

# Biology and origin of isolated north-easternmost populations of the common wall lizard, *Podarcis muralis*

Krzysztof Kolenda<sup>1,\*</sup>, Tomasz Skawiński<sup>2,\*\*\*</sup>, Tomasz Majtyka<sup>1</sup>, Monika Majtyka<sup>3</sup>,  
Natalia Kuśmierk<sup>4,\*\*\*\*</sup>, Agata Starzecka<sup>5</sup>, Daniel Jablonski<sup>6,\*\*\*\*\*</sup>

**Abstract.** The common wall lizard, *Podarcis muralis*, is a widely distributed European lizard which has been often introduced across the continent, including north of the continuous species range. Three such populations were recently discovered in the Strzelin Hills in Poland, but no information is available about their origin. We studied the morphological variation, demographic structure and ecology of these populations, as well as their possible origin based on cytochrome *b* mtDNA sequences. Between 2011 and 2019, the lizards were annually active from the first half of March to mid-October. Males attained significantly larger snout-vent length than females and had relatively larger heads. Almost half of all captured individuals exhibited at least one pileus scale anomaly. Analysis of colour polymorphism revealed the occurrence of three morphs: white, white-red and red. The oldest lizards reached the age of 8 years. These parameters of Polish populations do not deviate from those of other populations from similar latitudes. Molecular analysis revealed that they belong to the most common haplotype of Central European haplogroup I of the Central Balkan clade. This haplotype is widely distributed across the Czech Republic and Slovakia; however, genetic data do not allow determination of the exact origin of the Polish population. Human-mediated introduction from the closest localities, the Czech Republic or Slovakia, is probable but the relict status cannot at present be excluded.

**Keywords:** introduction, mtDNA, phylogeography, Poland, relict, thermophilic lizards.

## Introduction

The common wall lizard, *Podarcis muralis*, is one of the most widely distributed European lizards. It occurs across almost the entire south

of Europe, from Spain in the west to Bulgaria and Turkey in the east (Böhme et al., 2009; Sillero et al., 2014). Its distribution in the more northern parts of Europe is usually restricted to isolated populations, which are often introduced (e.g. Schulte et al., 2011; Jablonski et al., 2019). Because *P. muralis* is a xerothermic species associated mostly with the Mediterranean, its discovery in Poland (north of the Sudetes and Carpathians) was unexpected. Initially, Wirga and Majtyka (2013) described two breeding populations living in quarries (discovered in Strzelin in 2011 and in Przeworno in 2013) in the Strzelin Hills, Lower Silesia. Soon after, in 2014, a third quarry in the same region (Gęsiniec near Strzelin), was also identified as being inhabited by these lizards (Wirga and Majtyka, 2015a). These populations were initially considered to be introduced (Wirga and Majtyka, 2013, 2015a).

*Podarcis muralis* were introduced in numerous localities in Europe and North America (e.g. Allan, Prelypchan and Gregory, 2006; Schulte et al., 2011; Michaelides et al., 2015b), so the

- 1 - Amphibian Biology Group, Department of Evolutionary Biology and Conservation of Vertebrates, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland
- 2 - Department of Evolutionary Biology and Conservation of Vertebrates, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland
- 3 - Department of Gynaecology and Obstetrics, Wrocław Medical University, Bartla 5, 51-618 Wrocław, Poland
- 4 - Department of Parasitology, Institute of Genetics and Microbiology, University of Wrocław, Przybyszewskiego 63, 51-148 Wrocław, Poland
- 5 - Stawowa 11, 43-400 Cieszyn, Poland
- 6 - Department of Zoology, Comenius University in Bratislava, Mlynská dolina, Ilkovičova 6, 842 15 Bratislava, Slovakia

\*Corresponding author;

e-mail: krzysztof.kolenda@uwr.edu.pl

\*\*ORCID: <https://orcid.org/0000-0001-8683-9867>

\*\*\*ORCID: <https://orcid.org/0000-0002-1163-9366>

\*\*\*\*ORCID: <https://orcid.org/0000-0002-8213-7371>

\*\*\*\*\*ORCID: <https://orcid.org/0000-0002-5394-0114>

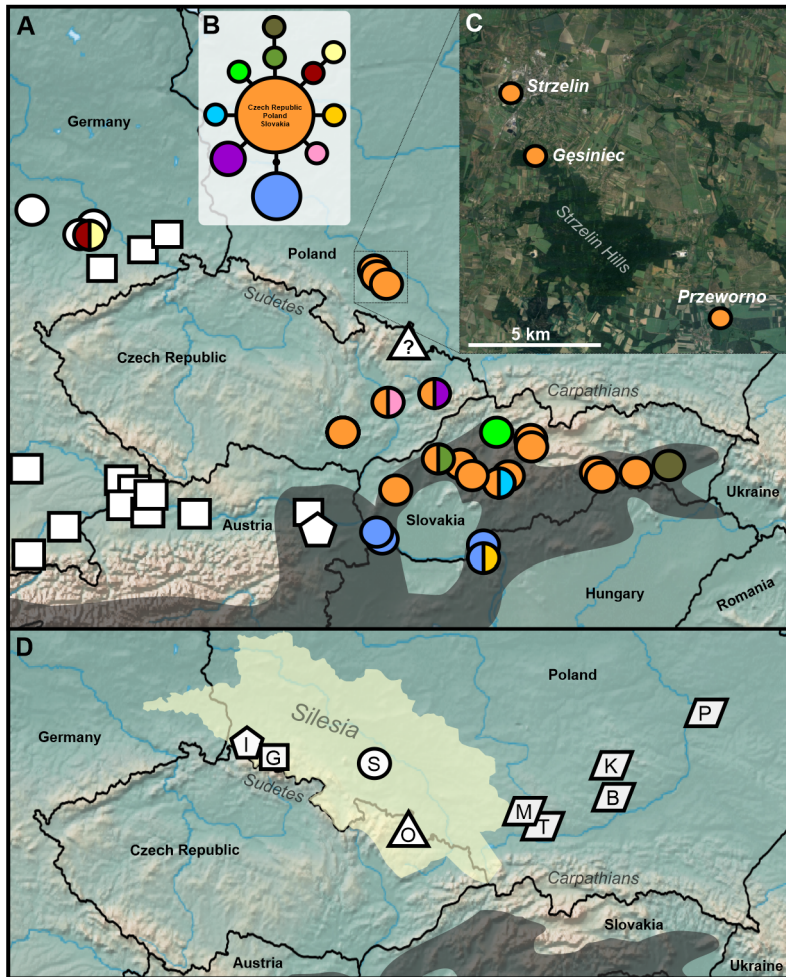
interpretation of *P. muralis* as introduced in Poland has been widely accepted (e.g. Sura, 2018). However, isolated populations located northerly to the continuous species range may represent relicts of a previously much larger Holocene range. Several European species of reptiles exhibited distributions reaching much farther north during the Holocene climatic optimum, ca. 9000 to 5000 years ago, and some relict northern populations still persist (e.g. in *Emys orbicularis*, *Lacerta viridis*, *Natrix tessellata*, *Zamenis longissimus*; Joger et al., 2010; Musilová et al., 2010; Marzahn et al., 2016). Therefore, the genetic evaluation of the origin and status of Polish populations of *P. muralis* is needed. It is also important to note that isolated (either relict or introduced) populations can differ significantly from ‘typical’ members of their species. *Podarcis* lizards, in particular, have a high potential for rapid ecological and behavioural adaptations to their environments, sometimes even developing unique morphologies (e.g. Herrel et al., 2008). *Podarcis muralis* is a highly variable species, showing great variation in morphology, ecology or longevity (e.g. Castanet and Roche, 1981; Bruner and Costantini, 2007; Pellitteri-Rosa, 2010; Eroğlu et al., 2018). For example, southern populations often inhabit humid or forest habitats, while northern populations occur in very dry, mostly rocky habitats (e.g. Böhme et al., 2009). We studied the biology and genetics of currently known *P. muralis* populations from Poland and compared our results with data on other Central European *P. muralis* populations. Previously published morphological and phenological data on two Polish populations (from Strzelin and Przeworno) of *P. muralis* were based on a relatively small sample (Wirga and Majtyka, 2013). Therefore, we provide more detailed information on the morphological variation, demographic structure and ecology of Polish populations of *P. muralis*, which are among the most northerly located. Such northern populations

can provide us important information about different (morphological, behavioural, physiological) adaptations to relatively cold climates and thus, studies of such populations are needed.

## Material and methods

### Study area

The Strzelin Hills are located in Lower Silesia region in the Sudetes Foothills (south-western Poland). Average altitude is 180–220 m a.s.l. with Gromnik (393 m a.s.l.) being the highest peak. This microregion varies between 4–8 km from west to east and about 17 km from north to south. The area is characterised by a mosaic of forests, mainly beech (*Fagus*) and oak (*Quercus*), arable fields and several abandoned or working open mines. The biggest town is Strzelin with an area of 10 km<sup>2</sup> and a population of almost 17 000 inhabitants. Mean annual temperature and mean annual precipitation reach 8.3°C and 563 mm, respectively. This area is characterised by the following climatic parameters (sensu Wirga and Majtyka, 2015b, with calculations based on data provided by Haylock et al., 2008): in summer no sub-zero temperatures are recorded (FD\_1 = 0); growing season length in autumn (GSL\_j) and spring (GSL\_w) lasts an average of 71 and 64 days, respectively; ice days in winter (ID\_z) are recorded at 24.5 days, summer days in summer (SU\_1) occur for 30.5 days; the minimum temperature in summer (TN\_1) is on average 11.18°C and the maximum temperature in summer (TX\_1) is 22.93°C; the minimum temperature in winter (TN\_z) and the maximum temperature in winter (TX\_z) are –3.88°C and 2.36°C, respectively. *Podarcis muralis* occur in three quarries (fig. 1A, C). Strzelin is an exploited granite quarry with a total area of ca. 82 ha. The extraction of raw material began in the thirteenth century; however, work on an industrial scale began around the mid-nineteenth century. *Podarcis muralis* occur in the north-eastern part of the quarry, mostly in a non-exploited area covered by grass, isolated trees and mounds of stones (fig. 2A, B). Gęsiniec is a granite quarry abandoned in 2010, with a total area of ca. 9.3 ha. The increased exploitation of the quarry probably started around the mid-nineteenth century. Currently, more than half of its surface is flooded with water. *Podarcis muralis* occur in the north-eastern part of the quarry, mainly on vertical walls and rock dumps (fig. 2C, D). Przeworno is a marble quarry abandoned in the mid-1990s, covering an area of ca. 2.4 ha. Marble was mined there since the beginning of the nineteenth century. Much of the quarry is currently flooded with water. Until spring 2019, this site was gradually overgrowing, until the east and north-west walls were re-exposed by cutting down the trees and shrubs and a general clean up by the new owner, who is currently building a diving centre there. *Podarcis muralis* inhabit part of the eastern slopes of the quarry and a small mound of stones situated between its eastern edge and a rapeseed field (fig. 2E, F). Strzelin and Przeworno are about 13 km apart. Gęsiniec is situated between them, 3 km south of Strzelin and 10 km north-west of Przeworno (fig. 1C).



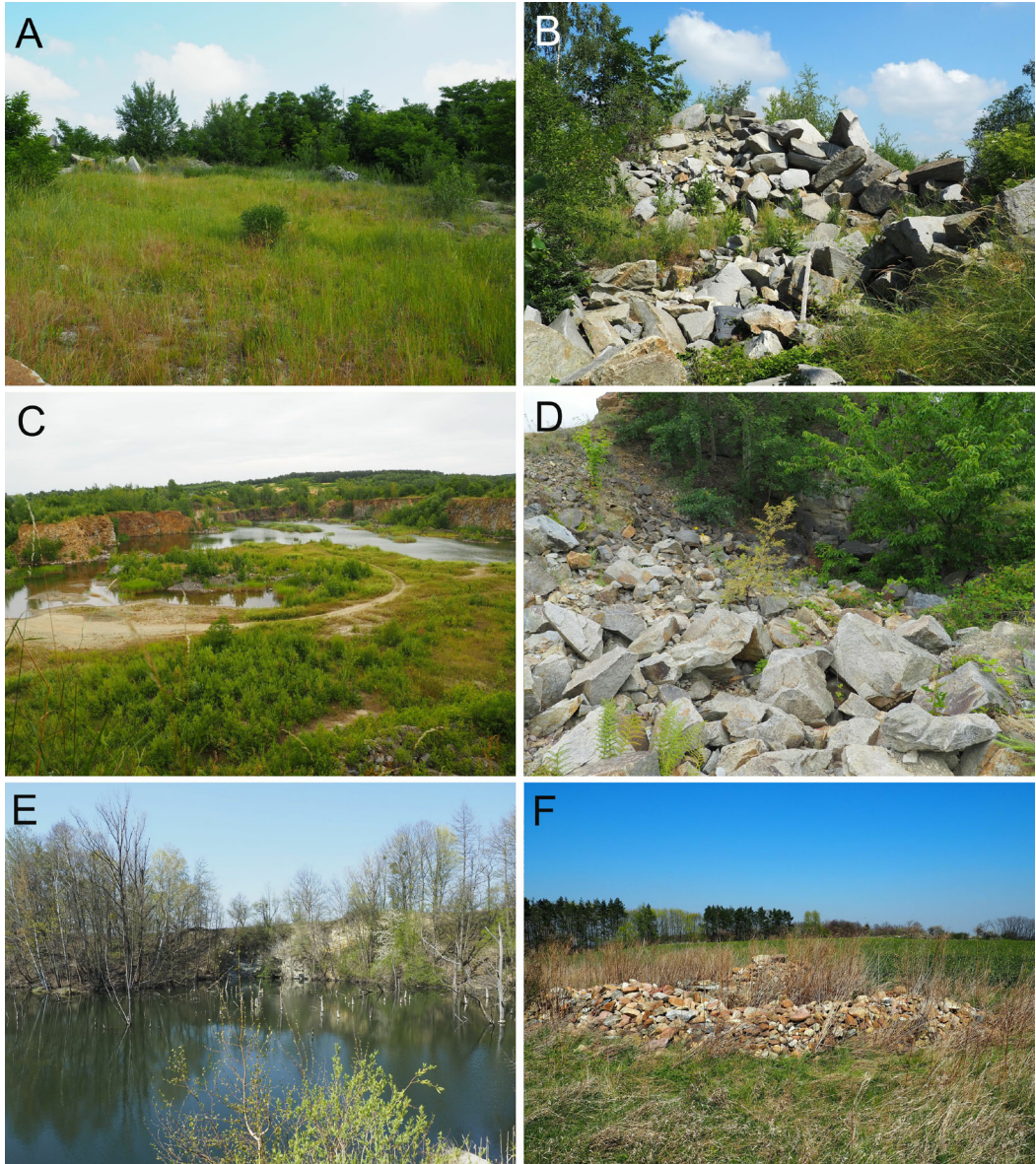
**Figure 1.** A. Distribution of haplotypes of the haplogroup I of the Central Balkan clade of *Podarcis muralis* in Central Europe. Members of this clade are represented by circles, squares represent members of exotic lineages, and a pentagon represents a probably native population of Austrian *P. muralis* (see Jablonski et al., 2019 for details). A population recently discovered in Krnov is represented by a triangle with a question mark. Shaded area represents the continuous species range. B. A haplotype network with colours corresponding to circles in the map. C. A satellite map showing three localities inhabited by Polish populations of *P. muralis*. D. Reported historical sites of *P. muralis* from Poland and cross-border areas. Populations from the Strzelin Hills (S) are in a circle. Pentagon (I) – Izera Mountains (Hännich, 1912); square (G) – Giant Mountains (Neumann, 1831); triangle (O) – Opava Silesia (Ens, 1835; Randík, 1957); parallelograms: (M) – Maczki-Sosnowiec, (T) – Trzebinia, (K) – Kielce, (B) – Busko, (P) – Puławy (Fejerváry, 1923). Shaded area represents the Silesia region (yellow) and the closest continuous range of *P. muralis* (grey).

#### Material collection

Phenological observations have been collected from 2011, when the first *P. muralis* were found in Poland (Wirga and Majtyka, 2013), to 2019. We identified easily noticeable phases such as the presence of basking or hunting individuals, gravid females, and freshly hatched individuals. From 2014 to 2018, we conducted observations throughout the year, including winter; in the remaining years, the obser-

vations were not continuous. For each phases we have given precise extreme dates of their observation.

Study on the morphology, demography and origin was conducted between April and October 2019. Lizards were captured by hand or by noosing and the sex of the animals was then determined. The snout-vent length (SVL), tail length (if autotomy had not taken place; TL), and head measurements were made using a digital calliper (Ecotone) to the nearest 0.01 mm. The length of the pileus (HL) was mea-



**Figure 2.** Habitats of *Podarcis muralis*. A, B – Strzelin, C, D – Gęsiniec, E, F – Przeworno. Photos by K. Kolenda.

sured from the tip of the rostral scale to the posterior border of the occipital scale. The height (HH) and width (HW) of the head were measured at the highest and widest points, respectively. Lizards were also weighed using Pesola 30 g ( $\pm 0.25$  g). Each individual was then photographed and classified according to known European colour morphs, including three pure phenotypes (white, yellow, red), and three intermediate ones (white-red, yellow-red and white-yellow; see Pellitteri-Rosa, 2010 for details). After that, lizards were individually marked by toe clipping, and immediately released back into their habitat. No lizards were killed for this

study. Toe clips were preserved in 80% pure ethanol and stored in  $-20^{\circ}\text{C}$  until further analysis.

#### *Wet lab and sequence analyses*

Five samples from Przeworno, three from Gęsiniec, and two from Strzelin were used for genetic analysis of their mitochondrial DNA (mtDNA; supplementary table S1). We used exactly the same procedures as described by Jablonski et al. (2019). DNA was extracted using the standard phenol-chloroform method. A 1143 bp sequence of

the cytochrome *b* (cyt *b*) gene was PCR-amplified using primers L14910 and H16064 according to Burbrink, Lawson and Slowinski (2000) and sequenced by Macrogen Inc. (Amsterdam, Netherlands; <http://www.macrogen.com>). A haplotype-network was constructed using the 95% limit of parsimony as implemented in TCS 1.21 (Clement, Posada and Crandall, 2000). For the haplotype network analysis we used 47 sequences of Central European haplogroup I of the Central Balkan clade (CB) sensu Schulte et al. (2008) and Jablonski et al. (2019) from the Czech Republic, Germany, Hungary and Slovakia (see supplementary table S1 for details).

#### *Skeletochronological analysis*

Individual age was determined using skeletochronology following Rozenblut and Ogielska (2005) with slight modifications to the protocol. The phalanges devoid of soft tissue were decalcified in a 1:1 mixture of 10% formic acid and 4% formalin for 1-2 h, and then washed in pure water (three changes, 10 minutes each). The tissue sample of each lizard was then transferred into an embedded freezing medium in flat embedding molds and sliced into 10- $\mu$ m thick sections using a Leica CM 1900 freezing microtome. Slices were stained in 0.05% cresyl violet and the cross-sections were observed under a Carl Zeiss Axioscope 20 light microscope. At least 20 cross sections of the central part of a diaphysis per individual were examined at different magnifications, ranging from  $\times 10$  to  $\times 40$ . Lines of arrested growth (1 LAG = 1 hibernation) were considered as complete and sharp, circular lines.

#### *Morphologically related statistical analysis*

In the analyses of sexual dimorphism, we used only males and females with SVL exceeding 43.0 mm, and those that were at least three years old. Smaller and younger animals, even if they could be confidently assigned to either sex, were not included.

The sexual dimorphism in SVL (25 males, 22 females) was tested using the Wilcoxon-Mann-Whitney test in R 3.6.1 (R Core Team, 2018). Sexual dimorphism in head size (16 males, 16 females) was analysed using an analysis of covariance (ANCOVA), with SVL as a covariate and sex as a grouping variable. Because SVL is commonly a sexually dimorphic trait in lacertids (e.g. Braña, 1996; Kratochvíl et al., 2003; Borczyk et al., 2014; see below), in a second analysis, we used the pileus length as a covariate. These analyses were performed in IBM SPSS Statistics 20. All data were log<sub>10</sub>-transformed before analyses.

The frequency of pileus anomalies were compared between the study sites using  $2 \times 2$  contingency tables and Fisher's exact tests in Statistica 13.5. In this case, a statistical significance level of  $p < 0.01$  was defined in order to avoid type I error due to multiple comparisons.

## Results

### *Phenology*

The first appearance of lizards after the winter torpor – when individuals after this date appeared regularly – was recorded from March 11 (2014) to April 15 (2013). Mostly single individuals of both sexes and juveniles were recorded at that time. In 2014, we also noted the short-term appearance of single individuals earlier, on February 20 and 21. The last individuals, mostly juveniles and males, were recorded on October 14 (2012, 2018 and 2019). During warm and sunny weather, we recorded single individuals (only juveniles) basking even later, i.e. on November 2-5 (2014) and November 21-22 (2016). Gravid females were observed from April 25 (2013) to August 4 (2012). Freshly hatched individuals were recorded from July 29 (2016) to September 17 (2012; see fig. 3).

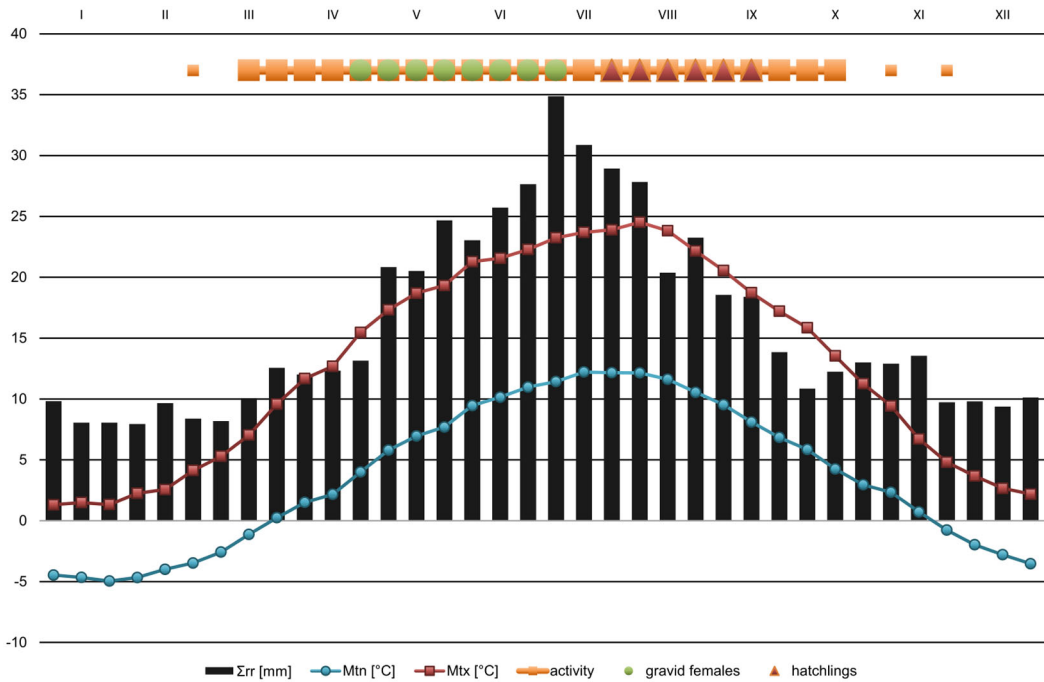
### *Morphometry*

In total, 60 lizards were collected from all three localities, including 26 males, 26 females and 8 juveniles. Half of males and 58% of females had an autotomised tail.

Males attain significantly larger SVL than females ( $W = 490$ ,  $p = 0.005$ ) (table 1). ANCOVA indicates that males have relatively longer ( $F = 37.253$ ,  $p < 0.001$ ), higher ( $F = 27.939$ ,  $p < 0.001$ ) and wider ( $F = 14.319$ ,  $p = 0.001$ ) heads than females at any given SVL (table 1). However, when the pileus length is taken as a reference point, males do not differ from females in head width ( $F = 0.392$ ,  $p = 0.536$ ), though they have higher heads ( $F = 6.554$ ,  $p = 0.016$ ).

### *Colour polymorphism*

Analysis of colour polymorphism revealed the occurrence of three morphs in Poland: white, white-red, and red (table 1, fig. 4). White-red morph dominate over white in females (17:9), and over red and white in males (13:12:1). The yellow colour morph was not recorded.



**Figure 3.** Phenogram of the annual activity (in decades) of *Podarcis muralis* against climatic conditions in Strzelin;  $\Sigma rr$  – sum of precipitation, Mtn – mean minimum temperature, Mtx – mean maximum temperature. The phenogram shows observations of the extreme dates of each phase.

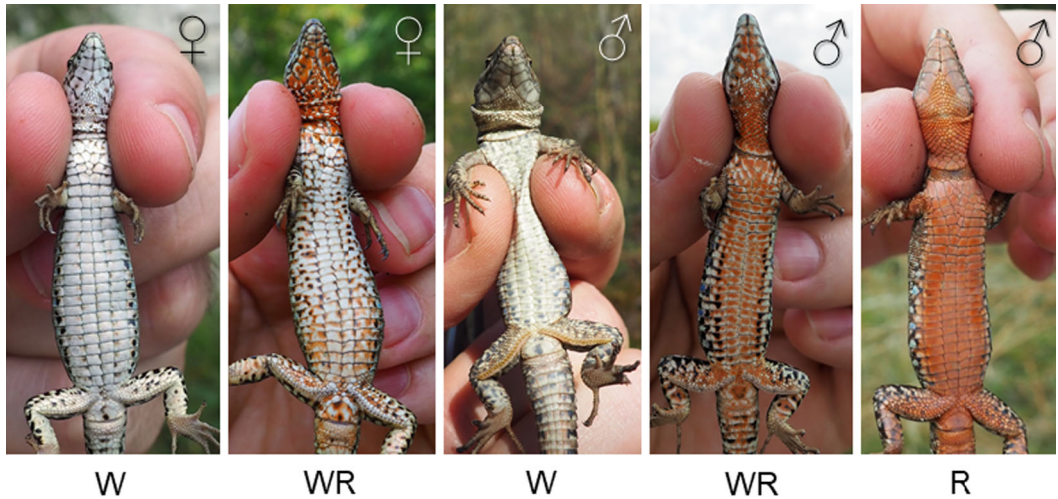
**Table 1.** Biometric data of *Podarcis muralis* from Poland.

Trait		Males	Females
SVL [mm]	Mean $\pm$ SD	57.40 $\pm$ 5.30	55.61 $\pm$ 6.66
	Range	37.03-63.50	39.70-64.20
HL [mm]	Mean $\pm$ SD	14.72 $\pm$ 0.80	11.84 $\pm$ 1.27
	Range	12.70-15.75	9.25-15.21
HH [mm]	Mean $\pm$ SD	6.02 $\pm$ 0.51	4.69 $\pm$ 0.68
	Range	5.17-6.90	3.09-5.84
HW [mm]	Mean $\pm$ SD	7.68 $\pm$ 0.46	6.34 $\pm$ 0.59
	Range	6.69-8.45	5.13-7.82
Colour [number of individuals]	White	1 (3.8%)	9 (34.6%)
	White-red	13 (50%)	17 (65.4%)
	Red	12 (46.2%)	0 (0%)
Age [years]	Range	2-8	1-8

### *Pholidosis*

The masseteric scale is present and surrounded by small temporals. Usually, there are five chin shields. The most anterior gulars are located between the second or third pair of chin shields. Four supralabials present anteriorly to the subocular. We have observed variation in several

other pholidotic traits. Most individuals exhibited a typical pattern in which the prefrontal scales are in wide contact, the interparietal and occipital scales are in contact, and the rostral and frontonasal scales are separated. However, in some individuals, the prefrontal scales contact only at a point ( $n = 2$ ) or are completely separated ( $n = 17$ ). This is achieved either by



**Figure 4.** Colour polymorphism of *Podarcis muralis* from Poland. W – white, WR – white-red, R – red. Photos by K. Kolenda.

an elongation of the frontonasal scale (fig. 5A), which may contact the frontal scale ( $n = 10$ ), or by the presence of an additional scale between the prefrontals (fig. 5C, D). This scale is of variable size: very small (it does not separate the prefrontals;  $n = 10$ ) or large enough to completely separate the prefrontals ( $n = 7$ ). Also, the interparietal and occipital scales can be either in contact ( $n = 44$ ), separated ( $n = 9$ ) or fused ( $n = 2$ ). The rostral and frontonasal scales were in contact in 5 lizards and separated in 55 individuals.

#### *Pileus anomalies*

In total, at least one scale anomaly was exhibited by 27 individuals (46.6%) – 12 females, 13 males and two juveniles. Two or more anomalies were present in 10 individuals (16.7%). However, the frequency of anomalies differed between the quarries; in Przeworno it was 30%, in Strzelin 50% and in Gęsiniec 61%. The frequency of anomalies was significantly different between Przeworno and Gęsiniec (Fisher's exact test,  $p < 0.001$ ) and Strzelin ( $p = 0.006$ ), but not between Strzelin and Gęsiniec ( $p = 0.15$ ).

The most common anomalies include the presence of an additional scale between the prefrontals (fig. 5C, D), which was present (regardless of its size) in 17 individuals (28.3%),

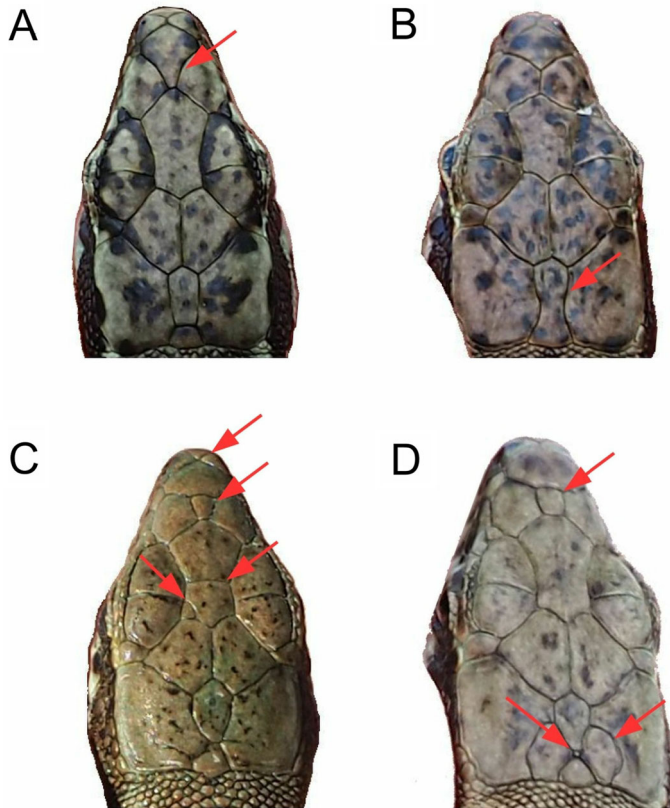
or the presence of an additional scale between the interparietal and occipital (5 individuals). Other types of anomalies, such as the fragmentation of the frontal (fig. 5C), parietal (fig. 5D) or supraocular scales, or fusion of the interparietal and occipital scales (fig. 5B), were present only in single individuals (see supplementary table S2).

#### *Longevity*

Individual age was successfully estimated in all examined individuals. Among juveniles we found freshly hatched (0 LAGs) and 1-year-old individuals. Females reached an age from 1 to 8 years, with 4- and 5-year-old individuals dominating. The age of males ranged from 2 to 8 with 6- and 7-year-old lizards dominating (table 1).

#### *Origin of populations from Poland*

The haplotype network analysis of *cyt b* sequences revealed that lizards from all three localities belong to the haplogroup I (sensu Jablonski et al., 2019), which also includes samples from the Czech Republic, Slovakia, eastern Germany and Hungary (fig. 1). 11 unique haplotypes have been detected among this Central European group. The most common one, which



**Figure 5.** Examples of pileus anomalies, highlighted by red arrows. A. An elongated frontonasal scale, separating the prefrontals. B. Fused interparietal and occipital scales. C. A contact between the rostral and frontonasal scales, an additional scale between the prefrontals, two divisions of the frontal scale (from anterior to posterior). D. An additional scale between the prefrontals, a divided parietal scale, an additional scale between the interparietal and the occipital (from anterior to posterior). Photos by K. Kolenda.

is widely distributed across the Czech Republic and Slovakia, also includes genetically studied lizards from Poland (fig. 1).

## Discussion

### *Biology of P. muralis from Poland*

In general, biological parameters of *P. muralis* from Poland do not deviate from those of other populations from localities in similar latitudes (e.g. Strijbosch, Bonnemayer and Dietvorst, 1980; Allan, Prelypchan and Gregory, 2006; Grosse and Seyring, 2015). For example, all phenological data are within the ranges characteristic of the northern native populations of this

lizard (Wirga and Majtyka, 2015b). One exception is the later appearance of hatchlings in the Netherlands in mid-October (Strijbosch, Bonnemayer and Dietvorst, 1980), while we have observed their first appearance in late July (this is also the case for the Canadian population; Allan, Prelypchan and Gregory, 2006). The annual activity of *P. muralis* does not, in principle, differ from the annual activity of the co-occurring sand lizard, *Lacerta agilis*, despite the fact that *P. muralis* is considered a more thermophilic species. It should be clearly noted that in 2013 such late appearance of lizards was caused by the fact that March of that year was extremely cold and the snow cover was still present in the first decade of April (IMGW, 2013).



There is no clear pattern in sexual size dimorphism within either lacertids (Cox, Butler and John-Alder, 2007) or within *P. muralis* (Žagar et al., 2012). In most of the studied populations of this species, males attain larger size (e.g. Gracceva et al., 2008; Moravec and Veselý, 2015), but female-biased sexual size dimorphism has been described in *P. muralis* from Slovenia (Žagar et al., 2012), while in the Netherlands and in an introduced population in Canada, both sexes attain similar sizes (Strijbosch, Bonnemayer and Dietvorst, 1980; Allan, Prelypchan and Gregory, 2006). In populations from the Strzelin Hills, males were larger than females, which agrees with the typical condition observed in *P. muralis*, including the most closely located populations from the Czech Republic (Moravec and Veselý, 2015).

Regardless of the type of sexual size dimorphism, males of lacertid lizards tend to have relatively larger heads (e.g. Gracceva et al., 2008; Scharf and Meiri, 2013; Borczyk et al., 2014). This is also the case in *P. muralis* from Poland.

We have observed several noteworthy pholidotic traits in *P. muralis* from the Strzelin Hills. In several individuals, the rostral and frontonasal scales contacted at a point. The separation of these scales is listed in the description of *Podarcis* (Arnold, Arribas and Carranza, 2007) and is sometimes used to distinguish *P. muralis* from other similar species of lacertids (Žagar et al., 2012). The contact between these scales was not previously reported from the Polish (Wirga and Majtyka, 2013) or Czech (Moravec and Veselý, 2015) populations of *P. muralis* but is known to occur, in a very low frequency, in *P. bocagei* and *P. carbonelli* (Kaliontzopoulou, Carretero and Llorente, 2005). The most common deviations from the norm were complete separation of the prefrontal scales and the presence of an additional scale between the prefrontals (in some individuals both these conditions were present). They were also recorded in a population from Štramberk in the Czech Republic (Moravec and Veselý, 2015).

Almost half of the studied lizards from Poland exhibited some anomalies in the pileus. This is less than in the Czech population of *P. muralis* from Štramberk, where 71.2% of males, 85.7% of females and 66.7% juveniles exhibited anomalies (Moravec and Veselý, 2015). The high frequency of scale anomalies was reported in populations that went through a genetic bottleneck (Gautschi et al., 2002), which is the case in many introduced populations, but also, for example, in hybrid individuals (Zinenko, 2004). The disturbances in developmental homeostasis that may lead to an increase in the frequency of scale anomalies are also more common in areas with strong anthropoppression (Lazić et al., 2013).

A relatively high frequency of the red colour morph and the absence of yellow-coloured lizards differentiates Polish populations of *P. muralis* from those from the Czech Republic and Slovakia, where the situation is slightly different. Moravec and Veselý (2015) mentioned the absence of a conspicuous red or yellow colouration in the population from Štramberk. However, the same situation as in Poland was described for members of the Central Balkan clade from eastern Germany (Schulte et al., 2011).

Although data concerning the longevity of *P. muralis* in Europe remain scarce, they are similar to those obtained in our study. In France (Castanet and Roche, 1981; Barbault and Mou, 1988) and Italy (Vollono and Guarino, 2002), the oldest lizards were reported to be 5 years old. In isolated populations in the Dobrudja region of Romania, the maximum age reached 7 years (Telea et al., 2018). The maximum longevity of *P. muralis* from Germany was stated to be 8-10 years (Grosse and Seyring, 2015). The highest longevity of this species has been found in Turkish lowland (14 years old) and highland (16 years old) populations (Eroğlu et al., 2018). In general, populations of lizards from colder climates (in particular, those from higher latitudes) grow and reach sexual maturity more slowly, which allows them to live longer

(e.g. Roitberg and Smirina, 2006; Cabezas-Cartes, Boretto and Iburgüengoytía, 2018). This may explain the slightly higher maximum age of lizards from Poland in comparison to those from more southern locations. However, other factors such as seasonality or precipitation (which in turn may affect the availability of food) can also affect longevity (e.g. Cabezas-Cartes, Boretto and Iburgüengoytía, 2018), which may explain the much higher longevity observed in Turkish populations (Eroğlu et al., 2018).

### *Species origin in Poland*

Since the discovery of *P. muralis* in Poland (Strzelin Hills), they have been considered an introduced species (Wirga and Majtyka, 2013, 2014, 2015a, b; Sura, 2018). This would not be unusual, because *P. muralis* were introduced in more than 150 locations in Europe and even North America (e.g. Michaelides et al., 2015b; Santos et al., 2019). This artificial, probably human-mediated origin in Poland was supported by the following arguments. Firstly, the reptile fauna of the Strzelin Hills has been investigated by several researchers (e.g. Chlebicki, 1988; Kołtowska, 2012; including several unpublished surveys and field observations) and none of them found any signs of the species. Secondly, the geographically closest populations (from the eastern Czech Republic and eastern Germany) were often recognised as most probably introduced (Schulte et al., 2011, Wirga and Majtyka, 2013; but see below). Thirdly, in the early twentieth century, there were numerous attempts to introduce southern European species in Central Europe. These include several Mediterranean species of reptiles introduced in the north-eastern Czech Republic (see details in Jablonski et al., 2019) or the common midwife toad, *Alytes obstetricans*, introduced in the Ślęża Massif, located less than 30 km from Strzelin (Udźziela, 1910).

It seems unlikely that several researchers overlooked or misidentified *P. muralis* in the

Strzelin Hills. However, such mistakes occasionally happen. For example, the first recorded specimens of *P. muralis* from the Czech Republic were initially recognised as the common lizard, *Zootoca vivipara*, and were only correctly identified more than 40 years later (Zavadil, 1999; Moravec and Beneš, 2000; Pavlík and Šuhaj, 2000 and see details in Jablonski et al., 2019). Additionally, Kołtowska (2012), in her study of amphibian and reptile fauna of the Strzelin Hills, did not explore the quarries in which these lizards were discovered several years later (Wirga and Majtyka, 2013). Chlebicki (1988) visited the quarries in Strzelin and Przeworno but the only lizards he observed were sand lizards, *Lacerta agilis*. However, his study was concentrated, in particular, on amphibian breeding sites (Chlebicki, 1988). Additionally, he began his study in 1979, soon after an exceptionally cold winter (e.g. Twardosz and Kossowska-Cezak, 2016). Because *P. muralis* is one of the most thermophilic reptiles currently living in Poland, such cold winters could have seriously limited its population size and thus make it more difficult to encounter. It is also worth noting that during the first several visits to the Gęsiniec quarry by Wirga and Majtyka, *P. muralis* were not observed (while other species of reptiles inhabiting the quarry, *L. agilis* and *Natrix natrix*, were noticed; Wirga and Majtyka, 2014, 2015a). This indicates that these lizards are not always easily detectable.

How can we explain the origin of *P. muralis* in the Strzelin Hills? Pax (1921, 1925) stated that a small number of individuals of this species were repeatedly introduced by herpetoculturists in Silesia (“in recent times”, i.e. most probably after World War I; Pax, 1925, p. 495), unfortunately, without specific information about localities. Are the lizards from the Strzelin Hills descendants of the animals introduced in those times? The first reports on the occurrence of *P. muralis* in Silesia precede Pax’s work by almost one century (see fig. 1D for details). Neumann (1831) reported the presence of *P. muralis* in the Giant Mountains and

similarly Hannich (1912) for the Iżera (Jizera) Mountains. However, it is possible that these observations resulted from misidentification of *Z. vivipara* (see also above). These records were regarded as unreliable by Pax (1925), mostly on the basis that no specimens were deposited in museum collections or mentioned in two recent books about German reptiles (Dürigen, 1897; Schreiber, 1912). However, it cannot be ruled out that some populations originally reported in the nineteenth century were already extinct by the time of Pax. Moreover, *P. muralis* were supposedly observed in Silesia (again, in an unspecified locality) also by Lichtenstein (cited by Tobias, 1865). A single observation of two individuals predated by a common buzzard, *Buteo buteo*, shot at Milotice nad Opavou (Opava Silesia, several kilometres from Krnov) was already published in 1957 (Randík, 1957). Unfortunately, these two specimens are now lost (Viček and Zavadil, 2019). Additionally, in the museum in Opava (currently, Silesian Museum), specimens of *P. muralis* supposedly collected in Opava Silesia, were already present in 1835 (Ens, 1835). Also, a previously unknown population of *P. muralis* was recently discovered in the Czech part of Silesia, near Krnov, very close to the Czech-Polish border and about 60 km in straight line from the Strzelin Hills populations. Although this population is probably introduced, genetic data are not yet available (Viček and Zavadil, 2019). It is also worth noting that *P. muralis* were allegedly present in other parts of present-day Poland. Hungarian naturalist Alexander Pongrácz collected these lizards from several localities in southern and eastern Poland (i.e. Kielce, Maczki-Sosnowiec, Trzebinia, Busko, Puławy; Fejerváry, 1923). These specimens were deposited in the Hungarian Natural History Museum in Budapest and studied by Fejerváry (1923), so their taxonomic identification is probably correct. However, it cannot be excluded that they were mislabelled and they do not, in fact, come from Poland

(Fudakowski, 1958). Currently, it is impossible to corroborate as the specimens were destroyed during the Hungarian Revolution in October 1956.

In light of all the facts, we demonstrated that *P. muralis* from Poland share the same haplotype that was found in the Czech and most Slovak populations (Jablonski et al., 2019). This is the most common (and presumably ancestral) haplotype of the haplogroup I of the Central Balkan clade of *P. muralis*. The presence of such ancestral haplotypes in isolated northern populations is consistent with their relict status (Joger et al., 2010). The same explanation applies to the Czech populations which may also be relicts rather than the result of introductions (especially the population in Štramberk, which is the closest to the Moravian Gate and contains also different haplotypes; Jablonski et al., 2019). This would reduce the geographic distance between populations from Lower Silesia and the closest native (or probably native) *P. muralis*.

The populations from Poland studied herein are consistent with the phylogeographic pattern of the species in Central Europe and these populations are not formed by exotic lineages (e.g. from the Balkans or Apennines), as is recorded in Germany or Austria (Schulte et al., 2008, 2011, 2012; Jablonski et al., 2019; fig. 1A). However, if Polish populations are introduced, Strzelin seems to be the most probable site of the original introduction, because it is inhabited by the largest population (several hundred individuals; see below). It is possible that *P. muralis* were accidentally transported by train from this quarry to the quarry in Przeworno where they then established another population (Dudek, 2014). This is supported by the fact that such dispersal by trains is well documented in *Podarcis* lizards (e.g. Santos et al., 2019), as these reptiles prefer habitats associated with railways (Gherghel and Tedrow, 2019). However, this still does not explain the origin of *P. muralis* in the Strzelin Hills. The genetic

data presented herein do not allow us to determine the origin of Polish populations. The introduction from the closest localities is probable, especially given the fact that an introduction of these lizards was attempted in Silesia about 100 years ago (Pax, 1925). However, if the Strzelin Hills wall lizards are indeed introduced, the source population must have been geographically close – located either in the Czech Republic or Slovakia. On the other hand, the relict status of Polish populations, although it needs further study, cannot be ruled out. Isolated northern populations of thermophilic reptiles are known for several species, such as the Aesculapian snake, *Zamenis longissimus*, and Eastern green lizard, *Lacerta viridis* (Böhme et al., 2007; Musilová et al., 2010; Allentoft et al., 2018), as well as *P. muralis* (Michaelides et al., 2015a).

#### *Perspectives for population persistence and further studies*

None of the Polish populations is seriously threatened at present and we do not anticipate any change in the immediate future. In Strzelin, the biggest studied quarry inhabited by the largest Polish population of *P. muralis*, lizards inhabit mostly an abandoned area; however, we also noticed individuals in exploited areas. We have seen at least a dozen to several dozen lizards in different parts of the quarry on each visit; therefore, we suppose the population size may reach several hundred individuals. Even an accidental destruction of the site where the lizards were most abundant (in 2013) did not significantly affect the population size, such actions may even be considered positive because they maintain the environment in the early stages of plant succession. Moreover, due to the occurrence of *Coronella austriaca*, a strictly protected species in Poland, in the abandoned area, a conservation plan aimed at removing excessive vegetation will soon be implemented. In Gęsiniec, we have observed up to 20 lizards in the most abundant area and over a dozen in other parts; thus we estimate that population

size is more than one hundred individuals. Currently, this quarry is used only for recreational purposes, and a further detailed management plan is uncertain. However, a possible geopark planned in this location should enhance protection and persistence of the population. In Przeworno, up to ten lizards have been noted on a pile of stones near the quarry and no more than 20 in the quarry; thus, the total number of lizards in this locality probably exceeds several dozen but no more than one hundred. Until spring 2019, this population was under the pressure due to the overgrowth of vegetation. However, the new owner of this place is building a diving centre in the quarry and has cut some trees and bushes which were growing on the slopes. According to our preliminary talks, he prefers to maintain the slopes partly uncovered. It is also noteworthy that, despite intense human activity in all three quarries, the populations seem to be relatively stable/unthreatened.

In the following years, explorations of other quarries in the Strzelin Hills will be conducted, including those studied in the past (Wirga and Majtyka, 2015a), as well as different potential habitats, especially along railway tracks situated between Strzelin and Przeworno.

Taking into account our considerations, we proposed to change the status of populations from the Strzelin Hills from ‘alien’ to ‘cryptogenic’ (sensu Carlton, 1996), which was approved by the Institute of Nature Conservation of the Polish Academy of Sciences – the organ responsible for the monitoring of alien species in Poland (IOP, 2019). Currently, this species is not protected in Poland and we suggest to retain the *status quo* until more detailed genetic analyses involving numerous nuclear markers are conducted.

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