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ORIGINAL PAPER

The mammal assemblage of the hominid site TM266 (Late Miocene, Chad Basin): ecological structure and paleoenvironmental implications

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Abstract Characterizing the paleoenvironmental context of the first hominids is a key issue for understanding their behavioral and morphological evolution. The present study aims at reconstructing the paleoenvironment of the TM266 vertebrate assemblage (Toros-Menalla, Northern Chad) that yielded the earliest known hominid *Sahelanthropus tchadensis* (7 Ma). For the first time, a quantitative analysis is carried out on the fossil mammal assemblage associated with that hominid. Two complementary approaches were applied: (1) the analysis of the relative abundances of taxa and their habitat preferences; and (2) the study of the distribution of taxa within three meaningful ecovariables: locomotion, feeding preferences, and body mass. The resulting taxonomic and paleoecological structures are used to reconstruct the diversity and the relative extent of the habitats in that part of northern Chad seven million years ago. The paleoenvironment was composed of open areas with dry and humid grasslands, prevailing over wooded habitats. Water was also widely available as freshwater bodies and certainly swamps. It appears that the high habitat diversity of the landscape is a common feature among paleoenvironments associated with early hominids.

Keywords Mammal paleocommunity · Paleoenvironments · Early hominids · Chad · Late Miocene

Introduction

In order to understand the evolution of early hominids, it is crucial to study in detail the paleoenvironmental context in which the first representatives of our lineage lived. This can be achieved using various approaches based on sedimentological features, climate models, stable isotopes, dental microwear, and fossil assemblage composition. Recent discoveries of Late Miocene hominids in Africa stress the importance of that research area, especially for the earliest known hominid *Sahelanthropus tchadensis* (Brunet et al. 2002, 2005). The site TM266 (Toros-Menalla, northern Chad) is the type locality of that species. It has yielded a rich vertebrate assemblage that is significant for multiple reasons. First, it belongs to the Toros-Menalla area, the only Late Miocene faunal record from Central Africa. Thus, it provides the opportunity to make comparisons with other contemporaneous African hominid-bearing assemblages. Second, it documents an important period of global climatic change (Cerling et al. 1997), associated with the opening of landscapes and the setting up of modern East African ecosystems through faunal migrations from Eurasia (Leakey et al. 1996).

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Vignaud et al. (2002) provided a description of the TM266 faunal assemblage and a first paleoenvironmental reconstruction, together with a biochronological estimation ca. 7 Ma. This age has been recently confirmed by a cosmogenic nuclide dating (Lebatard et al. 2008). Here, we present an updated faunal list for the TM266 mammal assemblage. We use a quantitative assessment of its taxonomic and paleoecological structure to investigate its paleoenvironmental significance. The purpose is to assess the diversity of the habitats recorded by the mammal assemblage of TM266.

Materials and methods

More than a thousand vertebrate remains have been collected and identified at TM266, among which 90% are assigned to mammals. Table 1 gives the updated faunal list of the TM266 mammal assemblage, represented by at least 31 species. The current dataset results from several fieldwork seasons during which mammals were exhaustively sampled. They were extracted from a sandstone level referred to as the Anthracotheriid Unit (Vignaud et al. 2002). This biostratigraphic unit represents a duration that is shorter than 0.36 My (Lebatard et al. 2008), a degree of accuracy of the same order of magnitude than those generally encountered in Miocene sites from East Africa. The screen-washing of the entire surface of the site was not possible and remained irregular. Together with the scattering of the smallest pieces by current aeolian deflation at the local scale, we can suspect the under-representation of micromammals (body mass <1 kg), a bias already observed in some other Mio–Pliocene vertebrate assemblages (Soligo and Andrews 2005).

Do TM266 fossils represent a homogeneous mammal paleocommunity or a condensed mixture of different paleocommunities? This crucial question is at the base of any paleoecological reconstruction and it should be considered on both temporal and spatial axes (e.g., Behrensmeyer and Hook 1992; Etter 1999). Waiting for the detailed taphonomical characterization of the TM266 material (work in progress), several observations enable us to address this issue. There is no sorting pattern in the sediment or among the specimens. Most fossil remains are disarticulated but they are generally well preserved, and a vast majority of them (>90%) show no evidence for aquatic polishing. These observations suggest a short and very limited fluvial transport, and they give strong indications for the autochtonous origin of the assemblage.

The question of time-averaging can be addressed by analyzing the way bones accumulated (e.g., Badgley 1986; Behrensmeyer 1991; Cutler et al. 1999; Palmqvist and Arribas 2001; Robb 2002), but current data for TM266 show that the accumulation process may have been either catastrophic, attritional, or both. The presence of various weathering stages seems to indicate an attritional process (Behrensmeyer 1978, 1981), whereas the presence of many types of bones and tooth-wear patterns, together with some articulated partial skeletons, favors a catastrophic event (e.g., Voorhies 1969). Nevertheless, other indices support the absence of aeolian-reworked material: most fossils were still embedded into the Anthracotheriid Unit sediments when collected and field observations show that a fossil cannot resist the aeolian deflation more than 3 years in the Djourab Desert; no fossil mammal was found above or below that fossiliferous level; and the TM266 assemblage is biochronologically homogeneous (Vignaud et al. 2002). It substantiates a limited time averaging for the Anthracotheriid Unit, that should not exceed 0.36 My. Such a small-scale time averaging is not detectable with the evolutionary features shown by the TM266 assemblage.

As a whole, the limited space and time averaging allows us to consider the TM266 mammal assemblage as a homogeneous entity carrying an ecological signal. It certainly represents several successive biological communities (as they would be defined by ecologists). As such, it is what some authors referred to as a metacommunity (Gilpin and Hanski 1991; Wilson 1992; Leibold et al. 2004; Maridet et al. 2007; Escarguel et al. 2008), a term that enables to consider the dynamics of natural systems in space and time (Parker 2002).

We explored this dataset using a taxonomic and a "taxon-free" approach. In the first one, the relative abundance of taxa was computed at a level of taxonomic inclusiveness that maximizes both the number of taxa and the number of specimens. Micromammals were excluded for their supposed under-representation. Usual abundance measures, such as the number of identified specimens (NISP) and the minimum number of individuals (MNI), were discarded. The use of the NISP is recommended for assemblages that accumulated under fluvial regime, causing the scattering of remains (Badgley 1986). On the other hand, the MNI is better suited to assemblages that did not suffer from any kind of transport, keeping the skeletal elements articulated or close to each other (Badgley 1986). The TM266 assemblage neither shows a large amount of articulated remains nor any evidence of important transport. These measures are thus certainly not appropriate for the TM266 data. Instead, abundances were estimated from the number of mandibles. They were counted regardless of the age of the individuals. The observation of the material suggests that the probability of counting a fragment of mandible belonging to the same individual is low in this assemblage. In order to increase the sample size, right and left branches, as well as fragmentary or entire mandibles were counted indifferently. The proportion of each taxon

Table 1 The updated faunal list of mammals from TM266, associated with their relative abundances and their assignations to ecological categories for the three ecovariables (body mass, feeding preferences, locomotion)

	Relative abundance	Body mass	Diet	Locomotion
Carnivora				
Hyaenidae				
Hyaenictitherium minimum	+	D	Ca	LT
Hyaenidae gen. et sp. indet. A	− −	EF	Ca	LT
Hyaenidae gen. et sp. indet. B	−	EF	Ca	LT
Felidae				
Machairodus kabir	− −	GH	Ca	LT
Machairodontinae gen. et sp. indet. cf. *Dinofelis* sp.	− −	EF	Ca	LT
Felidae gen. et sp. indet. (size *Profelis aurata*)	− −	D	Ca	ST
Mustelidae				
Lutrinae indet. aff. *Torolutra* sp.	− −	D	Ca	Aq
Lutrinae indet. aff. *Sivaonyx* sp. or *Djourabus* sp.	− −	EF	Ca	Aq
Herpestidae				
Galerella sanguinea		AB	I	ST
Primates				
Cercopithecidae				
Colobinae gen. indet. nov. sp. A	− −	C	Hb	ST
Hominidae	−			
Sahelanthropus tchadensis		EF	O/F?	ST?
Rodentia				
Sciuridae				
Xerus sp.		AB	O	ST
Muridae				
Murinae indet.		AB	–	–
Gerbillinae indet.		AB	O	ST
Hystricidae				
Hystrix sp.	− −	D	Hb/F	ST
Lagomorpha	−			
Leporidae				
Serengetilagus tchadensis		C	Hg	ST
Tubulidentata				
Orycteropodidae	− −			
Orycteropus abundulafus		D	I	ST
Perissodactyla				
Equidae	−			
Hipparion cf. *H. abudhabiense*		EF	Hg	LT
Proboscidea				
Gomphotheriidae				
Anancus kenyensis	−	GH	Hg	LT
Elephantidae				
Loxodonta sp. aff. *L. cookei*	− −	GH	Hg	LT
Artiodactyla				
Suidae				
Nyanzachoerus syrticus	− −	GH	O	LT
Anthracotheriidae	++			
Libycosaurus petrocchii		GH	Hb/Hg	Aq
Hippopotamidae	−			
Hexaprotodon garyam		GH	Hg	Aq
Giraffidae				
Sivatherium aff. *S. hendeyi*	− −	GH	Hb/Hg	LT
Giraffa sp.	− −	GH	Hb	LT
Bovidae				
Antilopini	++			
Gazella sp.		D	Hb/Hg	LT
Reduncini	+	EF	Hg	LT

Table 1 (continued)

	Relative abundance	Body mass	Diet	Locomotion
Hippotragini	++			
Saheloryx solidus gen. et sp. nov.		EF	Hg	LT
Tchadotragus sudrei gen. et sp. nov.		EF	Hg	LT
Bovini indet.	− −	GH	Hg?	LT
Aepycerotini	− −			
Aepyceros sp.		EF	Hb	LT

Sources used: Hendey (1981), Kingdon (1997), Eisenmann and Whybrow (1999), Gagnon and Chew (2000), Brunet et al. (2002), Harris and Leakey (2003), Harris et al. (2003), Leakey et al. (2003), Lihoreau (2003), Franz-Odendaal and Solounias (2004), Merceron et al. (2004), Boisserie et al. (2005), de Bonis et al. (2005), Peigné et al. (2005a, b), Lehmann et al. (2006), Jacques (2007), Lopez-Martinez et al. (2007), Sanders (2007), Geraads et al. (2008), Peigné et al. (2008), Blondel (pers. com.), Guy (pers. com.), and Viriot (pers. com.)

The abundances of taxa have been computed at the genus level from the count of mandibles. They are expressed as: ++: very common (>16 individuals); +: common (nine to 16 individuals); −: rare (two to eight individuals); −: very rare (one individual)

A arboreal, *AB* <1 kg, *Aer* aerial, *Aq* aquatic, *C* 1–10 kg, *Ca* carnivorous, *D* 10–45 kg, *EF* 45–180 kg, *F* frugivorous, *GH* >180 kg, *Hb* browser, *Hg* grazer, *I* insectivorous, *LT*: large terrestrial, *O* omnivorous, *S* scansorial, *ST* small terrestrial

was qualified as follows (Table 1): very common (>10.1%), common (10.1% to 5.2%), rare (5.1% to 1%), and very rare (<1%). The relative abundance of taxa carrying paleoenvironmental information makes it possible to infer the paleohabitats present and their relative extent.

The TM266 fossil mammal assemblage was ecologically characterized using a so-called taxon-free approach. This widely applied method (Andrews et al. 1979; Gagnon 1997; Reed 1997; Fernandez-Jalvo et al. 1998; Kovarovic et al. 2002; Rodriguez 2004; Fara et al. 2005) consists in assessing paleoenvironments using the ecological structure of the paleocommunity, defined as the range of ecological niches occupied by the species of the corresponding assemblage (Andrews 1996). The niche of a species combines several ecological components, or ecovariables, such as feeding preferences, locomotion, and body mass. Each ecovariable was divided into categories, expressed as a percentage of the number of taxa. The categories, taken from Andrews et al. (1979), are broad in order to include a sufficient number of taxa and they should suffice for detecting the ecological structure of the assemblage (Reed 1997). They were chosen also because they include body mass, a variable that carries a paleoenvironmental signal (e.g., Peters 1983; Reynolds 2007). The assignation of these categories to taxa was based on anatomy, geochemistry, and tooth-wear patterns. The distribution of each ecovariable was then compared to those obtained by Andrews et al. (1979) on modern African environments.

Results

At least six species of bovids are identified (Table 1). This group dominates the assemblage by gathering 58% of the individuals (Fig. 1). Only one species of anthracothere is present but still includes 14% of the individuals (Table 1 and Fig. 1). Carnivores are well diversified (nine species) and account for 11% of the individuals (Table 1 and Fig. 1). Remaining families and orders are less well represented, each one not exceeding 4% of the individuals (Fig. 1).

Table 1 shows that three taxa dominate the TM266 assemblage: Hippotragini (38% of the individuals) and Anthracotheriidae and Antilopini (about 13% each). *Hyaenictitherium* and Reduncini are both common (relative abundance close to 6%). Among rare taxa (1–5%), there

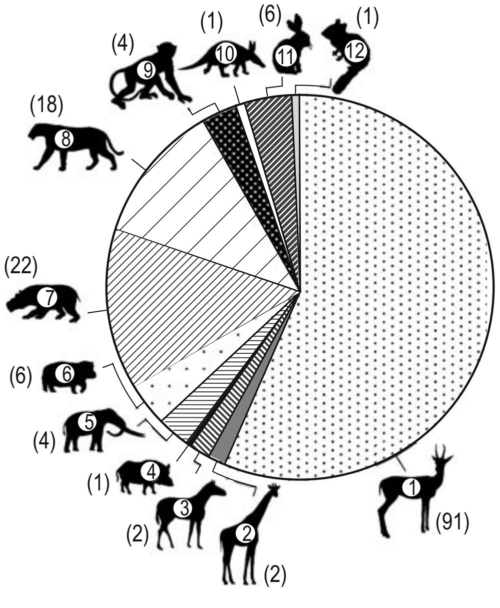
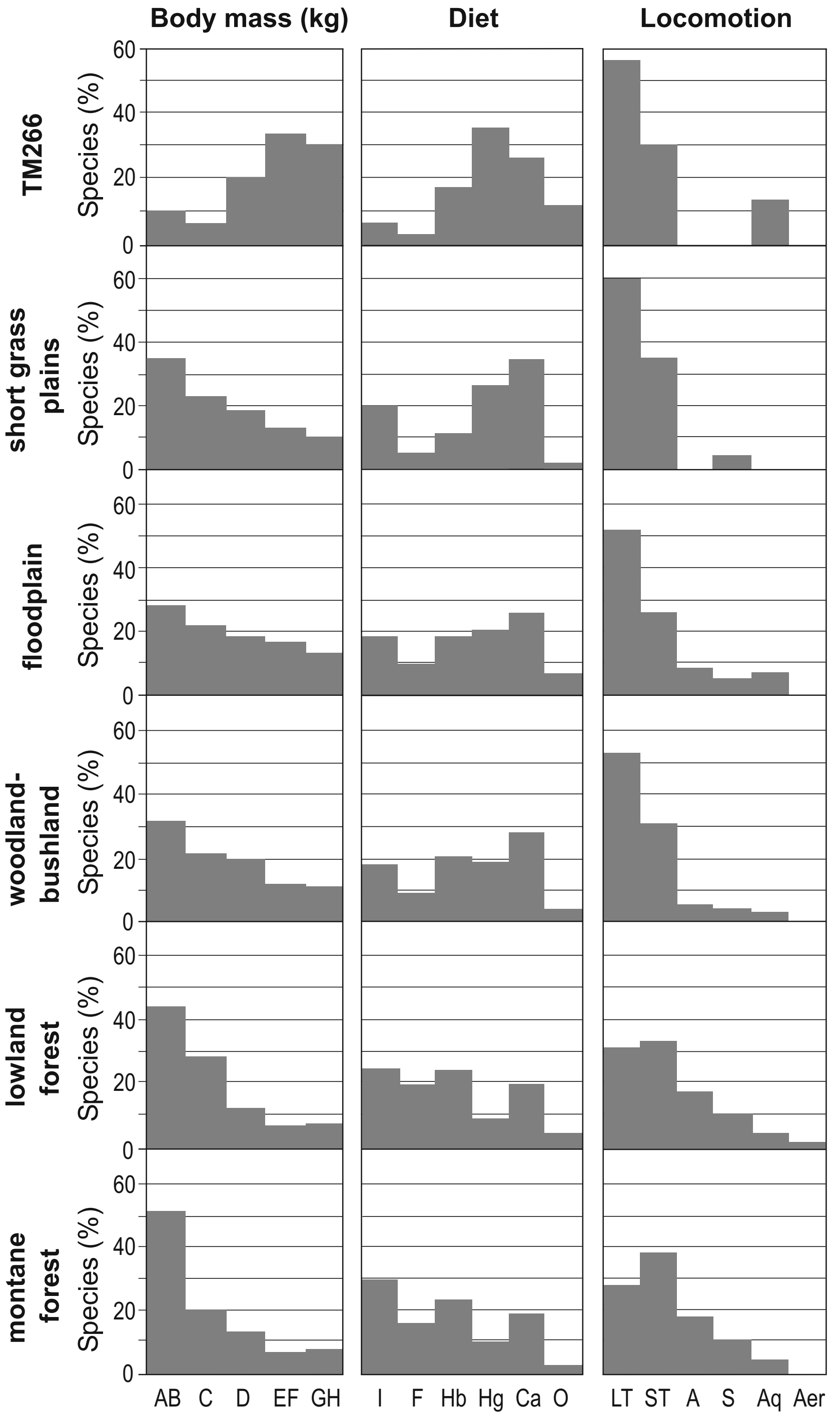


Fig. 1 Relative abundances of TM266 mammalian families and orders, computed from the count of mandibles (numbers in brackets). *N*=158 individuals. (*1*) Bovidae; (*2*) Giraffidae; (*3*) Equidae; (*4*) Suidae; (*5*) Proboscidea; (*6*) Hippopotamidae; (*7*) Anthracotheriidae; (*8*) Carnivora; (*9*) Primates; (*10*) Orycteropodidae; (*11*) Lagomorpha; (*12*) Rodentia

are *Anancus*, Hippopotamidae, *Sahelanthropus*, *Hipparion*, and Lagomorpha. The dominance of anthracotheres over hippos is certainly representative of a genuine ecological signal because their semi-aquatic representatives are considered as ecological analogues (Pickford 1991; Ducrocq 1997; Boisserie et al. 2005; Lihoreau et al. 2006). The very rare (<1%) but ecologically informative taxa are Giraffidae, *Nyanzachoerus*, Colobinae, Orycteropodidae, *Loxodonta*, *Machairodus*, and Lutrinae.

The ecological structure of the TM266 mammal assemblage (Fig. 2) has common features with some of the environments compiled by Andrews et al. (1979). Among the latter, the proportion of frugivorous species tends to decrease from forested to more open environments. The same is true for browsers (although to a lesser extent), whereas carnivorous species and grazers show the reverse tendency (Fig. 2). The proportion of carnivores and browsers in the TM266 assemblage (respectively, 27%

Fig. 2 Distribution of TM266 species within ecological variables (body mass, feeding preferences, locomotion), compared with patterns observed in modern African environments (estimated from Andrews et al. 1979). For abbreviations, see Table 1



and 17%) comes closer to those observed in the faunas of woodland–bushlands and floodplains. The amount of frugivorous species (3%) is close to the one observed in the short-grass plains. Grazers represent 35% of the species at TM266, which is much higher than the proportion observed in extant environments (note that the highest value characterizes short-grass plains). Insectivorous and omnivorous diets hardly help to differentiate the various environments. Nevertheless, the TM266 assemblage has peculiar values: omnivorous taxa are more numerous (12%) than in modern faunas, and insectivorous taxa are less well represented (7%). The above-mentioned bias against small species should be responsible, at least in part, for the low representation of insectivorous taxa.

Patterns for locomotor categories converge with those obtained for diet preferences: the TM266 assemblage is close to faunas from woodland–bushlands, floodplains and short-grass plains (Fig. 2). The fossil assemblage shows a high proportion of terrestrial mammals, among which the majority (57%) is exclusively restricted to the ground, the other species being fossorial or semi-arboreal. The high proportion of aquatic species suggests a stronger affinity with the woodland–bushland and floodplain environments, because those taxa are absent in short-grass plains. The TM266 assemblage does not yield strictly arboreal, scansorial, or aerial species. Again, the under-representation of micromammals certainly contributes to these absences, especially for scansorial and aerial species.

Finally, the body mass distribution in the TM266 assemblage has no equivalent among extant environments (Fig. 2). Large (45–180 kg) and very large (>180 kg) mammals prevail and they represent about 30% of the taxa each. Medium-sized (10–45 kg) and small (<10 kg) mammals are less represented and account for 20% and 17% of the taxa, respectively. By contrast, the number of species decreases from the smallest to the largest ones in extant faunas. The high proportion of very large species is intriguing because it is never observed in modern environments (Andrews et al. 1979; Gagnon 1997; Fernandez-Jalvo et al. 1998; Kovarovic et al. 2002; Soligo and Andrews 2005). This can result from various biasing processes but we cannot exclude the presence of a paleoecological signal. Indeed, such a high proportion is frequent in many Cenozoic assemblages (Soligo and Andrews 2005), albeit with different taphonomical and sedimentological contexts.

Discussion

The analysis of the structure of the TM266 mammal assemblage enables us to infer the corresponding paleoenvironment, provided that this structure reflects the one of the original mammal metacommunity from which it actually derives (Behrensmeyer 1982; Badgley 1986; Kidwell and Flessa 1995; Etter 1999; Hadly 1999; Soligo and Andrews 2005). A fossil assemblage is only a partial picture of the original metacommunity that may have been altered by taphonomical processes and sampling biases. Here, the relative abundances of taxa are not or are little affected by biasing taphonomical processes, such as sorting and selective preservation. In fact, all skeletal elements are represented in similar proportions in the entire mammal assemblage. Furthermore, these skeletal elements, especially mandibles, are evenly distributed among the four abundance categories used in our analysis (Fig. 3), yet gathering species covering wide taxonomic and ecological ranges, including body size. The relative abundances of the TM266 taxa thus likely provide a good estimation of the proportion of taxa in the original metacommunity.

Nevertheless, one must keep in mind that the full ecological spectrum of the original metacommunity is not accessible because of the under-representation of small mammals and micromammals. Some other limitations must be considered. The first one concerns the use of modern relatives as ecological analogues for fossil species. This method is generally adopted (Gentry 1970; Vrba 1980; Shipman and Harris 1988; Dodd and Stanton 1990; WoldeGabriel et al. 1994), especially in cases where the phylogeny and the ecology of the lineage are correlated (Fernandez-Jalvo et al. 1998). However, others (Shotwell 1955; Solounias and Dawson-Saunders 1988) warned that these analogies become more hazardous with older fossils. A second limitation involves the inference of the extension of paleohabitats from the proportion of indicator species in the taxonomic approach. The underlying assumption is that these two parameters are directly correlated but this

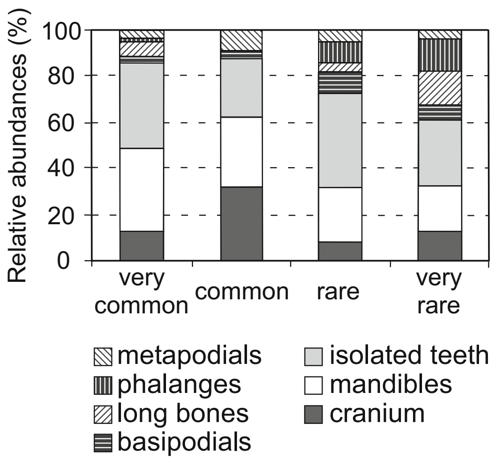


Fig. 3 Proportion of skeletal elements represented within each relative abundance category defined for the TM266 taxa

hypothesis has yet to be substantiated. For instance, mammal population size can differ between closed and open landscapes in relation to different physiological characteristics of species. It is then generally larger in the latter (Estes 1992; Kingdon 1997).

In spite of these limitations, the structure of the large mammal assemblage from TM266 makes it possible to extract three main environmental components.

The first one is composed of permanent aquatic habitats, as attested by the high abundance of large semi-aquatic mammals (anthracotheres and hippos) and by the presence of two semi-aquatic otters. This is confirmed by the abundant remains of freshwater fish, crocodiles, and aquatic turtles found at TM266 (Vignaud et al. 2002; Otero et al. 2007, 2008).

The second component corresponds to dense to moderately dense woodlands with trees and bushes, as suggested by the affinities that the TM266 assemblage shows with woodland-bushland environments (Fig. 2) and by the presence of several taxa: *Giraffa* sp. (Harris 1991), *Sivatherium* aff. *S. hendeyi* (Hamilton 1973; Harris 1991), *Anancus kenyensis* (Maglio 1973; Smart 1976; Cerling et al. 1997; Jacques 2007), *Loxodonta* (Kingdon 1997), *Nyanzachoerus syrticus* (Harris and White 1979; Bishop and Hill 1999; Jacques 2007), *Machairodus kabir* (Peigné et al. 2005b), and a species of colobus monkeys (Oates 1994). In spite of this high taxonomic richness, these species were rare or very rare in the landscape. Together with the moderate abundance of browsers and the scarcity of frugivorous taxa, it suggests the reduced extent of these wooded habitats.

The third environmental unit is an open landscape of grasslands, mainly inhabited by the hippotragines (Estes 1992; Kingdon 1997) *Tchadotragus sudrei* and *Saheloryx solidus* (Geraads et al. 2008), a *Gazella* (Estes 1992; Kingdon 1997), and the small hyena *Hyaenictitherium minimum* (de Bonis et al. 2005). The high abundance of these taxa and of grazing species points out the prevalence of open habitats over closed ones. This area was interspersed by humid zones (floodplains and swamps) occupied by water-dependent bovids (Reduncini; Estes 1992; Kingdon 1997), as well as dry areas with gerbils, ground squirrels (*Xerus*) and fossorial species such as *Orycteropus abundulafus* and *Serengetilagus tchadensis* (Lehmann et al. 2005; Lopez-Martinez et al. 2007). These results are strengthened by the similarity between the TM266 assemblage and extant faunas living in short-grass plains and floodplain environments.

The taxonomic and the ecological structures converge toward a common paleoenvironmental reconstruction for the TM266 area. This is all the more remarkable since these two approaches are based on different kinds of data, namely abundance of specimens and number of species. The results confirm the first paleoenvironmental reconstruction proposed by Vignaud et al. (2002) for the TM266 vertebrate assemblage and bring new information on the extent of paleohabitats. Three environmental components have been distinguished: (1) aquatic habitats made of permanent water bodies; (2) woodlands with trees and bushes; and (3) a dominating open landscape of grasslands interspersed by humid zones (floodplains and swamps) and dry areas. The absent or limited transport suggests that these habitats were locally interwoven and could form a mosaic environment. As already suggested by Brunet et al. (2005), a modern analogue of this mosaic landscape could be the Okavango Delta in Botswana. It is composed of a mosaic of seasonally flooded swamps and grasslands to riverine woodlands and dry savannas never under water (Ramberg et al. 2006). This environment has already been proposed as representing a suitable environment in which the emergence of early hominids may have occurred (Wrangham 2005). Alternatively, open landscapes and closer ones could have succeeded one another through time by the migration of the ecotone that separated them. In both cases, the environment was highly diversified.

S. tchadensis was probably rare in this landscape and had a wide variety of habitats at its disposal, as for the two other Late Miocene hominids. *Orrorin tugenensis* (Lukeino Fm., Kenya, 6.0–5.7 Ma; Senut et al. 2001; Sawada et al. 2002) may have evolved in well wooded to forested conditions margining lakes and streams with open countryside in the vicinity (Pickford and Senut 2001; Mein and Pickford 2006), whereas *Ardipithecus kadabba* (Adu-Asa Fm., Ethiopia, 5.77–5.54 Ma; Haile-Selassie 2001) is associated with a mosaic of riverine forests, woodlands, and grassy woodlands (Haile-Selassie et al. 2004). These landscapes have in common high habitat diversity, but it seems that those at TM266 were more open than those of the two other hominid-bearing sites. This is also evidenced from the pattern of abundances exhibited by bovids. Indeed, the TM266 assemblage shows a high proportion of open habitat dwellers such as Hippotragini, Antilopini, and Reduncini. To the contrary, rather closed habitat dwellers dominate in the Adu Asa and Lukeino assemblages: Tragelaphini and Boselaphini for the former, Aepycerotinae for the latter. Whether *S. tchadensis* preferred open, closed, or both kinds of habitats cannot be established here, but we can wonder how bipedalism could have provided a selective advantage to early hominids over quadrupedal primates. Bipedalism makes it easier to move from patch to patch or to exploit food from open habitats. Many hypotheses have been proposed to illustrate this benefit, such as the energy saving that bipedal locomotion enables for walking (Rodman and McHenry 1980; Sockol et al. 2007), or the decreasing of the body surface exposed to solar radiation (Wheeler 1991a, b). The woodland would have still been necessary to supply food and shelters to these hominids (Wrangham 2005).

Exhaustive comparisons between these early hominid assemblages require a good knowledge of their taphonomical context and a quantitative characterization of modern environmental analogues, especially of mosaic landscapes. This would ultimately allow researchers to infer some climatic parameters that constrained the ecosystem where the earliest hominids evolved.

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