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Authors: De Bellocq, Joëlle Goüy, Fornůsková, Alena, Ďureje, L'udovít, Bartáková, Veronika, Daniszová, Kristina, et al.

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First record of the greater white-toothed shrew, *Crocidura russula*, in the Czech Republic

Joëlle GOÛY DE BELLOCQ^{1*}, Alena FORNŮSKOVÁ¹, Ľudovít ĎUREJE¹, Veronika BARTÁKOVÁ¹, Kristina DANISZOVÁ², Malahat DIANAT^{1,3}, Matouš JANČA^{1,3}, Petr ŠABATA¹, Nikola ŠENEKLOVÁ¹, Tadeáš STODŮLKA^{1,3}, Barbora VOŠLAJEROVÁ BÍMOVÁ² and Miloš MACHOLÁN²

¹ Institute of Vertebrate Biology of the Czech Academy of Sciences, Brno, Czech Republic; e-mail: joellegouy@gmail.com, a.fornuskova@seznam.cz, dureje@gmail.com, bartakova.v@ivb.cz, malahatdianat2002@yahoo.com, matous.janca@gnj.cz, petr.sabata04@seznam.cz, nikcaseneklova@seznam.cz, stodulka.tadeas@gmail.com

² Institute of Animal Physiology and Genetics, Czech Academy of Sciences, Brno, Czech Republic; e-mail: carlosik.hs@gmail.com, voslajerova@iapg.cas.cz, macholan@iach.cz

³ Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

This article is dedicated to Prof. Jan Zima for his great contribution to European mammalogy.

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Abstract. While sampling house mice in 2022 in the westernmost region of the Czech Republic, we also captured other small mammal species in and around farms. The sympatric shrew species were pre-identified based on morphological characteristics and genotyped using the mitochondrial cytochrome *b* marker. Among them, 14 specimens from five different localities were identified as the greater white-toothed shrew (*Crocidura russula*). With previous records from southern Saxony in Germany, our findings are the easternmost records of *C. russula* distribution in Europe and the first report of this species in the Czech Republic. The four other shrew species captured during fieldwork (*C. suaveolens*, *C. leucodon*, *Sorex minutus*, and *S. araneus*) are widely distributed in this country. The checklist of Eulipotyphla from the Czech Republic, which currently lists ten species (*C. leucodon*, *C. suaveolens*, *S. alpinus*, *S. araneus*, *S. minutus*, *Neomys milleri*, *N. fodiens*, *Talpa europaea*, *Erinaceus europaeus*, *E. roumanicus*), should now be updated with this new entry. The arrival of *C. russula* in the Czech Republic should be closely monitored as this species has been regularly reported for its competitive behaviour leading to the local extinction of resident shrew species.

Key words: Eulipotyphla, *Crocidura russula*, Czech Republic, range expansion, climate change, cytochrome *b*

Introduction

The checklist of insectivores of the Czech Republic, recently updated by Anděra & Hanzal (2022), reports the occurrence of ten species from three families: seven species of shrews (Soricidae), two species of hedgehogs (Erinaceidae), and one species of mole (Talpidae). Some

of these taxa are widely distributed over the territory (*Sorex araneus*, *S. minutus*, *Neomys fodiens*, *N. milleri*, *Crocidura suaveolens*, *Talpa europaea*, *Erinaceus europaeus*), while the other three (*S. alpinus*, *C. leucodon*, *E. roumanicus*) have a more regional distribution (Anděra & Hanzal 2022). The occurrence of these ten species has been relatively stable in recent decades,

* Corresponding Author

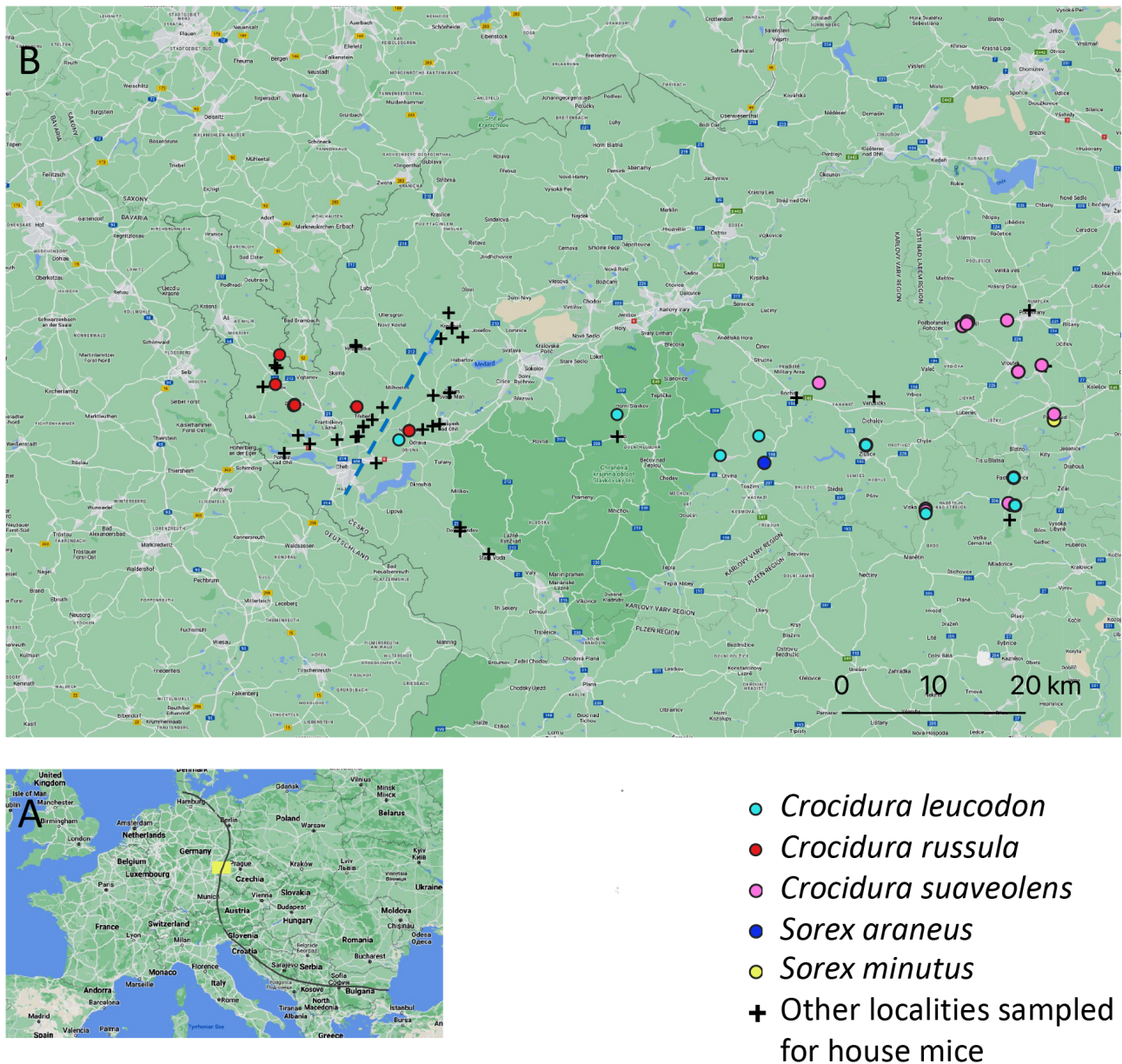


Fig. 1. A) Course of the European house mouse hybrid zone (in dark grey); the yellow rectangle shows the position of the studied area. B) Map of the westernmost part of the Czech Republic showing the localities where different shrew species were accidentally captured during sampling house mice. The grey line is the border between Germany and the Czech Republic. The dashed blue line represents the consensus house mouse hybrid zone centre estimated by Macholán et al. (2008). The red dots are the five localities where *Crocicidura russula* individuals were found for the first time in the Czech Republic. The crosses are the localities targeted for house mice but where no shrews were sampled. The maps were created using the Free and Open Source Geographic Information System QGIS v. 3.30 (QGIS.org 2023).

except for two species, *C. leucodon* and *N. milleri*: the first, *C. leucodon*, shows a large number of new geographic records in the last 30 years, showing its evident spread in the territory; the second, *N. milleri*, originally considered a rare species in the Czech Republic, is now reported in more than two-thirds of the territory due to intensive faunistic surveys in the 1980s and 1990s. Two species of shrews, the Millet's shrew or crowned shrew, *Sorex coronatus*, and the greater white-toothed shrew, *Crocicidura russula*, are regularly mentioned in the insectivore checklists of the Czech Republic as never recorded in the country

but with potential future occurrence because these species are found near the western Czech Republic border (Anděra 2010, Anděra & Hanzal 2022).

Crocicidura russula is a widespread species of shrew that occurs from sea level to elevations of 1,200 m, although it can reach up to 2,000 m in Mediterranean landscapes (Aulagnier et al. 2021). The species is found in northern Africa, from Morocco to Tunisia, and in southern and western Europe to the western-central regions of Switzerland and Germany (Brändli et al. 2005, Aulagnier et al. 2021, see also <https://www.iucnredlist>).

org/fr/species/29652/197503499 for an overview of the species range). It also occurs on some Mediterranean and Atlantic islands (Cosson et al. 1996, 2005, Vogel et al. 2003) and has been reported as a rapidly spreading species in Ireland from 2007 (Tosh et al. 2008, McDevitt et al. 2014) and recently as a new species for Great Britain (Bond et al. 2022). Genetic studies suggest that the species originated in Africa, with a subsequent northward expansion of eastern and western lineages (Lo Brutto et al. 2004, Brändli et al. 2005, Cosson et al. 2005, Nicolas et al. 2015). This scenario is essentially supported by greater nucleotide diversity and some evidence that population expansion in Morocco preceded that in Europe (Brändli et al. 2005). An eastern subclade groups individuals from Tunisia and the Mediterranean islands, whereas a western subclade comprises individuals from Morocco, eastern Algeria and mainland Europe. The eastern known distribution limit of *C. russula* on mainland Europe is in Germany, where it runs from western Bavaria through Saxony and western Brandenburg and from there northward, roughly following the course of the River Elbe to the North Sea (Kapischke 2009). The limit is thus very close to the Czech Republic border, a region where intensive fieldwork has been carried out in the last two decades on the hybrid zone between two subspecies of the European house mouse, *Mus musculus musculus* and *M. m. domesticus* (Macholán et al. 2007, 2011, Baird et al. 2012, Goüy de Bellocq et al. 2015, 2018). This hybrid zone runs for more than 2,500 km across Europe, from Scandinavia to the Black Sea, crossing the Czech Republic just a few kilometres from its westernmost border with Germany (Ďureje et al. 2012) (see Fig. 1A).

While sampling mice in the westernmost part of the Czech Republic in 2022, we also collected other small mammals that entered the traps. Mice and the sympatric rodent species were our main targets to characterise their shared viral community. A subset of the sympatric small mammals that accidentally entered the traps were shrews. The animals were provisionally determined morphologically and subsequently genotyped to confirm their identification. In this study, we report the first detection of *C. russula* in the Czech Republic, together with morphometric and mitochondrial cytochrome *b* (*cytb*) data of the shrews from this region.

Material and Methods

Sampling

Two trapping sessions were organised in 2022, five days in mid-May and ten days in late September, to sample house mice in the westernmost region of the

Czech Republic where the house mouse hybrid zone between *M. m. musculus* and *M. m. domesticus* crosses the country (Macholán et al. 2007, Ďureje et al. 2012). We sampled 68 localities across a transect starting in the south of the Ústecký/north of the Plzeňský regions and passing through the central part of the Karlovarský region to the border with Germany (Fig. 1). We used live traps (wooden, Sherman, plastic and Ugglan) with oat flakes mixed with sardine oil as bait. At each locality selected for trapping, most of the traps were placed inside farm buildings to catch house mice, with a small number of traps placed around the walls of the buildings or in bushes nearby to catch mice and other sympatric rodent species. The number of traps was adjusted to the size of the farm/buildings so that different numbers of traps were placed in different localities. Generally, traps were set at a locality for one to three nights, depending on trapping success. Traps were checked for the presence of rodents, and animals were transferred to transport boxes. In several cases, shrews entered the traps as unintended bycatch and were found dead during trap checks. These non-targeted samples were collected and frozen for later determination and to be archived in the Genetic Bank of the Institute of Vertebrate Biology. Sample collection was conducted under Czech region permit numbers 3152/ZZ/16-4, 11656/ENV/17, 274/530/17, ZN/3820/ŽP/16, ZN/3820/ŽP/16, ŽP/17139/16.

Morphological measurements, genotyping and sequence analysis

Shrew individuals were weighed, measured (head, body, tail, ear, and hind foot length) and sexed. Small pieces of tissue from the tail, ear or foreleg were preserved in 96% ethanol and used for subsequent genotyping. A piece of liver and muscle was also preserved in 96% ethanol and deposited in the Genetic Bank of the Institute of Vertebrate Biology, Czech Academy of Sciences, which is part of the National Animal Genetic Bank of the Czech Republic. DNA was extracted from the sample tissue using an Invisorb DNA tissue HTS 96 kit (Strattec Molecular, Berlin, Germany) and eluted in 100 µL of elution buffer. We used primers L14723 and H15915 to amplify the mitochondrial *cytb* gene (Lecompte et al. 2002). The polymerase chain reaction (PCR) was performed in a volume of 20 µL containing 0.4 µM of each primer, 0.2 mM of each dNTP, 2.5 mM MgCl₂, 1X DreamTaq buffer, 0.6 unit of DreamTaq DNA polymerase (Fermentas, Germany), and 2 µL of the DNA template. The thermal cycling profile was as follows: an initial denaturation step at 95 °C for 2 min, followed by 35 cycles at 95 °C for 45 sec, 53

Table 1. Morphological measurements of individuals from five shrew species captured in the westernmost part of the Czech Republic in 2022. Values from the literature are in grey. Ref. 1: Burgin et al. (2018); Ref. 2: Anděra & Hanzal (2022). Imma: immatures.

Species	N	Body mass (in g)		Head-body (in mm)		Tail (in mm)		Hindfoot (in mm)		Ear (in mm)	
		mean (SD)	Min-Max	mean (SD)	Min-Max	mean (SD)	Min-Max	mean (SD)	Min-Max	mean (SD)	Min-Max
<i>S. araneus</i>											
Male	0										
Female	1	5.84	5.84-5.84	63	63-63	x	x	11.3	11.3-11.3	x	x
Total	1	5.84	5.84-5.84	63	63-63	x	x	11.3	11.3-11.3	x	x
Ref 1			5-14.5 (imma 5-10)		56-82		37-52		12-14		
Ref 2			4.5-13		60-80		35-50		11.8-13.5		
<i>C. leucodon</i>											
Male	12	7.66 (0.86)	6.39-9.10	70.4 (4.55)	63.4-80.8	32.7 (2.60)	28.4-36.1	12.4 (0.45)	11.5-13.0	7.45 (0.44)	6.62-8.08
Female	6	6.78 (0.82)	5.95-8.23	70.9 (2.88)	66.7-73.6	34.0 (1.58)	32.4-36.7	12.3 (0.45)	11.5-12.7	7.28 (1.20)	5.47-7.96
Total	18	7.37 (0.93)	5.95-9.1	70.6 (3.99)	63.4-80.8	33.2 (2.30)	28.4-36.7	12.4 (0.44)	11.5-13.0	7.4 (0.69)	5.47-8.08
Ref 1			5.9-11.1		59-72		31-41		11-15		
Ref 2			7-15		70-90		25-35		11-13		
<i>S. minutus</i>											
Male	1	2.79	2.79-2.79	51.6	51.6-51.6	39.6	39.6-39.6	10.4	10.4-10.4	x	x
Female	1	2.85	2.85-2.85	49.8	49.8-49.8	40.2	40.2-40.2	10.3	10.3-10.3	x	x
Total	2	2.82 (0.04)	2.79-2.85	50.7 (1.22)	49.8-51.6	39.9 (0.37)	39.6-40.2	10.4 (0.05)	10.3-10.4	x	x
Ref 1			2.6-7		40-64		33-45		9-12		
Ref 2			2.5-5		40-60		40-46		10-11		
<i>C. russula</i>											
Male	10	8.58 (1.34)	7.18-10.95	72.6 (4.11)	63.5-76.8	40.7 (2.50)	36.0-43.8	12.8 (0.73)	11.5-13.8	7.76 (1.33)	5.46-9.83
Female	4	8.52 (2.61)	6.0-11.21	70.5 (8.98)	60.2-76.5	44.3 (3.69)	41.2-48.4	12.9 (0.25)	12.7-13.2	8.74 (0.03)	8.71-8.76
Total	14	8.57 (1.58)	6.0-11.21	72.1 (5.19)	60.2-76.8	41.7 (3.15)	36.0-48.4	12.8 (0.64)	11.5-13.8	8.01 (1.22)	5.46-9.83
Ref 1			5-16		44-86		24-47		10-14		5-11
<i>C. suaveolens</i>											
Male	20	4.49 (0.49)	3.14-5.28	61.7 (2.92)	55.1-68.4	37.4 (1.85)	33.8-40.6	11.6 (0.36)	11.0-12.3	7.38 (0.62)	5.68-8.34
Female	13	4.58 (0.63)	3.70-5.86	61.2 (3.91)	55.6-69.3	36.7 (2.27)	30.4-39.8	11.2 (0.31)	10.7-11.8	7.16 (0.75)	5.29-8.29
Total	33	4.52 (0.54)	3.14-5.86	61.5 (3.3)	55.1-69.3	37.1 (2.04)	30.4-40.6	11.5 (0.39)	10.7-12.3	7.29 (0.67)	5.29-8.34
Ref 1			6.5-9.4 (imma 4-6.5)		47-80		25-40				
Ref 2			3-11		55-70		25-35		10-12		

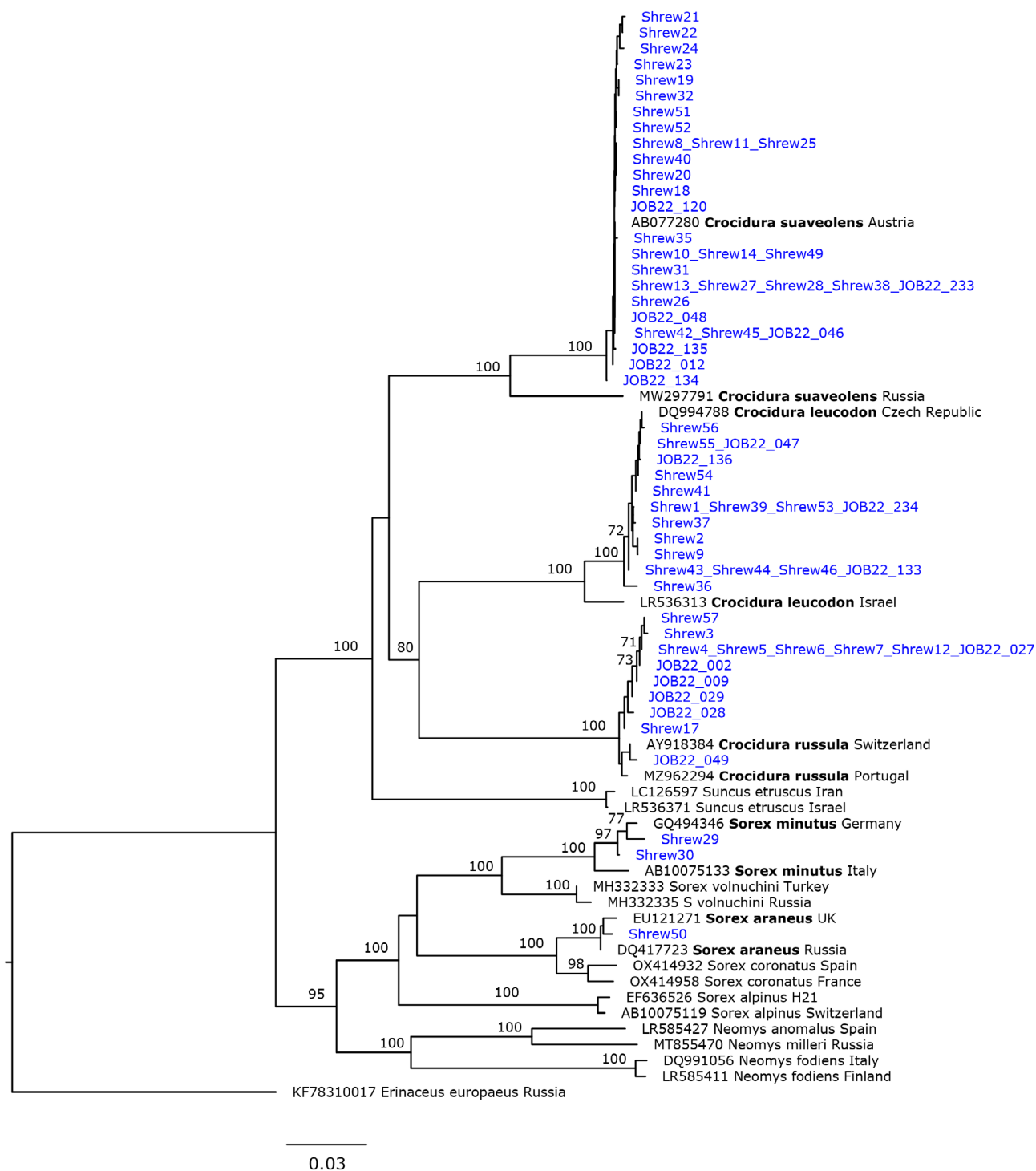


Fig. 2. Neighbor-Joining tree of cytochrome *b* sequences from shrew samples captured during the 2022 fieldwork in the westernmost part of the Czech Republic. A sequence of *Erinaceus europaeus* was used as the outgroup. The evolutionary distances were computed using the Kimura2-parameter model. Bootstrap values based on 1,000 pseudoreplicates are shown next to branches. The scale bar represents the expected number of substitutions per site under the K2P model. For GenBank sequences, the accession number and the country of origin are mentioned.

°C for 30 sec, and 72 °C for 1 min and ending with an extension step of 72 °C for 5 min. PCR products were visualised on a 1.5% agarose gel, purified, and Sanger sequenced from a single direction at Eurofins Genomics (Ebersberg, Germany) using primer L14723. Sequences were visually inspected in Geneious Prime software and trimmed to remove

low-quality bases. Sequence length varied between 851 and 1,092 nucleotides. For species identification, sequences were compared to the GenBank nucleotide database on the NCBI BLAST homepage (<https://blast.ncbi.nlm.nih.gov>) (Johnson et al. 2008). To obtain a visual representation of the identified sequences, we performed a Neighbor-Joining (Saitou & Nei 1987)

phylogenetic reconstruction in MEGAX (Kumar et al. 2018) with evolutionary distances computed using the Kimura2-parameter and 1,000 replicates for the bootstrap test. Reference sequences of sorcid species known to occur in Europe were added to the dataset for comparison, and a sequence of *E. europaeus* was used to root the tree. Identical sequences in terms of length and nucleotides were combined before phylogenetic analysis.

Results and Discussion

In total, we captured 446 small mammals. The large majority of them were rodents (84.8%), including house mice (*M. musculus*, $n = 258$; 57.8% of captures), woodmice (*Apodemus* sp., $n = 62$; 13.9%), harvest mice (*Micromys minutus*, $n = 27$; 6.1%), common voles (*Microtus arvalis*, $n = 22$; 4.9%), bank voles (*Clethrionomys glareolus*, $n = 6$; 1.3%), and brown rats (*Rattus norvegicus*, $n = 3$, 0.7%). The remaining 15.2% of the untargeted bycatch were shrews. Preliminary identifications made in the field allowed us to distinguish red-toothed shrews (*Sorex*; $n = 3$) from white-toothed shrews (*Crocidura*; $n = 65$) based on the colour of the teeth and the presence/absence of long thin hairs on the tail. *Sorex minutus* and *S. araneus* could further be distinguished based on body weight (Table 1). Among the white-toothed shrews, the bicoloured white-toothed shrew (*C. leucodon*) individuals ($n = 18$) were recognisable due to the marked dark dorso-ventral brown/white colour difference. The remaining white-toothed shrews, i.e. 47 individuals, which we suspected to be the lesser white-toothed shrew, *C. suaveolens*, had body masses ranging from 3.14 to 11.21 g, which are above the range of 4–9.4 g reported by Burgin et al. (2018) for this species but fits within the range reported by Anděra & Hanzal (2022) (see Table 1). Therefore, we could not distinguish whether these were juveniles and adults of a single species or two different species.

Shrew species are not easily identified in the field, and *cytb* barcoding is regularly used to confirm species identity (Nicolas et al. 2015, Mori et al. 2020). We used this approach to confirm our preliminary species identification. BLAST analysis showed that 54 sequences have > 99% identity with sequences of species known to occur in the Czech Republic: *S. araneus*, *S. minutus*, *C. leucodon* and *C. suaveolens* (Table S1). The remaining 14 sequences showed > 99% identity with *cytb* sequences of *C. russula*. These 14 individuals are represented by three different *cytb* haplotypes. The results can be visualised on the Neighbour-Joining tree (Fig. 2), showing that all 68

shrew samples clustered with high bootstrap support with reference sequences of five species.

The morphological characteristics of each species are summarised in Table 1. In our sampling, while there was some overlap between *C. suaveolens* and *C. russula* in head-body, tail, hindfoot and ear length measurements, there was no overlap in body mass, with the largest captured *C. suaveolens* individual weighing 5.86 g and the smallest captured *C. russula* individual weighing 6 g. Thus, of the morphological traits we used, body mass is the most reliable characteristic in our sampled individuals to distinguish the two species.

The spatial distribution of the different shrew species is shown in Fig. 1B. The 14 specimens of *C. russula* were found in five different localities covering approx. 60 km² (Table S1 and Fig. 1B), suggesting the species arrived in the Czech Republic a few years ago. The presence of *C. russula* in this country has been suspected for some time (Anděra 2010, Anděra & Hanzal 2022), but no faunistic survey has confirmed its presence in the Czech Republic. Anděra & Hanzal (2022) reviewed the facts that suggested that the presence of *C. russula* could be expected in the Czech Republic: the species is relatively common in the Dresden agglomeration (about 20 km from the border with the Czech Republic) and was found further south, less than 10 km from the borderline, on the ridges of the Ore Mountains (Krušné hory Mountains) (see also Mitchell-Jones et al. 1999). Thus, its range expansion could have been expected along the Elbe Valley between Hřensko and Děčín or in the depression below the Ore Mountains in the Kraslice region. The situation was similar in the Aš region, where *C. russula* was reported in north-eastern Bavaria (Hof and surroundings), only about 15 km from the Czech Republic border. Our study confirms that expansion via the Aš region was a good prediction.

Crocidura russula has been reported to be a competitor with resident shrew species resulting in local extinctions. This species is an invasive species in Ireland, first reported in 2007, spreading rapidly to the detriment of *S. minutus* (McDevitt et al. 2014, Browett et al. 2023). In continental Europe, *C. russula* has been reported to spread in several regions at the expense of *C. suaveolens* in Bavaria, Germany (Kraft 2000), or *C. leucodon* in Switzerland (Vogel et al. 2002) and north-western Germany (Frank 1984). In the localities where we caught at least two shrew individuals, *C. russula* was not found with other

shrew species, except in Nebanice, the easternmost *C. russula* locality, where three individuals of this species were captured together with one *C. leucodon* (Table S1). Only *C. russula* individuals were captured on the west of Nebanice. However, suggesting that *C. russula* has already displaced resident shrew species in synanthropic habitats may be premature, as this may be due to a trap-type effect, as more wooden traps, which are perhaps less suited to capturing small shrew species, were used in the west of the field sampling. More Ugglan traps, which capture a wider range of shrews, were used in the east of the sampling area. If the greater white-toothed shrew is a strong competitor leading to the exclusion of resident congeneric or confamilial species, then it is likely that the dynamics of insectivore occurrence in this part of the Czech Republic will change in the coming years, and this deserves attention, as replacement may be exacerbated by climate change (Frank 1984, Kraft 2000, Vogel et al. 2002). Moreover, such invasive mammalian species can be a vector of novel zoonotic pathogens (Nally et al. 2016). For now, the checklist of Eulipotyphla from the Czech Republic should be updated with this new record.

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Author Contributions

All authors performed the fieldwork; L. Ďureje, M. Dianat and J. Goüy de Bellocq performed morphological measurements; J. Goüy de Bellocq performed molecular work and genetic analysis and drafted the first version of the manuscript. All authors provided editorial advice and approved the final manuscript.

Data Availability Statement

Sequences were deposited to GenBank under accession numbers OQ928961–OQ929028. Tissue samples were deposited in the Genetic Bank of the Institute of Vertebrate Biology, Czech Academy of Sciences, under accession numbers IVB-M-7739–IVB-M-7806. Five carcasses were deposited in the National Museum in Prague under accession numbers NMP 97751–NMP 97755, and the others are available at the Institute of Vertebrate Biology, Research Facility Studenec.

Literature

- Anděra M. 2010: Current distributional status of insectivores in the Czech Republic (Eulipotyphla). *Lynx*, n.s. 41: 15–63.
- Anděra M. & Hanzal V. 2022: Atlas of distribution of insectivores of the Czech Republic. *Agentura ochrany přírody a krajiny ČR, Praha, Czech Republic*. (in Czech)
- Aulagnier S., Hutterer R., Kryštufek B. et al. 2021: *Crocidura russula* (amended version of 2016 assessment). The IUCN Red List of Threatened Species 2021: e.T29652A197503499. <https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T29652A197503499.en>
- Baird S.J., Ribas A., Macholán M. et al. 2012: Where are the wormy mice? A reexamination of hybrid parasitism in the European house mouse hybrid zone. *Evolution* 66: 2757–2772.
- Bond I., Gilford E., McDevitt A. et al. 2022: First records of the greater white-toothed shrew *Crocidura russula* from Great Britain. *Mammal Commun.* 8: 23–28.
- Brändli L., Handley L.J., Vogel P. & Perrin N. 2005: Evolutionary history of the greater white-toothed shrew (*Crocidura russula*) inferred from analysis of mtDNA, Y, and X chromosome markers. *Mol. Phylogenet. Evol.* 37: 832–844.
- Browett S.S., Synnott R., O'Meara D.B. et al. 2023: Resource competition drives an invasion-replacement event among shrew species on an island. *J. Anim. Ecol.* 92: 698–709.
- Burgin C.J., He K., Haslauer R. et al. 2018: Family Soricidae (Shrews). In: Wilson D.E. & Mittermeier R.A. (eds.), *Handbook of the mammals of the world*, vol. 8: insectivores, sloths and colugos. *Lynx Edicions, Barcelona, Spain*: 332–551.
- Cosson J.F., Hutterer R., Libois R. et al. 2005: Phylogeographical footprints of the Strait of Gibraltar and Quaternary climatic fluctuations in the western Mediterranean: a case study with the greater white-toothed shrew, *Crocidura russula* (Mammalia: Soricidae). *Mol. Ecol.* 14: 1151–1162.
- Cosson J.F., Pascal M. & Bioret F. 1996: Origine et répartition des musaraignes de genre *Crocidura* dans les îles bretonnes. *Vie Milieu/Life & Environment*: 233–244.
- Đureje L., Macholán M., Baird S. & Piálek J. 2012: The mouse hybrid zone in Central Europe: from morphology to molecules. *Folia Zool.* 61: 308–318.
- Frank F. 1984: Zur Arealverschiebung zwischen *Crocidura russula* und *C. leucodon* in NW-Deutschland und zum wechselseitigen Verhältnis beider Arten. *Z. Säugetierkd.* 49: 65–70.
- Goüy de Bellocq J., Baird S.J., Albrechtová J. et al. 2015: Murine cytomegalovirus is not restricted to the house mouse *Mus musculus domesticus*: prevalence and genetic diversity in the European house mouse hybrid zone. *J. Virol.* 89: 406–414.
- Goüy de Bellocq J., Ribas A., Bryja J. et al. 2018: Holobiont suture zones: parasite evidence across the European house mouse hybrid zone. *Mol. Ecol.* 27: 5214–5227.
- Johnson M., Zaretskaya I., Raytselis Y. et al. 2008: NCBI BLAST: a better web interface. *Nucleic Acids Res.* 36: W5–W9.
- Kapischke H.-J. 2009: Hausspitzmaus *Crocidura russula* (Hermann, 1780). In: Hauer S., Ansorge H. & Zöphel U. (eds.), *Atlas der Säugetiere Sachsens. Sächsischen Landesamt für Umwelt, Landwirtschaft und Geologie, Dresden, Germany*: 107–109.
- Kraft R. 2000. Ehemalige und aktuelle Verbreitung von Hausspitzmaus, *Crocidurus russula* (Hermann, 1780), und Gartenspitzmaus, *Crocidura suaveolens* (Pallas, 1811), in Bayern. *Bonn Zool. Beitr.* 49: 115–129.
- Kumar S., Stecher G., Li M. et al. 2018: MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Mol. Biol. Evol.* 35: 1547–1549.
- Lecompte É., Granjon L., Peterhans J.K. & Denys C. 2002: Cytochrome b-based phylogeny of the *Praomys* group (Rodentia, Murinae): a new African radiation? *C.R. Biol.* 325: 827–840.
- LoBrutto S., Azeuleo M. & Sarà M. 2004: Mitochondrial simple sequence repeats and 12S-rRNA gene reveal two distinct lineages of *Crocidura russula* (Mammalia, Soricidae). *Heredity* 92: 527–533.
- Macholán M., Baird S.J.E., Dufková P. et al. 2011: Assessing multilocus introgression patterns: a case study on the house mouse X chromosome in Central Europe. *Evolution* 65: 1428–1446.
- Macholán M., Baird S.J.E., Munclinger P. et al. 2008: Genetic conflict outweighs heterogametic incompatibility in the mouse hybrid zone? *BMC Evol. Biol.* 8: 271.
- Macholán M., Munclinger P., Šugerková M. et al. 2007: Genetic analysis of autosomal and X-linked markers across a mouse hybrid zone. *Evolution* 61: 746–771.
- McDevitt A.D., Montgomery W.I., Tosh D.G. et al. 2014: Invading and expanding: range dynamics and ecological consequences of the greater white-toothed shrew (*Crocidura russula*) invasion in Ireland. *PLOS ONE* 9: e100403.
- Mitchell-Jones A., Amori G., Bogdanowicz W. et al. 1999: The atlas of European mammals. *Poyser, London, UK*.

- Mori E., Brambilla M., Ramazzotti F. et al. 2020: In or out of the checklist? DNA barcoding and distribution modelling unveil a new species of *Crocidura* shrew for Italy. *Diversity* 12: 380.
- Nally J.E., Arent Z., Bayles D.O. et al. 2016: Emerging infectious disease implications of invasive mammalian species: the greater white-toothed shrew (*Crocidura russula*) is associated with a novel serovar of pathogenic *Leptospira* in Ireland. *PLOS Negl. Trop. Dis.* 10: e0005174.
- Nicolas V., Jacquet F., Stoetzel E. et al. 2015: Identification moléculaire et histoire phylogéographique et démographique des musaraignes du Maroc septentrional. Molecular identification, phylogeographic and demographic history of shrews from northern Morocco. *Travaux de l'Institut Scientifique Série Générale* 8: 141–150.
- QGIS.org 2023: QGIS Geographic Information System. QGIS Association. <http://www.qgis.org>
- Saitou N. & Nei M. 1987: The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* 4: 406–425.
- Tosh D.G., Lusby J., Montgomery W.I. & O'Halloran J. 2008: First record of greater white-toothed shrew *Crocidura russula* in Ireland. *Mammal Rev.* 38: 321–326.
- Vogel P., Cosson J.-F. & López Jurado L.F. 2003: Taxonomic status and origin of the shrews (Soricidae) from the Canary islands inferred from a mtDNA comparison with the European *Crocidura* species. *Mol. Phylogenet. Evol.* 27: 271–282.
- Vogel P., Jutzeler S., Rulence B. & Reutter B. 2002: Range expansion of the greater white-toothed shrew *Crocidura russula* in Switzerland results in local extinction of the bicoloured white-toothed shrew *C. leucodon*. *Acta Theriol.* 47: 15–24.

Supplementary online material

Table S1. Data on localities, genotyping, individual characteristics and accession numbers of the shrew samples (<https://www.ivb.cz/wp-content/uploads/JVB-72-2023-Gouy-De-Bellocq-et-al.-Table-S1.pdf>).