Original study

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A taxonomic revision of fat dormice, genus *Glis* (Rodentia)

<https://doi.org/10.1515/mammalia-2020-0161>

Received October 26, 2020; accepted January 7, 2021;

published online March 12, 2021

Abstract: We address in this study the taxonomic status of the two major phylogenetic lineages of fat dormice, genus *Glis*. These lineages show unique mutations at 43 positions of the cytochrome *b* alignment and are classified as two distinct species, the European fat dormouse *Glis glis* (Linnaeus, C. [1766]. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis synonymis, locis*, Vol. 1. Laurentii Salvii, Holmiae [Stockholm]) and the Iranian fat dormouse *Glis persicus* (Erxleben, I.C.P. [1777]. *Systema regni animalis per classes, ordines, genera, species, varietates cum synonymia et historia animalium*. Classis I. Mammalia. Impensis Weygandianis, Lipsia [Leipzig]). The European dormouse is widespread in Europe, Asia Minor and the Caucasus, while the Iranian dormouse occupies the southern Caspian coast in Iran. Ranges are presumably delimited in Azerbaijan by rivers Kura and Aras. The two species differ categorically in size of the glans penis, size and shape of the baculum and in width of the posterior extension of the premaxilla. The Iranian fat dormouse has on average a more blackish distal half of the tail, a higher count for abdominal nipples, and a longer maxillary tooth-row. Intraspecific structuring in

G. glis indicates a taxonomic complexity which is not yet understood and requires a comprehensive systematic revision. To define the nominal taxon objectively we designate voucher PMS 27369 (Slovenian Museum of Natural History) as the neotype for *G. glis*, therefore restricting the type locality for the species to Mt. Krim in Slovenia.

Keywords: baculum; *Glis glis*; *Glis persicus*; neotype; species delimitation.

1 Introduction

The genus of fat dormice (*Glis*) embodies the largest extant dormice, which are externally characterized by a grey dorsal pelage, a sharply delimited white belly and a bushy tail. They are nocturnal occupants of deciduous, mixed, and sclerophyllous evergreen forests in temperate and Mediterranean Europe and adjacent southwest Asia (Kryštufek 2010). Several species were recognized in the genus during the late 19th (Barrett-Hamilton 1898, 1899) and early 20th century (Thomas 1907; Trouessart 1910), but Miller (1912) considered all of them to be conspecific and admitted only a single polytypic species. Miller's view was unequivocally accepted by subsequent authors (Corbet 1978; Ellerman and Morrison-Scott 1951; Kryštufek 2010; Rossolimo et al. 2001; Storch 1978; Vietinghoff-Riesch 1960) and challenged only recently in phylogenetic analyses based on mitochondrial sequences. Current opinions are nonetheless utterly divergent. While some authors understood the genus as containing a single monotypic species *Glis glis* (Holden-Musser et al. 2016), others stressed the complexity of phylogenetic trees, which in their view points on more than a single species of *Glis*. Naderi et al. (2014a) suggested for dormice from the south Caspian coast in Iran to represent a distinct species, and Gippoliti (2013) and Gippoliti and Groves (2018) proposed a separation of *Glis italicus* as a species on its own. Advocates of taxonomic splitting in the genus *Glis*, however, form the minority and the genus continues to be treated as monotypic in major recent reviews (Amori et al. 2016; Holden-Musser et al. 2016; Loy et al. 2019). A taxonomic revision is badly needed, and in this

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paper, we address the taxonomic implications of the basal divergence in *Glis* as reported earlier in Naderi et al. (2014a).

Naderi with co-authors showed that fat dormice from refugial Hyrcanian forests in northern Iran separate from those occupying Europe and Turkey by a genetic distance that exceeds the intraspecific divergence and is well within the range between congeneric rodent species (cf. Baker and Bradley 2006). The phylogeographic pattern was explained by a fragmentation of the ancestral *Glis* population at 5.74 mya (95% CI = 5.44–6.22; Ahmadi et al. 2018) which was putatively triggered by a dramatic environmental change during the Messinian Salinity Crisis at the end of the Miocene. The Iranian isolate presumably persisted throughout the entire Pliocene and the glacial-interglacial dynamics of the Pleistocene in a comparatively small Hyrcanian refugium. Such a scenario is not exceptional but follows a high degree of endemism among mesic temperate mammals from the southern Caspian coast (e.g. Darvish et al. 2015; Dubey et al. 2007; Mahmoudi et al. 2018, 2020).

This paper results from a synthesis of published information with our observations on preserved material. We shall subsequently expose morphological differences between the two major lineages of fat dormice, which were retrieved in Naderi et al. (2014a). These dissimilarities are not consistent with the current taxonomic arrangement of fat dormice into a single species and support the idea that the genus *Glis* consists of more than one species.

2 Materials and methods

2.1 Sequence data

We downloaded from GenBank 49 sequences of the mitochondrial cytochrome *b* (*cytb*) gene representing all phylogeographic lineages of the genus *Glis*. Geographic scope and accession numbers are reported in Supplementary Table S1. Because the *cytb* phylogeny of *Glis* is well known and was recently reassessed in Ahmadi et al. (2018), we saw no need for a duplication of these results. Instead, we focused on unique mutations in the two major lineages of dormice, the Iranian lineage versus all the remaining haplotypes combined. Comparisons were performed in MEGA v7.0 (Kumar et al. 2016).

2.2 Morphological data

We examined 1402 museum specimens (skins, skulls, and wet specimens), deposited in 15 collections. Vouchers originated from 28 countries and represent the great majority of named taxa (see Appendix 1 and Figure 1). To obtain statistically meaningful samples, we pooled individuals that were assumed to belong to interbreeding populations in a landscape of topographical and climatic continuity. In no case we

transgressed borders between subspecies or phylogeographic lineages. Six population samples were created that way: (1) Slovenia (Kočevski Rog Mt.; Krim Mt.; Postojna; Prestranek; Snežnik Mt.); (2) Germany (Bavaria, Munich); (3) western North Macedonia (Bistra Mt.; Galičica Mt.; Karadica Mt.; Korab Mt.; Kožuf Mt.; Pretor; Skopska Crna Gora); (4) Peninsular Italy (Aspromonte; Florence; Monte Aspro; Monte Gargano); (5) Sardinia; (6) North Iran (Alborz; Gilan; Gorgan; Mazandaran). These samples are hereafter referred to as populations. Populations were assigned to two major mitochondrial (*mt*) lineages, the *glis* lineage (populations one to six), and the *persicus* lineage (population seven). The *glis* lineage was further sub-structured into three phylogeographic sub-lineages (Figure 1): the European sub-lineage (populations one, two and three), Macedonian sub-lineage (population four), and Italian sub-lineage (populations five and six). All *persicus* samples belonged to the Western Iranian sub-lineage (sensu Ahmadi et al. 2018). For further details, see Figure 1 and references quoted in the figure caption.

Skins were examined visually and external measurements were obtained from specimen tags. Seven craniodental measurements were scored by a vernier calliper to the nearest 0.1 mm. Acronyms and definitions for variables used in this study are: BWt–body mass; HBL–length of head and body; TL–length of the tail; HfL–length of hind-foot (without claws); EL–length of the ear. Cranial measurements: CbL–condylobasal length of skull; MxT–length of maxillary tooth-row; DiL–length of diastema; ZgW–width across zygomatic arches; IoC–width of interorbital constriction; BcB–greatest width of braincase; BcH–height of braincase (without bullae). Dormice were classified as adults if they overwintered at least once. Age was estimated from the date of capture, body size, fur colouration, presence/absence of deciduous teeth (Donaurov et al. 1938), and molar abrasion (Gaisler et al. 1977).

Penes were obtained from fresh specimens, from carcasses preserved in alcohol, and from dry study skins. Among 329 samples (Appendix 2) we selected 180 adult specimens which were assigned to four populations: (1) Slovenia (Kočevski Rog Mt.; Korin; Krim Mt.; Postojna; Snežnik Mt.; Šentjernej; Vransko); (2) Littoral Croatia (Brač Is.; Hvar Is.; Korčula Is.; Krk Is.; Mljet Is.; Pelješac); (3) North Macedonia (Galičica Mt.; Karadica Mt.), and (4) Iran (Gilan; Golestan). Glans penes were photographed in dorsal and lateral views using a Canon EOS 450D. Bacula were stained following the modified protocol of Anderson (1960). Specifically, the terminal part of each penis with the baculum imbedded in the glans was removed and placed in a vial containing a 2% solution of KOH stained with a small amount of Alizarin red-S in a saturated alcoholic solution. After 24 h the glans was moved to a 2% KOH solution and macerated until the soft tissue could be removed. Stained bacula were transferred to glycerol and photographed in a dorsal view using a stereoscopic zoom microscope Nikon SMZ 800 with a mounted digital camera Nikon DS-Fi2, and processed with NIS-Elements D 4.20 software. The following dimensions were scored from digital photographs using the TpsDig2 software (Rohlf 2017): GpL–greatest length of glans; GpW–greatest width of glans; GpH–greatest depth (height) of glans penis; BaL–length of baculum; BaW–width of baculum across the base.

Secondary sexual dimorphism (SSD) in cranial size was tested in four geographic samples (Slovenia, Germany, N Macedonia, and Iran), using a *t*-test. Six pairwise tests out of a total of 28 were significant (at $p < 0.05$). Visual examination of bivariate plots for pairs of such variables revealed an almost complete overlap between males and females (not shown). Furthermore, when a sex dimorphism was present, it was

Figure 1: Geographic range of fat dormice (*Glis*) with sampling points of museum vouchers used in this study. Circles—*Glis glis*; triangles—*G. persicus*; stars—type localities with names of species group taxa. Top insets show distribution of phylogeographic lineages (left) and simplified phylogenetic tree of the genus (right). Acronyms for sublineages: A – Italian; E – European; M – Macedonian; G – Greek; S – Sicilian; 1 – Western Iranian; and 2 – Eastern Iranian (modified from Ahmadi et al. 2018; Hürner et al. 2010; Koren et al. 2015; Lo Brutto et al. 2011; Naderi et al. 2014a, 2016). The range follows Kryštufek (2010).

dwarfed by the interpopulation differences. Effect sizes were consequently small (Cohen's $d < 0.01$) what encouraged us to pool sexes in further analyses.

Metrical variables of adult dormice were analysed using uni- and multi-variate statistical tests. Kolmogorov–Smirnov and Bartlett tests detected no substantial departures from normality and/or homoscedasticity (both $p > 0.05$), respectively, therefore legitimizing parametric tests.

To characterize the morphological variation among samples and to find patterns in our high dimensional data, we used principal components analysis (PCA), which was performed on the correlation matrix of $\log_{10}$ -transformed cranial variables. Statistical analyses were run using Statistica software (StatSoft, Inc. 2004).

3 Results and discussion

3.1 Molecular data

3.1.1 Phylogenetic relationships

Naderi et al. (2014a) showed that fat dormice are phylogenetically structured into two main lineages, the *glis* and the *persicus* lineages (Figure 1). The *glis* lineage is further

sub-structured into five sub-lineages: (1) the widespread European sub-lineage which is present also in Asia Minor (Hürner et al. 2010); (2) the Italian sub-lineage from the Apennine peninsula, Sicily and Sardinia (Hürner et al. 2010; Lo Brutto et al. 2011), (3) the Macedonian sub-lineage, known from few sites in western North Macedonia (Koren et al. 2015), (4) the Greek sub-lineage, known on the basis of a single haplotype from the Aegean Island of Alonissos (Castiglia et al. 2012); and (5) the Sicilian sub-lineage from eastern Sicily (Hürner et al. 2010). The *persicus* lineage is subdivided into two sub-lineages: (1) the Western Iranian sub-lineage in Ardabil, Gilan, and Mazandaran (probably also Azerbaijan), and (2) the Eastern Iranian sub-lineage in Golestan (Ahmadi et al. 2018).

3.1.2 Unique substitutions

The length of analysed sequences varied between 568 and 1140 base pairs and the two lineages (*glis* and *persicus*) showed unique mutations at 43 positions of the *cytb* alignment (Table 1).

Table 1: Unique mutations identified in the cytochrome *b* sequences for the two major lineages of fat dormice *Glis*.

Position	156	174	198	199	207	228	240	270	274	280	282	309	327	357	366
<i>glis</i>	T	T	T	A	C	C	C	C	A	T/A	A	T	T	C	T
<i>persicus</i>	C	C	C	T	T	T	T	T	G	C	T	C	C	T	C
	396	399	405	456	492	510	528	543	549	588	591	603	639	669	694
<i>glis</i>	C/T	C	A	C	T	A	C	T	T	C	T	C	A	T	C
<i>persicus</i>	A	T	G	T	C	G	A	C	C	T	C	T	T	C	T
	699	705	771	777	822	873	880	901	909	916	921	939	954		
<i>glis</i>	C	C	C	C	T	C	C	T	T/C	G/C	T	G	C		
<i>persicus</i>	T	T	T	T	C	A	T	C	A	A	C	A	T		

3.2 Phenotypical traits

3.2.1 External morphology

Interpopulation differences in size are well documented in *Glis* and were widely used in subspecific taxonomy (Miller 1912; Storch 1978). It was, therefore, not a surprise when the one-way ANOVA retrieved a significant heterogeneity among the six geographic populations in all external variables except for the length of the ear (Table 2). Dormice from Iran, with the largest mean length of head and body, were on average 22.8% longer than dormice from N Macedonia which were the shortest; the difference in the hind foot scored for 22.3%.

Miller (1912: 574) described the dorsal pelage in the fat dormouse as “ranging from a yellowish broccoli-brown to bluish smoke-grey, a little darkened on back by a sprinkling of long blackish hairs”. In skins that we saw the colour varied between populations in the intensity of the brownish shade and the extension of the longer blackish hairs which noticeably darkened the ground greyish tint in some individuals. The tail was frequently darker than the back, particularly along its terminal half. We noted a pronouncedly dark or even black tail in the majority of dormice from Iran (Figure 2). A blackish tail was also common in dormice from peninsular Italy, Sicily and Sardinia. Individual variation was considerable as was observed already by Miller (1912: 578), that even within a single population (*Glis glis italicus*) the tail was either “drab, slaty, or ... blackish”.

The morphology of the hind foot and its sole (planta) is rather invariant in *Glis*. The only difference we noticed between the two lineages concerned the relative length of digits. In the *glis* lineage, digit IV was the longest and digit V was approximately of the same length as digit II. In the *persicus* lineage, digit IV was approximately of the same length as digit III and digit V was shorter than digit II (Figure 3). Colouration and size of the dorsal metacarpal

and metatarsal stripe (Figure 3C) was in the past frequently involved in subspecies diagnostics (Barrett-Hamilton 1898; Miller 1912; Ondrias 1966; Kryštufek and Vohralík 2005). Variation is significant, and we could not distinguish between the two lineages on this ground.

Glis females have a high and unstable number of nipples (range = 8–14; Kryštufek 2010). Median, mean and maximum values are higher in the *persicus* lineage (Table 3) and the difference between Iranian and Slovenian dormice was significant (two-sample Kolmogorov-Smirnov test $p < 0.001$). The number of nipples is 2 pectoral, 1–2 abdominal and 1–2 inguinal pairs in the *glis* lineage, and 2 pectoral, 2–3 abdominal and 1–2 inguinal pairs in the *persicus* lineage. An asymmetric count of 11 nipples was reported in both lineages with frequencies of 13.7% (*glis*; Kryštufek 2004) and 7.1% (*persicus*; Naderi et al. 2014b).

3.2.2 Glans penis and baculum

Our observations on the shape of the glans penis were concordant with descriptions and figures of earlier authors (Hrabě 1968; Kratochvíl 1973; Simson et al. 1995). The glans was of a similar shape in all studied samples but its size differed between the *glis* and *persicus* lineages (Table 4). The difference was categorical for length but in the remaining variables overlapped to a lesser (width) or larger (depth) extent. One-way ANOVA retrieved highly significant differences between the two lineages in all parameters ($F > 27$, $p < 0.00001$).

The difference between lineages was even more apparent in the baculum. The *persicus* lineage had a much longer baculum with a wider base and ranges for length and width did no overlap with the ranges for *glis* (Table 5). Furthermore, in the *glis* lineage the baculum tapered gradually from the expanded base towards the apical tip giving a triangular appearance of the bone (Figure 4A). Baculum was robust in *persicus* throughout the majority of its length but close to the tip narrowed abruptly; the

Table 2: Descriptive statistics for six *Glis* populations.

	Slovenia	Germany	N Macedonia	Italy	Sardinia	Iran	One-way ANOVA
							F-value p
BWt	(118) 182.15 ± 51.55 62–300	(32) 86.38 ± 15.51 54–127	(9) 114.89 ± 34.30 75–192	(5) 193.40 ± 51.69 135–243	(3) 276.0 ± 107.4 211–400		29.28 0.0000
HBL	(118) 183.94 ± 10.87 149–206	(36) 160.58 ± 10.09 136–180	(50) 151.86 ± 10.66 123–177	(14) 175.79 ± 14.06 151–149	(4) 165.75 ± 12.97 154–184	(28) 186.43 ± 21.67 148–253	58.11 0.0000
TL	(112) 150.87 ± 10.40 105–173	(31) 125.84 ± 7.59 110–141	(42) 128.02 ± 8.14 111–145	(14) 154.21 ± 18.09 126–191	(4) 136.25 ± 3.86 134–142	(25) 154.24 ± 23.47 115–200	38.38 0.0000
HfL	(116) 31.30 ± 1.694 27.2–35.0	(36) 29.51 ± 1.186 27.0–32.0	(49) 27.22 ± 1.446 22.8–30.3	(14) 31.89 ± 2.462 28.0–37.0	(4) 31.50 ± 1.000 30.0–32.0	(28) 33.28 ± 2.366 30.0–38.0	8.79 0.0000
EL	(116) 18.67 ± 1.067 16.0–21.2	(36) 18.94 ± 0.977 17.0–20.5	(49) 17.74 ± 1.133 15.0–20.3	(14) 20.64 ± 2.706 14.0–24.0	(4) 20.00 ± 0.000 20.0–20.0	(28) 23.36 ± 1.962 20.0–26.0	0.74 0.60
CbL	(179) 39.87 ± 1.021 37.5–42.0	(69) 35.57 ± 1.188 32.8–38.3	(52) 35.60 ± 1.240 33.2–38.1	(19) 41.08 ± 1.583 38.3–43.0	(13) 38.42 ± 1.194 36.1–40.3	(21) 40.93 ± 1.990 35.4–44.6	167.3 0.0000
MxT	(179) 7.40 ± 0.245 6.9–8.1	(69) 6.92 ± 0.198 6.4–7.3	(52) 7.17 ± 0.265 6.5–7.9	(19) 8.26 ± 0.378 7.5–8.7	(13) 7.90 ± 0.339 7.3–8.4	(22) 8.43 ± 0.467 7.3–9.3	158.5 0.0000
Dil	(179) 10.40 ± 0.442 9.3–11.4	(69) 9.04 ± 0.380 8.0–10.0	(52) 9.20 ± 0.447 8.4–10.3	(20) 10.41 ± 0.455 9.6–11.2	(13) 9.85 ± 0.504 8.9–10.7	(22) 10.49 ± 0.620 9.2–11.7	126.7 0.0000
ZgW	(179) 24.54 ± 0.796 23.0–29.6	(69) 22.63 ± 0.877 22.7–24.4	(52) 22.56 ± 0.847 16.5–19.2	(19) 25.69 ± 1.038 23.8–27.1	(11) 24.29 ± 1.283 22.4–26.1	(20) 25.75 ± 0.967 23.9–27.6	71.70 0.0000
loC	(179) 5.12 ± 0.121 4.9–5.5	(69) 4.98 ± 0.099 4.8–5.2	(52) 4.97 ± 0.148 4.7–5.3	(20) 5.51 ± 0.195 5.2–6.1	(13) 5.29 ± 0.108 5.1–5.5	(22) 5.37 ± 0.173 5.0–5.6	17.05 0.0000
BcB	(176) 19.50 ± 0.411 18.4–20.6	(68) 17.93 ± 0.470 17.0–19.0	(45) 18.07 ± 0.574 16.5–19.2	(18) 19.81 ± 0.823 18.7–22.2	(11) 18.59 ± 0.767 17.3–19.7	(16) 19.42 ± 0.757 17.7–20.7	47.0 0.0000
BcH	(178) 11.15 ± 0.302 9.6–11.7	(69) 10.34 ± 0.274 9.9–11.0	(52) 10.61 ± 0.309 10.0–11.3	(19) 10.95 ± 0.291 10.4–11.6	(13) 10.86 ± 0.320 10.4–11.4	(21) 11.16 ± 0.402 10.4–12.0	81.1 0.0000

Given are sample size (in parentheses), arithmetic mean ± standard deviation (upper row) and range (lower row). The right-hand column reports the results (F-value and p-level) obtained in one-way ANOVA. For character acronyms see the text.

Figure 2: *Glis glis* (A) from Mt. Kočevski Rog, Slovenia, and *G. persicus* (B) from Ramsar, Mazandaran, Iran. Note the difference in tail coloration. Photo B. Kryštufek (A) and M. Naderi (B).

Figure 3: Left hind foot in the *glis* (A, C) and *persicus* (B) lineages of fat dormice *Glis*. Insets A and B show plantar surfaces and inset C depicts the dorsal side. Digits are indicated by Roman numbers (thumb = I) and interdigital pads are shown by Arabic numbers. Capital letters indicate the lateral (L) and medial (M) metatarsal pads, respectively. Note differences in relative length of toes. Arrow points on a dark metatarsal stripe (C). Based on PMS vouchers 27319 (A; Mt. Snežnik, Slovenia), 26297 (B; Kalaleh, Golestan, Iran), and 27320 (C; Mt. Krim, Slovenia).

terminal portion (about 1/5 of the total length) was stick-like (Figure 4B). In spite of the considerable overlap in bacular dimensions among the *glis* samples (Figure 4), dormice from Slovenia had a significantly longer and wider

baculum than their counterparts from Littoral Croatia ($F > 45, p < 0.0001$; cf. Table 4). Nevertheless, it is clear from Figure 4 that the interpopulation variation within the *glis* lineage is an entirely different phenomenon from the differentiation between the two major lineages.

3.2.3 Cranial and dental morphology

Interpopulation differences among six geographic samples were highly significant in all cranial variables and *F*-values were particularly high ($F > 120$) for CbL, MxT, and DiL (Table 2). We proceeded with a PCA using a complete matrix of seven cranial measurements on 372 individuals. Craniometric relationships between five samples are portrayed by a plot of individuals on the first two principal components (PCs; Figure 5). These components had eigenvalues of 4.758 and 0.934, respectively, and explained 81.3% of the total variance. The matrix of eigenvectors showed that PC1 was loaded with positive eigenvectors for variables describing all major dimensions of the skull, namely length (CbL, DiL), width (ZgW, BcB) and height (BcH; Figure 5). As a consequence, samples segregated along this axis according to the overall size and neatly clustered into two groups; the right-hand cluster contained large dormice samples from Slovenia, Italy and Iran, while small dormice samples from Germany and N Macedonia grouped together on the left-hand side of the

Table 3: Descriptive statistics for number of nipples in four geographic samples of fat dormice belonging to two phylogenetic lineages (*glis* and *persicus*).

Lineage	Country	n	Median	Mean ± SD	Min–max	Source
<i>glis</i>	Slovenia	51	10	10.2 ± 0.50	10–12	Kryštufek (2004)
<i>glis</i>	N Italy	20		11.3 ± 0.85	10–12	Marin and Pilastro (1994)
<i>glis</i>	Mt. Gargano	3		10.7 ± 0.58	10–11	ZFMK specimens
<i>persicus</i>	Iran	56	12	12.6 ± 1.02	11–14	Naderi et al. (2014b)

Table 4: Descriptive statistics for dimensions (mm) of glans penis in two phylogenetic lineages of fat dormice (*glis* and *persicus*).

Lineage (n)	Length of glans		Width of glans		Height of glans	
	Mean $\pm$ SD	Min–max	Mean $\pm$ SD	Min–max	Mean $\pm$ SD	Min–max
<i>glis</i> (46)	7.977 $\pm$ 0.709	7.09–10.42	3.841 $\pm$ 0.542	2.85–4.95	3.114 $\pm$ 0.521	1.99–4.37
<i>persicus</i> (14)	15.542 $\pm$ 1.720	12.79–18.19	5.595 $\pm$ 0.650	4.83–6.78	3.967 $\pm$ 0.636	2.81–5.20
F-value	666.08		108.40		27.30	
P	<0.000001		<0.000001		0.000002	

Results of one-way ANOVA for each trait are reported in the bottom lines.

Table 5: Descriptive statistics for length and width (mm) of the baculum in two phylogenetic lineages of fat dormice (*glis* and *persicus*).

Lineage	Country (n)	Length of baculum		Width of baculum	
		Mean $\pm$ SD	Min–max	Mean $\pm$ SD	Min–max
<i>glis</i>	Slovenia (113)	8.992 $\pm$ 0.379	7.99–9.83	2.523 $\pm$ 0.089	2.09–2.86
<i>glis</i>	Littoral Croatia (47)	8.431 $\pm$ 0.303	7.64–9.06	2.346 $\pm$ 0.116	2.05–2.61
<i>glis</i>	N Macedonia (2)	8.711 $\pm$ 0.407	8.42–9.00	2.579 $\pm$ 0.041	2.55–2.61
<i>persicus</i>	Iran (18)	14.903 $\pm$ 0.776	13.75–16.65	4.330 $\pm$ 0.465	3.51–5.51

axis. PC2 had high negative loadings for interorbital width and length of maxillary tooth-row (Figure 5). Samples from Germany, Slovenia and N Macedonia with narrow interorbital region and short tooth-row (cf. Table 1) had high scores for PC2. The two overlapping samples of Italian and Iranian dormice were characterized by a wide interorbital region and a long tooth-row. It is evident at

glance from Figure 5 that cranial morphology did not follow the phylogeographic structuring in fat dormice. Dormice from the *glis* lineage spread over the entire morphospace. Furthermore, the Italian sub-lineage overlapped with the Iranian lineage but showed nearly no similarity with the remaining *glis* samples. Of the two samples of the European sub-lineage, the one from Germany separated from Slovenian sample by smaller size but overlapped perfectly with the sample of the Macedonian lineage (Figure 5).

Ognev (1947) used the width of the posterior extension of the premaxilla (*processus nasalis ossis intermaxillaries* in his terminology) to diagnose subspecies of fat dormice: 1.4–2.0 mm in the nominate subspecies and *tshetshenicus* (*glis* lineage as defined here) versus 2.4–2.8 mm in *caspius* (*persicus* lineage). Our observations confirmed the taxonomic utility of this trait (Figure 6). The quotient of the width of the premaxilla with the width of the nasal (both measured at their posterior extension) as denominator ranged between 0.67 and 1.25 in dormice from throughout Europe, Anatolia and the Caucasus (including Armenia and northern Azerbaijan), and 1.25–2.17 in those from Iran and southern Azerbaijan. So far known, this is the only cranial difference permitting a secure discrimination between the two major phylogenetic lineages of *Glis*.

A projection of the length of the maxillary tooth-row against condylobasal length (Figure 7) retrieved similar relationships between the five samples, as summarized in Figure 5. It is clearly obvious that dormice from Slovenia, despite being of comparable size to Iranian and Italian samples, have shorter tooth-rows (Figure 8). Apart from

Figure 4: Bivariate plot of the width of baculum against its length (in mm) in fat dormice *Glis* from both phylogenetic lineages, *glis* (A) and *persicus* (B). Abbreviations of populations: 1 – Slovenia; 2 – Littoral Croatia; 3 – North Macedonia; 4 – Sila Mts., Calabria, Italy (from Simson et al. 1995); 5 – Iran. The *glis* lineage contains three sublineages, the European (1, 2), Macedonian (3), and Italian (4). Bacula (in dorsal view) are depicted to scale. They are vouchers (A) PMS 17288 (Croatia, Bregana; BaL = 8.31 mm) and (B) MNC 8BK (Iran, Siakhal; BaL = 13.97 mm).

Figure 5: Bivariate plot of five *Glis* populations onto the first two principal components (PC) derived from ordination of seven cranial measurements (transformed to log10). The percentage of variance explained by individual PC is in parentheses. The character vector diagram (left-upper inset) illustrates the relative contribution of the original variables (see text for acronyms) to the principal components. Population identifiers: 1 – Slovenia; 2 – Germany; 3 – North Macedonia; 4 – Italy (including Sardinia); 5 – Iran. Polygon for the Iranian sample is shaded grey and polygon for the Italian sample is shown by an interrupted line.

this clear difference in size, we noticed no dissimilarity in the arrangement of transverse enamel ridges between *glis* and *persicus* (Figure 8).

3.3 Taxonomy

Our comparisons retrieved categorical differences between the two major phylogenetic lineages of *Glis* (*glis* and *persicus*) in three traits: (1) nucleotide sequences, (2) length of the glans penis and size and shape of the baculum (Tables 3 and 4 and Figures 4), and (3) width of the premaxilla. As stressed already by Naderi et al. (2014a), mitochondrial metrics on its own justifies a taxonomic split of *Glis* because the average genetic distance is confidently placed beyond the intraspecific heterogeneity and well within the range for interspecific differentiation (Baker and Bradley 2006). We add to this argument the categorical difference in size and shape of the baculum. A number of functions have been proposed for the mammalian baculum during copulation (Lemaître et al. 2012; Ramm 2007). Although the role of the baculum is not fully understood, its presence and shape associates with male reproductive success (Milligan 1979; Stockley 2002). Sexual selection predicts a higher variation in sexually selected traits than in non-sexually-selected traits and their variation is frequently informative in taxonomy (Miller 2010). A categorical difference in the glans penis and baculum between the two lineages suggests different copulatory behaviours. This topic, which was so far not addressed, remains a challenge for further studies.

We conclude that the genus *Glis* consists of two well-differentiated allopatric species which are detailed subsequently. The list of synonyms is an upgraded and

Figure 6: Dorsal rostrum in dormice showing the difference in relative width of the posterior extension of the nasal (1a) against the posterior extension of the premaxilla (2a; insets C and F). Top (*glis* lineage): A – Slovenia, Mt. Snežnik (PMS 27319); B – Turkey, Rize, Çat, Çeymakçur Yayla (ZSM 67/29 HMS); C – Italy, Monte Gargano (ZFMK 66.415). Bottom (*persicus* lineage): D – Iran, Golestan, Kalaleh (PMS 26297); E – Iran, Gilan, Asalem (ZSM 68.443 HMS); F – Azerbaijan, Lerik region (ZIN 71740). Bones: 1 – nasal; 2 – premaxilla; 3 – maxilla; 4 – lachrymal; 5 – frontal. Not to scale; only the right half of the rostrum is shown in insets B, C, E, and F.

Figure 7: Bivariate plot of the maxillary tooth-row length against condylobasal length of the skull (in mm) in five *Glis* populations. Explanation is the same as for Figure 5.

Figure 8: Occlusal surface of cheek teeth in dormice belonging to two lineages (*glis* and *persicus*). Based on PMS vouchers 27319 (*glis*; Slovenia, Mt. Snežnik) and 26297 (*persicus*; Iran, Golestan, Kalaleh). Note that skulls of these individuals are of comparable size: CbL = 38.1 mm in *glis* and 37.2 mm in *persicus*. Upper and lower case letters refer to maxillary and mandibular premolars (P/p) and molars (M/m), and numbers indicate their position in the row.

completed version of the earlier version in Kryštufek (2010).

3.4 *Glis glis* (Linnaeus 1766) – European fat dormouse

Sciurus glis Linnaeus 1766: 87. Type locality “Habitat in Europa australi [lives in southern Europe]”; type locality was erroneously restricted to “Germany” (Miller 1912: 577); emended by Violani and Zava (1995: 111) to “Southern

Carniola in Slovenia”. Type locality is further restricted by the neotype (see below) to “above Preserje, Mt. Krim, Slovenia; coordinates 45.924620N 14.439479E”.

Glis esculentus Blumenbach 1779: 79. Type locality is “im südlichen Europa [in southern Europe]”. Miller (1912: 577) erroneously reported the type locality as “Central Europe”. Blumenbach refers to “Valvassor” (i.e. Valvasor 1689: 437) who quoted the fat dormouse, as “Billich” [German] or “Pouh” [Slovenian] for “Krain [Carniola]”. Therefore, *esculentus* has the same type locality as *S. glis* Linnaeus.

Glis vulgaris Oken 1816: 868. Oken intentionally renamed many species already named; besides, his work has been rejected for nomenclatural purposes (International Commission on Zoological Nomenclature 1956). *Nomen nudum*.

Myoxus Giglis Cuvier 1832: 444. *Nomen nudum* (Miller 1912: 577).

Myoxus avellanus Owen 1840: 25 + plate 105. No locality.

Glis italicus Barrett-Hamilton 1898: 424. Type locality is “Siena”, Italy.

Glis insularis Barrett-Hamilton 1899: 228. Type locality is “Monte Aspro, near Palermo”, Sicily, Italy.

Myoxus glis orientalis Nehring 1903: 533. Type locality is “Gebirge Alem-Dagh, nordöstlich von Scutari, in Kleinasien [Üskudar, Alem Dağı Mts., İstanbul, Turkey in Asia].

Glis glis spoliatus Thomas 1906: 220. Type locality is “Khotz [Çosandere; Kryštufek 2010: 196], near Trabizond [Trabzon]. Alt. 100 m”, Turkey in Asia.

Glis Melonii Thomas 1907: 445. Type locality is “Marcurighè, Urzulei, Ogliastro, Sardinia”, Italy.

Glis glis pyrenaicus Cabrera 1908: 193. Type locality is “Navarre Pyrenees, North Spain” “All, province of Navarre.”

Glis italicus intermedius Altobello 1920: 22. Type locality is not specified, the name however was proposed for dormice from the Abruzzi and Molise Province (now two different provinces, the Abruzzo and the Molise), central Italy.

Glis glis subalpinus Burg 1920: 419. Type locality is “Münstertal [Val Müstair]”, Canton of Graubünden, Switzerland.

Glis glis tshetschenicus Satunin 1920: 150. Type locality is “р. Шара-Аргунь [River Shara-Argun]”, a tributary of the Terek (Ognev 1947: 465), Chechen Republic, Russian Federation.

Glis glis postus Montagu 1923: 866. Type locality is “Veliki Dergonel [Veliki Drgomalj; Kryštufek 2010: 196], the Gorski Kotar, Croatia.”

Glis glis abrutti Altobello 1924: 35. Type locality (“Abruzzi e [and] Molise”) is identical to *Glis italicus intermedius* Altobello and the two are synonymous.

Glis glis minutus Martino 1930: 60. Type locality is “Predejane. 30 klm. S. from Leskovac, Serbia”.

Glis glis vagneri V. E. Martino and E. V. Martino 1941: 9. Type locality is “Vrhpolje, Kamnik, Kamniške Alpe, Slovenia.”

Glis glis intermedius V. E. Martino and E. V. Martino 1941: 9. Type locality is “Presača [Pesača], Donji Milanovac, N. E. Serbia.” Preoccupied by *Glis italicus intermedius* Altobello.

Glis glis argenteus Zimmermann 1953: 28. Type locality is “Wälder der Weissen Berge, Kreta [White Mts., Samaria, 1000 m elevation, Island of Crete; Ondrias 1966: 28].”

Glis esculantus: Vietinghoff-Riesch 1960: 16. Incorrect subsequent spelling of *esculentus* Blumenbach.

Glis glis abrutii: Vietinghoff-Riesch 1960: 19. Incorrect subsequent spelling of *Glis glis abrutti* Altobello.

Glis glis martinoidi Mirić 1960: 36. New name for *Glis glis intermedius* V. E. Martino and E. V. Martino.

G.[lis] g.[lis] wagneri: Dulić and Tortić 1960: 7. Incorrect subsequent spelling of *Glis glis vagneri* V. E. Martino and E. V. Martino.

Glis glis pindicus Ondrias 1966: 25. Type locality is: “Moni Stomiou, near Konitsa, Epirus, Greece, at an altitude of 1600 m”.

M. glis martinoidi Grekova 1969: 66. Not Greova (Gromov and Erbajeva 1995: 174). Type locality is “Limanchik, Abraudyurso, Krasnodarskiy kray”, Russia. Preoccupied by *Glis glis martinoidi* Mirić 1960.

M. glis germanicus Violani and Zava, 1995: 112. Type locality is “Marxheim, Bavaria, Germany”.

M. glis grekova Baranova 2003 (in Baranova and Gromov 2003: 27). New name for *M. glis martinoidi* Grekova 1969.

Designation of a neotype: *G. glis*, as defined here, is wide-ranging, extending from the Pyrenees as far east as the Caucasus area and the Volga River. Morphological variation among geographic samples is extensive in this species and the list of synonyms involves over 20 names which were in the past tentatively classified into nine subspecies (Corbet 1978; Ellerman and Morrison-Scott 1951). Nucleotide diversity (Ahmadi et al. 2018; Hürner et al. 2010; Koren et al. 2015) and extensive morphological variation among populations (this paper) indicate a taxonomic complexity which is not yet understood and requires a comprehensive systematic revision on its own (see also Gippoliti 2013; Gippoliti and Groves 2018). An objective definition of taxa is essential for a stable taxonomy and nomenclature, which induced us to designate a neotype for *G. glis* as a firm standard for further taxonomic work in the group.

We propose voucher PMS 27369 as the neotype for *G. glis*. This specimen was collected by Marjan Zavodnik on 10 October 2020 above Preserje, Mt. Krim, Slovenia; coordinates 45.924620 N 14.439479 E. Preserved in ethanol with skull extracted; visceral organs fixed in 10% solution of formaldehyde and subsequently transferred to 75% ethanol; baculum kept in glycerol in a separate vial; tissue sample preserved in non-denaturated 96% ethanol and refrigerated; photographs of glans penis in dorsal, lateral and ventral view deposited in the PMS database. The tissue is also deposited in ZFMK (ZFMK-TIS-54202).

Dimensions of the neotype: BWt–282 g; HBL–195 mm; TL–152 mm; HfL–31.4 mm; EL–16.7 mm; CbL–40.6 mm; MxT–7.4 mm; DiL–10.1 mm; ZgW–25.4 mm; IoC–5.2 mm; BcB–19.8 mm; BcH–11.5 mm; GpL–10.42 mm; GpW–4.67 mm; GpH–3.58 mm; BaL–8.44 mm; BaW–2.75 mm.

An illustration of the neotype skull is to be found in this paper in Figure 9.

The International Code for Zoological Nomenclature (International Commission on Zoological Nomenclature 1999; subsequently referred to as the Code) stipulates conditions under which the designation of a neotype is justified. Specifically, “a neotype is not to be designated as an end in itself” (Article 75.2 of the Code) but only when “a name-bearing type is necessary to define the nominal

Figure 9: Dorsal, ventral and lateral views of the skull and labial side of the mandible in *Glis glis* (top) and *G. persicus* (bottom). Based on vouchers PMS 27369 (*G. glis*; Slovenia, Mt. Krim) and ZSM 68.443 HS (*G. persicus*; Iran, Gilan, Asalem).

taxon objectively” (Article 75.1). We believe that the neotype of *G. glis* will remove doubts regarding the taxonomic scope of this species against *Glis persicus* on the one hand and will facilitate a taxonomic revision within *G. glis* as it is defined here. As stated earlier on, Gippoliti (2013) and Gippoliti and Groves (2018) already extracted *italicus* (with *insularis*) from the scope of *G. glis*, but a thorough taxonomic revision still remains to be done. Furthermore, the taxonomic status of a highly divergent phylogeographic lineage from the Balkans (Macedonian lineage) was not addressed yet. Therefore, a comprehensive taxonomic revision of *G. glis* may retrieve a higher species diversity that is still not appreciated.

In addition to the above justification for a valid designation of the neotype we met other qualifying conditions specified by the Code. In detail:

- (1) We provide characters that differentiate *G. glis* from *G. persicus* (stipulated by Article 75.3.2. of the Code) and demonstrate that the neotype matches the traits which are characteristic for *G. glis*. Hürner et al. (2010) sequenced five dormice from Mt. Krim which all retrieved a single *cytb* haplotype (Hap02) characteristic for the European sublineage of *G. glis*. Furthermore, the locality of the neotype is well inside the range of the North-Western Balkan microsatellite group of *G. glis* which occupies Slovenia, North-Eastern Italy and Croatia (Michaux et al. 2019).
- (2) We describe in words and in figures the neotype specimen, hence meeting the provision of Article 75.3.3.
- (3) As shown by Violani and Zava (1995), the type of *S. glis* had not been designated and Linnaeus himself never saw the animal. The description in the 12th edition of *Systema Naturae* (Linnaeus 1766) is almost verbatim a summary from the letter sent to Linnaeus on 7th April 1763 by Joannes A. Scopoli, his correspondent from the Austrian province of Carniola (now Slovenia). “Habitat in Europa australi”, which is the Linnean type locality for *S. glis*, is based on “Carniola, in primis inferiore” in Scopoli’s letter. Miller (1912: 577) erroneously restricted the type locality to “Germany”, possibly a reminiscence of the fact that Carniola was, at the time of correspondence between Linnaeus and Scopoli, part of the Holy Roman Empire which occasionally had an unofficial extension “of the German Nation.” Miller’s restriction was emended to “Southern Carniola in Slovenia” (Violani and Zava 1995: 111).
- (4) The neotype comes from Mt. Krim which is located in the southern part of the former Carniola Province and is therefore inside the type locality as validly restricted by Violani and Zava (1995) (Article 75.3.6.).
- (5) The neotype is deposited in the Slovenian Museum of Natural History, i.e. in a “recognized scientific ...

institution”, which “maintains a research collection, with proper facilities for preserving name-bearing types, and ... makes them accessible for study” (Article 75.3.7.). In provision with Article 76.3. of the Code (“Type locality determined by the neotype”), “above Preserje, Mt. Krim, Slovenia” is the type locality for *G. glis*.

Diagnosis: Identical to a cluster of five sub-lineages (European, Italian, Sicilian, Macedonian and Greek; Figure 1) as retrieved in the phylogenetic analysis of the mitochondrial *cytb* gene (Ahmadi et al. 2018; Hürner et al. 2010). In our dataset, *G. glis* has unique mutations in comparison with sequences of *G. persicus* at 43 positions of the *cytb* alignment (Table 1). *G. glis* has a shorter glans penis (GpL < 10.5 mm; GpL > 12.5 mm in *persicus*), a shorter and narrower baculum (BaL < 10 mm and BaW < 3.0 mm vs BaL > 13.5 mm and BaW > 3.5 mm in *persicus*), and a narrower posterior extension of the premaxilla (Figure 6A–C).

Description: The morphology of *G. glis* is thoroughly documented in Miller (1912), Ognev (1947), Storch (1978), Rossolimo et al. (2001), and Kryštufek (2010). Subsequently we list traits which, despite some interspecific overlap, signalize a divergence between *G. glis* and *G. persicus*.

- (1) The tail is usually only slightly darker than the back in *G. glis* while it is normally blackish in *G. persicus*; dormice from the Italian sub-lineage resemble in the tail colouration *persicus* rather than *glis*.
- (2) On the hind foot, digit IV is of the same length than digit III in *G. persicus*, but it is the longest digit in *G. glis*.
- (3) The number of abdominal nipples is 1–2 in *G. glis* and 2–3 in *G. persicus*.
- (4) The maxillary tooth-row is longer in *G. persicus* (MxT > 7.0 mm) than in *G. glis* (MxT < 8.1 mm in majority of populations); dormice from the Italian sub-lineage are intermediate in this trait (MxT = 7.3–8.7 mm).

Distribution: *G. glis* occupies the majority of the genus’ range in Europe, northern Anatolia, and the Caucasus area. The European range was mapped by Storch (1978) and Kryštufek (1999), the range in Russia, Belarus, Ukraine and Moldova by Likhachev (1972), in Anatolia by Kryštufek and Vohralík (2005), and in the Caucasus by Shidlovsky (1962). Local updates are summarized in Holden (2005). Along the south-western Caspian coast, the ranges of *G. glis* and *G. persicus* are presumably delimited by rivers Kura and Aras (cf. Map 2 in Shidlovsky 1962).

Miscellaneous: Earlier authors noted that *italicus* (Ellerman and Morrison-Scott 1951: 547) and also *melonii* (Ognev 1947: 470) resemble *persicus* (or *caspius*) closer than their counterparts from the rest of Europe. As shown here, the differences are obvious in the tail colouration and in the

length of the maxillary tooth-row. Contrary to Gippoliti and Groves (2018) we are hesitant to propose the elevation of *italicus* to a species in its own right for the following reasons:

- (1) If *italicus* would be defined to include the Italian and Sicilian sub-lineages, then it would be paraphyletic in the *cytb* tree.
- (2) Dormice from the Italian region are in two highly divergent *cytb* sub-lineages which are sympatric in Sicily (Hürner et al. 2010). Relationships between these sub-lineages on the island are not known.
- (3) Different markers (*cytb* and *COI*) retrieved non-congruent phylogeographic patterning in Italy (cf. Hürner et al. 2010 vs Lo Brutto et al. 2011).
- (4) The contact zone between the Italian and the European sub-lineages is not known. Based on morphological variation in a subspecies *italicus*, Miller (1912: 579) concluded that “northern specimens [from the region of Turin and at Porlezza] are probably best treated as intermediates between *glis* and *italicus*”.

Classification of *G. glis* as a monotypic species (Holden-Musser et al. 2016) contradicts the phylogeographic structuring of the species (Figure 1) and the morphological variation (Ognev 1947; Storch 1978). The pattern of variation is complex and the size classes, upon which the traditional subspecies mainly rely on, do not match the phylogenetic lineages. In this study, the populations from Germany and Macedonia overlapped perfectly in cranial dimensions (Figure 5), although they belong to distant phylogenetic groups. Contrary to this, populations from Germany and Slovenia (both from the European sub-lineage) hardly overlapped in morphospace (Figure 5). An infraspecific revision of *G. glis* is therefore left unresolved.

Not considered in this review is a single *mt* haplotype from the Aegean Island of Alonissos which clusters with other *G. glis* sequences (Castiglia et al. 2012). Only a single individual is known from the island and we did not see the voucher.

3.5 *Glis persicus* (Erxleben 1777) – Iranian fat dormouse

Sciurus persicus Erxleben 1777: 417. Type locality is “... in Persiae provincia Gilan [in the Iranian Province of Gilan]”, subsequently restricted to “Rasht” “Iran: Ghilan [Gilan] Province” (Lay 1967: 193).

M. glis caspius Satunin 1905: 55. Two topotypes were collected “въ Чулійскомъ ущель въ 40 верстахъ отъ

Асхабада [in the Chuli George, 40 versts (= 42.6 km) from Ashgabat]” (p. 56), Turkmenistan.

M. glis caspius Satunin 1905–1906: 54. Unjustified emendation of *caspius* Satunin (cf. Pavlinov and Rossolimo 1987: 147).

Glis glis petruccii Goodwin 1939: 1. Type locality is “Gouladah foothills of the Kurkhud Mountains, District Bujnurd, northeastern Iran; alt. about 3000 feet [915 m]”.

Erxleben’s name is occasionally applied to the Caucasian squirrel *Sciurus anomalus* G黤denst鋎t, 1785 (Gromov et al. 1963: 277; Kuznetsov 1944: 281; Martirosyan and Papanyan 1983: 42; Ognev 1940: 422; Trouessart 1904: 317; Vinogradov and Argyropulo 1941: 100). Already Ellerman (1940: 433) refuted such practice claiming that “there is reason to believe that this name [*S. persicus*] was based on a Dormouse, *G. glis*.” Note that Erxleben referred to an animal from Gilan while the Caucasian squirrel does not occupy Hyrcanian forests and is nowhere in Iran sympatric with the fat dormouse (cf. Yusefi et al. 2019).

The type of *G. persicus* was not selected. For reasons detailed under *G. glis*, the neotype should be designed also for *G. persicus*. The neotype should preferably originate from Mazandaran and consists of at least a skin, a skull, a tissue sample and a penis or a baculum. Since we are not aware of the existence of such a museum voucher, we refrained from designating a neotype.

Diagnosis: Identical to the Iranian lineage as retrieved in the phylogenetic analysis of the mitochondrial *cytb* gene (Naderi et al. 2014a). In our dataset, *G. persicus* has unique mutations in comparison with sequences of *G. glis* at 43 positions of the *cytb* alignment (Table 1). *G. persicus* has a longer glans penis (GpL > 12.5 mm; GpL < 10.5 mm in *glis*), a longer and wider baculum (BaL > 13.5 mm and BaW > 3.5 mm vs BaL < 10 mm and BaW < 3.0 mm in *glis*), and a wider posterior extension of the premaxilla (Figure 6D–F).

For further comparison with *G. glis*, see under that species.

Distribution: Endemic to the Caspian Hyrcanian mixed forests in south-east Azerbaijan (south of Kura and Aras; cf. Shidlovsky 1962) and Iran as far east as the eastern-most Golestan (Yusefi et al. 2019). Known in Turkmenistan only from two syntypes of *M. glis caspius* Satunin (Zykov 1991); the type material was lost already in 1918 (Ognev 1947: 467).

Miscellaneous: Subspecies are not thoroughly studied. Ognev (1947: 470) recognized a single subspecies (*caspius*) for the entire Caspian coast between the south-east Transcaucasia and Kopet Dag. Subsequent authors followed this practice (Gromov et al. 1963: 361; Lay 1967: 194; Shidlovsky 1962: 78), although Vietinghoff-Riesch (1960) admitted three subspecies. Size varies between populations with

large dormice in Gilan and Mazandaran (Table 1) and small dormice in Azerbaijan (mean $\pm$ SD condylobasal length is 36.57 ± 1.412 ; range = 34.9–38.8 mm; $n = 7$); the type of *petruccii* is even smaller (CbL = 30 mm; Goodwin 1939: 6). Eftekhari et al. (2018) reported on the variation in mandibular shape along the Caspian coast in Iran and Ahmadi et al. (2018) retrieved a deep divergence (1.19 mya; CI = 0.55–1.9 mya) between the Iranian Western lineage (Gilan and Mazandaran) and the Iranian Eastern lineage (Golestan). A further taxonomic split in *G. persicus* is therefore likely.

Acknowledgments: Access to collections was granted (alphabetically; for collection acronyms see Appendix 1): Paula Jenkins (BMNH), the late William Stanley (FMNH), the late Jan Zima (IVB), Gabor Csorba (MNM), Linda Gordon (NMNH), Petr Benda (NMP), Barbara Herzig Straszil (NMW), Milan Paunović (PMBg), the late Gerhard Storch and Katrin Krohmann (SMF), Alexandra Davydova (ZIN), Vladimir Lebedev (ZMMU), and Anneke van Heteren and Richard Kraft (ZSM). The PMS collection of dormice benefitted tremendously from the enthusiastic help of traditional dormouse hunters Marjan and Andrej Zavodnik, Stane Kumelj, Dušan Pavlin and their colleagues; a significant portion of specimens thus assembled were processed and curated by Mojca Jernejc Kodrič.

Author contributions: B.K. conceived the study, provided and elaborated material, examined museum vouchers, made part of statistical analyses, and wrote the text; M.N. provided material, examined museum vouchers, and commented the drafts; F.J. elaborated material, performed statistical tests and commented the drafts; R.H. supervised the study and commented the drafts; D.B. elaborated material; A.M. performed molecular analyses and commented the drafts.

Research funding: The study received funding support from *Javna agencija za raziskovalno dejavnost Republike Slovenije* (Slovenian Research Agency) through research core funding nos. P1-0255 (B.K.), P1-0403 and J1-2457 (F.J.).

Conflict of interest statement: The authors declare no known conflict of interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix 1: List of museum vouchers used in this study

Material is organised according to countries which are reported from the north-west to south-east. Localities inside the countries are listed alphabetically. Sample size in the

collection is in parentheses and follows the collection acronym.

Collection acronyms

BMNH, Natural History Museum, London, UK

FMNH, Field Museum of Natural History, Chicago, USA

IVB, Institute of Vertebrate Biology, Academy of Sciences of the CR, Brno, Czech Republic

MNC, collection of Morteza Naderi, Qom, Iran

MNM, Hungarian Natural History Museum, Budapest, Hungary

NMNH, National Museum of Natural History, Washington D.C., USA

NMP, National Museum, Prague, Czech Republic

NMW, Natural History Museum Vienna, Vienna, Austria

PMBg, Natural History Museum Belgrade, Belgrade, Serbia

PMS, Slovenian Museum of Natural History, Ljubljana, Slovenia

SMF, Senckenberg Research Institute and Natural History Museum, Frankfurt a/M, Germany

ZFMK, Zoological Research Museum A. Koenig, Bonn, Germany

ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia

ZMMU, Zoological Museum of Moscow State University, Moscow, Russia

ZSM, Zoological State Collection Munich, Munich, Germany

***Glis glis* ($n = 1313$).** **Andorra** (BMNH 2). **United Kingdom** ($n = 35$): Bovingdon (BMNH 1); Chesham (BMNH 1); Cholesbury (BMNH 1); England, no locality (PMS 27); Tring (BMNH 5). **France** ($n = 6$): Bouches-du-Rhône (BMNH 2); Nîmes (BMNH 4, NMNH 1). **Switzerland** ($n = 8$): Bale (BMNH 1); Geneva (BMNH 1); Gotthard (BMNH 1); Interlaken (ZFMK 1); Lucerne (BMNH 1); Thayingen (BMNH 2); Zürich (NMNH 1). **Germany** ($n = 138$): Frankfurt a/M (SMF 2); Friedrichsdorf, Bad Homburg (SMF 1); Gelnhausen (SMF 7); Heppenheim (NMW 20); Herborn (SMF 1); Kalbacher (NMW 20); Kronberg (SMF 1); Ludwigsburg nr. Stuttgart (SMF 1); München and vicinity (BMNH 1, ZSM 69); Reitenbraitbach (NMW 3); Stromberg (NMW 4); Taunus Mts. (SMF 6); Wächtersbach (SMF 2); **Italy** ($n = 62$): Aspromonte (BMNH 1); Bressanone (NMW 7); Florence (BMNH 1); Genoa, Borzoli (BMNH 1); Monte Aspro (BMNH 1); Monte Galbiga (SMF 2); Monte Gargano (ZFMK 7, ZSM 9); Ponte di Nava (BMNH 1); Porlezza (SMF 1); Sardegna Is.: Marcuringhe, Orgovi, Urzulei (BMNH 5, NMW

4, SMF 1, ZIN 2, ZFMK 2); Sicily Is.: Ficuzza, Messina, Palermo (BMNH 1, NMW 1, SMF 1, ZSM 1); Siena (BMNH 8); Trento, Monte Baldo (SMF 2); Trieste (BMNH 1); Val d'Aosta (SMF 2). **Austria** ($n = 47$): Landl (PMS 5); Kals am Grossglockner (NMW 1); Königstetten (NMW 4); Lesachtal (NMW 2); Steyr (NMW 25); Wiefleck (NMW 1); Vienna (NMW 9). **Czech Republic** ($n = 9$): Prague (NMP 9). **Slovenia** ($n = 436$): Bistrica pri Črnomlju (PMS 18); Bohinj, Ukanc (PMS 1); Cerknica, Škocjan (PMS 2); Divača (PMS 11); Goriška brda (PMS 1); Hotedrška (PMS 6); Jelovica, Goška ravan (PMS 3); Kamnik, Vrhpolje (ZIN 2); Kamniške Alpe, Mokrica (PMS 1); Kočevski Rog Mt.: Podstene; Rdeči kamen (PMS 19); Korin, Krka (PMS 7); Kranj (PMS 1); Krim Mt. (PMS 207); Lendava, Dobrovnjak (PMS 1); Poljčane, Modraž (PMS 9); Postojna, Hudičevac (PMS 5); Prestranek (PMS 33); Prevalje (PMS 1); Razdrto (PMS 4); Semič, Mirna gora (PMS 5); Šentjernej (PMS 2); Sežana (PMS 5); Slovenska Bistrica, Cigonca (PMS 4); Snežnik Mt.: Mašun, Okroglina, Sviščaki (PMS 64); Srednje Gamelje (PMS 1); Travnica gora (PMS 1); Vransko, Jeronim (PMS 10); Vremščica Mt. (PMS 12). **Croatia** ($n = 166$): Biokovo Mt. (PMS 5, PMBg 3); Brač Is.: Dračevica, Nerežišća (PMS 35); Bregana (PMS 9); Cres Is., Beli (PMS 3); Gorski Kotar, Mrkopalj (PMS 24); Hvar Is., Jelsa (PMS 1); Korčula Is.: Brna, Žrnovo (PMS 20); Krk Is.: Baška, Dobrinj, Šilo (PMBg 4, PMS 4, SMF 8); Mljet Is.: Babino polje, Prozurska Luka (PMS 6); Mosor Mt., Kosa (SMF 2); Novska (ZIN 1); Pazin, Vela Traba (PMS 3); Pelješac, Žuljana (PMS 18); Plitvice Lakes (PMS 1); Svilaja Mt., Maovice (PMS 5); Velebit Mt.: Alan, Apatiška duliba, Krasno, Prezdid, Štirovac (NMW 2, PMBg 3, PMS 2); Zagreb, Maksimir (SMF 7). **Poland** ($n = 1$): Białowieża (BMNH 1). **Hungary** ($n = 20$): between Győr and Sopron (MNM 15, ZIN 1); Komárom (MNM 4). **Bosnia and Herzegovina** ($n = 40$): Bosanski Petrovac, Brozgač (ZIN 1); Gacko, Mangorj (PMS 2); Foča–Kalinovik (PMS 1); Igman Mt. (ZIN 4); Klekovača Mt., Vrljetina (PMBg 3); Ljubinja (PMS 1); Prenj Mt.: Boračko jezero, Doljani, Kalinovik, Osobac (BMNH 4, PMBg 5, ZIN 1); Šator Mt., Šatorsko jezero (PMS 4); Sječina (ZIN 1); Velež Mt., Rujište (PMS 1); Zelengora Mt.: between Čemerno and Orlovat, Donje Bare (PMS 12). **Slovakia** ($n = 69$): Drienovec (NMP 10); Jeseníky (NMP 21); Slavec (NMP 37); Smolenice (NMP 1). **Serbia** ($n = 81$): Arandjelovac (ZIN 1); Basarski kamen (PMBg 4); Beograd: Avala, Košutnjak, Resnik, Topčider (PMBg 3, ZIN 2); Boljevac (PMBg 1); Čuprija, Ravanička pećina (PMBg 1); Djerdap, Ploča (PMBg 22); Donji Milanovac: Greben, Pesača (BMNH 2, PMBg 10, ZIN 3); Dževrin potok (PMBg 2); Fruška gora, Čortanovci (PMS 13); Golija, Biser voda (PMS 1); Južni Kučaj, Troglan Bare (PMBg 11); Kopaonik Mt., Lukovo (ZIN 2); Kraljevo, Čukujevac (ZIN 1); Leskovac, Predejane (BMNH 2, PMBg 7); Ljuboten (ZIN 2); Ljubovija, Gornja Trešnjica (PMBg 6);

Majdanpek, Domena (BMNH 1); Povlen, Mravinci (PMBg 13); Priština, Gazivoda (PMS 1); Rtanj, Mirovsko vrelo (PMBg 8); Ruj Mt., Vučji Do (PMBg 2); Sip, Kašajna potok (PMBg 1); Srem, Bojčin (PMBg 1); St. George, Temska district (PMBg 2); Tara Mt., Beli Rzav (PMS 1); Veliki Jastrebac (PMBg 4); Zvonačka Banja (PMBg 2). **Greece** ($n = 6$): Leivaditis (PMS 1); Mirsini (NMW 1); Ossa Mt. (ZIN 1, ZFMK 3). **Montenegro** ($n = 39$): Bjelasica Mt., Biogradsko jezero (PMBg 11); Cetinje: Hum, Soko (NMNH 2, PMBg 2, ZIN 3); Durmitor Mt., Žabljak, Crno jezero (PMBg 8); Kučište (ZIN 3); Orjen Mt., Vrbanje (PMS 2); Komovi Mt., Trešnjevik (PMBg 1); Lovćen Mt.: Čekanje, Ivanova korita (PMBg 1, PMS 4, ZIN 1); Ulcinj (PMBg 1). **North Macedonia** ($n = 49$): Bistra Mt., Senečke suvati (BMNH 1, ZIN 4); Galičica Mt.: Asan Đura, Elen vrv, Oteševo (PMBg 1, PMS 2); Karađica Mt. (PMS 1); Korab Mt.: Brodac, Ničipur, Štirovica (BMNH 12, ZIN 1); Kožuf Mt.: Asan česma, Keči-kaja (BMNH 18, ZIN 2); Pretor (PMS 5); Skopska Crna Gora (PMS 2). **Romania** ($n = 4$): Băile Herculane (BMNH 1); Galben (BMNH 1); Hateg (BMNH 1); Rastolita (BMNH 1). **Bulgaria** ($n = 17$): Kalofer (ZIN 4); Rila Mt. (ZIN 3); Ropotamo (IVB 1); Vitosha Mt. (ZIN 8, ZSM 1). **Ukraine** ($n = 1$): Perehinski Zapovednik (ZIN 1). **Moldova** ($n = 3$): Sadovo (ZIN 3). **Turkey** ($n = 17$): Artvin (ZIN 1); Demirköy (PMS 3, SMF 2); Rize: Çat, Çeymakçur Yayla (ZSM 7); Tekirdağ (SMF 1); Uludağ Mt. (SMF 1); Trabzon, Khotz (BMNH 2). **Russian Federation** ($n = 33$): Adygeyskaya Avtonomnaya Oblast, Nikel' (ZIN 8); Daghestan, Khasav-Yurt (ZIN 1); Daghestan, Khanzauskiy raion (ZIN 1); Kabardino-Balkarian Republic, Nalchik (ZIN 1); Krasnodarsky krai, Adzhanovka (ZIN 3); Krasnodarsky krai, Limanchik (ZIN 6); Krasnodarsky krai, Maikopsky raion (ZIN 8); North Ossetia, Alagir (ZIN 1); Samarska Luka (ZIN 4). **Georgia** ($n = 19$): Abkhazia, Pehu (ZIN 15); Mtskheta (ZMMU 4). **Armenia** ($n = 8$): Delizhan (ZIN 7); near Quba (ZMMU 1). **Azerbaijan** ($n = 1$): Zakatal (ZIN 1).

Glis persicus ($n = 43$). **Azerbaijan** ($n = 4$): Lenkaran (BMNH 3); Lerik regiona (ZIN 3). **Iran** ($n = 37$): Alborz (BMNH 6); Gilan, Asalem (ZSM 3); Gilan, 12 km W Chalus (FMNH 7); Gilan, Javaher dasht (PMS 1); Gilan, Lavandevl (MNC 2); Gilan, Rasht (BMNH 1); Gilan, Rezwandeh (FMNH 9); Golestan, Kalaleh (PMS 1); Gorgan, Rud-e-Ziarat (SMF 1); Gilan, Siahkal (MNC 1); Gilan, Toutaki (MNC 1); Mazandaran, 25 km east of Gorgan (NMNH 2); Mazandaran, south of Nowshar (ZSM 2); Mazandaran, Ramsar (MNC 2); Mazandaran, Sama (FMNH 1).

We saw the following types:

BMNH 98.10.2.14 – *Glis italicus* Barrett-Hamilton 1898;
 BMNH 98.10.6.4 – *Glis insularis* Barrett-Hamilton 1899;
 BMNH 6.5.1.38 – *Glis glis spoliatus* Thomas 1906;
 BMNH 8.4.6.1 – *Glis melonii* Thomas 1907;
 BMNH 1934.11.26.14 – *Glis glis postus* Montagu 1923;

BMNH 1911.1.1.103 – *Glis glis germanicus* Violani and Zava 1995;

ZIN 33745 – *Glis glis minutus* V. E. Martino 1930;

ZIN 33780 – *Glis glis vagneri* V. E. Martino and E. V. Martino 1941

ZIN 33766 – *Glis glis intermedius* V. E. Martino and E. V. Martino 1941;

We also saw eight paratypes of *M. glis martinoidi* Grekova 1969 (ZIN 47001, 47002, 47003, 47004, 47005, 47006, 47007, 47008).

Appendix 2: List of penial and bacular samples examined in this study

For collection acronyms see Appendix 1.

Glis glis ($n = 309$). **Slovenia** ($n = 268$): Kočevski Rog Mt. (PMS 5); Korin, Krka (PMS 23); Krim Mt. (PMS 209); Postojna (PMS 17); Šentjernej (PMS 2); Snežnik Mt. (PMS 8); Prevalje (PMS 1); Slovenska Bistrica, Cigonca (PMS 2); Vransko, Jeronim (PMS 2). **Croatia** ($n = 55$): Brač Is. (PMS 20); Bregana (PMS 6); Hvar Is. (PMS 1); Korčula Is. (PMS 13); Krk Is. (PMS 2); Mljet Is. (PMS 4); Pazin, Vela Traba (PMS 3); Pelješac, Žuljana (PMS 4); Svilaja Mt., Maovice (PMS 2). **Bosnia and Herzegovina** ($n = 2$): Šator Mt., Šatorsko jezero (PMS 1); Zelengora Mt. (PMS 1). **North Macedonia** ($n = 2$): Galičica Mt. (PMS 1); Karađica Mt. (PMS 1). **Turkey** ($n = 1$): Demirköy (PMS1).

***Glis persicus*, Iran** ($n = 18$): Gilan, Lavandevl (MNC 2); Gilan, Siahkal (MNC 13); Golestan, Kalaleh (PMS 1); no locality (MNC 2).

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Supplementary Material: The online version of this article offers supplementary material (<https://doi.org/10.1515/mammalia-2020-0161>).