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A review of bristly ground squirrels Xerini and a generic revision in the African genus *Xerus*

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Abstract: Bristly ground squirrels Xerini are a small rodent tribe of six extant species. Despite a dense fossil record the group was never diverse. Our phylogenetic reconstruction, based on the analysis of cytochrome *b* gene and including all known species of Xerini, confirms a deep divergence between the African taxa and the Asiatic *Spermophilopsis*. Genetic divergences among the African Xerini were of a comparable magnitude to those among genera of Holarctic ground squirrels in the subtribe Spermophilina. Evident disparity in criteria applied in delimitation of genera in Sciuridae induced us to recognize two genera formerly incorporated into *Xerus*. The resurrected genera (*Euxerus* and *Geosciurus*) are clearly distinct between each other and from *Xerus* in nucleotide sequences and in external, cranial and dental morphology. They occupy discrete ranges and show specific environmental adaptations. *Atlantoxerus* is more likely a sister to the remaining African genera than being nested inside them. We readdress nomenclatural issues associated with Xerini, list and reference all names above the species groups, and detail in words and figures those characters which differentiate the taxa. We propose *Tenotis* Rafinesque, 1817 (type species is *Tenotis griseus* Rafinesque, 1817), which is occasionally synonymized with *Euxerus,* as a not identifiable name (*nomen dubium*).

Keywords: *Atlantoxerus*; cytochrome *b*; *Euxerus*; *Geosciurus*; *Spermophilopsis*.

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Introduction

Bristly ground squirrels from the arid regions of Central Asia and Africa constitute a coherent monophyletic tribe Xerini sensu Moore (1959). The tribe contains six species in three genera of which *Atlantoxerus* and *Spermophilopsis* are monotypic. The genus *Xerus* in its present scope (Thorington and Hoffmann 2005), consists of four species in three subgenera: *X. inauris* and *X. princeps* (subgenus *Geosciurus*), *X. rutilus* (subgenus *Xerus*), and *X. erythropus* (subgenus *Euxerus*). Recent phylogenetic reconstruction based on molecular markers retrieved *Xerus* to be paraphyletic with respect to *Atlantoxerus* (Fabre et al. 2012), therefore challenging the suitability of the generic arrangement of the group.

We address in this paper the current taxonomic division of Xerini and its concordance with various sources of evidence. Specifically, we (i) review the taxonomic history of bristly ground squirrels, (ii) reconstruct phylogenetic relationships among the extant species using a complete mitochondrial gene for cytochrome *b* (cyt*b*), (iii) confront genetic distances among bristly ground squirrels with distances between the genera of Holarctic ground squirrels, (iv) analyse phenotypical traits of taxa, (v) their biogeography and fossil history, and (vi) propose a novel generic taxonomy for the group which consents to the available body of evidence. We conclude that classification of African taxa into four genera, as proposed around a century ago by Thomas (1909) and Pocock (1923), is more in accordance with operational criteria which are currently in use for the delimitation of genera in squirrels (e.g. Helgen et al. 2009) than is a two-genera system advocated by the majority of recent authors (cf. Thorington and Hoffmann 2005).

Taxonomic history

The only Asiatic species, “the curious prairie-dog-like *Spermophilopsis leptodactylus*” (Moore 1959), is morphologically and geographically so remote from the African Xerini, that the two were only rarely treated simultaneously. Genus *Spermophilopsis*, coined by Blasius (1884) for a species known since 1823 as *Arctomys leptodactylus*, was ignored by Pocock (1923), and classified together with Palaearctic ground squirrels (now in *Spermophilus* and *Urocitellus*) by Obolenskij (1927). Ognev (1940) cherished the uniqueness of *Spermophilopsis* among the squirrels occupying the Palaearctic Asia by placing it into a subfamily on its own, emphasizing simultaneously its close resemblance to the African bristly ground squirrels. Ellerman (1940) formally grouped *Spermophilopsis* with *Xerus* and *Atlantoxerus* and his arrangement, not seriously challenged ever since (but see Simpson 1945: 79), received support from several molecular phylogenetic reconstructions (Herron et al. 2004, Fabre et al. 2012, Ge et al. 2014).

Xerus was originally proposed as a subgenus of *Sciurus* (Hemprich and Ehrenberg, 1833). Already Waterhouse (1839) used *Xerus* as a full genus, and he was followed by the majority of subsequent authors (Temminck 1853, Brandt 1855, Murray 1866, Gray 1867, Alston 1876, etc.). Two other generic names were introduced for bristly ground squirrels shortly after the paper by Hemprich and Ehrenberg (1833), *Geosciurus* (Smith 1834) and *Spermosciurus* (Lesson 1836), while *Euxerus* was coined with considerable delay (Thomas 1909). The Barbary ground squirrel, known (as *Scyurus* [sic!] *getulus*) already to Gessner (1551 n.v., and subsequent editions: 1569, 1583), was recognized as a member of its own subgenus *Atlantoxerus* (within *Xerus*) only towards the end of the 19th century (Forsyth Major 1893). Earlier on this animal was classified either into *Sciurus* (Brisson 1762, Erxleben 1777, Smith 1834, Murray 1866, Jentink 1882, Lataste 1885) or into *Xerus* (Temminck 1853, Gray 1867, Flower and Lydekker 1891, Forsyth Major 1893, Trouessart 1897). In the 19th century the taxonomic scope of *Xerus* was understood very differently than it is now and the genus contained also squirrels which are currently classified into the tribes (sensu Thorington and Hoffmann 2005) Sciurini and Protoxerini (Huet 1880, Trouessart 1880, Forsyth Major 1893, Palmer 1904). Gray (1867) defined the scope of *Xerus* as agreed at present and Jentink (1882) correctly concluded that the genus contains three species; *Geosciurus princeps* as the fourth species was recognized much later (Thomas 1929).

The early 20th century saw two generic classifications of fundamental importance for understanding the taxonomic relationships among African bristly ground squirrels. Thomas (1909) based his taxonomic system on dentition, evidently following Forsyth Major (1893) who claimed that "squirrels should be classified by their dental and cranial characters just as other rodents are, and [...] not [...] on such superficial characters as the presence or absence of stripes or similar external characters". Pocock (1923), on the other hand, created his classification on the baculum, a heterotopic bone which was shown by Thomas (1915) to be in squirrels a superior taxonomic character relative to skull and dentition. Importantly, although Thomas (1909) and Pocock (1923) based their revisions on non-overlapping character sets, they both recognized four genera, i.e. all listed hereafter in the account on taxonomy.

Ellerman (1940) concluded that genera of African bristly ground squirrels are based "on the least or vaguest excuses" and retained only *Xerus* (with *Geosciurus* and *Euxerus* as subgenera) and *Atlantoxerus*. This arrangement was adopted in nearly all subsequent major revisions and taxonomic lists (Simpson 1945, Amtmann 1975, Carleton 1984, Corbet and Hill 1980, 1986, Honacki et al. 1982, Hoffman et al. 1993, Nowak 1999, Thorington et al. 2012, Waterman 2013a, Monadjem et al. 2015). Allen (1954), in his list of African mammals, retained the system of three genera, but after 1940 such a view was accepted only by few mammalogists: Hill and Carter (1941), Schouteden (1947), Roberts (1951), Setzer (1956), Rosevear (1969), Depierre and Vivien (1992), Kingdon (1997), Osborn and Osbnornová (1998), and Reiner and Simões (1998). In his influential taxonomic arrangement of diurnal squirrels, Moore (1959) accepted *Euxerus* and *Geosciurus* as subgenera of *Xerus*, but at the same time commented that a generic position might be more appropriate solution.

Materials and methods

Our analysis is based on published evidence and on examination of archived museum material representing all extant species of Xerini. For practical reasons we subsequently use *Xerus* in its narrow sense (containing only *X. rutilus*), and refer to *Euxerus* and *Geosciurus* as to genera.

Molecular phylogeny

Phylogenetic relationships among bristly ground squirrels were assessed using 25 published sequences for cyt*b* gene representing *Xerus*, *Euxerus*, both species of *Geosciurus* and *Spermophilopsis* (Supplemental Appendix 1). In addition to data downloaded from GenBank we sequenced cyt*b* gene for *Atlantoxerus getulus*. Restriction of our analysis to a single gene marker ensured a complete taxonomic sampling of Xerini, which is an advantage with respect to previous phylogenetic assessments. Because our aim was to achieve a generic system of Xerini which will be comparable to generic divisions in other groups of squirrels we quantified the cyt*b* intergeneric variation in Holarctic ground squirrels from the subtribe Spermophilina which were recently generically revised (Helgen et al. 2009). Intergeneric metrics in Spermophilina served as standard for setting genera in Xerini. We therefore downloaded from GenBank further 138 cyt*b* sequences representing 39 species of Holarctic ground squirrels in nine genera. For taxonomic scope and accession numbers see Supplemental Appendix 1.

DNA of *Atlantoxerus getulus* (voucher PMS 19301; Supplemental Appendix 2) was extracted using a QIAamp® DNA Mini kit (Qiagen, Valencia, CA, USA), following the manufacturer's conditions. Cyt*b* was amplified using the trans-mammalian primers L14727-SP and H15497-SP (Irwin et al. 1991). Amplification was performed using a 20 µl reaction containing 2.5 mm $MgCl_2$, 0.5 µm of forward and reverse primer, 0.2 mm of dNTPs and one unit of Fermentas Taq in the supplied ammonium buffer. Cycling conditions consisted of an initial stage of 95°C for 5 min followed by 40 cycles of denaturation (40 s at 94°C), primer annealing (40 s at 48°C) and extension (1 min at 72°C). Sequencing was performed on an ABI PRISM 3130 Genetic Analyzer using BigDye Terminators chemistry (Applied Biosystems, Foster City, CA, USA). Sequences were edited manually using CodonCode aligner software (CodonCodes Inc., Ewing et al. 1998).

Phylogenetic relationships among bristly ground squirrels were assessed using sequences from all extant species of Xerini and 39 species of Holarctic Spermophilina (Supplemental Appendix 1). An assembled alignment file consisting of 171 sequences with 1140 bp length was aligned with Clustal W (Thompson et al. 1997) algorithm using BioEdit 7.0.5 (Hall 1999). As pseudogenes are known to represent source of error for mitochondrial phylogeny (Triant and DeWoody 2009), cyt*b* sequences were checked for the absence of stop codons and indels.

The most appropriate evolutionary model of sequences was estimated based on Akaike Information Criterion (AIC) using Modeltest software (Posada and Crandall 1998). The phylogenetic relationships among haplotypes were reconstructed using two different optimality criteria: Maximum Likelihood (ML) and Bayesian inference of phylogeny (BI). ML tree was inferred in RaxML (Silvestro and Michalak 2012) with a general time-reversible model (GTR)+gamma distribution (G)+proportion of invariable sites (I) (G=0.8596 and I=0.3815) using rapid hill-climbing algorithm. Node robustness values were estimated using both rapid bootstrapping and ML heuristic search options. BI analysis based on the same model was performed with four Markov chain Monte Carlo (MCMC), as two simultaneous analyses using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003), which started from random trees and were run for 4,000,000 iterations. The first 5000 trees were discarded as burn-in, afterward the trees were sampled every 100th generation. The branch supports for BI were assessed with Bayesian posterior probabilities (BPP). Five species belonging to the family Gliridae (*Graphiurus murinus, Muscardinus avellanarius, Eliomys quercinus, Dryomys nitedula, Glis glis* and *Glirulus japonicus*) were used as outgroups for rooting trees.

The cyt*b* intergeneric variation among nine genera of Spermophilina and between five genera of Xerini was quantified assuming Kimura 2 parameter (K2P) substitution model in MEGA6 (Tamura et al. 2013).

Phenotypical analyses

We studied 181 museum vouchers housed in ten different collections (Supplemental Appendix 2). Information on sex, locality, and external dimensions was deduced from specimen tags. Skull morphology was quantified with traditional morphometric methods using a set of nine cranial variables. The following linear measurements were scored using a Vernier calliper with accuracy to the nearest 0.1 mm: condylobasal length, length of rostrum from premaxilla to 3rd molar, length of rostrum from premaxilla to margin of hard palate, length of upper diastema, length of upper tooth row, breadth across zygomatic arches, breadth of braincase, occipital height, and length of mandible. To minimize the effect of ontogenetic growth, only adult individuals were used in analyses. Age was assessed following the criteria in Helgen et al. (2009).

To characterize the morphological variation among samples and to find patterns in our data of high dimensions we used principal components analysis (PCA) which was performed on the correlation matrix of $\log_{10}$-transformed cranial variables. Transformation of data to logarithms has the advantage of normalizing the distribution of the measurements, equalizing the variances, and preventing dominance of the analysis by large values at the expense of small ones. First few principal components (PC) usually explain a high proportion of variance in the original data set which allows a reduction of the dimensionality of a multivariate dataset and facilitates visualization of the relations among the studied objects. Statistical tests were run in Statistica (Version 5.5, StatSoft, Tulso, OK, USA, 1999).

Results and discussion

Molecular phylogeny

We analyzed simultaneously all the sequences. The 165 samples yielded 144 different cyt*b* haplotypes. For the 1140 bp-long sequence, 644 polymorphic sites (56.5%) were found with a total of 930 mutations, 574 of which were parsimony informative. No stop codons, insertions or deletions were observed in the alignment. As expected under neutral evolution (Martin and Palumbi 1993), the majority of polymorphic sites were at third positions (369 variable sites, 57.3% of all variable sites), followed by first positions (157 variable sites, 24.4% of all variable sites) and second positions (118 variable sites, 18.3% of all variable sites). The mean transition/transversion ratio was 4.61. The nucleotide composition was characterized by a deficit of guanines (5.9%), similar to that described in other mammals (Irwin et al. 1991).

Phylogenetic relationships that were reconstructed by the two different methods (ML and BI) yielded very similar results. Both approaches retrieved a basal dichotomy into two lineages which matched Xerini and Spermophilina, respectively. Within the latter, a branching pattern yielded an identical topology to those published by Harrison et al. (2003) and Herron et al. (2004); consequently, only the inset of the BI tree with Xerini is shown in Figure 1. All nodes were highly supported in both analyses (BP>95%, BPP>0.89). The Central-Asiatic *Spermophilopsis* hold a basal position in the tree. Chaining hierarchy of African genera retrieved *Atlantoxerus* at the basal position and *Geosciurus* as the most derived group.

The only published phylogenetic reconstruction of all recent Xerini is by Fabre et al. (2012) who used four markers, two mitochondrial (cyt*b* and gene encoding 12S RNA) and two nuclear markers (Interphotoreceptor retinoid-binding protein exon IRBP and Recombination activating gene 1 RAG-1). The cladogram retrieved the basal position of *Spermophilopsis* (Figure 1). Within the African taxa *Euxerus* holds the basal position which, however, benefited low support (BP<70%) while *Atlantoxerus* is in a strongly supported (BP≥95%) sister position against *Xerus*. Sister relationships between *Xerus*+*Atlantoxerus* and *Geosciurus* benefited moderate support (70%≤BP≤95%). Evidently, phylogenetic trees failed to provide robust and conclusive results on the evolutionary relationships within African Xerini. One of possible reasons for discrepancy between the two trees is in incomplete sampling in Fabre et al. (2012) since their matrix (6 species×4 genes) contained high proportion (=42%) of missing values.

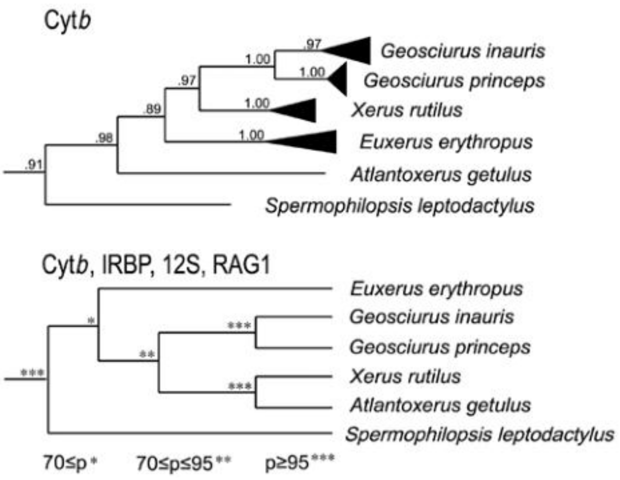

Figure 1: Bayesian inference tree (above) reconstructed from cytochrome *b* sequences of six species of Xerini. Numbers on the branches correspond to posterior probability values; bootstrap supports at all nodes were >95% (not shown). Below is cladogram depicting the highest-likelihood topology for relationships among Xerini, with symbols indicating bootstrap supports (from Fabre et al. 2012). Sequences used in tree constructions: Cyt*b* – cytochrome *b*, IRBP – Interphotoreceptor retinoid-binding protein exon, 12S – gene encoding 12S RNA, RAG-1 – Recombination activating gene 1. Both trees are insets from wider phylogenetic analyses, considering 45 species of squirrels (six species of Xerini and 39 species of Spermophilina), and rooted with six species of Gliridae (above), and 1265 species of rodents (below).

As a next step we explored inter- and intrageneric genetic K2P distances in two lineages of squirrels, the Xerini and the Spermophilina (Table 1). In Xerini, the intergeneric K2P estimates ranged between 13.8 and 22.5% (n=6) and were mainly within the margins observed among nine genera of Spermophilina (range=12.4–20.5%; mean 16.7%±2.43; n=36). The intergeneric divergences clearly exceeded intrageneric heterogeneity which ranged between 3.7 and 4.7% (n=3) in Xerini and from 0.2 to 9.6% (mean=5.5%±3.4; n=9) in Spermophilina. It is therefore safe to conclude that metrics of K2P genetic distances provides strong support for a generic split of the African bristly squirrels.

Table 1: Pairwise K2P genetic distances (in percent; mean±SD) among genera of Xerini.

	1	2	3	4
1. *Atlantoxerus*	–			
2. *Xerus*	20.9±1.3	*4.7±0.6*		
3. *Euxerus*	17.9±2.1	14.8±2	*3.7±0.7*	
4. *Geosciurus*	22.4±1.4	13.8±1	17.5±2.1	*4.5±0.4*
5. *Spermophilopsis*	25.1±1.7	21.4±1.4	24.6±2.6	23.9±1.5

Italicized are average intrageneric distances on diagonal (not estimated in *Atlantoxerus* and *Spermophilopsis*).

Chromosomes

Chromosomal data are available for *Spermophilopsis* (Liapunova and Zholnerovskaya 1969, Nadler et al. 1969) and for all African bristly ground squirrels: *Atlantoxerus* (Petit et al. 1984), *Xerus* (Nadler and Hoffmann 1974, Baskevich et al. 1995), *Euxerus* (Dobigny et al. 2002, Granjon and Duplantier 2009), and both species of *Geosciurus* (Robinskon et al., 1986). All species share identical diploid number (2n) of 38 pairs of chromosomes. With the exception of one pair of acrocentrics, the remaining chromosomes are metacentric and submetacentric, resulting in a fundamental number of autosomal arms (NFa) of 70. The X chromosome is submetacentric in all species while the small Y chromosomes is acrocentric in *Euxerus* and metacentric in *Xerus*, both species of *Geosciurus* and *Spermophilopsis*; the details are not known for *Atlantoxerus*. Differences in morphology of the Y chromosome most probably originate from the pericentric inversion which is the predominant drive of chromosomal change in squirrels (Richard and Dutrillaux 2012). Such differences provide little useful information for phylogenetic reconstructions of interrelationships in Sciuridae because of convergent and reverse rearrangements of the karyotype (Romanenko et al. 2011, Richard and Dutrillaux 2012). Evidently, Xerini have retained a conservative karyotype which remains similar to the ancestral condition in squirrels (Li et al. 2006, Beklemisheva et al. 2011).

Phenotypical traits

Morphological evidence is thoroughly documented in Flower and Lydekker (1891), Forsyth Major (1893), Thomas (1909), Pocock (1922, 1923), Ellerman (1940), Ognev (1940), Moore (1959), Rosevear (1969), and Denys et al. (2003).

External morphology

All bristly ground squirrels are externally modified for terrestrial life. They are of moderate size according to squirrel standards and grade in length of head and body (in mm; parenthesized are mean±SD) as follows: *Atlantoxerus* (175.8±12.42, n=28) <*Xerus* (222.8±8.80, n=12) <*Geosciurus inauris* (238.3±11.87, n=12) ≈*Spermophilopsis* (243.5±17.62, n=22) ≈*G. princeps* (247.8±12.83, n=6) ≈*Euxerus* (249.3±15.46, n=26). One-way ANOVA retrieved highly significant (F>90, p <0.0001) heterogeneity among species in all external measurements.

Secondary sexual dimorphism in size (SSDS) is not a major source of intraspecific variation in Xerini. The SSDS is reportedly not readily apparent in *Xerus* (O'Shea 1991), *Geosciurus* (Smithers 1971, Waterman and Herron 2004, Skurski and Waterman 2005) and *Euxerus* (Waterman 2013b). Usually, males are slightly larger and heavier than females. We tested SSDS using two variables (length of hind foot and condylobasal length of skull) utilized by Matějů and Kratochvíl (2013) in their assessment of the phenomenon in Spermophilina. *Geosciurus princeps* was excluded due to a small sample of females. ANOVA on the remaining species failed to retrieve significant difference in any comparison (F<3.3, p>0.1). Based on these results we pooled sexed in subsequent statistical tests.

Fur is short, coarse or rush (brittle), with some hairs flattened and grooved. *Xerus* has the most pronouncedly spiny pelage, followed by *Euxerus* and *Geosciurus princeps*; *G. inauris* has less bristly hair. Ventral side is more sparsely haired and is even partly bare. Basic color varies from cinnamon or sandy to dark chocolate-brown but is most frequently red sandy to red brown. Differences in color among local populations may depend on rainfall (Waterman 2013a,b). Additionally, skins in *Xerus* and *Euxerus* are frequently stained from the soil what changes the color of the feet, tail, and even the entire body (Hollister 1919). Dorsal pelage is monochromatic (*Xerus* and *Spermophilopsis*) or striped (the remaining species). The pattern is simple, with a single flank stripe of all-white hairs in *Euxerus* and *Geosciurus*. *Atlantoxerus* has an indistinct spinal line in addition to lateral stripes (Figure 2).

African Xerini are relatively long-tailed for ground-dwelling squirrels (Figure 2). Length of tail relative to length of head and body ranks between species as follows (in%; parenthesized are mean±SD): *Atlantoxerus* (70.42±6.79, n=10) <*Euxerus* (80.6±8.45, n=26) <*Xerus* (84.2±7.95, n=12) <*Geosciurus inauris* (86.9±7.10, n=12) <*G. princeps* (103.2±6.27, n=6). The long clawed ground squirrel *Spermophilopsis* (Figure 3) is decidedly short-tailed (29.2±4.42, n=21). The tail is dorso-ventrally flattened (distichous) with long hairs directed sideways rather than bushing out evenly all around. Long tail hair is monochromatic in *Xerus*, but has white and black bands in the remaining genera. In *Spermophilopsis* the black and white pattern is restricted to the terminal half of the tail and is most extensive on its ventral side. The tail in Xerini serves multiple purposes, i.e. in thermoregulation (in hot days as a parasol to prevent overheating; Bennett et al. 1984), in social interactions (Herron and Waterman 2004) and in antipredatory behavior, either by alarming conspecifics (Sludskiy et al. 1969) or mobbing and harassing snakes by sideway flicking (Apps 2000).

Figure 2: Representatives of genera in African bristly ground squirrels Xerina: 1 – *Atlantoxerus getulus* (Fuerteventura, Canary Islands; photo courtesy Alenka Kryštufek); 2 – *Geosciurus inauris* (Etosha National Park, Namibia; photo courtesy Emmanuel Do Linh San); 3 – *Xerus rutilus* (Samburu National Park, Kenya; photo by Jan Matějů); 4 – *Euxerus erythropus* (captive; photo courtesy Klaus Rudloff).

Figure 3: Long-clawed ground squirrel *Spermophilopsis leptodactylus* (Kyzyl Kum, Kazakhstan; photo courtesy Nedko Nedyalkov).

Pocock (1922) stressed that African Xerini are unique in having "a supplementary superciliary tuft of long vibrissae over the posterior angle of the eye" (i.e. superciliary or supraorbital vibrissae), and Sokolov and Kulikov (1987) reported a cluster of vibrissae on the outer antebrachium about halfway between the elbow and the wrist (the antebrachial vibrissae; Figure 4) as a distinctive trait in *Spermophilopsis*. As a matter of fact, both types of vibrissae are present in all species of Xerini.

Feet of Xerini are peculiar among squirrels in being of perissodactyle type, i.e. having digit III the longest and digits II and IV of about same length (Figure 4). *Atlantoxerus* deviates from other genera in having the feet more slender and in retaining metatarsal pads. The remaining African species display stouter feet with small plantar pads and lack the metatarsal pads; *Geosciurus* has the most robust and fossorial feet of all genera. *Spermophilopsis* differs from African genera in having much enlarged claws and densely haired paws and soles (Figure 4). There was significant heterogeneity among species in length of hind foot relative to length of head and body (One-way ANOVA of $\log_{10}$-transformed quotients: $F=15.61$, $p<0.0001$). *Xerus* (relative length of hind foot: 29.5±0.57,

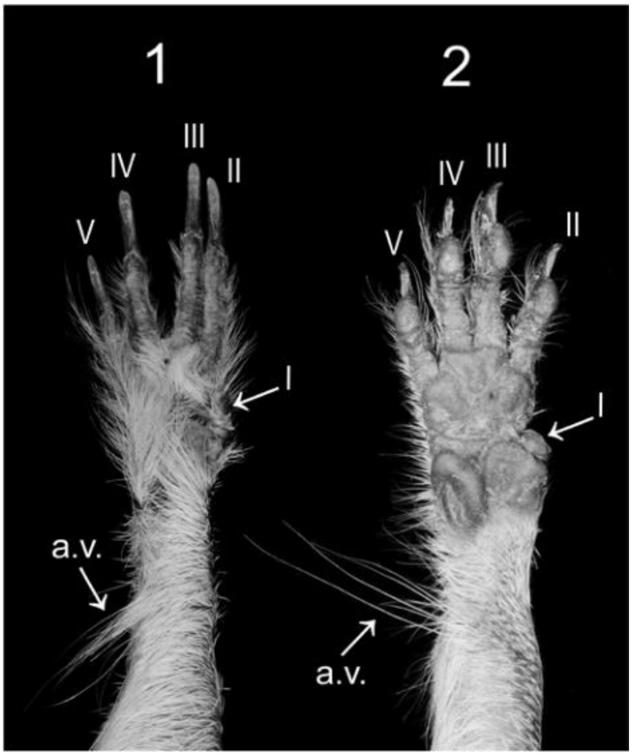

Figure 4: Right front paw (ventral view) in (1) *Spermophilopsis leptodactylus* (ZFMK 92.478) and (2) *Atlantoxerus getulus* (NMW 28084). Roman numerals correspond to digits (No. I is the thumb); a.v. – antebrachial vibrissae. Note that digit III is longer than either digits II and IV. Also note differences in length of claws (decidedly longer in *Spermophilopsis*) and in hairiness of the palm (nude in *Atlantoxerus*). Not to scale.

n=12) and both species of *Geoscirus* (*G. inauris*: 28.1±0.57, n=12; *G. princeps*: 29.3±0.80, n=6) had relatively the longest foot. Hind foot was the shortest in *Spermophilopsis* (23.9±0.48, n=17); *Atlantoxerus* (29.5±0.568, n=12) and *Euxerus* (25.7±0.41, n=23) were intermediate in this respect.

The ear conch is usually reduced in ground dwelling squirrels and this holds also for Xerini. In *Atlantoxerus*, *Xerus* and *Euxerus*, the ear is relatively large, with its margin staying away from head. The ear is reduced to a thick fold of skin in *Geosciurus* and *Spermophilopsis*. The orifice is sheltered by a tragus in *Euxerus*, *Xerus*, and *Spermophilopsis*, but is exposed in *Atlantoxerus* (which still retains the tragus) and *Geosciurus* (which lacks the tragus).

Atlantoxerus and *Spermophilopsis* have four pairs of nipples: one pectoral, two abdominal and one inguinal pair, respectively (Figure 5). *Xerus* and *Geosciurus* have two pairs (the posterior abdominal and the inguinal). Typical count in *Euxerus* is three pairs (both abdominal and the inguinal), however of 14 lactating females examined, four individuals from Senegal and Uganda lacked the inguinal pair hence retaining only both abdominal pairs. For *Spermophilopsis* occupying Afghanistan, Obolenskij (1927) reports three pairs of nipples, however, we counted four pairs on each of two female skins from the country (ZFMK 92.478, 92.479; Figure 5). Similarly to our results, Ognev (1940) identified four pairs in *Spermophilopsis*.

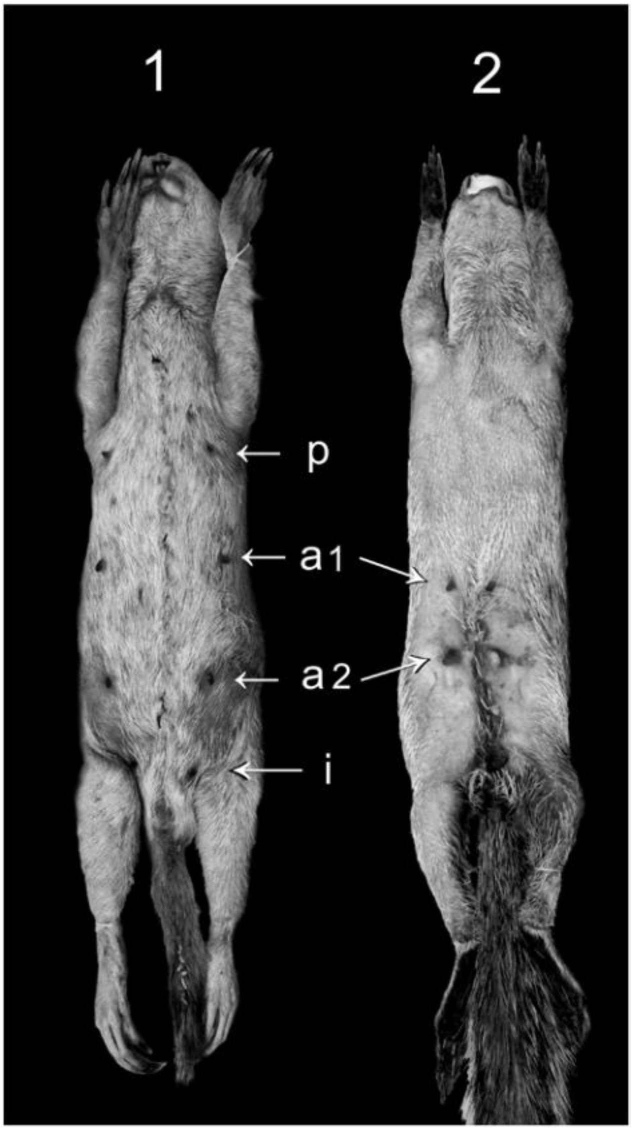

Figure 5: Nipples in (1) *Spermophilopsis leptodactylus* (ZFMK 92.496) and (2) *Euxerus erythropus* (ZFMK 76.38): p – pectoral; a1 and a2 – 1st and 2nd abdominal; i – inguinal. Not to scale.

Glans penis is relatively large with well-developed baculum. The baculum is terminally situated and consists of a compressed blade which carries a cartilaginous or partly ossified crest; the crest expands posteriorly and represents the distal dorsal crest of the glans. In all its aspects the baculum in Xerini differs profoundly from this structure in Arctomyinae (Pocock 1923, Ognev 1940).

Cranial and dental morphology

We assessed the overall cranial similarity by subjecting nine linear skull measurements to PCA. First principal component (PC1) explained 72.7% of variation in the original data set and had high (>0.76) positive loadings for all variables. PC2 (9.5% of variance explained) had moderately high loadings for zygomatic width (0.52) and breadth of braincase (0.44). Projection of specimens' scores onto PC1 and PC2 retrieved clear differences among the taxa (Figure 6). Species grouped along PC1 according to size, from *Atlantoxerus* (the smallest) on the left hand side to *Geosciurus* (the largest) on the right hand size. Evidently, the majority of Xerini are large, and *Xerus* is the only genus of intermediate size. PC2 sorted taxa according to their relative breadth of skull. Most extreme were *Spermophilopsis* (the broadest skull) and *Euxerus* (the narrowest skull). Wide skulls are evidently more common in Xerini than narrow skulls.

Ellerman (1940) and Moore (1959) stressed the cranial similarity between *Geosciurus* and *Spermophilopsis*, which is clearly retrieved also from our results. It is equally well evident that the similarity is superficial due to a robustness of our approach. Namely, the nine parameters we used to quantify each skull missed many details of cranial shape which are grasped at glance already on a dorsal profile of the skull (Figure 6). For example, *Spermophilopsis* has a longer rostrum tapering towards its apex and relatively shorter brain case while the rostrum is short and blunt in *Geosciurus*, and the braincase is longer. African genera were widely apart in the morphospace defined by the first two principal components and did not overlap at all. Groups are not defined in advance in the PCA, therefore morphometric distances between the objects are not biased, e.g. by minimizing variance within each group and maximizing variance among groups as is the case in a discriminant analysis. Plot in Figure 6 therefore reflects the actual relationships what allows the conclusion of significant cranial differentiation among the genera of African Xerini.

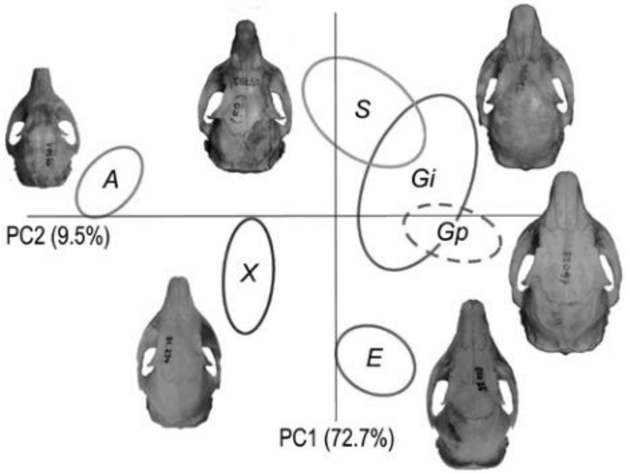

Figure 6: Bivariate plot of six Xerini species onto the first two principal components (PC) derived from ordination of nine cranial measurements (transformed to $\log_{10}$). Percentage of variance explained by individual PC is in parentheses. 95% confidence ellipses show the dispersion of all specimens within each species and letters indicate group centroids. Skulls (in dorsal view) are depicted to scale: *A – Atlantoxerus getulus* (PMS 19301); *E – Euxerus erythropus* (ZFMK 47.972); *Gi – Geosciurus inauris* (NMW 32092); *Gp – Geosciurus princeps* (NMW 32097); *S – Spermophilopsis leptodactylus* (NMW 25782); *X – Xerus rutilus* (ZFMK 81.234).

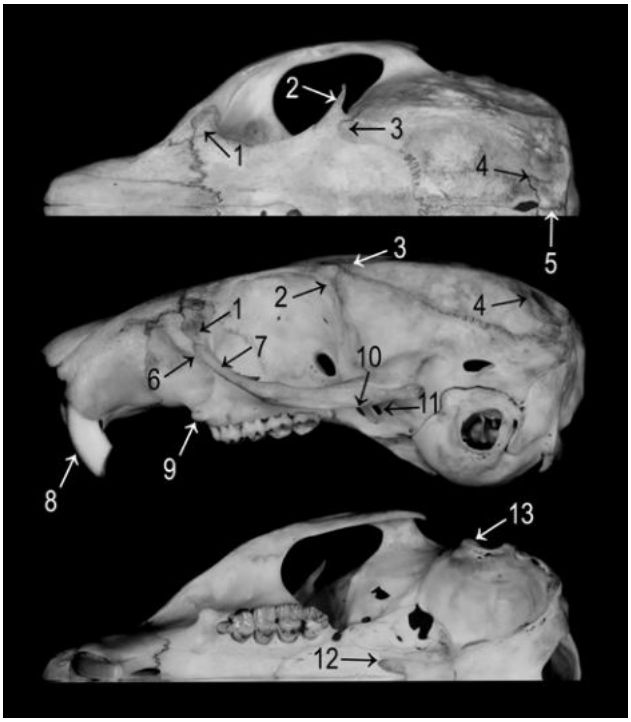

Figure 7: Skull of *Atlantoxerus getulus* (NMW 43000) in dorsal, lateral and ventral views (from top to bottom). Arrows point on traits which are informative for taxonomic ranking of Xerini. 1 – lacrimal bone; 2-postorbital process of the frontal bone; 3 – anterior extension of the squamosal bone; 4 – parieto-interparietal suture; 5 – interparietal suture; 6 – anteriorly projected external ridge on the front face of the zygomatic plate; 7 – jugal bone; 8 – opisthodont upper incisor; 9 – masseteric tubercle; 10 – buccinator foramen; 11 – masticatory foramen; 12 – posterior margin of hard palate; 13 – external *meatus acusticus*.

The upper incisors are thickened and opisthodont (Figure 7), with the antero-posterior diameter exceeding the transverse diameter. The front surface has shallow grows in *Atlantoxerus* but is smooth in the remaining genera. Among the characteristic features of cheek-teeth morphology shared by all fossil and recent Xerini are (i) metaloph disconnected from protocone, and (ii) a presence of ectolophid and hypoconulid in lower molars. The morphological trends recorded in the group are limited to size increase and moderate hypsodonty development on the basis of the bunodont dental pattern (Denys et al. 2003). *Atlantoxerus* is the most bunodont and brachyodont, and *Spermophilopsis* is distinctly hypsodont, likely an adaptation to a marked herbivorous diet. The mandibular tooth-row is more distinctly bunodont than the maxillary. Low cusps and ridges became obliterated into wide re-entrant folds fairly early in life. *Atlantoxerus, Spermophilopsis* and *Euxerus* retain the 3rd upper premolar (Figure 8). This tooth, invariably small and peg-like, is frequently missing in *Euxerus* (absent in seven skulls of 39 examined, i.e. 18%) and may be occasionally absent also in *Atlantoxerus* and *Spermophilopsis*.

Cladistic analysis of African Xerini, based on 13 cranial and 9 dental traits (Denys et al. 2003), did not unambiguously resolve phylogenetic relationships among species and branching topology depended on a taxonomic sampling. *Atlantoxerus*, however, emerged as the most distinct with a putative sister position against the remaining species.

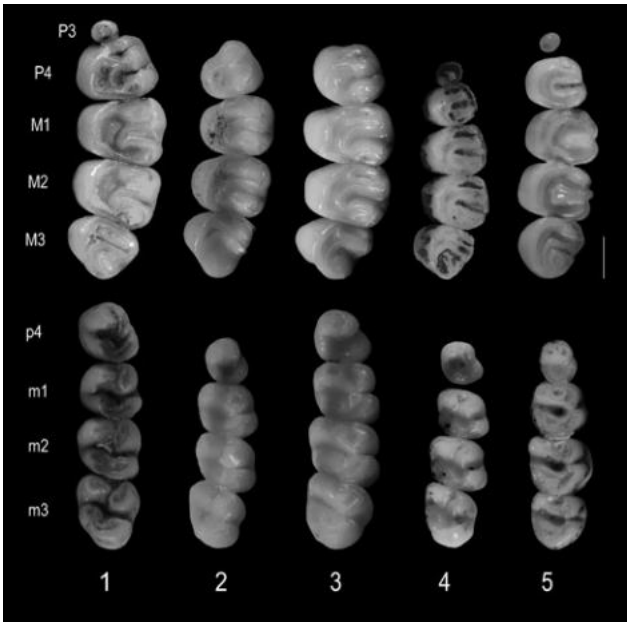

Figure 8: Left maxillary (above) and right mandibular (below) tooth-rows in Xerini: 1 – *Euxerus erythropus* (NHML 69.10.24.18/ZFMK 97.467), 2 – *Xerus rutilus* (ZFMK 81.234/ZFMK 96.251); 3 – *Geosciurus inauris* (ZFMK 55.147); 4 – *Atlantoxerus getulus* (PMS 19301 / ZFMK 88.195); 5 – *Spermophilopsis leptodactylus* (ZFMK 92.497/ZFMK 92.496). Abbreviations for cheek-teeth: P/p – upper/lower premolar, M/m – upper/lower molar; numbers refer to a position in the tooth-row. Scale bar=2 mm.

Fossil history

The ranges of extant Xerini are disjunct. The main occupation in Africa (*Atlantoxerus* and *Xerus* sensu lato), and a smaller one in western Asia (*Spermophilopsis*) reflect the much more extensive former distribution (Figure 9). The fossil record is surprisingly dense, particularly during the Miocene in Eurasia and northern Africa. The group however was never diverse, being represented at most by two or three genera at a time.

The earliest true Xerini are known from the Late Oligocene and belong to two closely related fossil genera: *Kherem* Minjin, 2004 from Mongolia (Maridet et al. 2014) and *Heteroxerus* Stehlin and Schaub, 1951 (*Aragoxerus* Cuenca, 1988 is a synonym), from west Europe (Baudelot and Olivier 1978, Werner 1994). Their widely scattered distributional records indicate an extensive trans-Palaearctic distribution of Xerini at the very beginning of their known history.

Heteroxerus and *Atlantoxerus* are the best know genera of Xerini in the Eurasian and North African record throughout the Miocene. Both had a cuspate bunodont dental pattern but differed in size. The larger *Atlantoxerus,* known since the Early Miocene of Europe (Aguilar 2002) and China (Qiu et al. 2013), occupied Asia (northern and north-western China, Mongolia, Pakistan, Thailand, Kazakhstan, Arabia, Anatolia), south-western Europe (Italy, France, Spain), and northern Africa. The smaller *Heteroxerus* hold a stable range in the western Mediterranean and was also recorded from the Early Miocene of western Kazakhstan (Kozhamkulova and Bendukidze 2005), from the Middle Miocene of Siwalik, Indostan (Flynn and Wessels 2013), and from the Middle and Late Miocene of South Africa (Winkler et al. 2010). The Middle Miocene marks the maximum range expansion and abundance of Xerini in Eurasia. This peak was followed by the extinction of *Kherem* and *Heteroxerus* in the Middle (Maridet et al. 2014) and Late Miocene (de Bruijn, 1999), respectively, and by the emergence of *Xerus* sensu lato, which appeared for the first time in the early Late Miocene of Ethiopia (Geraads 2001). The second earliest record (tentatively *Xerus* sensu stricto) comes from late Late Miocene of Kenya (Manthi 2007).

In the Pliocene and Early Pleistocene the fossil record of Xerini clearly declined throughout Eurasia, and the formerly continuous range became increasingly fragmented. The genus *Atlantoxerus* survived until Early Pliocene in Spain and persisted into the earliest Pleistocene in northern China. In northern Africa, where *Atlantoxerus* still had an extensive trans-regional distribution during the Late Miocene, the range contracted to Morocco and

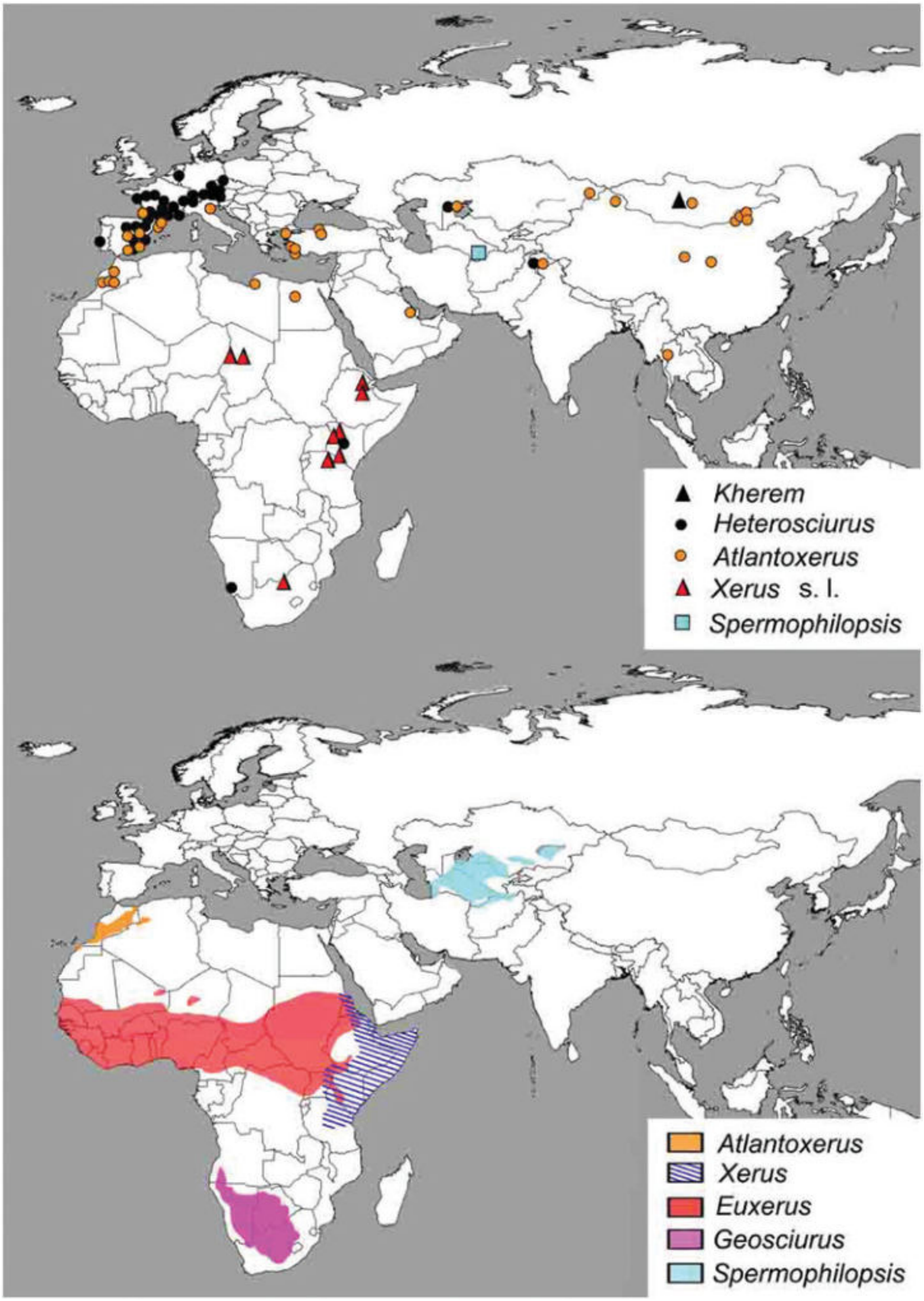

Figure 9: Distributional ranges of Xerini. Fossil (Late Oligocene to Early Pleistocene) records (top inset) are based on Fortelius (2015) with corrections and additions from Gromov and Erbajeva (1995), Kozhamkulova and Bendukidze (2005), Winkler et al. (2010), Flynn and Wessels (2013), and Maridet et al. (2014). Map of recent ranges (inset below) does not show the isolate of *Euxerus erythropus* in Morocco, and the population of *Atlantoxerus getulus* introduced to Fuerteventura, Canary Islands.

Algeria by the Early Pliocene, and to Morocco by the Early Pleistocene.

The African record of *Xerus* sensu lato is patchy. The group is known throughout the Pliocene from East Africa (Kenya, Tanzania, Ethiopia), during the Early Pleistocene from Chad, and during the Late Pleistocene from central South Africa (Winkler et al. 2010). The Early Pleistocene emergence of *Spermophilopsis* in deposits of Badkhyz, southern Turkmenistan (Gromov and Erbajeva 1995), marks the presence of the genus within its modern range. The increase of dryness towards the end of the Miocene and the opening of savannahs may have directed the evolution of Xerini towards adaptations to arid environments.

The phylogenetic reconstruction of the Xerini is quite straightforward, due to low taxonomic diversity and good fossil record. Geologically, the oldest representative is *Heteroxerus* which is the smallest and the most plesiomorphic in dental morphology. By the Early Miocene *Heteroxerus* may have given rise to *Atlantoxerus* (Jaeger 1977). *Xerus* presumably diverged from a primitive *Atlantoxerus* stock during the Early to Late Miocene (Denys et al. 2003). Similarly, proto-*Spermophilopsis* possibly emerged after the late Middle Miocene from a population fragment of *Atlantoxerus* in south-Central Asia. A palaeoecological analysis of the chronological distribution of Xerini (*Atlantoxerus* and *Heteroxerus*) during the Neogene of Spain retrieved a marked positive dependence of taxonomic diversity on increase in temperature. The group “flourished during the late Early to Middle Miocene thermal optimum in Spain and declined during the subsequent Middle Miocene cooling episode” (Van Dam and Weltje 1999).

Systematics and nomenclature

The two available phylogenetic trees confirm a basal dichotomy into an African and an Asiatic lineage, but suggest very different relationships within the African bristly ground squirrels. For the latter, the most probable is a basal position of *Atlantoxerus*, which was retrieved in our molecular reconstruction and in a cladistic analysis of cranial and dental traits (Denys et al. 2003). *Atlantoxerus* shares with *Spermophilopsis* several traits (two upper premolars, high number of nipples, and opened parieto-interparietal suture) what induced Moore (1959) to presume close phylogenetic links between the two. *Atlantoxerus* is also unique among the African species in its relatively soft fur, in retaining metatarsal pads and in the shape of the suture between the jugal and the lacrimal (see below). At least some of these traits are probably plesiomorphic for Xerini.

Although the phylogenetic relationships remain unresolved, metrics of genetic distances requires a taxonomic partition of African Xerini. The genetic disparity is fully concordant with the ecomorphological discrepancy therefore a division of the genus *Xerus* (sensu Ellerman 1940) into three genera more properly reflects the taxonomic relationships among the sub-Saharan bristly ground squirrels. Also noteworthy, the generic split of *Xerus* creates genera of Xerini which are separated by genetic distances comparable to those in another lineage of ground dwelling squirrels, the Spermophilina (cf. above).

Subsequently we list and reference all names above the species group in Xerini. Species group names are compiled in Ellerman (1940), Allen (1954), Ognev (1940) and, Pavlinov and Rossolimo (1987). Type localities and other relevant passages where quoted as originally published (shown by quotation marks). For each taxon above the species group we provide a brief diagnosis, understanding a diagnosis as “A statement in words that purports to give those characters which differentiate the taxon from other taxa with which it is likely to be confused” (ICZN 1999).

Subfamily Xerinae Murray

Xeri Murray, 1866, p. 256. Type genus is *Xerus* (by tautonomy). Emended to Xerini (Kryštufek and Vohralik 2013).

Xerinae Osborn, 1910, p. 535. Type genus is *Xerus* (by tautonomy).

Xerini Simpson, 1945, p. 79. Type genus not defined. Simpson evidently changed the rank from Osborn’s (1910) subfamily to a tribe, without altering its scope.

In the past, the subfamily Xerinae was usually defined to include the African genera *Xerus* and *Atlantoxerus*, and the Asiatic *Spermophilopsis* (Osborn 1910, Pocock 1923). Steppan et al. (2004) redefined the scope of Xerinae by including also Arctomyinae Grey, 1821 (Marmotinae Pocock, 1923 is a synonym; cf. Kryštufek and Vohralik 2013). A phylogenetic reconstruction of Fabre et al. (2012) retrieved Xerinae to consist of two lineages, which are appropriately classified as tribes (Kryštufek and Vohralik 2013), the Xerini (cf. below) and the Callosciurini Simpson, 1945. The scope of Callosciurini is identical to the content of the subfamily Callosciurinae of Steppan et al. (2004). Close relationships between Xerini and Callosciurini are evident from chromosomal data (O’Shea 1991).

Tribe Xerini Murray: Bristly ground squirrels

For synonyms see under Xerinae.

Ground squirrels with coarse, bristly or spiny fur during at least one season; hair is usually scanty; the feet is elongate and slender, the 3rd digit longer than 4th (Figure 4); the claws are long and comparatively straight (fossorial); pinna minute or reduced to a stiffened skin fold, antitragal thickening set near the middle of the posterior edge of pinnae; membranous cheek-pouches are missing. Xerini have supplementary superciliary vibrissae and the antebrachial vibrissae (Figure 4). The baculum consists of a compressed blade which carries a cartilaginous or partly ossified crest. Number of nipples is two to four pairs (Figure 5).

Skull (Figure 7) is typically with (i) the bony palate considerably prolonged beyond the ends of the tooth-row, (ii) enlarged lacrimal bone, (iii) well developed and anteriorly projected external ridge on the front face of the zygomatic plate, (iv) the squamosal bone extending up to the base of postorbital process of the frontal bone, (v) a powerful masseteric tubercle, (vi) a short and massive pterygoid processes, and (vii) the opisthodont upper incisors (Flower and Lydekker 1891, Pocock 1922, Ellerman 1940, Ognev 1940, Moore 1959). The karyotype is conservative (2n=38).

Xerini occupy dry open habitats in the Palaearctic region (central Asia and the area of the Atlas Mts.), and of sub-Saharan Africa (the Sudano-Guinean, Somali-Masai, and Zambezian savannas; Denys 1999). Genera occupy exclusive non-overlapping ranges, except for slight overlap between *Xerus* and *Euxerus* in Eritrea, Ethiopia, Uganda and Kenya (Figure 9). Four genera of total five are monotypical what induced Moore (1959) to speculate that Xerini are in the contracting phase of their evolution.

Xerini, as typical ground squirrels, dig underground burrows and do not climb trees; *Atlantoxerus* seeks shelter among rocks and easily climbs on rock slopes. *Spermophilopsis* is a habitat specialist, mainly dependent on moving sands. All species are diurnal and do not practice torpor.

No common name is in use for the African and the Asiatic Xerini combined. We propose "bristly ground squirrels", a name capturing an evident character in common to these animals.

The tribe contains two subtribes: Xerina of Africa and Spermophilopsina of Central Asia.

Subtribe Xerina Murray: African bristly ground squirrels

For synonyms see under Xerinae.

Subtribe Xerina includes African members of the tribe Xerini, with long tail and a pelage which is bristly (rough in *Atlantoxerus*) at all seasons; a bold light (whitish) ring is surrounding the eye, and three genera of totally four have flank stripes (Figure 2). Soles and plants are nude (Figure 4); the pollex bears a tiny nail, claws on the remaining digits are not enlarged (<10 mm in length); two tufts of supraorbital vibrissae are present; the cerebral *dura mater* has no melanocits; the external *meatus acusticus* lacks a bony tube (except in *Geosciurus*); buccinator and masticatory foramina are separate (Figure 7).

Few common names were in use in the past for Xerina: "spiny (or bristly) squirrels" (Murray 1866, Flower and Lyddeker 189, Osborn 1910) and "African ground squirrels" (Pocock 1922, Simpson 1945, Li et al. 2006). Pocock (1922) was perhaps the first who used the combination "bristly ground squirrels".

Genus *Xerus* Hemprich and Ehrenberg: Unstriped ground squirrels

Xerus Hemprich and Ehrenberg, 1832, Plate IX. Type species is *Sciurus (Xerus) brachyotus* Hemprich and Ehrenberg (=*Xerus rutilus*).

Spermosciurus Lesson, 1842, p. 110. Type species is *Sciurus rutilus* Cretzschmar (cf. below). *Spermosciurus* was proposed as a subgenus of *Sciurus*.

Content. – A monotypic genus, containing only *X. rutilus*.

Xerus rutilus (Cretzschmar): Unstriped ground squirrel

Sciurus rutilus Cretzschmar, 1828, p. 59, plate 24. Type locality is "eastern slope of Abysinnia"; probably Massawa (cf. Thorington and Hoffmann 2005), today in Eritrea.

Amtmann (1975) recognized eight subspecies but also noted that subspecific classification is uncertain.

Etymology. – *Xerus* is Greek for "dry"; "called from the character of the fur, which is harsh and often spiny" (Palmer 1904). Species name *rutilus* is Latin for "red" or "golden red" in allusion to the colouration of the pelage.

Diagnosis. – *Xerus rutilus* is a medium-sized member of the subtribe Xerina and the only one with a plain, unstriped pelage (Figure 2). The ears are moderately large, with the tragus present. Metatarsal pads are absent (Pocock 1922). Females have posterior abdominal and the inguinal pairs of nipples (four nipples totally). The baculum (length=6 mm) is typified by a wide and spearhead-shaped upper surface of the blade and a low dorsal median crest (Pocock 1923). Skull is moderately wide (Figure 6) and the 3rd upper premolar is absent (Figure 8); the jugal bone is bluntly truncated against the lacrimal.

Distribution. – Endemic to a Somali-Masai savannah (Denys 1999), occupying dry bushland and savannah in

Somalia, Ethiopia, Eritrea, Kenya, Tanzania and eastern Uganda (O'Shea 1991) (Figure 9). A century ago reported for Sinkat (Anderson 1902) in what is today Sudan, but current presence in Sudan questioned by O'Shea (1991).

Remark. – *Xerus rutilus* is reviewed in O'Shea (1991) and Waterman (2013c).

Genus *Euxerus* Thomas: Striped ground squirrels

Euxerus Thomas, 1909, p. 473. Type species is *Sciurus erythropus* E. Geoffroy.

Tenotis Rafinesque 1817 , p. 362. Type species is *Tenotis griseus* Rafinesque. *Tenotis griseus* is listed in Palmer (1904: 668) and Kretzoi and Kretzoi (2000: 403) but ignored in other nomenclatural sources. Rafinesque proposed *T. griseus* under "*Sciurus erithopus*. Geoffr." (a misprint for *erythopus*) and defined *Tenotis* as "contain[ing] all the squirrels with pouches [...] who live under ground"; as such *Tenotis* does not match Xerini which lack internal pouches. Locality for *T. griseus* is not known and we propose the name *Tenotis* as not identifiable (*nomen dubium*).

Content. – A monotypic genus, containing only *E. erythropus*.

Euxerus erythropus (É. Geoffroy Saint-Hilaire): Striped ground squirrel

Sciurus eyrthoupus (sic) É. Geoffroy Saint-Hilaire, 1803, p. 178. Type locality: "Inconnue" (=unknown). A specimen from Senegal, acquired by Florent Prévost in November 1820 and deposited in Muséum National d'Histoire Naturelle, Paris (MNHN-ZM-MO-2000-601), was designated as neotype (Rode 1943). Type locality is therefore ("probably") Senegal (Allen 1954). The ICZN (1971: 224) ruled *erythoupus* by Geoffroy Saint-Hilaire to be an incorrect original spelling for *erythropus*, placed *erythoupus* on the Official Index of Rejected and Invalid Specific Names in Zoology, and validated the emendation of the specific name *erythoupus* to *erythroupus*. Wilson and Reeder (1993) regarded Geoffroy Saint-Hilaire (1803) ("a very rare book"; Jentink 1882) as not validly published, what was rebuffed in Corbet and Hill (1994); with reference to Hill 1980).

Six subspecies were recognized by Amtmann (1975) and tentatively mapped in Herron and Waterman (2004).

Etymology. – "Eu" is Greek for "typical"+*Xerus*; i.e. "a typical bristly ground squirrel". The species name *erythropus* is from "eruthros" (red) and "pous" (a foot, both Greek), i.e. "a red-footed", although "there is nothing to indicate why Geoffroy should have chosen the name... as it is [red-footed] in fact not one which has any particular application to any known form [of *E. erythropus*]" (Rosevear 1969: 132); note the above claim by Hollister (1919) who stated that feet and other parts of body are often stained with the soil what changes the color.

Diagnosis. – *Euxerus erythropus* is a large member of the subtribe Xerina, recognizable by a combination of flank stripe (Figure 2), narrow skull (Figure 6), and a high incidence of the 3rd upper premolar (present in ~80% of individuals; Figure 8). The ears are moderately large, with tragus present. Metatarsal pads are absent and plantar pads are more reduced in size than in any other African species (Pocock 1922). Females have two (Figure 5) or three pairs of nipples (mean=2.71±0.469, n=14). The baculum (length=8–9 mm) consists of a cylindrical proximal part and distal compressed blade; the dorsal crest ossifies only partly (Pocock 1923). The Y chromosome is acrocentric (biarmed in the remaining Xerini). The jugal bone is bluntly truncated against the lacrimal (i.e. without a short wedge-like extension between the lacrimal and maxillary; Figure 10).

Distribution. – Endemic to the Sudano-Guinean savannah (Denys 1999). *E. erythropus* is a habitat generalist (Rosevear 1969) occupying a wide subtropical and tropical belt between the equator and the transition of the Sahelian zone and Sahara (Granjon and Duplantier 2009, Monadjem et al. 2015). Range extends from the Atlantic coast in the west to Eritrea, western Ethiopia and north-western Kenya in the east (Figure 10). There is an isolate in the Souss region in western Morocco (Blanc and Petter 1959). Remnants of the Neolithic age from Bir Kiseiba in southern Egypt (Osborn and Osbnornová 1998) are another evidence of a wider occurrence in Palaearctic Africa during the Holocene. The 19th century records for Egypt (Jansen 1882) and "Nubia" (Supplemental Appendix 2) however most probably refer to what is now Sudan (cf. Anderson 1902).

Remarks. – *Euxerus erythropus* is reviewed in Rosevear (1969), and (as *Xerus erythropus*) in Herron and Waterman (2004) and Waterman (2013b).

Genus *Geosciurus* Smith: South African ground squirrels

Geosciurus Smith 1834, p. 128. Type species is "*X. capensis*" (synonym of *Sciurus inauris* Zimmermann), subsequently designated by Thomas (1897, p. 933).

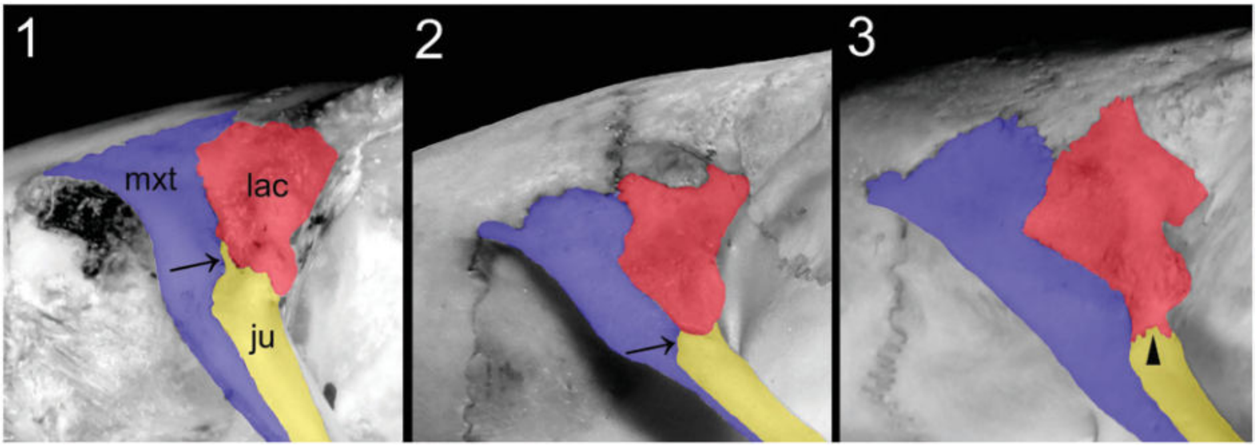

Figure 10: Anterior zygomatic arch in three genera of Xerini to show differences in a suture between the lacrimal (lac), the maxillary (max) and the jugal (ju) bones. 1 – *Spermophilopsis leptodactylus* (NMW 32092); 2 – *Atlantoxerus getulus* (NMW 43000); 3 – *Euxerus erythropus* (ZFMK 97.472). Arrow points on a wedge-like extension of the jugal between the lacrimal and maxillary in *Spermophilopsis* and *Atlantoxerus*. A bluntly truncated top of jugal bone at the lacrimal bone which is distinctive of sub-Saharan Xerina, is shown by triangle. Not to scale.

Content. – *Geosciurus* contains two species which differ morphologically (de Graaff 1981, Herzig-Straschil et al. 1991) and in nucleotide sequences (Herron et al. 2005).

Geosciurus inauris (Zimmermann): Cape ground squirrel

Sciurus inauris Zimmermann 1780, p. 344. Type locality is "Kaffirland, 100 miles north of the Cape of Good Hope" (Skurski and Waterman 2005).

A monotypical species which however includes three deeply divergent phylogeographic lineages (Herron et al. 2005).

Geosciurus princeps Thomas: Damara (Kaokoveld) ground squirrel

Geosciurus princeps Thomas, 1929, p. 106. Type locality is "Otjitundua, Central Kaokoveld, Namibia, Africa."

A monotypical species.

Etymology. – The name *Geosciurus* is derived from "geos" (Greek for earth)+*Sciurus* (Greek for a squirrel, from "skia" for "shade"+"oura" for "tail" (both Greek), i.e. "a shade-tail" "on account of the way a squirrel holds his bushy tail over his back" (Gotch 1995); *Geosciurus* is therefore "a ground squirrel" (allusion on its habits). The species name *inauris* consists of "in" (not, without)+"auris" (ear; both Latin) in allusion "to the very small ear pinnae of the species" (de Graaff 1981). The name *princeps* (Latin for "first" or "primary") "may refer to the larger than average size, brighter coloration and more profusely ringed tail of this species in contrast to the somewhat smaller, drabber *inauris*." (de Graaff 1981).

Diagnosis. – More fossorial than other African bristly ground squirrel. Size is large, fur is bristly; flanks with a stripe (Figure 2); hind foot robust, metatarsal pads absent; the ear extremely reduced to a rounded thickened rim, tragus absent; two pairs of nipples (posterior abdominal and the inguinal). Baculum (length is 8 mm in *G. inauris*) consists of long proximal cylindrical portion and elongated distal part; the upper surface of the blade is narrow and strongly constricted; dorsal crest is long (Pocock 1923). Skull is broad and deep, with a short rostrum and elongate braincase (Figure 6); jugal bone is bluntly truncated against the lacrimal. Cheek-teeth are relatively hypsodont; the 3rd upper premolar is absent (Figure 8).

Distribution. – The genus *Geosciurus* is endemic to Zambezian savannah (Denys 1999; Figure 9); *G. inauris* occupy open savannahs in Botswana, Republic of South Africa, and Namibia (Herzig-Straschil 1979) but possibly disappeared during the last century from Zimbabwe (Skurski and Waterman 2005). *G. princeps* is restricted to the western escarpment in Namibia and very marginally occurs in Republic of South Africa and Angola. Although ranges of the two species overlap, they select different habitats and segregate in behavior (Herzig-Straschil and Herzig 1989).

Remarks. – Both species of *Geoscirus* are well covered (as *Xerus*) in general faunal reviews of the mammals occupying the southern African subregion (de Graaff 1981, Skinner and Chimimba 2005). For other reviews see Skurski and Waterman (2005), Waterman and Herron (2004) and Waterman (2013d,e).

Genus *Atlantoxerus*: Barbary ground squirrels

Atlantoxerus Forsyth Major, 1893, p. 189. Type species is "X. *getulus* (Gesn[er])" (=*Sciurus getulus* Linnaeus). *Atlantoxerus* was proposed as a subgenus of *Xerus*.

Scope. – A monotypic genus, containing only *A. getulus*.

Atlantoxerus getulus (Linnaeus): Barbary ground squirrel

Sciurus getulus Linnaeus 1758, p. 64. The type locality ("Habitat in Africa" = Lives in Africa) was restricted to "Barbary" (= Mediterranean Africa between Egypt and the Atlantic coast) by Thomas (1911: 149), and to "Agadir" (Morocco) by Cabrera (1932: 217). On p. 218 Cabrera justified this step as follows (our translation from Spanish): "(1) Imports of animals and other goods from Morocco in the 17th and 19th century came mostly from the port "Santa Cruz de Berberia", the current name of which is Agadir. Examples are squirrels figured in the painting "Arche Noah" by the Dutch artist P. Breughel [actually Jan Breughel the Elder, 1568–1625], now in the Prado in Madrid [Prado holds one of the later versions while the original is in the J. Paul Getty Museum; Kolb 2005], and in the book by Gessner from 1551. The picture in Gessner subsequently inspired Ray (1693, Synops. Method. Anim. Quadrup., p. 216) to discuss this squirrel. (2) Linnaeus based his name on the reports of Ray (as above), and of Edwards 1751 (A natural history of birds, vol. 4, plate 198), who reported and figured a squirrel from "Santa Cruz (on the Western Coast of Barbary, bordering on the Atlantic Ocean)". The specimen figured in Gessner (1551), argues Cabrera, should be regarded as the type of the species.

No subspecies are recognized.

Etymology. – The name *Atlantoxerus* was coined from Greek "Atlas" or "Atlantos" (=the Atlas Mts. in Morocco)+"Xerus" (dry in Greek) in allusion to the arid habitat. The species name is derived from Gaetulia (Romanized for a Berber Getulia), an ancient district in Northern Africa around the Atlas Mts.

Diagnosis. – The smallest species of Xerini, and the only one having a light spinal stripe (Figure 2), present metatarsal pads, a paired interparietal bone (Figure 7), upper incisor with traces of a groove, and brachiodont and bunodont cheek-teeth. Among the African Xerina, *Atlantoxerus* is unique in having rough, but not bristly (spiny) fur, four pairs of nipples, exposed orifice which is not sheltered by a tragus, in retaining the parieto-interparietal suture (Figure 7), and in having a short wedge-like extension of the jugal bone between the lacrimal and maxillary (Figure 10). Baculum (length=7 mm) has a long proximal portion and simple blade which is asymmetrical in dorsal view and has a medial crest (Pocock 1923). The 3rd upper premolar is present (Figure 8).

Distribution. – Endemic to north-western Africa (Figure 9) in Morocco and present very marginally also in western Algeria (Aulagnier and Thevenot 1986, Kowalski and Rzebik-Kowalska 1991). In 1966–1970 introduced to Fuerteventura, the Canary Islands (Bertolino 2009). Prefers open rocky habitats.

Remarks. – *Atlantoxerus getulus* is reviewed in Aulagnier (2013).

Subtribe Spermophilopsina Ognev: Long-clawed ground squirrels

Spermophilopsinae Ognev 1940, p. 432. Type genus is *Spermophilopsis* (by tautonomy).

Genus *Spermophilopsis* Blasius: Long-clawed ground squirrels

Spermophilopsis Blasius, 1884, p. 325. Type species: *Arctomys leptodactylus* Lichtenstein, 1823.

Content. – A monotypic genus.

Spermophilopsis leptodactylus (Lichtenstein): Long-clawed ground squirrel

Arctomys leptodactylus Lichtenstein, 1823, p. 119. Type locality is "140 Werst diesseits Buchara", interpreted as "vicinity of Kara-Ata, 140 km north-west from Buchara, Uzbekistan" (Ognev 1940: 452). Thorington et al. (2012: 202) erroneously fixed the type locality to "Dagestan, Russia".

Gromov and Erbajeva (1995) recognized three subspecies which differ in size and color.

Etymology. – "*Spermophilus*" (a genus of ground squirrels) from "sperma" (seed) and "phylos" (loving; both

Greek) in allusion to the animal's principal food+"opis" (Greek) "of appearance"; i.e. "of same appearance as ground squirrel". The species name is from "leptos" (slender)+"dactylos" (finger, both Greek), on allusion on slender fingers bearing excessively long claws.

Diagnosis. – A large and short-tailed bristly ground squirrel with a seasonally dimorphic pelage (bristly and sparse in summer, long, dense and silky in winter); dorsal color is plain, with no stripes (Figure 3). The external ear is extremely reduced to a rounded thickened rim, the tragus and the antitragus however are present. Soles and plants are densely clothed with hair; the pollex is clawed; claws on the remaining digits are heavily thickened and enlarged (>10 mm in length) (Figure 4); 1 tuft of supraorbital vibrissae. Melanocits are present in the cerebral *dura mater* (Sokolov 1963). Skull is wide and deep, with short braincase (Figure 6); external *meatus acusticus* has a bony tube; the parieto-interparietal suture is retained in adults; jugal bone has a short wedge-like extension between the lacrimal and maxillary (Figure 10); buccinator and masticatory foramina fused. Cheek-teeth are strongly hypsodont; the 3rd upper premolar is present (Figure 8).

Distribution. – The long-clawed ground squirrel is restricted to sandy deserts ("peski" in Russian) of Central Asia, from the Caspian Sea in the west to Lake Balkash in the east, and from the Sea of Aral in the north to northern Afghanistan in the south (Figure 9). The majority of distributional area is in Turkmenistan, Uzbekistan and southern Kazakhstan.

Remarks. – Abundant information on various biological issues of *Spermophilopsis leptodactylus* exists in Russian (Sludskiy et al. 1969, Komarova 1980, Zubov and Svidenko 2005) which however is unknown to the English speaking community (cf. Thorington et al. 2012). For general review in English see Ognev (1966) and for a study of the ecology (in French) see Ružić (1967).

Conclusions

1. Bristly ground squirrels (tribe Xerini) inhabit arid regions of Central Asia and Africa. Their disjunctive range witnesses a much more extensive former distribution. The group is known since the Late Oligocene. In the Middle Miocene the Xerini peaked in range expansion and abundance but declined afterwards. Despite of a dense fossil record, the group was never diverse taxonomically.
2. Extant Xerini are arranged into six species and three genera of which *Atlantoxerus* and *Spermophilopsis* are monotypic. The genus *Xerus* is further split into three subgenera.
3. Phylogenetic reconstruction based on mitochondrial gene for cyt*b* retrieved deep divergences in African Xerini, which are of comparable magnitude to those among genera of Holarctic ground squirrels in the subtribe Spermophilina (subfamily Arctomyinae). Herein we recognize two genera (*Euxerus* and *Geosciurus*), formerly incorporated in *Xerus*, which are clearly distinct in external, cranial and dental morphology, occupy discrete ranges and show specific environmental adaptations.
4. A multigenic phylogenetic reconstruction by Fabre et al. (2012) nested *Atlantoxerus* within the African Xerini. This may be an artefact of incomplete genetic sampling across taxa which left a high proportion of missing values in the data matrix. Our cyt*b* reconstruction and morphological analyses, together with published odontological analyse by Denys et al. (2003) suggest *Atlantoxerus* to be in a sister position against the remaining African taxa. All analyses confirm the sister position of the Asiatic *Spermophilopsis* against the African Xerina.
5. We propose *Tenotis* Rafinesque, 1817 (type species is *Tenotis griseus* Rafinesque, 1817), which is occasionally synonymized with *Euxerus*, as a not identifiable name (*nomen dubium*).
6. Generic classification for the African Xerina proposed herein:
    - Family Sciuridae
        - Subfamily Xerinae, new content
            - Tribe Xerini
                - Subtribe Xerina
                    - Genus *Xerus*, new content
                    - Genus *Euxerus*, new rank
                    - Genus *Geosciurus*, new rank
                    - Genus *Atlantoxerus*
                - Subtribe Spermophilopsina
                    - Genus *Spermophilopsis*

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References

Aguilar, J.-P. 2002. Les sciuridés des gisements karstiques du Miocène inférieur à moyen du sud de la France: nouvelles espèces, phylogénie, paléoenvironnement. Geobios 35: 375–394.

Allen, G.M. 1954. A checklist of African mammals. Bull. Mus. Comp. Zool. 1954: 1–763.

Alston, E.R. 1876. On the classification of the order Glires. Proc. Zool. Soc. Lond. 1876: 61–98.

Amtmann, E. 1975. Family Sciuridae. In: (J. Meester and H.W. Setzer, eds.) The mammals of Africa: an identification manual. Part 6. 1. Smithsonian Institution Press, Washington, DC. (not continuously paginated).

Anderson, J. 1902. Zoology of Egypt: Mammalia. Hugh Rees, London.

Apps, P. 2000. Smither's mammals of southern Africa: a field guide. Struik, Cape Town.

Aulagnier, S. and M. Thevenot. 1986. Catalogue des mammiferes sauvages du Maroc. Travaux de l'Institut Scientifique, Sér. Zool. 41: 1–164.

Aulagnier, S. 2013. *Atlantoxerus getulus* Barbary ground squirrel. In (D.C.D. Happold, ed.) Mammals of Africa. Vol. III: Rodents, hares and rabbits. Bloomsbury, London. pp. 42–44.

Baskevich, M.I., V.N. Orlov, A. Bekele and A. Mebrate. 1995. New data on the karyotype of Ethiopian small mammals (Insectivora, Rodentia). In: (V.E. Sokolov, ed.) Theriological investigations in Ethiopia. Nauka, Moscow. pp. 58–72 (in Russian, with summary in English).

Baudelot, S. and P. Olivier. 1978. Les rongeurs (Mammalia, Rodentia) de l'Oligocene terminal de Dieupentale (sud-ouest de la France: Tarn et Garonne). Geobios 11: 5–19.

Beklemisheva V.R., S.A. Romanenko, L.S. Biltueva, V.A. Trifonov, N.V. Vorobieva, N.A. Serdukova, N.V. Rubtsova, O.V. Brandler, P.C.M. O'Brien, F. Yang, R. Stanyon, M.A. Ferguson-Smith and A.S. Graphodatsky. 2011. Reconstruction of karyotype evolution in core Glires. I. The genome homology revealed by comparative chromosome painting. Chromosome Res. 19: 549–565.

Bennett, A.F., R.B. Huey, H. John-Alder, and K.A. Nagy. 1984. The parasol tail and thermoregulatory behaviour of the Cape ground squirrel *Xerus inauris*. Physiol. Zool. 57: 57–62.

Bertolino, S. 2009. Animal trade and non-indigenous species introduction: the world-wide spread of squirrels. Div. Distr. 15: 701–708.

Blanc, G. and F. Petter. 1959. Presence au Maroc de l'Ecureuil terrestre du Senegal *Xerus erythropus*. Mammalia 23: 239–241.

Blasius, W. 1884. Ueber eine bisher zu den Zieseln (*Spermophilus*) gerechnete neue Nagethiergattung aus Turkestan. Tageblatt der 57. Versammlung Deutscher Naturforscher und Aerzte in Magdeburg 5: 324–325.

Brandt, J.F. 1855. Beiträge zur nähern Kenntniss der Saügethiere Russlands. Mém. a l'Acad. Imp. Sci. St. Petersbourg 6–9: 1–375.

Brisson, M.J. 1762. Le regnum animale in classes IX distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem dibvisionem in ordines, sectiones, genera & species. T. Haak, Paris.

Cabrera, A. 1932. Los Mamíferos de Marruecos. Trabajos del Museo National de Ciencias Naturales, Ser. Zool. 57: 209–222.

Carleton, M.D. 1984. Introduction to rodents. In: (S. Anderson and J.K. Jones Jr., eds.) Orders and families of Recent mammals of the world. John Wiley and Sons, New York. pp. 255–265.

Corbet, G.B. and J.E. Hill. 1980. A World list of mammalian species. British Museum (Nat. Hist.), London.

Corbet, G.B. and J.E. Hill. 1986. A World list of mammalian species. 2nd ed. British Museum (Nat. Hist.), London.

Corbet, G.B. and J.E. Hill. 1994. Wilson, D. E., and D. M. Reeder (eds.). 1993. Mammal species of the World: a taxonomic and geographic reference, 2nd edition. Smithsonian Institution Press, Washington D.C., xviii + 1206 pp. ISBN 1-56098-217-9. Price (hardcover), $75.00 ($60.00 to members of The American Society of Mammalogists). The view from the Old World. J. Mammalogy 75: 239–243.

Cretzschmar, J. 1828. Säugethiere. Atlas zu der Reisen im Nördlichen Afrika von Eduard Rüppell. Abt. 1. Zoologie. Partie 1. H.L. Brönner, Frankfurt a.M.

de Bruijn, H. 1999. Superfamily Sciuroidea. In: (G.E. Rössner and K. Heissig, eds.) The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, München. pp. 271–280.

de Graaff, G. 1981. The rodents of southern Africa. Butterworths, Durban.

Denys, C. 1999. Of mice and men. Evolution in East and South Africa during Plio-Pleistocene times. In: (T. Bromage and F. Schrenk, eds.) African Biogeography, Climate Change and Human Evolution. The Human Evolution series, Oxford University Press. pp. 226–252.

Denys, C., L. Viriot, R. Daams, P. Pelaez- Campomanes, P. Vignaud L. Andossa and M. Brunet. 2003. A new Pliocene xerine sciurid (Rodentia) from Kossom Bougoudi, Chad. J. Vert. Pal. 23: 676–687.

Depierre, D. and J. Vivien. 1992. Mammiferes sauvages du Cameroun. Office National des Forêts, Fontainebleau.

Dobigny, G., A. Nomao and J.-C. Gautun. 2002. A cytotaxonomic survey of rodents from Niger: implications for systematics, biodiversity and biogeography. Mammalia 66: 495–523.

Ellerman, J.R. 1940. The Families and Genera of Living Rodents. Volume I. Rodents other than Muridae. British Museum (Natural History), London.

Erxleben, J.C.P. 1777. Systema regni animalis per classes, ordines, genera, species, varietates, cum synonymia et historia animalium. Classis I. Mammalia. Weygandianis, Lipsiae.

Ewing, B., L. Hillier, M.C. Wendl and P. Green. 1998. Base-calling of automated sequencer traces using Phred. I. Accuracy assessment. Genome Res. 8: 175–185.

Fabre, P.-H., L. Hautier, D. Dimitrov and E.J.P. Douzery. 2012. A glimpse on the pattern of rodent diversication: a phylogenetic approach. BMC Evol. Biol. 12: 88.

Flower, W.H. and R. Lydekker. 1891. An introduction to the study of mammals living and extinct. Adam and Charles Black, London.

Flynn, L. and W. Wessels. 2013. Paleobiogeography and South Asian small mammals. Neogene latitudinal faunal variation. In: (X. Wang, L. Flynn and M. Fortelius, eds.) Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia Univ. Press, New York. pp. 445–460.

Forsyth Major, C.J. 1893. On some Miocene squirrels, with remarks on the dentition and classification of the Sciurinae. Proc. Zool. Soc. Lond. 1893: 179–215.

Fortelius, M. (coordinator). 2015. New and Old Worlds Database of Fossil Mammals (NOW). Univ. Helsinki. http://www.helsinki.fi/science/now/. Accessed on April 7, 2016.

Ge D.Y., X. Liu, X.F. Lv, Z.Q. Zhang, L. Xia and Q.S. Yang. 2014. Historical biogeography and body form evolution of ground squirrels (Sciuridae: Xerinae). Evol. Biol. 41: 99–114.

Geoffroy Saint-Hilaire, É. 1803. Catalogue des Mammifères du Muséum national d'Histoire naturelle. Paris.

Geraads, D. 2001. Rongeurs du Miocène supérieur de Chorora (Ethiopie): Murinae, Dendromurinae et conclusions. Paleovertebrata 30: 89–109.

Gessner C. 1569. Thierbuch. Wilhelm Gerlins, Franckfurt am Main.

Gessner C. 1583. Thierbuch. Froschover, Zürich.

Gotch, A.F. 1995. Latin names explained. A guide to the scientific names of reptiles, birds & mammals. Cassell plc, London.

Granjon, L. and J.-M. Duplantier. 2009. Les rongeurs de l'Afrique sahélo-soudanienne. Faune et Flore tropicales 43. IRD éds., Institut de recherce pour le développement, Marseille.

Gray, J.E. 1867. Synopsis of the African squirrels (Sciuridae) in the collection of the British Museum. Ann. Mag. Nat. Hist., 3rd ser., 20: 323–334.

Gromov, I.M. and M.A. Erbajeva. 1995. The mammals of Russia and adjacent territories. Lagomorphs and rodents. Russian Acad. Sci., St. Petersburg. (in Russian).

Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl. Acids Symp. Ser. 41: 95–98.

Harrison, R.G., S.M. Bogdanowicz, R.S. Hoffmann, E. Yensen and P.W. Sherman. 2003. Phylogeny and evolutionary history of the ground squirrels (Rodentia: Marmotinae). J. Mamm. Evol. 10: 249–276.

Helgen. K.M., F.R. Cole, L.E. Helgen and D.E. Wilson. 2009. Generic revision in the Holarctic ground squirrel genus *Spermophilus*. J. Mammal. 90: 270–305.

Hemprich, F.G. and C.G. Ehrenberg. 1833. Symbolae Physicae seu icones et descriptiones corporum naturalium novorum aut minus cognitorum, quae ex itineribus per Libyam, Aegyptum, Nubiam, Dongalam, Syriam, Arabiam et Habessiniam. Decas 1. Pars zoologica I-II, vol. I., Mammalia. V. Mittlero (pages not numbered).

Herron, M.D. and J.M. Waterman. 2004. *Xerus erythropus*. Mammalian Species 748: 1–4.

Herron M.D., T.A. Castoe and C.L. Parkinson. 2004. Sciurid phylogeny and the paraphyly of Holarctic ground squirrels (Spermophilus). Mol. Phyl. Evol. 31: 1015–1030.

Herron M.D., J.M. Waterman and C.L. Parkinson. 2005. Phylogeny and historical biogeography of African ground squirrels: the role of climate change in the evolution of Xerus. Mol. Ecol. 14: 2773–2788.

Herzig-Straschil, B. 1979. *Xerus inauris* (Rodentia, Sciuridae) – an inhabitant of the arid regions of southern Africa. Folia Zool. 28: 119–124.

Herzig-Straschil, B. and A. Herzig. 1989. Biology of *Xerus princeps* (Rodentia, Sciuridae). Madoqua 16:41–46.

Herzig-Straschil, B., A. Herzig and H. Winkler. 1991. A morphometric analysis of the skulls of *Xerus inauris* and *Xerus princeps* (Rodentia: Sciuridae). Z. Säugetierkunde 56: 177–187.

Hill, J.E. 1980. The status of *Vespertilio borbonicus* E. Geoffroy, 1803. Zool. Meded. 55: 287–295.

Hill, J.E. and T.D. Carter. 1941. The mammals of Angola, Africa. Bull. Am. Mus. Nat. Hist. 78: 1–211.

Hoffman, R.S., C.G. Anderson, R.W. Thorington and L.R. Heaney. 1993. Family Sciuridae. In: (D.E. Wilson and D.-A.M. Reeder, eds.) Mammal Species of the World. 2nd ed. Smithsonian Institution Press, Washington DC. pp.: 419–465.

Hollister, N. 1919. East African mammals in the United States National Museum. Part II. Rodentia, Lagomorpha, and Tubulidentata. US Nat. Mus. Bull. 99: iii-vii + 1–175 + 44 Plates.

Honacki, J.H., K.E. Kinman and J.W. Koeppl. 1982. Mammal species of the world: A taxonomic and geographic reference. Allen Press, Lawrence, KS.

Huet M. 1880: Recheches sur les Écureuils Africains. Nouv. Arch. Mus. Nat. d'Hist. Nat., ser. 2, 3: 131–158.

ICZN [International Commission on Zoological Nomenclature]. 1971. Opinion 945. *Sciurus ebii* Pel, 1851 (Mammalia): supressed under the plenary powers. Bull. zool. Nomencl. 27: 224–225.

ICZN [International Commission on Zoological Nomenclature]. 1999. International code of zoological nomenclature. The International Trust for Zoological Nomenclature, London.

Irwin, D.M., T.D. Kocher and A.C. Wilson. 1991. Evolution of the cytochrome *b* gene of mammals. J. Mol. Evol. 32: 128–144.

Jaeger, J.-J. 1977. Rongeurs (Mammalia, Rodentia) du Miocene du Beni-Mellal. Paleovertebrata 7: 91–125.

Jentink, F.A. 1882. A monograph of the African squirrels, with an enumeration of the specimens in the Leyden Museum. Notes Leyden Mus. 4: 1–53.

Kingdon, J. 1997. The Kingdon field guide to African mammals. Academis Press, London.

Kolb, A.F. 2005. The entry of the animals into Noah's Ark. The J. Paul Getty Museum, Los Angeles.

Komarova, L.V. 1980. The distribution and some ecological features of the long-clawed ground squirrel. Fauna i Ekologiya Gryzunov 14: 201–23172 (in Russian, with summary in English).

Kowalski, K. and B. Rzebik-Kowalska. 1991. Mammals of Algeria. Polish Academy of Sciences, Wroc ław.

Kozhamkulova, P.A. and O.G. Bendukidze. 2005. New data on a find of mastodont (Gomphotherium cf. angustidens) in north-eastern Usturt. Trudy Instit. Zool. Almaty 49: 37–41. (in Russian).

Kretzoi, M. and M. Kretzoi. 2000. Fossilium Catalogus Animalia. Index Generum et Subgenerum Mammalium. Backhuys Publ., Leiden.

Kryštufek, B. and V. Vohralik. 2013. Taxonomic revision of the Palaearctic rodents (Rodentia). Part 2. Sciuridae: *Urocitellus*, *Marmota* and *Sciurotamias*. Lynx n.s. 44: 27–138.

Lataste, F. 1885. Étude de la Faune des Vertébrés de Barbarie (Algérie, Tunisie et Maroc). Catalogue provisoire des

Mammifères apélaqiues sauvages. Actes Soc. Linn. Bordeaux 39: 129–289.

Lesson, R.P. 1842. Nouveau tableau du Règne Animal. Mammifères. Arthus Bertrand, Paris.

Li, T., J. Wang, W. Su, W. Nie and F. Yang. 2006. Karyotypic evolution of the family Sciuridae: inferences from the genome organizations of ground squirrels. Cyt. Gen. Res. 112: 270–276.

Liapunova, E.A. and E.I. Zholnerovskaya. 1969. The chromosome complements of the some species of Sciuridae. Pp. 57-59, In: (N.N. Vorontsov, ed.) The mammals: Evolution, Karyology, Taxonomy, Fauna. Academy of Sciences of the USSR, Siberian branch, Novosibirsk. pp. 167. (in Russian, title translated to English).

Lichtenstein, H. 1823. Reise von Orenburg nach Buchara von Eduard Eversmann. Verlag von E. H. Christiani, Berlin.

Linnaeus, C. 1758. Systema naturae per regna tria naturae: secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus 1. Ed. dec., ref. Laurentii Salvii, Holmiae.

Manthi, F.K. 2007. Preliminary review of the rodent fauna from Lemudong'o, southwestern Kenya and its implication to the Late Miocene palaeoenvironments. Kirtlandia 56: 92–105.

Maridet, O., G. Daxner-Höck, D. Badamgarav and U.B. Göhlich. 2014. New discoveries of sciurids (Rodentia, Mammalia) from the Valley of Lakes (Central Mongolia). Ann. Naturhist. Mus. Wien, Serie A, 116: 271–291.

Martin, A.P. and S.R. Palumbi. 1993. Protein evolution in different cellular environments: cytochrome *b* in sharks and mammals. Mol. Biol. Evol. 10: 873–891.

Matějů, J. and L. Kratochvíl. 2013. Sexual size dimorphism in ground squirrels (Rodentia: Sciuridae: Marmotini) does not correlate with body size and sociality. Front Zool 10: 1–10.

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

Moore, J.C. 1959. Relationships among the living squirrels of the Sciurinae. Bull. Am. Mus. Nat. Hist. 118: 157–206.

Murray, A. 1866. The geographical distribution of mammals. Day & Son Ltd., London.

Nadler, C.F., D.M. Lay and J.D. Hassinger. 1969. Chromosomes of three Asian mammals: *Meriones meridianus* (Rodentia: Gerbillinae), *Spermophilopsis leptodactylus* (Rodentia: Sciuridae), *Ochotona rufescens* (Lagomorpha: Ochotonidae). Experientia 25: 774–775.

Nadler, C.F. and R.S. Hoffmann, 1974. Chromosomes of the African ground squirrel, *Xerus rutilis* (Rodentia: Sciuridae). Experientia 30: 889–891.

Nowak, R.M. 1999. Walker's mammals of the World. Vol. II, 6th ed. John Hopkins Univ. Press, Baltimore.

O'Shea, T.J. 1991. *Xerus rutilus*. Mammalian Species 370: 1–5.

Obolenskij S.I. 1927. A preliminary review of the Palaearctic sousliks (*Citellus* and *Spermophilopsis*). Dokl. Akad. Nauk SSSR, Ser. A 1927(11): 188–193.

Ognev S.I. 1940. The Mammals of the USSR and Adjacent Countries (The Mammals of Eastern Europe and northern Asia). Volume 4. Izdatel'stvo Akademii Nauk SSSR, Moskva & Leningrad, pp. 615 (in Russian).

Ognev, S.I. 1966. Mammals of the U.S.S.R. and Adjacent Countries. Mammals of Eastern Europe and Northern Asia. Vol. IV. Rodents. Israel Program for Scientific Translations, Jerusalem.

Osborn, D.J. and J. Osbnornová. 1998. The mammals of ancient Egypt. The Natural History of Egypt 4. Aris & Phillips Ltd., Warminster.

Osborn, H. F. 1910. The age of mammals in Europe, Asia and North America. The Macmillan Co., New York.

Palmer, T.S. 1904. Index Generum Mammalium. A list of genera and families of mammals. North Amer. Fauna 23: 1–984.

Pavlinov, I.Ya. and O.L. Rossolimo. 1987. Systematics of mammals of the USSR. Arch. Zool. Mus. Moscow State Univ. 25: 1–284 (in Russian).

Petit, D, J. Couturier, E. Viegas-Péquignot, M. Lombard and B. Dutrillaux. 1984. Très grande similitude entre le caryotype ancestral des écureils (rongeurs) et celui des primates et des carnivores. Ann. Génét. 27: 201–12.

Pocock, R.I. 1922. On the external characters of the beaver (Castoridae) and of some squirrels (Sciuridae). Proc. Zool. Soc. Lond. 1922: 1171–1212.

Pocock, R.I. 1923. The classification of the Sciuridae. Proc. Zool. Soc. Lond. 1923: 209–246.

Posada, D. and K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14: 817–818.

Qiu, Z.-X., Z. Qiu, T. Deng, C.-K. Li, Z.Q. Zhang, B.-Y. Wang and X. Wang. 2013. Neogene land mammal stages/ages of China. Toward the goal to establish an Asian land mammal stage/age scheme. In: (X. Wang, L. Flynn and M. Fortelius, eds.) Fossil mammals of Asia: Neogene biostratigraphy and chronology. Columbia Univ. Press, New York, NY. pp. 29–90.

Rafinesque, C.S. 1817. New species of Mammifers, noticed in the Notes to the (Tableau methodique des Mammiferes) Methodical Picture of the Mammifers, by D. Desmarets, in the 24th and last volume of the French New Dictionary of Natural History. Paris, 1804. Translated and improved by C.S. Rafinesque. Am. Month. Mag. Crit. Rev. 1: 361–363.

Reiner, F. and P. Simões. 1998. Mamíferos selvagens da Guiné-Bissau. Projecto Delfim, Lisboa.

Richard, F. and B. Dutrillaux. 2012. Low, complex and probably reticulated chromosome evolution of Sciuromorpha (Rodentia) and Lagomorpha. Cytogenet. Genome Res. 137: 218–232.

Robinskon, T.J., J.D. Skinner and A.S. Haim. 1986. Close chromosomal congruence in two species of ground squirrel: *Xerus inauris* and *X. princeps* (Rodentia: Sciuridae). S. Afr. J. Zool. 21: 100–105.

Roberts, A. 1951. The mammals of South Africa. Trustees of "The Mammals of South Africa" Book Fund.

Rode, P. 1943. Catalogue des types de mammifères du Muséum National d'Histoire Naturelle. Odre des Rongeurs. I. Sciuromorphes. Bull. Mus. Nat. d'Hist. Nat., 2^{e} Sér. 15: 382–385.

Romanenko, S.A., P.L. Perelman, V.A. Trifonov and A.S. Graphodatsky. 2011. Chromosomal evolution in Rodentia. Heredity 108: 4–16.

Ronquist, F. and J.P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Rosevear, D.R. 1969. The rodents of West Africa. British Museum (Nat. Hist.), London.

Ružić, A. 1967. Contribution a l'ecologie de *Spermophilopsis leptodactylus* Lich. dans le desert au sud de Buchara. Mammalia 31: 173–185.

Schouteden, H. 1947. Les mammiferes du Congo Belge et du Ruanda-Urundi. Ann. Mus. Congo Belge. C. Zool. Sér. II Tome III 1–3:1–576.

Setzer, H.W. 1956. Mammals of the Anglo-Egyptian Sudan. Proc. US Nat. Mus. 106: 447–587.

Silvestro, D. and I. Michalak. 2012. raxmlGUI: a graphical front-end for RAxML. Org. Div. Evol. 12: 335–337.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist. 85: 1–350.

Skinner, J.D. and C.T. Chimimba. 2005. The mammals of the Southern African subregion. Cambridge Univ Press, Cambridge, UK.

Skurski, D.A. and J.M. Waterman. 2005. *Xerus inauris*. Mammalian Species 781: 1–4.

Sludskiy, A.A., S.N. Varshavsky, M.I. Ismagilov, V.I. Kapitonov and I.G. Shubin. 1969. Mammals of Kazakhstan. Vol. 1, Part 1. Rodents (Marmots and ground squirrels). “Science” of the Kazakh SSR, Alma-Ata. (in Russian).

Smith A. 1834. An epitome of African zoology; or, A concise description of the objects of the animal kingdom inhabiting Africa, its islands and seas. S. Afr. Quart. J. 2: 113–128.

Smithers, R.H.N. 1971. The mammals of Botswana. Museum Memoir No. 4, National Museum of Rhodesia, Salisbury.

Sokolov, W. 1963. Pigment in the dura mater of mammals. Nature 4875: 105–106.

Sokolov, V.E. and V.F. Kulikov. 1987. The structure and function of the vibrissal apparatus in some rodents. Mammalia 51: 125–138.

Steppan, S.J., L.S. Brian and R.S. Hoffmann. 2004. Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. Mol. Phyl. Evol. 30: 703–719.

Tamura, K., G. Stecher, D. Peterson, A. Filipski A. and S. Kumar. 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. Mol. Biol. Evol. 30: 2725–2729.

Temminck, C.J. 1853. Esquisses zoologiques sur la côte de Guiné. Brill, Leiden.

Thomas, O. 1897. On the Mammals obtained by Mr. A. Whyte in Nyasaland, and presented to the British Museum by Sir H. H. Johnston, K. C. B.; being a fifth contribution to the mammal fauna of Nyasaland. Proc. Zool. Soc. Lond. 1897: 924–938.

Thomas, O. 1909. The generic arrangement of the African squirrels. Ann. Mag. Nat. Hist. 8th ser. 3: 467–475.

Thomas, O. 1911. The mammals of the tenth edition of Linnaeus; an attempt to fix the types of the genera and the exact bases and localities of the species. Proc. Zoo. Soc. Lond. 1911: 120–158.

Thomas, O. 1915. The penis-bone, or “baculum”, as a guide to the classification of certain squirrels. Ann. Mag. Nat. Hist. 8th ser. 15: 383–287.

Thomas, O. 1929. On mammals from the Kaoko-Veld, South West Africa, obtained during Captain Shortridge’s fifth Perey Sladen and Kaffrarian Museum Expedition. Proc. Zool. Soc. Lond. 99: 99–111.

Thompson, J.D., Gibson T.J., F. Plewniak, F. Jeanmougin and D.G. Higgins. 1997. The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res. 25: 4876–4882.

Thorington, R.W. and R.S. Hoffmann. 2005. Family Sciuridae. In: (D.E. Wilson and D.-A.M. Reeder, eds.) Mammal species of the World. A taxonomic and geographic reference. 3rd ed., Vol. 2. John Hopkins University Press, Baltimore, MD. pp. 754–818.

Thorington, R.W. Jr., J.L. Koprowski, M.A. Steele and J.F. Whatton. 2012. Squirrels of the World. The Johns Hopkins Univ. Press, Baltimore.

Triant, D.A. and J.A. DeWoody. 2009. Integrating numt pseudogenes into mitochondrial phylogenies: comment on ‘Mitochondrial phylogeny of Arvicolinae using comprehensive taxonomic sampling yields new insights’. Biol. J. Linn. Soc. 97: 225–226.

Trouessart, E.L. 1880. Révision du genre écureuil (*Sciurus*). Le Naturaliste: 290– 315.

Trouessart, E.L. 1897. Catalogus mammalium tam viventium quam fossilium. Tomus 1. R. Friedländer and Sohn, Berlin.

Van Dam, J.A and G.J. Weltje. 1999. Reconstruction of the Late Miocene climate of Spain using rodent palaeocommunity successions: an application of end-member modelling. Palaeogeog., Palaeoclimat., Palaeoecol. 151: 267–305.

Waterhouse, G.R. 1839. Observations on the Rodentia with a view to point out groups as indicated by the structure of the crania in this order of mammals. Mag. Nat. Hist. 2nd ser. 3: 90–96.

Waterman, J.M. and M.D. Herron. 2004. *Xerus princeps*. Mammalian Species 751: 1–3.

Waterman, J.M. 2013a. Genus *Xerus* Ground squirrel. In: (D.C.D. Happold, ed.): Mammals of Africa. Volume III: Rodents, hares and rabbits. Bloomsbury, London. pp. 93–94.

Waterman, J.M. 2013b. *Xerus erythropus* Stripped ground squirrel (African ground squirrel, West-African ground squirrel, Geoffrey’s ground squirrel). In: (D.C.D. Happold ed.): Mammals of Africa. Volume III: Rodents, hares and rabbits. Bloomsbury, London, pp. 94–96.

Waterman, J.M. 2013c. *Xerus rutilus* Unstripped ground squirrel (Pallid ground squirrel). In: (D.C.D. Happold ed.): Mammals of Africa. Volume III: Rodents, hares and rabbits. Bloomsbury, London, pp. 100–101.

Waterman, J.M. 2013d. *Xerus inauris* Cape ground squirrel (South African ground squirrel). In: (D.C.D. Happold ed.): Mammals of Africa. Volume III: Rodents, hares and rabbits. Bloomsbury, London, pp. 96–98.

Waterman, J.M. 2013e. *Xerus princeps* Damara ground squirrel (Mountain ground squirrel, Kaokoveld ground squirrel). In: (D.C.D. Happold ed.): Mammals of Africa. Volume III: Rodents, hares and rabbits. Bloomsbury, London, pp. 99–100.

Werner, J. 1994. Beiträge zur Biostratigraphie der Unteren Süßwasser-Molasse Süddeutschlands: Rodentia und Lagomorpha (Mammalia) aus den Fundstellen der Ulmer Gegend. Stuttgarter Beitr. Naturkd. (B) 200: 1–220.

Wilson, D.E. and D.-A.M. Reeder (eds.). 1993. Mammal species of the World: A taxonomic and geographic reference, 2nd edition. Smithsonian Institution Press, Washington DC.

Winkler, A., C. Denys and D.M. Avery. 2010. Fossil Rodents of Africa. In: (L. Werdelin and W.J. Sanders, eds.) Cenozoic Mammals of Africa. Univ. California Press, Oakland, CA. pp. 263–304.

Zimmermann, E.A.W. 1780. Geographische geschichte des menchen, und der allgemein verbreiten vierfeussigen thiere: nebst einer hieher geheorigen zoologischen weltcharte. In der Weygandschen Buchhandlung, Leipzig.

Zubov, V.V. and A.A. Svidenko. 2005. Long-clawed ground squirrel (*Spermophilopsis leptodactylus* Lichtenstein, 1823). In: (V.V. Kučeruk and L.A. Hlyap, eds.): Lagomorphs and Rodents of the Central Asian Deserts. GEOS, Moscow. pp. 40–64. (in Russian).

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