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Extinct or just overlooked – does the Northern white-breasted hedgehog *Erinaceus roumanicus* occur in Germany?

(Mammalia, Erinaceidae)

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The European hedgehog (*Erinaceus europaeus*) and the Northern white-breasted hedgehog (*E. roumanicus*) are the only members of their genus occurring in Central Europe. The two morphologically cryptic species are distributed parapatrically, overlapping in two contact zones with limited areas of sympatry. The Central European contact zone largely coincides with the Eastern border of Germany to Poland, the Czech Republic, and Austria, but only *E. europaeus* is widespread and common in Germany. *Erinaceus roumanicus*, on the other hand, has been presumed extinct from Germany since the end of World War II, though without obvious reasons. This study uses DNA-based species identification of mostly road-killed hedgehogs collected from two states along the Eastern border of Germany, Bavaria and Brandenburg, to test for the presence of *E. roumanicus*. The mitochondrial D-loop marker was sequenced and used to identify 39 samples. Six different haplotypes of *E. europaeus* in eastern Bavaria and one widespread haplotype in eastern Brandenburg were identified, but no *E. roumanicus* was present in our sampling. Our results suggest the general assumption that *E. roumanicus* has become extinct in Germany, although our sampling may have been insufficient to detect any relict populations of *E. roumanicus* among the widespread *E. europaeus* populations. Further targeted surveying for *E. roumanicus* is needed to clarify its continuous presence in Eastern Germany. Potential hotspots for its rediscovery might be in areas where natural distribution barriers are permeable, for example, along low elevation passes across the mountains of the Bavarian Forest or in the valley of the river Elbe, where it traverses the Elbe Sandstone Mountains.

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Introduction

Central Europe is inhabited by two closely related hedgehog species of the genus *Erinaceus* – the European hedgehog (*Erinaceus europaeus* Linnaeus, 1758) and the Northern white-breasted hedgehog (*E. roumanicus* Barrett-Hamilton, 1900). After first being described as a subspecies of *E. europaeus* by Barrett-Hamilton (1900), *E. roumanicus* was considered a subspecies of the Southern white-breasted hedgehog (*E. concolor* Martin, 1838) until ca. 20 years ago (Mitchell-Jones et al. 1999), but it was elevated to species status based on morphological and molecular evidence (Holz 1978, Santucci et al. 1998, Suchentrunk et al. 1998, Seddon et al. 2001, Kryštufek 2006).

The distribution of *E. europaeus* and *E. roumanicus* is largely parapatric, currently overlapping in two contact zones: one in Central Europe including Poland, the Czech Republic, Austria, and Italy and the other in Northeastern Europe including Latvia, Estonia, and Eastern Russia to the Ural mountains (Mitchell-Jones et al. 1999, Hutterer 2005). Successful crosses of the two species have been achieved in captivity (Herter 1935, Poduschka & Poduschka 1983). However, strong evidence for ongoing introgressive hybridization is currently known for wild populations only within the eastern contact zone (Bogdanov et al. 2009, Zolotareva et al. 2020). While a small number of potential hybrid individuals have been detected in the central contact zone (Bolfíková et al. 2017, Curto et al. 2019), there is not enough evidence to confirm that natural interspecies hybridization is occurring, which suggests that reproductive isolating mechanisms have formed and the two species exist there largely in sympatry (Suchentrunk et al. 1998, Bolfíková & Hulva 2011). Compared to the

Table 1. Sample ID, species identity, localities and GenBank accession numbers for all hedgehog specimens included in this study.

Sample ID	Species	Locality / Country	Latitude	Longitude	Accession No.	Haplotype
5	*Erinaceus europaeus*	Passau, BY, Germany	48.56387	13.45290	MW497258	H1
82	*E. europaeus*	Furth im Wald, BY, Germany	49.31343	12.84423	MW497259	H1
26	*E. europaeus*	Cham, BY, Germany	49.20757	12.63841	MW497260	H1
60	*E. europaeus*	Cham, BY, Germany	49.16490	12.80569	MW497261	H1
62	*E. europaeus*	Cham, BY, Germany	49.20229	12.93116	MW497262	H1
64	*E. europaeus*	Arrach, BY, Germany	49.19697	12.97583	MW497263	H1
72	*E. europaeus*	Cham, BY, Germany	49.20757	12.63841	MW497264	H1
74	*E. europaeus*	Hohenwarth, BY, Germany	49.19934	12.93134	MW497265	H1
77	*E. europaeus*	Cham, BY, Germany	49.23247	12.77457	MW497266	H1
78	*E. europaeus*	Rimbach, BY, Germany	49.21480	12.89170	MW497267	H1
79	*E. europaeus*	Hohenwarth, BY, Germany	49.20870	12.92327	MW497268	H1
61	*E. europaeus*	Eschlkam, BY, Germany	49.27058	12.93256	MW497269	H3
63	*E. europaeus*	Cham, BY, Germany	49.24507	12.65158	MW497270	H3
65	*E. europaeus*	Hohenwarth, BY, Germany	49.20149	12.92061	MW497271	H3
66	*E. europaeus*	Hohenwarth, BY, Germany	49.20979	12.91426	MW497272	H3
70	*E. europaeus*	Arnschwang, BY, Germany	49.26143	12.80585	MW497273	H3
75	*E. europaeus*	Rimbach, BY, Germany	49.22905	12.87850	MW497274	H3
71	*E. europaeus*	Rimbach, BY, Germany	49.23191	12.86061	MW497275	H4
84	*E. europaeus*	Bad Kötzting, BY, Germany	49.18723	12.85761	MW497276	H4
30	*E. europaeus*	Kirchdorf am Inn, BY, Germany	48.24616	12.97267	MW497277	H6
32	*E. europaeus*	Simbach am Inn, BY, Germany	48.26118	13.03263	MW497278	H5
67	*E. europaeus*	Cham, BY, Germany	49.16407	12.68081	MW497279	H2
68	*E. europaeus*	Cham, BY, Germany	49.21870	12.77351	MW497280	H2
69	*E. europaeus*	Cham, BY, Germany	49.14693	12.68701	MW497281	H2
76	*E. europaeus*	Hohenwarth, BY, Germany	49.20526	12.92559	MW497282	H2
23	*E. europaeus*	Passau, BY, Germany	48.58465	13.40413	MW497283	H1
24	*E. europaeus*	Passau, BY, Germany	48.59712	13.78480	MW497284	H1
29	*E. europaeus*	Simbach am Inn, BY, Germany	48.27353	13.03801	MW497285	H1
38a	*E. europaeus*	Falkenberg, BB, Germany	52.77917	13.90554	MW497286	H2
41	*E. europaeus*	Cham, BY, Germany	49.24485	12.67085	MW497287	H3
9a	*E. europaeus*	Wreizen, BB, Germany	52.70177	14.11615	MW497288	H2

Eastern European contact zone, the phylogeography of *E. europaeus* and *E. roumanicus* in the Central European contact zone has been widely studied (e.g., Herter 1934, Santucci et al. 1998, Seddon et al. 2001). Still, whether the western-most distribution of *E. roumanicus* extends beyond the current eastern political border of Germany, both historically and currently, remains unclear.

For several years, *E. roumanicus* was widely assumed to inhabit the entire eastern border region of Germany (Herter 1934, Angermann 1974, Ansorge 1987). In the former German Democratic Republic (DDR), the White-breasted hedgehog was protected as rare species ("geschützte seltene Tierart") but, nevertheless, the species has not been reliably recorded in Germany since the end of World War II (Ansorge 1987). In the Red List of endangered vertebrates in Germany, Nowak et al. (1994) considered the White-breasted hedgehog (then under the species name *E. concolor*) as one of ten extinct mammal species in Germany, speculating that the species might have become extinct at the beginning of the 20th century. Meinig et al. (2009, 2020) listed the species as extinct in Germany sometime before 1945. These assessments are based on the absence of reliable records of *E. roumanicus* from Germany in recent decades, emphasizing the poor knowledge about this species in the country.

Herter (1934) recorded several localities of the Northern white-breasted hedgehog within the current borders of the German state of Brandenburg (BB), including Berlin (an enclave within Brandenburg) and the regions of Oderbruch and Hasenfelde, close to the border with Poland. These specimens, assumed initially to be *E. concolor*, were later identified as *E. roumanicus*, endorsing that both species

Table 1. (continued)

Sample ID	Species	Locality / Country	Latitude	Longitude	Accession No.	Haplotype
34a	*E. europaeus*	Falkenberg, BB, Germany	52.77917	13.90554	MW497289	H2
33	*E. europaeus*	Falkenberg, BB, Germany	52.77917	13.90554	MW497290	H2
7a	*E. europaeus*	Forst, BB, Germany	51.72372	14.58177	MW497291	H2
5a	*E. europaeus*	Wiesenau, BB, Germany	52.22698	14.59570	MW497292	H2
10a	*E. europaeus*	Erkrath, NRW, Germany	51.20667	6.94473	MW497293	H2
6a	*E. europaeus*	Falkenhagen, BB, Germany	52.40868	14.29333	MW497294	H2
2a	*E. europaeus*	Lietzen, BB, Germany	52.47295	14.34387	MW497295	H2
3a	*E. europaeus*	Neutrebbin, BB, Germany	52.65585	14.28749	MW497296	H2
MK510251	*E. europaeus*	Alicante, Spain	–	–	MK510251	–
MK510245	*E. europaeus*	Algarve, Portugal	–	–	MK510245	–
MK510244	*E. europaeus*	Alentejo, Portugal	–	–	MK510244	–
MK510239	*E. europaeus*	Castilla-Leon, Spain	–	–	MK510239	–
MK510229	*E. europaeus*	Minho, Portugal	–	–	MK510229	–
MK510227	*E. europaeus*	Douro Litoral, Portugal	–	–	MK510227	–
AF379715	*E. roumanicus*	Austria	–	–	AF379715	–
AF379736	*E. roumanicus*	France	–	–	AF379736	–
AF379712	*E. roumanicus*	Netherlands	–	–	AF379712	–
AF379735	*E. roumanicus*	Switzerland	–	–	AF379735	–
MK510249	*E. roumanicus*	Olympus, Greece	–	–	MK510249	–
MK510248	*E. roumanicus*	Kedriki Makedhonia, Greece	–	–	MK510248	–
MK510247	*E. roumanicus*	Kedriki Makedhonia, Greece	–	–	MK510247	–
KY366260	*E. roumanicus*	Macedonia	–	–	KY366260	–
KY366259	*E. roumanicus*	Balkans	–	–	KY366259	–
KY366255	*E. roumanicus*	Serbia	–	–	KY366255	–
KY366254	*E. roumanicus*	Serbia	–	–	KY366254	–
KY366253	*E. roumanicus*	Serbia	–	–	KY366253	–
KY366249	*E. roumanicus*	Montenegro	–	–	KY366249	–
KY366248	*E. roumanicus*	Montenegro	–	–	KY366248	–
MK510246	*E. concolor*	Caucaso, Armenia	–	–	MK510246	–
MK510241	*E. concolor*	Firat, Turkey	–	–	MK510241	–
MK510318	*Atelerix algirus*	Oujda, Morocco	–	–	MK510318	–

of European hedgehog were present at some point in Brandenburg (Herter 1934, Ansorge 1987). From the northern-most German state along the contact zone of the two species, Mecklenburg-Vorpommern (MV), a single historical record of *E. roumanicus* was reported from the island Usedom (Herold 1934). Labes et al. (1991) has since listed *E. roumanicus* as extinct in MV, citing competition with *E. europaeus* as a potential cause. Herold (1939) reported two historic observations of hedgehogs that resembled *E. roumanicus* near Mittelsohland in the eastern upper Lusatia region of Saxony (SY). However, the records are questionable given ontogenic variability in the breast fur coloration of *E. europaeus.* Thus, there is no current verifiable evidence of the White-breasted hedgehog from Saxony (Ansorge 1987, Hauer 2009).

Meinig et al. (2009) questioned whether *E. roumanicus* has ever occurred in autochthonous populations in Germany and speculated that existing records might be partly or entirely based on introduced individuals, as was already suggested by Ansorge (1987) and Herter (1934). In particular, two isolated records of *E. roumanicus*-type hedgehogs that were found near Berlin (Herter 1934, Ansorge 1987) and Munich in Bavaria (BY) (Nowak 1975) were believed to be introduced based on their distance from the eastern German border. It is also possible that these historical, isolated records of *E. roumanicus* in Eastern Germany were simply misidentifications. A recent genetic study of hedgehog populations in Berlin and its suburbs detected no *E. roumanicus* among 143 *E. europaeus* samples (Barthel et al. 2020) but confirmed that the Central European contact zone extends close to Germany. Several confirmed populations of *E. roumanicus* approach the border with Bavaria and Saxony, including those in the Eferdinger Becken west of Linz in Austria, ca. 30 km from the German border (Blumenschein 2007), and records in the Czech Republic less than 15 km from the German border (Kratochvíl 1966, Anděra 2010, Bolfíková & Hulva 2011).

Currently, few researchers, conservationists, and naturalists seem to be aware of the possible existence of two hedgehog species in Germany. Hedgehogs can be immediately recognized as members of the genus *Erinaceus*, but most conservationists are not aware that the contact zone of two hedgehog species is situated close to the eastern borders of Germany. Additionally, the study of *E. europaeus* and *E. roumanicus* is complicated due to the fact that the two species do not voluntarily show their diagnostic ventral coloration when encountered and instead retract themselves into a 'ball of spines'. Furthermore, the two species often cannot be easily distinguished by external morphological characteristics alone, making identification in the field unreliable. Thus, the presence of *E. roumanicus* in Germany may have been overlooked, especially given that distinguishing between the two species is rather difficult in the field, and researchers may not even know about the existence of an additional hedgehog species along the eastern border.

The aim of this study is to test for individuals of *E. roumanicus* in hedgehog samples collected in Eastern Bavaria and Brandenburg near the Central European contact zone. Older studies used a combination of morphological characters, including skull morphology, number of spines, and the colour of the breast to distinguish the species (Ruprecht 1972, Kratochvíl 1974, Holz 1978, Zaitsev 1982, Zaitsev 1984). However, many diagnostic traits vary within the species and interspecific overlap is present, making morphology-based species identification difficult, especially in zones of sympatry. For example, Bolfíková et al. (2020) found the skull morphology of the *E. roumanicus* and *E. europaeus* individuals to be more similar within the Central European contact zone than those living outside the contact zone. More recent investigations into nuclear and mitochondrial DNA polymorphisms (Bannikova et al. 1995, Bannikova et al. 2003, Santucci et al. 1998, Seddon et al. 2001, Berggren et al. 2005, Bolfíková & Hulva 2011, Bolfíková et al. 2017, Curto et al. 2019) revealed that the two species are genetically divergent and, thus, easily distinguished when in sympatry using molecular data. In this study, we use molecular sequencing data (Sanger) isolated from the mitochondrial D-loop coding region to identify hedgehog samples collected mostly as road kill (and on which morphological identification would be difficult if not impossible in many cases). Information on the continued presence of *E. roumanicus* in Germany would not only contribute to a more accurate understanding of mammalian diversity in this country but also impact the population monitoring and conservation management of both *E. europaeus* and *E. roumanicus* populations in Germany.

Materials and methods

Our sampling included DNA from a total of 52 mostly road-killed hedgehogs collected in eastern Bavaria by the Landesbund für Vogelschutz e. V. (LBV) and in Brandenburg by F., K., and T. Glaw. A single sample from North Rhine-Westphalia was also collected.

We extracted total genomic DNA from tissue and hair samples using the DNeasy Blood & Tissue Kit (QIAGEN, Hilden, Germany), following the manufacturer's protocol. We sequenced the D-loop region in-

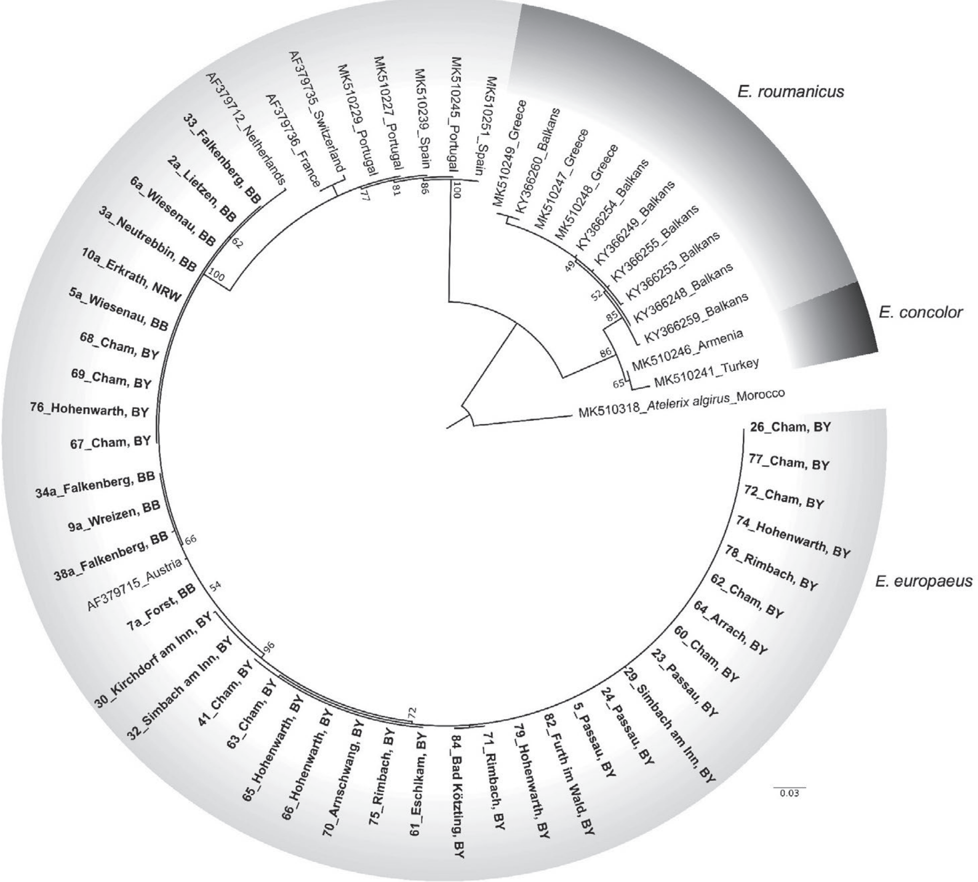

Fig. 1. Maximum Likelihood tree of hedgehogs (*Erinaceus*), including newly sequenced samples (highlighted in bold) and sequences retrieved from GenBank. Node values indicate ultrafast bootstrap support. Tree figure was edited using FigTree v1.4.4 (Rambaut 2018). Acronyms after sample numbers include the region of origin within Germany: BB = Brandenburg, BY = Bavaria, NRW = North Rhine-Westphalia.

stead of the standard marker for DNA barcoding, Cytochrome C Oxidase I (COI; Hebert et al. 2003), because D-loop provided better results and more sequence data of this marker are available for hedgehogs in databases (Bolfíková & Hulva 2011). The primers ProL-He (5′-ATACTCCTACCATCAACACCCAAAG-3′) and DLH-He (5′-GTCCTGAAGAAAGAACCAGATGTC-3′) were used to isolate the 430 bp mitochondrial D-loop coding region (Seddon et al. 2001).

PCR was performed with initial denaturation for 3 min at 94 °C, followed by 35 cycles of 30 s denaturation at 94 °C, 30 s annealing at 60 °C, 60 s elongation at 72 °C, and a final elongation step of 10 min at 72 °C. We then purified the PCR products using MagSi-NGSPREP plus beads according to the manufacture's protocol. Sequencing was conducted using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) on ABI 3730 and ABI 3130 xl capillary sequencers (Life Technologies) at the Ludwig-Maximilians-Universität sequencing center in Munich, Germany.

The D-loop sequences were assembled, quality-controlled, and edited using Geneious v8.0.5 (Kearse et al. 2012). DNA sequence data produced in this study are available under GenBank accession numbers MW497258 to MW497296. In order to identify the new hedgehog specimens from Bavaria and Brandenburg, we included D-loop sequences of known *E. roumanicus*, *E. europaeus*, and *E. concolor* retrieved from GenBank in our analyses (Table 1). An additional sequence of the North African hedgehog *Atelerix algirus* (Lereboullet, 1842) from GenBank was included as an outgroup. All hedgehog sequences were aligned in MEGA X v10.1.7 (Kumar et al. 2018). We constructed a phylogenetic tree using a Maximum Likelihood (ML) approach in W-IQ-TREE (Trifinopoulos et al. 2016), which implemented the ModelFinder function (Kalyaanamoorthy et al. 2017)

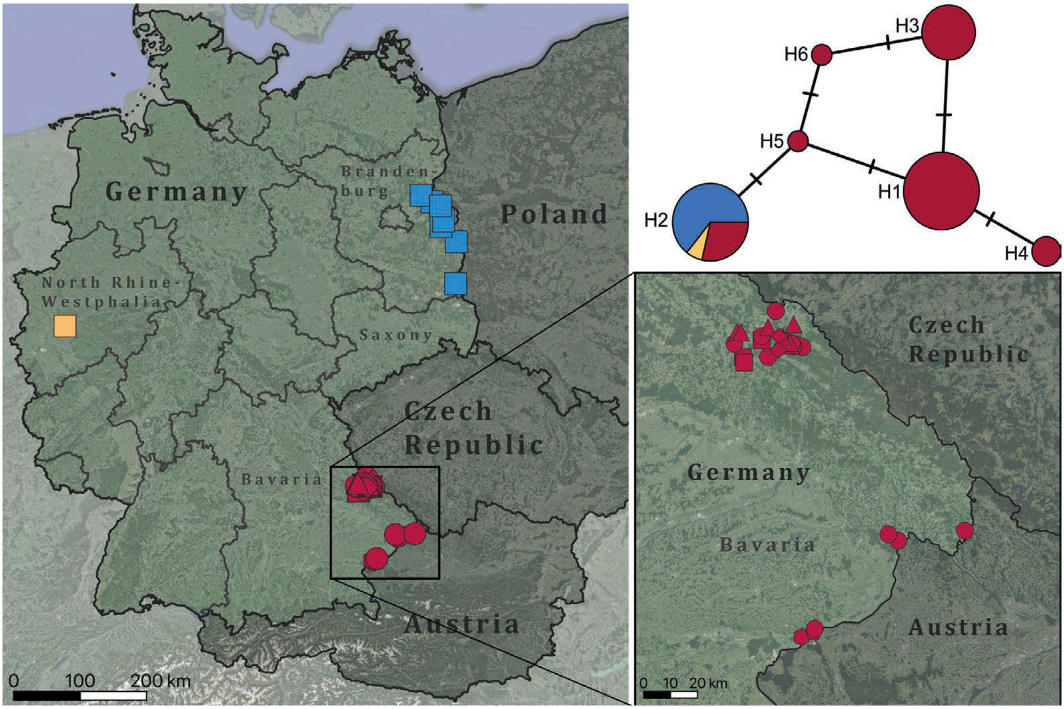

Fig. 2. Haplotype network (TCS network) of the German *Erinaceus europaeus* samples and maps showing locations of individuals sampled in North Rhine-Westphalia (●), Brandenburg (●) and Bavaria (●). Shapes correspond to haplotypes and colours indicate the German states that the hedgehogs were sampled from. Map created in QGIS v3.4.15 (QGIS Development Team 2020). Haplotypes: ● H1; ■ H2; ▲ H3; ◆ H4; ⬟ H5; ⬢ H6.

to determine the best-fitting model for the data. Ultrafast bootstrap approximation (Hoang et al. 2017) with 1000 bootstrap replicates was used to assess branch support. Finally, we created a TCS haplotype network (Clement et al. 2002) of the *E. europaeus* specimens from Bavaria, Brandenburg and North Rhine-Westphalia using PopART (Leigh & Bryant 2015).

Results

We obtained quality sequences from 39 out of 52 total samples and removed the poor-quality sequences from subsequent analysis. According to the well-supported molecular phylogeny (Fig. 1), all high-quality sequences from eastern border regions of Bavaria and Brandenburg clearly cluster together with the previously identified sequences of *E. europaeus*. Since there is a significant molecular divergence between *E. europaeus* and *E. roumanicus*, we are confident that none of the 39 hedgehog samples from Bavaria and Brandenburg included in the analyses belong to *E. roumanicus*, although our approach is unable to detect mitochondrial introgression. According to the TCS network (Fig. 2), we identified six *E. europaeus* haplotypes present in the Eastern German hedgehog samples. All the northern specimens collected in Brandenburg share the haplotype (H2) with the single specimen collected in North Rhine-Westphalia and four specimens from Bavaria. Six haplotypes are present in the Bavarian *E. europaeus* population alone. Two haplotypes in particular (H1 and H2) were most prevalent in the hedgehogs sampled. Haplotypes differ in a maximum of only two mutation steps (Fig. 2).

Discussion

The nine individuals of the European hedgehog *E. europaeus* sampled in Brandenburg all shared a single haplotype, whereas we found six haplotypes in the 29 individuals from Bavaria. Overall, the variation among haplotypes was found to be very limited with a maximum of two mutational steps. Given the limited sample size and restricted geographic sampling along the political borders, no further conclusions on migration or biogeography are justified.

No individuals of the Northern white-breasted hedgehog were present in the German hedgehog samples analysed in this study. Although several observations of *E. roumanicus* were historically recorded along the eastern border region (Herold 1934, Herter 1934, Herold 1939), the results of our opportunistic surveying in Brandenburg and Bavaria support the claim that no verifiable evidence of *E. roumanicus* in Germany remains after the morphologically confirmed records of Herter (1934). This result could be interpreted as a confirmation of the prevailing assumption that *E. roumanicus* has become extinct in Germany (Nowak et al. 1994, Meinig et al. 2009, 2020). However, our data are insufficient to make any confident assumptions regarding the current status of *E. roumanicus* in Germany based on our data since a much denser sampling along the eastern German border would be necessary to exclude the existence of *E. roumanicus* populations with any certainty.

The political border of Eastern Germany often follows natural geographical barriers such as the Oder River, the Ore Mountains (Erzgebirge) in Saxony, and the Bavarian Forest. Given the observations that *E. roumanicus* prefers lower altitudes (Bauer 1976) and large rivers have been known to function as boundaries between subpopulations (Bolfíková & Hulva 2011), potential hotspots for the rediscovery of *E. roumanicus* might be in areas where these natural barriers are permeable. For instance, corridors along low elevation passes across the mountains of the Bavarian forest or in the valleys of the rivers Elbe, Danube, Flöha, and Bahra might represent part of the boundary between the two species (Naturschutzinstitut Freiberg 2003).

Even though we did not find any *E. roumanicus* among the road-killed hedgehogs opportunistically sampled in this study, our results provide valuable biodiversity data on the fauna of Eastern Germany and additional support for the known distribution ranges of European hedgehogs.

We also reiterate the usefulness of DNA-based species identification as a reliable tool to quickly identify cryptic mammal species without relying on morphological features, useful when specimens are incomplete, damaged, or hard to identify by morphological features alone, such as the road-killed hedgehog individuals from this study. Future research and monitoring on the Central European contact zone should entail continued thorough morphological and molecular surveying for *E. roumanicus* in the eastern border states of Germany. A completed inventory of the extant hedgehog species in Germany is not only of faunistic and biogeographical interest, e. g., to identify distribution range limits, but it is also essential for conservation management and monitoring of European hedgehogs.

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