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1 **Quaternary terrestrial microvertebrates from Mediterranean northwestern Africa: state-**
2 **of-the-art focused on recent multidisciplinary studies.**

3
4 Emmanuelle STOETZEL ^{1*}, Aude LALIS ², Violaine NICOLAS ², Stéphane AULAGNIER ³, Touria
5 BENAZZOU ⁴, Yannicke DAUPHIN ², Mohammed Abdeljalil EL HAJRAOUI ⁵, Ahmed EL HASSANI
6 ⁶, Soumia FAHD ⁷, Mohammed FEKHAOUI ⁶, Eva-Maria GEIGL ⁸, François-Joseph LAPOINTE ⁹,
7 Raphaël LEBLOIS ¹⁰, Annemarie OHLER ², Roland NESPOULET ¹, Christiane DENYS ²

8
9 ¹ Histoire Naturelle de l'Homme Préhistorique (HNHP), UMR 7194, Muséum national d'Histoire
10 naturelle, CNRS, Sorbonne Universités, UPVD, Paris, France (emmanuelle.stoetzel@mnhn.fr,
11 roland.nespoulet@mnhn.fr).

12 ² Institut de Systématique, Evolution, Biodiversité (ISYEB), UMR 7205, Muséum national d'Histoire
13 naturelle, CNRS, Sorbonne Universités, EPHE, Université des Antilles, Paris, France
14 (aude.lalis@mnhn.fr, violaine.colin@mnhn.fr, yandauph@yahoo.fr, annemarie.ohler@mnhn.fr,
15 christiane.denys@mnhn.fr).

16 ³ Comportement et Ecologie de la Faune Sauvage, INRA, Castanet Tolosan, France
17 (stephane.aulagnier@toulouse.inra.fr).

18 ⁴ Faculty of Sciences, Mohammed V University, Rabat, Morocco (touriabenazzou@hotmail.com).

19 ⁵ Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco
20 (maelhajraoui@gmail.com).

21 ⁶ Institut Scientifique, Mohammed V University, Rabat, Morocco (elhassani@israbat.ac.ma,
22 fekhaoui@israbat.ac.ma).

23 ⁷ Faculté des Sciences de Tétouan, Université Abdelmalek Essaâdi, Tétouan, Morocco
24 (sfahd@uae.ac.ma)

25 ⁸ Institut Jacques Monod, Equipe Epigénome et Paléogénome, Paris, France (geigl.eva-
26 maria@ijm.univ-paris-diderot.fr).

27 ⁹ Département de sciences biologiques, Université de Montréal, Québec, Canada (francois-
28 joseph.lapointe@umontreal.ca).

29 ¹⁰ Centre de Biologie pour la Gestion des Populations (CBGP), UMR 1062, INRA, Montferrier-sur-Lez,
30 France (raphael.leblois@inra.fr).

31 * Corresponding author: Emmanuelle STOETZEL (emmanuelle.stoetzel@mnhn.fr).

32
33
34 **Abstract**

35 Northwestern Africa is today characterized by high geographical, climatic and ecological
36 diversity; it is recognized as a hotspot of biodiversity and a major area for both human and
37 faunal evolution. Studies of North African fossil microvertebrates have increased
38 considerably in recent years, but they no longer just provide palaeontological descriptions of
39 the species found in the assemblages. They also aim at better understanding the evolution of
40 faunal communities in relation to Quaternary climate changes and at reconstructing the
41 palaeoenvironmental background of prehistoric human occupations, in well-established
42 taphonomic and chronological contexts. These studies are also increasingly adopting an
43 integrative approach by combining archaeology, palaeontology, (palaeo)genetics,

1 taphonomy, palaeoecology and systematics, and using new methods such as geometric
2 morphometrics and isotopic analyses on both fossil and modern specimens. This paper aims
3 to present a history of the studies on Quaternary terrestrial microvertebrates from
4 northwestern Africa, and show how recent multidisciplinary studies have provided new
5 perspectives and evidence on the respective influences of climate change and increasing
6 human pressure on their evolution.

7
8 **Keywords:** Micromammals; Herpetofauna; Maghreb; integrative approach.

9 10 11 **1. Introduction**

12
13 Northwestern Africa (Morocco, Algeria, Tunisia) is characterized by unique ecological
14 systems, with sharp ecotone gradients going from coastal forest to desert, lowland and
15 upland. This region is today recognized as a hotspot of biodiversity and a major area for both
16 human and faunal evolution. Numerous archaeological sites allow us to better understand
17 the biological and cultural evolution of several hominin species in North Africa in parallel to
18 Quaternary climatic changes. Algeria has recently yielded some of the oldest lithic industries
19 (~1.9–2.4 Ma; Sahnouni *et al.*, 2018) and Morocco some of the oldest *Homo sapiens* remains
20 (~300 ka BP; Richter *et al.*, 2017) from throughout Africa, further increasing the interest of
21 the scientific community in this region. Microvertebrates, and especially micromammals
22 such as rodents, are of prime importance for obtaining palaeoclimatic, palaeoenvironmental,
23 biochronological and taphonomic information. They also allow us to establish a high-
24 resolution palaeoenvironmental background for human evolution, which contributes to a
25 better understanding of the human–environment relationship and its evolution throughout
26 time. During the Late Cenozoic, depending on the opening or closing of dispersal routes for
27 tectonic and/or climatic causes, northwestern Africa alternatively represented faunal
28 refuges, “cul-de-sac”, or crossroads of immigration waves from tropical Africa and Eurasia
29 (Aulagnier, 1992; Dobson and Wright, 2000; Husemann *et al.*, 2014). The aim of this paper is
30 to give an updated synthesis on the studies performed on Quaternary terrestrial
31 microvertebrates (rodents, shrews, hedgehogs, amphibians, squamates) from northwestern
32 Africa, in the frame of recent multidisciplinary, or integrative, approaches. We especially
33 focus on the Mediterranean area *s.l.*, as the arid and Saharan areas yielded very few (or no)
34 stratified or well-dated archaeological sequences with microvertebrate assemblages.

35 36 37 **2. Historical studies of Quaternary northwestern African microvertebrates**

38 39 *2.1. Before 1970*

1 During the 19th century and the beginning of the 20th century, researchers observed the
2 presence of some rodent remains in Plio-Quaternary deposits, especially in Algeria (Pomel,
3 1878, 1892, 1893–1898; Thomas, 1884; Pallary, 1892, 1934; Doumergue, 1893, in Cadenat,
4 1948; Arambourg, 1931, 1949), but the first studies focusing on fossil small vertebrates from
5 northwestern Africa only date from the 1950's, most notably concerning the Miocene site of
6 Beni Mellal in Morocco (Figure 1a). Even if the latter is not of Quaternary age, and is thus
7 beyond the scope of this article, this site is of primary importance, as it was the first in
8 northwestern Africa to have yielded a rich and diversified microfauna that was further
9 studied in detail, including small mammals (Lavocat, 1952, 1961, Sigé, 1976; Jaeger, 1977a;
10 Sigé and Legendre, 1983; Coiffait-Martin, 1991; Butler, 1998; Vergilino, 1999; Lopez-
11 Antoñanzas and Knoll, 2011; Hugueney *et al.*, 2015), herpetofauna (Hecht *et al.*, 1961;
12 Hoffstetter, 1961; Vergnaud-Grazzini, 1966; Rage, 1976; Hossini, 2002) and birds (Brunet,
13 1961). In the 50's and 60's, microvertebrates received little attention and few studies were
14 dedicated to Quaternary sites, although we can cite the researches of Coque (1957, 1962) in
15 the Tunisian Plio-Pleistocene site of Aïn Brimba; Arambourg (1957), Arambourg and
16 Hoffstetter (1954, 1955) and Jaeger (1969) in the famous Middle Pleistocene site of
17 Tighennif (Ternifine) in Algeria; Ginsburg *et al.* (1968) and Petter (1968) in the Late
18 Pleistocene site of Jebel Filfila in Algeria; Biberson (1961) in the Middle Pleistocene site of
19 Sidi Abderrahmane in Morocco; Ennouchi (1962) in Jebel Irhoud in Morocco; Ruhlmann
20 (1951) in the Late Pleistocene site of Dar-es-Soltan in Morocco; Vaufrey (1955) in various
21 Late Pleistocene and Holocene sites in Morocco, Algeria and Tunisia (these latter are not
22 represented on the maps Figure 1). Most of these references deal with fauna in general, and
23 records of small vertebrates mostly contain simple mentions of rodents, hedgehogs or
24 chelonians found among large mammal assemblages; only Petter (1968) and Jaeger (1969)
25 specifically focused on rodents.

26

27 2.2. 1970–1990

28

29 From the 70's to the 90's, we observe a considerable increase in studies, notably through the
30 fundamental work of Jaeger, focusing either on particular taxa (*Paraethomys*: Jaeger *et al.*,
31 1975; *Ellobius*: Jaeger, 1988) or sites (e.g., Jebel Irhoud: Jaeger, 1970; Ichkeul: Jaeger, 1971;
32 Oued Zra: Jaeger and Martin, 1971) or more general data on Mio-Plio-Quaternary fossil
33 rodents from northwestern Africa (Jaeger, 1973, 1975a, 1975b, 1977a, 1977b, Jaeger *et al.*,
34 1973, 1977, 1987). Important studies were also provided by Ameur (1976a) and Ameur-
35 Chehbeur (1988) on Neogene and Quaternary rodents from Algeria; Tong (1989) on
36 Gerbillinae from several sites in Morocco, Algeria and Tunisia; and Rzebik-Kowalska (1988)
37 on Plio-Pleistocene soricids from Morocco and Algeria. These represent the basis of all
38 subsequent studies on Neogene and Quaternary micromammals in North Africa. In addition,
39 several other studies were made on specific sites such as those by Cheddadi (1986) and
40 Michel (1988) in Aïn Bahya (Morocco, Middle Pleistocene); Denys *et al.* (1984, 1987) in
41 Tighennif (Algeria, Middle Pleistocene); Ameur (1976b) in Aïn Meftah (Algeria, Middle

1 Pleistocene); and Ameur-Chabbar *et al.* (1975) in Djebel Orouse, also named Djebel Kristel
2 (Algeria, Early Pleistocene). Shorter descriptions of small vertebrates were also made among
3 large mammal remains by Michel (1990) in several Moroccan sites (not represented on the
4 maps [Figure 1](#)), by Hadjouis (1985) and Chaïd Saoudi (1987) in several Late Pleistocene and
5 Holocene Algerian sites (not represented on the maps [Figure 1](#)), and by Gilman (1975) in the
6 Holocene Achakar caves in Morocco. Although all of the Maghreb is represented, the studied
7 sites date mainly to the Early or Middle Pleistocene ([Figure 1b](#)). Between the 70's and the
8 90's, no study was published on Quaternary northwestern fossil herpetofauna (amphibians
9 or squamates).

10 11 2.3. 1990–2000

12
13 In the 90's, there was a global decrease in microvertebrate studies in North Africa ([Figure](#)
14 [1c](#)). Nevertheless, Coiffait-Martin (1991) and Benammi (1997) focused their PhD research on
15 Neogene rodents from Algeria, and Geraads conducted important studies on fossil
16 micromammals and mammal biochronology in Morocco, especially in the Casablanca region:
17 Late Miocene (Lissasfa: Geraads, 1998; Raynal *et al.*, 1999), Early Pleistocene (Ahl-al-
18 Oughlam: Raynal *et al.*, 1990; Geraads 1995; Geraads *et al.*, 1998) and Middle Pleistocene
19 (Oulad Hamida 1 or “Grotte des Rhinocéros”: Geraads, 1993, 1994). Sporadic studies were
20 also conducted on Quaternary micromammal material from Algeria (Tighennif: Dauphin *et*
21 *al.*, 1994, 1999), and Tunisia (Jebel Ressay: Mein and Pickford, 1992). In addition, Hutterer
22 (1991) and Vergilino (1999) reviewed the fossil soricids from northwestern Africa, and
23 Renaud *et al.* (1999) the *Paraethomys* lineages from Morocco and Algeria. Again, only a few
24 studies concerned herpetofauna between 1990 and 2000, including the study of Bailon
25 (2000) in Ahl-al-Oughlam (Morocco, Early Pleistocene), Ould-Sabar and Michel (1996) in
26 Doukkala (Morocco, Middle-Late Pleistocene), and the reviews of Gmira (1995) and
27 Lapparent de Broin (2000) on the (North) African fossil Chelonians.

28 29 2.4. 2000–2010

30
31 In the 2000's, we observe a renewal of interest for Quaternary North African
32 microvertebrates, but almost only in Morocco ([Figure 1d](#)). The only exceptions are
33 Columnata and Taza 1 in Algeria, where some hedgehog, toad and lizard remains were
34 described by Merzoug (2005). Geraads and colleagues were still working on the Early and
35 Middle Pleistocene sites of Casablanca (Geraads, 2002, 2010; Raynal *et al.*, 2002, 2010;
36 Geraads *et al.*, 2010; Gunnell *et al.*, 2011; Gmira *et al.*, 2013), but most of the new studies
37 concerned Late Pleistocene and Holocene sites ([Figure 1d](#)). Among the major studies leading
38 to a better understanding of the Late Quaternary microvertebrate communities in Morocco,
39 we can cite the study of rodents from El Harhoura 1 (Aouraghe and Abbassi, 2002), Oulad
40 Hamida 2 or “Grotte des Félin” (Raynal *et al.*, 2008; Geraads *et al.*, 2010), Chrafate and Ez
41 Zarka (Ouahbi *et al.*, 2003), the review of the fossil *Mus spretus* from Morocco by Darviche *et*

1 *al.* (2006) (including fossil material from Doukkala), and Stoetzel's PhD research in the
2 Rabat–Temara region which includes a large synthesis (Stoetzel, 2009). Some micromammal
3 species were also mentioned, but not studied in detail, at other sites, such as Taforalt (Late
4 Pleistocene; Bouzouggar *et al.*, 2007), Kef el Hammar (Late Pleistocene; Barton *et al.*, 2005),
5 Hassi Ouenzga (Holocene; Linstädter, 2004) and several Pleistocene and Holocene sites in
6 Morocco (Ouchaou, 2000; Mouhsine, 2003; not represented on the maps [Figure 1](#)). In
7 addition, Hossini (2001, 2002), Bailon and Aouraghe (2002), Stoetzel *et al.* (2008) and
8 Stoetzel (2009) undertook studies on amphibians and squamates.

9

10 2.5. Since 2010

11

12 The increase in studies on Quaternary northwestern microvertebrates observed since the
13 2000's continues today, with an expansion throughout the Maghreb ([Figure 1e](#)).

14 Geraads and colleagues recently published new data on the microvertebrates from the
15 Moroccan site of Jebel Irhoud (Middle Pleistocene; Geraads *et al.*, 2013) and a synthesis on
16 rodents (Geraads, 2016a) and insectivores (Geraads, 2016b) from the “Grotte des
17 Rhinocéros” (Oulad Hamida 1, Middle Pleistocene, Morocco). Several other Early and Middle
18 Pleistocene sites were also considered: Guefaït-4 in Morocco (Early Pleistocene; Agusti *et al.*,
19 2017, 2018), Wadi Sarrat in Tunisia (Middle Pleistocene; Martinez-Navarro *et al.*, 2014;
20 Mtimet, PhD in progress), and Ben Kerat in Algeria (Middle Pleistocene; Stoetzel and
21 Pickford, 2018).

22 Here again, most of the recently studied sites are Late Pleistocene and Holocene in age. In
23 Morocco, we can notably cite the research on the microvertebrate assemblages from El
24 Harhoura 2 on the Atlantic Moroccan coast (Late Pleistocene-Holocene) and the
25 relationships between fossil and modern populations (Stoetzel *et al.*, 2010a, 2011a, 2012a,
26 2013, 2014, 2017; Cornette *et al.*, 2015a, 2015b; Jeffrey, 2016). In the same region and for
27 the same period, studies were also conducted at Contrebandiers Cave (Reed and Barr, 2010;
28 Amani *et al.*, 2012a), El Mnasra Cave (Amani *et al.*, 2012b; Stoetzel *et al.*, 2011b, 2014), and
29 Dar-es-Soltan 1 (Bouzouggar *et al.*, 2018). Other studies in Morocco focused on the
30 Casablanca region (Tamaris or “Grotte des Gazelles”: Bougariane *et al.*, 2010; Geraads *et al.*,
31 2010; Stoetzel *et al.*, 2017), northeastern Morocco (Ifri el Baroud: Potì *et al.*, 2019; Ifri
32 N'Ammar: Hutterer, 2010; Rhafas: Stoetzel *et al.*, 2018; Taforalt: Stoetzel, in progress;
33 Guenfouda: Aouraghe *et al.*, 2010; Lopez-Garcia *et al.*, 2013; Stoetzel *et al.*, 2017; Mhamdi
34 and Aouraghe, 2018; Mhamdi, PhD in progress), and central Morocco (M'Tsogatin: Sens *et al.*,
35 2016). Studies or reviews of amphibians and squamates from Moroccan Quaternary sites
36 remain rare (Bailon *et al.*, 2011; Stoetzel *et al.*, 2012b; Bailon, 2016; Bailon *et al.*, 2017).

37 In Algeria, some studies on microvertebrates (micromammals and herpetofauna) were
38 started in Gueldaman (Holocene; Saidani *et al.*, 2016), Medjez I and II (Late Pleistocene-
39 Holocene; Saidani *et al.*, 2017), and Abri Alain (Late Pleistocene; Campmas *et al.*, 2017).
40 Faunal lists including some microvertebrate taxa were also given by Chaïd Saoudi (2012),

1 notably for Tin Hanakaten (Holocene), located in a more arid area, and for which a revision
2 of the material would be needed.

3 In Tunisia, an inventory and a study of the entire microvertebrate material from Late
4 Pleistocene and Holocene archaeological sites stored at the *Institut National du Patrimoine*
5 of Tunis was recently initiated, but little material is available for each site (Stoetzel, 2017a;
6 [Figure 1e](#)).

7 We should also mention the revision of Lopez-Antoñanzas and Knoll (2010, 2011) on the
8 North African fossil Ctenodactylidae; the biochronological synthesis elaborated by Stoetzel
9 (2013) on the micromammal fauna from northwestern Africa from the Miocene to the
10 Holocene; the syntheses of Stoetzel (2017b), Stoetzel and Bougariane (2017), and Geraads
11 (2017) on the origin, evolution and biogeographic history of Moroccan mammals; the
12 synthesis of Gardner and Rage (2016) on African fossil lissamphibians; and Bailon *et al.*
13 (2017) on amphibians and lepidosaurs from the Cenozoic of Morocco.

14

15 2.6. What kinds of studies?

16

17 Until recently, the studies on Quaternary northwestern microvertebrates mainly provided
18 palaeontological descriptions of the species found in the assemblages and some
19 biochronological syntheses for small and large mammal faunas.

20 However, during the last 20 years, research problematics and methodologies have
21 diversified. In the second part of this paper we highlight the benefits brought by these new
22 integrated approaches. Indeed, combining archaeology, palaeontology, taphonomy, and
23 palaeoecology with geometric morphometrics, genetics, microstructural, compositional and
24 isotopic studies offers invaluable precisions for the interpretations of fossil Quaternary small
25 vertebrate communities.

26 Our examples come from recent studies that were mainly conducted within the framework
27 of a French–Moroccan project (ANR-09-PEXT-004 ‘MOHMIE’, 2009-2014, dir. C. Denys), in
28 which several researchers from different fields were involved. The project was two-fold:
29 focusing on both modern and fossil small vertebrates from the northern half of Morocco,
30 and trying to understand the 6th extinction of terrestrial small vertebrates in the Maghreb.

31 Trapping small vertebrates and collecting the pellets and scats of various predators enabled
32 the modern Moroccan biodiversity to be better studied and solid osteological and
33 taphonomic referentials to be set – a prerequisite for the reliable interpretation of fossil
34 assemblages (Stoetzel *et al.*, 2010b, 2012c; Denys *et al.*, 2015). Trapped animals were used
35 for osteological collections and isotopic, genetic and morphometric analyses (see below).
36 Pellets and scats were analysed for DNA preservation (Guimaraes *et al.*, 2015), isotopic
37 calibration (Jeffrey *et al.*, 2015) and taphonomic analyses (Dauphin *et al.*, 2015; Denys *et al.*,
38 2018; Campmas *et al.*, 2018). The microstructures and composition of bones and teeth
39 extracted from trapped animals, as well as modern pellets and fossil samples were also
40 analysed to decipher changes due to predation and diagenesis, but neither are presented

1 here (Dauphin and Massard, 2015, 2017; Dauphin *et al.*, 2012, 2018; Farre *et al.*, 2014;
2 Massard and Dauphin, 2017).

3 Concerning fossil data, although several North African archaeological and palaeontological
4 sites were considered for these studies, most of the results came from the Moroccan cave El
5 Harhoura 2, located on the Atlantic Coast near Rabat. This site has yielded large amounts of
6 microvertebrate remains over a sequence of more than 100,000 years (see references
7 above). We will look at some examples of the morphological, genetic and biogeographical
8 evolution of some microvertebrate species, and the relationships between fossil and modern
9 populations.

10

11

12 **3. Quaternary palaeoenvironmental changes and regional faunal particularities in** 13 **northwestern Africa**

14

15 *3.1. Complex phylogeographic histories in northwestern Africa: East vs West*

16

17 Several recently published genetic studies have helped us understand the phylogeographic
18 history of numerous small vertebrates in North Africa. Even if fossil data are not directly
19 considered here, they allow us to answer some questions of interest for palaeontologists
20 relating to species systematics and identifications, and their evolution and biogeographic
21 history through time, for instance. Phylogenetic analyses also allow us to demonstrate the
22 existence of cryptic species inducing taxonomic changes that must be considered in studies
23 on fossil material.

24 For example, the North African white-toothed shrew *Crocidura pachyura*, a sister species of
25 *Crocidura russula*, was thought to occur only in Tunisia and some Mediterranean islands,
26 while *C. russula* was supposed to exist only in Morocco and Algeria (e.g., Contoli and Aloise,
27 2001; Brandli *et al.*, 2005). But a recent study (Nicolas *et al.*, 2014a) has shown that *C.*
28 *pachyura* also occurs in Kabylia, Algeria, without evidence of sympatric occurrence or
29 hybridization between these species. Consequently, studies on Algerian and Tunisian fossil
30 assemblages have to consider these new results for the identification of fossil specimens.
31 However, to date, few data are available on the dental and osteological characters that
32 would enable discrimination of the two species, and additional morphological and
33 morphometric analyses are required.

34 Concerning the *Meriones shawii/grandis* complex, genetic analyses on modern specimens
35 (Lalis *et al.*, 2016a) has evidenced the existence of two main clades: a western clade
36 (northwestern Morocco) and an eastern clade (eastern Morocco, Algeria, Tunisia).
37 Morphometric analyses (Stoetzel *et al.*, 2017) have attempted to solve long-lasting
38 taxonomic difficulties by giving a species name to each clade, and to follow their evolution.
39 First, the comparison with museum specimens (including types) has allowed us to identify
40 the modern western clade as *M. grandis*, and the eastern clade as *M. shawii*, representing
41 distinct species. Second, the geometric morphometric analysis of fossil specimens has shown

1 that both species were present in Atlantic Morocco during the Late Pleistocene, with a west–
2 east re-organization during the Holocene. However, prior to this study, almost all jirds of
3 “modern” morphology dating to the Late Quaternary in Morocco were assigned to *M. shawii*
4 (Stoetzel, 2013) and thus deserve a revision.

5 Nicolas *et al.* (2014b) and Bouarakia *et al.* (2019) have produced a complex phylogeographic
6 pattern for *Gerbillus campestris* in North Africa, with seven genetic lineages occurring in
7 western Morocco; one in eastern Morocco, Algeria and Tunisia; one in Mali and Niger
8 (mainly in the Adrar des Iforas and Air Mountains); and one in Egypt, Libya, Niger and Mali.
9 In Morocco, these genetic lineages correspond to distinct morphometric groups. The rise of
10 these lineages was probably caused by the combined effects of habitat changes and marine
11 transgressions, notably on the Atlantic Moroccan coast, during the successive cycles of
12 cooling and warming that characterized the end of the Pleistocene. Large rivers, such as the
13 Moulouya, Bou Regreg and Sebou rivers in Morocco, may also have contributed to the
14 present phylogeographic pattern. Populations were probably restricted to distinct areas
15 during unfavorable periods of the Pleistocene, leading to allopatric differentiation, and
16 expanded again during more favorable periods.

17 Such east vs west phylogeographic divergence was also observed among amphibians and
18 squamates (see examples and references listed in Nicolas *et al.*, 2014b, p. 247). For these
19 groups, however, the divergence events appear more ancient (Messinian Salinity Crisis or
20 Plio-Pleistocene boundary), suggesting different causes for the initial differentiation and
21 subsequent preservation of the east and west lineages in climatic refugia in the west and the
22 east of the Maghreb (Beddek *et al.*, 2018).

23 For instance, modern populations of the frog *Pelophylax saharicus* (Nicolas *et al.*, 2015a)
24 belong to two main clades (one in Morocco, one in Algeria and Tunisia) that may have split
25 around 2.6 Mya, and whose divergence may have been reinforced by Pleistocene climatic
26 changes. In addition, the Moroccan clade shows genetic differentiation between the
27 populations north and south of the Atlas (Lansari *et al.* 2015).

28 Among painted frogs (*Discoglossus*), there is a strong phylogeographic structuration
29 between western Morocco on the one side (*D. scovazzi*), and eastern Morocco, Algeria and
30 Tunisia on the other (*D. pictus*), without any sympatry (Zangari *et al.*, 2006; Vences *et al.*,
31 2014). Vences *et al.* (2014) have shown that it is probably not the Moulouya River itself that
32 played the role of biogeographic barrier, but rather the wide arid valley extending along
33 much of the river. Within Morocco, these authors have also shown a weak phylogeographic
34 structure of *D. scovazzi*, with the exception of populations from high elevations in the Atlas
35 Mountains, suggesting these populations originated from an ancestral population that
36 diverged in a refugial area, possibly located in the Atlas.

37 On the contrary, other species show very weak intraspecific differentiation across North
38 Africa, notably among toads: *Bufo boulengeri* (Nicolas *et al.*, 2018) and *Sclerophrys*
39 *mauritanicus* (Nicolas *et al.*, unpublished). This low genetic diversity at a continental scale
40 contrasts with the east–west divergence that has been commonly found in other
41 phylogeographic studies. We hypothesize that a combination of high vagility and

1 continuously suitable habitats across North Africa during glacial and interglacial periods
2 facilitated species dispersal and the subsequent gene flow, which could explain the unusual
3 lack of mitochondrial differentiation between eastern and western North Africa.

4 5 *3.2. Regional faunal differences within Morocco*

6
7 In addition to major faunal differences at a continental scale between western and eastern
8 northwestern Africa, regional differences can also be recorded. This is particularly true in
9 Morocco, which is today characterized by a high geographical, climatic and ecological
10 diversity, leading to strong habitat heterogeneities throughout the territory, which probably
11 existed in the past too.

12 In order to highlight potential “palaeo-ecozones”, we performed a Correspondance Analysis
13 based on the micromammal faunal lists (presence/absence of species; PAST software) of the
14 main Moroccan Late Pleistocene and Holocene sites for which microvertebrates have been
15 studied, irrespective of their chrono-cultural attribution (Figure 2).

16 We observed a clear discrimination between sites located on the Atlantic Coast and those
17 located in northern and eastern Morocco, regardless of their age. For example, the eastern
18 sites (Taforalta, Guenfouda, Ifri N’Ammar, Rhafas) are characterized by the presence of taxa
19 such as *Elephantulus/Petrosaltator* and *Ctenodactylus*, which we do not find in western or
20 northern parts of Morocco (Aulagnier *et al.*, 2017). This result may reflect the impact of the
21 Atlas and Rif Mountains, but also bioclimate and relative humidity, on the microvertebrate
22 communities. For example, *Ctenodactylus gundi* is associated with the arid bioclimatic zones,
23 in areas receiving between 50 and 400 mm of mean annual precipitations (MAP) –
24 hygrometry is too high for this species near the Atlantic and Mediterranean coasts.
25 *Elephantulus rozeti* has a wider distribution because it is more tolerant to humidity; it
26 frequents the semi-arid bioclimatic zones and its distribution corresponds to the limit of 400
27 mm MAP. Phylogeographic studies have also highlighted the recent role of the Moulouya
28 valley as an ecological barrier, isolating eastern Morocco from the rest of the country,
29 leading to a closer resemblance with the Algerian and even Tunisian fauna (see previous
30 chapter).

31 Considering the geographic and habitat heterogeneities inside Morocco, and more generally
32 in northwestern Africa, we conclude that climatic changes were acting differently in different
33 regions, and that small vertebrate faunas presented different responses. Thus, for the
34 palaeoecological interpretations and comparisons between sites to be valid, it is important
35 to consider different regional bioclimatic areas.

36 More numerous data from sites located in different bioclimatic areas are needed to better
37 understand this issue and describe the existence of other “ecozones”, notably in more
38 southern and arid areas.

39 40 *3.3. Late Pleistocene palaeoenvironmental reconstructions in Atlantic Morocco*

41

1 Throughout the Quaternary, northwestern Africa went through alternations of arid and
2 more humid periods, accompanied by modifications in the environment, such as more open
3 steppic habitats during arid periods, and more ponds, grasslands, and more or less densely
4 wooded areas during humid periods (e.g., Hooghiemstra *et al.*, 1992; DeMenocal, 1995,
5 2004; Carto *et al.*, 2009; Trauth *et al.*, 2009; Stoetzel *et al.*, 2011a). Along the North Atlantic
6 coast of Morocco, altitudinal variations are both due to regional tectonic events (e.g., Chabli
7 *et al.*, 2014) and sea level variations influenced by global climatic changes, which may have
8 impacted both the landscape and cave occupations by humans and other predators (Stoetzel
9 *et al.*, 2014; Campmas *et al.*, 2015).

10 At El Harhoura 2, the standard analyses of microvertebrate assemblages were
11 complemented by isotopic analysis on rodent teeth in order to better assess palaeoclimatic
12 fluctuations. Stable carbon (^{13}C) and oxygen (^{18}O) isotopes were explored both on modern
13 and fossil *Meriones gr. shawii-grandis* (Jeffrey *et al.*, 2015; Jeffrey, 2016). Results showed
14 that the ^{18}O composition of *Meriones* teeth was strongly correlated with mean annual
15 precipitation (MAP), reflecting moisture availability (or lack of it) in arid settings. The $\delta^{13}\text{C}$
16 values of the *Meriones* teeth reflect the dietary inputs of C_3 and C_4 plants; however, arid and
17 mesic sites could not be distinguished because of the high variability displayed by the ^{13}C
18 composition. At El Harhoura 2, isotopic analyses indicated that levels 11 to 7 (dated to MIS
19 5) encountered more humid conditions than today, while levels 6 to 3 (dating from MIS 5 to
20 3) presented conditions similar to the present day, indicating a relatively open environment
21 throughout the Late Pleistocene. Level 2 (dated to MIS 2) appears more arid, which is
22 consistent with the MIS 2 aridification of the region (for datings, see Janati-Idrissi *et al.*,
23 2012; Jacobs *et al.*, 2012; Nespoulet *et al.*, 2015; Ben Arous, 2016; Ben Arous *et al.*, 2019).
24 This latter period is contemporaneous with a clear cultural change: the end of the Middle
25 Stone Age (MSA) Aterian culture and the appearance of the Late Stone Age (LSA)
26 Iberomaurusian culture (e.g., Linstädter *et al.*, 2012; Stoetzel *et al.*, 2014).

27 When comparing these results with previous palaeoecological data (Stoetzel *et al.*, 2011a,
28 2012a; [Figure 3](#)) we observe common trends, but also some discrepancies, notably in levels
29 7, 6 and 5: isotopic results indicate relatively humid conditions in levels 7 and 5 and more
30 arid ones in level 6, while faunal communities indicate the opposite. These discrepancies
31 could be due to several causes, notably differences in the signals recorded from a set of
32 species communities and those from individuals within a single species which can adapt
33 differently to environmental changes. Moreover, carbon isotopes may either reflect the
34 arid/open C_3 vegetation around the cave, or just the preferred habitats and diet of *Meriones*.
35 Each of the methods mentioned before has its own biases. For faunal abundance analyses,
36 we have to work with the material that is brought into the site by predators, and that may
37 not faithfully reflect the biocenosis. Several parameters may impact oxygen isotope
38 composition – e.g., source and amount of precipitation, and pathway of moisture impact
39 strongly on Rayleigh distillation; at groundlevel there are effects related to soil moisture and
40 evapotranspiration in plants. Further calibration analyses still need to be performed to refine
41 isotopic analyses. Nevertheless, these results are consistent with the fact that C_3 vegetation

1 dominated throughout the Late Pleistocene, and that such a coastal region never
2 experienced the hyper-aridity associated with the present desert steppe environments south
3 of the Atlas Mountains and in eastern Morocco (Jeffrey, 2016; Jeffrey *et al.*, 2016).
4 Consequently, the North Atlantic Coast of Morocco would have played the role of refugia for
5 some species during arid periods.

7 3.4. Demographic history of Moroccan rodent populations

9 Multidisciplinary analyses can also infer the demographic history of populations, and the
10 assessment of the relative role of climate and humans in detected population size changes.

11 The rodent *Mus spretus* is an example, as fossil data (Stoetzel *et al.*, 2011a), geometric
12 morphometry on molars (Stoetzel *et al.*, 2013), genetic analyses and ecological niche
13 modelling (Lalis *et al.*, 2019) are all available. From the Late Pleistocene onwards, we
14 observe very few molar size and shape variations until the Middle Holocene, despite several
15 climatic changes. This is consistent with genetic and climatic niche modeling analyses,
16 showing that climatically suitable habitats probably occurred in the Rabat region throughout
17 the Late Quaternary, which explains the relative stability in the species representation
18 observed in the El Harhoura 2 cave. Morphometric analysis has shown a recent, post-
19 Neolithic size decrease in modern Moroccan populations, together with an increase in
20 morphological variability (Khammes-El Homsy and Aulagnier, 2010; Stoetzel *et al.*, 2013).
21 Genetic analyses have evidenced a Neolithic dispersion from the Maghreb towards Western
22 Europe accompanied by a strong population expansion during the Middle Holocene (~5000
23 years BP), followed by a recent bottleneck in some North African populations (~600 BP). All
24 these recent phenomena (size decrease, demographic collapse) are probably due to the
25 combined effects of global aridification, growing human impact on natural habitats and
26 especially competition and hybridization events with the commensal mouse *Mus musculus*
27 *domesticus*, which probably arrived in northwestern Africa 3000 years ago, after the first
28 millennium BC (Orth *et al.*, 2002; Bonhomme *et al.*, 2011; Cucchi *et al.*, 2012; Stoetzel *et al.*,
29 2013; Lalis *et al.*, 2019).

30 Similar studies were performed on the *Meriones shawii/grandis* complex enabling a better
31 understanding of the demographic and geographic history of this group. In the Late
32 Pleistocene fossil record, *Meriones* were well represented and generally dominated the
33 assemblages. Geometric morphometric analysis of *Meriones* molars from several modern
34 and fossil Moroccan populations (Stoetzel *et al.*, 2017) has shown that during the Late
35 Pleistocene, both *M. shawii* and *M. grandis* were present in western Morocco. Few changes
36 occurred throughout this period despite several climatic changes, indicating that suitable
37 habitats probably always occurred in the region, as was the case for *Mus spretus* (Lalis *et al.*,
38 2019). Fossils from El Harhoura 2 cave, dating from ~5.8 ka BP to at least 44 ka BP, have
39 yielded the oldest ancient DNA sequences obtained from Africa (Guimaraes *et al.*, 2017).
40 Similar clades of *M. grandis* were evidenced both in modern and fossil populations (Lalis *et*
41 *al.*, 2016a; Guimaraes *et al.*, 2017), demonstrating their apparent stability in this area over

1 tens of thousands of years. In addition, during the Middle Holocene, palaeontological and
2 morphometric analyses have evidenced a change in the faunal spectrum and species
3 distribution, with *M. grandis* only represented in Morocco, and *M. shawii* in Algeria and
4 Tunisia, as is the case today (Lalis *et al.*, 2016a; Stoetzel *et al.*, 2017). Statistical analyses
5 based on genetic results indicate a clear demographic collapse during the Early–Middle
6 Holocene (Lalis *et al.*, 2016a). We therefore suggest that during the humid period of the
7 Middle Holocene, when Mediterranean forests expanded, the semi-arid open steppe
8 habitats, more suitable for *Meriones* (Aulagnier *et al.*, 2008), decreased drastically in the
9 northern half of Morocco, leading to population collapses and changes in their geographic
10 distribution. *Meriones* of the *shawii/grandis* complex were not able to extend their range
11 further south, where other more arid-adapted *Meriones* species already occurred (*M.*
12 *crassus*, *M. libycus*). This may have led to a west–east re-organization of the *M.*
13 *shawii/grandis* distribution, maintained with the subsequent establishment of a marked arid
14 zone in the Moulouya Valley of eastern Morocco. Present-day *Meriones* are very common in
15 cultivated and abandoned fields, representing a major pest for farming communities in
16 North Africa (e.g., Adamou-Djerbaoui *et al.*, 2010, 2013; Ghawar *et al.*, 2011; Derbali *et al.*,
17 2012). We therefore hypothesize that after the drastic decrease and species shift in the
18 Middle Holocene, *Meriones* were able to profit from both the increasing aridity and the
19 development of agriculture since the Neolithic (Lalis *et al.*, 2016a; Stoetzel *et al.*, 2017). This
20 means that, contrary to what is generally expected, recent environmental changes in
21 synergy with anthropogenic pressure could have benefitted the development of some
22 indigenous rodents, like *M. grandis* in Morocco and *M. shawii* in Algeria and Tunisia,
23 although it created disequilibrium in the ecosystem (Stoetzel *et al.*, 2017).
24 Integrative studies combining paleontological, archaeological and genetic data may thus lead
25 to a better understanding of the relative impact of climatic changes and human pressure on
26 the evolution and biogeographic history of several species. They can also allow us to infer
27 the routes and timing of dispersal between distinct regions.

28
29

30 **4. Investigating the roles of climate change and human impact in faunal diversity and** 31 **dispersal in northwestern Africa**

32
33
34

35 *4.1. Intra-African microfaunal (and human) dispersal events*

36 During the whole Quaternary period, North Africa experienced, especially in the Saharan
37 area, several climatic and vegetation changes that had a strong influence on the evolution,
38 adaptation and dispersal of faunas and humans in and out of Africa (e.g., Carto *et al.*, 2009;
39 Trauth *et al.*, 2009; Compton, 2011; Garcea, 2012; Whiting Blome *et al.*, 2012; Drake *et al.*,
40 2013). Morocco, Algeria and Tunisia, located in the extreme northwest of Africa, may have
41 acted as a faunal refuge or a “cul-de-sac” at some periods, especially arid ones. During these
times, any species that was confined by geographical barriers (e.g., Atlas mountains, Sahara,

1 oceans and seas) could have become extinct, or adapted to local environmental pressure,
2 leading to numerous fossil and living endemic species (notably among *Paraethomys*, *Mus*,
3 *Praomys*, *Gerbillus*, *Meriones*, *Crociodura* genera). However, at other times, northwestern
4 Africa may also have acted as a major crossroads of immigration waves from Europe (e.g.,
5 *Apodemus sylvaticus*, *Squamata* spp., *Alytes*, *Pleurodeles*, and possibly *Pelodytes*), the
6 Middle East (e.g., *Eliomys*, *Ellobius*, and possibly *Jaculus*), and tropical Africa (e.g.,
7 *Petrosaltator rozeti*, *Xerus erythropus*, *Mus jotterandi*, *Arvicanthis*, *Lemniscomys*, *Mastomys*,
8 *Golunda*, *Crociodura viaria*, *C. lusitania*, *Bitis*, *Dasypeltis*) (Dobson and Wright, 2000; Stoetzel,
9 2013; Aulagnier *et al.*, 2017; Bailon *et al.*, 2017). Among large mammals, we observe a global
10 “Panafricanism” of the faunas during the whole Quaternary (North African faunas similar to
11 those from East Africa), with only an increase of Eurasian species in North Africa at the end
12 of the Pleistocene (e.g., Geraads, 2002, 2012; Geraads *et al.*, 2010). Large mammals would
13 therefore have always been able to migrate over long distances, leading to continuous
14 exchanges between North and sub-Saharan Africa independently to climatic changes.
15 However, it seems that only the largest, most mobile mammals would have been able to
16 cross large stretches of desert successfully, while smaller mammals would have taken
17 advantage of wetter periods and the development of vegetation, rivers and lakes in the
18 Sahara (Dobson and Wright, 2000; Stoetzel, 2013). Passages along the Atlantic Coast would
19 also have been followed by some small species (Aulagnier, 1992). This was notably the case
20 for *Mastomys erythroleucus*. No fossil specimen was attributed with certainty to this species
21 (Stoetzel 2013), but phylogeographic analyses (Brouat *et al.*, 2009) have shown that modern
22 Moroccan populations, today restricted to the southwestern part of the country, may have
23 encountered a south–north shift of their distribution area during a Late Quaternary humid
24 period, from West to North Africa.

25 The genus *Arvicanthis* is today composed of seven species, all living in sub-Saharan savannas
26 and the Nile Valley (Monadjem *et al.*, 2015). The taxonomic status and geographic
27 distribution of some genetic clades is still debated, notably in East Africa (Bryja *et al.*, 2019).
28 This taxon is today absent from northwestern Africa, but it appeared several times during
29 the Quaternary (Stoetzel, 2013, 2017c), dispersing either along the Atlantic Coast, the Nile
30 Valley and the Mediterranean Coast, or through the Sahara during wet periods. *Arvicanthis*
31 was notably found in the early Late Pleistocene (during MIS 5) in Morocco, most recently in
32 El Mnasra, Rhafas and Taforalt caves (Stoetzel *et al.*, 2018, unpublished data). Genetic
33 studies on modern populations of *Arvicanthis niloticus* show a phylogeographic pattern
34 strongly linked to climatic and vegetation changes (Abdel-Rahman *et al.*, 2008; Dobigny *et al.*,
35 2013). According to these studies, in sub-Saharan Africa, allopatric genetic divergence
36 within savanna refuges occurred during humid periods and dispersal during arid ones. But it
37 is likely that the development of grassland habitats in the Sahara also allowed expansion
38 northwards during humid periods. Moreover, *Arvicanthis niloticus* underwent a major
39 expansion at the Middle–Late Pleistocene boundary (Abdel-Rahman *et al.*, 2008).
40 Considering its current anthropophilic habits, Abdel-Rahman *et al.* (2008) have linked this
41 phase of expansion in *Arvicanthis* populations with the expansion and dispersal of early

1 *Homo sapiens* from East Africa and the increase in human population density. We cannot
2 exclude, however, the hypothesis of “behavioral convergence”, *i.e.* a similar response from
3 *Arvicanthis* and humans to the same environmental change (a more humid period and
4 greening of the Sahara). Whether we consider that rats followed humans, or that they both
5 followed a “common route”, in both cases *Arvicanthis* argues for passages of faunas, and
6 probably of humans, between the south and the north of the Sahara in the early MIS 5. This
7 hypothesis is fully consistent with the presence of numerous contemporary MSA
8 archaeological sites in the Sahara, linked to the development of extensive palaeorivers and
9 palaeolakes (Scerri *et al.*, 2014; Campmas *et al.*, 2017), and the emergence in North Africa of
10 the Aterian culture, which is associated with anatomically modern humans and new cultural
11 innovations, similar to those observed in South Africa at the same period (e.g., d’Errico *et al.*,
12 2009; Campmas *et al.*, 2016, 2017; Will *et al.*, 2019). For now though, the dispersal route(s)
13 remain unknown and we await further studies.

14

15 4.2. Late Quaternary human-mediated dispersal from and towards Europe

16

17 By combining palaeontological, archaeological and genetic data, we were able to show a link
18 between the dispersal of the wood mouse, *Apodemus sylvaticus*, and the diffusion of the
19 Cardial Neolithic from Western Europe to the Maghreb, through the Strait of Gibraltar
20 during the Middle Holocene (Libois *et al.*, 2001; Michaux *et al.*, 2003; Lalis *et al.*, 2016b;
21 Stoetzel, 2017c). This hypothesis was recently confirmed by genomic data from ancient
22 human populations (Fregel *et al.*, 2018). The Middle Holocene coincides with the last climatic
23 optimum, which allowed the development of Mediterranean forests in northwestern Africa,
24 probably facilitating the establishment of this semi-arboreal rodent there. Interestingly, the
25 Algerian mouse, *Mus spretus*, followed the reverse path to Western Europe from
26 northwestern Africa during the same period (Lalis *et al.*, 2019), evidencing the existence of
27 two-way exchanges through the Strait of Gibraltar in the Middle Holocene.

28 Other examples of recent dispersal can be found among Eulipotyphla. *Atelerix* sp. is
29 represented in the northwestern African fossil record since the Early Pleistocene (Stoetzel,
30 2013). Today, the Algerian hedgehog, *Atelerix algirus*, can also be found in the eastern
31 Iberian Peninsula (Aulagnier *et al.*, 2008). Genetic studies (Khaldi *et al.*, 2016) support the
32 recent colonization of Spain, and the Balearic and Canary Islands by this species (Holocene),
33 probably mediated by humans. Osteological data from archaeological and recent contexts
34 confirm the results of molecular studies (Hutterer, 1983; Borg, 2005; Morales and Rofes,
35 2008).

36 The greater white-toothed shrew, *Crocidura russula*, is known in northwestern Africa since
37 the Early Pleistocene (Stoetzel, 2013), and is today widespread in Western Europe (Aulagnier
38 *et al.*, 2008). When taking into account the whole fossil record, Rofes and Cuenca-Bescós
39 (2011) indicated that *C. russula* is known in Western Europe from the Middle Pleistocene
40 onwards, or even from the Early Pleistocene in Italy (only one record; Pasa, 1947). These
41 authors propose that the first waves of dispersal from Africa to Europe occurred during the

1 Early Pleistocene through the Middle East, rather than through the Strait of Gibraltar.
2 However, this hypothesis is not supported by genetic data. Phylogeographic studies
3 performed by Cosson *et al.* (2005) have proved the North African origin of *C. russula*, which
4 seems to have reached the Iberian Peninsula only during the Late Pleistocene, probably by
5 crossing the Strait of Gibraltar by natural or, more probably, anthropic overwater dispersal.
6 New phylogeographic and demographic analyses have confirmed the colonization of Europe
7 by *C. russula* via the Strait of Gibraltar in recent times from a reduced number of individuals
8 (Nicolas *et al.*, 2015b). The discrepancy between the European fossil record and genetic data
9 can have several causes. On the one hand, the identification of fossil shrew species and the
10 assignment of fossil records to present species is not always straightforward for such old
11 periods. Even the taxonomy of actual *Crociodura* species is often challenging, as seen for *C.*
12 *pachyura* for example (Nicolas *et al.*, 2014a). On the other hand, the genetic data of present-
13 day populations cannot exclude that some populations could have migrated in Europe
14 without leaving any descendants or trace in the genome of the sampled populations. More
15 European populations need to be analysed. It could be that either there are new
16 undescribed fossil species, or their history is much more complicated than reconstructed
17 based on the genetics of present-day populations. But the question cannot be solved using
18 the current state of knowledge and therefore calls for the paleogenomic analysis of fossils.
19 Concerning the herpetofauna, we take the example of the Mediterranean tree frog, *Hyla*
20 *meridionalis*. This species is found today in northwestern Africa and in southwestern Europe.
21 Dufresnes *et al.* (2019) recognized two main clades within North African *Hyla*, separating the
22 populations of Tunisia and Algeria as a distinct species, *Hyla carthaginiensis*. Thus, *Hyla*
23 *meridionalis* is now limited to the populations from Morocco, the Canary Islands and
24 southwestern Europe. The relationship with the European populations is complex, and at
25 least three independent dispersal events were proposed leading to the colonization of Spain,
26 France, Italy, and the Canary Islands (Recuero *et al.*, 2007; Dufresnes *et al.*, 2019). The
27 transportation of frogs by humans from northwestern Africa to Europe is plausible, as the
28 effect of human activity on the distribution of taxa has been especially strong in the
29 Mediterranean Basin (e.g., Cheylan, 1991; Dobson, 1998; Blondel and Aronson, 1999). This
30 was possibly the case for several reptile species, such as *Chamaeleo chamaeleon* (Paulo *et*
31 *al.*, 2002), *Tarentola mauritanica* (Harris *et al.*, 2004), and *Mauremys leprosa* (Verissimo *et*
32 *al.*, 2016). However, dating very recent divergence events is challenging when trying to
33 distinguish Late Pleistocene colonizations from anthropogenic introductions. *Testudo*
34 *graeca*, for example, reached the Iberian Peninsula during the latest Pleistocene, but it
35 remains difficult to ascertain with confidence whether such species naturally crossed the
36 Strait of Gibraltar during low sea level stands or were introduced by humans (Gracia *et al.*,
37 2013).

38

39

40 **5. Conclusion**

41

1 In this paper we have presented a review of the research undertaken in recent years on
2 Quaternary microvertebrates in northwestern Africa, and the interest of combining data
3 from a wide range of disciplines. Studies are still ongoing to obtain more data from
4 palaeontological and archaeological sites located in different bioclimatic areas, in order to
5 better understand environmental changes and their impact on faunal communities and
6 human populations, notably for site occupations, dispersal events and cultural changes. It is
7 also important to consider the whole vertebrate spectrum (mammals, amphibians,
8 squamates, birds, fishes) to obtain complementary results for taphonomic purposes and
9 palaeoenvironmental reconstructions. Collaborations between archaeologists,
10 palaeontologists, biologists and geneticists appear fruitful, with such integrative approaches
11 allowing new interpretations of species evolution over time, their evolutionary relationships
12 with current populations, and changes in their geographical and ecological ranges, which can
13 be influenced by both climate changes and increasing human pressure on the environment.
14
15

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10

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14

15 **Figure captions**

16 Figure 1. Location of the main sites that yielded microfauna, cited in the text, which were
17 studied: a) before 1970, b) between 1970 and 1990, c) between 1990 and 2000, d) between
18 2000 and 2010, e) since 2010.

19 Figure 2. Results from the Correspondance Analysis performed on the micromammal faunal
20 lists (presence/absence of taxa; PAST software) of several Moroccan Late Pleistocene and
21 Holocene sites: CB = Contrebandiers (Reed and Barr, 2010), CHR1 and CHR2 = Chrafate 1 and
22 2 (Ouahbi *et al.*, 2003), DES1 = Dar-es-Soltan 1 (Bouzouggar *et al.*, 2018), EH2-1 to EH2-8 = El
23 Harhoura 2 levels 1 to 8 (Stoetzel *et al.*, 2011a), EM-3 to EM-13 = El Mnasra levels 3 to 13
24 (Stoetzel *et al.*, 2011b, unpublished data), GF = Guenfouda (Lopez-Garcia *et al.*, 2013;
25 Mhamdi and Stoetzel, unpublished data), IB = Ifri el Baroud (Potì *et al.*, 2019), KB = Kehf el
26 Baroud (Ouchaou, 2000), MT = M'Tsogatin (Sens *et al.*, 2016), NAM = Ifri N'Ammar (MSA
27 levels; Hutterer, 2010), OH2 = Oulad Hamida 2 (Raynal *et al.*, 2008; Geraads *et al.*, 2010),
28 RHAF = Rhafas (MSA levels; Stoetzel *et al.*, 2018), TAF = Tatoralt (MSA levels; Bouzouggar *et*
29 *al.*, 2007; Stoetzel, unpublished data), TAM = Tamaris (Bougariane *et al.*, 2010; Geraads *et*
30 *al.*, 2010; Stoetzel, unpublished data), ZRK1 and ZRK—2 = Ez Zarka 1 and 2 (Ouahbi *et al.*,
31 2003).

32 Figure 3. Comparison of palaeoecological data for El Harhoura 2 cave (inspired from Jeffrey,
33 2016, Fig. 7.1, modified): a) Taxonomic Habitat Index based on microfaunal communities
34 (Stoetzel *et al.*, 2011, 2012a, 2014), b) proportion of aquatic species (Stoetzel, 2009), and c)
35 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopic analyses (Jeffrey, 2016), with cultural and chronological context for
36 each studied levels. ^{14}C = radiocarbon dating (Nespoulet *et al.*, 2008, 2015; Ben Arous *et al.*,
37 2019); OSL = Optical Stimulated Luminescence dating (Jacobs *et al.*, 2012); ESR-U/Th =
38 combined Electron Spin Resonance - Uranium series dating (Janati *et al.*, 2012; Ben Arous,
39 2016; Ben Arous *et al.*, 2019).

Figure 1

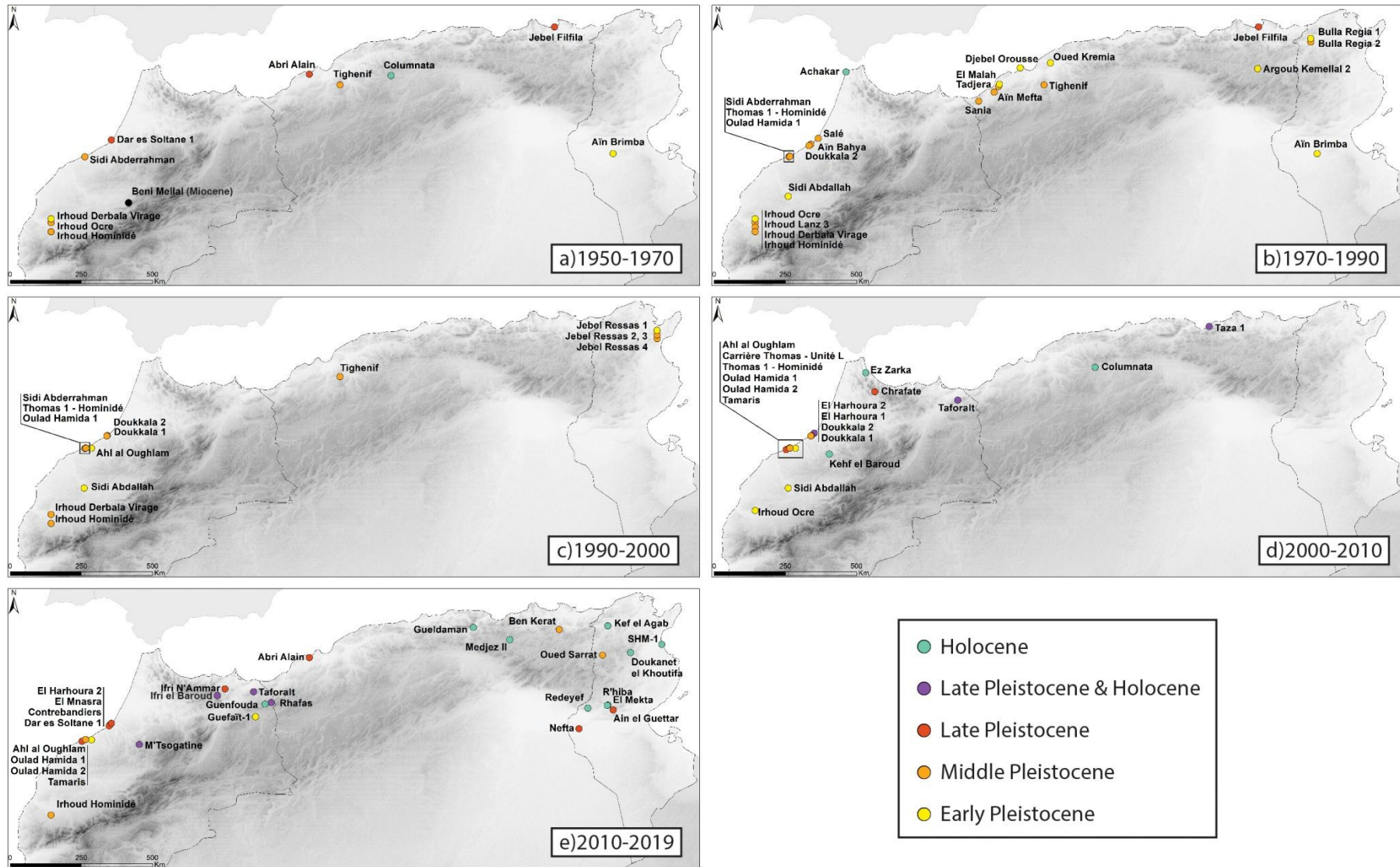


Figure 2

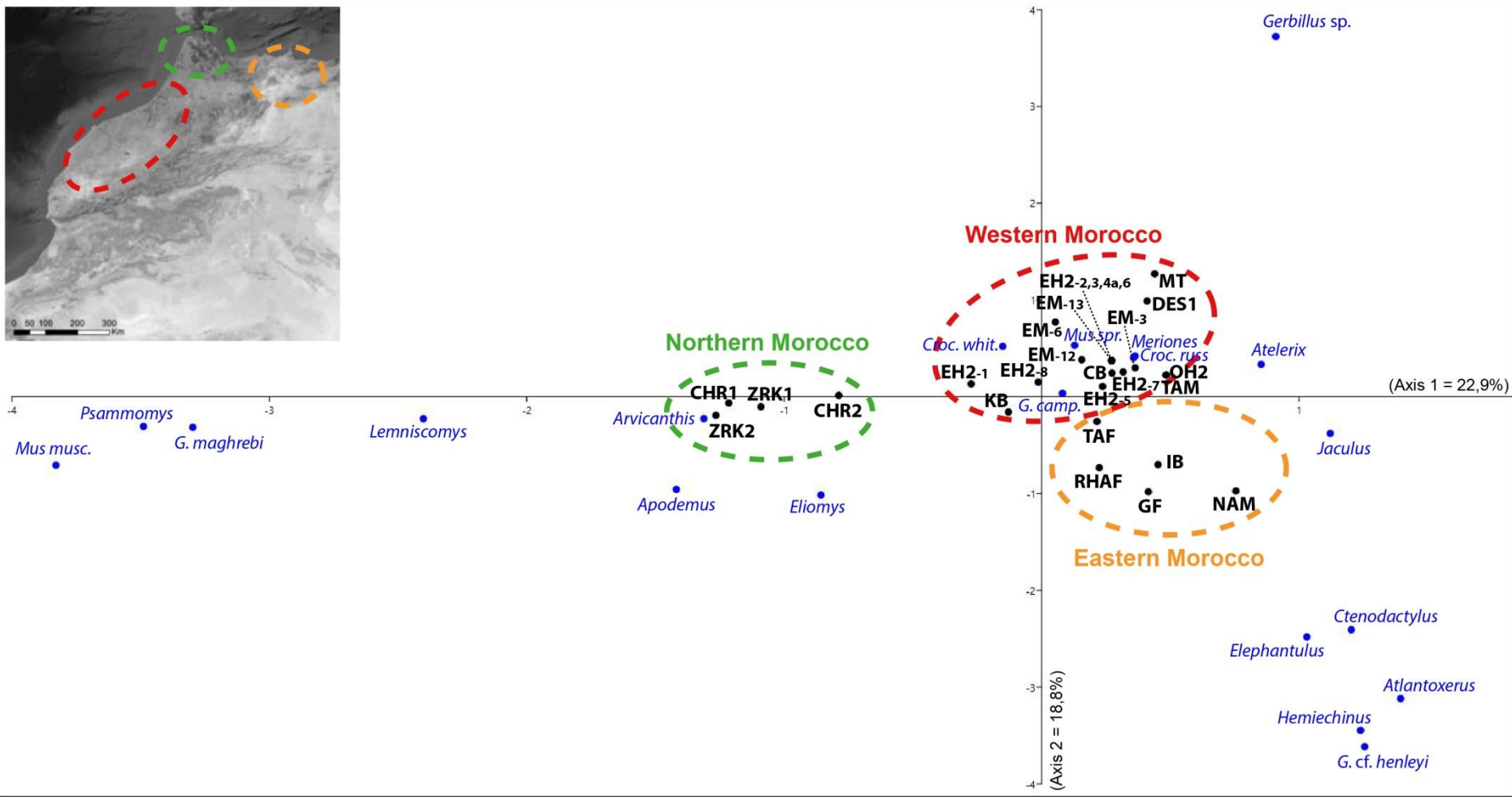


Figure 3

