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Hicham Mhamdi, Emmanuelle Stoetzel, Oussama Bouarakia, Hassan Aouraghe, Mohammed Souhir. Morphological, biometric and taphonomic analyses of Holocene gerbils from Guenfouda (Eastern Morocco) and first mention of *Gerbillus henleyi* in a fossil record. *Historical Biology*, In press, 35 (5), pp.623-636. 10.1080/08912963.2022.2057227 . hal-03633540

HAL Id: hal-03633540

<https://hal.science/hal-03633540>

Submitted on 7 Apr 2022

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Morphological, biometric and taphonomic analyses of Holocene gerbils from Guenfouda (Eastern Morocco) and first mention of *Gerbillus henleyi* in a fossil record

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Abstract

The Guenfouda cave, located in eastern Morocco, has yielded an abundant macro- and microvertebrate fauna associated with a rich lithic industry attributed to several cultures (Middle Stone Age, Later Stone Age and Neolithic). Among the microfauna, on the basis of new morphological and biometric data of the upper and lower first molars, we identified two gerbillines of the genus *Gerbillus* collected from the upper levels of an Holocene age. *Gerbillus henleyi* is here identified for the first time in the fossil record of North Africa, while *G. campestris* has been cited previously at this site and in many other Pleistocene and Holocene sites in the Maghreb. The taphonomic study concluded that a medium-sized nocturnal predator (possibly *Tyto alba*) was likely to be the source of the accumulation of small mammals in the filling of the Guenfouda cave. The palaeoecological reconstruction based on the whole faunal spectrum indicates a semi-open steppic landscape, with patches of more wooded areas and water ponds or streams, which is also characteristic for this region at present.

Keywords: Rodents; Gerbillinae; Holocene; eastern Morocco; palaeontology; taphonomy; palaeoenvironments

Introduction

As in other countries of North Africa, the microvertebrates of Morocco are still poorly documented and often underrepresented in the archaeological context (Stoetzel 2017; Stoetzel et al. 2019). The information obtained from the discovery of abundant microvertebrate remains in the Holocene levels of the Guenfouda cave in eastern Morocco (Aouraghe et al. 2010; López-García et al., 2013) shed new lights on the paleoenvironments and paleoclimates in which the prehistoric human populations of the region evolved. This discovery also filled some gaps in the fossil record of the concerned taxa in eastern Morocco and in the Maghreb in general.

By their abundance, and adaptations to well-defined habitats and precise climatic conditions, micromammals are good ecological markers and allow a fine reconstruction of palaeoenvironments (e.g., Chaline 1970). However, the accumulation of the remains of small vertebrates at an archaeological or palaeontological site is generally (but not exclusively) the result of the intervention of one or more predators, and also of various post-deposition processes (e.g., Denys 1985; Andrews 1990; Fernandez-Jalvo and Andrews 1992; Desclaux et al. 2011). A taphonomic analysis is therefore necessary in order to determine the main accumulating agent as well as the factors that may have affected the assemblage secondarily. This, in turn, ensures the reliability of the palaeoenvironmental reconstructions deduced from the faunal lists and the application of palaeoecological indices.

Previous studies in Guenfouda focused on the fauna in general (Aouraghe et al. 2010), and small mammals in particular (López-García et al. 2013). In the present work, we focused on the gerbillines of the genus *Gerbillus*, because during the review of the material it became clear that at least two species of very distinct size were present, something unheard of in a Moroccan Holocene site. The genus *Gerbillus* appeared in the Maghreb during the Pliocene (Tong 1989; Geraads 1995), and underwent significant diversification during the Pleistocene, a period characterised by strong climatic and environmental variations (Stoetzel 2013; Ndiaye et al. 2016). It is probably the establishment of increasingly long and marked arid periods in the Lower and Middle Pleistocene that would have particularly favoured the diversification of Gerbillinae in North Africa. But at the boundary between the Middle and Upper Pleistocene, we observe a significant decrease in diversity within micromammals, with the disappearance of many fossil species (and even entire lineages) including within the subfamily Gerbillinae (Geraads et al. 2013; Stoetzel 2013). At the Upper Pleistocene, within the genus *Gerbillus*, only *G. campestris*, and very occasionally *G. maghrebi*, are recorded in the archaeological and palaeontological sites of the Maghreb.

The systematics, phylogeny and phylogeography of the current Gerbillinae have undergone a significant development in recent years (e.g., Chevret and Dobigny 2005; Pavlinov 2008; Abiadh et al. 2010; Ito et al. 2010; Ndiaye et al. 2012, 2016; Aghova et al. 2017; Alhajeri 2018; Nanova et al. 2020; Bryja et al. 2022). However, there is still no consensus on the position of some taxa such as *Dipodillus*, which is, according to the authors, considered as a synonym of *Gerbillus* (e.g., Chevret and Dobigny 2005), a separate genus (e.g., Musser and Carleton 2005; Pavlinov 2008) or a sub-genus of *Gerbillus* (e.g., Abiadh et al. 2010; Ndiaye et al. 2012; Nicolas et al. 2014; Alhajeri et al. 2015). This debate is not part of the objectives of the present study, and consequently we chose to use the name *Gerbillus* in a broad sense.

The aim of this study is twofold: first, to identify the gerbilline species present in the Guenfouda cave using morphological and biometric criteria, and second, to study the taphonomic context of the assemblage in order to ensure the age of these remains and the reliability of the palaeoenvironmental reconstructions.

The site

The Guenfouda cave (also known as Ghar Zebouj) is located 6 km from the village of the same name and 30 km SW of the city of Oujda in eastern Morocco (Figure 1a).

The cave cut through a cliff of dolomite and oolitic limestone (Figure 1b) of Aaleno-Bajocian age (about 175 million years old), a formation deposited in a marine platform environment. Orographically, it is located on the eastern part of the Oujda Mountains at 930 m above sea level, and it occupies a panoramic position overlooking the plain of Beni Yala (Figure 1c). The arched porch, which opens to the east, rises 4.35 m from the ground at the entrance. The cave is mostly unichamber from the entrance until a central stalagmitic pillar located at the back. From that pillar, the cave starts to divide into two cavities (Figure 1d): a chamber on the right which is about 6 m long and 3.5 m wide, and a smaller room on the left of 3.5 m length by 2.5 m width.

Its large area, good aeration, easy access and its location in a place which overlooks the surrounding areas (Figure 1c) make the cave a suitable place for a human habitat. Indeed, regularly excavated since 2004 by Professor H. Aouraghe and his team from Mohamed First University, the Guenfouda cave yielded abundant and varied archaeological material (lithic and bone industries, ceramics, faunal and human remains) attributed to several cultures (mainly from the Neolithic, but also to the Later Stone Age, and to the Middle Stone Age) (Aouraghe et al. 2008).

The filling of the excavated area extends over two metres in depth and comprises the succession of several stratigraphic levels of different sedimentological natures (Figure 2). These levels have recorded several human occupations ranging from the Middle Stone Age (MSA) to the Neolithic. The cave's stratigraphy studied so far is divided into five layers (Figure 2), which are, from top to bottom:

- Layer C0: this surface layer consists of powdery silts and limestone blocks. It yielded bone remains, lithic and bone tools and ceramic shards attributed to the Neolithic.
- Layer C1a: characterised by an alternation of beds rich in ashes (whitish levels), charcoals (dark levels) or clays (brown levels). The little disturbed appearance of these layers suggests the good conservation of the underlying strata. A polished axe and a handstone characteristic of the Neolithic have been discovered in this layer. This layer is also particularly rich in terrestrial gastropod shells.
- Layer C1b: made up of light brown powdery silts, without any visible structure, encasing limestone blocks mainly fallen from the walls of the cave and various faunal and lithic remains. This layer yielded ceramic furniture of the Cardial type, corresponding to an ancient phase of the Neolithic
- Layer C2: made up of dark brown clay, with an aggregate structure, thicker than layer C1b. The transition with the latter is irregular, but clear. Charcoals are relatively numerous and allowed a ^{14}C dating which resulted in an age of $11,150 \pm 50$ BP (11,162–10,904 cal BC) at the top of Layer C2. This layer has yielded archaeological material attributed to Neolithic cultures (lithic and bone industries).

Other levels have been reached during the recent excavations, but were not yet studied in detail and are not represented on Figure 2:

- Layer C3: divided into three sublevels (C3a, C3b, C3c). The basal part (C3c) of this layer is dominated by powdery ashy clays. This is then topped by an irregular stony level (C3b) formed by centimetric, or even decimetric, angular limestone elements. An irregular and finely laminated limestone crust forms the third sublevel (C3a) which caps

the layer. Sub-layer C3c has provided lithic tools of the 'slats with knocked back' type (Later Stone Age).

- Layer C4: provisionally divided into two parts. The basal part (C4b) is relatively friable, quite ashy, and rich in charcoal debris. The top part (C4a) is characterised by its orange colour, a relative induration and a clear lamination. Also, the charcoal remains are very abundant, and scattered centimetric limestone fragments are present. In 2021, this layer provided lithic tools of the Levallois type (Middle Stone Age).
- Both layers (C3 and C4) yielded abundant faunal remains (which are still under study).

Archaeological excavations have reached a depth of up to two metres in some places, but they have not yet reached the base of the filling. To specify its extent, an electric tomography campaign was carried out by Professor D. Khattach (Aouraghe et al. 2014) and assessed the depth of the filling at 5 m at the edges next to the cave walls.

A Neolithic burial was discovered in Layer C2 as well as isolated human remains including teeth, post cranial bones, and some bones of hands and feet (Aouraghe and Haddoumi, 2012; Aouraghe et al., 2005).

The Guenfouda cave also yielded abundant faunal remains (Table 1) represented by at least 15 taxa of larger fauna (Aouraghe et al. 2008, 2010; Aouraghe and Haddoumi 2012; Bougariane 2013), and 34 taxa of small vertebrates. Micromammals are composed of two soricomorphs (*Crocidura russula*, *C. whitakeri*), one macroscelid (*Petrosaltator rozeti*), two bats (*Myotis blythii*, *Rhinolophus hipposideros*) and seven rodents (*Mus spretus*, *Meriones shawii*, *Apodemus sylvaticus*, *Gerbillus campestris*, *Eliomys* sp., *Atlantoxerus getulus*, *Ctenodactylus* sp.) (López-García et al, 2013).

However, recent reviews of the material have shown that some of the previously identified taxa need reappraisal. For instance, Stoetzel et al. (2017) showed that it is rather *Meriones grandis*, and not *M. shawii*, that is represented at Guenfouda. We also revealed that the remains previously attributed to *Ctenodactylus* sp. belong actually to *Jaculus* sp. (Mhamdi and Stoetzel, pers. obs.), and that a second species of gerbil is present (present work).

Materials and methods

Sampling

The material studied in this work originates from the Layers C0 to C2, excavated in 2016, 2017 and 2019. These excavations were carried out by independent subdivisions of 5 cm thick layers, while respecting the limits of sedimentary layers and archaeological soils. Each bucket of sediment removed during the excavations bore the indications of its origin (number of the square, depth [Z] level measured by laser theodolite). The sediments were then water-sieved on two superimposed sieves of 3 mm and 1 mm mesh in order to recover the smaller archaeological materials (bones of small animals, ostrich eggshell beads, micro-flint shards, etc). The sieved material came mainly from squares I39, I40, J39, J40, K39 and L39 (Figure 1d) which had been the subject of extensive excavations. After drying in the sun, a first selective sorting using tweezers allowed us to recover the remains of microvertebrates. These were then packed in micro-mount boxes bearing the indications of the sample's origin (number of the square, layer, Z level and date).

Because of their proximity to the stalagmitic column, the majority of the fossils from square J40 were covered by concretions, which made their taxonomic and taphonomic study very difficult. To clean them, the samples were submerged in a 10% acetic acid solution for 10

minutes before being rinsed with clean water. These were considered separately for the taphonomic analysis.

Species identification

Gerbillus species were identified mainly according to the anatomical identification criteria established by Tong (1989), Aulagnier et al. (1993), Stoetzel (2009), López-García et al. (2013) and Aulagnier et al. (2017). The dental nomenclature followed here is that used by Tong (1989) (Figure 3).

Direct observation of the morphological characters was made thanks to a stereomicroscope (OPTIKA SZM GEM1, magnification x7 to x40). For comparisons, we consulted current genotyped specimens from the collection of O. Bouarakia deposited at the 'Biodiversity, Ecology and Genome Laboratory', Faculty of Sciences, Mohammed V University, Rabat, as well as photos of specimens from the MNHN in Paris and BMHN in London taken by E. Stoetzel. Materials recovered from rejected pellets and dead individuals collected by H. Mhamdi in the vicinity of the site, made available at the Oujda University Museum, were also used.

The dimensions of the upper (M1) and lower (m1) first molars can be very useful at differentiating certain groups of rodents (Geraads 1994). The list of current and fossil material used in this work is presented in Table 2. The Guenfouda fossil assemblage studied includes 107 molars (40 M1: 13 right M1 and 27 left M1; 67 m1: 32 right m1 and 35 left m1), corresponding to a minimum of 35 individuals. The molars were photographed in occlusal view with a camera (OPTIKAM 2350) coupled to a stereomicroscope (OPTIKA SZM GEM1, magnification x40) at the Faculty of Sciences of Oujda. Measurements of different molar distances, indicated in mm, were then taken using the Digimizer software (trial period). The measurements used in this work follow those of Tong (1986) and Stoetzel (2009): the length and width of the molars correspond to the greatest anteroposterior distance and the width of the median lobe, respectively.

After entering all data in an Excel table, the usual statistical calculations (sum, mean, standard deviation, and variance) as well as plotting the graphs were carried out using the PAleontological STatistics (PAST) software (version 3.22).

High-resolution photos used for illustrations and some taphonomic observations were taken with the Scanning Electron Microscope (SEM) of the Faculty of Sciences of Oujda.

Taphonomic observations

The taphonomic study of a fossil assemblage requires observing several criteria such as faunal and skeletal representation, fragmentation, and surface alterations such as traces of digestion (e.g., Denys 1985, 2014, 2020; Andrews 1990; Fernandez- Jalvo and Andrews 1992). A criterion used alone is rarely sufficient to interpret a fossil assemblage; this is why it is often necessary to combine several approaches to obtain a global vision of the taphonomic processes that have affected an assemblage. In the case of an accumulation by predation, the faunal spectrum, the percentage of digested elements and the intensity of digestion, however, remain the most reliable criteria to identify the predator. The anatomical representation and the fragmentation are often subject to post-deposition factors which may mask the signal of the predator's digestion (Stoetzel 2014). Thus, in the context of this preliminary taphonomic study, we only focused on the observation of bone surfaces.

Results

Species identification

In this work, we identified, based on morphological and biometric criteria, two gerbil species from the Guenfouda material: *Gerbillus campestris* and *Gerbillus henleyi*. Below we present a description of the material and discuss the geographical range and ecology of the current and fossil populations.

Gerbillus campestris (Loche, 1867)

List of the studied material

6 maxilla (with M1, M2 and M3 *in situ*); 14 maxilla (with M1 and M2 *in situ*); 10 maxilla (with M1 *in situ*); 5 isolated M1; 2 mandibles (with m1, m2 and m3 *in situ*); 28 mandibles (with m1 and m2 *in situ*); 15 mandibles (with m1 *in situ*) and 9 isolated m1.

Previous mentions in the Maghreb fossil record

Forms related to *G. campestris* are present in the Maghreb fossil record from the Lower Pleistocene, in particular at Jebel Ressay in Tunisia or at Oued Melah in Algeria (Ameur-Chehbeur 1988; Tong 1989; Mein and Pickford 1992). Later, the species became more frequently recorded during the Middle Pleistocene in Morocco (Hominid cave and Rhinoceros Cave, Geraads et al. 2010; Salé, Tong 1989; Jebel Irhoud; Geraads et al. 2013; Sidi Abderrahmane, Tong 1989), as well as in Algeria (Aïn Mefta; Tong 1989) or in Tunisia (Jebel Ressay; Mein and Pickford 1992). In the Upper Pleistocene and the Holocene, with the exception of a mention of *G. maghrebi* at Chrafate and Ez-Zarka in northern Morocco (Ouahbi et al. 2003), *G. campestris* became the only gerbil species cited throughout different sites in Morocco (El Harhoura 2, Stoetzel et al. 2010; Contrebandiers Cave, Reed and Barr 2010; Felids Cave, Geraads et al. 2010; Chrafate and Ez Zarka; Ouahbi et al. 2003; Oued Assaka, Wengler et al. 2002; Ifri-el-Baroud; Poti et al. 2019; Guenfouda, M et al. 2013; Ifri N 'Ammar, Mouhsine 2003; Kehf-el-Baroud; Barton et al. 2005; Kahf-That-El-Ghar, Ouchaou 2000; Gazelles Cave, Geraads et al. 2010; Hassi Ouenzga, Linstädter 2004) and in Algeria (Gueldaman, Saidani et al., 2016).

Description and comparison

The upper first molars (M1) (Figure 3a) present a protocone that is offset mesially from the paracone. These two tubercles are not individualised and are linked on little-worn teeth by a short ridge. The longitudinal ridges (anterolophule and neolophe), are relatively well developed (high) and alternate (Aulagnier et al. 1993; Stoetzel 2009).

On the lower first molars (m1) (Figure 3b), the anteroconid is asymmetrical. The anterolophulid connects the latter to the protoconid with a labial position (taking sometimes a more median position). The metaconid and the protoconid are not individualised and are in the opposite position. The longitudinal ridges are well developed, reaching almost the same height as the tubercles (as is the case on M1). Finally, anterolophulid and neolophulid are aligned (Tong 1989; Stoetzel 2009).

In addition, a m1 (G115-L39) presents an anterior cingulum, as well as a posterior cingulum (Figure 3c). This characteristic can be found frequently in certain fossil gerbil species (*G. cingulatus*, *G. grandis*), or in old populations of *G. campestris* (1989; Stoetzel 2009). Thus, our material is similar to the extant populations of *G. campestris*, and the presence of an anterior

and posterior cingulum on some m1 would reflect a primitive character displayed by some individuals.

Measurement

The upper, and especially the lower, molars of *G. campestris* from Guenfouda appear on average somewhat smaller than other fossil (Table 3, Figure 5) or current (Table 2, Figure 6) populations of this species. But this difference, which does not seem to be significant, could just as well be due to a difference in the measurement method between observers. The values remain within the overall size variability of the species (Table 2, Figures 5, 6).

Current distribution and ecology

The North African gerbil *G. campestris* is widespread in the Mediterranean region of North Africa, from Morocco to Egypt, west of the Nile. It is also present, but more scattered, in the Sahara Desert and the Sahel region (in Mali, Niger and Sudan) (Happold 2013; Granjon 2016). In Morocco, this species is widely distributed from the north of the country to the Drâa Valley in the south, with some isolated populations in the Sahara. This gerbil lives in a variety of habitats, ranging from sub-humid to arid regions, with the exception of high mountains, forests and sandy desert areas. It occupies steppes, arable land, rocky habitats and oases (Nicolas et al. 2014; Aulagnier et al. 2017; Bouarakia et al. 2019a).

Gerbillus henleyi (Winton, 1903)

List of the studied material

1 maxilla (with M1, M2 and M3 *in situ*); 3 maxilla (with M1 and M2 *in situ*); 1 maxilla (with M1 *in situ*); 6 mandibles (with m1 and m2 *in situ*); 6 mandibles (with m1 *in situ*) and 1 isolated m1.

Previous mentions in the Maghreb fossil record

To our knowledge, this is the first mention of this species in a fossil or sub-fossil state in the Maghreb, or even in the whole of North Africa. Note that a mention of another small gerbil, *G. nanus*, was made at Ti-n-Torha in Libya, also dated to the beginning of the Holocene (Gautier and Van Neer, 2011, in Masseti 2010). However, African populations of *G. nanus* were reattributed to *G. amoenus* according to recent molecular studies (Ndiaye et al. 2013; Bouarakia et al. 2019b).

Description and comparison

On the M1 (Figure 4a) the anterocone is squeezed on its lingual and labial flanks. The protocone and the paracone, which are slightly offset mesially, are individualised on little worn teeth. The ridges joining the tubercles are lower than these. With wear, save rare exceptions, tubercles progressively fuse in the order anteroconus-protocone-paracone-metacone. The hypocone and metacone are not very distinct on young teeth; with wear, they form a single transverse lophe.

On m1 (Figure 4b), the anteroconid joins the metaconid by the anterolophulid, and later with wear it joins the protoconid as well. The metaconid and the protoconid are individualised and are in opposite position along a lingo-labial axis. The posterior lophe (hypoconid-entoconid), is individualised and directed inwards and a little backwards. The mesosinusid (between metaconid and entoconid) is directed forward in its labial part, almost isolating the metaconid when the teeth start to wear. The longitudinal ridges are less developed, and are slightly offset

in young teeth (Baker and Amr 2003; Siah sarvie and Darvish 2007; Stoetzel et al. al., 2011; Aouraghe and Haddoumi 2012; Geraads et al. 2013; Amr et al. 2018).

Measurements

G. henleyi from Guenfouda exhibit slightly smaller molars than the comparative material, but they remain within the overall size variability of current populations (Table 3, Figures 5, 6). However, these can be considered as preliminary observations, pending on a larger sample from current populations.

Current distribution and ecology

The pygmy gerbil *G. henleyi* lives in the Sahel region and in the southern and northern limits of the Sahara Desert, with an extension into the Middle East and Arabia (Musser and Carleton 2005; Granjon 2013; Monadjem et al. 2015). In Morocco, the distribution area appears sparse with a few capture points or traces of presence reported in the south and southeast of the country (Aulagnier et al. 2017). Recent captures and molecular identifications have confirmed the extension of its distribution range in northeastern Morocco in the *Hauts Plateaux* (Bouarakia et al. 2018). This gerbil occupies desert to semi-desert regions and prefers coastal sand dunes covered with halophytes, salt marshes, cultivated fields, wadi beds, stony plains and hamadas (Granjon 2013; Aulagnier et al. 2017).

Discussion

The morphology as well as the size of the *G. campestris* Guenfouda material is similar to specimens described from the neighbouring and contemporary Ifri N'Ammar deposit (Afsou, Nador) by Mouhsine (2003). However, some differences were observed compared to the current populations of the species. In particular, we noted a slightly smaller size of the molars (Table 3, Figures 5, 6) and the persistence of primitive characters (anterior and posterior cingulum) in certain individuals. But these differences remain within the overall variability of the species.

The morphological and biometric study enabled us to identify with certainty *G. henleyi* at Guenfouda. These specimens did not differ from their present-day counterparts except by their slightly smaller size (Table 3, Figures 5, 6). *G. henleyi* is now part of the current fauna of eastern Morocco, with an expansion of 370 km to the north-east of the country according to the most recent record of this species from south of Tafilalt from rejection pellets (Aulagnier et al. 2017; Bouarakia et al. 2018). This expansion could be interpreted as the result of the ongoing desertification process in North Africa and the increasing aridification advancing northwards to regions such as eastern Morocco (Jalut et al. 2009; Tabel et al. 2016; Bouarakia et al. 2018, 2021). Similar to the case of *G. henleyi*, Sundevall's Jird *Meriones crassus* Sundevall, 1842, a gerbilline species widespread in the desert regions of North Africa and Asia, was also recently discovered in eastern Morocco (Bouarakia et al. 2021).

Taphonomic observations

For a study of digestion, a total of 357 Gerbil fossil remains were considered (114 femoral heads, 136 incisors and 107 M1 and m1 molars). When considering the entire material, the analysis of the bone and dental surface under a stereomicroscope and with a scanning electron microscope (SEM) shows a low percentage of digested elements (13.2% of the femoral heads, 16.2% of the incisors and 7.5% of the molars) (Table 4), with mostly low to moderate digestion grades (Figures 7 and 8).

While the exact identification of the raptor species responsible for the accumulation of the assemblage is always a difficult exercise, it is nevertheless possible to determine a predation category comprising a number of potential predators with similarities in their taphonomic signals. In Guenfouda, the alteration produced by digestion highlights the probable role of category 1 or 2 nocturnal predator(s) according to the classification by Andrews (1990) and Fernández-Jalvo et al. (2016). These categories include, for example, the barn owl *Tyto alba*, an accumulator of small vertebrates which is also present in the region. Note that the presence of a few remains with stronger alterations may come from the occasional contribution of other predators, or young barn owls which tend to digest more strongly than adults (Bruderer and Denys 1999).

Concerning the post-depositional processes, we observed traces of plant roots which are relatively few, and traces of corrosion caused by soil acidity. We also noted some rodent burrows especially at the level of layers C1a and C1b, which testify a very local disturbance of the deposits, but these were well identified during the excavations and the archeo-stratigraphic context seems to be well preserved.

The slight alteration of the tooth and bone elements suggests that their accumulation is probably linked to a category 1 or 2 nocturnal raptor, possibly *Tyto alba*. Such predators are known to be opportunistic hunters and to give a good representation of the diversity of the prey-species in the environment, in the limit of their size, nocturnal habits and hunting territory (e.g., Andrews 1990).

Paleoenvironments

The presence of gerbils such as *G. campestris*, and especially *G. henleyi*, reflects open and arid environments in the vicinity of the cave during the period in which they were accumulated. But the use of only gerbils to reconstruct palaeoenvironments is too reductive, and we need to enlarge the spectrum of the considered taxa.

In the previous study of López-García et al. (2013) on Guenfouda small mammals, the authors used the method of Taxonomic Habitat Index (THI). We adjusted these results in replacing *Ctenodactylus* sp. by *Jaculus orientalis*, *Meriones shawii* by *Meriones grandis*, and in adding *Gerbillus henleyi* to the faunal list. The taxonomic name of some other species has been updated as well. We used the habitat categories established by Stoetzel et al. (2014) and Saidani et al. (2016) in including the whole microvertebrate faunal spectrum, and not only micromammals (Table 5). However, Gekkonidae sp., Lacertidae sp. and *Chalcides* sp. were not included, due to the large differences in the ecology of the species belonging to these groups. We also used the Climatogram method, by weighting the habitats frequented by the species by their abundance (reflected by the MNI = Minimum Number of Individuals) and using the ecological groups defined by Saidani et al. (2016) (Table 6). This method, however, assigns each species to a single habitat, and does not take into account their ecological plasticity. Moreover, it may be biased by the preferred prey and hunting territory of the predator responsible for the accumulation. Nevertheless, this method provides an interesting and complementary insight to the THI.

The results obtained by both methods (Figure 9) indicate that during the early-middle Holocene the environment of the Guenfouda cave was dominated by a semi-open steppic landscape, with patches of more wooded areas and water ponds. Considering the climatogram method, the open habitats (meadows, steppes) are much more dominant than in the THI, mainly due the abundance of *Mus spretus* in the assemblage. But this species can also frequent 'intermediate' habitats and open forests. All the identified species still occur today in the region.

Although the presence of *Natrix maura* and amphibian species indicate the punctual presence of water points, it should be mentioned that only *Pelophylax saharicus* strictly needs permanent water; *Sclerophrys mauritanicus*, *Bufo boulengeri* and even *Discoglossus pictus* (to a lesser extent) are more terrestrial and can burrow themselves during the dry season (Bons & Geniez, 1996; Escoriza and Ben Hassine 2019). Rocky soils were dominant, but soft and sandy soils were also represented, notably through the presence of burrowing species, and especially *G. henleyi*. Our results are globally in line with those previously obtained by López- García et al. (2013), with however a lower representation of open-dry and rocky habitats with the THI method, mainly due to the actual absence of *Ctenodactylus* in the assemblage. Comparative analyses with other contemporaneous (Holocene) sites are difficult, because small vertebrate analyses are scarce in eastern Morocco, and there exist important regional differences in the Maghreb, in particular in Morocco (Stoetzel et al. 2019). The results obtained for the Holocene levels of Guenfouda indicate an environment close to what is known today in the region, i.e., an arid Mediterranean climate, and a landscape dominated by steppes and scrubs (especially with the climatogram method), together with patches of more wooded areas and water ponds or streams.

Conclusions

This work contributes to the knowledge of the diversity, geographical and chronological occurrence of gerbil species in North Africa. A total of 405 fossil remains were analysed and measured (114 femoral heads, 136 incisors and 107 molars). The morphological and biometric analysis, as well as the comparison with current and fossil specimens, allowed us to attribute the fossil material of the Guenfouda gerbils to *G. campestris* and *G. henleyi*. The latter is cited in a fossil state for the first time in North Africa.

The taphonomic analysis shows that a nocturnal raptor (probably *Tyto alba*) was the source of the assemblage. Some burrows observed during excavations argue for few local disturbances of the deposits, without major mixing of sediments or archaeological material.

The abundance of gerbillines in the Guenfouda assemblage indicates an open and dry environment, which is also characteristic for this region at present.

Data availability statement: The authors confirm that the data supporting the findings of this study are available within the article.

Acknowledgments

The Faculty of Sciences of Mohamed First University at Oujda provided us with the logistical means to carry out excavations in the Guenfouda cave; our thanks go to the excavation team. ¹⁴C dating was performed on charcoal remains at the *Centre de Datation par le Radiocarbon*, Lyon, France (Lyon-15389-SacA-53713). We also thank the technical team of the Scanning Electron Microscope (SEM) of the Faculty of Sciences of Oujda for helping us to take high-resolution pictures, and the “Biodiversity, Ecology and Genome” Laboratory of the Faculty of Sciences of Rabat, for allowing us to use its collections of current specimens. We warmly thank Salvador Bailon (MNHN, Paris) for providing us information about the identification and counts of amphibians and squamates of Guenfouda. We thank also Pr Hamid Hadoumi for his contribution to the description and illustration of the stratigraphic sequence, and Mohamed Amezian for the English revision. Finally, we would like to thank the two anonymous reviewers for their valuable corrections and comments that allowed to improve the manuscript.

Disclosure statement: No potential conflict of interest was reported by the author(s).

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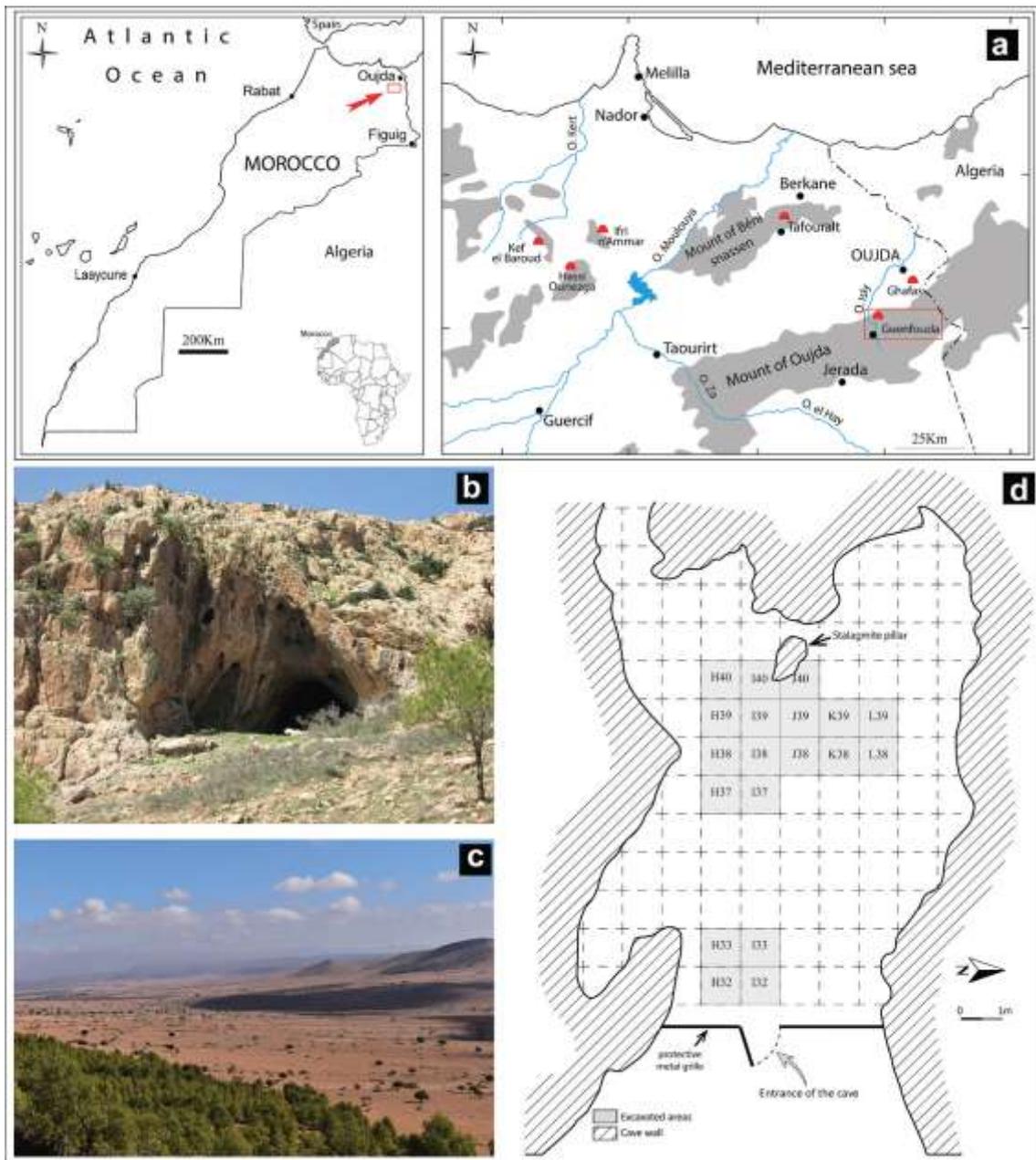


Figure 1. a) Location of the Guenfouda Cave and representation of the main archaeological sites of Eastern Morocco; b) Close-up view of the cave, carved out of the Jurassic limestone (Photo Aouraghe. H); c) Panoramic view from the interior of the cave and the strategic position of the place (Photo Aouraghe. H); d) Plan of the excavation of Guenfouda cave (Aouraghe et al. 2014).

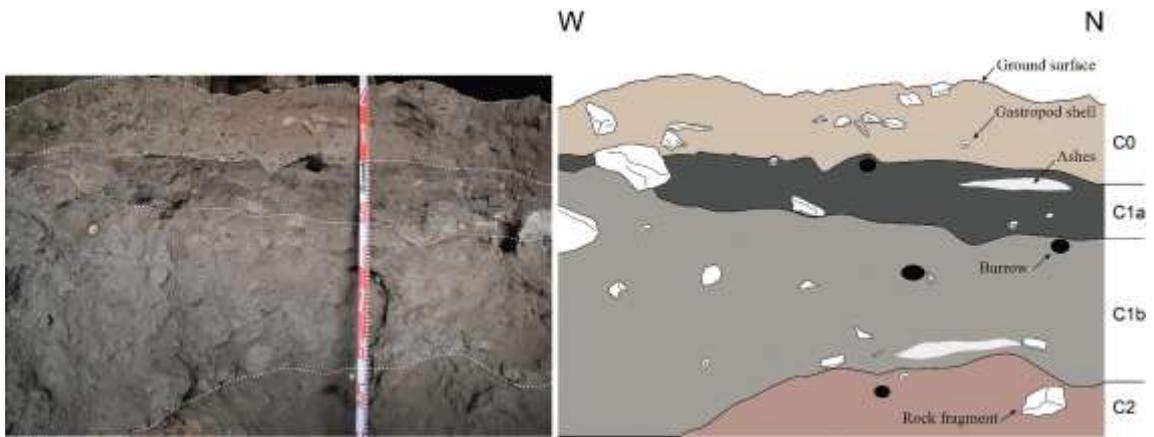


Figure 2. Stratigraphic section of the Guenfouda cave (square J40) (picture and infography Hamid Haddoumi).

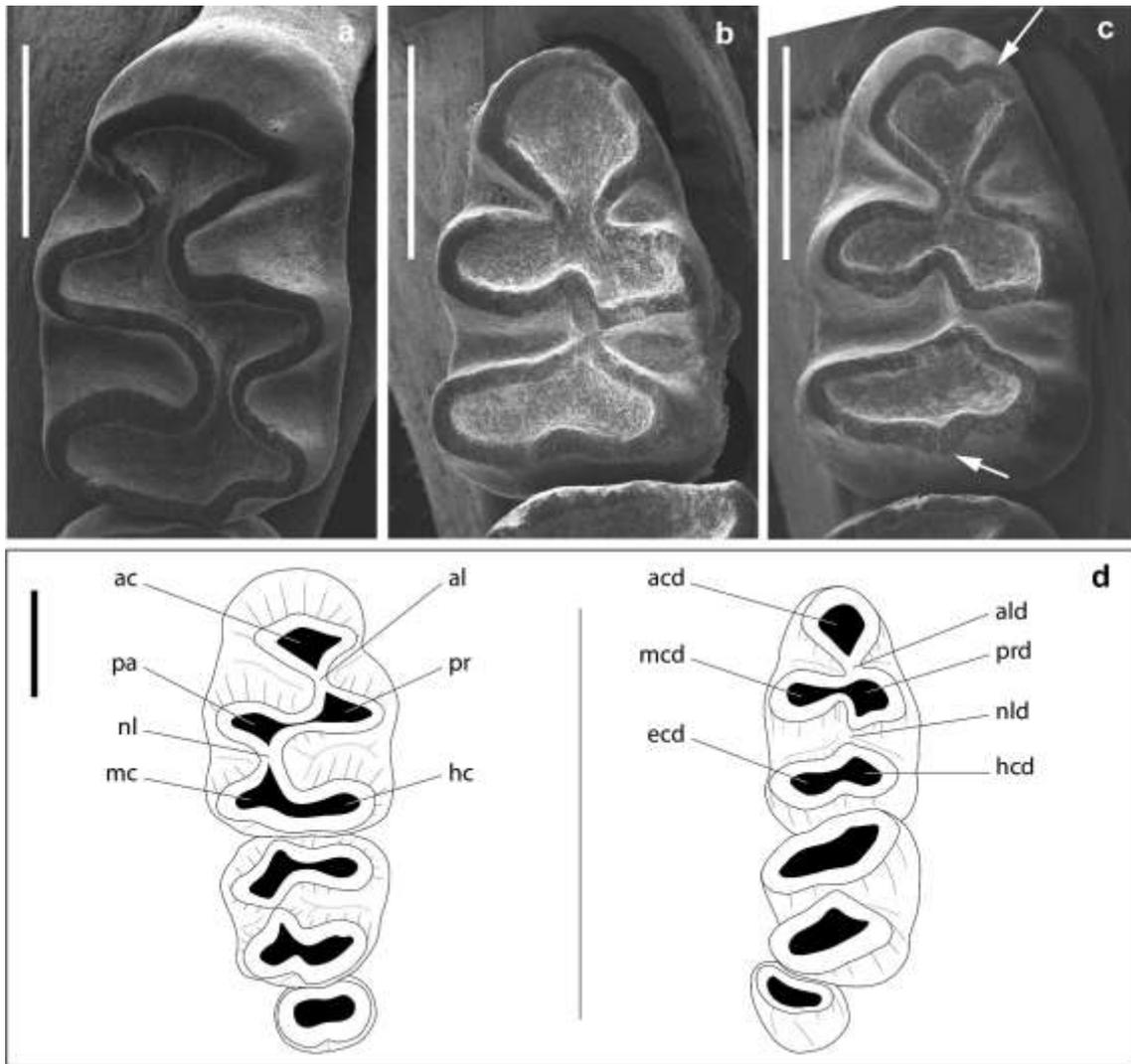


Figure 3. Examples of first molars of *G. campestris* from Genfouda. a = M1L (G054-I39); b = m1R (G123-K39); c = m1R (G115-L39) displaying anterior and posterior cingulum; d = upper (left) and lower (right) dental rows of a modern *G. campestris* from Fritissa (Morocco), specimen (MAR15-FRT17) trapped and genotyped by O. Bouarakia in 2015 (drawing H. Mhamdi). Scale = 1 mm. Dental nomenclature of the Gerbillinae (following Tong 1989): ac = anterocone; acd = anteroconid; al = anterolophule; ald = anterolophulid; ecd = entoconid; hc = hypocone; hcd = hypoconid; mc = metacone; mcd = metaconid; nl = neolophe; nld = neolophulid; pa = paracone; prd = protoconid; pr = protocone.

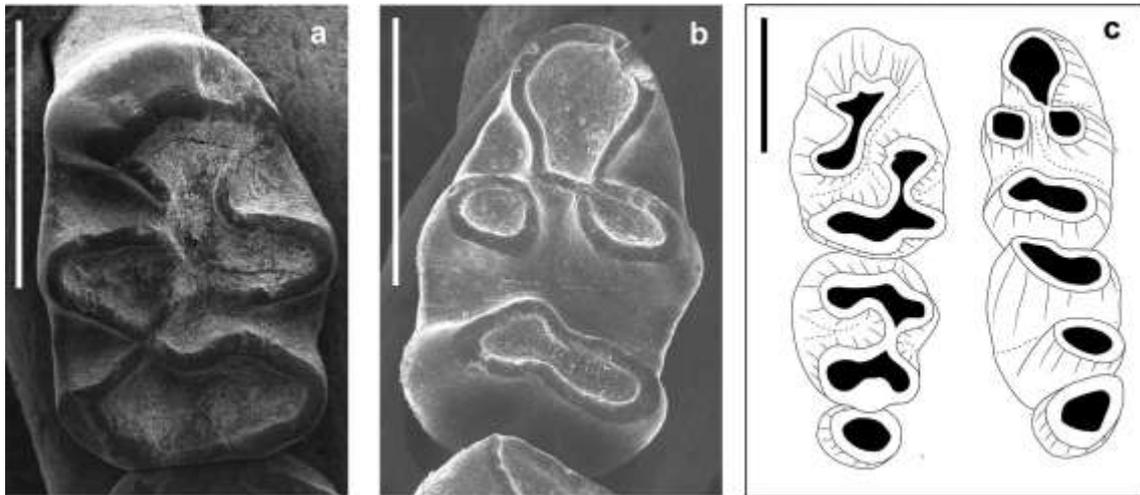


Figure 4. Examples of first molars of *G. henleyi* from Guenfouda. a = M1R (G055-I39); b = m1L (G125-K39); c = upper (left) and lower (right) dental rows of a modern *G. henleyi* from Ain Beni Mathar (Morocco), specimen (MAR14-BMT1) trapped and genotyped by O. Bouarakia in 2014 (drawing H. Mhamdi). Scale = 1 mm.

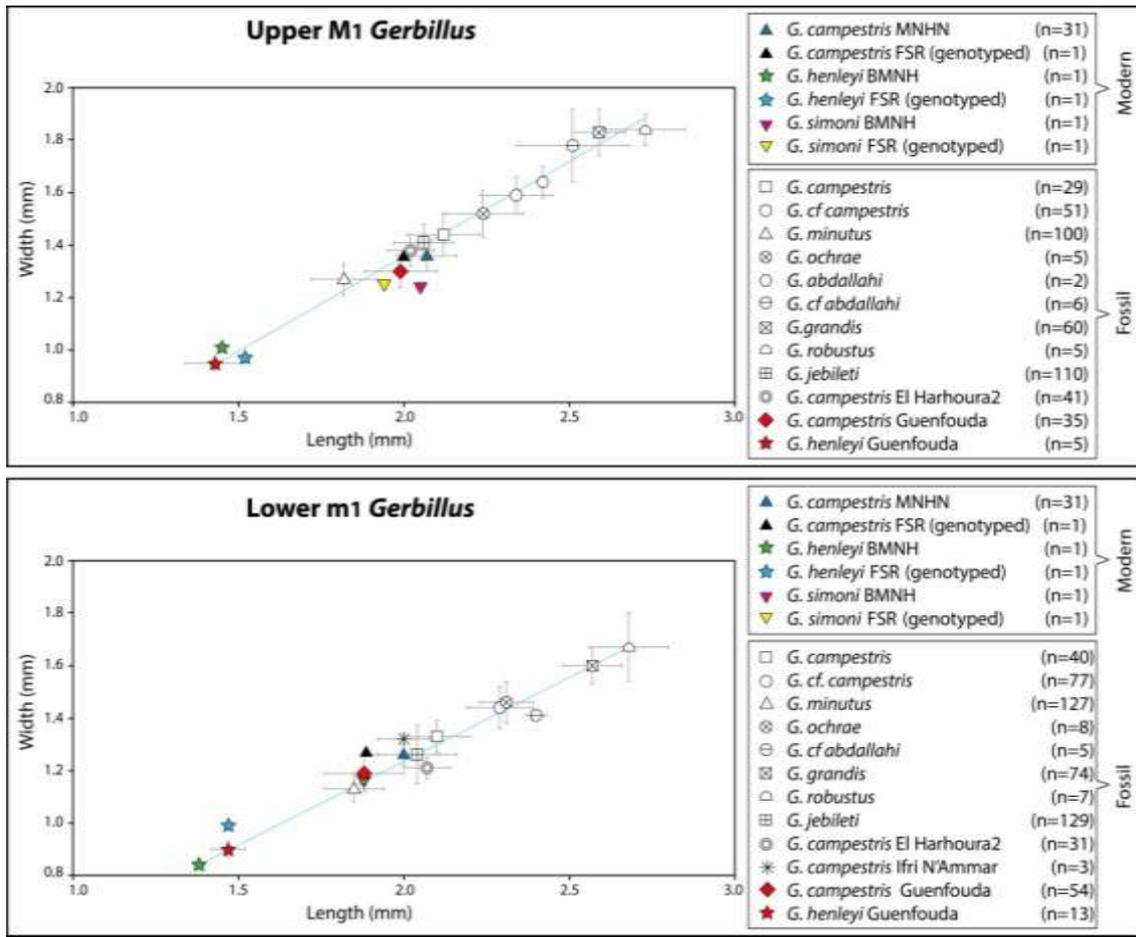


Figure 5. Comparison of mean size of upper and lower first molars of different fossil and modern *Gerbillus* species, standard deviation in brackets. n = number; MNHN = Muséum National d’Histoire Naturelle, Paris, France; FSR = Faculty of Sciences of Rabat, Morocco; BMNH = British Museum of Natural History, London, UK.

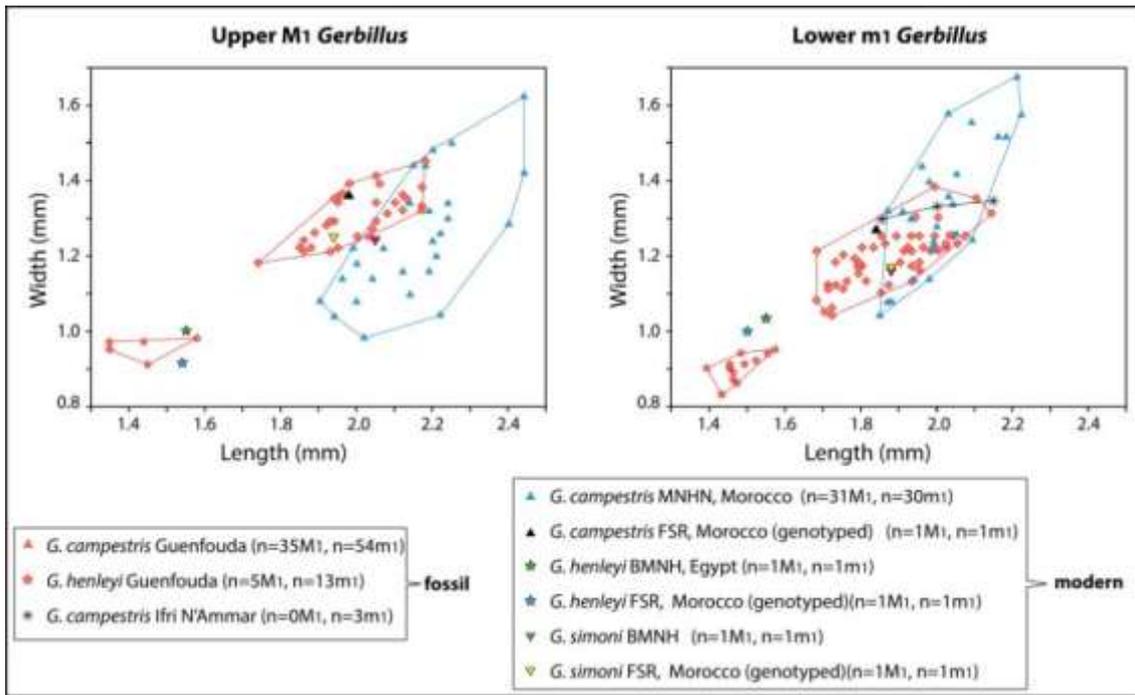


Figure 6. Bivariate diagram of measurements (length x width in mm) of upper (M1) and lower (m1) first molars of fossil and modern *Gerbillus* species. n = number; MNHN = Muséum National d’Histoire Naturelle, Paris, France; FSR = Faculty of Sciences of Rabat, Morocco; BMNH = British Museum of Natural History, London, UK.

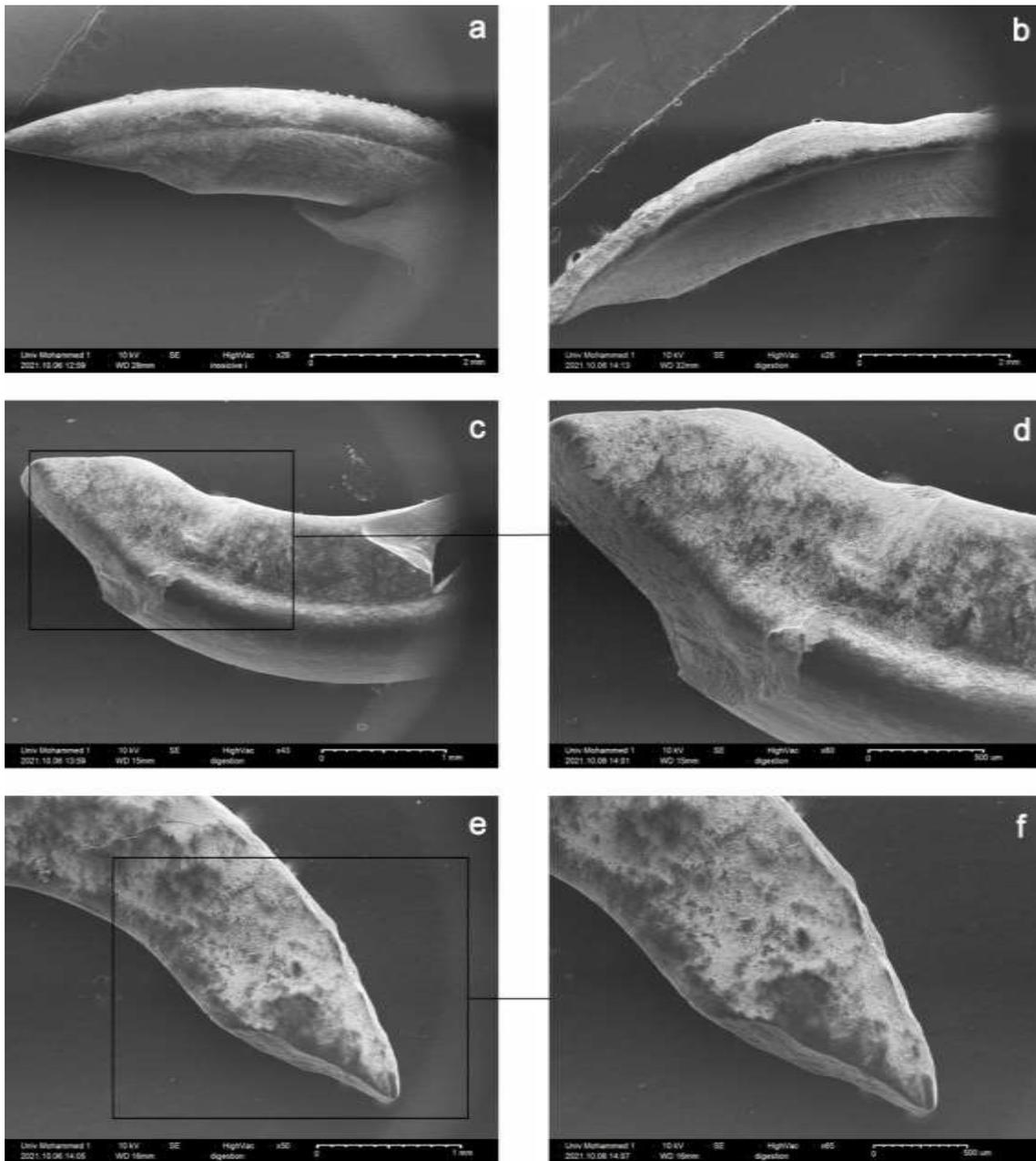


Figure 7. Examples of rodent digested incisors from Guenfouda. a: non digested gerbil *in situ* lower incisor; b: lightly digested gerbil lower incisor (enamel surface pitting on the tip); c-d: moderately digested rodent upper incisor (enamel and dentine dissolved on the tip); e-f: heavily digested rodent upper incisor (enamel removed from most of the tooth, dentine strongly altered).

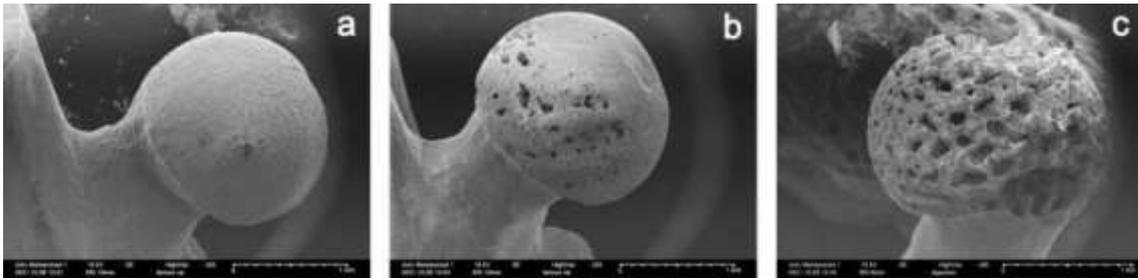


Figure 8. Examples of digested *Gerbillus* femoral heads from Guenfouda. a: Femur head without any digestion; b: light digestion (slight penetration of the head); c: moderate digestion (advanced penetration of the whole head with osteocyte lacunae well visible). Scale = 1 mm.

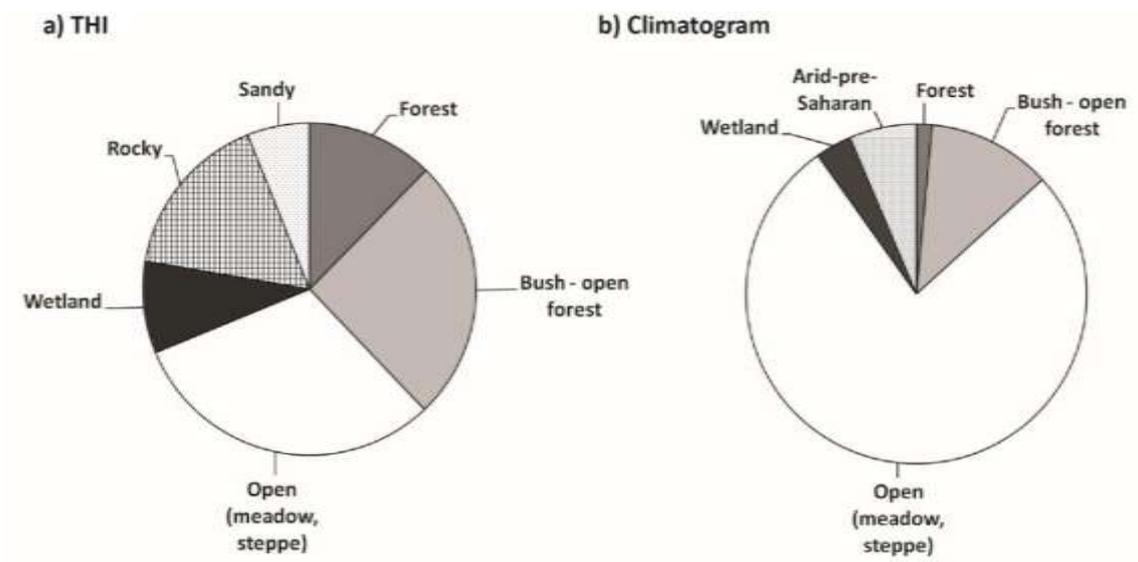


Figure 9. Representation of the THI (a) and climatogram (b) results based on the microvertebrate species from the Holocene levels of Guenfouda.

Groups	Order	Family	Species	HS	C.0	C.1	C.2		
Mammalia	Carnivora	Canidae	<i>Canis lupus f. familiaris</i>	+	+	-	-		
			<i>Vulpes vulpes</i>	+	-	+	-		
		Felidae	<i>Leptailurus serval / Caracal caracal</i>	-	-	+	-		
			<i>Mellivora capensis</i>	-	-	+	-		
		Perissodactyla Artiodactyla	Mustelidae	Indeterminate Carnivora	+	-	-	-	
				Equidae	<i>Equus sp.</i>	+	+	+	-
			Suidae Bovidae	<i>Sus scrofa</i>	+	-	+	-	
				<i>Bos primigenius f. taurus</i>	+	+	+	+	
				<i>Alcelaphus buselaphus</i>	+	-	+	-	
				<i>Connochaetes taurinus</i>	+	-	+	-	
	<i>Oryx sp.</i>			+	-	-	-		
	<i>Gazella sp.</i>			+	+	+	-		
	<i>Ammotragus lervia</i>			+	-	+	-		
	<i>Capra hircus</i>			+	-	+	+		
	<i>Ovis aries</i>	+	-	+	-				
	Lagomorpha	Leporidae	Indeterminate bovids	+	+	+	+		
			<i>Lepus capensis</i>	+	-	+	-		
		Rodentia	Murinae	<i>Oryctolagus cuniculus</i>	+	-	+	-	
				Indeterminate Leporidae	+	-	+	-	
			Gerbillinae	<i>Mus spretus</i>	+	+	+	+	
				<i>Apodemus sylvaticus</i>	+	+	-	-	
				<i>Meriones grandis</i>	+	+	+	+	
				<i>Gerbillus campestris</i>	+	+	+	+	
				<i>Gerbillus henleyi</i>	+	+	+	+	
				<i>Eliomys sp.</i>	+	+	+	+	
	Gliridae Sciuridae Dipodidae Hystricidae	<i>Atlantoxerus getulus</i>	+	+	+	+			
		<i>Jaculus orientalis</i>	+	+	-	-			
		<i>Hystrix cristata</i>	+	+	-	-			
		Soricomorpha	Soricidae	<i>Crociodura russula</i>	+	+	+	+	
	<i>Crociodura whitakeri</i>			+	+	+	+		
	Erinaceomorpha Macroscelidea		Erinaceidae	<i>Atelerix algirus</i>	+	-	+	-	
			Macroscelididae	<i>Petrosaltator rozeti</i>	-	+	+	+	
	Chiroptera	Vespertilionidae	<i>Myotis blythii</i>	+	+	+	+		
			<i>Rhinolophus hipposideros</i>	+	+	+	+		
		Anura	Alytidae	<i>Discoglossus pictus</i>	-	+	-	-	
			Bufonidae	<i>Sclerophrys mauritanica</i>	+	+	+	-	
	<i>Bufo boulangeri</i>	+		+	+	+			
	Sauropsida	Testudines	Ranidae	<i>Pelophylax sp.</i>	+	+	-	-	
			Testudinidae	<i>Testudo sp.</i>	+	+	+	+	
			Emydidae	<i>Emys sp.</i>	+	+	+	+	
Geoemydidae			<i>Mauremys sp.</i>	+	+	+	+		
Squamata			Trogonophidae	<i>Trogonophis wiegmanni</i>	+	+	+	+	
			Agamidae	<i>Agama cf. bibronii</i>	+	+	+	+	
			Chamaeleonidae	<i>Chamaeleo chamaeleon</i>	+	+	+	+	
			Scincidae	<i>Eumeces sp.</i>	+	+	+	+	
				<i>Chalcides sp.</i>	+	+	+	+	
				Gekkonidae	sp.	+	+	+	+
Lacertidae		sp.		+	+	+	+		
Aves		Lamprophiidae	<i>Malpolon sp.</i>	+	+	-	-		
		Colubridae	<i>Coronella cf. girondica</i>	+	+	-	-		
			<i>Natrix maura</i>	+	+	-	-		
		Struthionidae	<i>Struthio camelus</i>	+	+	+	+		
		Unstudied birds	spp.	+	+	+	+		
		Gastropoda	Stylommatophora	Helicidae	<i>Helix sp.</i>	+	+	+	+

Table 1. Taxonomic list of the large and small vertebrates of Guenfouda cave (Aouraghe et al. , 2008; Aouraghe and Haddoumi 2012; Bougariane 2013; López-García et al. 2013; Stoetzel et al. 2017, present work). The names of some amphibian species have been updated according to recent works in taxonomy and systematics (Escoriza & Ben Hassine, 2019). + = presence, - = absence, HS = not in stratigraphy.

	Genus	Species	Collection	Type specimens	N° collection	Collector	Year	Country	Locality	Sex	Genotyped
	<i>Gerbillus</i>	<i>campestris</i>	FSR	/	MAR15-FRT17	O. Bouarakia	2015	Morocco	Fritissa	F	Yes
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-395	J.A. Rioux	1972	Morocco	Blahrna	juv	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-396	J.A. Rioux	1972	Morocco	Blahrna	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-397	J.A. Rioux	1972	Morocco	Blahrna	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-399	J.A. Rioux	1972	Morocco	Blahrna	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-400	J.A. Rioux	1972	Morocco	Blahrna	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-402	J.A. Rioux	1972	Morocco	Blahrna	juv	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-404	J.A. Rioux	1972	Morocco	Blahrna	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-407	J.A. Rioux	1972	Morocco	Blahrna	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-408	J.A. Rioux	1972	Morocco	Blahrna	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-409	J.A. Rioux	1972	Morocco	Blahrna	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-762	M. Tranier	/	Morocco	Haut Atlas	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-765	M. Tranier	/	Morocco	Essaouira	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-768	M. Tranier	/	Morocco	Essaouira	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-769	M. Tranier	/	Morocco	Essaouira	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-770	M. Tranier	/	Morocco	Haut Atlas	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-771	M. Tranier	/	Morocco	Haut Atlas	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-772	M. Tranier	/	Morocco	Haut Atlas	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-773	M. Tranier	/	Morocco	Haut Atlas	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-774	M. Tranier	/	Morocco	Taliouine, Igris	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1973-775	M. Tranier	/	Morocco	Taliouine, Igris	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1974-223	M. Tranier	/	Morocco	Essaouira	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1974-224	M. Tranier	/	Morocco	Essaouira	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1974-225	M. Tranier	/	Morocco	Essaouira	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1974-226	M. Tranier	/	Morocco	Haut Atlas	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1974-227	M. Tranier	/	Morocco	Haut Atlas	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1980-260	Lesne	1976	Morocco	/	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1990-700	T. Benazzou	/	Morocco	El Jadida	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1990-701	T. Benazzou	/	Morocco	Essaouira	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1990-702	T. Benazzou	/	Morocco	Rabat	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1990-718	T. Benazzou	/	Morocco	/	M	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	ZM-MO-1990-822	F. Pette	/	Morocco	Taounate	F	/
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	MOHME-SB10	E. Stoetzel	2007	Morocco	Sidi Boughaba	F	Yes
	<i>Gerbillus</i>	<i>campestris</i>	MNHN	/	MOHME-SB22	E. Stoetzel	2007	Morocco	Sidi Boughaba	F	Yes
	<i>Gerbillus</i>	<i>henleyi</i>	BMNH	HOLOTYPE	3-8-1-34	Rothschild	/	Egypt	Wady Natron	M	/
	<i>Gerbillus</i>	<i>henleyi</i>	FSR	/	MAR14-BMT2	O. Bouarakia	2014	Morocco	Ain Beni Mathar	F	Yes
	<i>Gerbillus</i>	<i>henleyi</i>	FSR	/	MAR14-BMT1	O. Bouarakia	2014	Morocco	Ain Beni Mathar	M	Yes
	<i>Gerbillus</i>	<i>simoni</i>	FSR	/	MAR14-BMT3	O. Bouarakia	2014	Morocco	Ain Beni Mathar	M	Yes
	<i>Gerbillus</i>	<i>simoni</i>	BMNH	COTYPE	81-10-8-1	Lataste	/	Algeria	Oued Magra	M	/
	<i>Gerbillus</i>	<i>simoni</i>	BMNH	COTYPE	81-10-8-3	Lataste	/	Algeria	Hodna	/	/
	<i>Gerbillus</i>	<i>simoni</i>	BMNH	PARALECTOTYPE	19-7-7-1550	Lataste	publi 1888	Algeria	Oued Magra	/	/
	<i>Gerbillus</i>	<i>simoni</i>	BMNH	LECTOTYPE	19-7-7-2426	Lataste	/	Algeria	Oued Magra	F	/
	<i>Gerbillus</i>	<i>campestris</i>	FSO	/	Several samples	H. Mhamdi	2017-2019	Morocco	Guenfoada	/	/
	<i>Gerbillus</i>	<i>campestris</i>	INSAP	/	Several samples	E. Stoetzel	2005-2008	Morocco	El Harhoura 2	/	/
	<i>Gerbillus</i>	<i>campestris</i>	INSAP	/	Several samples	T. Mouhsine	1997-1999	Morocco	Ifri N' Ammar	/	/
	<i>Gerbillus</i>	<i>henleyi</i>	FSO	/	Several samples	H. Mhamdi	2017-2019	Morocco	Guenfoada	/	/

Table 2. Current and fossil comparative material used in the present study. FSR = Faculty of Sciences of Rabat, Morocco; INSAP = Institut National de l'Archéologie et du Patrimoine, Rabat, Morocco; FSO = Faculty of Sciences of Oujda, Morocco; MNHN = Muséum National d'Histoire Naturelle, Paris, France; BMNH = British Museum of Natural History, London, UK.

Species	Collection source	Upper M1										Lower m1							
		N	Length				Width				N	Length				Width			
			mean	min	max	SD	mean	min	max	SD		mean	min	max	SD	mean	min	max	SD
<i>G. campestris</i>	MNHN	31	2.07	1.92	2.24	0.05	1.36	1.28	1.48	0.03	30	2	1.84	2.22	0.11	1.26	1.12	1.44	0.04
<i>G. campestris</i>	Bouarakia, 2020	1	1.98	1.98	1.98	0	1.36	1.36	1.36	0	1	1.84	1.84	1.84	0	1.27	1.27	1.27	0
<i>G. henleyi</i>	Bouarakia, 2020	1	1.52	1.52	1.52	0	0.97	0.97	0.97	0	1	1.47	1.47	1.47	0	0.99	0.99	0.99	0
<i>G. simoni</i>	Bouarakia, 2020	1	1.94	1.94	1.94	0	1.25	1.25	1.25	0	1	1.88	1.88	1.88	0	1.17	1.17	1.17	0
<i>G. henleyi</i>	BMNH	1	1.45	1.45	1.45	0	1.01	1.01	1.01	0	1	1.38	1.38	1.38	0	0.84	0.84	0.84	0
<i>G. simoni</i>	BMNH	1	2.05	2.05	2.05	0	1.24	1.24	1.24	0	1	1.88	1.88	1.88	0	1.16	1.16	1.16	0
<i>G. campestris</i>	Tong, 1989	29	2.12	1.96	2.33	0.11	1.44	1.34	1.6	0.08	40	2.10	1.95	2.28	0.10	1.33	1.23	1.42	0.06
<i>G. cf. campestris</i>	Tong, 1989	51	2.34	2.13	2.5	0.11	1.59	1.50	1.75	0.07	77	2.29	2.08	2.48	0.10	1.44	1.32	1.59	0.08
<i>G. minutus</i>	Tong, 1989	100	1.82	1.65	2.14	0.1	1.27	1.09	1.42	0.06	127	1.85	1.69	2	0.09	1.13	1.05	1.23	0.05
<i>G. ochrae</i>	Tong, 1989	5	2.24	2.05	2.37	0.12	1.52	1.39	1.63	0.09	8	2.31	2.17	2.38	0.08	1.46	1.29	1.56	0.08
<i>G. abdallahi</i>	Tong, 1989	2	2.42	2.41	2.42	0.01	1.64	1.59	1.68	0.06	0	/	/	/	/	/	/	/	/
<i>G. cf. abdallahi</i>	Tong, 1989	6	2.51	2.35	2.69	0.17	1.78	1.69	1.94	0.14	5	2.40	2.37	2.42	0.03	1.41	1.39	1.42	0.02
<i>G. grandis</i>	Tong, 1989	60	2.59	2.48	2.74	0.08	1.83	1.70	1.99	0.09	74	2.57	2.44	2.72	0.09	1.60	1.49	1.71	0.07
<i>G. robustus</i>	Tong, 1989	5	2.73	2.60	2.85	0.12	1.84	1.76	1.92	0.06	7	2.68	2.51	2.79	0.12	1.67	1.48	1.84	0.13
<i>G. jebilei</i>	Tong, 1989	110	2.06	1.80	2.36	0.09	1.41	1.19	1.54	0.07	129	2.04	1.87	2.19	0.12	1.26	1.11	1.40	0.11
<i>G. campestris</i> EH-2	Stoetzel, 2009	41	2.02	1.91	2.10	0.07	1.38	1.31	1.44	0.06	31	2.07	1.85	2.04	0.07	1.21	1.18	1.28	0.04
<i>G. campestris</i> Ifr NA	Mouhsine, 2003	0	/	/	/	/	/	/	/	/	3	2.00	2.00	2.15	0.08	1.32	1.30	1.35	0.02
<i>G. campestris</i> Guenf	This work	35	1.99	1.74	2.18	0.11	1.30	1.18	1.45	0.06	54	1.88	1.68	2.14	0.12	1.19	1.04	1.38	0.07
<i>G. henleyi</i> Guenf	This work	5	1.43	1.35	1.58	0.09	0.95	0.91	0.98	0.03	13	1.47	1.39	1.57	0.05	0.90	0.83	0.95	0.03

Table 3. Dental measurements (in mm) of first molar of the modern and fossil *Gerbillus* and source collection of the studied material. Abbreviations are ‘SD’ for Standard deviation; ‘EH2’ for El Harhoura 2 cave, Morocco; ‘Guenf’ for Guenfouda cave, Morocco; ‘Ifr NA’ for Ifri N’Ammar cave, Morocco; ‘FSR’ for Faculty of Sciences of Rabat, Morocco; ‘FSO’ for Faculty of Sciences of Oujda, Morocco; ‘INSAP’ for Institut National des Sciences de l’Archéologie et du Patrimoine, Rabat, Morocco; ‘MNHN’ for Muséum National d’Histoire Naturelle, Paris, France; ‘BMNH’ for British Museum of Natural History, London, UK.

Femoral heads	No digestion	86.8%
	Low digestion	8.8%
	Moderate digestion	2.6%
	High digestion	1.8%
	Total PD	13.2%
Incisors	No digestion	83.8%
	Low digestion	13.2%
	Moderate digestion	3%
	High digestion	0%
	Total PD	16.2%
Molars	No digestion	92.5%
	Low digestion	5.6%
	Moderate digestion	1.9%
	High digestion	0%
	Total PD	7.5%

Table 4. Percentages and grades of digestion of *Gerbillus* species incisors, molars, and femoral heads from Guenfouda. PD = Percentage of Digestion %.

	Forest	Bush - open forest	Open (meadow, steppe)	Wetland	Rocky	Sandy
Chiroptera						
<i>Myotis punicus</i>	0.00	0.60	0.30	0.00	0.10	0.00
<i>Rhinolophus hipposideros</i>	0.40	0.40	0.10	0.00	0.10	0.00
Macroscelidea						
<i>Petrosaltator rozeti</i>	0.00	0.00	0.30	0.00	0.50	0.20
Soricomorpha						
<i>Crocidura russula</i>	0.20	0.40	0.30	0.05	0.05	0.00
<i>Crocidura whitakeri</i>	0.10	0.30	0.40	0.05	0.10	0.05
Rodentia						
<i>Eliomys munbyanus</i>	0.30	0.30	0.10	0.00	0.30	0.00
<i>Apodemus sylvaticus</i>	0.60	0.30	0.05	0.05	0.00	0.00
<i>Mus spretus</i>	0.10	0.30	0.40	0.10	0.05	0.05
<i>Gerbillus campestris</i>	0.05	0.20	0.55	0.00	0.10	0.10
<i>Gerbillus henleyi</i>	0.00	0.00	0.60	0.00	0.10	0.30
<i>Meriones grandis</i>	0.00	0.20	0.60	0.00	0.10	0.10
<i>Atlantoxerus getulus</i>	0.00	0.10	0.20	0.00	0.70	0.00
<i>Jaculus orientalis</i>	0.00	0.00	0.60	0.00	0.30	0.10
Amphibia						
<i>Sclerophrys mauritanica</i>	0.05	0.15	0.30	0.30	0.15	0.05
<i>Bufoes boulengeri</i>	0.20	0.20	0.20	0.30	0.05	0.05
<i>Pelophylax saharicus</i>	0.20	0.20	0.20	0.40	0.00	0.00
<i>Discoglossus pictus</i>	0.20	0.20	0.20	0.30	0.05	0.05
Squamata						
<i>Trogonophis wiegmanni</i>	0.15	0.35	0.20	0.00	0.10	0.20
<i>Agama bibronii</i>	0.00	0.00	0.30	0.00	0.70	0.00
<i>Chamaeleo chamaeleon</i>	0.10	0.80	0.10	0.00	0.00	0.00
<i>Eumeces algeriensis</i>	0.05	0.25	0.40	0.00	0.15	0.15
<i>Malpolon monspessulanus</i>	0.05	0.20	0.50	0.05	0.15	0.05
<i>Coronella girondica</i>	0.10	0.50	0.30	0.05	0.05	0.00
<i>Natrix maura</i>	0.10	0.20	0.20	0.50	0.00	0.00
Total	2.95	6.15	7.40	2.15	3.90	1.45

Table 5. Values of the Taxonomic Habitat Index (THI) of the microvertebrate species from the Holocene levels of Guenfouda. Adapted and completed from López-García et al. (2013), Stoetzel (2014) and Saidani et al. (2016).

Ecological groups	Forest	Bush - open forest	Open (meadow, steppe)	Wetland	Arid - pre-Saharan
Species (MNI)	<i>Apodemus sylvaticus</i> (2)	<i>Crocidura russula</i> (18)	<i>Crocidura whitakeri</i> (15)	<i>Discoglossus pictus</i> (2)	<i>Petrosaltator rozeti</i> (3)
	<i>Rhinolophus hipposideros</i> (1)	<i>Eliomys munbyanus</i> (1)	<i>Mus spretus</i> (89)	<i>Sclerophrys mauritanica</i> (2)	<i>Gerbillus henleyi</i> (7)
		<i>Myotys blythii/punicus</i> (1)	<i>Gerbillus campestris</i> (27)	<i>Bufoetes boulengeri</i> (1)	<i>Atlantoxerus getulus</i> (1)
		<i>Trogonophis wiegmanni</i> (1)	<i>Meriones grandis</i> (23)	<i>Pelophylax saharicus</i> (1)	<i>Jaculus orientalis</i> (1)
		<i>Chamaeleo chamaeleon</i> (2)	<i>Eumeces algeriensis</i> (1)	<i>Natrix maura</i> (1)	<i>Agama bibronii</i> (1)
		<i>Coronella girondica</i> (1)	<i>Chalcides</i> spp. (1)	<i>Malpolon monspessulanus</i> (1)	
Total MNI	3	24	157	7	13

Table 6. Classification of the Guenfouda microvertebrates in ecological groups for the establishment of a climatogram. MNI = Minimum Number of Individuals (in brackets). Adapted and completed from Saidani et al. (2016).