



Common lizards break Dollo's law of irreversibility: Genome-wide phylogenomics support a single origin of viviparity and re-evolution of oviparity

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ABSTRACT

Dollo's law of irreversibility states that once a complex trait has been lost in evolution, it cannot be regained. It is thought that complex epistatic interactions and developmental constraints impede the re-emergence of such a trait. Oviparous reproduction (egg-laying) requires the formation of an eggshell and represents an example of such a complex trait. In reptiles, viviparity (live-bearing) has evolved repeatedly but it is highly disputed if oviparity can re-evolve. Here, using up to 194,358 SNP loci and 1,334,760 bp of sequence, we reconstruct the phylogeny of viviparous and oviparous lineages of common lizards and infer the evolutionary history of parity modes. Our phylogeny supports six main common lizard lineages that have been previously identified. We find strong statistical support for a topological arrangement that suggests a reversal to oviparity from viviparity. Our topology is consistent with highly differentiated chromosomal configurations between lineages, but disagrees with previous phylogenetic studies in some nodes. While we find high support for a reversal to oviparity, more genomic and developmental data are needed to robustly test this and assess the mechanism by which a reversal might have occurred.

1. Introduction

There are numerous examples for the loss of a complex trait in the animal kingdom throughout evolution. Dollo's law of irreversibility states that once such a complex trait has been lost, it cannot be regained (Gould, 1970). Some exceptions to this rule have been discovered, though it remains a very rare phenomenon in evolution (Collin and Miglietta, 2008; Lynch and Wagner, 2010). Oviparity (egg-laying) is an example for such a complex trait and has been lost on several independent occasions throughout animal evolution (Lee and Shine, 1998; Murphy and Thompson, 2011). While there are more than a hundred independent transitions from oviparity to viviparity (live-bearing) in reptiles (Blackburn, 2006; Sites et al., 2011), only one robust example for the re-evolution of the eggshell is known to date (Lynch and Wagner, 2010). Molecular mechanisms by which reversals in complex traits such as reproductive mode occur are to date unknown.

The common lizard (*Zootoca vivipara*) is the most widespread extant terrestrial reptile species. Its distribution covers nearly the whole of Europe, northern and central Asia and as far as Japan in its easternmost range. Within this distribution, common lizards have adapted to various extreme environments. Arguably the most salient of these adaptations is

the evolution of viviparity, unique within European lizards that are otherwise oviparous. As one of the youngest transitions from oviparity to viviparity known in vertebrates (Pyron and Burbrink, 2014; Surget-Groba et al., 2006), common lizards are an emerging model system for the study of viviparity (Freire et al., 2003; Le Galliard et al., 2003; Murphy and Thompson, 2011). However, not all common lizards are live-bearing: of the six currently recognized common lizard lineages, two are oviparous and four are viviparous (Surget-Groba et al., 2006; Fig. 1). One oviparous lineage is restricted to northern Spain and southwestern France, allopatric to all other common lizard lineages. A second oviparous lineage occurs in the southern part of the Alps. Four viviparous lineages cover the rest of the Eurasian distribution (Mayer et al., 2000; Surget-Groba et al., 2006; Fig. 2).

The phylogenetic relationships within *Zootoca* have not been fully resolved. The evolutionary history of the two different parity modes has been controversial depending on which data were used to interpret the phylogenetic relationships. In a first study using a single mitochondrial gene, both oviparous lineages were found to be sister to all other viviparous lineages, consistent with a single origin of viviparity (Surget-Groba et al., 2001; Fig. 1A). However, subsequent analyses on the karyotype of common lizards resulted in a more complex evolutionary

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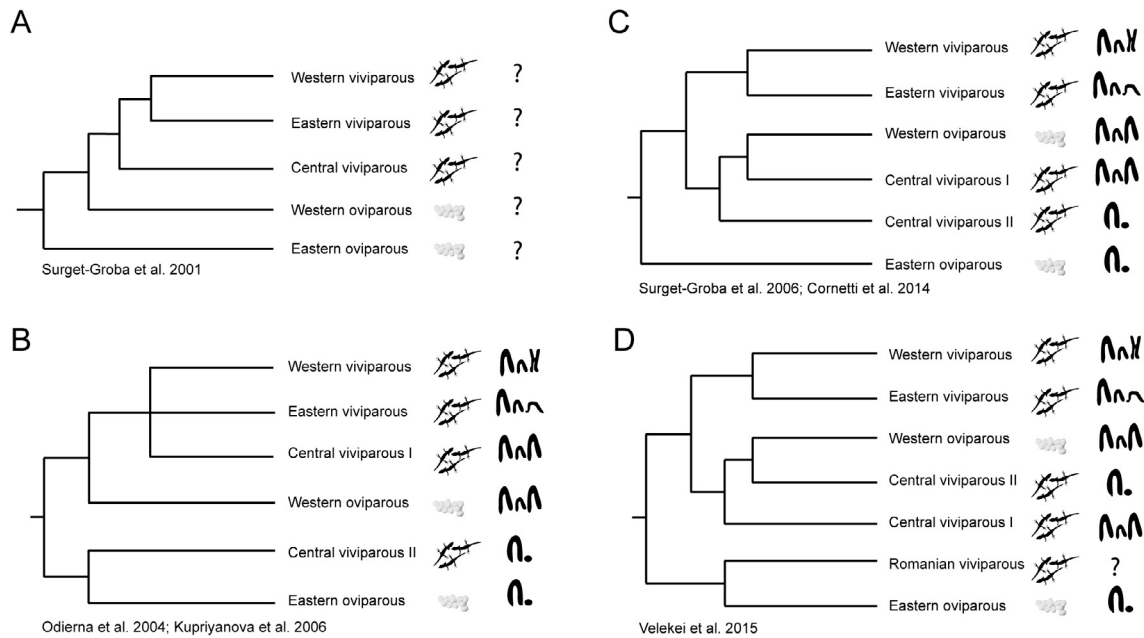


Fig. 1. Alternative hypotheses for phylogenetic relationships of common lizards and parity mode evolution. Parity mode and sex chromosome configuration (ZW or Z_1Z_2W ; Odierna et al., 2004) are illustrated next to each respective lineage. Phylogenetic tree (A) involves a single origin of viviparity and was supported by one mtDNA gene. The second tree (B) is based on karyological studies and suggests two independent origins of viviparity. Hypothesis (C) suggests a reversal to oviparity as most parsimonious scenario, based on mtDNA and a few nuclear genes. The last phylogeny (D) includes a recently discovered viviparous lineage in the Carpathians, which was found to be closely related to the eastern oviparous lineage. Parity mode evolution in this scenario involves two independent origins of viviparity and a reversal to oviparity.

scenario, arguing for two origins of viviparity based on sex-chromosome evolution (Z_1Z_2W or ZW) (Odierna et al., 2004; Surget-Groba et al., 2006; Fig. 1B). More extensive geographic sampling and sequencing of mitochondrial genes instead favored a scenario of a single origin of viviparity followed by a reversal to oviparity in the Spanish western oviparous lineage (Cornetti et al., 2014; Surget-Groba et al., 2006; Fig. 1C), though this phylogeny was incompatible with a single origin of the Z_1Z_2W sex chromosome system. Finally, a population inhabiting the Carpathian region in Romania was discovered recently and was found to be most closely related to the phylogenetically basal eastern oviparous lineage based on mtDNA (Velekei et al., 2015; Fig. 1D). The reproductive mode of this lineage was not reported, but since all other common lizard populations in its geographic proximity are viviparous (Surget-Groba et al., 2006), this would suggest another independent origin of viviparity. However, all phylogenies to date have had limited support at deeper nodes essential for the interpreting the evolutionary scenarios of parity mode evolution. Moreover, phylogenies reconstructed only from mitochondrial DNA have limited information and frequently misrepresent the ‘true’ phylogenetic relationships (Ballard and Whitlock, 2004; Near and Keck, 2013; Wallis et al., 2017). Therefore, it is essential to incorporate high resolution nuclear DNA sequencing to resolve difficult topologies. Moreover, coalescent-based approaches for disentangling incomplete lineage sorting effects and hybridization have considerably advanced phylogenetic reconstruction (Bouckaert et al., 2014; Pickrell and Pritchard, 2012; Posada, 2016).

The evolutionary implications for models involving several origins of viviparity and/or a reversal to oviparity are significant. A reversal to oviparity from viviparity is considered a very unlikely evolutionary scenario, presumably breaking Dollo’s law of irreversibility (Lee and Shine, 1998). Common lizard parity mode evolution could represent one of the very few examples for an exception to this ‘law’ (Surget-Groba et al., 2006). Further, the evolution of both oviparity and viviparity are difficult to study from a molecular genetic perspective because they have most frequently occurred at deep evolutionary time scales. Common lizards provide an example of recent parity mode

changes and therefore a critical insight to usually more ancient evolutionary events.

To tackle this outstanding evolutionary question, we use genome-wide phylogenomics with data from double-digest restriction-site associated DNA sequencing (ddRADSeq), a next generation sequencing (NGS) technique, to identify DNA polymorphisms across all common lizard lineages (Peterson et al., 2012; Recknagel et al., 2015, 2013). Using broad geographic sampling of 67 individuals, we reconstructed a nuclear phylogeny of up to 1.33 million nucleotides, and a mitochondrial DNA phylogeny based on cytochrome *b*, using coalescent, Maximum Likelihood, and Maximum Parsimony methods. We performed topological tests and model-based ancestral state reconstructions to assess the likelihood of alternative scenarios for parity mode evolution. Our results strongly support a single origin of viviparity in common lizards and a subsequent reversal to oviparity in one derived lineage as the most probable scenario of reproductive mode evolution.

2. Material and methods

2.1. Sampling

Samples and specimens were obtained from the Natural History Museum in Vienna, the Royal Ontario Museum, and fieldwork during 2013–2016 (see Table S1 for specimens and Fig. 2 for a map of collecting localities). Lizards were collected by diurnal opportunistic searches. Tail clips (up to 2 cm) were extracted and preserved in 95–99% ethanol and lizards were released thereafter. Mode of reproduction was assessed by observation of an individual retained in captivity until oviposition/parturition or from data on other individuals at the same site.

2.2. Generation of molecular data

DNA was extracted from tissue using a Dneasy Blood and Tissue Kit (Qiagen) following the manufacturer’s protocol. Three genomic libraries were constructed using double-digest restriction-site associated

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