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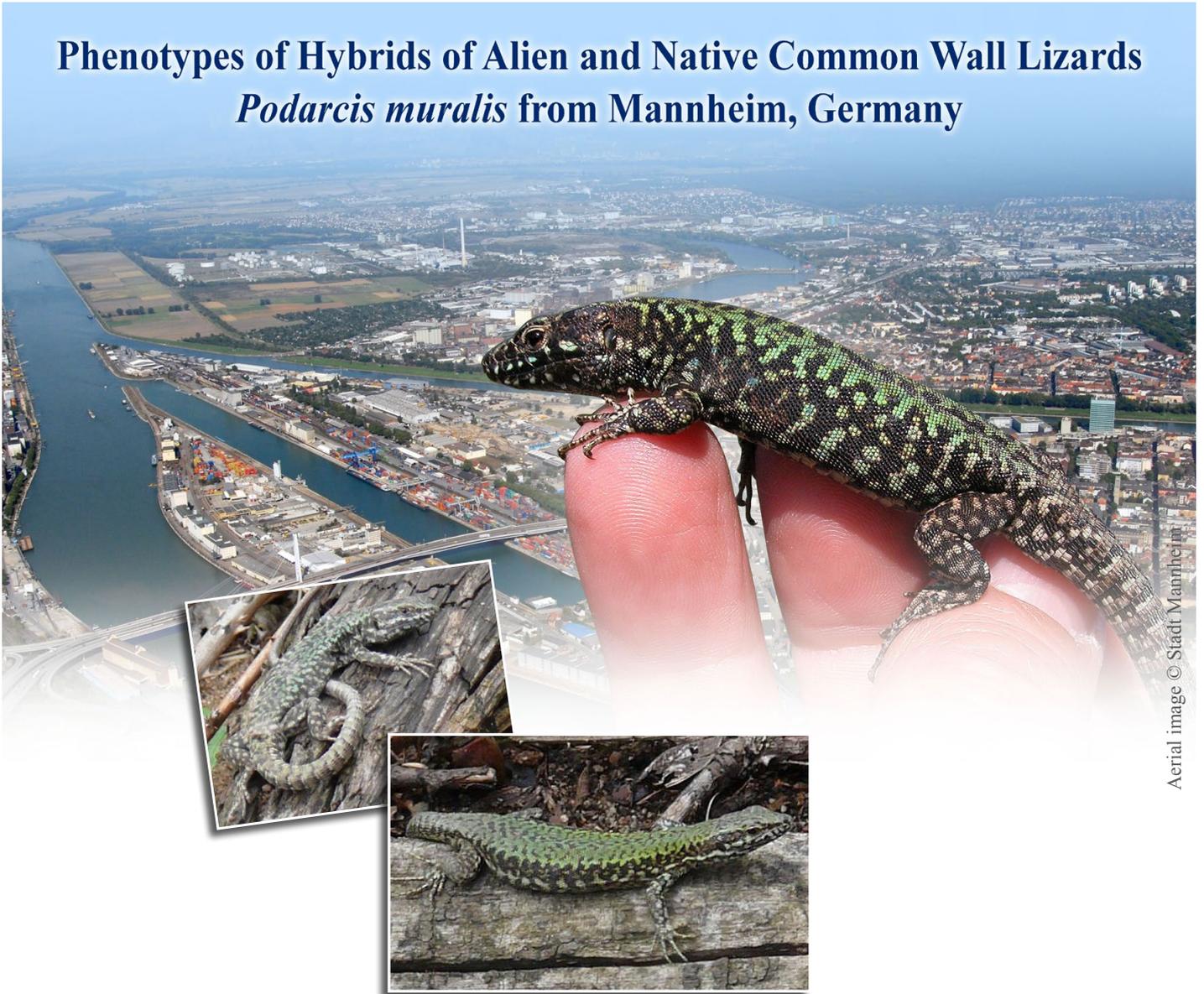
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Phenotypes of Hybrids of Alien and Native Common Wall Lizards *Podarcis muralis* from Mannheim, Germany



Aerial image © Stadt Mannheim

GUNTRAM DEICHSEL, ULRICH SCHULTE and JOSCHA BENINDE, September 2015

Motivation

With this series of images we want to demonstrate the diversity of hybrids of the Common Wall Lizard, stressing that an assessment of the hybrid statuses of Wall Lizards based on phenotypic characteristics alone is difficult and often only possible in a speculative way.

The **phenotype** of an individual is defined as the sum of its observable traits, i.e. morphology. It is determined by nuclear DNA encoding the genome, which contains both maternal and paternal DNA, as well as the environment, which may limit resources and thus affect phenotypes differentially.

The taxonomic units within species, i.e. subspecies, were described predominantly by their phenotypes in the past. This presents many problems when dealing with diversity within species and the common wall lizard is no exception.

Here, taxonomic units within this species, i.e. subspecies, are not congruent with evolutionary units, as derived from mitochondrial DNA analyses. This method was used up to the beginning of the 21st century in taxonomy and compares sequences of mitochondrial DNA, reflecting its evolutionary history. The advantage of mitochondrial DNA is that it is easier to sequence, since it contains only one copy of parental heritage information, i.e. the **haplotype**. The haplotype is a sequence of bases within a mitochondrial gene, which codes proteins for cellular processes, and is not directly reflected in observable traits of an individual. Since mitochondria are only passed down the maternal line, they provide only „half the story“ – a limitation making it impossible to infer hybridization events within populations based solely on this method.

Since the beginning of the 21st century, analysis of nuclear DNA became an established method of studying such population genetic processes. Including both maternal and paternal DNA of nuclei, the hybrid status of individuals can be determined. Most commonly, this is carried out by means of so-called microsatellite analyses. These can provide insight into the history of gene flow, such as between individuals of populations, known to harbor different lineages of the common wall lizard. However, after multiple generations of hybridization, populations of the common wall lizard have been shown to represent a homogenous genetic mixture of all individuals, and are then termed hybrid swarms. In such a case, individuals do not belong to a specific lineage, but to this newly emerged hybrid swarm. At the same time, it is possible to count haplotypes of such a population. Hence one can determine nominally genetic lineages existing in a population and calculate their relative frequencies. This can deliver interesting information on the putative origin of populations but, from a conservation point of view, it is fundamentally questioned whether such hybrid-populations with non-native lineages still possess conservation value at all.

Examinations of Common Wall Lizards from the location

SCHULTE et al. (2011, 2012) report on a population of 640 individuals of the Common Wall Lizard from an area next to the Ried Railway Bridge in the City of Mannheim. After microsatellite analyses, the authors assign the population to the Venetian

and the Southern Alps lineages (*Podarcis muralis maculiventris*). Further, they consider the population to have originated from a deliberate release and mention hybridisation with native *P. m. brongniardii* of the Eastern France lineage. In addition, BENINDE (unpublished data) found a few specimens of the Western France lineage of *P. m. brongniardii* within Mannheim's city boundary. Judging from the fact that three alien lineages are occupying the area, repeated rafting on rail freight appears to be very likely in addition to deliberate release.

The area inhabited is a little-used industrial rail track, adjacent allotment gardens and a dumping site for garden waste. Individuals of all mentioned lineages hybridize with each other, but the Italian lineages interbreed in a dominant way, suppressing the native lineage (SCHULTE et al. 2012). Below we present images of a few of these individuals from Mannheim after a description of the appearance of genetically pure individuals.

Description of pure phenotypes

Pure native *P. m. brongniardii* of the Eastern France lineage are dorsally brown to brownish grey with small black marks, which may be absent. A thin black line, which may be broken or missing, runs along the middle of the dorsum. The venters are white, isabelline, orange or red (rarely yellow) with few or no black marks. In individuals with white venters, often only the throats are coloured. Individuals of the Eastern France lineage are smaller than those of the Venetian and the Southern Alpine lineage.

Pure *P. m. brongniardii* of the Western France lineage chiefly differ from individuals of the Eastern France lineage by their generally more coarse pattern. Pure native *P. m. maculiventris* of the Southern Alpine lineage are dorsally brown to brownish grey with small black marks and frequently display a net-like (reticulated) pattern. Along the middle of the dorsum runs a broader (than in *P. m. brongniardii*) row of black marks, which may merge into a line in some animals and which is missing only in very rare cases. There are also individuals displaying light marks on a dark base coloration. Venters are white, isabelline, frequently yellow, ochreous, orange or red. Black marks on venters are, if present, small.

Pure *P. m. maculiventris* of the Venetian lineage are dorsally brown or brownish grey and patterned more coarsely than individuals of the Southern Alpine lineage. Venter are purely white with coarse black flecks. There are also individuals with green dorsa. WERNER MAYER (personal information) postulates the hypothesis, that the green coloration of Venetian individuals stems from male *P. m. nigriventris* of the Tuscany lineage which crossed the Apennines to NE Italy after the last ice age in warmer climatic periods, leaving their “green traces”. This hypothesis explains the fact that the number of individuals with green dorsa increases towards the northern border of the Apennines,

starting from the city of Bologna. Occasionally single individuals of the Tuscany type “Mendel out” in a phenotypically almost pure form and can be found from the northern border of the Apennines up to the region around Bologna. These individuals are dark green, coarsely black patterned and often display a largely broken broad black irregular zigzag stripe on the dorsum, having black venters with white marks (fig. [2], [3]). Thus natural hybrids of the Venetian and the Tuscany lineage exist in NE Italy. Without knowledge of the origin of such individuals, there is no way to decide if they were introduced as hybrids or if hybridisation took place only at the site of introduction.

In what follows we present and comment on some phenotypes from the area next to the Ried Railway bridge in Mannheim.



Fig. 1 – Industrial rail track bordering allotment gardens. The slope of the rail bed is SE-exposed, bending towards NE. Photo by Guntram Deichsel, 19 June 2015



Fig. 2 – Lateral view of a hybrid male phenotype *P. m. nigriventris* at the garden waste dumping site. His haplotype is that of the Venetian lineage of *P. m. maculiventris* which is not reflected in observable traits, however. In particular, the coloration lacks brown elements which are typical of *P. m. maculiventris*. Photo by Marcus Schrenk, 11 May 2006



Fig. 3 – Ventral aspect of the individual in [2]. In this hybrid the black base coloration of the underside is restricted to the throat. In pure *P. m. nigriventris* of the Tuscan lineage, the proportion of black on the venter is higher. Photo by Marcus Schrenk, 11 May 2006.



Fig. 4 – Swabbing the oral mucosa of an individual of the Venetian lineage's haplotype. Besides the green dorsum, there are brown elements in the coloration. Such animals are found as natural hybrids with the Tuscany lineage between Bologna and the northern border of the Apennines. Photo by Guntram Deichsel, 5 July 2010



Fig. 5 – Male hybrid (with partially shed skin) of the Venetian x Southern Alps lineage with rudimentary green coloration – a trace of the Tuscan impact on the Venetian lineage. The broken stripe on the dorsum is frequently found in this form on individuals of the Southern Alpine lineage and more frequently in the Eastern France lineage. Photo by Guntram Deichsel, 5 July 2010



Fig. 6 – Ventral aspect of the individual in [5] which is typical of the Venetian lineage.
Photo by Guntram Deichsel, 5 July 2010



Fig. 7 – Female hybrid of the Venetian x Southern Alpine lineage with a more marked green coloration than in the individual in [5, 6]. This stronger impact of the Tuscan lineage is also reflected in the broad stripe breaking down to blotches, on the middle of the dorsum. Photo by Guntram Deichsel, 5 July 2010



Fig. 8 – Underside of the individual in [7]. The throat is only moderately dark with light marks – another indication to the closeness to the Tuscan type. Photo by Guntram Deichsel, 5 July 2010



Fig. 9 – Male hybrid of the Venetian x Southern Alpine lineage. In this individual the impact of the Tuscan lineage is even stronger than in [5-8]: the dorsum displays a broad “tattered”, and partially dissolved, irregular black zigzag stripe. Photo by Guntram Deichsel, 5 July 2010



Fig. 10 – Underside of the individual in [9]. Closeness to the Tuscan lineage is reflected here by the black white-flecked throat. Photo by Guntram Deichsel, 5 July 2010



Fig. 11 – Female Venetian x Southern Alpine hybrid. The dorsal pattern is typical of the Southern Alpine lineage. Photo by Guntram Deichsel, 5 July 2010



Fig. 12 – Underside of the individual in [11] – typical of the Venetian lineage.
Photo by Guntram Deichsel, 5 July 2010



Fig. 13 – A pair of hybrids with unclear status. Phenotypically, the small marks on the male indicate the Southern Alpine lineage and the almost uniform dorsum of the female indicates the Eastern France lineage. Green indicates the Venetian lineage.
Photo by Guntram Deichsel, 19 June 2015



Fig. 14 – Male of the Venetian lineage during the skin-shedding period, showing a heavy impact of the Tuscan lineage. Photo by Guntram Deichsel, 19 June 2015



Fig. 15 – In this female an allocation to the Eastern France or the Southern Alpine lineage is not possible. It is also possible that it is a hybrid of both lineages. Photo by Guntram Deichsel, 19 June 2015



Fig. 16 – Male multiple hybrid of the Eastern France lineage with involvement of at least two further lineages.
Photo by Joscha Beninde 2012



Fig. 17 – Underside of the individual in [16]. The high proportion of red indicates an only weak involvement of the Venetian lineage.
Photo by Joscha Beninde 2012



Fig. 18 – Multiple hybrid of the Eastern France lineage. The very weak proportions of green on the borders of the dorsum indicate an involvement of the Venetian lineage which is, however, not reflected in the small marks. Photo by Joscha Beninde 2012



Fig. 19 – Underside of the specimen in [18]. Isabelline venters like that shown here are found on individuals of the Eastern, Western France and Southern Alps lineage. The marking does not offer reliable clues for an allocation to a lineage as well. Photo by Joscha Beninde 2012.



Fig. 20 – Female Eastern France x Venetian lineage hybrid and a male with unclear status. The phenotype of the male is frequent on the northern border of the Apennines where individuals of the Venetian haplotype are strongly influenced by the Tuscan lineage. Photo by Guntram Deichsel, 15 June 2015



Fig. 21 – Male multiple hybrid of the Western France haplotype with genotypic components of the Eastern France and the Southern Alps lineage. Photo by Joscha Beninde 2012



Fig. 22 – Ventral aspect of the individual in [21]. Photo by Joscha Beninde 2012



Fig. 23 – Male multiple hybrid of the Western France haplotype with genotypic components of the Eastern France, the Southern Alps and the Venetian lineage. Photo by Joscha Beninde 2012



Fig. 24 – Ventral aspect of the individual in [23]. Photo by Joscha Beninde 2012

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Credit:

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