Research Article

Towards a better knowledge of the molar morphology and ecology of extant and fossil grass rats (Muridae: *Arvicanthis* Lesson, 1842)

Emmanuelle Stoetzel[a]* 🆔, Helder Gomes Rodrigues[b] and Raphaël Cornette[c]

[a]Histoire Naturelle de l'Homme Préhistorique - UMR 7194, CNRS / MNHN / UPVD, Musée de l'Homme—Palais de Chaillot, 17 place du Trocadéro, 75016 Paris, France.; [b]Centre de Recherche en Paléontologie-Paris - UMR 7207, CNRS / MNHN, CP38, 8 rue Buffon, 75005, Paris, France. and [c]Institut de Systématique, Evolution, Biodiversité - UMR 7205, CNRS / MNHN / EPHE / Université des Antilles, CP50, 57 rue Cuvier, 75005 Paris, France.

Abstract

African rodents of the genus *Arvicanthis* are presently restricted to sub-Saharan savannas and to the Nile Valley. In contrast, their distribution during the Quaternary included most of northern Africa, leading to the emergence of local fossil species. To date, there have been no comprehensive studies of *Arvicanthis* populations in northern Africa, neither to clarify their taxonomy nor their paleoecology. The present study aims to explore both morphology and diet of modern and fossil *Arvicanthis* species using geometric morphometric and dental microwear analyses on first upper molars. The geometric morphometric analysis efficiently discriminates the studied extant and fossil *Arvicanthis* species and allowed for the identification of probable geographical variations within the *A. niloticus* group. Although all extant species of the genus *Arvicanthis* are predominantly grass-eaters, microwear analyses also highlighted diet differences in various modern populations of *A. niloticus*, as well as paleodiet inferences in the *A. arambourgi* fossil species, but no clear link between molar size or shape and diet can be established. This work helps set the stage for a complete revision of the fossil remains of *Arvicanthis* from northern African Quaternary deposits, and for a better understanding of the geographical and temporal morphological variability of this genus in Africa.

Keywords: Rodents, Africa, Quaternary, Geometric morphometrics, microwear analyses

(Received 22 August 2022; accepted 1 February 2023)

INTRODUCTION

Throughout the Quaternary period, Africa experienced climatic and vegetation changes that had strong influences on the evolution, adaptation, and dispersal of faunas and humans in and out of Africa (e.g., DeMenocal, 1995, 2004; Carto et al., 2009; Trauth et al., 2009; Compton, 2011; Abbate and Sagri, 2012; Whiting Blome et al., 2012; DeMenocal and Stringer, 2016; Lazagabaster et al., 2021). Morocco, Algeria, and Tunisia, located in northwestern-most Africa, may have alternately played the role of "dead-end," refuge area or crossroads for faunas and humans between western Europe, the Near East, and sub-Saharan Africa. During wetter periods, the development of vegetation, rivers, and lakes in the Sahara may have favored the passage of faunas and humans (e.g., Osborne et al., 2008; Castañeda et al., 2009; Balter, 2011; Garcea, 2012; Coulthard et al., 2013; Drake et al., 2013; Scerri, 2017). These events can be documented through the study of fossil faunas, and especially micromammals such as rodents, found in archaeological sites. Indeed, rodents are recognized as good paleoenvironmental proxies (e.g., Chaline, 1972, 1973; Avery, 1982; Andrews, 1990; Cuenca-Bescos et al., 2011; Stoetzel, 2017), and can help us to better understand human population movements and their effect on the environment (e.g.,

Abdel Rahman et al., 2008; Jones et al., 2013; Stoetzel, 2017; Weissbrod et al., 2017; Cucchi et al., 2020; Lazagabaster et al., 2021).

We investigate here fossil and extant specimens of the Grass Rat *Arvicanthis*, which is a good example to address issues related to dispersal events and relationships to environmental changes and human populations through time in Africa. The genus *Arvicanthis* most probably originated in eastern Africa during the Mio-Pliocene transition (Winkler, 2002; Manthi, 2007) and is today represented by (at least) seven species: *A. abyssinicus*, *A. ansorgei*, *A. blicki*, *A. nairobae*, *A. neumanni*, *A. niloticus*, and *A. rufinus* (Musser and Carleton, 2005; Monadjem et al., 2015; Denys et al., 2017). However, the taxonomic status of some taxa is still debated, notably in western (Happold, 2013) and eastern (Castiglia et al., 2006; Bryja et al., 2019) Africa, where several cryptic species seem to exist, and relationships between most species are not yet resolved. The data also suggest a rapid radiation, probably during the Early–Middle Pleistocene (Bryja et al., 2019). Now restricted to sub-Saharan savannas and the Nile Valley, its past distribution during the Pleistocene and the Early Holocene included parts of the Middle East and northern Africa (Tchernov, 1968, 1975; Jaeger, 1975; Stoetzel, 2013, 2017).

Genetic studies on modern populations of *A. niloticus* showed a phylogeographic pattern that suggests a strong link to climatic and vegetation changes through the Quaternary (Abdel Rahman et al., 2008; Dobigny et al., 2013; Bryja et al., 2019). According to these studies, in sub-Saharan Africa, allopatric genetic divergence within savanna refugia occurred during humid periods

Table 1. Modern and fossil *Arvicanthis* specimens used in the present study. N. sp. = number of specimens, GM = geometric morphometrics, Mw = microwear analyses. Detailed list of specimens in Appendix (Supplementary Table 1).

Species	Modern/fossil	Country	N. sp. GM	N. sp. Mw
Arvicanthis abyssinicus	modern	Ethiopia	13	17
Arvicanthis ansorgei	modern	Mali	15	17
Arvicanthis blicki	modern	Ethiopia	19	17
Arvicanthis neumanni	modern	Ethiopia	13	10
Arvicanthis niloticus	modern	Niger	16	18
Arvicanthis niloticus	modern	Mali	12	11
Arvicanthis niloticus	modern	Sudan	23	21
Arvicanthis arambourgi	fossil	Algeria	24	14
TOTAL			**135**	**125**

(development of forests, reduction and fragmentation of savannas), while dispersals occurred during arid periods (reduction of forests and expansion of savannas). But it is likely that the development of grassland habitats in the Sahara also allowed expansion across this area during humid periods. Moreover, this rodent has undergone a major population expansion at the Middle-Late Pleistocene boundary, corresponding in time with the expansion of early *Homo sapiens* within and out of Africa (Abdel Rahman et al., 2008; Weissbrod and Weinstein-Evron, 2020).

To date, there have been no comprehensive studies of *Arvicanthis* populations in northern Africa, either to try to clarify specific attributions or to better understand how these savanna rodents adapted to steppe and Mediterranean environments in regions farther north than their current distribution. A local endemic species, *A. arambourgi*, has been described in the Early–Middle Pleistocene site of Tighennif in Algeria (Jaeger, 1975), and another one, *A. ectos*, has been described in the Levant for the Middle Pleistocene (e.g., Tchernov, 1968, 1975). But most of the remains coming from the other sites North of the Sahara were assigned to *Arvicanthis* sp. or *A. niloticus*, without thorough analysis.

The aim of the present study is not to solve the current taxonomic issues related to the genus *Arvicanthis*, but to find a method to efficiently discriminate both extant and extinct species on the basis of molar shape that will facilitate future analyses of *Arvicanthis* fossil remains. In archaeological and paleontological contexts, complete crania and mandibles are quite rare, while molars (either isolated or in situ) are generally numerous and well preserved, facilitating the use of Geometric Morphometric methods. We also highlight some aspects of the diet and ecological specificities of selected *Arvicanthis* species using molar microwear analyses, with application to the fossil population from Tighennif.

MATERIAL AND METHODS

Modern specimens

The current reference specimens used for Geometric Morphometrics (GM) and microwear analyses come from the rodent collections of the Muséum national d'Histoire naturelle (MNHN) of Paris. As far as possible, we used the same specimens for both GM and microwear analyses, but more specimens were considered for GM in order to enhance the significance of discrimination.

Five species of *Arvicanthis* from different localities in Africa were considered for this study (Table 1; Figs. 1, 2): *A. abyssinicus* and *A. blicki* (both endemics of Ethiopia), *A. neumanni* (eastern Africa), *A. ansorgei* (western Africa), and four populations of the widespread *A. niloticus*. No specimen was available or usable for *A. nairobae* (eastern Africa) or *A. rufinus* (western Africa). Data concerning the distribution and ecology of extant species mainly come from the International Union for Conservation of Nature (IUCN) database (www.iucnredlist.org) and Monadjem et al. (2015), as well as more specific references when cited.

Fossil specimens

Various paleontological and archaeological northern African sites have yielded *Arvicanthis* remains (Stoetzel, 2013, 2017), but generally in low numbers, preventing any analysis at a populational level. One of the possible explanations for the scarcity of *Arvicanthis* remains may be the diurnal habits of this rodent, which meant they were likely not often hunted by owls, the major accumulators of small mammal assemblages. However, in other geographical areas, *Arvicanthis* remains are well represented in fossil assemblages produced by owls (e.g., Stoetzel et al., 2018). Another explanation would be that this sub-Saharan rodent, which has only made occasional incursions into the region, would have been much less abundant in the environment than the local rodent species, notably Gerbillinae. It is also less likely that remains of *Arvicanthis* would be fossilized and preserved if the incursion of this taxon in the region was brief.

Only two Middle Pleistocene sites from northwestern Africa have yielded large numbers of *Arvicanthis* remains: Tighennif in Algeria (N = 457) and Irhoud Derbala Virage in Morocco (N = 67), both studied by Jaeger (1975). Both collections were supposed to be stored at the Institut des Sciences de l'Evolution de Montpellier (ISEM, France), but only the Tighennif collection could be analyzed for the present study (Table 1), while the *Arvicanthis* remains from Irhoud Derbala Virage currently are not accessible.

Geometric morphometrics

Geometric morphometric (GM) methods represent useful tools to precisely quantify and describe anatomical shapes of biological objects (e.g., Zelditch et al., 2012; Adams et al., 2013). Several studies in classical and geometric morphometrics have been carried out on *Arvicanthis* (Bekele et al., 1993; Corti and Fadda,
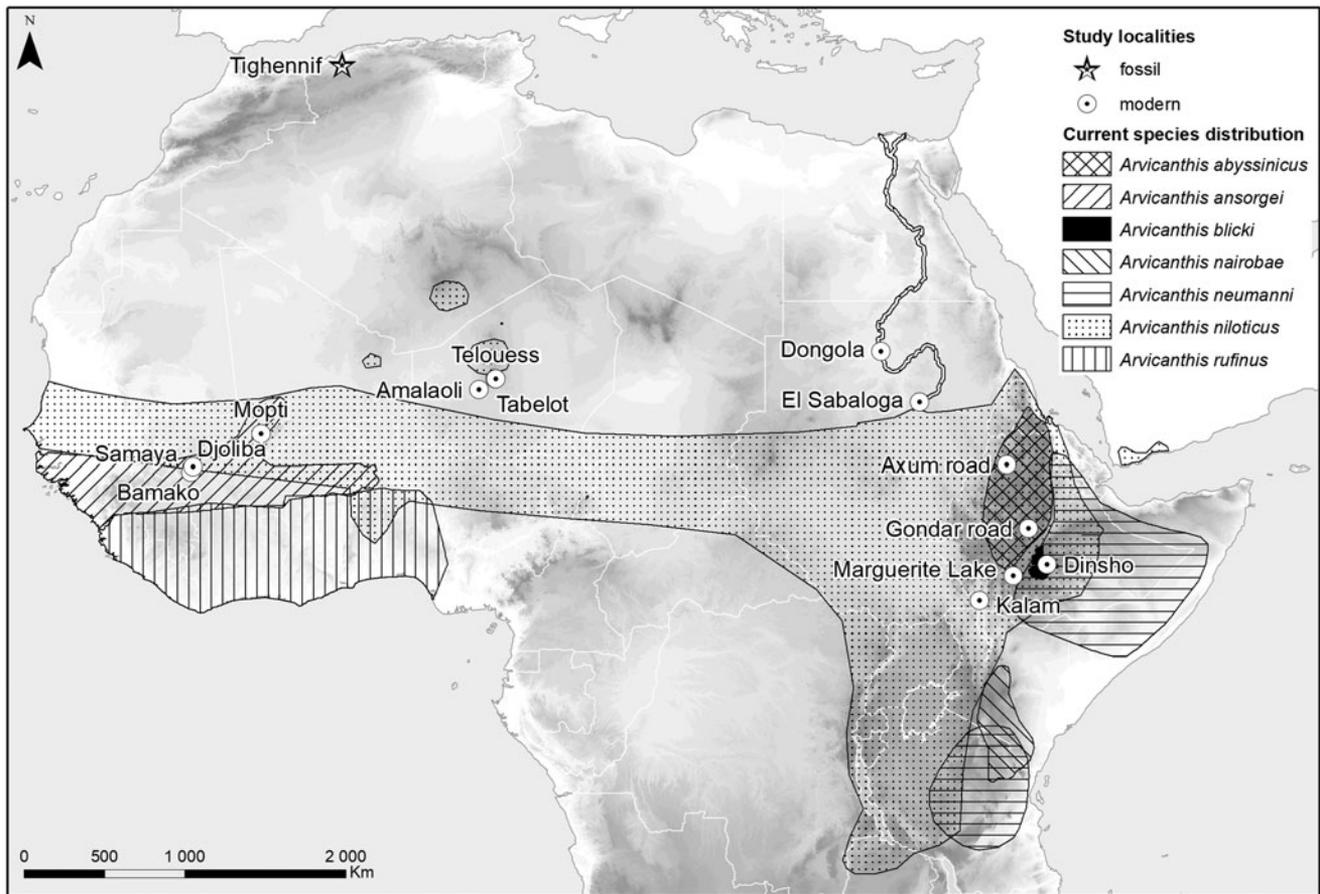
Figure 1. Current distribution of the modern *Arvicanthis* species and localities from which the modern and fossil *Arvicanthis* specimens used in the present study originate.

1996; Fadda and Corti, 2001), but they have focused mainly on the skull. These studies are unlikely to be applicable in archaeological or paleontological contexts, because complete skulls are extremely rare, and the best preserved and most abundant identifiable remains are usually isolated molars or in situ molars embedded in fragmented mandibles and maxillae. Moreover, some authors have shown that in murine rodents the upper molars are more diagnostic and show a faster evolution than the lower molars (e.g., Renaud et al., 1999, 2011), which is why we primarily focused on the first upper molars (M1).

In the present study, we analyze both the outline and the relative position of cusps on M1, by combining anatomical landmarks (LM) and sliding semi-landmarks (SLM) (Gunz and Mitteroecker, 2013), a method that has proven effective in several studies on modern and fossil murid rodents (e.g., Macholan, 2006; Kimura et al., 2013; Stoetzel et al., 2017; Hulme-Beaman et al., 2019; Cucchi et al., 2020). The position of LM was based partially on Janzekovic and Krystufek (2004), Siahsarvie and Darvish (2008), and Matthews and Stynder (2011).

The 11 LM are located on the local maximum curvature of the outline of the *Arvicanthis* M1 associated with cusps and valleys between cusps (Macholan, 2006; Kimura et al., 2013) as follows (Fig. 2):

1. Apex = most anterior point of the prelobe.
2. Maximum curvature of the valley between the prelobe and the cusp t1.

3. Maximum curvature of the valley between cusps t1 and t4 = most posterior point of the cusp t1 on the outline of the tooth.
4. Maximum curvature of the valley between cusps t4 and t8 = most posterior point of the cusp t4 on the outline of the tooth.
5. Maximum curvature of the valley between cusps t8 and t9 = junction between t8 and t9.
6. Most posterior point of the cusp t6 on the outline of the tooth.
7. Maximum curvature of the valley between cusps t6 and t3 = most posterior point of the cusp t3 on the outline of the tooth.
8. Junction between cusps t3 and t2.
9. Junction between cusps t2 and t1.
10. Junction between cusps t6 and t5.
11. Junction between cusps t5 and t4.

In addition, a series of 60 SLM was placed between the LM along the outline of the tooth (Fig. 2), which makes a total of 71 points.

After verification of their state of preservation, the fossil and recent *Arvicanthis* molars were photographed following a precise protocol allowing GM analyses. The photographs were all taken by the same person (E.S.) and with the same equipment (Nikon D750FX camera with a macro lens 85mm 1:3.5 G positioned on a stand with double side lighting or in a lightbox). A picture of
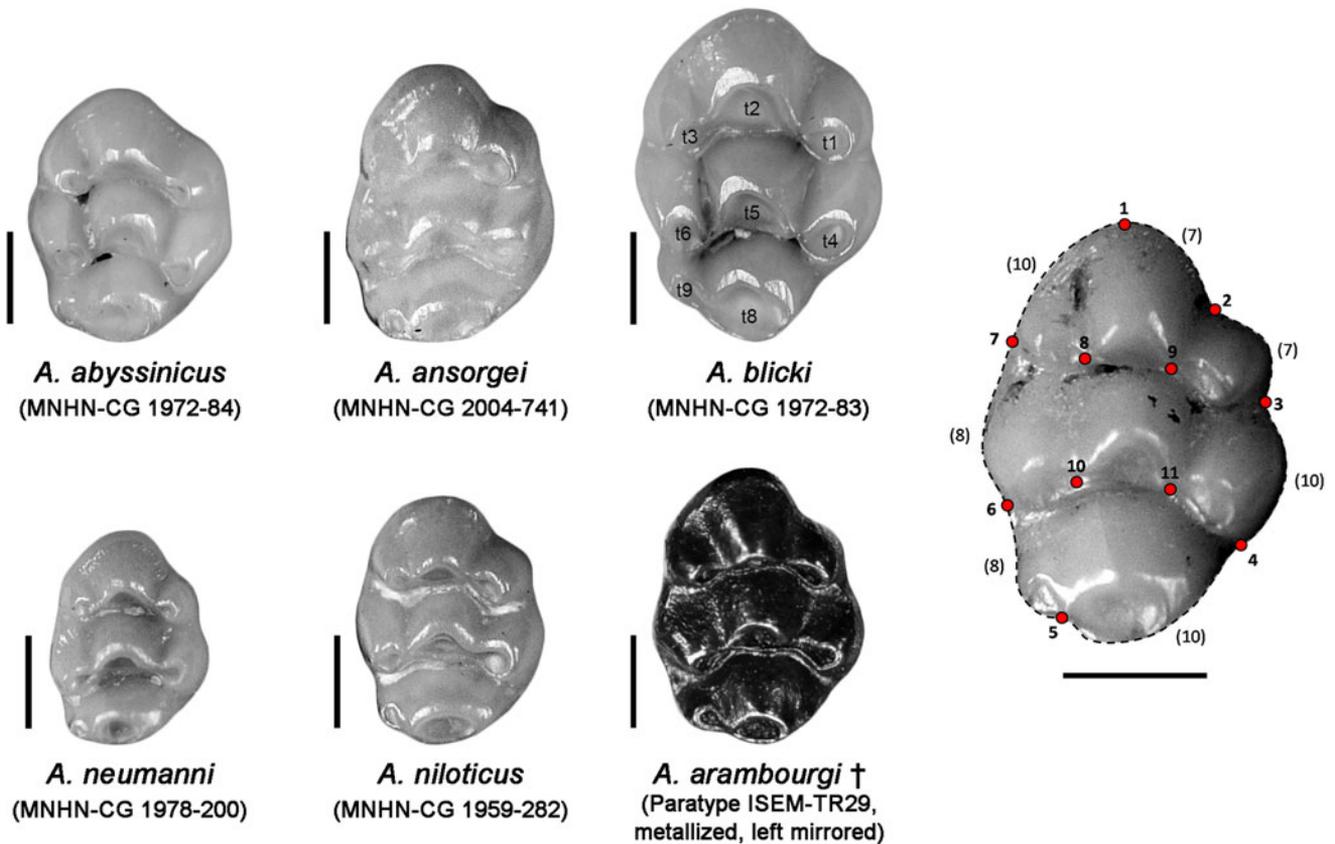
Figure 2. Examples of right first upper molars of each studied modern and fossil *Arvicanthis* species, nomenclature of cusps (t1–t9), and positions of the landmarks (LM, red points) and sliding semi-landmarks (SLM, dashed lines, numbers in parentheses) used in this study. CG = collection number of the MNHN specimens; TR = collection number of the ISEM specimen. Scale = 1 mm.

the same ruler was taken at each session in order to check the scale. Each tooth was positioned with the most horizontal occlusal surface possible. Only the right side was considered, except for modern specimens in which the right M1 was absent or damaged, and fossils, for which all molars have been considered. In these cases, the picture of the left side was mirrored before positioning LM and SLM. To avoid any bias related to the age of the individuals, only sub-adults and adults were considered (thus excluding juveniles and old individuals). Age classes were based upon tooth-wear stages (juvenile: distinct cusps and incipient wear, m3/M3 unerupted or partially erupted; sub-adult: little wear beginning to unite cusps into laminae, exposed dentine of the cusps not yet fused; adult: intermediate wear, cusps united transversely but still discernible, dentine-bridge between the cusps becomes progressively wider as the cusps wear down; old: advanced wear, cusps no longer discernible, different rows/laminae become confluent).

The image set was assembled using TpsUtil (Rohlf, 2019a), and LM and SLM were positioned with TpsDig2 (Rohlf, 2017). To remove information on position, scale, and orientation from the Cartesian coordinate configurations, we performed a generalized Procrustes analysis (Rohlf and Slice, 1990) using TpsRelw (Rohlf, 2019b) to produce a new set of shape coordinates. The semi-landmarks were allowed to slide, minimizing the bending energy between each specimen and the mean conformation of all specimens (Bookstein, 1997; Gunz and Mitteroecker, 2013). The resulting Procrustes shape coordinates from this superimposition were used as shape variables for subsequent statistical

analyses. The centroid size was measured using the square root of the sum of the squared distances between each point and the centroid of the configuration.

A standard preliminary repetition procedure of orienting-digitizing and landmark positioning was performed on molars. Three specimens of the same species and from the same locality (*A. niloticus* from Dongola, Sudan) were photographed 10 times, and the LM and SLM were positioned manually on each of the 30 pictures. A Principal Component Analysis (PCA) revealed that the intra-specimen measurement variability, corresponding to the repetition, was significantly lower than the inter-specimen variability (Supplementary Figure 1).

Size differences between groups were investigated using ANOVA with pairwise t-tests using Bonferroni correction. Patterns of shape variation were investigated using a PCA and shape differences between groups were tested using a MANOVA and pairwise comparisons using t-tests with Bonferroni correction. To compare shape differences between modern and fossil specimens or between modern populations, we performed a Canonical Variate Analysis (CVA) on the n axes of the PCA, representing 95% of the total variance (Baylac and Friess, 2005)—in our case, the first 14 axes of the PCA. Because of the potential presence of several clades/species among the *A. niloticus* group (Bryja et al., 2019), the four localities were considered separately, and specific analyses on this group were performed to explore possible population differences. The k-Nearest Neighbors (KNN) algorithm was used to compute the cross-validated correct classification percentages. This method allows us to classify a

particular object in a group, taking into account its KNN by Euclidian distance after a leave-one-out cross validation. This method is less sensitive to small sample size than linear discriminant analysis (e.g., Hanot et al., 2020). In order to increase the efficiency of the discriminations, size was included in the KNN analysis. Statistical analyses and graphical representations were performed using PAST, MorphoJ, and R software programs.

Microwear analyses

Dental microwear patterns reflect abrasion resulting from contact between tooth enamel and food items consumed by an animal in the last few days prior to its death (e.g., Walker et al., 1978; Teaford and Oyen, 1989). The protocol of dental microwear analyses was adapted to muroid rodents in order to infer the dietary habits of extinct or extant taxa (Gomes Rodrigues et al., 2009, 2012, 2013; Renaud et al., 2015; Kerr et al., 2017). Casts of first upper molars (M1) were analyzed using transmitted light stereomicroscopy (LEICA M205C). Three different variables were quantified using ImageJ: the number of fine scratches (Nfs, more numerous in grass-dominated feeders, GDF), wide scratches (Nws, more numerous in fruit-dominated feeders, FDF), and large pits (Nlp, more numerous in animal-dominated feeders, ADF).

A PCA was performed using Statistica on the three microwear variables (Nfs, Nws, and Nlp) to infer the main dietary components of *Arvicanthis* species when compared to the reference database (MUROIDEA, Gomes Rodrigues et al., 2009, 2012, from which two populations of *Arvicanthis niloticus* from Sudan, previously belonging to GDF, have been removed). MANOVA and post-hoc tests, namely multiple means comparison tests, Fisher's least significant difference (LSD), and the more conservative Tukey's honestly significant difference (HSD), were then realized on rank-transformed data (to meet parametric assumptions,

see Conover and Iman, 1981) to test for significant differences with dietary categories and between species.

RESULTS

Geometric morphometrics

The ANOVA performed on the log of the centroid size shows significant differences between groups ($p = 4.85 \times 10^{-61}$). *Arvicanthis blicki* is the largest species, while *A. neumanni* is the smallest (Fig. 3; Table 2). *Arvicanthis abyssinicus* and all the studied populations of *A. niloticus* display a similar mean size, while *A. ansorgei* is a bit larger (but not statistically significant). The fossil species *A. arambourgi* displays a size close to the upper range of *A. ansorgei*.

The MANOVA performed on the shape variables (first 14 axes of the PCA) also reveals significant differences between groups ($p = 1.949 \times 10^{-93}$) (Table 3), and the CVA allows species discrimination (Figs. 4, 5). The negative extremity of the first axis, isolating the largest species *A. blicki*, is characterized by a proportionally wider tooth in its anterior part and thinner in its posterior part, a significantly shorter prelobe, and a more individualized t9 located closer to the t6. Generally, *A. blicki* shows higher, more rounded, and individualized tubercles (t1 and t4 are generally isolated in young individuals). *Arvicanthis arambourgi*, located on the positive parts of the two first axes, plots apart from all the modern species (Fig. 4). On the first axis, at the opposite of *A. blicki*, the fossil species is characterized by a proportionally longer prelobe (but of similar size than most of the other species). On the second axis, compared to all other modern species, *A. arambourgi* shows a more developed t1 and a narrower posterior part (Fig. 5). Generally, the t9 is less reduced than in all the studied modern species. *Arvicanthis ansorgei* and
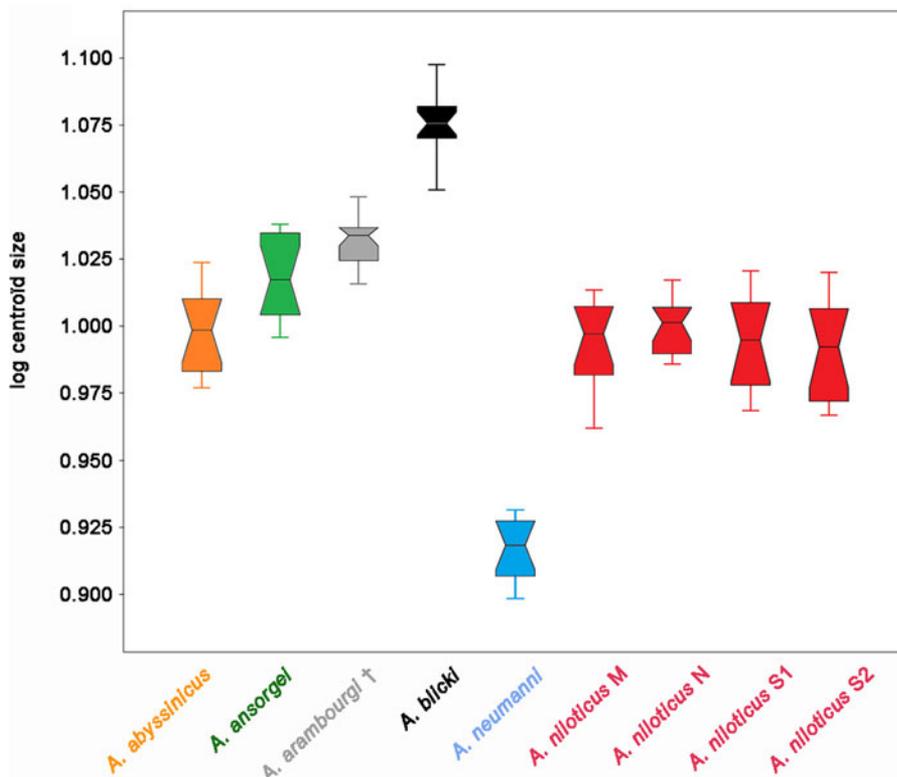

Figure 3. Box plot representation of the size differences (log of the centroid size) between the considered modern and fossil (†) *Arvicanthis* groups. M = Mali, N = Niger, S1 = Sudan (El Sabaloga), S2 = Sudan (Dongola).

Table 2. Results of the ANOVA with pairwise t-tests comparisons on the log of the centroid size of the considered modern and fossil *Arvicanthis* groups. Significant p values (<0.05) are represented in bold.

Bonferroni correction	A. abyssinicus	A. ansorgei	A. arambourgi	A. blicki	A. neumanni	A. niloticus Mali	A. niloticus Niger	A. niloticus Sudan1	A. niloticus Sudan2
								Uncorrected	
A. abyssinicus		**0.005**	**<0.001**	**<0.001**	**<0.001**	0.765	0.709	0.476	0.305
A. ansorgei	0.178		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**0.003**	**0.001**
A. arambourgi	**<0.001**	0.383		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
A. blicki	**<0.001**	**<0.001**	**<0.001**		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
A. neumanni	**<0.001**	**<0.001**	**<0.001**	**<0.001**		**<0.001**	**<0.001**	**<0.001**	**<0.001**
A. niloticus Mali	1	**0.036**	**<0.001**	**<0.001**	**<0.001**		0.501	0.921	0.724
A. niloticus Niger	1	0.079	**<0.001**	**<0.001**	**<0.001**	1		0.329	0.228
A. niloticus Soudan1	1	0.108	**<0.001**	**<0.001**	**0.002**	1	1		0.687
A. niloticus Soudan2	1	0.053	**<0.001**	**<0.001**	**<0.001**	1	1	1	

A. neumanni are well discriminated against each other on the fourth axis. *Arvicanthis neumanni*, the smallest species, is located on the positive part of axis 4 and displays a narrower tooth with a proportionally longer prelobe, and a t6 markedly shifted posteriorly. In *A. ansorgei*, located in the negative parts of axes 3 and 4, the prelobe is relatively short and the t9 appears relatively well developed and slightly offset posteriorly. *Arvicanthis abyssinicus* and *A. niloticus*, generally located in the middle parts of the CVA axes, display similar molar size and morphological features. Although their molars are relatively large with a short prelobe compared to the other species, in *A. abyssinicus*, the tubercules appear less aligned than in *A. niloticus* (especially the t4, which is generally located more posteriorly).

Since size is an important discriminating criterion for some species, we chose to include the log of the centroid size in the CVA analysis in order to increase the efficiency of the discriminations. Applying the KNN method, both on shape and size parameters, we obtained 100% of correct classification for specimens belonging to *A. neumanni* and *A. blicki* (Table 4). The fossil species *A. arambourgi* is well separated from the modern groups (83.3% of correct classification). *Arvicanthis abyssinicus* and *A. ansorgei* give values of 61.5% and 66.7%, respectively. Concerning the *A. niloticus* group, only the population from Niger displays relatively good values of correct classification (68.8%). Most of the misclassified *A. niloticus* specimens fall in other *A. niloticus* populations, or in *A. abyssinicus*.

In order to explore possible population differences within *A. niloticus*, we performed a separate analysis on the four considered populations of *A. niloticus*. While the ANOVA performed on size does not show significant differences (Fig. 3; Table 2), the MANOVA performed on the shape variables reveals significant differences between these four groups ($p = 7.728 \times 10^{-9}$). In

Table 3. Results of the MANOVA with pairwise t-tests comparisons on the shape variables of the considered modern and fossil *Arvicanthis* groups. Significant p values (<0.05) are represented in bold.

| Bonferroni correction	A. abyssinicus	A. ansorgei	A. arambourgi	A. blicki	A. neumanni	A. niloticus Mali	A. niloticus Niger	A. niloticus Sudan1	A. niloticus Sudan2
								Uncorrected	
A. abyssinicus		**0.004**	**<0.001**	**<0.001**	**0.020**	**0.029**	**0.006**	**0.040**	**0.003**
A. ansorgei	0.1467		**<0.001**	**<0.001**	**0.005**	0.073	**0.006**	**0.012**	**0.003**
A. arambourgi	**<0.001**	**<0.001**		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
A. blicki	**0.029**	**<0.001**	**<0.001**		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
A. neumanni	0.728	0.186	**<0.001**	**<0.001**		**0.049**	**0.030**	**0.042**	**0.009**
A. niloticus Mali	1.068	2.628	**<0.001**	**<0.001**	1.769		0.308	0.067	**0.018**
A. niloticus Niger	0.210	0.229	**<0.001**	**<0.001**	1.097	11.105		0.065	**0.016**
A. niloticus Sudan1	1.452	0.440	**0.001**	**<0.001**	1.509	2.397	2.355		0.614
A. niloticus Sudan2	0.103	0.096	**<0.001**	**<0.001**	0.337	0.663	0.563	22.098	
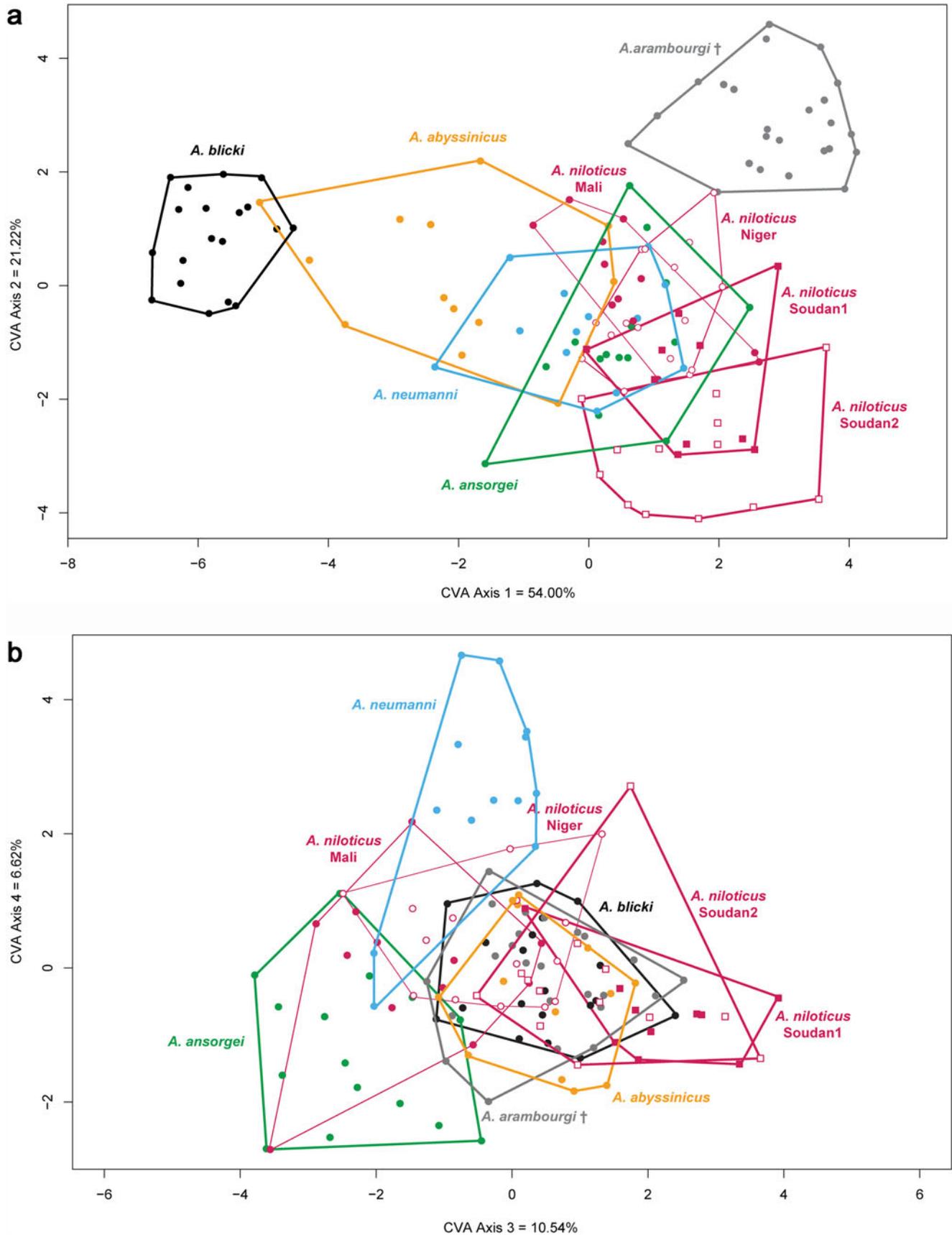
Figure 4. Representation of axes 1 and 2 (**a**) and axes 3 and 4 (**b**) of the Canonical Variate Analysis (CVA) based on the first 14 axes of the PCA.

Figure 5. Reconstruction of the mean shapes at the extremities of the first four axes of the CVA (difference ×5 for a better visualization). Gray = negative extremity of the axes, Orange = positive extremity of the axes.

looking at the pairwise comparisons (Table 5), the two populations from Sudan can be distinguished from the two other populations (Mali and Niger), although these differences are not significant considering the Bonferroni-corrected p-values (Table 5).

Microwear analyses

Dental microwear data quantified for each population of *Arvicanthis* are shown in Table 6, and results of the multivariate analyses based on the number of fine scratches (Nfs), wide scratches (Nws), and large pits (Nlp) are shown in Table 7 and Figures 6 and 7. The global results are relatively homogeneous, however, the post-hoc tests show finer differences, notably concerning the *A. niloticus* specimens coming from Sudan, which were split into two groups according to their origin (S1: El Sabaloga, S2: Dongola). Indeed, most of the studied specimens belonging to modern species such as *A. blicki*, *A. niloticus* (S1, Mali, Niger), *A. abyssinicus*, *A. ansorgei*, and *A. neumanni*

Table 4. Classifications provided by the k-Nearest Neighbors (KNN) method using both size and shape variables (k = 1).

	A. abyssinicus	A. ansorgei	A. arambourgi	A. blicki	A. neumanni	A. niloticus Mali	A. niloticus Niger	A. niloticus Soudan1	A. niloticus Soudan2	% correct
A. abyssinicus	8	0	2	0	0	3	1	0	0	61.54
A. ansorgei	0	10	1	0	0	2	0	0	0	66.67
A. arambourgi	1	1	20	0	0	0	1	0	0	83.33
A. blicki	0	0	0	19	0	0	0	0	0	100.00
A. neumanni	0	0	0	0	13	0	0	0	0	100.00
A. niloticus Mali	1	2	0	0	0	3	1	2	1	25.00
A. niloticus Niger	2	2	1	0	0	3	11	2	2	68.75
A. niloticus Sudan1	1	0	0	0	0	0	0	2	5	20.00
A. niloticus Sudan2	0	0	0	0	0	1	2	4	5	38.46
Total	13	15	24	19	13	12	16	10	13	

Table 5. Results of the MANOVA with pairwise t-tests comparisons on the shape variables of the four *Arvicanthis niloticus* populations. Significant p values (<0.05) are represented in bold.

	Uncorrected			
Bonferroni correction	A. niloticus Mali	A. niloticus Niger	A. niloticus Sudan1	A. niloticus Sudan2
A. niloticus Mali		0.090	0.073	**0.017**
A. niloticus Niger	0.544		**0.046**	**0.010**
A. niloticus Sudan1	0.438	0.279		0.525
A. niloticus Sudan2	0.102	0.059	3.154	

fall into the GDF group (grass-dominated feeders). But the *A. niloticus* specimens coming from Dongola (S2) are clearly included in the FDF group (fruit-dominated feeders). Concerning the fossil specimens of *A. arambourgi* from Tighennif, we see that they do not fall into a precise category according to the statistical tests, even if they tend to be closer to the GDF group (grass-dominated feeders) on the PCA (Fig. 7). They also display the smallest differences with *A. ansorgei* according to the LSD test on the number of fine scratches.

Table 6. Dental microwear data quantified for each population of *Arvicanthis*. Nfs = number of fine scratches, Nws = number of wide scratches, Nlp = number of large pits.

		Mean			Standard deviation		
Species	N	Nfs	Nws	Nlp	Nfs	Nws	Nlp
A. niloticus Sudan 1	10	20.9	2.3	1.5	5.4	1.1	2.0
A. niloticus Sudan 2	11	15.8	8.2	4.7	6.0	3.4	2.6
A. niloticus Mali	11	20.5	1.7	4.4	5.3	1.3	2.7
A. niloticus Niger	18	23.6	2.4	4.9	7.2	1.7	3.1
A. abyssinicus	17	23.8	3.1	3.8	6.2	2.0	2.9
A. ansorgei	17	16.9	3.3	6.3	4.8	2.1	2.0
A. neumanni	10	21.0	3.9	4.4	5.1	2.0	3.0
A. blicki	17	24.9	1.8	2.7	5.7	1.3	2.0
A. arambourgi	14	12.2	2.4	5.5	5.3	1.7	2.4

Table 7. Pairwise comparison tests performed on dental microwear data. ADF = animal-dominated feeders, FDF = fruit-dominated feeders, GDF = grass-dominated feeders, Nfs = number of fine scratches, Nws = number of wide scratches, Nlp = number of large pits. Significance at $\alpha = 0.05$ is indicated in bold for both LSD and HSD tests, and in normal letters for only LSD test.

Diet	ADF	GDF	FDF
A. blicki	**Nfs, Nws, Nlp**	Nfs, Nws	**Nfs, Nws, Nlp**
A. arambourgi	**Nws**, Nlp	**Nfs**, Nws	**Nws**
*A. niloticus*_S1	**Nfs, Nws, Nlp**	Nlp	**Nfs, Nws, Nlp**
*A. niloticus*_S2	Nfs, **Nlp**	Nfs, **Nws**	Nlp
*A. niloticus*_Mali	**Nfs, Nws**, Nlp	Nws	**Nfs, Nws**, Nlp
*A. niloticus*_Niger	**Nfs, Nws, Nlp**	Nws	**Nfs, Nws**, Nlp
A. abyssinicus	**Nfs, Nws, Nlp**		**Nfs, Nws, Nlp**
A. ansorgei	**Nfs, Nws**, Nlp	Nlp	Nfs, **Nws**
A. neumanni	**Nfs**, Nws, **Nlp**		**Nfs, Nws**, Nlp

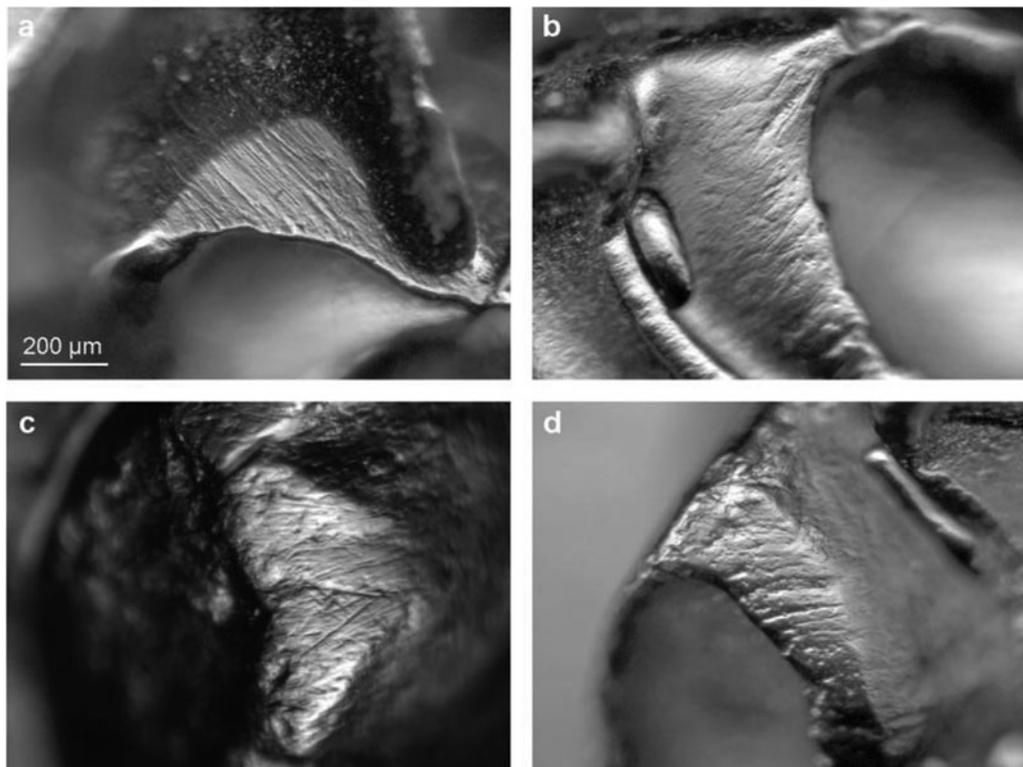|	*A. blicki*	*A. arambourgi*	*A. niloticus*_S1	*A. niloticus*_S2	*A. niloticus*_Mali	*A. niloticus*_Niger	*A. abyssinicus*	*A. ansorgei*
A. arambourgi	**Nfs**, Nlp							
*A. niloticus*_S1		**Nfs**, Nlp						
*A. niloticus*_S2	**Nfs, Nws**	**Nws**	Nfs, **Nws**, Nlp					
*A. niloticus*_Mali		**Nfs**		Nfs, **Nws**				
*A. niloticus*_Niger		**Nfs**	Nlp	Nfs, **Nws**				
A. abyssinicus		**Nfs**		Nfs, **Nws**				
A. ansorgei	Nfs, **Nlp**	Nfs	**Nlp**	**Nws**		Nfs	Nfs, Nlp	
A. neumanni	Nws	**Nfs**	Nlp	Nfs, **Nws**	Nws			

Figure 6. Examples of dental microwear patterns. (**a**) *Arvicanthis blicki* (MNHN-ZM-MO-1972-77), (**b**) *A. niloticus* Niger (MNHN-ZM-MO-1959-267), (**c**) *A. niloticus* Sudan (MNHN-ZM-MO-2003-511), (**d**) *A. arambourgi* (UM 7). Scale for all images shown in (**a**).
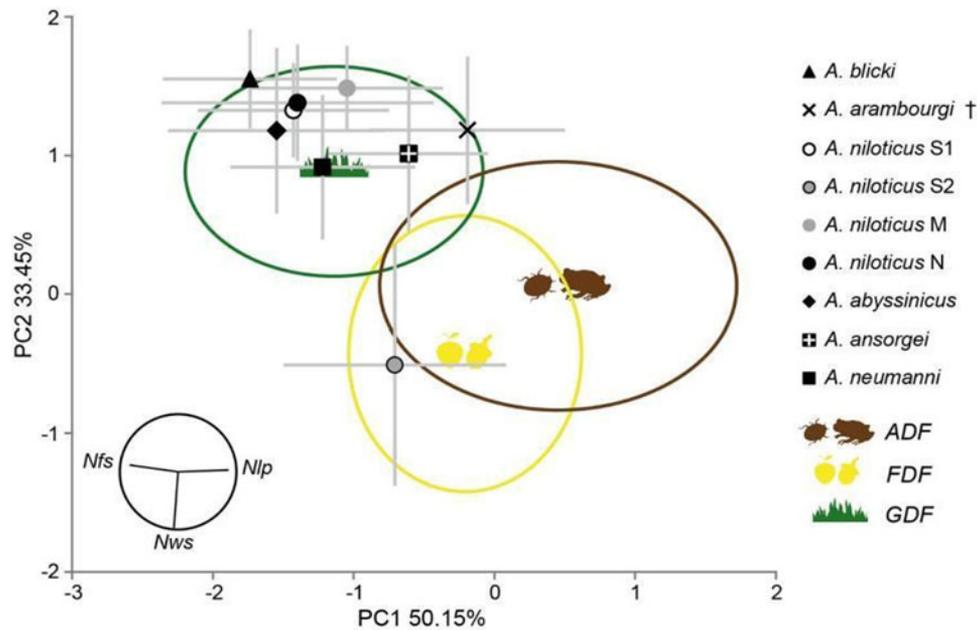
Figure 7. Visualization of the two first axes of the PCA performed on the results of the microwear analysis. ADF = animal-dominated feeders, FDF = fruit-dominated feeders, GDF = grass-dominated feeders, Nfs = number of fine scratches, Nws = number of wide scratches, Nlp = number of large pits, M = Mali, N = Niger, S1 = Sudan (El Sabaloga), S2 = Sudan (Dongola). See Gomes Rodrigues et al. (2009, 2012) for the reference database (MUROIDEA).

DISCUSSION

Arvicanthis *species discrimination, relation to diet and ecology*

Considering the upper first molar size, *A. blicki* is the largest species, while *A. neumanni* is the smallest. *Arvicanthis abyssinicus* and *A. niloticus* display a similar mean size, while *A. ansorgei* and *A. arambourgi* are a bit larger. These results are in line with previous studies (Bekele et al., 1993; Corti and Fadda, 1996; Fadda and Corti, 2001) with, however, *A. blicki* displaying larger M1s relative to its skull size, thus confirming a marked macrodonty (Monadjem et al., 2015).

Considering both size and shape parameters, despite some overlap, we were able to efficiently discriminate the different modern and fossil *Arvicanthis* species. This is especially true for the three eastern African modern species *A. blicki*, *A. neumanni*, and *A. abyssinicus*, and the extinct northern African species *A. arambourgi*. The western African modern species *A. ansorgei* appears relatively close in size and shape to the widespread *A. niloticus* group.

According to some authors, differences in *Arvicanthis* species morphology and size may reflect adaptations to different ecological niches (Bekele et al., 1993; Fadda and Corti, 2001), especially in Ethiopia where geographical, climatic, and ecological contrasts possibly triggered the emergence of several endemic species and/ or clades (Bryja et al., 2019). Fadda and Corti (2001) showed that in western Africa the skull shape is mainly correlated with latitude and mean temperature, while in eastern Africa, the main factors explaining morphological variation are elevation and latitude. The close relationship with geo-climatic variables strongly suggests that morphometric variation in *Arvicanthis* skulls can be linked to local climatic conditions (Fadda and Corti, 2001). For example, the eastern African species *A. abyssinicus*, *A. blicki*, and *A. neumanni*, which display very different skull and molar sizes and shapes, also have different ecological requirements (Table 8). *Arvicanthis abyssinicus* and *A. blicki* are found in

mid- and high-elevation grasslands of the Ethiopian High Plateau (1600–3600 m and 2500–4050 m, respectively), while *A. neumanni* occupies dry savanna habitats, at a maximum of 1000 m of elevation. Following the theory of a close relationship between morphology and ecology, *A. ansorgei* and *A. niloticus*, which display similar external body and molar morphologies, should thus share a similar ecology. Although they are morphologically close, they belong to two different genetic clades among the *Arvicanthis* genus (Bryja et al., 2019). Moreover, the literature highlights some ecological differences (Table 8): *A. ansorgei* occupies bush and woodland savannas and is presumably herbivorous, while *A. niloticus* is found across a very large geographic range (Fig. 1) and shows a broader diet. Nonetheless, the global microwear results are relatively homogeneous (most species are grass-dominated feeders), which is not very surprising, since microwear data show mostly dietary trends and are not always very discriminating within the same genus (especially among the Muridae family; Gomes Rodrigues et al., 2009). This was previously observed for other murids, such as *Mus* and *Apodemus* (Renaud et al., 2015; Kerr et al., 2017). Indeed, the diet of the *Arvicanthis* species seems quite homogeneous (mainly herbivores—grass, leaves, seeds—and occasional consumption of insects) (e.g., Granjon and Duplantier, 2009; Denys et al., 2017; Hirpasa et al., 2022), but because most of the data refer to *A. niloticus*, the precise ecology and diet of some species remain poorly known. Moreover, even if some population differences were observed (see below), no link between morphological changes and dietary changes could be established.

Therefore, the variability in M1 size and shape within *Arvicanthis* cannot be explained only by dietary niche and habitat. It is likely that several factors are intertwined, including joint action of environmental pressure, genetic drift, and isolation driving the morphological differences, thus confirming what had been previously stated by Corti and Fadda (1996) and Fadda and Corti (2001).

Table 8. Ecological information (distribution, habitat, and diet) on the considered *Arvicanthis* species.

Species	Distribution	Habitat	Diet	References
A. abyssinicus	Eastern Africa	Mid- and high-elevation grasslands of the Ethiopian High Plateau, from 1600–3600 m of elevation	Predominantly herbivorous, but can also include other resources, such as arthropods	Monadjem et al., 2015; Hirpasa et al., 2022; <www.iucnredlist.org>
A. ansorgei	Western Africa	Bush and woodland savannas of the Sudanian domain	Presumably herbivorous, including probably also seeds and insects	Granjon and Duplantier, 2009; Monadjem et al., 2015; <www.iucnredlist.org>
A. blicki	Eastern Africa, restricted area on the East of the Rift Valley	Alpine grasslands at very high elevations (2500–4050 m)	Mainly herbivorous, consuming monocots and dicots	Monadjem et al., 2015; <www.iucnredlist.org>
A. neumanni	Eastern Africa	Dry savanna habitats, at a maximum of 1000 m of elevation	Presumably herbivorous	Monadjem et al., 2015; <www.iucnredlist.org>
A. niloticus	Widespread on the Sahelian strip south of the Sahara + Nile Valley	Savannas, grasslands, and shrublands	Broad diet, including leaves, shoots, seeds of grasses, cultivated crops, and insects + can display a temporary arboreal lifestyle in acacia trees, especially during dry season and/or pullulation periods, feeding on seeds, twigs, bark, and gum	Galat and Galat-Luong, 1977; Poulet, 1982; Granjon and Duplantier, 2009; Monadjem et al., 2015; <www.iucnredlist.org>

Geographic variations in Arvicanthis morphology and diet

Arvicanthis niloticus is an adaptable and ubiquitous species with a broader diet than the other *Arvicanthis* species (Table 8). This may reflect a higher ecological plasticity for this species, and/or the existence of several clades with their own ecological particularities throughout the geographical range of this group (Dobigny et al., 2013; Bryja et al., 2019), the two being not exclusive. Regarding this issue, the discriminant analysis performed on the molar size and shape variables revealed some differences between the considered *A. niloticus* populations (Table 4, Fig. 5), separating the two Sudanese populations on one side, and the populations from Mali and Niger on the other, and highlighting morphological differences between eastern and central/western African populations. This would be in line with the existence of two different clades within this group, as evinced by Bryja et al. (2019): *A. niloticus* sensu stricto in northeastern Africa, and *A. niloticus* clade "C2-C4" in southeastern, central, and western Africa.

Moreover, microwear analyses highlighted dietary differences between two populations of *A. niloticus*, but different from those highlighted by the GM analysis. Here, the populations are both coming from Sudan: specimens from El Sabaloga (S1) are grass-dominated feeders, while specimens from Dongola (S2) are fruit-dominated feeders (Fig. 7). These important differences, especially regarding the higher number of large features quantified in specimens from S2, could be explained by the fact that these specimens were found mainly in deserts, contrary to specimens from S1, which were found in less-arid semi-desertic areas (Abdel Rahman et al., 2008). Even if both populations probably lived in grassy patches in the riparian fringe of the Nile River, living in drier environments would induce a larger consumption of hard and tough items, such as tree bark, rather than fruits (Poulet, 1982), but can also include consumption of insects and ingestion of grit, which might result in larger microwear features. Moreover, some large areas adjacent to the Nile in Sudan are used for agriculture. Consequently, some populations could have fed on crops, which could have resulted in the observed differences in the microwear patterns. But for the moment, we lack information on the types of crops potentially present in the regions at the time of trapping, as well as on the type of traces they could have left on the teeth. Such geographical differences in microwear within a species were also evident in other rodent taxa, such as *Apodemus sylvaticus* (Gomes Rodrigues et al., 2013; Kerr et al., 2017).

Previous studies have highlighted geographic differences in skull size and shape within the *A. niloticus* complex correlated to ecological and/or geographic parameters (e.g., Bekele et al., 1993; Fadda and Corti, 1998). These geographical variations and their potential link with habitat and/or species competition deserve to be explored more deeply, especially in light of the recent results on the phylogeographic structure of this group (Bryja et al., 2019).

Application to a fossil population

It is interesting to note that most divergences leading to current *Arvicanthis* species diversity occurred simultaneously in eastern Africa at the beginning of the Early Pleistocene (Bryja et al., 2019). This period is characterized by fundamental shifts and high variability in African climate, with alternation of warm-humid and cooler, drier, and more open conditions leading to the periodic expansion of savanna grasslands (e.g., Cerling, 1992; DeMenocal, 2004; Trauth et al., 2009; Levin, 2015). Most *Arvicanthis* species have adapted well to savanna environments and have been sensitive to the climatic variations affecting these habitats, as have other mammalian species at various periods (e.g., Abdel Rahman et al., 2008; Bryja et al., 2010; McDonough et al., 2015; Kaya et al., 2018). The geographic range and population demographics of *Arvicanthis* probably followed the evolution of savannas over time. Reduction and fragmentation of savanna habitats most likely led to contraction and isolation of *Arvicanthis* populations. This isolation could have resulted in the disappearance of certain populations and/or speciation and/or adaptation to new habitats. Conversely, the expansion of savanna areas in other periods allowed geographic and demographic expansion of *Arvicanthis*. After the Early Pleistocene,

repeated dispersals of *Arvicanthis* populations occurred to the west (Sudano-Guinean savannas) and to the south (Masai steppe) (Bryja et al., 2019), but also possibly to the north, as suggested by the first appearance of *Arvicanthis* remains in a northern African site dating from the Early Pleistocene (Jebel Ressas 8, Tunisia; Mein and Pickford, 1992). However, the route taken to reach the Maghreb is still unknown, and several hypotheses are possible: Nile valley and lybico-Egyptian route, Saharan reliefs or hydrographic network, Atlantic coast (e.g., Compton, 2011; Garcea, 2012; Aulagnier et al., 2017; Scerri, 2017; Stoetzel, 2017).

Thus, the fossil northern African species *A. arambourgi*, dating to the Early–Middle Pleistocene, could have originated from an in situ speciation in the Maghreb from an ancient population that arrived from eastern Africa during the Early Pleistocene, and which did not leave any current descendant, at least in northwestern Africa (evolutionary dead-end). To date, *A. arambourgi* is only known in northwestern Africa and was not recorded in other regions of Africa. During subsequent wetter periods, it could have migrated southwards or eastwards in the "Green Sahara," but it could have been in competition with other populations coming from the south and/or the east, such as *A. niloticus* (or its ancestor). Since the fossil record is extremely poor or non-existent in central-western Africa, the hypothesis of the potential occurrence of *A. arambourgi* south of the Sahara at certain periods cannot be totally ruled out.

Paleoenvironmental data available for the Tighennif site suggest an open and arid environment of dry steppe/savanna, with persistence of some more wooded areas (Jaeger, 1975; Geraads, 1981; Meunier et al., 2020). Microwear analyses have shown that the *Arvicanthis* from Tighennif do not fall into a precise diet category; they are close to the GDF group (grass-dominated feeders), with a low number of scratches compared to extant species, but at the limit with the ADF group (animal-dominated feeders) (Fig. 7). One possibility is that *Arvicanthis* had a diet more oriented towards insects (or hard food in general), which is consistent with more arid environments (less available plant material, and soft food in general). This has been verified for *A. ansorgei*, for which aridity induces a decrease in the consumption of plants compensated by that of non-orthopteran arthropods, and the diversity of plants consumed decreases with aridity (Atteynine, 2017). But for other species, such as *A. niloticus*, the diversity of plants consumed increases with aridity (Atteynine, 2017), with a switch first to dicotyledonous plants and then almost completely to grasses during the wet and dry seasons, respectively (Taylor and Green, 1976; Addisu and Bekele, 2014). Moreover, there is an increase in insect consumption during the wet season in this species (e.g., Taylor and Green, 1976; Rabiu and Fisher, 1989; Rabiu and Rose, 1997), which makes the issue more complex, especially for fossil species.

Paleobotanical data do not show any extension of savanna environments stricto sensu as far north as in the Maghreb during the Quaternary period (e.g., Dupont and Agwu, 1992; Le Houerou, 1997; DeMenocal, 2004; Hooghiemstra et al., 2006). Therefore, the northern African populations of *Arvicanthis* must have adapted to other types of vegetation (probably steppes) and fed on other plant species than what they were used to in sub-Saharan savannas. The fact that *A. arambourgi* does not fall into a precise diet category might reflect a specific ecological niche, or an ecological plasticity that allowed it to better adapt to new habitats (climatic changes and/or geographic expansions), but this cannot be confirmed with certainty in the current state of knowledge.

CONCLUSION AND PERSPECTIVES

The GM method applied in the present study on first upper molars allowed us to efficiently discriminate various modern and fossil species belonging to the genus *Arvicanthis*. The Early–Middle Pleistocene fossil species *A. arambourgi* is distinct from the modern species, although relatively close in molar size and shape to recent specimens of the western African species *A. ansorgei*. However, we caution that morphological similarity does not necessarily imply phylogenetic proximity (e.g., due to homoplasy).

The microwear analysis revealed a relatively homogeneous diet for all the modern and fossil species considered (i.e., grass-dominated feeders), except the specimens from Dongola, Sudan, which appear to be mostly fruit-dominated feeders. Moreover, the studied specimens of *A. arambourgi* and *A. ansorgei* likely also included a significant component of animals (insects) in their diet.

The present work represents a promising exploratory study, and geographical differences in morphology and diet deserve to be explored more deeply. This would be especially important for species with a relatively large distribution range such as *A. niloticus*, but also *A. neumanni* (in eastern Africa: Ethiopia, Somalia, Kenya, Tanzania), *A. ansorgei* (in western Africa: from Senegal and Guinea to Niger and Burkina Faso), and for two species not investigated here, *A. nairobae* (in eastern Africa: Kenya, Tanzania) and *A. rufinus* (in western Africa: Ghana, Benin, Cameroon, Central African Republic).

Additional GM studies also have to be performed on recently trapped and genotyped individuals to better characterize the morphological variability within the genus *Arvicanthis*, and to compare the phenotype to phylogenetic and phylogeographic data (Bryja et al., 2019). Moreover, in order to maximize our chances of identifying the northern African fossil remains, which are quite rare and represented by different teeth, we should apply GM not only on M1, but on all upper and lower molars.

This work thus helps set the stage for a potential revision of the fossil remains of *Arvicanthis* from northern African Quaternary deposits in order to (1) clarify their specific attribution and their relationship with present-day sub-Saharan populations; (2) characterize the variations in their diet in relation to Quaternary climatic and environmental changes; and (3) deduce hypotheses on their area of origin, evolution, and dispersal routes in relation to the development of savanna-like areas that also facilitated the passage of humans across the Sahara, which will be the subject of the continuation of our project.

References

Abbate, E., Sagri, M., 2012. Early to Middle Pleistocene *Homo* dispersals from Africa to Eurasia: geological, climatic and environmental constraints. *Quaternary International* **267**, 3–19.

Abdel Rahman, A.E.H., Ducroz, J.F., Mitchell, A., Lamb, J., Contrafatto, G., Denys, C., Lecompte, E., Taylor, P.J., 2008. Phylogeny and historical demography of economically important rodents of the genus *Arvicanthis* (Mammalia: Muridae) from the Nile Valley: of mice and men. *Biological Journal of the Linnean Society* **93**, 641–655.

Adams, D.C., Rohlf, F.J., Slice, D.E., 2013. A field comes of age: geometric morphometrics in the 21st century. *Hystrix, the Italian Journal of Mammalogy* **24**, 7–14.

Addisu, A., Bekele, A., 2014. Habitat preferences, seasonal abundance and diets of rodents in Alage, Southern Ethiopia. *African Journal of Ecology* **52**, 284–291.

Andrews, P., 1990. *Owls, Caves and Fossils*. Natural History Museum Publications, London.

Atteynine, S.A., 2017. *Changement Climatique et Rongeurs Ravageurs des Cultures: Effet Attractif des Cultures de Saison Sèche sur les Espèces du Genre* Arvicanthis *au Mali*. PhD Dissertation, Aix-Marseille University, France and University of Bamako, Mali.

Aulagnier, S., Cuzin F., Thévenot, M., 2017. *Mammifères Sauvages du Maroc: Peuplement, Répartition, Ecologie*. Société Française pour l'Etude et la Protection des Mammifères, Castanet Tolosan, France.

Avery, D.M., 1982. Micromammals as paleoenvironmental indicators and an interpretation of the late Quaternary in the Southern Cape Province. *Annals of the South African Museum* **85**, 183–374.

Balter, M., 2011. Was North Africa the launch pad for modern human migrations? *Science* **331**, 20–23.

Baylac, M., Friess, M., 2005. Fourier descriptors, Procrustes superimposition, and data dimensionality: an example of cranial shape analysis in modern human populations. In: Slice, E. (Ed.), *Modern Morphometrics in Physical Anthropology*. Springer, Boston, MA, pp. 145–165.

Bekele, A., Capanna, E., Corti, M., Marcus, L.F., Schlitter, D.A., 1993. Systematics and geographic variation of Ethiopian *Arvicanthis* (Rodentia, Muridae). *Journal of Zoology* **230**, 117–134.

Bookstein, F.L., 1997. Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. *Medical Image Analysis* **1**, 225–243.

Bryja, J., Colangelo, P., Lavrenchenko, L.A., Meheretu, Y., Sumbera, R., Bryjova, A., Verheyen, E., Leirs, H., Castiglia, R., 2019. Diversity and evolution of African Grass Rats (Muridae: *Arvicanthis*)—from radiation in East Africa to repeated colonization of northwestern and southeastern savannas. *Journal of Zoological Systematics and Evolutionary Research* **57**, 970–988.

Bryja, J., Granjon, L., Dobigny, G., Patzenhauerova, H., Konecny, A., Duplantier, J.M., Gauthier, P., *et al.*, 2010. Plio-Pleistocene history of West African Sudanian savanna and the phylogeography of the *Praomys daltoni* complex (Rodentia): the environment/geography/genetic interplay. *Molecular Ecology* **19**, 4783–4799.

Carto, S.L., Weaver, A.J., Hetherington, R., Lam, Y., Wiebe, E.C., 2009. Out of Africa and into an ice age: on the role of global climate change in the Late Pleistocene migration of early modern humans out of Africa. *Journal of Human Evolution* **56**, 139–151.

Castañeda, I.S., Mulitza, S., Schefuß, E., Lopes dos Santos, R.A., Sinninghe Damsté, J.S., Schouten, S., 2009. Wet phases in the Sahara/Sahel region and human migration patterns in North Africa. *Proceedings of the National Academy of Sciences* **106**, 20159–20163.

Castiglia, R., Bekele, A., Makundi, R., Oguge, N., Corti, M., 2006. Chromosomal diversity in the genus *Arvicanthis* from east Africa: a taxonomic and phylogenetic evaluation. *Journal of Zoological Systematic and Evolutionary Research* **44**, 223–235.

Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology* **97**, 241–247.

Chaline, J., 1972. Le rôle des rongeurs dans l'élaboration d'une biostratigraphie et d'une stratigraphie climatique fine du Quaternaire. *Mémoires du BRGM* **77**, 375–379.

Chaline, J., 1973. Biogéographie et fluctuations climatiques au Quaternaire d'après les faunes de rongeurs. *Acta Zoologica Cracoviensia* **18**, 141–160.

Compton, J.S., 2011. Pleistocene sea-level fluctuations and human evolution on the southern coastal plain of South Africa. *Quaternary Science Reviews* **30**, 506–527.

Conover, W.J., Iman, R.L., 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *The American Statistician* **35**, 124–129.

Corti, M., Fadda, C., 1996. Systematics of *Arvicanthis* (Rodentia, Muridae) from the Horn of Africa: a geometric morphometrics evaluation. *Italian Journal of Zoology* **63**, 185–192.

Coulthard, T.J., Ramirez, J.A., Barton, N., Rogerson, M., Brücher, T., 2013. Were rivers flowing across the Sahara during the last interglacial? Implications for human migration through Africa. *PLoS ONE* **8**(9), e74834. https://doi.org/10.1371/journal.pone.0074834.

Cucchi, T., Papayianni, K., Cersoy, S., Aznar-Cormano, L., Zazzo, A., Debruyne, R., Berthon, R., *et al.*, 2020. Tracking the Near Eastern origins and European dispersal of the western house mouse. *Scientific Report* **10**, 8276. https://doi.org/10.1038/s41598-020-64939-9.

Cuenca-Bescos, G., Melero-Rubio, M., Rofes, J., Martínez, I., Arsuaga, J.L., Blain, H.A., Lopez-Garcia, J.M., Carbonell, E., Bermudez de Castro, J.M., 2011. The Early–Middle Pleistocene environmental and climatic change and the human expansion in Western Europe: a case study with small vertebrates (Gran Dolina, Atapuerca, Spain). *Journal of Human Evolution* **60**, 481–491.

DeMenocal, P., 1995. Plio-Pleistocene African climate. *Science* **270**, 53–59.

DeMenocal, P., 2004. African climate change and faunal evolution during the Plio-Pleistocene. *Earth and Planetary Science Letters* **220**, 3–24.

DeMenocal, P., Stringer, C., 2016. Human migration: climate and the peopling of the world. *Nature* **538**, 49–50.

Denys, C., Taylor, P.J., Aplin, K.P., 2017. Family Muridae. In: Wilson, D.E., Lacher, T.E., Jr, Mittermeier, R.A. (Eds.), *Handbook of the Mammals of the World, Volume 7: Rodents II*. Lynx Edicions, Barcelona, Spain.

Dobigny, G., Tatard, C., Gauthier, P., Ba, K., Duplantier, J.M., Granjon, L., Kergoat, G.J., 2013. Mitochondrial and nuclear genes-based phylogeography of *Arvicanthis niloticus* (Murinae) and sub-Saharan open habitats Pleistocene history. *PLoS One* **8**(11), e77815. https://doi.org/10.1371/journal.pone.0077815.

Drake, N.A., Breeze, P., Parker, A., 2013. Palaeoclimate in the Saharan and Arabian deserts during the Middle Palaeolithic and the potential for hominin dispersals. *Quaternary International* **300**, 48–61.

Dupont, L.M., Agwu, C.O.C., 1992. Latitudinal shifts of forest and savanna in N.W. Africa during the Brunhes chron: further marine palynological results from site M 16415 (9°N 19°W). *Vegetation History and Archaeobotany* **1**, 163–175.

Fadda, C., Corti, M., 2001. Three dimensional geometric morphometrics of *Arvicanthis*: implications for systematics and taxonomy. *Journal of Zoological Systematics and Evolutionary Research* **29**, 585–696.

Galat, G., Galat-Luong, A., 1977. Démographie et régime alimentaire d'une troupe de *Cercopithecus aethiops sabaeus* en habitat marginal au nord Sénégal. *Revue d'Ecologie, Terre et Vie, Société Nationale de Protection de la Nature* **31**, 557–577.

Garcea, E.A.A., 2012. Successes and failures of human dispersals from North Africa. *Quaternary International* **270**, 119–128.

Geraads, D., 1981. Bovidae et Giraffidae (Artiodactyla, Mammalia) du Pléistocène de Ternifine (Algérie). *Bulletin du Museum national d'Histoire naturelle, Paris* **4**, ser. C3, 47–86.

Gomes Rodrigues, H., Marivaux, L., Vianey-Liaud, M., 2012. Expansion of open landscapes in northern China during the Oligocene induced by dramatic climate changes: paleoecological evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* **358–360**, 62–71.

Gomes Rodrigues, H., Merceron, G., Viriot, L., 2009. Dental microwear patterns of extant and extinct Muridae (Rodentia, Mammalia): ecological implications. *Naturwissenschaften* **96**, 537–542.

Gomes Rodrigues, H., Renaud, S., Charles, C., Le Poul, Y., Solé, F., Aguilar, J.P., Michaux, J., *et al.*, 2013. Roles of dental development and adaptation

in rodent evolution. *Nature Communications* **4**, 2504. https://doi.org/10.1038/ncomms3504.

Granjon, L., Duplantier, J.M., 2009. *Les Rongeurs d'Afrique Sahélo-Soudanienne*. IRD Editions, Publications Scientifiques du Muséum, Marseille.

Gunz, P., Mitteroecker, P., 2013. Semilandmarks: a method for quantifying curves and surfaces. *Hystrix, the Italian Journal Of Mammalogy* **24**, 103–109.

Hanot, P., Gerber, S., Guintard, C., Herrel, A., Verslype, L., Cornette, R., 2020. Reconstructing the functional traits of the horses from the tomb of King Childeric. *Journal of Archaeological Science* **121**, 105200. https://doi.org/10.1016/j.jas.2020.105200.

Happold, D., 2013. *Mammals of Africa: Vol. 3, Rodents, Hares and Rabbits*. Bloomsbury Publishing, London, UK.

Hirpasa, T., Wondimu, E., Tadele, A., 2022. Distribution, diet, and trophic level of *Arvicanthis abyssinicus* and *Tachyoryctes splendens* around the area of recently extinct Ethiopian Wolf *Canis simiensis* on Mount Guna, northwestern Ethiopia. *Journal of Threatened Taxa* **14**, 20539–20549.

Hooghiemstra, H., Lézine, A.M., Leroy, S.A.G., Dupont, L., Marret, F., 2006. Late Quaternary palynology in marine sediments: a synthesis of the understanding of pollen distribution patterns in the NW African setting. *Quaternary International* **148**, 29–44.

Hulme-Beaman, A., Claude, J., Chaval, Y., Evin, A., Morand, S., Vigne, J.D., Dobney, K., Cucchi, T., 2019. Dental shape variation and phylogenetic signal in the Rattini Tribe species of mainland Southeast Asia. *Journal of Mammalian Evolution* **26**, 435–446.

Jaeger, J.J., 1975. *Evolution des Rongeurs du Miocène à l'actuel en Afrique Nord-Occidentale*. PhD Dissertation, Université de Montpellier, France.

Janzekovic, F., Krystufek, B., 2004. Geometric morphometry of the upper molars in European wood mice *Apodemus*. *Folia Zoologica* **53**, 47–55.

Jones, E.P., Eager, H.M., Gabriel, S.I., Johannesdottir, F., Searle, J.B., 2013. Genetic tracking of mice and other bioproxies to infer human history. *Trends in Genetics* **29**, 298–308.

Kaya, F., Bibi, F., Žliobaitė, I., Eronen, J.T., Hui, T., Fortelius, M., 2018. The rise and fall of the Old World savannah fauna and the origins of the African savannah biome. *Nature Ecology & Evolution* **2**, 241–246.

Kerr, E., Cornette, R., Gomes Rodrigues, H., Renaud, S., Chevret, P., Tresset, A., Herrel, A., 2017. Can functional traits help explain the coexistence of two species of *Apodemus*? *Biological Journal of the Linnean Society* **122**, 883–896.

Kimura, Y., Jacobs, L.L., Flynn, L.J., 2013. Lineage-specific responses of tooth shape in murine rodents (Murinae, Rodentia) to Late Miocene dietary change in the Siwaliks of Pakistan. *PLoS ONE* **8**(10), e76070. https://doi.org/10.1371/journal.pone.0076070.

Lazagabaster, I.A., Rovelli, V., Fabre, P.H., Porat, R., Ullman, M., Davidovich, U., Lavi, T., et al., 2021. Rare crested rat subfossils unveil Afro-Eurasian ecological corridors synchronous with early human dispersals. *Proceedings of the National Academy of Sciences* **118**(31), e2105719118. https://doi.org/10.1073/pnas.2105719118.

Le Houerou, H.N., 1997. Climate, flora and fauna changes in the Sahara over the past 500 million years. *Journal of Arid Environments* **37**, 619–647.

Levin, N.E., 2015. Environment and climate of early human evolution. *Annual Review of Earth and Planetary Sciences* **43**, 405–429.

Macholan, M., 2006. A geometric morphometric analysis of the shape of the first upper molar in mice of the genus *Mus* (Muridae, Rodentia). *Journal of Zoology* **270**, 672–681.

Manthi, F.K., 2007. A preliminary review of the rodent fauna from Lemudong'o, southwestern Kenya, and its implication to the Late Miocene paleoenvironments. *Kirtlandia, The Cleveland Museum of Natural History* **56**, 92–105.

Matthews, T., Stynder, D.D., 2011. An analysis of the *Aethomys* (Murinae) community from Langebaanweg (Early Pliocene, South Africa) using geometric morphometrics. *Palaeogeography, Palaeoclimatology, Palaeoecology* **302**, 230–242.

McDonough, M.M., Sumbera, R., Mazoch, V., Ferguson, A.W., Phillips, C.D., Bryja, J., 2015. Multilocus phylogeography of a widespread savanna-woodland-adapted rodent reveals the influence of Pleistocene

geomorphology and climate change in Africa's Zambezi region. *Molecular Ecology* **24**, 5248–5266.

Mein, P., Pickford, M., 1992. Gisements karstiques Pléistocènes au Djebel Ressas, Tunisie. *Comptes Rendus de l'Académie des Sciences de Paris, Serie II* **315**, 247–253.

Meunier, M., Stoetzel, E., Souttou, K., Sekour, M., Moussa, H., Boukhemza, M., Doumandji, S., Denys, C., 2020. Mise à jour de la liste des rongeurs d'Algérie, biogéographie et implications paléoécologiques. *Bulletin de la Société Zoologique de France* **145**, 413–474.

Monadjem, A., Taylor, P.J., Denys, C., Cotterill, F.P.D., 2015. *Rodents of Sub-Saharan Africa. A Biogeographic and Taxonomic Synthesis*. De Gruyter, Berlin.

Musser, G.G., Carleton, M.D., 2005. Superfamily Muroidea. In: Wilson D., Reeder D.M. (Eds.), *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd ed. Johns Hopkins University Press, Baltimore, MD.

Osborne, A.H., Vance, D., Rohling, E.J., Barton, N., Rogerson, M., Fello, N., 2008. A humid corridor across the Sahara for the migration of early humans out of Africa 120,000 years ago. *PNAS* **105**, 16444–16447.

Poulet, A.R., 1982. Pullulation de Rongeurs dans le Sahel: Mécanismes el Déterminisme du Cycle d'abondance de *Taterillus pygargus* et d'*Arvicanthis niloticus* (Rongeurs, Gerbillidés et Muridés) dans le Sahel du Sénégal de 1975 à 1977. PhD Dissertation, University Paris 6, Editions ORSTOM, Paris, France.

Rabiu, S., Fisher, M., 1989. The breeding season and diet of *Arvicanthis* in northern Nigeria. *Journal of Tropical Ecology* **5**, 375–386.

Rabiu, S., Rose, R.K., 1997. A quantitative study of diet in three species of rodents in natural and irrigated savanna fields. *Acta Theriologica* **42**, 55–70.

Renaud S., Benammi M., Jaeger J.-J., 1999. Morphological evolution of the murine rodent *Paraethomys* in response to climatic variations (Mio-Pleistocene of North Africa). *Paleobiology* **25**, 369–382.

Renaud, S., Gomes Rodrigues, H., Ledevin, R., Pisanu, B., Chapuis, J.L., Hardouin, E.A., 2015. Fast evolutionary response of house mice to anthropogenic disturbance on a Sub-Antarctic island. *Biological Journal of the Linnean Society* **114**, 513–526.

Renaud S., Pantalacci S., Auffray J.-C., 2011. Differential evolvability along lines of least resistance of upper and lower molars in island house mice. *PLoS ONE* **6**(5): e18951. https://doi.org/10.1371/journal.pone.0018951.

Rohlf, F.J., 2017. *TpsDig2, Digitize Landmarks and Outlines, Version 2.31*. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.

Rohlf, F.J., 2019a. *TpsUtil, File Utility Program, Version 1.78*. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.

Rohlf, F.J., 2019b. *TpsRelw, Relative Warps Analysis, Version 1.70*. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.

Rohlf, F.J., Slice, D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology* **39**, 40–59.

Scerri, E.M.L., 2017. The North African Middle Stone Age and its place in recent human evolution. *Evolutionary Anthropology* **26**, 119–135.

Siahsarvie, R., Darvish, J., 2008. Geometric morphometric analysis of Iranian wood mice of the genus *Apodemus* (Rodentia, Muridae). *Mammalia* **72**, 109–115.

Stoetzel, E., 2013. Late Cenozoic micromammal biochronology of northwestern Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **392**, 359–381.

Stoetzel, E., 2017. Adaptations and dispersals of anatomically modern humans in the changing environments of North Africa: the contribution of microvertebrates. *African Archaeological Review* **34**, 453–468.

Stoetzel, E., Cornette, R., Lalis, A., Nicolas, V., Cucchi, T., Denys, C., 2017. Systematics and evolution of the *Meriones shawii/grandis* complex (Rodentia, Gerbillinae) during the late Quaternary in northwestern Africa: exploring the role of environmental and anthropogenic changes. *Quaternary Science Reviews* **164**, 199–216.

Stoetzel, E., Sime, W.B., Pleurdeau, D., Asrat, A., Assefa, Z., Desclaux, E., Denys, C., 2018. Preliminary study of the rodent assemblages of Goda Buticha: new insights on late Quaternary environmental and

cultural changes in southeastern Ethiopia. *Quaternary International* **471**, 21–34.

Taylor, K.D., Green, M.G., 1976. The influence of rainfall on diet and reproduction in four African rodent species. *Journal of Zoology* **180**, 367–389.

Tchernov, E., 1968. *Succession of Rodent Faunas During the Upper Pleistocene of Israel*. Verlag Paul Parey, Berlin.

Tchernov, E., 1975. XVI. Rodent faunas and environmental changes in the Pleistocene of Israel. In: Prakash, I., Ghosh, P.K. (Eds.), *Rodents in Desert Environments*. Junk, The Hague, pp. 331–362.

Teaford, M.F., Oyen, O.J., 1989. In vivo and in vitro turnover in dental microwear. *American Journal of Biological Anthropology* **80**(4), 447–460.

Trauth, M.H., Larrasoana, J.C., Mudelsee, M., 2009. Trends, rhythms and events in Plio-Pleistocene African climate. *Quaternary Science Reviews* **28**, 399–411.

Walker, A., Hoeck, H.N., Perez, L., 1978. Microwear of mammalian teeth as an indicator of diet. *Science* **201**, 908–910.

Weissbrod, L., Marshall, F.B., Valla, F.R., Khalaily, H., Bar-Oz, G., Auffray, J.C., Vigne, J.D., Cucchi, T., 2017. Origins of house mice in ecological niches created by settled hunter-gatherers in the Levant 15,000 y ago. *Proceedings of the National Academy of Sciences* **114**, 4099–4104.

Weissbrod, L., Weinstein-Evron, M., 2020. Climate variability in early expansions of *Homo sapiens* in light of the new record of micromammals in Misliya Cave, Israel. *Journal of Human Evolution* **139**, 102741. https://doi.org/10.1016/j.jhevol.2020.102741.

Whiting Blome, M., Cohen, A.S., Tryon, C.A., Brooks, A.S., Russel, J., 2012. The environmental context for the origins of modern human diversity: a synthesis of regional variability in African climate 150,000–30,000 years ago. *Journal of Human Evolution* **62**, 563–592.

Winkler, A.J., 2002. Neogene paleobiogeography and East African paleoenvironments: contributions from the Tugen Hills rodents and lagomorphs. *Journal of Human Evolution* **42**, 237–256.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D., 2012. *Geometric Morphometrics for Biologists: A Primer*. Academic Press, Amsterdam.