Population and Evolutionary Genomics of Lizards and Snakes

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Abstract

With an extraordinary diversity in body plans, colour patterns and lifestyles, and over 12,000 living species, squamate reptiles (lizards, snakes, and amphisbaenians) provide unparalleled opportunities to apply genomic tools for answering biological questions. From desert runners to rainforest climbers, high-mountain dwellers to sea snakes, squamates have repeatedly evolved remarkable innovations, including giving birth to live young (viviparity) and reproduction without males (parthenogenesis). This chapter explores how population and evolutionary genomics is used to understand squamate evolution, opening with a survey of the genomic resources currently available. Our own work on Mediterranean wall lizards serves as a case study, showing how genomes can illuminate evolutionary histories and allow inference about the genetic underpinnings of novel phenotypes. Research on the repeated evolution of viviparity and parthenogenesis is used to exemplify ongoing research to uncover the genomic and developmental genetic basis of phenotypic evolution. We conclude by looking ahead to the expanding role of genomics in countering the worldwide ongoing decline of squamates.

Key words: Squamates, diversification, innovation, phylogenomics, conservation genomics, wall lizards

Running head: Lizard and Snake Genomics

1. Introduction

With more than 12,000 extant species, squamate reptiles, or squamates, are the most species-rich order of vertebrates [1]. Squamates include the familiar lizards and snakes, the less-familiar worm lizards (amphisbaenians), and several extinct groups, such as mosasaurs. Both snakes and amphisbaenians (as well as mosasaurs) are nested within the squamate phylogenetic tree, which makes lizards a paraphyletic assemblage of different groups, such as geckos, chameleons, skinks and lacertids [2]. Since their origin some 240 million years ago [3], squamates have radiated into a diversity of lifestyles and adapted to many different environments, including deserts, rain forests, high mountains, and the sea. As of 2025, squamates include nearly 8000 described species of lizards, more than 4000 species of snakes and 203 species of amphisbaenians [The Reptile Database; accessed July 2025; 1]. In contrast, the closest relatives of squamate reptiles are represented by a single extant species - the tuatara (*Sphenodon punctatus*) of New Zealand - the sole survivor of a once-diverse clade [4].

This chapter examines how population and evolutionary genomics, which is the study of genome-wide variation within and between populations and species, has advanced our understanding of evolutionary diversification and innovation in squamate reptiles. We begin by summarizing the genomic resources currently available for this group. We then use our own research on Mediterranean wall lizards as a case study to illustrate how genomic data can be applied to reconstruct evolutionary history and uncover both the genetic basis and adaptive spread of complex phenotypes. Next, we review how genomic approaches have shed light on the evolution of novelty, focusing on two striking features of squamates that have repeatedly evolved: viviparity, which is giving birth to live young, and parthenogenesis, which is the capacity for reproduction without fertilization. Finally, we discuss the growing role of population genomics in informing conservation strategies for squamate reptiles.

2. Genomic resources for squamate reptiles

Squamates, in particular lizards, have long been model systems in evolutionary ecology, providing some of the most iconic examples of adaptive radiation [5]. In recent years, they have increasingly entered the genomic era of biological research, with the reconstruction of genome-wide sequence resources serving as a crucial step along the way. These genomic resources, initially restricted to selected regions (e.g., ultraconserved elements, anchored phylogenomic loci [6]), enable the extraction of thousands of phylogenetic markers that enable investigations of taxonomic relationships at an unprecedented level of detail. A major success stemming from these phylogenomic approaches was the clarification of phylogenetic relationships of the order of squamates at higher taxonomic levels [7, 8]. In addition, phylogenomics uncovered genomic regions with discordant histories, such as those shaped by introgression or incomplete lineage sorting [9]. Beyond the use of selected genomic regions, the assembly of entire reference genomes provides another crucial step forward and opens up new avenues of research. It allows, for example, an exploration of the natural history of genomes, for example through comparative genomics or 'pan-genomic' approaches that can reveal structural variation and lineage-specific innovation of genome content and organisation [10, 11]. At lower taxonomic levels, reference genomes serve as anchors for mapping individual-level sequence data, thereby enabling powerful population genomic analyses. While cross-species mapping is often feasible, its success declines with increasing evolutionary divergence due to sequence mismatches, in particular in fast-evolving regions of the genome. This makes the generation of clade-specific reference genomes a priority for the squamate research community. Broad and representative genomic coverage will greatly enhance the accuracy and resolution of comparative and population-level studies across the entire squamate radiation.

To assess the current state of squamate reference genomes, we conducted a survey of all currently available genome assemblies on the NCBI database (database accessed: July 2025). For an overview of our survey method, see **Note 1** or access github page https://github.com/FeinerUllerLab/SquamateGenomics). To put the status of squamate reference genomes into a broader context, we conducted equivalent surveys for mammals, birds and amphibians [see 12 for a detailed comparison].

The first published squamate genome was that of the green anole (*Anolis carolinensis*) in 2011 [13]. Since then, the number of publicly available reference genomes has steadily increased. As of July 2025, genome assemblies are available for 302 squamate species and most of the major clades of squamates are represented by at least one such genome assembly (Fig. 1A and B). Of these, 79 species, that is 0.6% of all squamate species, possess genome assemblies that are at chromosome-level and 32 include phased haplotypes, which is considered the current gold standard. The proportion of species with high-quality reference genomes (i.e., chromosome-level) is comparable to that of amphibians (0.5%), but lower than that of mammals (4.9%) and birds (1.9%; Fig. 1C). Given that amphibian genomes are particularly challenging due to their large size and high repeat content [14], the primary reason for why squamate reference genomes lag behind those of mammals and birds is the comparatively lower investment and effort from the research community.

The 79 chromosome-level reference genomes of squamates are relatively evenly distributed across the major groups, but a reference is still lacking for the Scolecophidia, a group of fossorial blind snakes (Fig. 1B). In contrast, dedicated research efforts have produced a high density of reference genomes for certain groups, most notably the genus *Podarcis* (Mediterranean wall lizards), where 14 of the 28 recognized species are represented by at least one chromosome-level genome assembly [15-27, 28; Fig. 1]. These resources enable fine-scale studies of genome evolution and adaptation at both the genus and species levels.

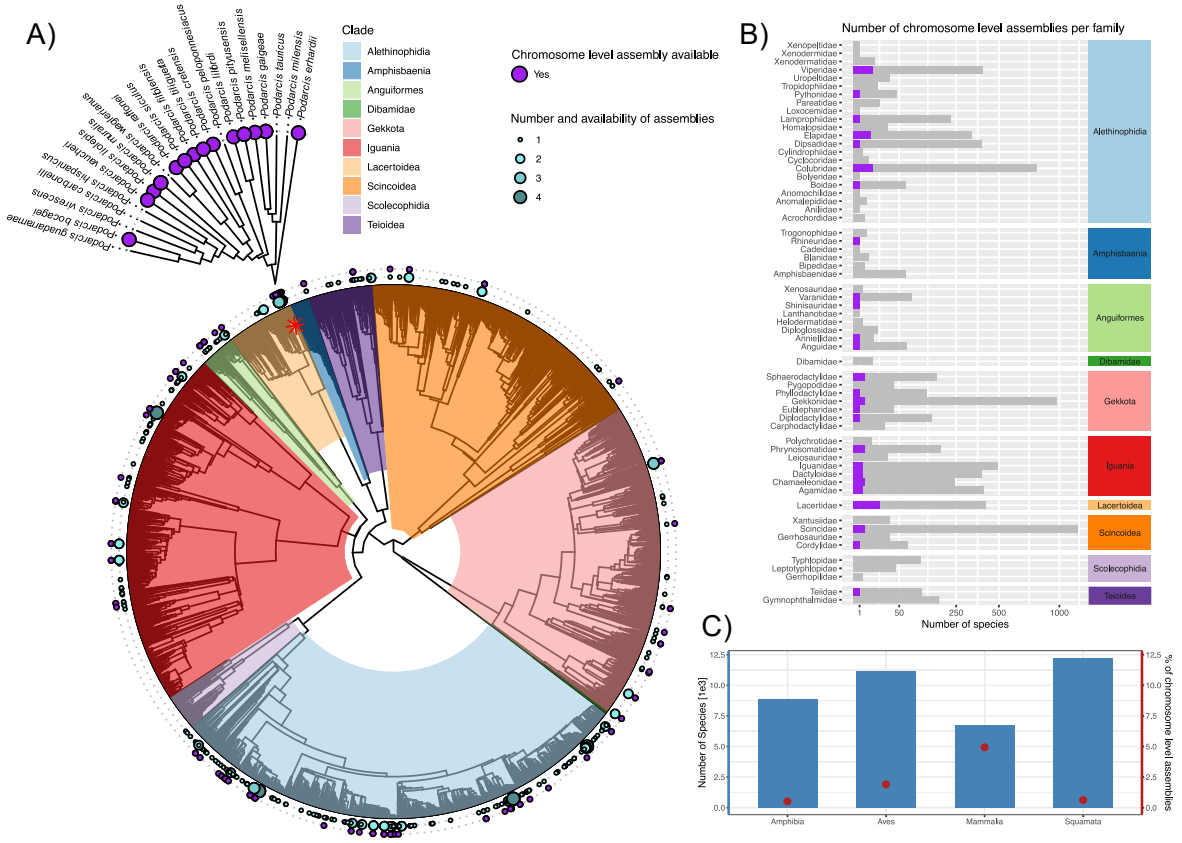

Fig. 1. Taxonomic distribution of genome assemblies across squamates. A) Phylogenetic tree of 6,885 species of squamates adapted from Title *et al.* [7] and the genus *Podarcis* is magnified at the top left. Note that this particular tree contains only 22 of the 28 described species of the genus *Podarcis* and that the tree topology does not entirely match the commonly accepted phylogenetic relationships [29, 30]. Color-coded circles on tips mark species that are represented by a reference genome at chromosome-level (purple) or at a lower quality (light blue). B) Overview of the distributions of chromosome-level reference genomes (purple bars) in relation to the number of described species (grey bars) at the family level across the ten major groups of squamates. C) Comparison of the percentages of available chromosome-level assemblies (red dots, right axis) in relation to the recognized number of species (blue bars, left axis) between squamates, amphibians, birds and mammals.

Squamate genomes range in size from approximately 0.9 to 2.8 Gb [31], with most assemblies falling between 1 and 2 Gb (Fig. 2). The quality of the existing 302 squamate genome assemblies is highly variable, which is reflected in scaffold N50 values and BUSCO scores

(Fig. 2). Scaffold N50, a measure of assembly continuity, ranges from 316 bp in *Xenodon rabdocephalus* to 390 Mbp in *Bradypodion pumilum*, with lower values indicating more fragmented assemblies. Low scaffold N50 values are often associated with lower BUSCO scores, which assess assembly completeness based on the presence of conserved orthologous genes. Note that this approach does not rely on genome annotations, but instead maps a reference protein database of universal single copy orthologs to genome sequences using 'miniprot'. Low BUSCO scores typically indicate incomplete or fragmented assemblies with missing or misassembled genomic regions. In general, variation in assembly quality poses challenges for comparative genomic applications, where incomplete gene repertoires or fragmented assemblies can lead to spurious results. Consequently, standardized protocols for genome assembly, such as those developed by ERGA [32] or the Darwin Tree of Life Project [33], are essential for producing high-quality reference genomes. These protocols ensure consistency, reliability, and compatibility across species, greatly enhancing the utility of squamate genomic resources in evolutionary and ecological research. Despite the overall high level of variation in terms of assembly quality, biologically interesting patterns can be observed even at this crude level of comparison. For example, the GC-content of snakes, with an average of 40.3%, is consistently lower than that of lizards, with 43.3% on average (Fig. 2). Identifying and systematically testing for such patterns can provide important insights into the evolution of genomes.

One shortcoming of the currently available resources is the widespread lack of gene annotations (Fig. 2). Until recently, obtaining high-quality gene annotations relied on the availability of transcriptomic datasets, ideally sourced from diverse tissues, which posed a challenge to many genome projects. Recent advances instead use deep-learning-based methods such as Tiberius and implement an *ab initio* (i.e., not based on transcriptomic data) pipeline

that rivals the quality of traditional gene annotations [34]. These developments may help to address the shortcoming of missing gene annotations in the near future.

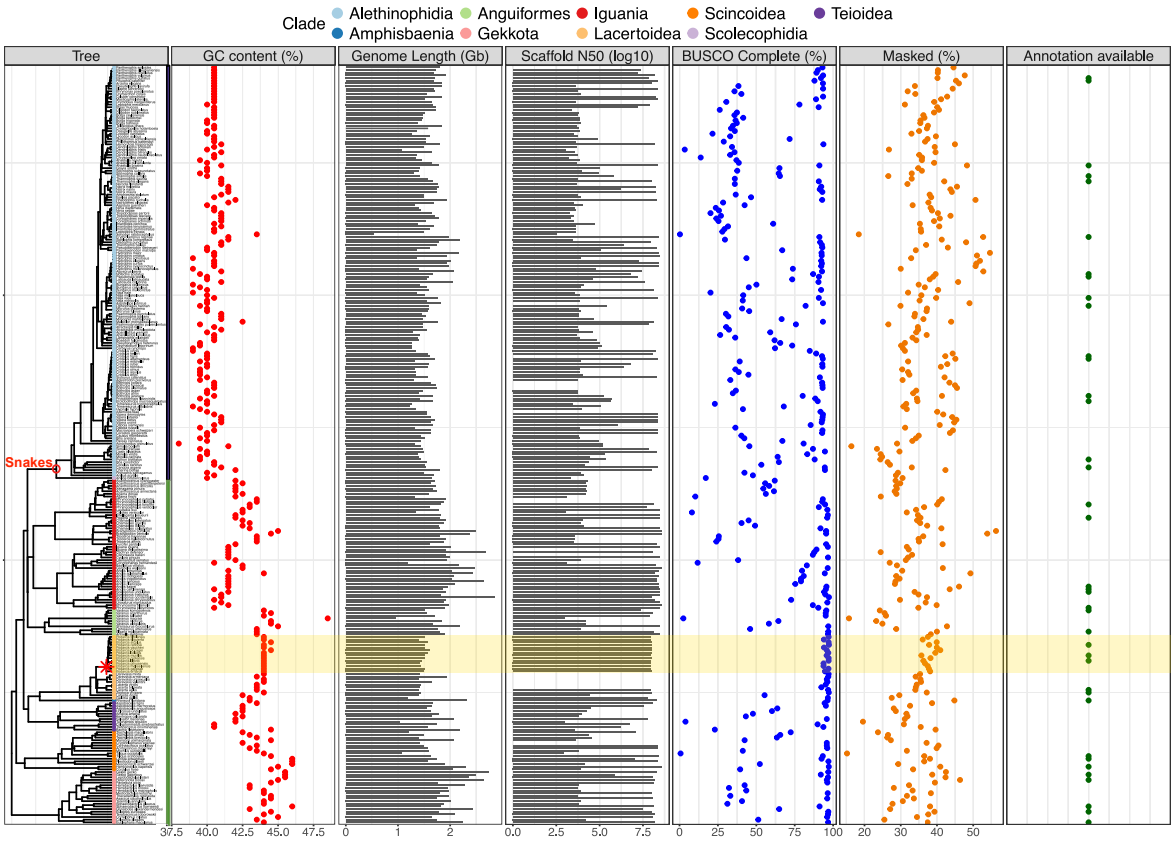

Fig. 2. Statistics and quality metrics of the 302 genome assemblies currently available for squamates. Columns present, from left to right, GC-content in percent, genome length in Gb, scaffold N50 values, BUSCO completeness scores in percent, percentage of genome that is masked, and whether a gene annotation is available (green dot for presence). The 14 species of *Podarcis*, a genus exceptionally densely covered with reference genomes, are highlighted with a yellow box. Note that missing data for scaffold N50 values indicates that assemblies are not at the scaffold level.

3. Evolution of *Podarcis* lizards in the Mediterranean Basin

3.1 Meet the wall lizards

Wall lizards of the genus *Podarcis* are small- to medium-sized, egg-laying members of the lacertid family, distributed across the western and northern Mediterranean region. Although a

few species are widespread on the mainland, it is their remarkable abundance and diversity on Mediterranean islands that has drawn particular attention [Fig. 3; 35, 36]. Insular populations often exhibit striking differences in body size and coloration and show frequent convergence among independently evolving populations and lineages [37]. Providing explanations for this "chaos of variation" has challenged researchers ever since the 19th century [38]. Moreover, the exceptional phenotypic variation has challenged the reconstruction of phylogenetic relationships among populations and lineages.

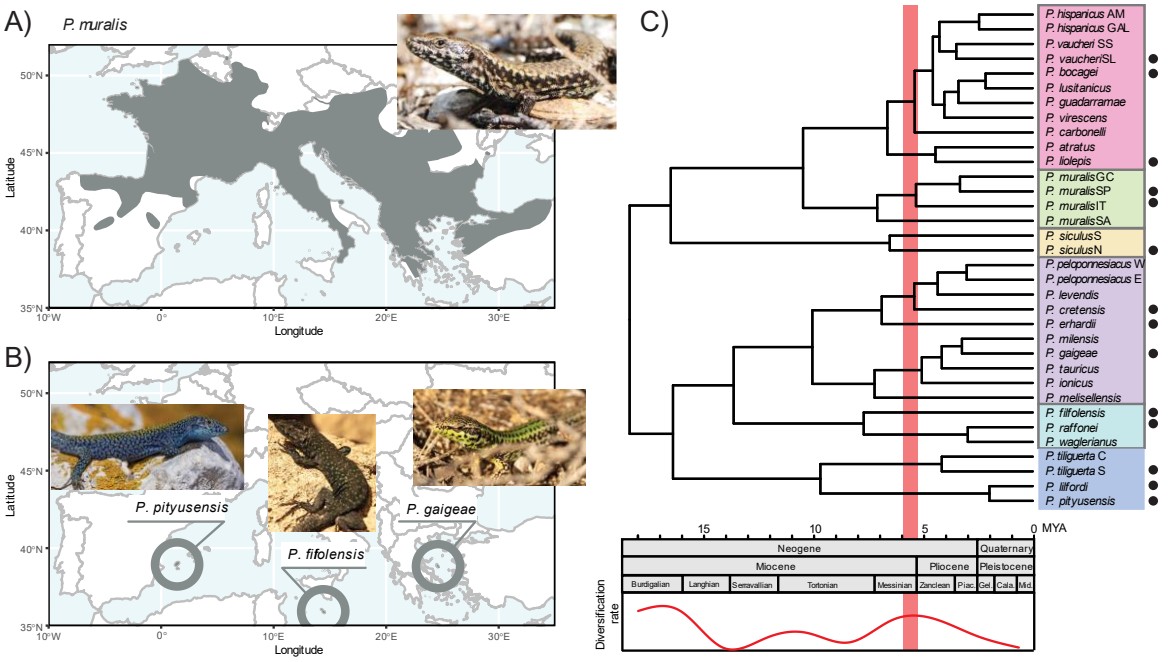

Fig. 3. Geographic distribution of selected species and phylogenetic relationships within the genus *Podarcis*. A) The common wall lizard *Podarcis muralis* occupies a broad distribution range that stretches from the Iberian Peninsula in the west to Asia Minor in the east. It is also native to extra-Mediterranean regions in western, central, and eastern Europe. B) In contrast, the Ibiza wall lizard (*P. pityusensis*), the Maltese wall lizard (*P. filfolensis*) and the Skyros wall lizard (*P. gaigeae*) are endemic to Mediterranean islands. Each of these species occupies one or two main islands and surrounding islets, some of which are very small. C) The time-calibrated maximum-likelihood phylogenetic tree of the 34 major lineages of wall lizards based on whole-genome sequences (outgroup not shown). All nodes were 100% supported with 1000 bootstrap replicates, but not across all local trees derived from 200 kb

windows [for details, see 29]. The lower panel shows the geological time scale of the evolutionary history of *Podarcis* and the estimated diversification rate. The thick red line indicates the Messinian Salinity Crisis (~6.0–5.3 MYA). The coloured rectangles on the tips of the tree denote geographically coherent groups of wall lizards. Dots to the left mark species or lineages for with chromosome-level genome assemblies are available. Panel C adapted from [29]. Picture credit: *P. muralis* and *P. filfolensis*, Nathalie Feiner; *P. pityusensis*, Day's Edge Productions; *P. gaigeae*, Javier Abalos.

3.2 Reconstructing evolutionary relationships within wall lizards

As an initial step towards resolving the evolutionary history of *Podarcis* wall lizards, we generated whole-genome resequencing data for 34 major lineages, encompassing all 26 recognized species at that time [29] (*see* **Note 2**). These sequences were aligned to the *Podarcis muralis* reference genome, and several phylogenomic analyses were conducted to infer evolutionary relationships among lineages. Both concatenated and multispecies coalescent approaches produced highly congruent phylogenies, consistently identifying two major clades. Estimates of divergence times, obtained using a relaxed molecular clock calibrated with the Lacertidae phylogeny, indicate that these clades diverged approximately 20 million years ago. One clade comprises deeply divergent lineages of the widely distributed common wall lizard (*P. muralis*) and the extant species that have their distribution centred on the Iberian or Italian peninsulas. The second major clade consists of three distinct subclades: two composed of insular species from the Western Mediterranean, and a third comprising all eastern-distributed lineages, several of which are also endemic to archipelagos.

The broad distribution and diversity of wall lizard lineages reflects the complex and dynamic geological history of the Mediterranean region. Notably, there is evidence for an increased rate of lineage diversification coinciding with the Messinian Salinity Crisis (5.9–5.3

million years ago), during which the Mediterranean Sea became largely isolated from the Atlantic Ocean. This isolation led to extensive evaporation and a dramatic drop in sea levels. The crisis ended abruptly with the reopening of the Strait of Gibraltar, triggering the rapid reflooding of the basin during the Zanclean flood that may have occurred in a period of less than two years [39].

Because wall lizards are generally poor overwater dispersers without human assistance, these events led to long-term isolation of many insular populations. Some of these lineages, such as the Balearic wall lizards, have since followed independent evolutionary trajectories [40, 41]. The geography of the Mediterranean Basin has also played a key role in shaping diversifications within species. For instance, the common wall lizard (*P. muralis*), which is widespread across southern and central Europe, comprises several deeply divergent lineages [dating from 6.2 to 2.5 million years ago; 42], each with distinct geographic distributions shaped by the Iberian, Italian, and Balkan Peninsulas [e.g., 43, 44]. On the European mainland, the distribution of this species was further influenced by climatic oscillations during the Pliocene and Pleistocene, with significant population declines during the Riss glaciation [ca. 200,000–100,000 years ago; 42]. Glacial cycles also strongly affected insular species, causing repeated episodes of fragmentation and reconnection within archipelagos [e.g., 45]. With the advent of genome-scale data, it is now possible to investigate how these dynamic historical processes have shaped phenotypic diversification, local adaptation, and genome evolution.

Although the phylogenetic relationships among *Podarcis* lineages appear well-resolved, extensive discordance was observed among local trees, supporting up to fifteen major instances of introgressive hybridization between major lineages [29]. In most cases, these events resulted in the introgression of approximately 5–10% of alleles from the minority ancestry. However, in several cases, hybridization led to a much more balanced genomic contribution from both parental lineages. A notable example is the clade of wall lizards

inhabiting Sardinia, Corsica, and the Balearic Islands, which exhibits roughly equal ancestry from the two major *Podarcis* clades. This pattern is consistent with a hybridization event estimated to have occurred approximately 10 million years ago [29], although this dating should be considered with caution. The geographic and ecological context for this event, and whether or not it represents a case of hybrid speciation, remain open questions for future research.

The transition from phylogenetics to phylogenomics has revealed that such instances of introgressive hybridization are widespread across many animal taxa. Similar to wall lizards, genome-scale data suggest that hybridization has played a prominent role in the evolutionary history of gemsnakes (Pseudoxyrhophiinae) [46], rattlesnakes (*Crotalus* and *Sistrurus*) [47], rock lizards (*Darevskia*) [48], and whiptail lizards (*Aspidoscelis*) [49]. Notably, in *Darevskia* and *Aspidoscelis*, hybridization has given rise to several parthenogenetic lineages (see below).

An illustrative counterexample is the gecko species *Heteronotia binoei*, a taxonomically unresolved radiation endemic to Australia that comprises >20 cryptic candidate species [50]. Despite relatively recent divergence times of the lineages within this species (2–5 million years ago), there is little evidence for introgression across the numerous contact zones. One possible explanation is that, unlike *Podarcis*, diversification in *Heteronotia binoei* appears to involve chromosomal rearrangements, which may act as strong barriers to gene flow. However, it is worth noting that contemporary gene flow is often limited also between *Podarcis* lineages [51, 52], despite extensive and widespread evidence of historical introgression [29]. More broadly, it remains a major challenge to infer when introgression occurred and its (bio)geographical and ecological contexts. Addressing this will require integrating genomic data with information on the physical geography, past species distributions, ecological dynamics, and spatial structure of hybrid zones.

Genomic data enable not only the reconstruction of evolutionary histories but also the identification of genes subject to positive selection [53]. In wall lizards, protein-coding genes of introgressed origin often exhibit elevated rates of molecular evolution compared to genes whose evolutionary histories align with the consensus phylogeny [29]. Furthermore, the co-introgression of mitochondrial genomes and nuclear genomic regions containing genes involved in energy metabolism and mitochondrial function provides additional evidence for adaptive evolution acting on introgressed genes [29]. We predict that more genomic data and refined methodology will provide important insights into the extent by which lineages 'mix and match' genetic elements and how selective processes shape genome evolution.

3.3 Origin and introgressive spread of a complex phenotype

Evolutionary change can be conceptualized as a two-step process: the emergence of a novel phenotype, followed by its spread within and across populations. While the latter step, the spread of a novel trait, is well understood theoretically, reconstructing the historical dynamics of this process has been challenging. In comparison, the origin of novel traits remains less well understood, both theoretically and empirically. Most empirical examples to date involve relatively simple traits controlled by a single locus, such as the difference between yellow and red plumage in parrots [54]. Genomic data now offer exciting opportunities to address these gaps by enabling researchers to uncover the developmental origins of complex traits and to trace their evolutionary trajectories across populations under selection. Here, we illustrate how this can be done using a case study of common wall lizards, *P. muralis*.

Across most of its range, the common wall lizard *Podarcis muralis* is a rather small, brownish wall lizard. In contrast, populations along the central west coast of Italy differ strikingly in both morphology and coloration. These lizards are significantly larger, with

disproportionately larger heads and strong bite force, and display rich and contrasting coloration, including extensive body melanisation, bright green dorsal coloration, and enlarged UV-blue lateral spots. These exaggerated characters are also accompanied by differences in behaviour, in particular higher aggression and dominance relative to the ancestral phenotype [55-57]. This distinctive suite of traits is most pronounced in populations described as the subspecies *P. muralis nigriventris*. However, the nigriventris traits vary quantitatively across central Italy and are consistently expressed together as a coordinated syndrome.

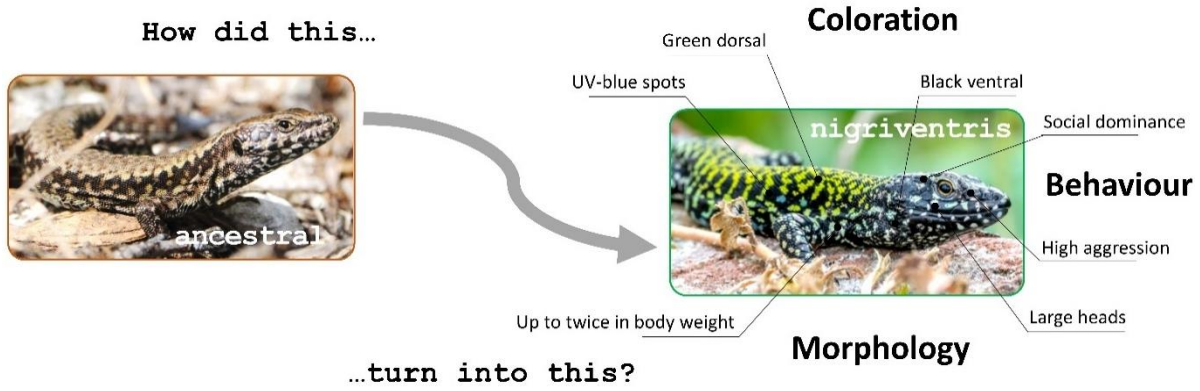

Fig. 4. Phenotypic difference between ancestral *P. muralis* and those with the nigriventris phenotype. Males are depicted and the key traits whose expressions differ between the two phenotypes are indicated on the right. Picture credit: Nathalie Feiner (left) and Arnaud Badiane (right).

We combined genomic and phenotypic data to reconstruct the origin and spread of the nigriventris phenotype in *P. muralis*. Analyses based on double digest restriction-site associated DNA sequencing (ddRADseq) confirmed that the nigriventris phenotype originated within the Central Italy lineage and subsequently introgressed into the distantly related Southern Alps lineage [58]. Although the hybrid zone is steep and relatively narrow, the introgression of nigriventris traits into the Southern Alps lineage is accompanied by asymmetric genomic introgression, consisting of approximately 3% of allelic variation. Notably, this asymmetry is absent in parts of the contact zone where both lineages share the

ancestral phenotype [51]. Experiments suggest that reproductive isolation between the Central Italy and Southern Alps lineages in areas of secondary contact is shaped more strongly by male than female mate choice [56]. These findings align with experimental enclosure studies showing that males expressing nigriventris traits outcompete ancestral males for access to high-quality territories and mates [55-57], suggesting that sexual selection drives the spread of the phenotype. Landscape-level analyses of phenotypic variation further indicate that the strength of sexual selection for the nigriventris syndrome is modulated by climate, with exaggerated morphological and coloration traits failing to spread into cooler regions such as the high Apennines [59].

The introgressive spread of the nigriventris syndrome offers an opportunity to identify candidate genes linked to this complex set of traits. In theory, selective co-introgression of multiple, genetically and developmentally complex traits could be facilitated by two main mechanisms. First, each trait might be controlled by separate genes, but inherited together because they lie within large, non-recombining genomic regions. A well-known example is the ruff, where a chromosomal inversion contains genes affecting coloration, body size, and reproductive behaviour, producing distinct morphs that are maintained by balancing selection [60]. Second, traits might be developmentally linked, so that changes in specific genes or regulatory elements cause multiple characters or character states to vary together.

In vertebrates, the coordinated evolution of coloration, morphology, physiology, and behaviour may be influenced by the biology of neural crest cells, an explanation proposed for the mammalian "domestication syndrome" [61]. The neural crest is a transient structure in early embryos whose migrating cells give rise to various tissues, including pigment cells, craniofacial structures, parts of the nervous system, and adrenal glands. Alterations in genes regulating neural crest cell development, such as their proliferation, migration, or differentiation, can simultaneously affect pigmentation, craniofacial features, and behaviour.

Therefore, while a single gene is unlikely to underlie the specific features of the nigriventris syndrome, developmental processes involving neural crest cells may facilitate the co-variation of certain characters, with the specific form of each character shaped by its own downstream developmental pathways. This hypothesis predicts that the ongoing introgressive spread of the nigriventris syndrome in *P. muralis* is enabled by one or more genes regulating neural crest cell development, while also drawing on locally available standing genetic variation across many additional loci to stabilize and refine functionally connected characters.

To identify candidate genes associated with the nigriventris syndrome, we leveraged two independent comparisons: one within the Central Italy (IT) lineage, where the syndrome originally evolved and spread, and another within the Southern Alps (SA) lineage, into which the syndrome later introgressed [62; Fig. 5A]. This paired design allowed us to perform F_{ST} (fixation index) outlier scans in both lineages using whole-genome resequencing data from 60 male individuals (Fig. 5B). By intersecting the outliers from these lineages, we identified 81 shared genomic regions (or "genomic islands"), which is 8.5 times more than expected by chance. These regions contained 45 protein-coding genes with biologically meaningful annotations. Notably, 24 of these genes (53%) could be linked to neural crest cell biology. In addition to F_{ST} outlier scans, we further validated candidate regions using lineage-specific genome-wide association studies (GWAS) based on an independent ddRADseq dataset, as well as analyses of genetic diversity indicative of historical selection [62].

Together, these analyses highlighted a particularly promising ~400-kb region of major effect on chromosome 12 (Fig. 5C). Patterns of gene flow suggest that this region likely introgressed from the IT lineage into SA populations that exhibit strong expression of the nigriventris phenotype. The genomic region is complex and shows two distinct peaks of differentiation between individuals with ancestral and nigriventris phenotypes: one located within the *Rab18* gene and the other within *Acbd5* (Fig. 5C). *Rab18* encodes a small GTPase

involved in vesicle trafficking and acts as a positive regulator of directed cell migration. *Acbd5* encodes a protein that binds long-chain acyl–coenzyme A and facilitates interactions between peroxisomes and the endoplasmic reticulum. It is unclear if and how these genes are related to neural crest cell biology, and it is possible that they are involved in more downstream fine-tuning of specific traits, such as coloration [although analyses of gene expression did not find any evidence for differential expression in green or brown skin; 62].

Between *Rab18* and *Acbd5* are multiple gene copies of *Pks* (polyketide synthase) and *Ptchd3* (patched domain-containing protein 3; Fig. 5C). Phylogenetic and structural analyses of the interpeak genomic region containing the *Pks* and *Ptchd3* genes suggest that these gene copies arose through both ancient (dating back to the origin of squamates) and more recent tandem duplications. Copy number variation in this region differs between individuals with the nigriventris and ancestral phenotypes. Despite this variation, there is no evidence for a large inversion or elevated transposable element density in the region. Long-read sequencing, Hi-C, and optical mapping, using one individual from an IT population fixed for the ancestral phenotype and one individual from an IT population fixed for the most extreme nigriventris phenotype, revealed substantial structural variation in the ~360 kb interpeak region.

Overall, these data suggest that the candidate region of major effect for the nigriventris syndrome is highly dynamic and structurally variable within and between populations and lineages, which may make it prone to act as a hotspot of genetic variation. This same genomic region has indeed been previously linked to subspecies differences in coloration and bill morphology in redpoll finches (*Acanthis* spp.) [63] and in a colour mutant of the budgerigar (*Melopsittacus undulatus*) [64], suggesting a broader functional role in vertebrate pigmentation and morphological variation.

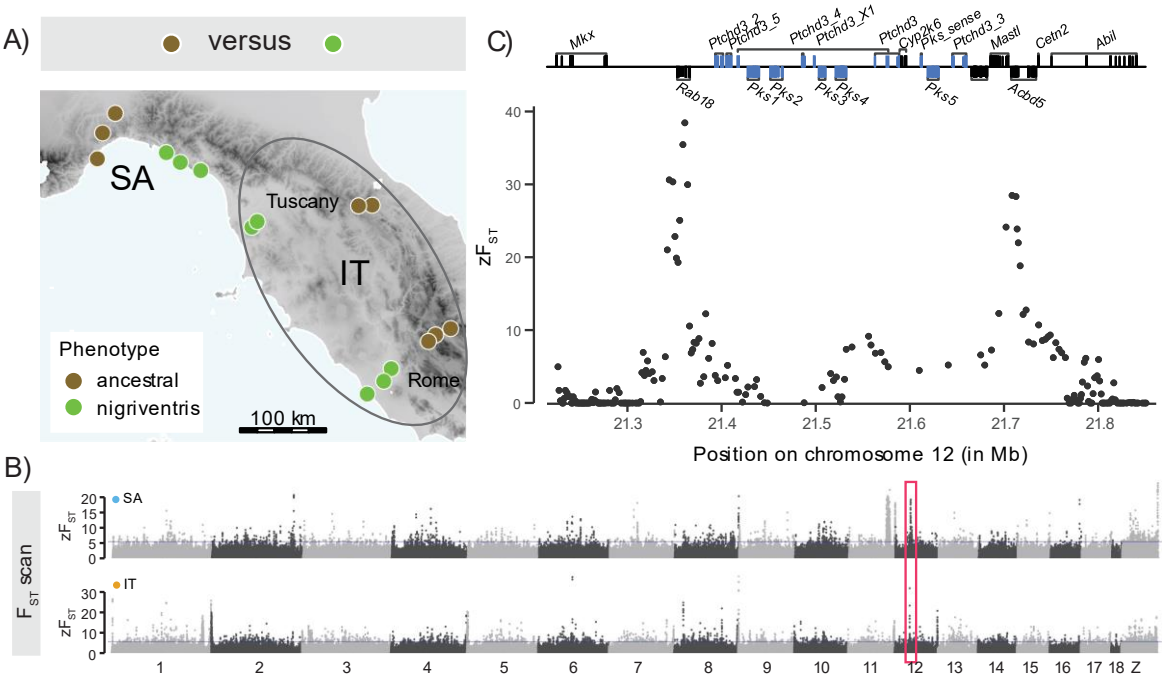

Fig. 5. The genetic basis of the nigriventris syndrome. A) Map of the focal region of the Italian Peninsula showing the contrasts that were used in F_{ST} outlier scans between ancestral and nigriventris phenotypes. Two contrasts were selected from the Central Italy (IT) lineage, and one from the Southern Alps (SA) lineage. Each dot represents a population from which several males were sourced and color indicates the phenotype. B) Genome-wide representation of the zF_{ST} scores in the SA lineage (top) and the IT lineage (bottom). Red box highlights the position of the candidate region on chromosome 12. C) Candidate region on chromosome 12 with zF_{ST} scores presenting the strength of differentiation between ancestral and nigriventris groups.

3.4 Evolution of colour polymorphism and its loss

In contrast to the complex genetic basis of the nigriventris syndrome, some trait variants have a simple genetic architecture. For example, allelic variation at a single locus can determine the expression of colours and patterns. When alternative alleles are maintained within a population, this can result in the stable coexistence of distinct morphs, inherited in a Mendelian fashion. Examples of such polymorphic traits include colour and pattern morphs found both in captive breeds, such as the 'Clown' morph in ball pythons [65], and in the wild, including the 'Diamond' morphs of female *Anolis sagrei* [66] and

the ventral coloration observed in many *Podarcis* species [15]. While the existence of allelic variants with major effects makes it tempting to consider the trait itself as having a "simple" genetic basis, the situation is better understood to reflect the role of specific alleles as difference-makers within the broader, complex dynamics of trait development.

In *Podarcis muralis*, individuals typically exhibit three main throat and ventral coloration morphs: yellow, orange, or white. Additional mosaic forms, yellow-orange and orange-white, are also observed. A pool-sequencing study of 154 individuals spanning five morphs identified two loci responsible for coloration [15]. Yellow coloration is associated with homozygosity (yy) at a locus upstream of *BCO2*, a gene encoding beta-carotene oxygenase 2, which cleaves carotenoids into colourless compounds. Orange coloration (including orange-white mosaics) is linked to homozygosity (oo) at a locus near *SPR*, which encodes sepiapterin reductase, a key enzyme in pterin metabolism. Yellow-orange individuals are homozygous at both loci (yy and oo), while white individuals are either heterozygous or homozygous for the alternative alleles (Y and O, respectively).

Colour polymorphism is widespread across the *Podarcis* genus and is typically maintained unless populations undergo severe bottlenecks. In *P. muralis*, the three main morphs have co-existed within all major lineages for millions of years [15; Uller et al., in press]. The reasons for this balancing selection that maintain polymorphism remain unclear but social interactions causing negative frequency-dependent selection likely play a major role. It has been shown that this balancing selection is disrupted following the (introgressive) spread of the sexually selected nigriventris syndrome, which leads to the selective elimination of the yellow and orange morphs (Uller et al. in press). By combining phenotypic and genomic data across 141 populations, alternative explanations for the morph loss based on genomic or developmental linkage could be ruled out. This is the first documented case of the collapse of a naturally occurring polymorphism through the origin and spread of a sexually selected phenotype.

4. The genomic basis of viviparity and parthenogenesis

With their diverse lifestyles and adaptations to a range of different environmental conditions, squamates offer excellent opportunities to study how innovations arise and how characters are transformed over evolutionary time. Understanding such evolutionary change prompts researchers to integrate genomic data in a comparative approach with mechanistic insight into how phenotypes develop. As examples of ongoing research programs in this area, we briefly review efforts to uncover the genomic and developmental genetic bases of transitions from oviparity to viviparity and from sexual reproduction to parthenogenesis. While viviparity and parthenogenesis are not unique to squamates, repeated evolution of both features in lizards and snakes offers excellent opportunities to explore the genetic basis of adaptive evolution.

4.1 Viviparity

Viviparity means that females give birth to live young. This reproductive mode has evolved independently more than 100 times in squamate reptiles, making them the vertebrate group with the highest number of transitions from the ancestral egg-laying condition to live-bearing [67, 68]. It is relatively well understood *why* viviparity evolves: carrying offspring within the body rather than exposing eggs to harsh environmental conditions can be a winning strategy in thermally challenging environments [69-71]. As ectotherms, squamates regulate their body temperature through behavioural thermoregulation, such as basking, which can significantly raise the temperature experienced by embryos compared to what conditions would have been like in a nest. This elevated and more stable thermal environment accelerates embryonic development and shortens gestation time, thereby increasing survival and allowing offspring to be born when conditions are more favourable [72].

While these adaptive benefits are well established, *how* viviparity evolves, including its underlying genomic changes and developmental mechanisms, remains less well resolved. Viviparity and oviparity are often treated as discrete reproductive modes but the evolution of viviparity is best understood as a gradual, continuous transformation [73, 74]. The evolutionary transformation from oviparity to viviparity begins with prolonged egg retention in the oviduct, meaning that the embryo is more advanced in development by the time of egg laying. For example, in lacertids, eggs are typically laid around the time of limb bud formation [75], but there can be biologically significant variation between and even within species [76]. Following the evolution of prolonged egg retention, a subsequent step is the thinning and eventual loss of the eggshell, allowing embryos to complete development entirely within the maternal reproductive tract. This also enables closer physiological interactions between mother and embryo, facilitating the evolution of placental-like structures that mediate nutrient and gas exchange. For such intimate maternal-fetal interactions to evolve, maternal immune responses must be modulated to prevent rejection of the embryo. These sequential modifications underscore the complexity of viviparity's genomic and developmental genetic basis: rather than being controlled by a single switch, it must involve a polygenic architecture encompassing a battery of genes that regulate shell reduction, nutrient transport, immune regulation, and uterine remodelling.

Most insights into the genomic and developmental genetic bases of viviparity come from comparative studies between viviparous and oviparous species, focusing on genomic differences or differential gene expression in the reproductive tracts of gravid females [e.g., 77, 78]. A study that compared gravid and non-gravid reproductive tissues of an ovi- and a viviparous species of skink found that thousands of genes were differentially expressed between pregnant and non-pregnant uterine tissue of the viviparous species, while gravidity in the oviparous species was only associated with few differentially expressed genes [78].

Similarly, another study contrasted closely related ovi- and viviparous species of the agamid genus *Phrynocephalus* and revealed that hundreds of genes are differentially expressed between gravid females of both reproductive modes [77]. Many differentially expressed genes are associated with egg gland formation, embryo attachment, egg retention and placenta development. The same study found 60 genes to be under positive selection in the viviparous *Phrynocephalus* species, none of which could be linked to reproductive biology [77]. This suggests that the evolutionary transitions to viviparity largely involve regulatory changes rather than changes to coding regions [77].

Particularly illuminating case studies involve species in which viviparity has evolved relatively recently and where it is possible to compare populations of viviparous and oviparous lineages. This is exemplified by the common lizard (*Zootoca vivipara*), which is widespread across Eurasia, as well as two Australian skinks: Bougainville's skink (*Lerista bougainvillii*) and the yellow-bellied three-toed skink (*Saiphos equalis*). In these species, oviparous populations often exhibit prolonged egg-retention and thus represent intermediate reproductive forms that are still functionally oviparous [79]. These transitional forms offer unique insights into the evolutionary transition from egg-laying to live-birth. A study by Recknagel *et al.* [80] leveraged a natural hybrid zone between ovi- and viviparous lineages of *Z. vivipara* that offered continuous variation and allowed the identification of genes associated with parity mode. Their genomic analyses identified 439 genes associated with gestation time and 38 genes associated with eggshell traits, and these genes were enriched for progesterone-binding functions, tissue remodelling and immune system pathways [80]. Given the extensive suite of changes involved, including modifications to morphology, reproductive physiology, and immune function, such a complex genetic architecture is to be expected.

The repeated evolution of viviparity in squamates and other vertebrates raises the question of whether similar genetic mechanisms are consistently involved. Comparative

genomic and transcriptomic studies suggest that the answer depends on the level of biological organization examined. Comparing convergent amino acid replacements associated with viviparity in four independent transitions in squamates, Gao *et al.* [77] did not find support for convergent evolution, suggesting that lineage-specific modifications are responsible for transitions to viviparity. However, some level of convergence between independent transitions to viviparity may still exist: comparing the set of genes that are active during pregnancy in mammals, fish and squamates, a core network of genes related to immunity, tissue remodelling and blood vessel generation was identified [80]. This may indicate that the same pathways are modified during the transition to viviparity, but that this does not leave a signature of selection on protein-coding genes, but rather involves 'tinkering' with the regulation of genes in ancient core pathways.

Beyond the study of shared versus unique changes to the squamate gene repertoires underpinning transitions to viviparity, this line of research relates to another unique source of genetic innovations: novel genes deriving from viruses. The gene *syncytin*, which functions as an envelope gene in retroviruses, has been domesticated by mammals for a function in the fusion of cells in the placenta [81]. Interestingly, a study of the viviparous *Mabuya* skink, whose placenta approaches mammalian placentas in complexity, found a *Mabuya*-specific *syncytin* gene that appears to function in the same way as mammalian *syncytins* [82]. This is a striking example of convergent evolution relying on domestication of foreign genetic elements. More genomic data from lineages that independently evolved viviparity in squamates may uncover further domestication events, which could help to understand how important viral genes are for evolutionary innovation.

4.2 Parthenogenesis

The ability to produce offspring without fertilization, known as parthenogenesis, has long captivated biologists and stirred the imagination of the public, even inspiring religious myths of "virgin birth" [83]. Although this reproductive strategy is relatively uncommon among animals, it occurs in a variety of groups, including insects, cartilaginous and teleost fish, and reptiles. In vertebrates, 99.9% of species rely on sexual reproduction. Obligate parthenogenesis, where reproduction occurs exclusively without fertilization, is restricted to lizards and results in all-female, unisexual species [84].

Both obligate and facultative parthenogenesis can have fitness benefits [83]. Isolated cases of parthenogenesis in reptiles, such as in captive Komodo dragons [85] and boa constrictors [86], are usually interpreted as being accidental or spontaneous, but given that this phenomenon is usually difficult to observe in the wild, it may be more common than widely assumed [87]. Independent of how frequent facultative parthenogenesis occurs in squamates, its existence demonstrates that lizards and snakes, in contrast to birds, have a biology that is conducive to generating parthenogenesis as a recurrent innovation. This, in turn, makes it possible for obligately parthenogenetic lineages to evolve and persist.

Obligate parthenogenesis is widespread and well documented in the whiptail lizards of the genus *Aspidoscelis* and in lacertid lizards of the genus *Darevskia*, each of which contains several unisexual species [84]. It also occurs in other distantly related lineages, such as the mourning gecko *Lepidodactylus lugubris* [88], the Bynoe's gecko *Heteronotia binoei* [89], the iguanian lizard *Liolaemus parthenos* [90] and the flowerpot snake *Indotyphlops braminus* [91]. The repeated and independent origin of parthenogenesis across squamates offers a powerful framework for applying evolutionary genomic tools to investigate the origins and mechanisms of asexual reproduction in vertebrates. Key questions include identifying which environmental,

ecological and population histories favour the emergence of unisexual lineages and uncovering the cellular and molecular mechanisms that enable embryo development in the absence of fertilization. Here, we summarize recent insights enabled by genomic data and outline promising directions for future research on the evolution of parthenogenesis.

The repeated and independent origins of unisexual lineages in the lizard genera *Aspidoscelis* and *Darevskia* enable investigation of the ecological and population genetic factors underlying the evolution of obligate parthenogenesis. A critical driver turns out to be hybridization and, specifically, hybridization between parental lineages that are sufficiently genetically divergent to disrupt normal meiosis or imprinting, yet not so divergent as to render offspring inviable or sterile [92]. This delicate balance creates a "Goldilocks zone" of genetic distance: the parental species must be neither too similar (failing to generate genomic novelty) nor too divergent (preventing viable hybrid offspring). Genome-wide analyses in both *Aspidoscelis* and *Darevskia* have consistently supported this pattern [48, 93], showing that unisexual lineages originate within a narrow phylogenetic window of relatedness.

Historically, obligately parthenogenetic species have been viewed as evolutionary dead ends that are unable to adapt to changing environments and thus destined for eventual extinction. This perspective stems from the assumption that unisexual populations lacking sexual reproduction are deprived of the genetic variation that recombination and segregation provide, which is essential for responding to selective pressures. Unisexual lineages of squamate reptiles are indeed relatively young in evolutionary terms [94]. However, recent studies challenge the deterministic view that they are doomed to extinction. This is because the mechanism of parthenogenesis plays a critical role in shaping genetic diversity and, by extension, evolutionary potential.

Most obligately parthenogenetic lineages initially form as diploids, but they can become triploid through backcrossing events with a sexual parent species [84, 91]. Triploidy

561 can enhance genomic stability in parthenogens by masking deleterious mutations. It may also
562 influence the cytogenetic mechanism of parthenogenesis. Broadly speaking, there are two
563 cytogenetic mechanisms that allow the egg cell to initiate embryonic development without
564 fertilization by a sperm. Premeiotic genome duplication involves a duplication of the genome
565 before meiosis, resulting in a diploid set of chromosomes that then undergoes meiosis. The
566 offspring produced are clonal, but heterozygosity is typically maintained. This is the dominant
567 cytogenetic mechanisms in obligately parthenogenetic lizards (e.g., *Aspidoscelis* and
568 *Darevskia*) [95, 96]. Alternatively, in the cytogenetic mechanism termed automixis, meiosis
569 proceeds normally, but diploidy is restored through fusion of the egg cell and one of the polar
570 bodies. Depending on which polar body the egg cell fuses with, heterozygosity is lost entirely
571 (fusion of sister chromatids involving the second polar body) or preserved to some extent
572 (fusion of non-sister chromatids involving the first polar body). Automixis is more commonly
573 observed in facultative or spontaneous parthenogenesis. Triploidy occurs when a
574 parthenogenetically produced diploid egg is fertilized by a sperm from a sexual species [84].
575 The evolutionary potential of a parthenogenetic lineage is influenced by the cytogenetic
576 mechanisms since automixis severely reduces heterozygosity and exposes recessive deleterious
577 mutations [92]. This can be detrimental to organismal survival, but it may also confer certain
578 advantages, such as the more efficient purging of deleterious recessive alleles, which might
579 reduce mutational load over time in stable environments. How these dynamics manifest in wild
580 populations remains poorly understood. Key questions remain regarding how long unisexual
581 lineages persist in nature, how they maintain sufficient genetic variation, and whether they can
582 respond adaptively to environmental change.

583 What genetic factors underpin premeiotic genome duplication and automixis? The
584 regulation of the cell cycle, in particular those related to meiosis, is likely to play a central role.
585 Supporting this idea, a study in the facultatively parthenogenetic fly *Drosophila mercatorum*

identified several cell cycle regulators (the genes *Polo*, *Myc*, and *Desat2*) whose expression levels correlate with sexual versus unisexual reproduction [97]. Remarkably, altering the expression of these genes in *Drosophila melanogaster*, a species normally considered obligately sexually reproducing, led to an increase in virgin births exceeding 1%. However, most embryos arrested development at early stages, indicating that simply manipulating the meiotic program may not be sufficient to establish stable parthenogenesis. To date, no studies have explored the genetic regulation of the cytogenetic mechanisms underlying parthenogenesis in lizards. This gap presents an exciting direction for future research.

5. Conservation genomics of squamate reptiles

Approximately 2,000 species of lizards and snakes, representing roughly 20% of global squamate diversity, are currently classified as threatened [98]. The primary causes of population decline include habitat loss and degradation due to agricultural expansion, logging, and urban development; biological invasions involving predation or competition by non-native species; and overexploitation through hunting and the pet trade. Climate change acts as a pervasive and compounding threat, not only intensifying these pressures but also directly altering the thermal and hydric environments that are critical for squamate survival and reproduction [99].

Conservation strategies aimed at mitigating these threats often overlap with those developed for other vertebrate taxa but must be adapted to the specific ecological and physiological characteristics of squamates. Many species exhibit limited dispersal ability and rely heavily on behavioural thermoregulation, making them particularly sensitive to habitat fragmentation and microclimatic changes.

Recent advances in genomic technologies provide valuable tools to support and refine conservation efforts. Genomic data can help to:

- Identify cryptic species and evolutionary lineages that may warrant separate conservation status
- Reconstruct historical and contemporary population structure and demographic trends
- Quantify gene flow, inbreeding, and genetic load, which are critical for assessing population viability
- Inform translocation and captive breeding programs by identifying genetically appropriate source individuals

Furthermore, genomic tools can be applied in wildlife forensics to trace the geographic origin of illegally traded individuals, enabling the identification of vulnerable source populations and the mapping of trade routes [100]. By integrating genomic insights with ecological and behavioural data, conservation strategies can be made more effective, targeted, and responsive to the unique challenges that squamates are facing.

An example of how genomic tools can inform conservation management is provided by efforts to preserve the Aeolian wall lizard (*Podarcis raffonei*), an island endemic with an extremely restricted distribution. This species is confined to three small islets and one peninsula north of Sicily and is estimated to comprise fewer than 2,000 individuals in total [101]. The most spectacular of the three islets inhabited by *P. raffonei* is La Canna sea stack, a columnar volcanic pinnacle of 70 m height (Fig. 6). Although a genome-wide assessment of genetic diversity and genetic load is currently lacking, the population of *P. raffonei* on this tiny islet is estimated to consist of around 100 animals, and genetic diversity estimated based on a single gene has been found to be zero [102].

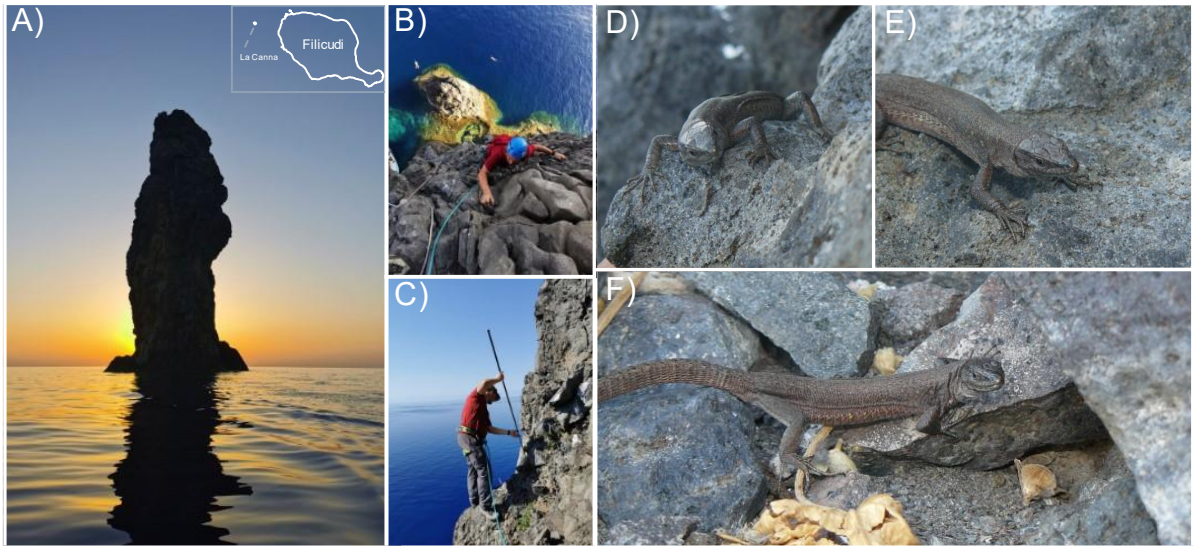

Fig. 6. The critically endangered Aeolian wall lizard *Podarcis raffonei*. A) Photograph of La Canna, one of three islets that is home to approximately 100 individuals of *P. raffonei*. B and C) The researcher Daniele Salvi on an expedition sampling the local lizard population. D to F) Photographs of individuals taken on La Canna. Adapted from [102] with permission from the author. Picture credit: Lorenzo Inzigneri (A-C) and Daniele Salvi (D-F).

Following the development of a chromosome-level reference genome [17], population genomic analyses revealed that *P. raffonei* populations have experienced exceptionally high and persistent levels of inbreeding, accompanied by markedly low levels of standing genetic variation [103]. Analyses of genetic load suggest some degree of purging of deleterious recessive alleles. However, it remains unclear whether this purging occurred recently and independently within each population, or if it reflects a longer-term demographic history involving repeated population bottlenecks. Understanding the timing and mechanism of purging remains a key question for assessing the species' long-term evolutionary potential and resilience.

An additional threat to the largest remaining population of *P. raffonei* is hybridization with the introduced Italian wall lizard (*P. siculus*), particularly on the peninsula Capo Grosso connected to Volcano island. Initial studies using limited genetic markers indicated high levels

of admixture [104], raising concerns about genetic swamping. However, more recent whole-genome data suggest that current hybridization events are rare and that there is little to no detectable introgression [103]. The availability of genomic resources has also been instrumental in guiding the establishment of ex-situ breeding programs and translocation of individuals to two sanctuary islands funded by a LIFE project from the European Union (LIFE22-NAT-IT-LIFE EOLIZARD/101114121). These efforts aim to safeguard against further decline and provide insurance populations for future reintroduction. This case highlights the value of genomic data not only for assessing population viability and evolutionary history but also for informing practical management strategies of critically endangered species.

Similar to the case of the Aeolian wall lizard, the development of genomic resources, including reference genomes [105, 106], for the highly endangered crocodile lizard (*Shinisaurus crocodilurus*; Fig. 7) has informed conservation efforts. High-resolution genomic analyses identified four genetically distinct conservation units within wild populations, revealing a previously unrecognized level of cryptic diversity [106]. The study also documented recent declines in both genetic diversity and effective population size, alongside evidence of genetic purging. While purging may have reduced the frequency of some deleterious alleles, *S. crocodilurus* remains vulnerable to the accumulation of genetic load, a risk that emphasizes the importance of maintaining sufficiently large and demographically stable populations. To this end, genomic data can help to evaluate the potential benefits and risks of genetic rescue strategies, including the use of captive breeding programs that incorporate individuals from different genetic lineages [107].

Fig. 7. The highly endangered crocodile lizard *Shinisaurus crocodilurus*. Resting adult from the captive breeding colony. Picture credit: Xia Qiu.

6. Notes

1. Methods for the survey of genomic resources of squamates, mammals, birds and amphibians

Phylogeny of squamates was obtained from Title *et al.* 2024 encompassing 6885 species. Species were annotated with family rank using NCBI taxonomy accessed with REST API via Rentrez R library (v1.2.3). The families were categorized into monophyletic groups according to the classification used in Title *et al.* 2024. The data was combined with the information on the currently available genome assemblies (as per July 2025) by accessing data from NCBI using REST API via the Rentrez R library (v1.2.3). Discrepancies in species names was resolved manually. Subspecies were grouped into species. In total 303 species were found to have at least 1 genome assembly available on NCBI and 286 overlapped with the phylogenetic tree. *Hydrophis hardwickii* (GCA_004023765.1) was removed from the analysis due to being labelled

in NCBI as contaminated. The number of assemblies per species were counted by including any haplotype resolved assemblies with two separate haplotypes as one. Fasta files for assemblies labelled "reference genome" were downloaded and checked for completeness with Busco v5 using the sauropsida_odb12 database. For species without an indicated reference genome any available assembly was used. Whether the assemblies were structurally annotated was identified through the search of gff files in the ftp directories using the RCurl R package (v 1.98-1.17). All assembly statistics were collected from *_assembly_stats.txt files available in the ftp directories. Proportion of masked genome was calculated as the sum of softmasked nucleotides relative to the whole genome size.

For comparison, a mammalian species list was obtained from The Mammal Diversity Database (MDD 2.2, accessed 16.06.2025), a bird species list was obtained from The World Bird Database (Avibase v2025, accessed 16.06.2025) and a amphibian species list was obtained from AmphibiaWeb (accessed 16.06.2025). The lists were combined with lists of available genome assemblies downloaded as metadata from NCBI datasets accessed via the web due to a limit on the number of records retrievable at a time using Rentrez R library. Species were grouped by order using the taxonomic annotation available from the aforementioned databases.

2. Note on the status of described species in the genus *Podarcis*

Since the publication of Yang *et al.* 2021, three taxa have been elevated to species level (*P. thais*, *P. latastei*, *P. galerai*), although these taxonomic revisions are not universally accepted. A further example of ongoing flux in *Podarcis* taxonomy is the case of *P. atratus*, which was split from *P. liolepis* and elevated to species status in 2005 [108]. However, this change has not been recognized by the Taxonomic Committee of the Societas Europaea Herpetologica [109] or the Reptile Database [110].

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