DISTRIBUTION OF THE COMMON OR VIVIPAROUS LIZARD, Zootoca vivipara (LICHTENSTEIN, 1823) (SQUAMATA: LACERTIDAE) IN CENTRAL EUROPE AND RE-COLONIZATION OF THE BALTIC SEA BASIN: NEW KARYOLOGICAL EVIDENCE

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The widely distributed viviparous lizard *Zootoca vivipara* (Lichtenstein 1823) revealed considerable differences in physiology, karyology, molecular genetics, and natural history. Based on chromosomal and mtDNA data several distinct karyotypic forms and haplotypes have been described from Central Europe. In an attempt to further clarify the geographic distribution of two karyologically different forms within the viviparous, nominotypic *Z. v. vivipara*, we studied the karyotypes of specimens from two NE German localities in West Pomerania (Baltic Sea) and Brandenburg, respectively, and also of those from Mt. Kopaonik in Serbia. All individuals karyotyped represented the western form of *Z. v. vivipara* that differs from other chromosomal forms of Central Europe in several karyotype characters. It inhabits the south coast of the Baltic Sea between the German harbor city of Kiel in the west and the Russian harbor city of Kaliningrad in the east. Recently, the eastern, so-called Russian form of *Z. v. vivipara* was recorded also in the Kaliningrad exclave, in Belarus near the border Belarus-Poland and even in easternmost Poland, then further eastwards along the Baltic Sea coast including Finland. Our data show that easternmost German populations still belong to the western form, as it is also the case in the SE European Serbian locality sampled. Together with previous data sets, our results document chromosomal uniformity within the western form of *Z. v. vivipara* from the Baltic Sea coast to the Carpathian basin and the central Balkans, and earlier hypotheses of the postglacial recolonization of the Baltic Sea basin by *Z. vivipara* are corroborated.

Keywords: viviparous *Zootoca vivipara*; central Europe; the Baltic Sea Basin; central Balkans; karyotype; western form of *Zootoca* v. *vivipara*; biogeography; re-colonization.

INTRODUCTION

The well-known viviparous lizard, *Zootoca* (formerly *Lacerta*) vivipara (Lichtenstein, 1823) is the world's widest-ranging terrestrial reptile species. Its huge distribution area ranges from the Cantabrian mountains and Ireland in the west through the entire Eurasian landmasses to Sakhalin (Russia) and Hokkaido (Japan) Islands in the east, and from the Pado valley (Italy) and central and southern Serbia and Bulgaria in the south to the Barents Sea in the north, where it considerably passed over the Polar Circle (Böhme, 1997). Until recently, the authorship of its species name was ascribed to the Austrian botanist Franz Josef von Jacquin (1787) (Jacquin, 1787) but his short, Latin account was not a species description but rather a simple description of its reproductive mode. It has been discussed by Böhme and Rödder (2006) and in more detail by Schmidtler and Böhme (2011). The nomen *vivipara*, certainly worth of being conserved, had therefore to be ascribed to the next author who used this name for the first time in a taxonomic and nomenclatural sense which, according to Schmidtler and Böhme (2011), was Lichtenstein (1823).

Despite the huge distribution range of Z. vivipara, the species was for long regarded as monotypic (see, e.g., Wermuth, 1951; Mertens and Wermuth, 1960). However, more recent taxonomic studies revealed considerable differences in physiology, karyology, natural history, and molecular genetics which resulted in the description and/or recognition of several subspecies, viz. sachalinensis Pereleshin and Terentyev, 1963, pannonica Lac and Kluch, 1968, carniolica Mayer, Böhme, Tiedemann and Bischoff, 2000, and louislantzi Arribas, 2010 (Dely and Böhme, 1997; Kupriyanova and Böhme, 1997; Ca-

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bela et al., 2001; Mayer and Böhme, 2000; Mayer et al., 2000; Odierna et al., 2000; 2004; Surget-Groba et al., 2001; Arribas, 2009; for a complete synonymy see Schmidtler and Böhme, 2011). One of these nominal subspecies, viz. the oviparous Z. v. carniolica, might even have approached already species status because it was possible to detect a hybridization zone between it and a viviparous Z. v. vivipara population where obviously selection against hybridization takes place (Lindtke et al., 2010) which can be interpreted as a beginning, incipient speciation process. Also, recent nuclear microsatellite DNA studies may support a distinct species range of the oviparous Z. v. carniolica (Cornetti et al., 2014, 2015). Subsequently, it became even possible (though still difficult) to distinguish these two taxa by external morphological character combinations (Clasen, 2001; Guillaume et al., 2006). Moreover, chromosomal and genomic data showed convincingly a multiple origin of viviparity in these lizards (Odierna et al., 2004; Kupriyanova et al., 2005b; 2006; Surget-Groba et al., 2006). All discovered chromosomal forms which partly fit the delimitations of current subspecies have their own karyotypic characteristics (see Table 1). Their distinct geographic distribution areas may show continuous or mosaic patterns, and they may be widely distributed or are relicts. In the latter case they certainly merit special attention and even protection

in some countries to prohibit their extinction before deeper studies as to their chromosomal and genetic characteristics as well as their subspecific status can be performed. The necessity for such studies is still important and even urgent for numerous European and Asian populations of *Z. vivipara*.

Recently, two widely distributed different forms have been discovered within the currently accepted nominotypic subspecies Z. v. vivipara based on their karyotypes. One has been called the viviparous "Russian form" with a diploid chromosome number 2n = 35 including the W-sex acrocentric/subtelocentric (A/ST) macrochromosome in the female, and the likewise viviparous western form, also 2n = 35, but with a W-sex submetacentric (SV) macrochromosome in the female (Fig. 1). As a result, at the southeastern coast of the Baltic Sea (i) the marginal populations of these two forms were discovered (ii) a parapatric contact zone between both of them was for the first time localized, and (iii) it was possible to demonstrate different habitat preferences between these two forms. Finally, the question of the taxonomic identity and rank of both forms was again raised (Kupriyanova, 2004; Kupriyanova and Melashchenko, 2011; Kupriyanova and Böhme, 2012). The Russian form has also been characterized genetically in that 12S- and 16S-RNA gene sequences practically agreed between a sample from

No.	2 <i>n</i> ♂*/♀	Size of sex chromosomes m/M	System of sex chromosomes Zw/Z_1Z_2W	Morpho- logy of sex chromo- somes	Mode of reproduction, O/V (ovi/viviparous)	Localities	Species, Subspecies, Chromosomal forms
			Th	e first group	o of karyotype		
1	36 A/36: 35 A + 1a	М	Zw	А	0	Central, South-western Europe, Carpathian region	Z. vivipara, now Z. v. carniolica
2	36 A/36: 35 A + 1a	М	Zw	А	V	Central Europe, Carpathian region	Z. vivipara, now Z. v. vivipara Hungarian form
			The	second grou	ip of karyotype		
3	36 A/35: 34 A + 1 A, A/ST	М	$Z_1 Z_2 W$	A, ST	0	Western Europe, the Pyrenees	Z. v. vivipara Pyrenean form, now Z. v. louislantzi
4	36 A/35: 34 A + 1ST	М	$Z_1 Z_2 W$	ST	V	Central Europe, Carpathian region	Z. vivipara, now Z. v. vivipara Austrian form; Z. vivipara (pannonian lowland)?
			Th	e third grou	p of karyotype		
5	36 A/35: 34 A + 1 A, A/ST	М	$Z_1 Z_2 W$	A, A/ST	V V	Asia, Eastern Europe, Fennoscandia, Baltic region, Carpathian region	Z. vivipara, now Z. v. vivipara Russian form
6	36 A/35: 34 A + 1 SV	М	$Z_1 Z_2 W$	SV	V	Western, Central Europe, Alps, Balkans, Carpathian region, Baltic region, Fennoscandia	Z. vivipara, now Z. v. vivipara Western form

TABLE 1. Karyotype Characteristics of Subspecies and Different Forms of *Zootoca vivipara* (Lichtenstein 1823) and their Distribution in Europe [a modification of the Table 1 of Kupriyanova et al. (2014)].

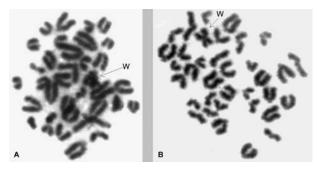


Fig. 1. Giemsa stained metaphase plates of females of *Zootoca vivipara*: A, Russian form of *Zootoca v. vivipara* with the W-sex acro/subtelocentric (A/ST) macrochromosome (M); B, western form of *Zootoca v. vivipara* with the W-sex submetacentric (SV) macrochromosom (M). Arrows point to the W-sex chromosomes. From Kupriyanova and Böhme (2012).

Sakhalin Island in the Far East and from St. Petersburg (Mayer and Böhme, 2000) and in sequences in mitochondrial cytochrome b between them from Sakhalin Island and from western Russia, from eastern Hungary (Surget-Groba et al., 2006; Velekei et al., 2014) and from Hokkaido Island and from Belorussia (Takeuchi et al., 2013). This finding raised the question as to how far west at the southeastern coast of central Europe the Russian form would be distributed. It turned out that this eastern form of Z. v. vivipara could be recorded in several populations in the Kaliningrad exclave, western Russia, in Belarus near the border Belarus - Poland and even in the northeast of Poland (a locality within the Suwalki gap) close to the Belarus and the Lithuanian border, as well as in several localities in eastern Europe (Estonia and northwest of Russia, around Stain-Petersburg). In the eastern part of the Baltic Sea seashore this form was described in several localities of Finland as well (Kupriyanova et al., 2005a, 2014; Kupriyanova and Melachshenko, 2011; Kupriyanova and Bazharev, 2012; Kupriyanova and Böhme, 2012) (Fig. 2).

However, the other, western form of *Z. v. vivipara*, was also discovered at the southern coast of the Baltic Sea, namely in Germany, in the Kaliningrad exclave of Russia and in the adjacent parts of northern Poland south-west of Kaliningrad Oblast, thus giving a first hint of a secondary contact zone between both forms in central Europe (Kupriyanova and Melashchenko, 2011; Kupriyanova and Böhme, 2012; Kupriyanova and Borczyk, in preparation) (Fig. 2).

Further chromosomal data, previous as well as modern ones, on Z. vivipara from the territory around the Baltic Sea Basin indicate that the geographical distribution of these two forms here is complex, and new secondary zones have been postulated in the northern and north-

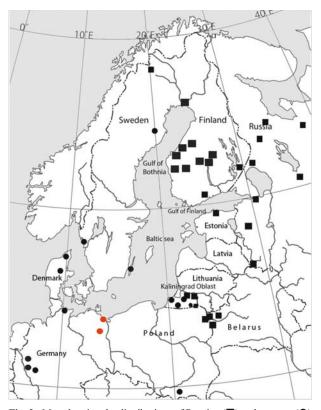


Fig. 2. Map showing the distributions of Russian (\blacksquare) and western (\bullet) forms of *Zootoca v. vivipara* in the Baltic Sea basin based mainly on their karyotypes. The locations sampled in this study presented as red circle mark (\bullet).

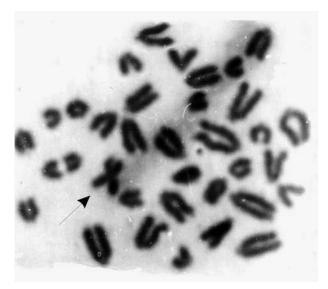
western parts of Fennoscandia as well as in the other parts of central and eastern Europe (Kupriyanova and Böhme, 2012; Kupriyanova et al., 2014). In an attempt to further clarify the situation in different areas of central Europe, we studied for the first time the karyotypes of viviparous *Z. vivipara* from two localities in West Pomerania, NE Germany, with special attention to Usedom Island in the Baltic Sea. In order to better understand a distribution of viviparous *Z. vivipara* and a direction of immigration of the species from a center of biodiversity in central Europe we examined also for the first time the karyotype of *Z. vivipara* from its southern area, namely in one site from the central Balkans, Serbia, and compared our data obtained with those available for other localities from central Europe.

MATERIAL AND METHODS

Four specimens (two females and two males) from two geographically distinct localities in North Germany were collected and analyzed in August – October 2015:

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Fig. 3. Giemsa stained metaphase plates of females of *Zootoca vivipa-ra* from: A, locality 1 near Fürstenberg, north of Germany; B, locality 2 from Usedom Island, north of Germany. 2n = 35M: 34A + 1 SV (W). Arrows point to the W-sex submetacentric (SV) macrochromosome (M). According to karyotype markers these females belong to the western form of *Z. v. vivipara*.



(Locality 1) near Fürstenberg, 80 km north of Berlin, and (Locality 2) Usedom Island, the Baltic Sea, north of Germany (Fig. 2). Additionally the karyotype of two females and one male (Locality 3) in Mt. Kopaonik (Pančićev vrh), Serbia, were analyzed in 2015.

No additional permits are required for research on this non listed species from central Europe. The specimens were deposited in the research collection in the Zoological Institute of the Russian Academy of Sciences.

Chromosomes were obtained according the scraping and air-drying method from intestinal epithelial cells, blood, lung and oviduct tissues (Odierna et al., 1993). The specimens were injected with 0.1% phytohemagglutinin M (PANECO) tree times during three weeks (0.08 ml/5 g of body weight) and then with 0.05% colchicines (Merk) 1 h before sacrificing animals. Slides were stained for 10 min with a 5% Giemsa solution (Kupriyanova and Melashchenko, 2011).

RESULTS AND DISCUSSION

The chromosomal analysis of the specimens of *Zootoca vivipara* revealed that females from the three geographically separate localities 1, 2, and 3 have 2n = 35:34 acrocentric (A) macrochromosomes (M) and 1 submetacentric (SV) W sex macrochromosome (Figs. 3 and 4). Males from the localities 1 - 3 have the typical pattern for all *Z. vivipara* males, viz. 36 acrocentric macrochromosomels, 2n = 36 A (Fig. 5). According to these chromosomal results the specimens studied here belong to the western form of *Z. v. vivipara*.

The females of the four other localities of central Europe, Germany, previously studied by us (1. near Bonn; 2. Maria Laach, Rhineland; 3. near Koblenz in

Fig. 4. Giemsa stained metaphase plate of female of *Zootoca vivipara* from locality 3 in Mt. Kopaonik (Pančićev vrh), Serbia. 2n = 35M: 34 A + 1 SV (W). Arrow points to the W-sex submetacentric (SV) chromosome. According to karyotype markers these females belong to the western form of *Z. v. vivipara*.

Rhineland; 4. near Kiel) had the same number of chromosomes, 2n = 35:34 acrocentric macrochromosomes (A) and characteristics of karyotype: 34 A and in addition they also showed one submetacentric W sex macrochromosome. Males from these localities had the typical 36 acrocentric macrochromosomes. From those data it was clear that those specimens belonged to the western form of Z. v. vivipara as well. However, females from the other localities from a northern part of central and eastern Europe (easternmost Poland, western Belarus, Estonia, western Russia and Finland) had in their karyotype A/ST W-sex macrochromosome (Figs. 1 and 2) (Kupriyanova and Böhme, 1997; Kupriyanova et al., 2006; Kupriyanova and Melashchenko, 2011; Kupriyanova and Böhme, 2012). All these finding corroborated the two population groups with two different karyotypic forms of viviparous Z. vivipara in the northern half of Europe, viz. the socalled Russian form and the so-called western form, both formally still included in the nominotypic subspecies Z. v. vivipara.

Our data presented here have provided some new information on the distribution of these two forms in central Europe, including its southern and northern parts. All chromosomal data obtained show that the western form is distributed in the central Balkans, Serbia, and at the south coast of the Baltic Sea, between the German harbor city of Kiel in the west and the Russian Kaliningrad oblast' in the east and additionally in the southwestern part of Baltic region, i.e., in western Fennoscandia. On the other hand, the other, Russian form, is present in the eastern part of the southern Baltic Sea seashore, i.e., in eastern and north-eastern Fennoscandia. As mentioned above, marginal populations of both forms have been found in parapatry in the central Kaliningrad oblast'. It can be assumed that parapatric contact may be also present in the eastern part of Poland and in western parts of Belarus and Lithuania. Moreover, we have to assume that zones of secondary contact between these two forms are to be localized also in other areas of northeast Europe. Additionally, some populations of these forms may be rare there and in need of protection and some territories may be very important for preserving and conservation of different forms and of biodiversity of the common species as a whole.

Moreover, also in the north or northwest of Fennoscandia both forms could co-occur in a zone of secondary contact (Kupriyanova et al., 2014; Fig. 2) as can be evaluated by karyotypic data. However, an interesting approach would also be to follow up the previous observations by Voipio (1961) who reported on the variability of pileus shield patterns in Finnish Z. vivipara populations.

Our results have thus further answered the question formulated already by Kupriyanova (1997): Is the Baltic Sea basin a zone of secondary contact between different forms of Zootoca vivipara? Yes, it certainly is. It seems certain now that the two forms colonized this area from a presumed center of evolution of different chromosomal forms in the Carpathian basin where a maximum of different chromosomal forms was revealed. They met there after their postglacial re-immigration from two different directions to the north of central Europe, from the southwest and from the southeast, respectively (Kupriyanova and Böhme, 1997; 2012; Odierna et al., 1998) (Fig. 2). This postglacial re-colonization pattern resembles that of other northerly distributed squamates, e.g., Natrix natrix and Vipera berus. However, particularly the comparison with N. natrix (Kindler et al., 2013) shows an important difference and underlines the importance of the Usedom Island vouchers of Zootoca vivipara. In contrast to N. natrix they represent the western form of the species and not, as is the case in the grass snake (see Kindler et al., 2013), a peculiar, distinct clade.

In addition, our present karyotype investigations of *Z. vivipara* from the central Balkans confirm an assumption about an unity of Carpathian-Balkan fauna (Kupriyanova, 2004) based on the chromosomal data of *Z. vivipara* from Carpathian. All these chromosomal data correlate with chromosomal and molecular data on the widely geographical distribution of western form in central Europe (the Alps, the Balkan, a western and partly an eastern Carpathian mountain systems) and other, Rus-

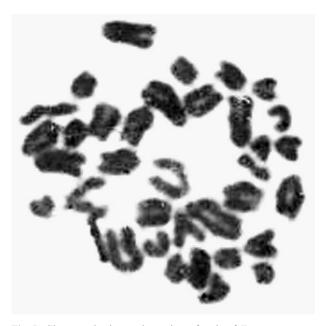


Fig. 5. Giemsa stained metaphase plate of male of *Zootoca vivipara* from locality 1 with 36 acrocentric (A) macrochromosomes (M). 2n = 36 A.

sian, form (eastern part of eastern and southern Carpathian Basin) and do not support the existence of a northsouth corridor of western chromosomal form in the eastern and southern Carpathians (Belcheva et al., 1986; Kupriyanova and Rudi, 1990; Guillaume et al., 1997; Kupriyanova, 2004; Surget-Groba et al., 2006; Ljubisavljevich et al., 2010; Velekei et al., 2014, 2015).

From the above we may notice also that on A. Isachenko classification (Isachenko, 1971) a western form mainly inhabits sub-and atlantic climatic zones of Europe while other, Russian, form – subcontinental one.

Although it is clear that a certain kind of variability cannot be excluded, additional samples from different areas should be examined and the chromosomal investigations should be extended in order to refine the distributional patterns of the two chromosomal forms and to identify more zones of secondary contact. Additionally, also the external morphology, particularly the variability of the pileus shield pattern in *Zootoca vivipara* should receive more attention.

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