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Taxonomic position and biogeography of *Mus callewaerti*, the largest species of the subgenus *Nannomys* (Rodentia: Muridae)

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Abstract. The Callewaert's mouse (*Mus callewaerti*) is shown as an ancient lineage of the African endemic subgenus *Nannomys*. Described in 1925 as a large-bodied species with proodont (forward pointing) incisors, it was long known only from a handful of localities in Angola and southern Democratic Republic of the Congo. Here, it is revealed identical with a genetically distinctive *Nannomys*, provisionally called *Mus* sp. "Nyika" in previous studies and reported from Nyika Plateau (Malawi) and the Angolan Escarpment. The skull shape analysis clearly associated the holotype of *M. callewaerti* with other specimens ascribed to the species (including the genotyped ones). It also pinpointed diagnostic features distinguishing *M. callewaerti* from other large bodied *Nannomys*, especially its sympatric *Mus triton*, for which the species was repeatedly mistaken. *Mus callewaerti* is presumably insectivorous and rare or not easy to capture. The divergence between its Malawian and Angolan populations is relatively shallow, dated to 0.32 million years ago, which suggests that at least in the past the species could be widespread. *Mus callewaerti* is known from grassy, locally moisty habitats. Together with a handful of other rodent taxa it provides evidence of persistence and historic connection of these habitats across the Zambezian region.

Key words. Zambezian region, skull shape, insectivory, phylogeography, integrative taxonomy

INTRODUCTION

The use of genetic data and molecular phylogenetic approaches in the last decades significantly improved our knowledge of biodiversity patterns and underlying evolutionary processes. For example, rapidly increasing amount of genetic information allows detection of cryptic species (Mayer & von Helversen 2001, Leaché & Fujita 2010, Struck et al. 2018), quantify the geographical distribution of evolutionary uniqueness (Robuchon et al. 2021) and even to understand the molecular mechanisms of adaptation of taxa to their environment (Hoekstra & Nachman 2003, Jones et al. 2012, Musilová et al. 2019). On the other hand, routine sequencing of DNA and unprecedented increase in availability of genetic data might complicate classical taxonomic approaches to biodiversity quantification. Discoveries of genetic lineages within species, often based on a single (mitochondrial) marker, lead to splitting species (using phylogenetic species

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concept) without any other support (Spinks et al. 2013, Chan et al. 2020). Furthermore, the frequent lack of morphological comparison of genotyped specimens with museum vouchers (including types) is against a good practice of integrative taxonomy and can lead to confusions in taxonomic implications.

Here we document pros and cons of molecular approaches in taxonomy using the example of a poorly known representative of African pygmy mice of the genus *Mus* (subgenus *Nannomys*). The subgenus *Nannomys* represents a highly diverse clade of African mammals that colonized Africa from Asia and started its African radiation in the early Pliocene, probably in mountains of eastern Africa (Bryja et al. 2014). One subclade of *Nannomys* colonized open savannah-like habitats and decreased the body size to about five grams, which makes them one of the smallest mammals on Earth. However, not all species of *Nannomys* are real "pygmy mice". For example, one of the ancient lineages of the subgenus, the Ethiopian endemic Ethiopian striped mouse *Mus imberbis*, has a body size comparable with most Eurasian species of the genus *Mus* (Meheretu Yonas et al. 2015).

In this study, we focus on another ancient lineage of *Nannomys*, represented by the Callewaert's mouse, *Mus callewaerti*. It was described by Thomas (1925) from the southern Democratic Republic of Congo (DRC) as the only member of a new genus *Hylenomys*. However, Misonne (1965) argued that the distinction of the genus *Hylenomys* from *Mus* (especially its subgenus *Nannomys*, called *Leggada* at that time) was based only on proodont (forward pointing) incisors, i.e., character present also in some other species of *Mus*, and synonymized *Hylenomys* with *Mus*. The species is very poorly known. Misonne (1965) summarized all reported records and counted only 21–22 known specimens (probably even fewer, as some of them in the American Museum of Natural History might represent the grey-belied pygmy mouse *Mus triton*; see Hatt 1940), all of them collected in Angola and southern DRC before 1948. Since that time, new records of *M. callewaerti* are mentioned in the literature only very scarcely. It was only in 2014, when Lamb et al. (2014) provided mitochondrial cytochrome *b* sequences of a taxon called in their study *M. callewaerti* from Angola (Mbala Nondolo village, Huambo province, 12.77° S, 15.73° E). However, they did not compare their specimens with the type material of *M. callewaerti* and very likely misidentified them with *M. triton* (see Krásová et al. 2019). Unfortunately, Bryja et al. (2014) continued in this confusion, because they used the name "*Mus* cf. *callewaerti*" for their geographically widespread "molecular operational taxonomic unit" (MOTU) 6, because their sequences clustered with Angolan sequences of Lamb's et al. (2014) *M. callewaerti*. Later integrative taxonomic revision of *Mus triton* by Krásová et al. (2019) unequivocally showed that (MOTU) 6 belongs to *M. triton* and all intraspecific clades of this species are morphologically very distinct from the holotype of *M. callewaerti*.

In the most comprehensive molecular phylogenetic study of *Nannomys*, Bryja et al. (2014) reported a very distinct ancient lineage, known from a single, relatively large individual (14 g), captured in the high plateau of Nyika Mts. in Malawi (ca. 2100 m a. s. l.) and called it *Mus* sp. "Nyika" (= (MOTU) 1 *sensu* Bryja et al. 2014). The cranium of this specimen (albeit broken) showed features like proodont incisors and slender mandibles, which indicates similarities with *M. callewaerti*. However, this record was very far from the nearest localities of *M. callewaerti* (in southern DRC), so nobody performed a comparison with its holotype. The situation changed when Krásová et al. (2021) reported another specimen of *Mus* sp. "Nyika" from Namba village (20 km south of Cassongue) in Angola (Fig. 1, Table 1), genetically very similar to the specimen from Malawi despite large geographical distance (more than 2100 km) and hypothesized that these two specimens might represent true *M. callewaerti*.

Table 1. Published records of *M. callewaerti*, verified by inspection of the specimens or at least by consulting the museum catalogues. Where available, the lengts of four standard body measurements (in mm) are provided (taken from the cited literature and collection catalogues); HB – head and body length; T – tail length; HF – hind foot length; E – ear length; for the collection abbreviations, see Material and Methods

specimens	locality	country	latitude	longitude	altitude	reference	HB	T	HF	E
BNHM 1925.4.2.1	Kananga (= Luluabourg)	DRC	–5.8833	22.4333	610	Thomas (1925)	95	43	12	10
AMNH M-86265	Kananga, Mission of St. Joseph	DRC	–5.9000	22.4167	635	Hatt (1940)	89	45	14	11
AMNH M-86666	Chitau	Angola	–11.2500	17.0167	1590	Hill & Carter (1941)	84	44	16.5	11.5
AMNH M-86668	Chitau	Angola	–11.2500	17.0167	1590	Hill & Carter (1941)				
AMNH M-86669	Chitau	Angola	–11.2500	17.0167	1590	Hill & Carter (1941)				
AMNH M-86671	Chitau	Angola	–11.2500	17.0167	1590	Hill & Carter (1941)	89	46	16.5	14
FMNH 80301	Muita	Angola	–7.7167	21.4167	710	Sanborn (1952)				
FMNH 80302	Muita	Angola	–7.7167	21.4167	710	Sanborn (1952)				
FMNH 80303	Muita	Angola	–7.7167	21.4167	710	Sanborn (1952)				
RBINS 11433	Lufwa	DRC	–8.9000	27.1333	1700	Misonne (1965)				
RBINS 11420	Mukana	DRC	–9.2167	27.1167	1810	Misonne (1965)	97	45	16	9.5
IVB ANG0267	Namba	Angola	–11.9110	14.8753	1752	Krásová et al. (2021)				
IVB M8x3025	Nyika NP	Malawi	–10.4959	33.8862	2099	Bryja et al. (2014)	74	49.3	15.7	13.3

In this contribution, we try to solve the taxonomy of this enigmatic taxon. We first compared the skulls of two recently collected and genotyped specimens of *Mus* sp. "Nyika" from Malawi and Angola with old museum material of *M. callewaerti* (including the holotype) and we show that they are conspecific. In the next step, we analyse the morphological distinctiveness of this species from *M. triton*, as both can be found in sympatry, as well as from *M. imberbis*, another large-bodied species of African *Mus* with proodont incisors. Finally, we used multi-locus dataset for the reconstruction of dated evolutionary history of African pygmy mice. Special attention is given to the ancient lineages of the subgenus *Nannomys*, for which we present a taxonomic summary.

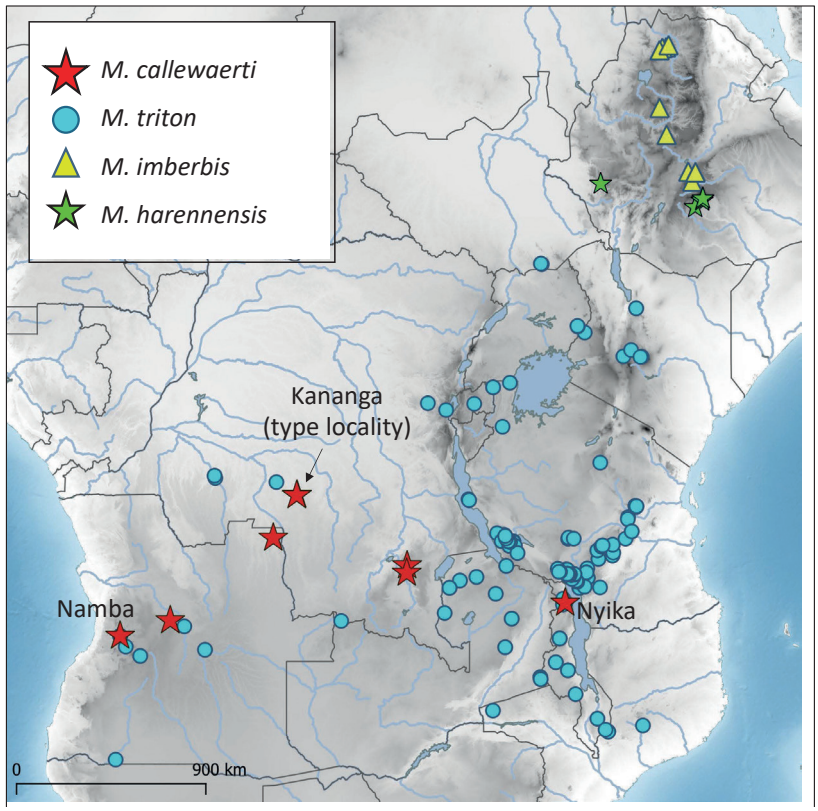

Fig. 1. Summary of the distribution of four ancient lineages of the genus *Mus*, subgenus *Nannomys*. All known localities of *Mus callewaerti* are shown by red stars (see also Table 1), the type locality (Kananga) and two localities with recently collected and genotyped specimens (Nyika, Namba) are highlighted by names. The distribution of the three remaining species is based on genetically identified specimens (taken from Krásová et al. 2022) and supplemented by recent unpublished data from Uganda and South Sudan and morphologically identified specimens of *M. imberbis* from FMNH in Chicago. The background in the scale of grey indicates elevation (higher is darker).

Table 2. Morphometric data set with species assignment and the area of origin is indicated. For the collection abbreviations, see Material and Methods

species	region	specimens
M. callewaerti	Angola	FMNH 80303, IVB ANG0267
	southern DRC	BMNH 1925.4.2.1
	Malawi	IVB M8x3025
M. triton	Angola	IVB ANG0205, ANG0236, ANG0243, ANG0260, ANG0261, ANG0264
	southern DRC	RMCA 97.021-M-0191, 97.021-M-0192, 97.021-M-0241, 97.021-M-0254, 97.021-M-0263, 97.021-M-0272, 97.021--M-0288, 97.021-M-0302, 97.021-M-0324, 97.021-M-0332
	Malawi / Zambia	IVB M8x0277, M8x3019, M8x3035, M8x3051, M8x3067, RS1226, RS1265, RS1368, RS1415, RS1548
M. imberbis	Ethiopian Highlands	FMNH 28664, 28667, 28668, 28671, 28672, 28674, 229648 BMNH ZD-1928.1.11.152, ZD-1928.1.11.153

MATERIAL AND METHODS

Sampling and data

The material and data analyzed in this study are based on specimens from various museum collections mentioned in Tables 1–3. Namely, American Museum of Natural History, New York, USA (AMNH); Field Museum of Natural History, Chicago, USA (FMNH); Institute of Vertebrate Biology of the Czech Academy of Sciences, Brno, Czech Republic (IVB); Natural History Museum, London, UK (BMNH); Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS); Royal Museum for Central Africa, Tervuren, Belgium (RMCA); Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia (SIEE); and University of Antwerp, Antwerp, Belgium (UA).

The morphological data set included skulls of 39 museum specimens: four referable to *Mus callewaerti* (including the holotype), 9 to *M. imberbis* and 26 to *M. triton*. The specimens of *M. callewaerti* and *M. triton* were from various parts of the species' distribution ranges, namely from Angolan Escarpment, south of the Congo Basin and from Malawi and the neighboring part of Zambia (Table 2). Sex and age of the individuals was not considered in the analysis, although none of the specimens was a typical juvenile, i.e., very small with conspicuously short rostrum.

The cranial morphology was studied on lateral view images of the skull, where the incisor procumbence is visible. The skull size and shape were captured by a set of 43 points (Fig. 2), including 14 landmarks and 29 sliding semilandmarks (Bookstein 1997). As the skulls of both genetically studied individuals were broken, the set is confined to their undamaged parts. The position of the incisor landmark (highlighted in Fig. 2) was *ad hoc* adjusted to account for the fact the incisor length can change during life. The landmark was shifted along the line joining it with the neighboring landmark at the base of the incisor and the shift secured that in all skulls the distance between these two landmarks was an equal fraction of centroid size calculated on all landmarks except for the shifted one. The photography protocol was set to be as repeatable as possible. In particular, the skulls rested with the underside on a horizontal support and their midplane was aligned with a line parallel to the camera lens.

The point configurations were then standardized by means of the generalized Procrustes analysis (Rohlf & Slice 1990) as implemented in the package geomorph (Adams et al. 2021) for R (R Core Team 2022). This method outputs skull size quantified as centroid size of the point configuration and shape in the form

Table 3. Molecular data set with species and population assignment, localities of origin and GenBank numbers of the sequences. Labels of populations indicate their mutual correspondence between *Mus callewaerti* and *M. triton* rather than precise area of origin. For the collection abbreviations, see Material and Methods; cc – country code: ETH = Ethiopia, ZAM = Zambia, TNZ = Tanzania, DRC = DR Congo, ANG = Angola, MWI = Malawi, KEN = Kenya, SNG = Senegal; lat. – latitude, long. – longitude

species	specimen	cc	locality	lat.	long.	CYTB	IRBP	RAG1	BFIB	SMO
M. imberbis	IVB ETH0121 FMNH	ETH	Galeme Range	7.518	39.310	KF928333	KF928334	OL616387	OL616303	OL616411
	WTS11979	ETH	Chennek	13.260	38.194	OL616363	OL616380	OL616404	OL616320	OL616428
M. harennensis	IVB ETH0211	ETH	Harenna Forest	6.415	39.437	KJ935743	KJ935875	OL616382	OL616298	OL616406
	SIEE LAV2274	ETH	Harenna Forest	6.700	39.733	KJ935744	OL616369	OL616384	OL616300	OL616408
M. triton	IVB RS1414	ZAM	Chishimba Falls	–10.108	30.918	MK011647	MK011812	MK011845	MH991382	MK011745
	IVB TA172	TNZ	Kyelele, Rumanyika GR	–1.278	30.806	KJ935756	KJ935878	MK011843	MH991380	MK011743
	UA KIK2086	DRC	Kwanga-Ngaza	–5.158	18.939	MK011566	MK011795	MK011828	MH991365	MK011728
	UA KIK5	DRC	Mbwambala	–5.058	18.909	MK011567	MK011796	MK011827	MH991364	MK011727
	IVB ANG0254	ANG	Namba	–11.911	14.875	MK011528	MK011819	MK011853	MH991390	MK011753
	IVB ANG0260	ANG	Namba	–11.911	14.875	MK011529	MK011820	MK011854	MH991391	MK011754
M. callewaerti	IVB ANG0267	ANG	Namba	–11.911	14.875	MW512154	OP747459	OP747461	OP747758	OP747460
	IVB M8x3025	MWI	Nyika NP, Safari Camp	–10.496	33.886	KJ935741	KJ935874	OL616396	OL616312	OL616420
M. mahomet	IVB ETH0095	ETH	Kuni Muktar	8.600	40.544	KJ935795	KJ935887	OL616386	OL616302	OL616410
	IVB ETH0526	ETH	Desea Forest	13.871	39.767	KJ935789	KJ935886	OL616389	OL616305	OL616413
M. proconodon	IVB ETH0299	ETH	Mago NP	5.466	36.264	KJ935767	KJ935883	OL616388	OL616304	OL616412
	SIEE LAV1145	ETH	Vanzaye	11.783	37.667	KJ935768	OL616377	OL616395	OL616311	OL616419

species	specimen	cc	locality	lat.	long.	CYTB	IRBP	RAG1	BFIB	SMO
M. bufo	IVB KE162	KEN	Maralal, Karisia Hills	1.096	36.756	OL616362	OL616376	OL616391	OL616307	OL616415
	IVB KE454	KEN	Mt Elgon NP, Endebess	1.034	34.825	KJ935783	KJ935885	OL616392	OL616308	OL616416
M. neavei	IVB M8x3049	MWI	Nyika NP, Jallawe valley	–10.371	33.799	KJ935805	KJ935890	OL616397	OL616313	OL616421
	IVB RS1228	ZAM	Mutinondo Wilderness	–12.392	31.323	KJ935808	KJ935891	OL616400	OL616316	OL616424
M. mattheyi	IVB NK894	SNG	Dar Salam	13.260	–13.203	OL616364	OL616378	OL616398	OL616314	OL616422
	IVB NK952	SNG	Dar Salam	13.260	–13.203	OL616365	OL616379	OL616399	OL616315	OL616423
M. gratus	IVB KE543	KEN	Taita Hills, Chawia Forest	–3.477	38.342	KJ935820	KJ935893	OL616393	OL616309	OL616417
	IVB TA077	TNZ	Minziro FR	–1.038	31.542	KJ935822	KJ935894	OL616401	OL616317	OL616425
M. minutoides	IVB KE600	KEN	Taita Hills, Vichwala	–3.469	38.341	KJ935855	KJ935902	OL616394	OL616310	OL616418
	IVB VM221	ZAM	Kacholola	–14.762	30.597	KJ935854	KJ935901	OL616403	OL616319	OL616427
M. gerbillus	IVB K3x3309	KEN	Marsabit NP	2.262	37.935	KJ935824	OL616375	OL616390	OL616306	OL616414
	IVB TZ27385	TNZ	Majawanga	–6.097	36.814	KJ935828	KJ935896	OL616402	OL616318	OL616426

of Procrustes shape coordinates, i.e. Cartesian coordinates of the points after accounting for differences in size and arbitrary position and orientation of the skulls (Dryden & Mardia 2016).

The molecular data set included two individuals of *M. callewaerti* and 26 others, together representing twelve species from all major lineages of *Nannomys* (Table 3). All individuals were sequenced at one mitochondrial locus, cytochrome *b* gene (*CYTB*), and four nuclear loci, namely, exon 1 of inter-photoreceptor retinoid-binding protein gene (*IRBP*), recombination activating gene 1 (*RAG1*), intron 7 of β-fibrinogen gene (*BFIB*) and intron 9 of smoothened frizzled class receptor gene (*SMO*). A large part of these data was already analyzed in Krásová et al. (2022), where also details of the laboratory protocol are given. In this study we newly generated four nuclear sequences of the Angolan specimen of *M. callewaerti*, which are accessible at GenBank under accessions OP747458–OP747461.

The holotype assignment and inter-specific differences

The skull shape differentiation was studied by means of between-group principal component analysis (bgPCA), which is PCA of group (= species) means followed by projection of individual shapes on the resulting axes (Yendle & MacFie 1989, Cardini et al. 2019). *Mus callewaerti* was represented by just three specimens, because the holotype was left aside for *post hoc* classification, in which it was assigned to the nearest species mean. Species distinctiveness was then inspected on a scatterplot resulting from the projection of individual shapes on bgPC1–2 axes and quantified by means of leave-one-out cross-validation which also classified the specimens to the nearest species means. The actual skull shape differentiation was shown by contrasting the mean shape of *M. callewaerti* with the mean shapes of the other two species. Also, the skull size of *M. callewaerti* holotype was shown in the context of skull size distributions in the three species. The analyses were performed using R functions available at https://github.com/onmikula/gmtools. Although we did not have sufficient material for the analysis of mandible form, we performed at least qualitative comparison by plotting mandibles of *M. callewaerti* specimens from Nyika and Namba village alongside with mandibles of the selected syntopic individuals of *M. triton*.

Finally, we compiled data on four standard body measurements, i.e., lengths of head and body, tail, hind foot, and ear. The latter three we expressed both in absolute units (mm) or as proportions (%) of the head and body length. For *M. callewaerti*, we compiled all available data (Hill & Carter 1941, Misonne 1965, and collection catalogues, see Table 1), while for the other two species we used samples of published data. For *M. triton*, we used data from Krásová et al. (2019), but we excluded their clade A, which is

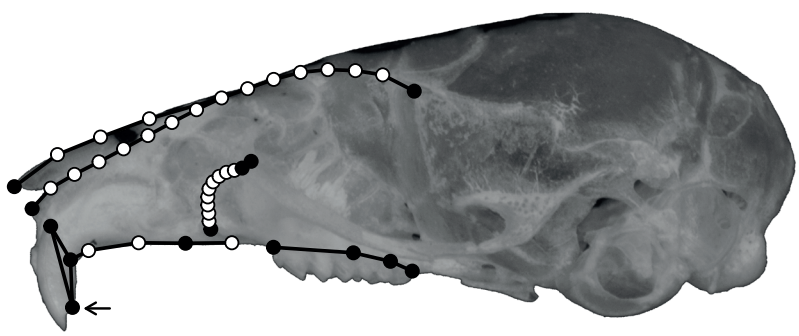

Fig. 2. Landmarks (in black) and semilandmarks (in white) used in the morphometric analysis of lateral size and shape of the skull of analysed species of *Mus*. The arrow marks the incisor landmark whose position was *ad hoc* adjusted.

extraterritorial to *M. callewaerti*. For *M. imberbis*, the data are taken from Yalden (2013), Meheretu Yonas et al. (2015), Monadjem et al. (2015), and from the FMNH catalogue.

Species tree inference

The species tree of subgenus *Nannomys* was inferred in StarBEAST 2 (Ogilvie et al. 2017), which is Bayesian implementation of the multispecies coalescent model (Rannala & Yang 2003). For the tree shape, we used birth-death prior (Rannala & Yang 1996) with uninformative hyperpriors on its parameters. The population size parameter was given uninformative prior and it was analytically integrated out as a part of the Markov Chain Monte Carlo sampling of the posterior. Each locus was assumed to have its own gene tree and clock rate. Nucleotide substitution models were set and protein-coding genes codon-partitioned according to the results of ModelFinder (Kalyaanamoorthy et al. 2017) in IQ-TREE software (Nguyen et al. 2015). For the purpose of this inference, species were set corresponding to the nominal species or to geographically separated populations, that have been inevitably separated for some period of time. The latter applies to three populations of *M. triton*, labelled 'Congo', 'Angola' and 'Malawi' to highlight their correspondence to sympatric populations of *M. callewaerti*, which were also treated as separate units called 'Malawi' and 'Angola' (for other nomenclature of *M. triton* populations, cf. Fig. 4 in Krásová et al. 2019).

Time-calibration of the tree was achieved by setting calibration gamma calibration density on the root (α=1.25, β=0.25, offset=4.4), which mimicked posterior distribution of the root age obtained in similar analysis by Krásová et al. (2022). The calibration is in units of million years (Ma) before the present. Molecular clock rates of genes and their partitions were given independent uninformative priors. Two independent runs of the analysis were conducted and their convergence was checked in Tracer 1.7 (Rambaut et al. 2018). The pooled posterior samples of species trees were summarized by the maximum credibility tree with common ancestor node heights in TreeAnnotator tool distributed with BEAST 2 (Bouckaert et al. 2019). The clade supports were quantified by their posterior probabilities (PP).

RESULTS

Morphological distinctiveness of *Mus callewaerti*

Given just three species were compared, differences between their mean shapes were fully accounted for by the first two bgPCA axes. In this plane the projected individual shapes created well separated species-specific clusters (Fig. 3), which was confirmed by 100% cross-validation success rate. The differentiation along bgPC2 (contrasting *M. callewaerti* to the other two species) seems to be correlated with the ontogenetic change as the outlying individuals in both *M. callewaerti* and *M. imberbis* are smaller than average. The holotype of *M. callewaerti* was unambiguously classified to *Mus* sp. "Nyika" (*sensu* Bryja et al. 2014), which justifies labelling of this species as *M. callewaerti* throughout this paper. The distance of the holotype to the mean of *Mus* sp. "Nyika" (already called *M. callewaerti* in Fig. 3) was 5.6 and 6.1 times lower than distances to the means of *M. triton* and *M. imberbis*, respectively.

When compared to the largely sympatric *M. triton*, the mean skull shape of *M. callewaerti* is characterized by the pronounced proodonty, shorter molar row, much higher zygomatic plate, and somewhat lower profile of the skull in its rostral part (Fig. 4). Compared to *M. imberbis*, it has longer rostrum, zygomatic plate shifted backwards and shorter molar row (Fig. 4). When examined in more detail, the shortening of molar row concerns especially the third upper molar. Expressed as a proportion of centroid size (the measure implicit in Fig. 4), the overall length of molar row was 0.147 in *M. callewaerti*, 87.9% of the value recorded in *M. imberbis* (0.168). The reduction was largely due to the third molar, however, whose relative length in *M. callewaerti* (0.018) was just 60.8% of that in *M. imberbis* (0.029), while in the first two molars the

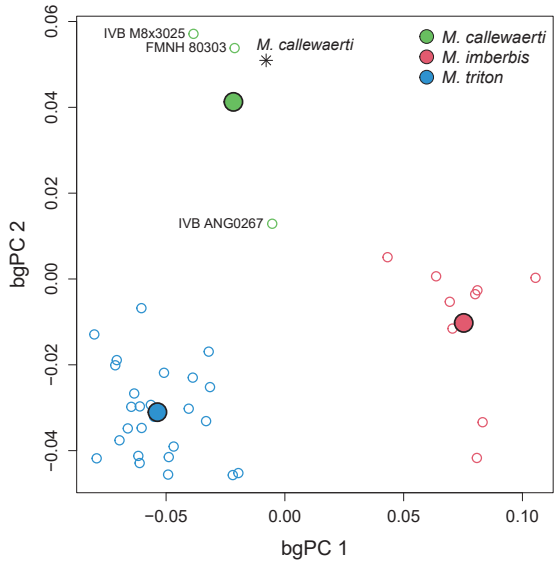

Fig. 3. Skull shape distinctiveness of *Mus callewaerti* in bgPCA scatter plot. The position of *M. callewaerti* holotype is indicated by the asterisk.

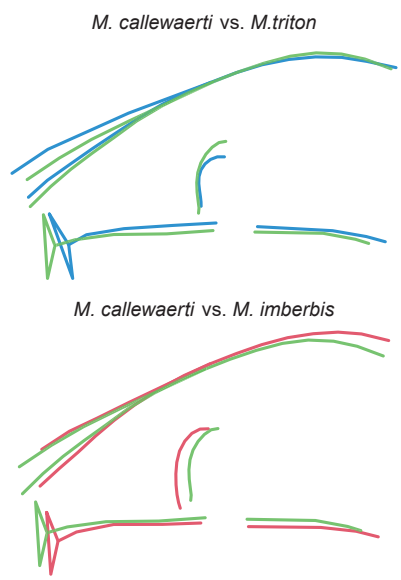

Fig. 4. Differences between mean skull shapes of the analysed species of *Mus* shown by wireframe plots. Landmarks are linked as indicated in Fig. 2, the colour code is the same as in Fig. 3.

Table 4. Body measurements of the three analysed species of *Mus*; means, minima, and maxima are given for the lengths of head and body, tail, hind foot, and ear. The latter three lengths are given in absolute units (mm) as well as proportions (%) of head and body length. The sample size (*N*) of each species is indicated. The hind foot of *Mus callewaerti* holotype was suspiciously low and excluded from the calculations

		head and body length			tail length			hind foot length			ear length		
		mean	min	max	mean	min	max	mean	min	max	mean	min	max
M. callewaerti	mm	88.0	74.0	97.0	45.4	43.0	49.3	15.7	14.0	16.5	11.6	9.5	14.0
(*N*=6)	%				52.2	45.3	66.6	18.3	15.7	21.2	13.3	9.8	18.0
M. triton	mm	72.4	57.0	91.0	50.6	39.0	65.0	15.0	13.6	16.6	12.0	10.0	16.5
(*N*=113)	%				70.5	51.3	96.5	20.9	16.7	26.5	16.7	13.7	24.6
M. imberbis	mm	80.0	70.0	92.0	49.1	44.0	55.0	17.9	16.0	26.0	12.0	11.0	13.0
(*N*=12)	%				58.4	48.9	71.4	21.4	18.5	32.5	14.6	13.0	16.3

percentage was 94.4% and 92.3%, respectively. The figures are similar when the comparison is made against *M. triton*. The mandibles of *M. callewaerti* are slender than those of *M. triton*, their processes are proportionately longer and the coronoid process points backwards, whereas it points up in *M. triton* (Fig. 5).

Mus callewaerti also appears to be the largest species in terms of the skull size (Fig. 6). The mean centroid sizes were 22.8 mm in *M. triton*, 24.2 mm in *M. imberbis*, and 25.2 mm in *M. callewaerti*. The holotype of *M. callewaerti* fitted the picture with its centroid size 26.6 mm. Body measurements are summarized in Table 4. Again, *M. callewaerti* is the largest species with the mean head and body (HB) length 88 mm (range 74–97 mm), while it was 85 mm (70–96 mm) in *M. imberbis* and only 71 mm (58–88 mm) in *M. triton*. Among the other measurements, *M. callewaerti* is outlying especially by its relatively short tail and hind foot. On average, its tail was just 52.2% of HB length, markedly less than 58.4% in *M. imberbis* and 70.5% in *M. triton*. Its hind foot had on average just 18.3% of HB length, while it was 20.9% in *M. triton* and 21.4% in *M. imberbis*.

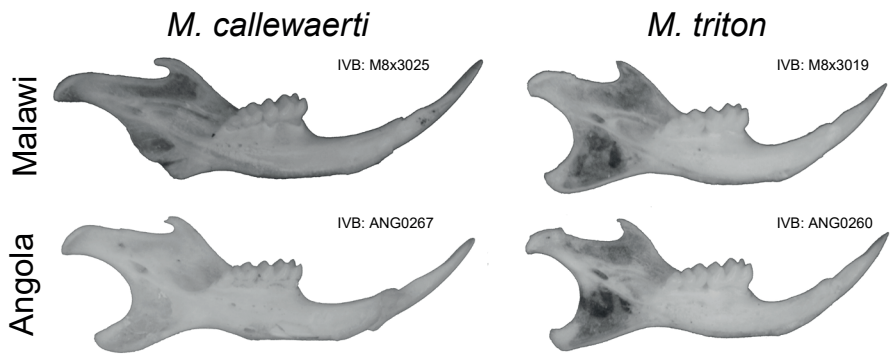

Fig. 5. Mandibles of two genetically analyzed individuals of *Mus callewaerti* and two examples of syntopic *M. triton*. All images are to the same scale.

Time-calibrated species tree of *Nannomys*

The species tree of *Nannomys* (Fig. 7) was almost completely resolved (PP≥1.00) with an exception of relationships in *mahomet-bufo-proconodon* clade (= *setulosus* species group of Bryja et al. 2014) and, notably, the most basal branching, which means the position of *M. callewaerti* relative to the other two major clades of the subgenus. In the maximum credibility tree, *M. callewaerti* is in a sister relationship to the *mahomet-neavei-minutoides* clade, but with PP=0.49 only. Significant alternative topologies were with *M. callewaerti* being sister to *imberbis-harennensis-triton* clade (PP=0.30) or to the rest of the subgenus (PP=0.20). In any case, *M. callewaerti* currently represents an isolated lineage, branching off in a supposedly fast basal radiation of *Nannomys* in the early Pliocene. It has no extant close relatives, and its origin was dated to 4.44 Ma with 95% highest posterior density (HPD) interval 3.88–4.97 Ma (conditional on its most probable phylogenetic position).

The divergence between 'Angola' and 'Malawi' populations of *M. callewaerti* (sister to each other with PP=1.00) was dated to 0.32 Ma (0.06–0.54 Ma). This estimate stands in contrast to the estimated divergence between 'Angola' and 'Malawi' of *M. triton*, which is 1.29 mm (0.79–1.74 Ma), and it is even younger than the divergence of geographically closer *M. triton*'s 'Angola' and 'Congo', dated to 0.63 Ma (0.29–0.94 Ma).

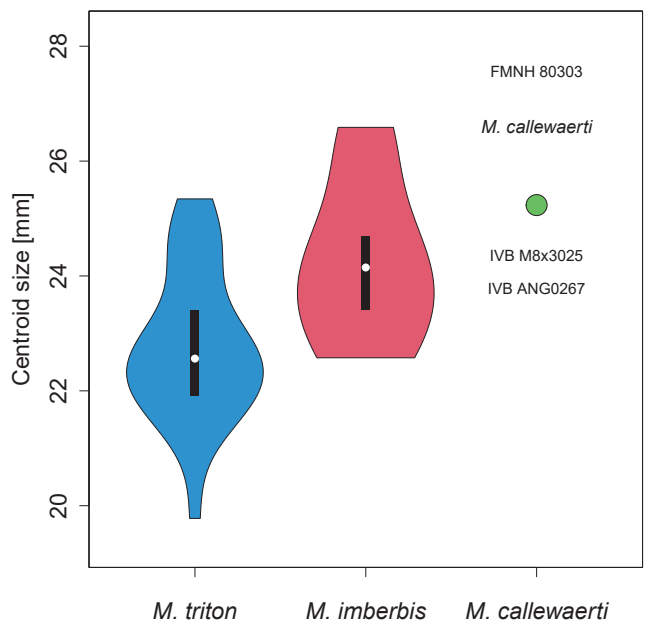

Fig. 6. Skull size differentiation of the three analysed species of *Mus*. Violin plots show distribution of individual centroid sizes with medians (white points) and interquartile ranges (black bars) indicated. Centroid sizes of the three specimens of *Mus callewaerti* are marked by their IDs, the green point is their mean. The size of the holotype is marked by the species' name. The figure was created using R package vioplot (Adler & Kelly 2021).

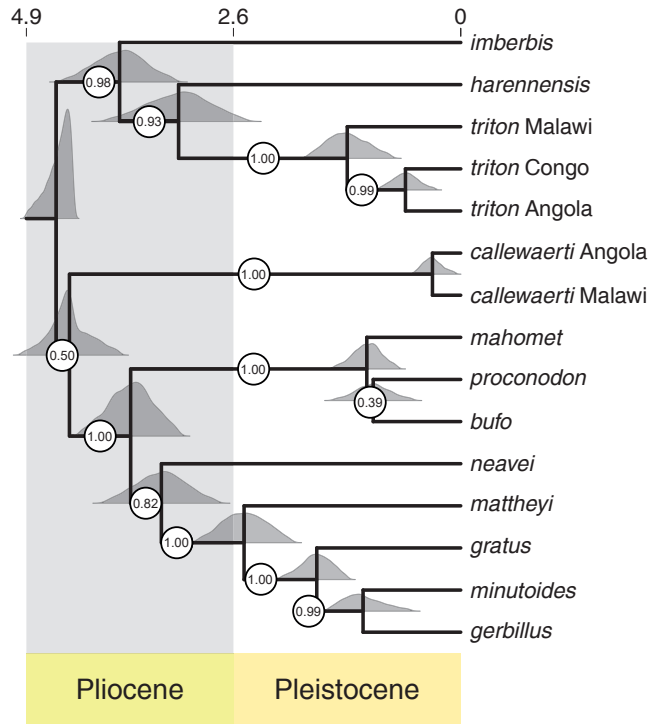

Fig. 7. Time-calibrated species tree of subgenus *Nannomys*. Posterior distributions of divergence times are displayed at the ancestral nodes as kernel density estimates. The numbers at branches supporting the nodes are posterior probabilities of the clades. The figure was created using R package MCMCtreeR (Puttick & Title 2019).

DISCUSSION

Our morphometric analysis unambiguously showed that the ancient lineage of *Nannomys* reported in previous phylogenetic studies (Bryja et al. 2014, Krásová et al. 2021) as *Mus* sp. "Nyika" is identical with *Mus callewaerti* of Thomas (1925). Furthermore, the species was shown to be remarkable from morphological and biogeographical point of view.

Morphological distinctiveness of *Mus callewaerti*

The most remarkable morphological feature of *Mus callewaerti* is its pronounced proodonty. This was the trait that convinced Thomas (1925) to describe the species as a member of a new genus *Hylenomys*, which he likened to another African genus, *Muriculus*, described earlier (Thomas 1902), largely based on the same character. Quite ironically, both these taxa turned out to belong to the genus *Mus* and even to its widespread African subgenus *Nannomys* (Misonne 1965, Meheretu Yonas et al. 2015). The character itself is often considered an adaptation to

insectivory (Martin et al. 2016) and, indeed, at least two other traits suggest *M. callewaerti* has insectivorous or, more generally, animal-dominated diet.

The species has remarkably short upper third molar, the condition found to be a good dental predictor of carnivory in murines (Kavanagh et al. 2007, Martin et al. 2016). Also, the mandibles of *M. callewaerti* are remarkably slender (Fig. 5), reminding the shapes suggested as typical for murine invertebrate-eaters (cf. Michaux et al. 2007: Fig. 4). Furthermore, the front face of incisors of *M. callewaerti* is not brownish yellow as in most rodents. Instead, it is "practically without pigment, the upper white, the lower very faintly yellowish" (Thomas 1925), the observation supported by the examination of specimens we had opportunity to study. The usual coloration is due to deposition of iron-rich pigments, which is supposed to affect mechanical and physical-chemical properties of teeth (Dumont et al. 2014). The difference in coloration can suggest, therefore, different functional demands put on the incisors and hence a difference in diet. Based on the present data, it can be therefore hypothesized that *M. callewaerti* represents a species with the most specialized animal-dominated diet of all *Nannomys*. Nevertheless, the hypothesis should be further tested by the inspection of stomach contents and by the analysis of dental microwear (expected to show fewer fine scratches, Gomes-Rodrigues et al. 2009) or occlusal surface complexity (expected to be low, Evans et al. 2007).

In addition, *M. callewaerti* is shown here as the largest African pygmy mouse, matched in its size only by *M. imberbis*, although more data would be needed for statistical comparison. The large size of *M. callewaerti* is particularly telling when compared to *M. triton*, which is already one of the larger species of *Nannomys* (Monadjem et al. 2015). The specificity of *M. callewaerti* phenotype is then apparent from relatively short body extremities, especially tail and hind foot, which may be related to a specific locomotor activity, possibly associated with its feeding specialization. Body mass data are largely missing for *M. callewaerti* with the only exception of the Nyika specimen (IVB M8x3025), which weighted 14 g.

Note, that both *M. callewaerti* and *M. imberbis*, i.e., the large-bodied, proodont, presumably insectivorous species, form isolated phylogenetic lineages originating in Pliocene basal radiation of *Nannomys*. It is tempting to speculate they survived for so long as the only members of their lineages because they occupy a specific niche, quite different from what is common in the subgenus.

Distribution and biogeography of *Mus callewaerti*

The present study shows *Mus callewaerti* as a typical element of the Zambezian bioregion (*sensu* Linder et al. 2012). After inclusion of the individual from Nyika plateau, its distribution range spans a vast area from northern Malawi through Katanga region of DRC and southern margin of the Congo River Basin to the northern end of the Angolan Escarpment. Currently, there is no record of the species east of the Great Rift Valley as the Tanzanian records currently available in Global Biodiversity Information Facility (GBIF) database are taxonomic mistakes (as they refer to Lamb et al. 2014). GBIF contains also a record from southern Malawi, but this should be checked as it refers to the specimen AMNH M-81367, which is exceedingly large (head and body = 142 mm) according to the museum catalogue.

The distribution of *M. callewaerti* is not unique among African rodents. Quite the opposite, there are several species with very similar distributional pattern. Most significantly, *M. triton* is sympatric with *M. callewaerti* over its known distributional range, although it occurs also further north in Tanzania and Kenya. Two other rodent species are known, among others, from

Nyika and then from Tundavala (14.81° S, 13.40° E; Krásová et al. 2021), a locality ca. 200 km further south of Namba village along the Angolan Escarpment. These two are the four-striped mouse, *Rhabdomys dilectus* (Ganem et al. 2020), and a species of climbing mouse, provisionally called *Poemys* sp. indet. 13 (Voelker et al. 2021). Another climbing mouse, captured directly in Namba, also bears the same biogeographical signal as *M. callewaerti*, as it belongs to *Poemys pecilei-nyikae* clade (Fig. 1; Voelker et al. 2021) distributed in the Congo Basin and the highlands of Malawi (Krásová et al. 2021: Fig. S2.3). Finally, the distribution of a rock rat *Aethomys nyikae* spans the same area with the westernmost record in northern Angola and the easternmost one in Nyika (Krásová et al. 2021: Fig. S2.7).

More surprising than the distribution itself is the apparent rarity of *M. callewaerti* in museum collections, which stands in contrast to abundant material of *M. triton* collected in the same regions and sometimes even in the same place. In the Nyika National Park, for instance, ten trapping nights spent in different elevations brought ten *M. triton*, five of them from the very same site as the single *M. callewaerti*. During a single night spent in Namba, eleven *M. triton* were captured compared to one *M. callewaerti*. The same applies on regional scale: there are many localities of *M. triton* across Malawi, Zambia, southern DRC, and Angola (Crawford-Cabral 1998, Leirs et al. 1999, Krásová et al. 2019), but just a handful of localities of *M. callewaerti* from the same area (Table 1). We suppose, therefore, *M. callewaerti* is not very abundant or not easy to capture. In any case, it is possible it just escapes attention at some sites, especially those with records of *M. triton*.

Another striking observation is the relatively shallow split between Angolan and Malawian populations of *M. callewaerti*. Their divergence time was estimated to 0.32 Ma, which coincides with the interglacial corresponding to the Marine Isotope Stage 9 (0.34–0.30 Ma; Lisiecki & Raymo 2005). The estimate should be taken with some caution because its 95% HPD interval spans almost 0.5 Ma, but it is precise enough to show the internal phylogeographic structure of *M. callewaerti* is much younger than that of *M. triton*, where the corresponding split was estimated to be as old as 1.29 Ma. This is quite counterintuitive as the isolation of relatively abundant populations of *M. triton* appears to be stronger and/or lasting longer compared to

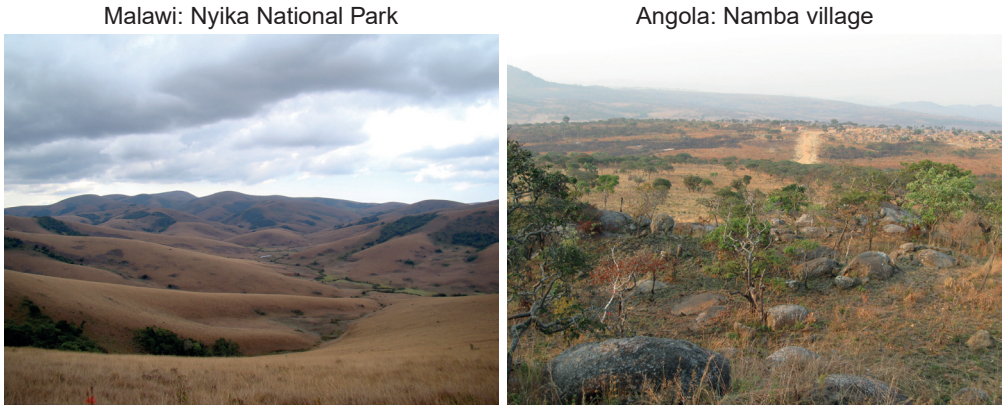

Fig. 8. Habitats of *Mus callewaerti* in Nyika National Park (Malawi) and Namba village (20 km south of Cassongue, Angola).

those of presumably rare *M. callewaerti*. Even the scarcely present species can be relatively widespread, however, or could be so in the past. We also consider the estimate accurate enough to conclude the effective divergence time between the populations is comparable to one or more glacial-interglacial cycles. It shows, therefore, the long-term persistence of the populations, or even their connectivity, despite major climatic changes.

The crucial in this respect is the persistence of suitable habitats. In the Nyika National Park in Malawi, *M. callewaerti* was captured in an undulating grassland with scattered shrubs and moisty places, placed on a plateau about 2100 m a. s. l. The surroundings of Namba village (1725 m a. s. l.) in Angola were also grassy and quite dry, but the trap line followed a stream rimmed with some shrubs. For the photos of both localities, see Fig. 8. It seems, therefore, *M. callewaerti* is associated with grassy and moist habitats, which would be consistent with its presumed insectivorous diet. Historically, therefore, the species' survival could depend on the prevalence of sparsely wooded landscape, which remains mesic throughout the year. At present, the species can be regionally widespread, because the habitat in Namba, for instance, fitted the common character of landscape in the region, i.e., the landscape of higher elevations at the northern end of the Angolan Escarpment. The species can be threatened, however, by severe and prolonged droughts and by the spread of more intensive cultivation.

Taxonomic summary

The large-bodied species of *Mus* (*Nannomys*) in Africa form long basal branches in the phylogenetic tree of *Nannomys* and they were referred either as "ancient mountain lineages" or the *triton* group by Bryja et al. (2014). Subsequent taxonomic work recognized them as belonging to four species, whose distribution is shown in Fig. 1; *M. triton* from the eastern Africa and the Zambezian region (Krásová et al. 2019), *M. harennensis* from the southern Ethiopia (Krásová et al. 2022), *M. imberbis* from the Ethiopian Highlands (Meheretu Yonas et al. 2015, Kostin et al. 2019, Craig et al. 2020), and *M. callewaerti*, another Zambezian species, for which we summarize available taxonomic information here.

Previous work on *Mus callewaerti* (Thomas, 1925)

Thomas (1925): *Hylenomys callewaerti*: species description, holotype BMNH 1925.4.2.1 (Fig. 9) from Kananga (= Luluabourg), DRC, 5.88° S, 22.43° E, 610 m a. s. l.
Misonne (1965): *Leggada callewaerti*: taxonomic notes, morphology, summary of known material.
Bryja et al. (2014): *Mus* sp. "Nyika": the first genetic data and the first record from Malawi.
Krásová et al. (2019): *Mus callewaerti*: morphological comparison of the holotype with *M. triton*.
Krásová et al. (2021): *Mus* sp. "Nyika": the first genetic data from Angola.

Diagnostic traits. *Mus callewaerti* is the largest representative of the subgenus *Nannomys*, with proodont incisors. From the sympatric (and sometimes even syntopic) *Mus triton*, it is distinguished by the form and colour of incisors, shorter third upper molar, and higher zygomatic plate. On average, it has also larger body size, relatively shorter tail, and hind foot (Table 4) and more reddish fur colouration (Misonne 1965).

Notes. The name "*callewaerti*" was incorrectly used for *Mus triton* in two previous phylogenetic papers. Lamb et al. (2014) used the name for a sequenced specimen from Angola but did not compare the morphology with the holotype. Based on this study, Bryja et al. (2014) subsequently used the name "cf. *callewaerti*" for all sequences in their MOTU 6, clustering with Lamb's et

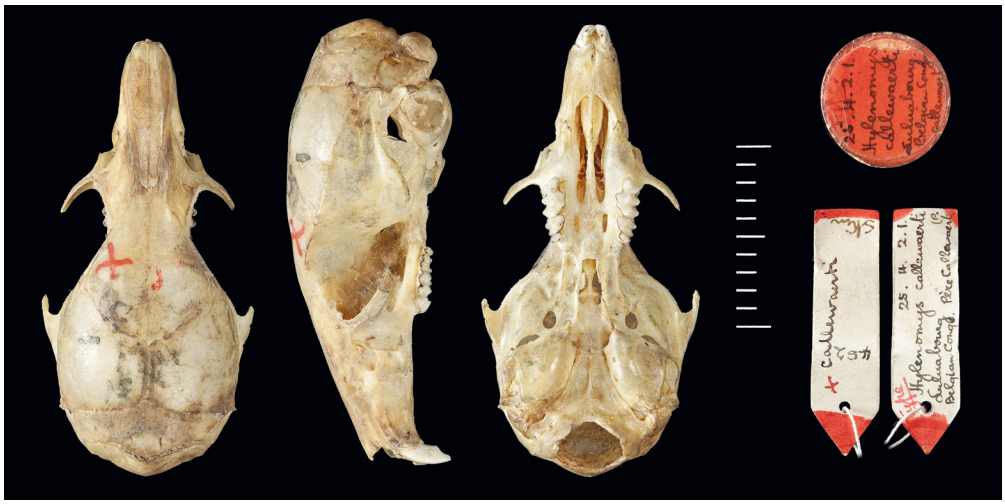

Fig. 9. The skull of the holotype of *Mus callewaerti*, BMNH 1925.4.2.1. The image provided by the Natural History Museum, London.

al. (2014) "*callewaerti*". However, MOTU 6 clearly represents intraspecific clades C and D of *M. triton* (see Krásová et al. 2019). The hindfoot of the holotype is unexpectedly short (in comparison with other specimens of this species) and should be re-analysed (Misonne 1965).

CONCLUSIONS

We performed an integrative taxonomic revision of the murid rodent species reported in the previous genetic studies as *Mus* sp. "Nyika". The recent finding and genotyping of another specimen in western Angola and the comparison with the museum material unequivocally confirmed that *Mus* sp. "Nyika" is conspecific with *M. callewaerti*, known till now only from a handful of localities in Angola and southern DRC. The species was shown morphologically distinct from *M. triton*, even if the two species are similar in external appearance and can occur in sympatry in the Zambezian bioregion. *Mus callewaerti* thus appears to be a widely distributed but perhaps uncommon member of Zambezian small mammal fauna, which split from its closest extant relatives in the early Pliocene, at the very beginning of radiation of the subgenus *Nannomys*. Together with *M. triton* and some other rodent species, it provides evidence about the biogeographic connection between the eastern and western side of the Zambezian region. *Mus callewaerti* also appears as the species of *Nannomys* most specialized to insectivory or, more generally, animal-dominated diet.

Acknowledgements

This paper is a part of a special issue devoted to our friend and teacher Hynek Burda, who performed a detailed and successful fieldwork of small mammals in the Nyika NP in Malawi in 1997. Even if he probably did not capture *Mus* sp. "Nyika" at that time, the results of his work in Africa were highly influ-

ential and there is no doubt that he attracted us to work on African rodents. The two genotyped specimens of *Mus callewaerti* were collected in the field by O. Mikula, J. Krásová and F. Vejmělka (Angola) and J. Šklíba and M. Lövy (Malawi). We thank A. Fergusson for allowing us to work on the collection of mammals in the FMNH (Chicago). This study was supported by the project of the Czech Science Foundation no. 20-07091J (to JB and RŠ) and the student project of the Grant Agency of the University of South Bohemia no. 018/2017/P (to JK).

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