 Paris, France
¶ Peabody Museum, Harvard University, 11 Divinity Avenue, Cambridge, Massachusetts, 02138, USA
 # Dept. Paleontología, Universidad Complutense, 28040 Madrid, Spain
☆ Centre des Sciences de la Terre, CNRS UMR 5125, Université Claude Bernard, 27-43 Bd du 11 novembre 1918, 69622 Villeurbanne, France
*** Centre National de Recherche Scientifique UMR 162 et Institut National de la Recherche Agronomique, Université Pierre et Marie Curie, 4 place Jussieu, 75252 Paris Cedex 05, France*

All six known specimens of the early hominid *Sahelanthropus tchadensis* come from Toros-Menalla site 266 (TM 266), a single locality in the Djurab Desert, northern Chad, central Africa. Here we present a preliminary analysis of the palaeontological and palaeoecological context of these finds. The rich fauna from TM 266 includes a significant aquatic component such as fish, crocodiles and amphibious mammals, alongside animals associated with gallery forest and savannah, such as primates, rodents, elephants, equids and bovids. The fauna suggests a biochronological age between 6 and 7 million years. Taken together with the sedimentological evidence, the fauna suggests that *S. tchadensis* lived close to a lake, but not far from a sandy desert, perhaps the oldest record of desert conditions in the Neogene of northern central Africa.

Since 1994, the Mission Paléoanthropologique Franco-Tchadienne (MPFT), a scientific collaboration between Poitiers University, Ndjaména University and the Centre National d'Appui à la Recherche (CNAR), Ndjaména, has conducted several field expeditions in the Djurab Desert of northern Chad (Fig. 1). Numerous Miocene and Pliocene vertebrate sites have been discovered, corresponding to four fossiliferous areas, all dated biochronologically—that is, by the evolutive degree of their faunas. These areas are Koro Toro, estimated at around 3.0–3.5 million years (Myr), which has already yielded hominid remains[1,2]; Kollé, between 4 and 5 Myr (ref. 3); and Kossom Bougoudi, dated close to the Mio-Pliocene boundary around 5.3 Myr (ref. 4). The fourth fossiliferous area, named Toros-Menalla, is the oldest: it was discovered in the western Djurab Desert by the MPFT in 1997. More than 300 vertebrate localities are already known from this area. One of them, TM 266, has yielded a vertebrate fauna (42 taxa) that includes more than 700 identifiable mammal fossils (24 taxa) and the oldest known hominid remains[5].

The Toros-Menalla fossiliferous area is located in the intracratonic Chad Basin (Fig. 1). This basin comprises a southern sub-basin that includes the present Lake Chad under semi-arid to wet conditions, and a northern sub-basin that forms the central Chad lowland, now a desert and subject to significant aeolian deflation. The Holocene 'Mega Lake Chad'[6] constitutes the last main lacustrine event in this region before aeolian erosion and the onset of the current desert conditions. Sediments in the Chad Basin are mainly lacustrine, fluviatile and aeolian. Fluviatile deposits are mainly due to episodic flash floods. Until now, no perennial fluvial systems have been recognized in Miocene deposits of the northern sub-basin.

Sedimentology

The Toros-Menalla outcrops consist of large flat to weakly undulating surfaces, sometimes dissected in small outliers. Stratigraphic sections are rarely thicker than a few metres. Outcrops are situated in the centre of the northern sub-basin and consist mainly of thick monotonous terrigenous series dominated by sands and weakly indurated sandstones interbedded with argillaceous pelites and diatomites (Fig. 2).

The section and the depositional facies described here (Fig. 2) correspond to the TM 266 hominid locality (1.5 km^2, hominids quarry about 5,000 m^2). Numerous sections (2–5 m thick) were examined and widely correlated. Having only small outliers, most of the sections were completed by excavations.

The lower part of the section (at least 4 m thick) is composed of fine to very fine white sands, poorly cemented, and is mainly constituted by numerous quartz grains, without matrix. The grains are well sorted, well rounded, matt and frosted, and are strong evidence for aeolian modelling. The foreset laminations (avalanche laminations in front of the aeolian dune) represent a typically aeolian deposit. These sands show cross-beddings that progressively decrease in size from the bottom (1–2 m) to the top (20 cm). This facies exhibits typical alternations of grain-fall and grain-flow laminations, characteristic of aeolian dune deposits[7,8]. Our interpretation is confirmed by frequent wind ripples at the foot of the fossil dunes, whose crests are perpendicular to the direction of dune progradation. These fossil dunes are, to our knowledge, the oldest evidence for desert conditions in the southern Sahara area. The measured currents of the larger-scale cross-bedding of the fossil dunes show a unimodal distribution that indicates a major wind direction towards the west-south-west (Fig. 2). This facies contains numerous rhizoliths (rocks formed from plant roots), their number increasing gradually from the bottom to the top. In contrast to the others, this unit contains no vertebrate fauna. The erosional surface at its top marks the end of the true desertic episode.

The middle part of the section (about 2 m thick) is informally named the anthracotheriid unit (AU). This unit yielded the hominid cranium and all the terrestrial vertebrate remains (Table 1). The hominid was embedded in a poorly cemented sandstone in the lowest metre of the unit (Fig. 2). The deposit is a moderately to well-cemented sandstone, generally well sorted but with a variable quartz grain maturity. The sandstone is characterized by a mixing of both inherited aeolian sand showing matt and frosted quartz grains, and other grains resulting from the lacustrine reworking. In contrast to the lower part of the section, these sandstones are often matrix supported (mainly pelites and diatomites). There are many millimetre- to centimetre-scale lacustrine joints that contain clay. In contrast to the lower part of the section, the cross-bedding sets are always small (generally 5–10 cm, exceptionally 20 cm). This root-rich unit yielded almost all the vertebrate remains, common fossilized dung beetle brood balls and rare termitaries[9,10]. In contrast to the lower aeolian facies, the occurrence of both current and wave ripples, as well as small sand bars of coarse pelitic sandstone, testify to water movements. However, in this unit the strong dispersion of the palaeocurrents in all directions (360°) (Fig. 2) is incompatible with a normal fluvial dynamic, in which currents never show such unusual dispersion (even in strongly meandering systems). This water circulation between the dunes represents the first manifestation of a northward lake transgression, which implicates episodic flooding and draining in a desert environment. The AU corresponds to a shallow perilacustrine environment, subject to frequent inundation due to recurrent lateral variations of the shoreline. For the present-day Lake Chad, such excursions may reach several tens of kilometres over one or two decades[11]. In this vegetated perilacustrine belt, numerous environments coexist, from aquatic habitats in the lake and along the shore, to very dry situations on the edge of the desert. The wide variation in palaeocurrent direction suggests the interdigitation and coexistence of lacustrine, perilacustrine and desert environments.

The upper part of the section (about 0.5 m thick) is weakly developed in the TM 266 site. It meets the middle part of the section at an erosional surface. It is a well-stratified green pelite and is interpreted as a true lacustrine environment. This upper unit yielded only aquatic vertebrates (fish and crocodilians).

Vertebrate fauna

The fauna recovered at TM 266 (Table 1) does not show evidence of fluviatile transport, consistent with the sedimentology.

There are more than ten taxa of freshwater fish. All identified taxa are known to have been present in the Nilo-Sudanese at least since the Upper Miocene; all have living representatives in Lake Chad except *Sindacharax*, which is a taxon from the Miocene and Pliocene of north equatorial Africa[12]. Turtles, lizards, snakes and crocodiles are represented by abundant skeletal material, but no bird remains have been recovered.

The carnivore fauna is particularly diverse. As in most Late

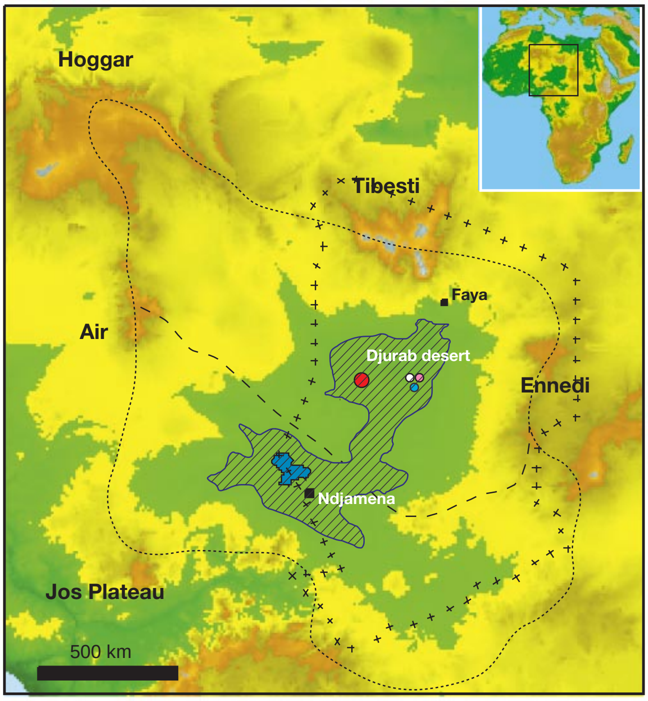

Figure 1 Map of the Chad basin showing the location of the Toros-Menalla area. The crossed line represents the Chad border. The boundaries of the ancient Lake Chad basin are shown as a dotted line (with northern and southern sub-basins divided by a dashed line). The inferred maximum extension of the Holocene 'Lake Mega Chad' is hatched in black; the small blue area within it corresponds to present-day Lake Chad. Red circle, the Toros-Menalla hominid site (TM 266); white circle, the Kossom-Bougoudi area; pink circle, Kollé area; blue circle, Koro-Toro area. Colours represent altitude: green, 280–430 m; yellow to grey, 430–850 m; brown, 850–2,000 m; grey-blue patches in Tibesti area, about 2,000–3,400 m.

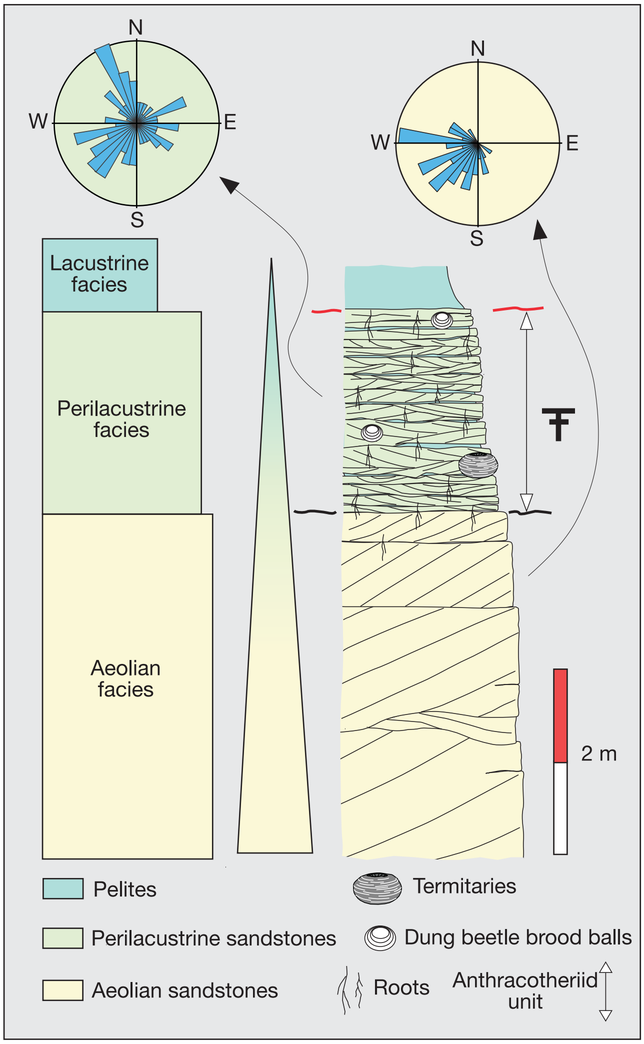

Figure 2 Idealized section and palaeoenvironmental vertical evolution in the TM 266 hominid site. Note the unimodal distribution of the direction of the currents measured in the aeolian facies (lower part of the section) in contrast to the variety of directions of the currents in the perilacustrine facies (middle part of section, anthracotheriid unit). The bottom of the crossed T indicates the precise location of the hominid remains.

Table 1 Flora and fauna of the TM 266 hominid locality

- FLORA
- LEGUMINOSAE
  - (?) Papilionoideae indet.

- ARTHROPODA
- COLEOPTERA
  - Scarabaeidae indet. (nests)
- ISOPTERA
  - Hodotermitidae indet. (nests)

- VERTEBRATA
- TELEOSTEI
- Mormyriformes
  - Gymnarchidae
    - *Gymnarchus* sp.
- Cypriniformes
  - Cyprinidae
    - *Labeo* sp.
- Characiformes
  - Characidae
    - *Hydrocynus* sp.
    - *Sindacharax* sp.
    - Alestini indet.
- Siluriformes
  - Bagridae
    - *Bagrus* group
  - Siluriformes indet.
- Perciformes
  - Perciformes indet.
- Tetraodontiformes
  - Tetraodontidae
    - *Tetraodon* sp.
- Polypteriformes
  - Polypteridae
    - *Polypterus* sp.

- REPTILIA
- Testudines
  - Trionychidae
    - Trionychidae indet.
  - Testudinidae
    - Testudinidae indet.
- Serpentes
  - Boidae
    - *Python* cf. *P. sebae*
  - Colubridae
    - Colubridae indet.
- Lacertilia
  - Varanidae
    - *Varanus* sp.
- Crocodylia
  - Crocodylidae
    - *Crocodylus niloticus*
    - *Euthecodon* cf. *E. nitriae*
  - Gavialidae
    - Gavialidae gen. et sp. nov.

- MAMMALIA
- Carnivora
  - Hyaenidae
    - *Hyaenictitherium* cf. *H. hyaenoides*
    - *Ictitherium* sp. (size of *I. taurinum*)
    - Hyaenidae indet. (size of *Protictitherium*)
  - Felidae
    - *Machairodus* cf. *M. giganteus*
  - Mustelidae
    - Lutrinae indet.
- Primates
  - Cercopithecidae
    - Colobinae indet.
  - Hominidae
    - Hominidae gen. et sp. nov.
- Rodentia
  - Sciuridae
    - *Xerus* sp.
  - Muridae
    - Murinae indet.
  - Hystricidae
    - *Hystrix* sp.
- Tubulidentata
  - Orycteropodidae
    - *Orycteropus* cf. *O. gaudryi*
- Perissodactyla
  - Equidae
    - *Hipparion* cf. *H. abudhabiense*
- Proboscidea
  - Gomphotheriidae
    - *Anancus kenyensis*
  - Elephantidae
    - *Loxodonta* sp. aff. *L.* sp.indet. "Lukeino stage"
- Artiodactyla
  - Suidae
    - *Nyanzachoerus syrticus*
  - Anthracotheriidae
    - *Libycosaurus petrocchii*
  - Hippopotamidae
    - *Hexaprotodon* sp. nov.
  - Giraffidae
    - *Sivatherium* cf. *S. hendeyi*
    - Giraffidae indet.
  - Bovidae
    - Antilopinae
      - Antilopini indet.
    - Caprinae
      - Ovibovini indet. aff. *Palaeoryx*
  - Bovinae
    - Bovini indet.
  - Hippotraginae
    - Reduncini
      - *Kobus* sp.
    - Hippotragini
      - cf. Hippotragini gen. et sp. nov.

Miocene localities, the hyaenids are the most numerous in both species and individuals. Three species can be identified: *Hyaenictitherium* cf. *H. hyaenoides*; *Ictitherium* sp., the size of *I. taurinum* but with different tooth morphology; and a third (Hyaenidae indet.) is small, like *Protictitherium*. The felid *Machairodus* cf. *M. giganteus* is represented only by very large mandibles. *Machairodus* is rare in Africa, and until now most of the referred material has been attributed to *Dinofelis*. Mustelids are represented only by a small species of lutrine (otter).

Except for the hominid remains[5], primates are represented by a single damaged maxilla referred to an indeterminate colobine monkey. Rodent remains are mainly attributable to Murinae, but some Sciuridae (*Xerus* sp.) and Hystricidae (*Hystrix* sp.) are also present. Among aardvarks, cranial and postcranial remains can be referred to *Orycteropus* cf. *O. gaudryi*, a species known in the Late Miocene of the eastern Mediterranean area[13]. A medium-sized equid shows strong affinities with *Hipparion abudhabiense* from the Upper Miocene of the United Arab Emirates[14]. Fossil remains of proboscideans are abundant. Numerous teeth of both the gomphothere *Anancus kenyensis* and the elephantid *Loxodonta* sp. aff. *L.* sp. indet. 'Lukeino stage'[15] have been found.

Suids are represented by *Nyanzachoerus syrticus*, smaller than *N. kanamensis* but larger than *N. devauxi*. The cheek teeth are very low crowned with robust premolars, including a double-rooted upper premolar P^1. The third molars show primitive features: the talon of upper M^3 comprises only one lingually located main cusp but lacks developed accessory cusps; the lower M_3 talonid is also simple. Morphology and size are congruent with *Nyanzachoerus syrticus* from Lothagam (Nawata formation, lower member)[16].

The AU receives its name from the abundance of anthracotheriid fossils (Fig. 2). These remains are referred to the north African *Libycosaurus petrocchii*. Together with the Anthracotheriidae, TM 266 yielded a new species of large hippopotamid, equivalent in size to *Hexaprotodon harvardi* from the Lothagam Nawata formation[17]. Nevertheless, mandibular morphology is dominated by a particularly high and massive symphysis, which clearly differs from the *H. harvardi* mandible. This primitive species is absent from the Miocene–Pliocene boundary and Early Pliocene sites in Chad, where a smaller and more-derived species is present.

Two giraffid taxa are represented, a large and a small form. The former, *Sivatherium* cf. *S. hendeyi*, is documented by mandibles and postcranial material. The latter is represented by postcranial bones, tentatively assigned to Giraffidae indet.

The hominid locality has yielded at least five bovid species, three of them being abundant. The smallest is a kob with short horns, similar to *Kobus subdolus* and *K. darti* from Langebaanweg (South Africa)[18], Sahabi (Libya)[19], Manonga (Tanzania)[20] and Mpesida (Kenya)[21], but smaller than in the first two sites. The teeth are more fully reduncine than in Langebaanweg[18] but teeth from this site are perhaps not illustrative of the teeth of primitive reduncines. The other two common taxa are of uncertain tribal affinities. One is attributed to cf. Hippotragini gen. et sp. nov., with a rather primitive skull morphology and long curved horns with a large basal sinus. It is probably an early hippotragine. The teeth are not strongly derived, but would confirm this identification. This species might be the same as ?*Hippotragus* sp. from Sahabi. The last of the three common taxa is a little larger, with massive, almost parallel, slightly curved and not very long horn cores, no sinus in the pedicle and large supraorbital pits. There are some similarities with the ovibovine *Palaeoryx* from the eastern Mediterranean Turolian, but also some differences, which make a close relationship unlikely. For the time being, it is referred to aff. *Palaeoryx* sp. The two less-abundant species are an antilopine and a bovine with primitive teeth. The bovid fauna from the Lothagam Nawata formation (lower member)[22] looks more modern than that of TM 266. It is dominated by the modern genus *Aepyceros* and by Boselaphini, which are absent from TM 266 but are known in other African sites close in age to the Miocene–Pliocene boundary, whereas two of the dominant TM 266 bovids (cf. Hippotragini and Ovibovini indet. aff. *Palaeoryx* sp.) are not present at Lothagam.

Biochronology

In the AU of TM 266, *Nyanzachoerus syrticus* is associated with an anthracotheriid (*Libycosaurus*). In younger sites from the Djurab area that have yielded *Nyanzachoerus kanamensis* (such as Kossom Bougoudi)[4], anthracotheriids are always absent. The evolutionary level of the upper and lower third molars of *Nyanzachoerus syrticus* from the hominid locality is very similar to that of related remains from the Lothagam Nawata formation[16]. The age of the Nawata formation fauna is estimated at about 5.2–7.4 Myr (ref. 23). The biochronological age estimate for the hominid locality is also supported by the evolutionary levels of several other mammalian groups (Anthracotheriidae, Proboscidea, Equidae and Bovidae). The *Libycosaurus* anthracotheriids are similar to those from Sahabi[24]; the fauna from this site is consistent with an Upper Miocene age[25]. Anthracotheriids are unknown from this time in East Africa and the remains from Libya and Chad may represent their last known occurrences in Africa.

The co-occurrence of *Anancus kenyensis* with *Loxodonta* sp. indet.

'Lukeino stage' is also seen in the Lukeino Formation, Kenya (∼6 Myr)[26,27]. However, the TM 266 proboscideans show more primitive characters than those from Lukeino[15,28] (thicker enamel and lower laminar frequency for *Loxodonta* sp. aff. *L.* sp indet. 'Lukeino stage'; a simpler crown pattern with less numerous tubercles and thicker enamel for *A. kenyensis*). These features support an older biochronological age for the TM 266 hominid site. This biochronological estimate is also supported by the presence of the equid *Hipparion* cf. *H. abudhabiense*, a species described from the Lower–Middle Turolian of Abu Dhabi[14]. Among carnivores, the co-occurrence of *Machairodus* cf. *M. giganteus*, small *Hyaenictitherium* and *Ictitherium* sp. is congruent with a Late Miocene age, equivalent to the European faunas of the Middle–Upper Turolian. Moreover, the five associated taxa of primitive bovids are also compatible with an Upper Miocene age. Among them, the two larger taxa do not fit easily into modern African bovid tribes, they suggest an earlier age than the Miocene–Pliocene boundary.

This evidence suggests that TM 266 is older than the Lukeino Formation[26,27], and may be equivalent in age with the base of the fossiliferous levels of the Nawata formation at Lothagam[23]. It is hoped that continuing studies on the fauna will clarify the precise chronological position of TM 266, but present evidence suggests that the faunal remains, including the hominid remains, were deposited between 6 and 7 Myr ago.

Environmental reconstruction

The diversity of aquatic and amphibious forms clearly demonstrates the presence of aquatic environments. Among fish, *Hydrocynus* (tiger fish) is a strict piscivore, hunting by sight in deep and well-oxygenated waters; many of the specimens are longer than 1 m, indicating extensive aquatic habitats. The frequency of piscivorous crocodilians, including *Euthecodon* and a new species of gavial, also clearly indicates large and permanent water bodies. Swampy, well-vegetated areas are suggested by the presence of the fish *Polypterus*, which can tolerate very poorly oxygenated waters. Likewise, *Gymnarchus* lives in swampy and turbid waters where its electrical sensorial system is advantageous. Moreover, there is a great abundance of taxa related to amphibious and bank habitats, particularly the well-preserved anthracotheriids and hippopotamids (including some complete skeletons), otters, trionychid turtles and the snake *Python* cf. *P. sebae*. The liana-like character of the papilionoid plants from TM 266 is compatible with a gallery forest bordering a lake.

The bovids represent about 55% of mammal remains from the TM 266 locality and amphibious mammals represent about 28%. The relatively high-crowned teeth of all the bovids and the lack of tragelaphines and boselaphines are strong evidence of open grassland. Thus, the faunal assemblage from the hominid site is compatible with a diversity of habitats including grassland (bovids), wooded savannah (proboscideans and giraffids), fresh water (fish, turtles, snakes, crocodilians, anthracotheriids, hippos and otters) and probably some gallery forest (primates).

The oldest known East African hominids (*Ororrin*, *Ardipithecus*) are contemporary with faunas associated with wooded environments[26,29,30]. Younger australopithecines lived in a wider range of habitats[31]. In contrast, the TM 266 vertebrate fauna contemporary of the Toros-Menalla hominid suggests a mosaic of environments from gallery forest at the edge of a lake area to a dominance of large savannah and grassland. Determining the precise habitat of the TM 266 hominid locality among the mosaic of environments available to it constitutes a research challenge to be met by further laboratory and field studies currently in progress. □

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Competing interests statement

The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to P.V. (e-mail: patrick.vignaud@univ-poitiers.fr).